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Growth and mortality of oak (*Quercus* spp.): a combined analysis of monitoring and tree-ring data from Swiss forest reserves

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Photo: Oak stems marked for data collection in
the forest reserve Les Follatères in Switzerland.

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Summary

Oaks (*Quercus* spp.) are of high ecological value since they feature the highest associated biodiversity of all Central European tree species. Due to their centuries-long facilitation through management, little is known about the current and future role of oaks in natural dynamics of Central European forests. On the one hand, reduced management may lead to oaks being increasingly outcompeted by more shade-tolerant tree species; on the other hand, oaks may gain relative competitiveness because of their drought tolerance as climate change proceeds. Hence, the overall goal of my thesis is the assessment of the natural potential of Central European oaks by investigating their growth and mortality under the exclusion of management. To this end, monitoring and tree-ring data collected in eleven forest reserves that comprise a large environmental gradient in Switzerland are analyzed. Particular emphasis is placed on (1) assessing the performance of oaks in changing stand structures after the abandonment of management, (2) identifying the key drivers of oak growth and mortality, and (3) developing a method for non-destructive estimation of tree age for oak.

In a first step, changes in stand structures after the abandonment of management were investigated, including the consequences for tree mortality (Chapter I). By using repeated diameter measurements from more than 17 600 individually tagged trees, stand dynamics in the reserves over the past 50 years were analyzed. Moreover, generalized linear mixed-effects models were fitted to quantify the effects of tree diameter, stand basal area, precipitation and slope on annual mortality rates of oak (*Q. petraea*, *Q. robur*, *Q. pubescens*) and its strongest competitor beech (*Fagus sylvatica*). Stand basal area strongly increased over time, whereas tree density decreased. The relative importance of oak decreased compared to beech at most sites. Mortality rates increased over time, with the increase being stronger for oak than for beech. Mortality rates of both species strongly decreased with increasing tree diameter, and showed an increasing tendency with precipitation. In addition, oak mortality strongly increased with stand basal area, whereas no such correlation was found for beech. These results indicate that (1) natural oak mortality in Central European oak-beech forests is mainly driven by stand structure, and (2) oaks are at risk of being increasingly outcompeted by beech, unless competition is reduced through management or disturbances.

As a second step in my thesis, the most important climatic drivers of oak diameter growth were identified along a gradient of soil moisture (Chapter II). To this end, tree-ring data from more than 300 oaks representing different vitality classes were sampled in the forest reserves. Response functions were calculated between tree-ring indices and monthly values of mean temperature, precipitation and a drought index. The time span from June of the previous year until September of the current year was considered as potentially influencing tree-ring widths. In general, tree-ring widths responded more strongly to precipitation than to temperature, with precipitation of the current summer months resulting in the highest positive responses. For the drought index, similar growth responses as for precipitation were identified. Whereas positive responses to precipitation and the drought index in June were identified along the whole soil moisture gradient, more positive responses for other months were identified at sites with comparably dry soil conditions. These growth responses indicate that, despite their drought-tolerance, oaks show reduced growth during dry summer periods, in particular if they are growing on dry soils.

In a third step, the development of oak diameters with age was investigated (Chapter III). The age-diameter relationships of the oaks growing in the Swiss forest reserves were determined based on the tree-ring samples introduced in Chapter II. To identify the key drivers that shape this relationship, nonlinear mixed-effects models were fitted with environmental variables included as covariates. Furthermore, a mean model was developed and its accuracy in predicting the age-diameter curves of independent oaks was assessed. The fixed effects elevation, slope and soil water holding capacity were identified as the most important covariates. Larger maximum diameters were associated with lower elevations, steeper slopes, north-facing aspects, higher water holding capacities and moister summers. Predictions based on the fixed effects were fairly accurate for most trees (root mean squared error between predicted and observed diameter < 6 cm for 75% of the trees) and the inclusion of random effects increased the accuracy for 86% of the trees. These results suggest that runoff plays a key role for oak diameter growth, likely accompanied by limiting temperature effects at higher elevations.

The fourth step of this thesis dealt with developing a method for the non-destructive estimation of tree age (Chapter IV). Age estimations derived from a traditional polynomial approach were compared to those derived from two alternative approaches that allow for bypassing tree-ring sampling in the future. In the first of these two alternative approaches (approach I), sequences of repeated diameter measurements from the monitoring in the reserves were fitted to a range of systematically varying age-diameter curves. In the second approach (approach II), the diameter sequences were fitted to the age-diameter curves that were predicted site-specifically for every tree from the fixed effects of the mean nonlinear model developed in Chapter III. The polynomial approach and approach II produced similarly accurate age estimations, whereas approach I was less accurate. Additionally including the random effects strongly improved the age estimations from approach II, such that relative errors were below 40% for 98% of the oaks. The included site information and the nonlinearity of this approach obviate the need for calibration in further applications, making it an entirely non-destructive alternative for tree age estimation.

Overall, the study of monitoring data revealed competition as the key driver of oak *mortality*, and the analysis of tree-ring data indicated strong effects of site characteristics and drought on oak *growth*. These findings indicate that targeted management is needed to retain the current proportion of oaks in Central European forests. The combination of monitoring and tree-ring data delivered a non-destructive method for tree age estimation, which is suggested to find application in the context of oak-related conservation.

Zusammenfassung

Eichen (*Quercus* spp.) sind ökologisch sehr wertvoll, da sie von allen Baumarten in Zentraleuropa die höchste assoziierte Biodiversität aufweisen. Aufgrund ihrer jahrhundertelangen Förderung durch gezielte Bewirtschaftung ist wenig über ihre derzeitige und zukünftige Rolle in der natürlichen Dynamik zentraleuropäischer Wälder bekannt. Einerseits könnte verminderte Bewirtschaftung dazu führen, dass Eichen zunehmend von schattentoleranteren Baumarten verdrängt werden; andererseits könnten Eichen aufgrund ihrer Trockenheitstoleranz im Zuge des fortschreitenden Klimawandels an relativer Konkurrenzstärke gewinnen. Das Hauptziel meiner Dissertation ist deshalb die Beurteilung des natürlichen Potenzials zentraleuropäischer Eichen anhand der Untersuchung ihrer Wachstums- und Mortalitätsprozesse unter Ausschluss von Bewirtschaftung. Zu diesem Zweck werden Monitoring- und Jahrringdaten analysiert, die in elf Waldreservaten entlang eines umfangreichen Umweltgradienten in der Schweiz erhoben wurden. Besondere Schwerpunkte sind dabei (1) die Beurteilung des Verhaltens von Eichen in sich ändernden Bestandesstrukturen nach der Einstellung der Bewirtschaftung, (2) die Identifizierung der Haupteinflussgrössen auf Eichenwachstum und -mortalität, und (3) die Entwicklung einer nicht-destruktiven Methode zur Altersschätzung bei Eichen.

In einem ersten Schritt wurde die Entwicklung der Bestandesstruktur nach der Einstellung der Bewirtschaftung untersucht, inklusive der Folgen für die Baummortalität (Kapitel I). Wiederholte Durchmessermessungen von mehr als 17 600 individuell gekennzeichneten Bäumen wurden verwendet, um die Bestandesdynamik in den Reservaten über die vergangenen 50 Jahre zu analysieren. Ausserdem wurden generalisierte lineare gemischte Modelle angepasst, um den Einfluss von Baumdurchmesser, Grundfläche des Bestandes, Niederschlag und Hangneigung auf die jährlichen Mortalitätsraten von Eichen (*Q. petraea*, *Q. robur*, *Q. pubescens*) und Buchen (*Fagus sylvatica*) zu quantifizieren. Die Grundfläche der Bestände stieg im Laufe der Zeit stark an, während die Baumdichte abnahm. Die relative Bedeutung der Eiche nahm im Vergleich zur Buche an den meisten Standorten ab. Die Mortalitätsraten stiegen über die Zeit an, wobei der Anstieg für die Eiche stärker ausfiel als für die Buche. Die Mortalitätsraten beider Arten nahmen mit zunehmendem Baumdurchmesser stark ab und zeigten eine zunehmende Tendenz mit zunehmenden Niederschlagsmengen. Ausserdem stieg die Eichenmortalität mit zunehmender Grundfläche des Bestandes stark an, die Buchenmortalität zeigte jedoch keine solche Abhängigkeit. Diese Resultate deuten darauf hin, dass (1) die natürliche Eichenmortalität in zentraleuropäischen Eichen-Buchen Wäldern hauptsächlich von der Bestandesstruktur beeinflusst wird und (2) Eichen Gefahr laufen, zunehmend von Buchen verdrängt zu werden, falls der Konkurrenzdruck nicht durch Bewirtschaftung oder Störungen reduziert wird.

Als zweiter Schritt in meiner Dissertation wurden die wichtigsten klimatischen Einflussgrössen auf den Durchmesserzuwachs von Eichen entlang eines Bodenfeuchtegradienten

bestimmt (Kapitel II). Dazu wurden in den Reservaten Jahrringdaten von mehr als 300 Eichen verschiedener Vitalitätsklassen erhoben. Response-Funktionen zwischen Jahrringindizes und monatlichen Werten der Durchschnittstemperatur, des Niederschlags und eines Trockenheitsindex wurden berechnet. Als potenziell beeinflussende Zeitspanne wurde Juni des vergangenen Jahres bis September des laufenden Jahres berücksichtigt. Im Allgemeinen reagierten die Jahrringbreiten stärker auf den Niederschlag als auf die Temperatur, wobei der Niederschlag im laufenden Sommer die grössten positiven Effekte erzielte. Der Trockenheitsindex äusserte sich in ähnlichen Wachstumseffekten wie der Niederschlag. Während die positiven Effekte des Niederschlags und des Trockenheitsindex im Juni entlang des gesamten Bodenfeuchtegradienten identifiziert wurden, traten für andere Monate mehr positive Effekte an Standorten mit vergleichsweise trockenen Bodenverhältnissen auf. Die identifizierten Wachstumseffekte zeigen, dass Eichen trotz ihrer Trockenheitstoleranz während trockenen Sommerperioden reduziertes Wachstum aufweisen, insbesondere auf trockenen Böden.

In einem dritten Schritt wurde die Entwicklung der Eichendurchmesser mit dem Alter untersucht (Kapitel III). Die Alters-Durchmesser Beziehung der Eichen in den Schweizer Waldreservaten wurde anhand der in Kapitel II erwähnten Jahrringdaten bestimmt. Um die Haupteinflussgrössen auf diese Beziehung zu ermitteln, wurden nichtlineare gemischte Modelle angepasst, in denen Umweltvariablen als Kovariablen einbezogen wurden. Ausserdem wurde ein gemitteltes Modell entwickelt und dessen Genauigkeit für die Vorhersage der Alters-Durchmesser Beziehung unabhängiger Eichen beurteilt. Die festen Effekte der Höhe über Meer, der Hangneigung und der Bodenwasserspeicherkapazität waren die wichtigsten Kovariablen. Grössere maximale Durchmesser standen in Zusammenhang mit tieferer Höhenlage, steileren Hängen, Nordexposition, höherer Bodenwasserspeicherkapazität und feuchteren Sommerperioden. Vorhersagen basierend auf den festen Effekten waren für die meisten Bäume ziemlich genau (die Wurzel aus der mittleren quadrierten Abweichung zwischen den vorhergesagten und den beobachteten Durchmessern betrug < 6 cm für 75% der Bäume), und der Einbezug von zufälligen Effekten erhöhte die Genauigkeit für 86% der Bäume. Diese Resultate deuten darauf hin, dass der Abfluss von Wasser eine zentrale Rolle für das Durchmesserwachstum der Eichen spielt, vermutlich in Kombination mit limitierenden Temperatureffekten in höheren Lagen.

Der vierte Schritt dieser Dissertation befasst sich mit der Entwicklung einer Methode zur nicht-destruktiven Schätzung des Baumalters (Kapitel IV). Die mittels eines traditionellen polynomialen Ansatzes geschätzten Baumalter wurden mit den Altersschätzungen zweier alternativer Ansätze verglichen, mit denen das Erheben von Jahrringdaten zukünftig umgangen werden könnte. Im ersten dieser zwei alternativen Ansätze (Ansatz I) wurden Durchmessersequenzen aus dem Monitoring der Reservate in systematisch variierende Alters-Durchmesser-Kurven eingepasst. Im zweiten Ansatz (Ansatz II) wurden die Durchmessersequenzen in diejenigen Alters-Durchmesser-Kurven eingepasst, die für jeden Baum standortsabhängig aus den festen Effekten des gemittelten Modells aus Kapitel III geschätzt wurden. Der polynomiale Ansatz und Ansatz II produzierten ähnlich genaue Altersschätzungen, während Ansatz I weniger genau war. Die zusätzliche Berücksichtigung von zufälligen

Effekten verbesserte die Altersschätzungen von Ansatz II, sodass der relative Fehler für 98% der Eichen geringer als 40% ausfiel. Die Standortsinformation und die Nichtlinearität dieses Ansatzes machen den Kalibrierungsschritt in weiteren Anwendungen unnötig, weshalb er eine vollständig nicht-destruktive Alternative für die Baumaltersschätzung darstellt.

Aus der Untersuchung der Monitoring-Daten ging die Konkurrenz als Haupteinflussgrösse der Eichen*mortalität* hervor, und die Analyse von Jahrringdaten zeigte starke Effekte von Standortsgrössen und Trockenheit auf das Eichen*wachstum*. Diese Resultate deuten darauf hin, dass gezielte Massnahmen nötig sind, um den derzeitigen Eichenanteil in den Wäldern Zentraleuropas zu erhalten. Die Kombination von Monitoring- und Jahrringdaten lieferte eine nicht-destruktive Methode zur Baumaltersschätzung, die in Eichenförderungsprojekten Anwendung finden könnte.

General introduction

Background

The ecological and economic importance of oaks

The increasing loss of biodiversity has become one of the most challenging topics in environmental sciences over the last decades (Pimm et al. 1995; Cardinale 2012). Current extinction rates are likely the highest ever in Earth's history, with estimations that 21-52% of the present species are becoming extinct in the near future (Barnosky et al. 2011). In the fight against biodiversity loss, forest ecosystems have an important role, since they harbour a disproportionately high amount of global biological diversity, with many of the involved species being endemic or endangered (Szaro and Johnston 1996; Hunter Jr. 1999).

In the context of the conservation of biodiversity in Central European forests, oak species (*Quercus* spp.) are exceedingly important because they feature the highest associated diversity of all present tree species. The presence of oak has been shown to be related to the diversity of a wide range of organisms, ranging from insects (Ranius and Jansson 2000) and birds (Caprio et al. 2009) to fungi (Bernicchia et al. 2008) and lichens (Frei 2003). In addition, the understory and herb layer in oak forests is typically highly species-rich (Barbier et al. 2008). According to their exceptionally high associated biodiversity, oaks are seen as umbrella species (cf. Wilcox 1984; Ehrlich and Murphy 1987). Hence, they have become the main focus of conservation efforts in many Central European forests (Bonfils et al. 2005).

In Switzerland, there are four native oak species (*Quercus petraea*, *Q. robur*, *Q. pubescens* and *Q. cerris*), which dominate in 2.1% of the forested area (Brändli 2010). Concerning relative volume proportions and relative stem numbers within these species, *Q. petraea* is the most abundant species, followed by *Q. robur* (Brändli 2010; Table 1). The occurrence of *Q. pubescens* is mainly restricted to the southwestern part of Switzerland and the Jura Mountains. Hence, it is much less frequent than *Q. petraea* and *Q. robur*. Since *Q. cerris* has its origin in southeastern Europe, its only occurrence in Switzerland lies in the southernmost part of the Ticino. Therefore, *Q. cerris* is not considered in this thesis.

The natural distribution of oaks in Switzerland is determined by a combination of their habitat requirements and their low competitiveness. *Q. petraea*, *Q. robur* and their strongest competitor *Fagus sylvatica* all show approximately the same optimum growth ranges, namely in mesic, moderately acid to alkaline and warm conditions (Ellenberg 2009). However, under such conditions *F. sylvatica* is much more competitive because of its higher shade tolerance. Therefore, oaks thrive close to the edges of their ecological amplitudes only, where *F. sylvatica* increasingly loses competitiveness. This results in the dominance of *Q. petraea* and *Q. robur* only in areas that are too dry or too acidic for beech (Table 1).

Additionally, *Q. robur* is able to grow under conditions that are too wet for beech (Ellenberg 2009). *Q. pubescens* mainly occurs at dry sites in competition to *Pinus sylvestris*.

The current distribution of oaks in Switzerland is heavily influenced by former forest management. Most of Switzerland's forests have been managed at some point in their history, but goals and priorities have varied strongly through the centuries. In medieval times, agroforestry and the coppice-with-standards management dominated, thus leading to an increased proportion of oak trees in the Swiss lowlands compared to natural conditions (Bürgi 1999b). For instance, semi-open stands of oak often served as pastures for pig feeding with acorns (Küchli and Thomet 2005). Big oak standards were used e.g. for barrels and ship building, whereas young coppiced stems often served as vine stakes, or their bark was collected for tanning (Küchli and Thomet 2005). Similar management histories have been described for oak forests in other parts of Europe (Haneca et al. 2005; Haneca et al. 2009). The high importance of oaks for pasturing and wood production essentially shaped the appearance of many forests, landscapes and villages at that time, which is still reflected in various toponyms and coats of arms throughout Europe (Meyer 1931; Figure 1).

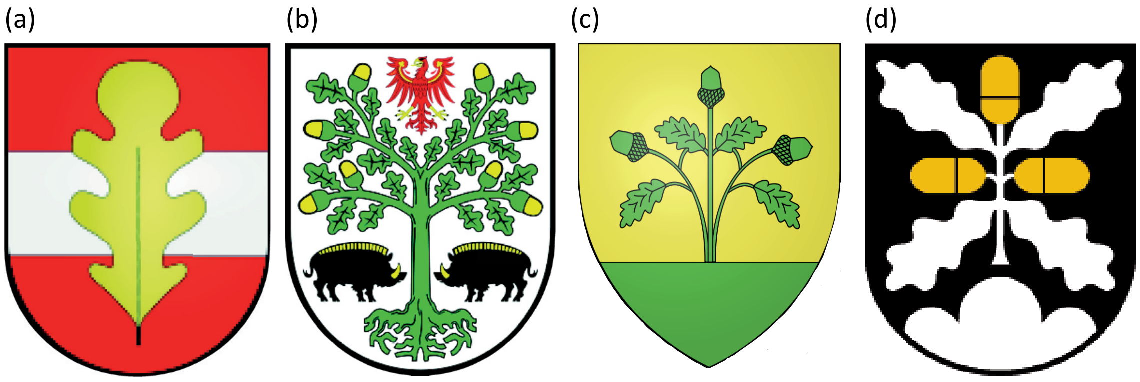
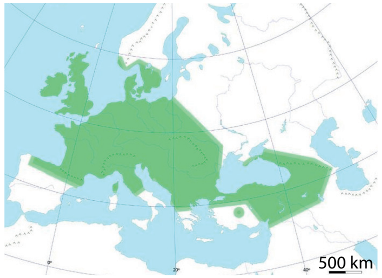
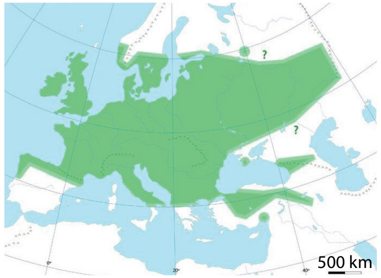
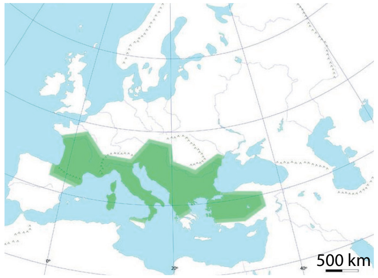
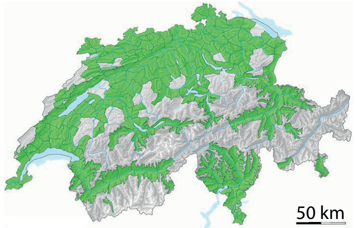
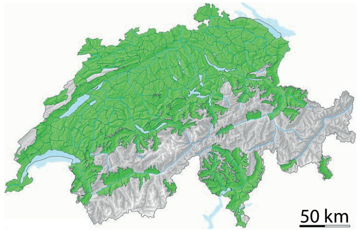
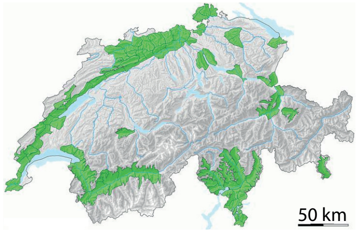
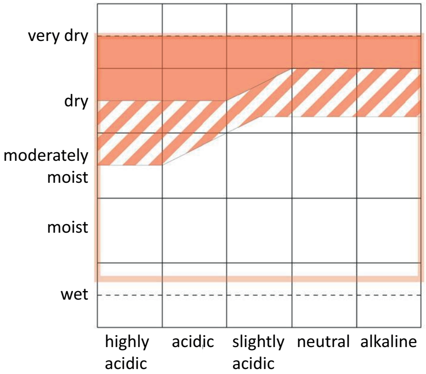
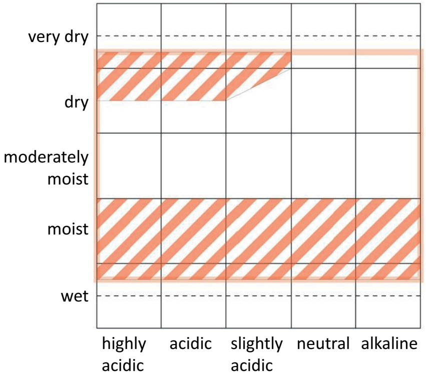
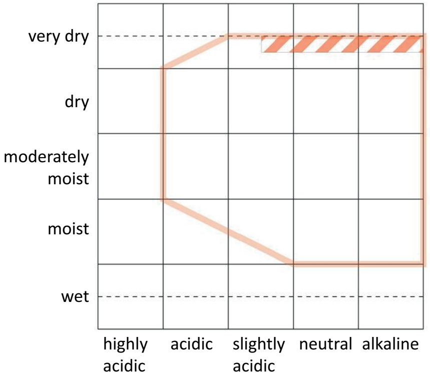


Figure 1. Local coats of arms containing oak motifs from (a) Siebnen in Switzerland, (b) Eberswalde in Germany, (c) Eichhoffen in France and (d) Eichenberg in Austria.

As a result of their centuries-long intensive facilitation through management, many oak trees are growing at sites where beech naturally would have been more competitive (cf. Mühlethaler 2008). Yet, in the course of the last two centuries, agroforestry and the coppice-with-standards management have largely been abandoned and replaced by high forest management (Bürgi 1999a). This transition has caused many oak stands to become denser, entailing increased competitive pressure among the trees. Due to the low relative competitiveness of oaks, their abundance in many Central European forests is thus likely to decrease in favour of beech.

Table 1. Distribution and abundance of oak species in Europe and in Switzerland.

	Quercus petraea	*Quercus robur*	*Quercus pubescens*
Distribution in Europe[1] © A. Rudow, ETH Zurich			
Distribution in Switzerland[1] © Swiss web flora			
Relative proportion of volume in Switzerland (%)[2]	55.7	39.7	4.1
Relative proportion of stem number in Switzerland (%)[2]	61.0	23.8	14.4
Ecogram[1] © A. Rudow, ETH Zurich ▬ Fundamental niche 🟥 Dominance within realized niche ▨ Co-dominance within realized niche			

[1] Taken from Baltisberger et al. (2012).

[2] According to Brändli (2010).

Note: *Quercus cerris* is not considered in this thesis because its occurrence in Switzerland is limited to the southernmost part of the Ticino with a relative proportion of volume of 0.5% and a relative proportion of stem number of 0.8%.

In recent times, oak regained attention not only because of conservation, but also in the context of adaptation strategies to climate change. For Switzerland, an increase in seasonal mean temperatures by 1.2-4.8°C is projected until the end of the 21st century (Weigel and Fischer 2011). Mean summer precipitation is simultaneously expected to decrease by 8-28%. In addition, more frequent and longer-lasting summer heat waves are likely (Fischer 2011). Under such generally warmer and drier conditions, the drought-tolerant and thermophile oak species may become more competitive relative to other co-occurring tree species (cf. Contran et al. 2012). For example, *Q. pubescens* has been shown to start replacing *P. sylvestris*, which experiences high mortality rates due to drought stress in several Central-Alpine dry valleys such as the Valais (Rebetez and Dobbertin 2004; Rigling et al. 2006; Weber et al. 2007). The question whether oaks could benefit from climate change in other parts of Central Europe, especially compared to beech, is discussed controversially (Rennenberg et al. 2004; Ammer et al. 2005; Rebetez and Kienast 2005; Brang et al. 2008). To be prepared for possible climate-induced changes in the performance of currently co-occurring tree species, oaks are increasingly becoming a focus in forest planning and policy (e.g. Mühlethaler 2008).

To determine the potential role of oaks in biodiversity conservation and climate adaptation strategies, accurate knowledge on their – possibly changing – behavior as a function of environmental factors is required. Such knowledge is a prerequisite to optimize Central European forest management in the face of current and future conservational and economic challenges. One crucial question is whether a less intensive management, e.g. complete protection or near-to-nature silviculture, would lead to oak being outcompeted through increased competitive pressure e.g. on the Swiss Plateau, or whether its relative competitiveness has already shifted as a consequence of climate change, and thus intensive management is not needed to retain an intended oak stock. The key to determine this natural potential of oak lies in the intensive, long-term investigation of the natural dynamics of oak forests.

Elements of natural forest dynamics

Natural forest dynamics are based on three key processes: growth, mortality and regeneration. Bearing in mind a tree's lifespan, it becomes obvious that extraordinarily long-lasting investigations are needed to capture these processes. In addition, all of them operate on multiple spatial scales, ranging from single trees to landscapes.

The study of tree growth has a long history in forest science and forestry. First systematic investigations concentrated on height growth under varying site conditions and emerged in the form of yield tables in the early 19th century (Tesch 1981). Thereafter, attention was increasingly paid to diameter growth, which was usually studied based on either repeated diameter measurements or tree rings. Indeed, the systematic study of tree rings created dendrochronology as an important branch of forest science (Douglass 1941; Stokes and Smiley 1968; Fritts 1976). In recent years, ecosystem-level aspects like total biomass, carbon stocks or the exchange of matter between forests and the atmosphere have additionally gained importance (McMahon et al. 2010). All of these efforts together revealed consensus about some general growth drivers: climate variability has been shown to strongly affect tree growth (Fritts 1976), but also soil properties or topographical characteristics such as aspect and slope (Oberhuber and Kofler 2000; Weber et al. 2007). As a further major growth-influencing feature, competition among trees plays a key role (Biging and Dobbertin 1995). However, quantifications of these influences – and their interactions – are largely missing for most tree species, as is the case for oak.

Natural tree mortality has become a main focus in forest science towards the end of the 20th century only (Manion 1981; Franklin et al. 1987). The conceptual theory by Manion (1981) suggests that predisposing, inciting and contributing factors together act in processes related to tree death. Four main mortality processes have been described. First, young trees usually grow closely together or are overtopped by larger trees and thus experience very high competition for light and other resources. Only the most vigorous trees succeed in growing older, whereas the majority dies – a process usually described as 'competitive self-thinning' (Adler 1996; Reynolds and Ford 2005). A second pulse of natural mortality occurs when trees reach their physiological age limit and die from senescence. Although reduced growth has been shown to often precede this mortality process (Bigler and Bugmann 2003), its physiological background is still poorly understood. As a third mortality process, prolonged physiological stress can lead to tree death, e.g. as a consequence of drought (Allen et al. 2010). A fourth mortality process that potentially affects trees of all ages is mechanical damage from disturbances such as avalanches, windstorms and fires. Since disturbances generally occur in a spatially and temporally unpredictable manner and forest dynamics driven by disturbances are not a main target of this thesis, this mortality process is not considered here.

Tree regeneration typically follows mortality events, when gaps in the formerly closed canopy allow high light levels to reach the ground (Szwagrzyk et al. 2001). Species present in the regeneration are not necessarily the same as those that are dominating the canopy (Parker and Leopold 1983), thus giving rise to succession and changes in species composition. However, the focus of this thesis is on growth and mortality processes.

Forest management strongly influences all these key elements of forest dynamics. Growth is affected mainly by the facilitation of target trees through thinning. Cutting of trees for economic reasons is human-induced mortality. Generation times in managed forests are usually set much shorter than in natural forest ecosystems to avoid a deterioration of wood quality and mortality from senescence. Thus, the omnipresent forest management in Central European oak forests is strongly modifying the processes of natural forest dynamics, which renders it very difficult to assess the natural potential of oak. Thus, there is only little knowledge on the natural dynamics of oak forests in Central Europe – both before and during the debate of climate change. The key to fill this gap lies in the study of long-term dynamics in forests actively protected from management.

Research approach

Swiss forest reserve network

With the goal in mind to provide a solid basis for reliable studies on natural forest dynamics, the Swiss forest reserve network was initiated by Professor Leibundgut at ETH Zurich in the late 1940s. From then on, reserves were established all over Switzerland, mostly in forests that had not been managed already for decades. The reserves were selected to represent as many of Switzerland's forest types as possible. After a re-organization in 2006, the reserve network is now jointly operated by ETH Zurich and the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), with considerable funding coming from the Swiss Federal Office for the Environment. Currently, the network consists of 49 reserves, which are guaranteed by contract and comprise areas between 1 ha and more than 5300 ha. Detailed information on the network can be found on www.waldreservate.ch or in Wunder (2007), Heiri (2009) and Brang et al. (2011).

A detailed guideline for setting up reserves and performing the monitoring activities was formulated in the early days of the network (Leibundgut 1959; Leibundgut 1962) and applied with only minor adjustments until today. The monitoring system aims for repeated data collection approximately every 5-10 years and includes three spatial scales with varying monitoring intensities (Figure 2):

(1) Full cruises are conducted in compartments, which represent subdivisions of the reserves that are homogeneous regarding site characteristics. During the full cruises, among others data on the tree species, diameters at breast height and whether a tree is dead or alive are collected.

(2) Within every reserve, one or more permanent plots (mostly < 1 ha) were established on which all trees are permanently tagged, allowing for individual-based analyses. In addition to the data collected in the compartments, several measures of vitality are assessed qualitatively for every tree, and tree height is determined for a random subsample.

(3) Detailed sketches on the size and location of all trees were drawn along transects of 6-10 m width ('profile strips'). However, these transects were given up in the 1980s due to financial constraints.

On the occasion of the re-organization in 2006, the monitoring system was complemented by guidelines concerning coarse woody debris, habitat structures, permanent photo series and inventory sampling procedures, which in the larger reserves are replacing the full cruises (Brang et al. 2011). With every additional monitoring campaign, the captured time frame of natural forest dynamics prolongs – and hence the value of the dataset increases.

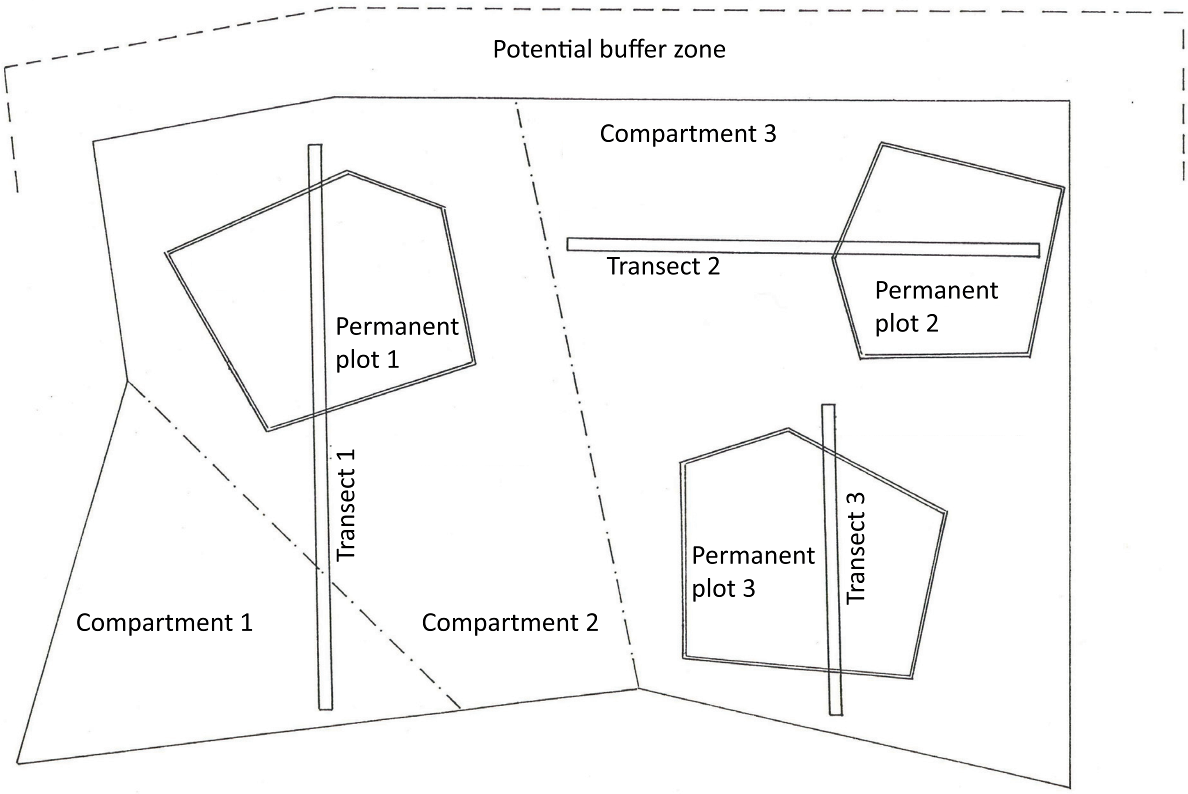


Figure 2. Design sketch for the establishment of a forest reserve according to the original guidelines by Leibundgut (1962). Adapted from Matter (2004).

The data collected in this way bear tremendous potential for long-term studies of natural forest dynamics as they are among the longest ecological data series worldwide and cover a wide range of environmental conditions (Brang et al. 2011). First analyses were restricted to descriptions of the initial data sets gathered in a few forest reserves (e.g. Hartl 1967; Eiberle 1969). Over time, the increasing amount of repeated measurements allowed also to focus on dynamic processes. Although their systematic analysis is still in the early stages, the reserve data have already delivered significant insights in some aspects of forest dynamics, e.g. growth-related mortality (Wunder 2007) and structural changes (Heiri 2009). While previous studies intensively dealt with *F. sylvatica* (Wunder et al. 2007; Heiri 2009), *Abies alba* (Wunder et al. 2007) and *Picea abies* (e.g. Hillgarter 1971), the reserve data have never been explored with respect to oak. Because the permanent plot data allow for a much richer analysis of key variables of forest dynamics, the present thesis focuses on this dataset rather than the full cruise data.

Dendrochronology

Besides monitoring data, tree-ring chronologies provide long-term information on tree growth, as mentioned above. The annual resolution of tree rings in the temperate and boreal zone contains a higher information content compared to the decadal resolution of monitoring data, allowing for different research foci. For instance, tree-ring widths have been shown to be highly sensitive to climate variability (Fritts 1976), but also to competition and site characteristics (Oberhuber and Kofler 2000; Weber et al. 2007). Dendrochronological studies thus provide the potential to deepen the understanding of growth responses of oak to climate and competition and how these responses vary among sites. For example, differing growth responses to drought have been identified for *Q. pubescens* and *P. sylvestris* in southwestern Switzerland (Weber et al. 2007). Insights in varying growth patterns of oaks excluded from management could contribute strongly to the assessment of their natural potential under climate change, but this has not been exploited so far.

Tree-ring studies have been employed in the Swiss forest reserve project right from the beginning. While first dendrochronological investigations intended to determine growth variability among trees in individual reserves (e.g. Leibundgut 1959), more recent studies focussed e.g. on mortality processes (e.g. Bigler and Bugmann 2003; Rohner 2008). In particular the typical growth decline prior to death was studied intensively based on increment cores taken in the reserves (Bigler and Bugmann 2003). However, only very few (yet large) tree-ring samples have been collected from living trees within the reserves so far, exclusively covering conifers (e.g. Leibundgut 1959; Hillgarter 1971).

The potential of combining monitoring and tree-ring data

A certain caution has evolved regarding the coring of living trees in protected and monitored forests, because negative impacts for the cored trees and thus biases in the collected data are feared. Dendrochronology always depends on invasive or even destructive data collection. While taking stem cross sections definitely kills a tree, there is large uncertainty regarding the long-term impacts of taking increment cores, e.g. the spread of pathogenic fungi (Hart and Wargo 1965). Coring seems to have no direct impact on the mortality of *Picea abies* (Wunder et al. 2011), but little is known on the susceptibility of other conifers, let alone deciduous tree species.

Besides studying growth processes, trees are often cored to determine their age, which is a crucial information in forest science and practice. For example, many forest growth models rely on tree age information (Thürig et al. 2005). In nature conservation, age acts as an indicator for the ecological value of a tree, because structural diversity generally increases with tree age (Michel and Winter 2009). Accurate tree age estimation is particularly important for oaks, because subsidies for their protection in the context of nature conservation projects are often determined as a function of their age (e.g. Kantonsforstamt St. Gallen 2003).

Combining monitoring data and tree-ring chronologies has the potential to obviate the need for future tree-ring sampling in attempts to determine tree age. If the age information stored in tree rings can be calibrated using monitoring data from the same trees, the age of further trees may be estimated based on monitoring data alone. Following this approach, invasive methods are only needed during calibration.

Objectives and research questions

The overall objective of this thesis is the assessment of the natural potential of Central European oaks by evaluating their growth and mortality under the exclusion of management impacts. Particular foci lie in (1) the identification of environmental variables that drive these processes, (2) the evaluation of whether oaks suffer from increased competition in unmanaged forests, or whether climate change is leading to an opposite trend, and (3) the development of a new approach for tree age estimation, which should satisfy the long-standing call for accurate, non-destructive methods for age determination. Hence, this thesis forms a basis for decisions in the context of forest-related nature conservation and attempts to adapt European forests to a changing climate, and delivers a non-destructive tool for the determination of tree age, which is important for both scientific and practical reasons.

From an *ecological* perspective, the following main questions are addressed regarding

(1) Stand structure
- *How does stand structure in oak forests change after the abandonment of management?*

(2) Mortality
- *Do oak and its strongest competitor beech show changing mortality patterns under the development towards near-natural stand conditions?*
- *What environmental variables are decisive for the mortality of oak and beech?*

(3) Growth
- *What are the most important climatic drivers of natural oak growth?*
- *What environmental variables limit the growth of oak diameters with age?*

The following research questions focus on *methodological* aspects:

- *How accurate are age-diameter relationships of oaks that are predicted based on site characteristics?*
- *How accurate are non-invasive tree age estimations for oaks based on nonlinear models?*

Structure of the thesis

This thesis is structured in four steps. In the first step, monitoring data with a decadal resolution are used to evaluate the development of stand structure in oak-beech forests after the abandonment of management, including the consequences for tree mortality (Chapter I). In the subsequent two steps, environmental drivers of oak growth are identified based on tree-ring data, first by focussing on growth responses to climate variability (Chapter II) and second by focussing on the age-diameter relationship (Chapter III). In the last step, the monitoring and tree-ring data are combined to develop a method that allows for non-destructive tree age estimation in the future (Chapter IV).

Chapter I: Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech

Qualitative descriptions of succession have suggested an increasing dominance of the shade-tolerant beech after management stops in Central European oak-beech forests. Under climate change, this trend may reverse as a consequence of the higher drought tolerance of oak compared to beech. However, structural changes and mortality processes in oak-beech forests developing towards natural conditions have only rarely been quantified. Thus, the first part of this thesis deals with identifying changes in stand structure and mortality rates – and their drivers – in twelve forest sites in ten forest reserves located along a large environmental gradient in Switzerland. Based on repeated measurements from more than 17 600 individually tagged trees, the development of stand basal area, stand density and the relative proportion of oak and beech are analyzed. In addition, generalized linear mixed-effects models are fitted to determine the differing effects of tree diameter, stand basal area, precipitation and slope on mortality rates of oak and beech.

Chapter II: Annual growth responses of oaks to temperature, precipitation and a drought index along a gradient of soil moisture in Swiss forest reserves

Knowledge on the relationship between climate and growth is a prerequisite for assessing the natural potential of oak, particularly under climate change. The second part of this thesis therefore aims at identifying the most important climatic drivers of natural oak growth in Central Europe. Furthermore, the question how these growth responses differ with site characteristics is addressed. To this end, increment cores from a total of 333 oaks representing different vitality classes are taken within the Swiss forest reserves, which represent a gradient of soil moisture conditions. Response functions of annual tree-ring indices to monthly temperature means, monthly precipitation and a monthly drought index are calculated. The time frame from June of the previous year until September of the current year is considered as potentially influencing oak growth. Furthermore, relating the responses to soil moisture conditions allows for identifying characteristically varying response intensities.

Chapter III: Estimating the age-diameter relationship of oak species in Switzerland using nonlinear mixed-effects models

The development of tree height growth with increasing age has been studied intensively in the context of traditional yield tables. However, the relationship between age and diameter has reached less attention so far, although a tree's diameter is a fundamental measure in forest science and forestry. Therefore, the main goal of the third part of this thesis is to identify the key environmental variables that shape the age-diameter relationship of oaks. For that purpose, the tree-ring samples introduced in Chapter II are used to determine the age-diameter relationship for the oaks growing in the Swiss forest reserves. Nonlinear mixed-effects models are fitted, with elevation, slope, aspect, soil water holding capacity and the most important climatic driver from Chapter II included as covariates. In addition, a mean model is developed and its accuracy in predicting age-diameter curves is assessed.

Chapter IV: Towards non-destructive estimation of tree age

Accurate tree age information is a prerequisite for many conservational, silvicultural and scientific questions such as assessing expected future growth. Although dendrochronological methods for tree age estimation have proved to be accurate, they are invasive or even destructive and thus often not applicable, e.g. in protected forests. The fourth part of this thesis therefore aims at developing a method for the non-destructive tree age estimation for oaks. To this end, age estimations derived from a traditional method are compared to those derived from two alternative approaches that allow for bypassing dendrochronological sampling in the future. In the first of these two approaches, diameter sequences determined during the forest reserve monitoring are fitted to a range of systematically varying age-diameter curves. In the second approach, the diameter sequences are fitted to the age-diameter curves that are predicted site-specifically for every individual tree from the mean model developed in Chapter III.

References

Adler, F. R. (1996) A model of self-thinning through local competition. Proceedings of the National Academy of Sciences 93: 9980-9984.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660-684.

Ammer, C., Albrecht, L., Borchert, H., Brosinger, F., Dittmar, C., Elling, W., Ewald, J., Felbermeier, B., H. von Gilsa, Huss, J., Kenk, G., Kölling, C., Kohnle, U., Meyer, P., Mosandl, R., Moosmayer, H.-U., Palmer, S., Reif, A., Rehfuess, K.-E. & Stimm, B. (2005) Zur Zukunft der Buche (*Fagus sylvatica* L.) in Mitteleuropa. Allgemeine Forst- und Jagdzeitung 176: 60-67.

Baltisberger, M., Frey, D. & Rudow, A. (2012) eBot. Version 4.0.2012. Institut für Integrative Biologie und Institut für Terrestrische Ökosysteme, ETH Zürich, Zürich.

Barbier, S., Gosselin, F. & Balandier, P. (2008) Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. (2011) Has the Earth's sixth mass extinction already arrived? Nature 471: 51-57.

Bernicchia, A., Benni, A., Venturella, G., Gargano, M. L., Saitta, A. & Gorjón, S. P. (2008) Aphyllophoraceous wood-inhabiting fungi on *Quercus* spp. in Italy. Mycotaxon 104: 445-448.

Biging, G. S. & Dobbertin, M. (1995) Evaluation of competition indices in individual tree growth models. Forest Science 41: 360-377.

Bigler, C. & Bugmann, H. (2003) Growth-dependent tree mortality models based on tree rings. Canadian Journal of Forest Research 33: 210-221.

Bonfils, P., Horisberger, D. & Ulber, M. (2005) Förderung der Eiche. Strategie zur Erhaltung eines Natur- und Kulturerbes der Schweiz. Schriftenreihe Umwelt Nr. 383. proQuercus; Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern.

Brändli, U.-B. (ed) (2010) Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf; Bundesamt für Umwelt BAFU, Bern.

Brang, P., Bugmann, H., Bürgi, A., Mühlethaler, U., Rigling, A. & Schwitter, R. (2008) Klimawandel als waldbauliche Herausforderung. Schweizerische Zeitschrift für Forstwesen 159: 362-373.

Brang, P., Heiri, C. & Bugmann, H. (2011) Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt, Bern.

Bürgi, M. (1999a) A case study of forest change in the Swiss lowlands. Landscape Ecology 14: 567-575.

Bürgi, M. (1999b) How terms shape forests: 'Niederwald', 'Mittelwald', and 'Hochwald', and their interaction with forest development in the Canton of Zürich, Switzerland. Environment and History 5: 325-344.

Caprio, E., Ellena, I. & Rolando, A. (2009) Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy. Landscape Ecology 24: 65-76.

Cardinale, B. (2012) Impacts of biodiversity loss. Science 336: 552-553.

Contran, N., Günthardt-Goerg, M. S., Kuster, T. M., Cerana, R., Crosti, P. & Paoletti, E. (2012) Physiological and biochemical responses of *Quercus pubescens* to air warming and drought on acidic and calcareous soils. Plant Biology (online). DOI: 10.1111/j.1438-8677.2012.00627.x.

Douglass, A. E. (1941) Crossdating in Dendrochronology. Journal of Forestry 39: 825-831.

Ehrlich, P. R. & Murphy, D. D. (1987) Monitoring populations on remnants of native vegetation. In: Nature conservation: the role of remnants of native vegetation (eds D. A. Saunders, G. W. Arnold, A. A. Burbidge & A. J. M. Hopkins), pp. 201-210. Surrey Beatty & Sons Pty Limited, Chipping Norton.

Eiberle, K. (1969) Die Bestandesverhältnisse im Waldreservat "Girstel" bei Gamlikon im Reppischtal. Schweizerische Zeitschrift für Forstwesen 120: 155-173.

Ellenberg, H. (2009) Vegetation ecology of Central Europe. Cambridge University Press, Cambridge.

Fischer, A. M. (2011) Expected changes in extremes. In: Swiss climate change scenarios CH2011 (eds T. Corti, A. M. Fischer, A. Kress & P. Pall), pp. 47-55. C2SM; MeteoSwiss; ETH; NCCR Climate; OcCC, Zurich.

Franklin, J. F., Shugart, H. H. & Harmon, M. E. (1987) Tree death as an ecological process. BioScience 37: 550-556.

Frei, M. (2003) Die Baumflechten des Eichenwitwaldes von Wildenstein. Mitteilungen der Naturforschenden Gesellschaften beider Basel 7: 157-172.

Fritts, H. C. (1976) Tree rings and climate. Academic Press, London.

Haneca, K., Acker, J. V. & Beeckman, H. (2005) Growth trends reveal the forest structure during Roman and Medieval times in Western Europe: a comarison between archaeological and actual oak ring series (*Quercus robur* and *Quercus petraea*). Annals of Forest Science 62: 797-805.

Haneca, K., Čufar, K. & Beeckman, H. (2009) Oaks, tree-rings and wooden cultural heritage: a review of the main characteristics and applications of oak dendrochronology in Europe. Journal of Archaeological Science 36: 1-11.

Hart, J. H. & Wargo, P. M. (1965) Increment borer wounds - penetration points for *Ceratocystis fagacerarum*. Journal of Forestry 63: 38-39.

Hartl, H. (1967) Die Soziologie der Urwälder Scatlè und Derborence. Schweizerische Zeitschrift für Forstwesen 118: 737-743.

Heiri, C. (2009) Stand dynamics in Swiss forest reserves: an analysis based on long-term forest reserve data and dynamic modeling. Ph.D. Thesis No. 18388. Swiss Federal Institute of Technology, Zürich.

Hillgarter, F. W. (1971) Waldbauliche und ertragskundliche Untersuchungen im subalpinen Fichtenurwald Scatlè/Brigels. Ph.D. Thesis No. 4619. Swiss Federal Institute of Technology, Zürich.

Hunter Jr., M. L. (1999) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Kantonsforstamt St. Gallen (2003) Konzept Waldreservate Kanton St. Gallen (ed T. Dietschi). Volkswirtschaftsdepartement des Kantons St. Gallen, St. Gallen.

Küchli, C. & Thomet, S. (2005) Lebendige Kulturgeschichte in Eichenwald. In: Förderung der Eiche. Strategie zur Erhaltung eines Natur- und Kulturerbes der Schweiz (eds P. Bonfils, D. Horisberger & M. Ulber), pp. 37-40. ProQuercus; Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern.

Leibundgut, H. (1959) Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. Schweizerische Zeitschrift für Forstwesen 110: 111-124.

Leibundgut, H. (1962) Richtlinien für Aufnahmen in Waldreservaten. Unpublished report. Institut für Waldbau, ETH Zürich, Zürich.

Manion, P. D. (1981) Tree disease concepts. Prentice-Hall, Englewood Cliffs.

Matter, J.-F. (2004) Waldreservate Professur Waldbau ETH-Zürich: Projekt-Dokumentation & Projekt-Stand. Unpublished report. Institut für Waldbau, ETH Zürich, Zürich.

McMahon, S. M., Parker, G. G. & Miller, D. R. (2010) Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences of the United States of America 107: 3611-3615.

Meyer, K. A. (1931) Geschichtliches von den Eichen in der Schweiz. Mitteilungen der Schweizerischen Centralanstalt für das forstliche Versuchswesen 16: 231-451.

Michel, A. K. & Winter, S. (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. Forest Ecology and Management 257: 1453-1464.

Mühlethaler, U. (2008) Ein Plädoyer für die Eichenförderung. Schweizerische Zeitschrift für Forstwesen 159: 98-102.

Oberhuber, W. & Kofler, W. (2000) Topographic influences on radial growth of Scots pine (*Pinus sylvestris* L.) at small spatial scales. Plant Ecology 146: 231-240.

Parker, G. R. & Leopold, D. J. (1983) Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of the Torrey Botanical Club 110: 482-488.

Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) The future of biodiversity. Science 269: 347-350.

Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85-94.

Rebetez, M. & Dobbertin, M. (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. Theoretical and Applied Climatology 79: 1-9.

Rebetez, M. & Kienast, F. (2005) Auswirkungen der Klimaerwärmung auf die Eichenwälder. In: Förderung der Eiche. Strategie zur Erhaltung eines Natur- und Kulturerbes der Schweiz (eds P. Bonfils, D. Horisberger & M. Ulber), pp. 33-34. ProQuercus; Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern.

Rennenberg, H., Seiler, W., Matyssek, R., Gessler, A. & Kreuzwieser, J. (2004) Die Buche (*Fagus sylvatica* L.) - ein Waldbaum ohne Zukunft im südlichen Mitteleuropa? Allgemeine Forst- und Jagdzeitung 175: 210-224.

Reynolds, J. H. & Ford, E. D. (2005) Improving competition representation in theoretical models of self-thinning: a critical review. Journal of Ecology 93: 362-372.

Rigling, A., Dobbertin, M., Bürgi, M., Gimmi, U., Pannatier, E. G., Gugerli, F., Heiniger, U., Polomski, J., Rebetez, M., Rigling, D., Weber, P., Wermelinger, B. & Wohlgemuth, T. (2006) Verdrängen Flaumeichen die Walliser Waldföhren? Merkblatt für die Praxis. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf.

Rohner, B. (2008) Trockenheitseffekte auf Wachstum und Mortalität der Waldföhren im Pfynwald, Wallis. Masterarbeit. Professur für Waldökologie, ETH Zürich, Zürich.

Stokes, M. A. & Smiley, T. L. (1968) An introduction to tree-ring dating. The University of Chicago Press, Chicago.

Szaro, R. C. & Johnston, D. W. (1996) Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York.

Szwagrzyk, J., Szewczyk, J. & Bodziarczyk, J. (2001) Dynamics of seedlig banks in beech forest: results of a 10-year study on germination, growth and survival. Forest Ecology and Management 141: 237-250.

Tesch, S. D. (1981) The evolution of forest yield determination and site classification. Forest Ecology and Management 3: 169-182.

Thürig, E., Kaufmann, E., Frisullo, R. & Bugmann, H. (2005) Evaluation of the growth function of an empirical forest scenario model. Forest Ecology and Management 204: 51-66.

Weber, P., Bugmann, H. & Rigling, A. (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. Journal of Vegetation Science 18: 777-792.

Weigel, A. P. & Fischer, A. M. (2011) Climate scenarios of seasonal means. In: Swiss climate change scenarios CH2011 (eds T. Corti, A. M. Fischer, A. Kress & P. Pall), pp. 29-39. C2SM; MeteoSwiss; ETH; NCCR Climate; OcCC, Zurich.

Wilcox, B. A. (1984) In situ conservation of genetic ressources: determinants of minimum area requirements. In: National parks, conservation, and development: the role of protected areas in sustaining society (eds J. A. McNeely & K. R. Miller), pp. 639-647. Smithsonian Institution Press, Washington.

Wunder, J. (2007) Conceptual advancement and ecological applications of tree mortality models based on tree-ring and forest inventory data. Ph.D. Thesis No. 17197. ETH Zürich, Zürich.

Wunder, J., Reineking, B., Hillgarter, F.-W., Bigler, C. & Bugmann, H. (2011) Long-term effects of increment coring on Norway spruce mortality. Canadian Journal of Forest Research 41: 2326-2336.

Wunder, J., Reineking, B., Matter, J.-F., Bigler, C. & Bugmann, H. (2007) Predicting tree death for *Fagus sylvatica* and *Abies alba* using permanent plot data. Journal of Vegetation Science 18: 525-534.

Chapter I

Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech

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Abstract

Question: What are the drivers of structural changes and mortality in oak–beech forests over 50 yrs of natural succession?

Location: Twelve unmanaged forest sites, comprising a large environmental gradient in the Swiss lowlands.

Method: By using repeated inventory data from more than 17 600 individually tagged trees, the dynamics of oak–beech stands over the past 50 yrs were analysed. Generalized linear mixed-effects models were fitted to quantify annual mortality rates of oak and beech based on DBH, stand basal area, precipitation and slope.

Results: Stand basal area increased, whereas tree density decreased over time. At most sites, the relative importance of oak decreased gradually compared to beech. Mortality increased over time for both oak and beech, but the increase was stronger for oak. Oak and beech mortality decreased with increasing DBH and tended to increase with precipitation. Additionally, oak mortality increased with stand basal area, whereas no such trend was found for beech.

Conclusion: Our study indicates that mortality in Central European oak–beech forests is driven by a combination of stand structures (i.e. tree size and stand basal area) and climate. However, the influence of climate on oak mortality is comparably low. Increasing oak mortality with stand basal area is a plausible consequence of its lower relative competitiveness and higher demand for light. Thus, in forests developing towards higher stand basal area, the ecologically important oak is increasingly outcompeted by beech, unless competition is reduced through management or disturbances.

Keywords: Akaike weight; *Fagus sylvatica*; forest dynamics; forest succession; generalized linear mixed-effects model; *Quercus* spp.; tree population.

Introduction

Natural forest succession has been a strong focus in vegetation ecology for a long time (Watt 1947; Peterken 1996). Understanding successional pathways in forests is crucial for a wide range of issues, among others timber production, conservation objectives and the assessment of ecological processes. A key driver of forest succession is tree mortality, as it causes changes in species composition and structural diversity (Franklin et al. 1987; Slik 2004).

In Central Europe, much attention has been paid to succession in mixed oak–beech forests since oak species are highly valuable for biodiversity (Ranius & Jansson 2000; Bernicchia et al. 2008; Bertiller & Müller 2010) whereas beech is the naturally dominant tree species of most lowland forests (Brzeziecki et al. 1993; Ellenberg & Leuschner 2010). Both taxa have approximately the same optimum growth ranges in mesic, moderately acidic to alkaline conditions (Ellenberg & Leuschner 2010). This causes high competitive pressure, under which succession typically leads to a dominance of beech due to its higher shade tolerance (Leibundgut 1984; Ellenberg & Leuschner 2010). Towards the edges of their range, relative competitiveness inverts, resulting in the dominance of oaks in areas that are too dry, too wet or too acidic for beech (Ellenberg & Klötzli 1972; Ellenberg & Leuschner 2010). However, human facilitation has increased the proportion of oak in many beech-dominated forests (Ellenberg & Leuschner 2010).

These descriptions of natural oak–beech succession are mainly of observational nature, whereas quantifications based on empirical data are largely lacking. Therefore, it is basically unknown to what extent and how rapidly stand structures change after the abandonment of forest management. In addition, little is known about natural mortality rates in oak–beech forests and the underlying drivers.

As a consequence of climate change, successional patterns are potentially shifting (Eastaugh 2008; Walther 2010). In Central Europe, increased temperatures, moister winters, drier summers and more frequent extreme events such as heatwaves and droughts are expected (Schär et al. 2004; OcCC 2008). Changes in the climate and its variability have been suggested to influence species ranges and mortality processes in forest ecosystems all over the world (e.g. Mueller et al. 2005; van Mantgem et al. 2009; Allen et al. 2010). There is an ongoing debate whether oaks could benefit from climate change in Central Europe, especially compared to beech (Brzeziecki et al. 1995; Bugmann 1997; Wohlgemuth et al. 2006; Wallnöfer & Hotter 2008).

The study of natural forest succession requires long-term data series from forests that have not been affected by human interventions. Such data sets are rare, which is likely the reason for the lack of quantitative studies on natural oak–beech succession. Unmanaged, but regularly inventoried, forest reserves provide an opportunity to fill this gap. However, relatively few long-term studies on successional pathways and tree mortality have been conducted in forest reserves (Bigler & Bugmann 2003; Wolf et al. 2004; Coomes & Allen 2007; Wunder et al. 2008; Heiri et al. 2009), and no study has focussed on the relationship between oak and beech. Therefore, we use a large set of permanent plots in Swiss forest reserves to quantify changes in stand structures and mortality rates of oak and beech and their potential drivers after the abandonment of management. We aim to elucidate whether natural succession leads to the dominance of beech over oak, or whether changes in climate variability may lead to an opposite trend. Hence, we focus on three main questions:

1) How do diameter distributions, stand basal area and the relative importance of oak and beech develop after the abandonment of management?
2) To what extent do mortality rates vary over time and differ between oak and beech?
3) What are the drivers of oak and beech mortality under natural succession?

Methods

Forest inventory data

We used data from the Swiss forest reserve network, which is jointly managed by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), ETH Zurich and the Swiss Federal Office for the Environment (FOEN). The network currently consists of 49 unmanaged forests located throughout Switzerland (for details see Wunder et al. 2007; Brang et al. 2008, 2011). Within many of these reserves, permanent plots have been established in which every tree with a diameter at breast height (DBH) ≥ 4 cm was individually tagged and its species recorded. During repeated inventory campaigns at intervals of approximately 5–10 yrs, the DBH and the status (dead/alive) of all trees was recorded. Ingrowing trees with a DBH ≥ 4 cm were also tagged and measured. The first campaigns took place in the late 1940s, and although the exact date of the last management interventions is unknown, it is documented that most forests had not been managed for several decades prior to incorporation in the reserve network (Brang et al. 2011). Thus, the data set covers more than half a century of natural forest succession.

Study sites

Twelve study sites were selected within the reserve network, which represent a wide range of oak and beech habitats varying in phytosociological associations, climatic conditions and slope (Table 1, see Appendix S1 for locations of the sites). The following criteria had to be met by the study sites: (1) the proportion of oaks, calculated as the importance value (IV = [relative density + relative basal area] / 2 × 100; Parker & Leopold 1983), was at least 10% in the last inventory; (2) at least three inventory campaigns have taken place; and (3) the phytosociological association had to be homogeneous within every study site. To meet the

Table 1. Detailed information on the study sites. 'Area' denotes the sum of the areas of the plots within one site; two values are given if the number of inventoried plots varied between campaigns. Phytosociological associations are indicated according to Ellenberg and Klötzli (1972), soil types are based on the FAO system (FAO 1998).

Site	Coordinates (northing, easting)	Elevation (m a.s.l.)	Slope (°)	Aspect*	Main soil type	Phyto-sociological association	Area (ha)	Number of plots	Inventory campaigns	Distance to climate station (km)
Adenberg (Ad)	47° 36' 50'' 8° 33' 40''	490-520	10	NW	Cambisol	*Galio odorati-Fagetum*	2.25	5	1970, 1980, 1990, 2002	4.3
Bannhalde (Ba)	47° 31' 28'' 8° 31' 15''	420	0	-	Cambisol	*Galio odorati-Fagetum*	0.50	1	1973, 1984, 1994, 2000	0.8
Bois de Chênes (Bo)	46° 26' 17'' 6° 13' 33''	510-520	5	N-S	Cambisol	*Carici albae-Fagetum caricetosum montanae*	2.67/4.46	7	1970-1974, 1984, 1995, 2007	4.2
Les Follatères (Fo)	46° 7' 39'' 7° 4' 26''	620-880	35	SE	Leptosol	*Arabidi turritae-Quercetum pubescentis*	3.17	14	1974, 1984-1986, 1995-1997	22.0
Josenwald (Jo)	47° 8' 5'' 9° 15' 19''	480-780	45	S	Leptosol	*Sileno nutantis-Quercetum*	0.84	3	1980-1981, 1990-1991, 2007	13.0
Krummenlinden (Kr)	47° 33' 27'' 8° 20' 8''	550	0	-	Cambisol	*Galio odorati-Fagetum luzuletosum*	0.74	3	1956, 1966, 1976, 1986, 1996	7.6
Langgraben (La)	47° 32' 49'' 8° 31' 36''	420	0	-	Luvisol	*Galio odorati-Fagetum luzuletosum (Galio silvatici-Carpinetum)*	0.49/0.92	4	1973, 1983, 1994, 2004	3.1
Strassberg (St)	47° 31' 55'' 8° 29' 40''	470-490	5	NW-SW	Cambisol	*Galio odorati-Fagetum*	2.03/2.16	5	1976, 1987, 2001	2.8
Vorm Stein 1 (Vo1)	47° 33' 7'' 8° 27' 13''	540	0	-	Luvisol	*Luzulo silvaticae-Fagetum typicum*	0.49/1.79	5	1972, 1986, 1999-2000	3.2
Vorm Stein 2 (Vo2)	47° 33' 7'' 8° 27' 13''	500-540	20	SW	Cambisol	*Coronillo coronatae-Quercetum (Cytiso-Pinetum silvestris)*	0.24/0.93	3	1972, 1986, 2000	3.2
Vorm Stein 3 (Vo3)	47° 33' 7'' 8° 27' 13''	480-500	10	SW	Cambisol	*Galio odorati-Fagetum (Pulmonario-Fagetum melittetosum)*	0.74	3	1972, 1986, 1999	3.2
Weidwald (We)	47° 24' 47'' 7° 59' 33''	600-680	25	S	Leptosol	*Asperulo taurinae-Tilietum,* *Cardamino-Fagetum typicum*	1.31	2	1976, 1987, 1998	1.9

* For sites with slope = 0°, aspect is not defined.

third criterion, the reserve Vorm Stein was split into three homogeneous sites. To keep the focus on late-successional processes, we excluded permanent plots with documented large-scale disturbances (mainly windthrow). The 12 selected study sites comprise a total area of nearly 20 ha.

Tree species

The three main oak species of Switzerland, *Quercus petraea* (Mattuschka) Liebl., *Quercus robur* L. and *Quercus pubescens* Willd., were analysed collectively (referred to as 'oak') for the following reasons: (1) in the inventory campaigns, *Q. petraea* and *Q. robur* were not discriminated because of their overlapping morphological attributes (cf. Kissling 1980; Aas 1998); (2) all three species tend to hybridize (Kissling 1980; Aas 1998); (3) the question whether they are different species at all is controversial (Aas 1998; Muir et al. 2000). The collective analysis of the three species resulted in a total of 8533 oak trees in the selected study sites.

Fagus sylvatica L. (referred to as 'beech') is the main competing species in most of the study sites. However, at two sites (Les Follatères and Josenwald; Table 1) beech was only marginally present. Therefore, the represented ecological gradient is slightly narrower for beech than for oak (e.g. slope, see Table 1). Nevertheless, 9086 beech trees were incorporated in the data set.

Data analysis

Development of stand structure

The temporal development of stand basal area was investigated for every study site. Site-specific changes in the relative importance of oak and beech were analysed based on stem density, basal area and IV. In addition, temporal changes in the diameter distributions of oak and beech were tested using a Kolmogorov–Smirnov test. All variables were standardized to 1 ha.

Mortality rates

Annual mortality rates m (Sheil & May 1996) were calculated at a population level as

$$m = 1 - (N_t/N_0)^{1/t} \tag{1}$$

where N_0 and N_t are the numbers of living trees at the beginning and at the end of the interval, respectively, and t is the inventory interval in years. Mortality rates m were only calculated if $N_0 \geq 10$. We did not investigate individual-based mortality since (1) most variables explaining variability in mortality (see below) were available only at the population level, and (2) comparisons among sites would have been difficult due to the differing inventory periods.

In populations containing trees with differing mortality probabilities, mortality rates decline with increasing inventory intervals, because the fraction of the population with a high mortality probability declines faster than the fraction with a low mortality probability (Sheil & May 1996). It follows that mortality rates calculated from diverse interval lengths can only be compared when calculated for subpopulations with homogeneous mortality probabilities (Sheil & May 1996). To account for the varying inventory intervals in our data set (Table 1), mortality rates (equation 1) were calculated separately for oak and beech, as well as for three DBH classes ('small', 'medium', 'large') to achieve the highest possible comparability.

For each site and inventory, we grouped all measured trees according to their DBH into three bins with equal numbers of trees ('small', 'medium', 'large'). The mean bin size across the three to five inventories per site was used to define the DBH classes for a specific site. The resulting site-specific variation of bin sizes takes into account that a tree with a given DBH can be completely suppressed at a productive site, while it may dominate at an unproductive site.

A paired Wilcoxon rank sum test was performed to analyse whether changes in mortality rates differed between oak and beech. For this purpose, the differences between the mortality rates of the first and the last inventory period were calculated separately for all sites and DBH classes, and pairs were defined as the corresponding differences of oak and beech.

Mortality models

Relationships between annual mortality rates and explanatory variables were identified using generalized linear mixed-effects models for proportions based on maximum likelihood, i.e. logistic regression models (Zuur et al. 2009). Models were fitted to the oak and beech data separately.

As fixed effects, characteristics related to the subpopulations, stands and sites were jointly considered. The DBH classes were treated as a factor with three levels (referred to as 'DBH'). As an indicator for the competitive situation in the stands, stand basal area (in m^2ha^{-1}) at the beginning of the respective interval was included as a further fixed effect (referred to as 'BA'). More complex competition indices could not be calculated due to the lack of spatial information at the tree level. Moreover, site-specific variations were considered based on both topography and regional climate. Topography was represented via the mean slope of all permanent plots within the individual study sites in degrees (referred to as 'SL'). Elevation was not considered as an explanatory variable due to the low variability among sites. To represent climate variability, precipitation sums during the growing season (April–September, referred to as 'PG') from the nearest climate station (Table 1) were included, since precipitation tends to be a limiting factor for trees in the Swiss lowlands (Ellenberg & Leuschner 2010). Mean precipitation sums of the intervals were standardized for every site separately to focus on within-site variations and thus to allow for comparisons among sites with different precipitation levels. Temperature was not included since it is not a limiting factor in the

Swiss lowlands (Ellenberg & Leuschner 2010), and it showed only low variability among the investigated sites.

Random effects were defined for the intercept with study sites as grouping factor. The inclusion of additional random effects for the variables did not improve the model performance and is therefore not shown in the results.

The four explanatory variables DBH, BA, SL and PG were tested for collinearity, which was quantified using variance inflation factors (VIF). All VIFs were < 1.5, indicating the absence of any critical collinearity (Zuur et al. 2009). Based on all possible combinations of the four explanatory variables, a set of 15 competing candidate models was formulated (Table 2). Interactions between explanatory variables were not considered due to limited sample sizes.

Table 2. Complete set of competing mixed-effects models for the mortality rates of oak and beech, and their results in the model ranking.

Model	Fixed effects				Random effect	Oak		Beech	
	DBH	SL	BA	PG	intercept	$\Delta AICc$	Weight (%)	$\Delta AICc$	Weight (%)
1	×				×	12.0	0.1	6.2	2.3
2		×			×	365.1	0.0	205.0	0.0
3			×		×	366.9	0.0	206.2	0.0
4				×	×	366.8	0.0	204.2	0.0
5	×	×			×	12.5	0.1	8.3	0.8
6	×		×		×	0.5	23.4	5.3	3.6
7	×			×	×	2.2	9.6	0.0	51.2
8		×	×		×	367.3	0.0	207.2	0.0
9		×		×	×	367.1	0.0	205.3	0.0
10			×	×	×	369.0	0.0	204.4	0.0
11	×	×	×		×	1.5	13.7	7.4	1.3
12	×	×		×	×	3.0	6.4	2.2	17.3
13	×		×	×	×	0.0	29.4	2.1	17.8
14		×	×	×	×	369.4	0.0	205.7	0.0
15	×	×	×	×	×	1.1	17.3	4.4	5.8

Diameter at breast height (DBH), slope (SL), stand basal area (BA) and standardized precipitation (PG) were considered as explanatory variables. The best-fitting models for oak and beech are highlighted in grey. $\Delta AICc$ is the difference in $AICc$ of the particular model and the model with the lowest $AICc$. Weight indicates the Akaike weights (equation 3) of the models. These weights can be interpreted as the probability of the particular model to be the best-fitting model for describing the data, given the complete set of candidate models (Burnham & Anderson 2002; Johnson & Omland 2004).

Model selection and model performance

The models that best explained mortality (referred to as 'best-fitting models') were identified according to an information-theoretic approach based on the corrected Akaike information criterion ($AICc$, Burnham & Anderson 2002), which is unbiased for small samples. For every model, the $AICc$ was calculated as

$$AICc = AIC + 2k(k+1)/(n-k-1) \quad (2)$$

where n is the sample size, k the number of parameters in the model, and AIC is defined as -2 × log(likelihood) + 2 × k (Burnham & Anderson 2002). The models were ranked based on Akaike weights, which are defined as

$$w_i = \left(e^{-\frac{1}{2}\Delta_i}\right) / \left(\sum_{i=1}^{15} e^{-\frac{1}{2}\Delta_i}\right) \quad (3)$$

where Δ_i is the difference in $AICc$ between model i and the model with the lowest $AICc$ (Burnham & Anderson 2002; Johnson & Omland 2004). Akaike weights may be interpreted as the probability that model i best describes the observed data, given the set of candidate models (Johnson & Omland 2004). Using this approach, the models with the best fit were identified separately for oak and beech.

In addition to single-model inference, multi-model inference (Burnham & Anderson 2002) was performed, since more than one model described mortality rates for oak fairly well. Therefore, the relative importance of the individual variables was calculated as the sum of the Akaike weights of all models in which the particular variable occurs (Burnham & Anderson 2002). We did not perform model averaging since quantitative prediction was not the main goal of the study (Burnham & Anderson 2002; Johnson & Omland 2004).

Model diagnostics were checked for the best-fitting models based on deviance residuals that were plotted against all variables and against the fitted values to detect possible undesirable structures in the residuals. In addition, Pearson correlations between observed and predicted mortality rates were calculated as an indicator of model performance. To assess the robustness of the results, we followed a leave-one-out approach by re-running the model selection procedure multiple times, each time excluding one study site.

All analyses were performed using R, a language and environment for statistical computing (R for Windows version 2.11.1; R Foundation for Statistical Computing, Vienna, Austria). For most visualizations, the packages *lattice* (R package version 0.18-8) and *latticeExtra* (R package version 0.6-14) were used. Models were fitted using the package *lme4* (R package version 0.999375-37).

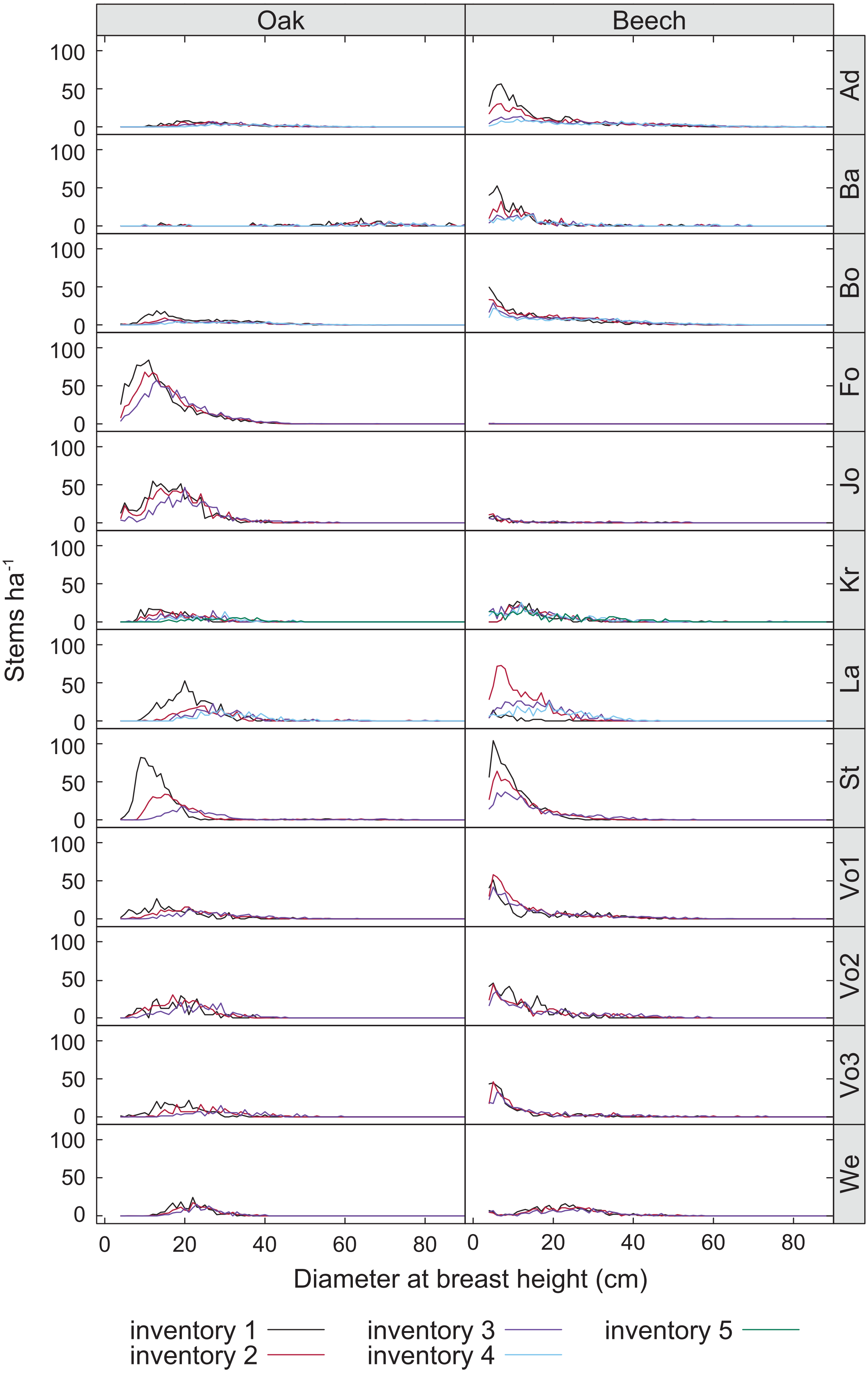


Figure 1. Development of diameter distributions of oak and beech at the study sites (4 cm ≤ DBH ≤ 100 cm). Site abbreviations are according to Table 1.

Results

Development of stand structure

Diameter distributions changed over time and differed between oak and beech as well as among sites (Fig. 1). For both species, trees up to 50 cm DBH were frequent at most sites; only Adenberg and Bannhalde contained a substantial proportion of larger trees (18% and 23% in the last inventory, respectively). For oak, the DBH distributions were generally bell-shaped with a positive skew, whereas for beech, variations from bell-shaped with a positive skew to inverse J-shaped were present. Overall, beech was relatively more frequent in the lowest diameter classes than oak. The diameter distributions of oak significantly shifted to larger DBHs at all sites, accompanied largely by a decreasing frequency of the lowest diameter trees (Kolmogorov–Smirnov test between the first and the last inventory, $P = 0.02$ at Bannhalde, $P < 0.01$ at all other sites). For beech, DBH distributions changed significantly at ten sites ($P = 0.02$ at Vorm Stein 1, $P < 0.01$ at all other sites), while only for Josenwald was no significant change recorded ($P = 0.51$). In Les Follatères, there were too few beech trees to perform a Kolmogorov–Smirnov test ($n = 5$ in the last inventory).

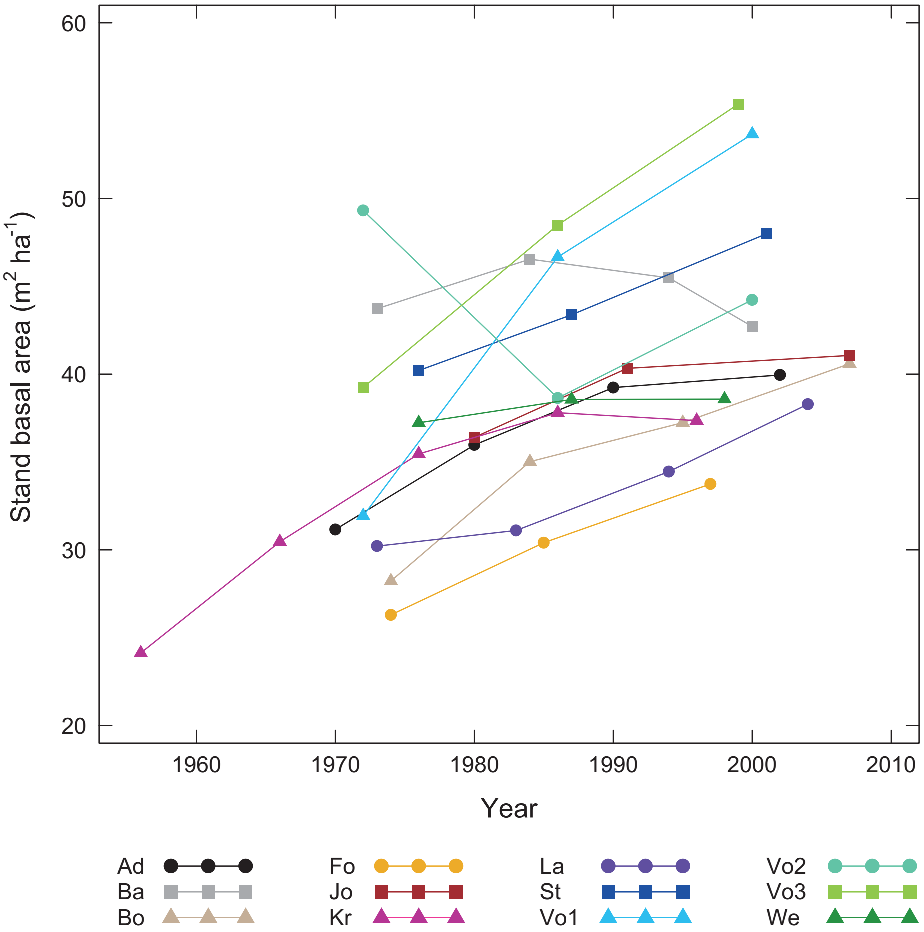


Figure 2. Development of stand basal area over time for all study sites (site abbreviations according to Table 1). At some sites, the inventoried areas changed between inventories (cf. Table 1).

Stand basal area monotonically increased over time at nine of the 12 study sites (Fig. 2). The increase from the first to the last inventory ranged from 4% (Weidwald) to 68% (Vorm Stein 1), with an average of 33% over all sites with an increase. In eight of the sites (Adenberg, Bois de Chênes, Les Follatères, Josenwald, Krummenlinden, Vorm Stein 1, Vorm Stein 3, Weidwald), the increase was more pronounced in earlier than later inventories. Stand basal area temporarily decreased at three sites (Bannhalde, Krummenlinden, Vorm Stein 2), although at Krummenlinden, only a marginal decrease was observed in the last inventory period. For Vorm Stein 2, the decrease was an artefact of the substantial expansion of the inventoried area from the first to the second inventory.

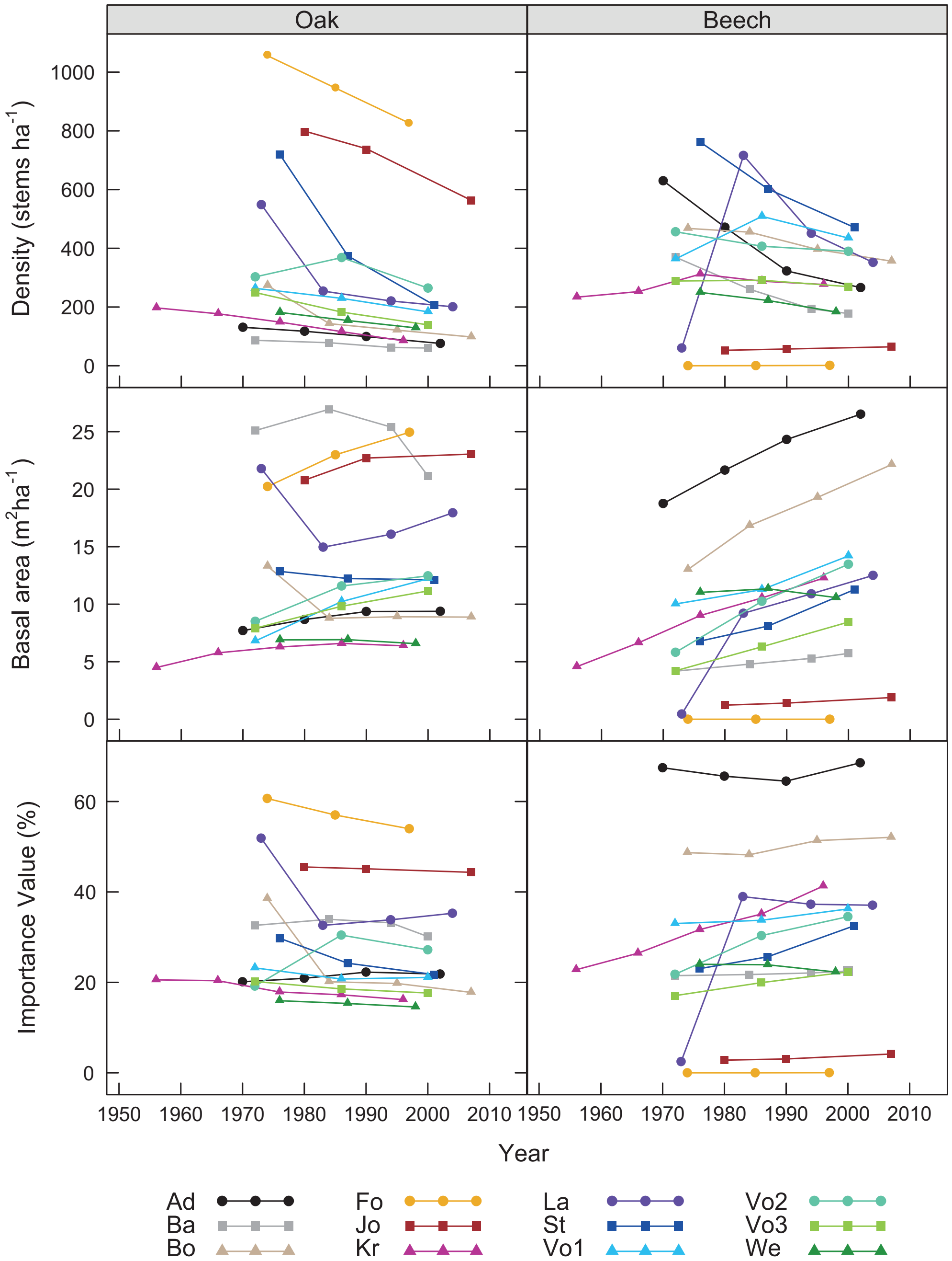


Figure 3. Development of stem density, basal area and importance values of oak and beech over time. Importance values were calculated as [relative density + relative basal area] / 2 × 100 (Parker & Leopold 1983). Site abbreviations are according to Table 1.

Stem density decreased from the first to the last inventory at all sites, and this effect was typically more pronounced for oak than for beech (Fig. 3, Appendix S2). Basal area of beech increased at all sites except Weidwald and Les Follatères, whereas no consistent trend was found for oak (Fig. 3). The combination of these patterns resulted in slightly decreasing IVs for oak and slightly increasing IVs for beech at the majority of the sites.

Mortality patterns

Annual mortality rates differed among tree sizes and species (Fig. 4). For oak, they ranged between 0% and 26% and thus were more variable and generally higher than those of beech, which did not exceed 9%. This holds true even if the highest two mortality rates of oak are omitted from the data set. Mortality rates showed an increasing trend over time, and the increase was significantly higher for oak than for beech (paired Wilcoxon rank sum test, P = 0.006). Furthermore, both species generally showed decreasing mortality rates with increasing tree size (cf. Appendix S3).

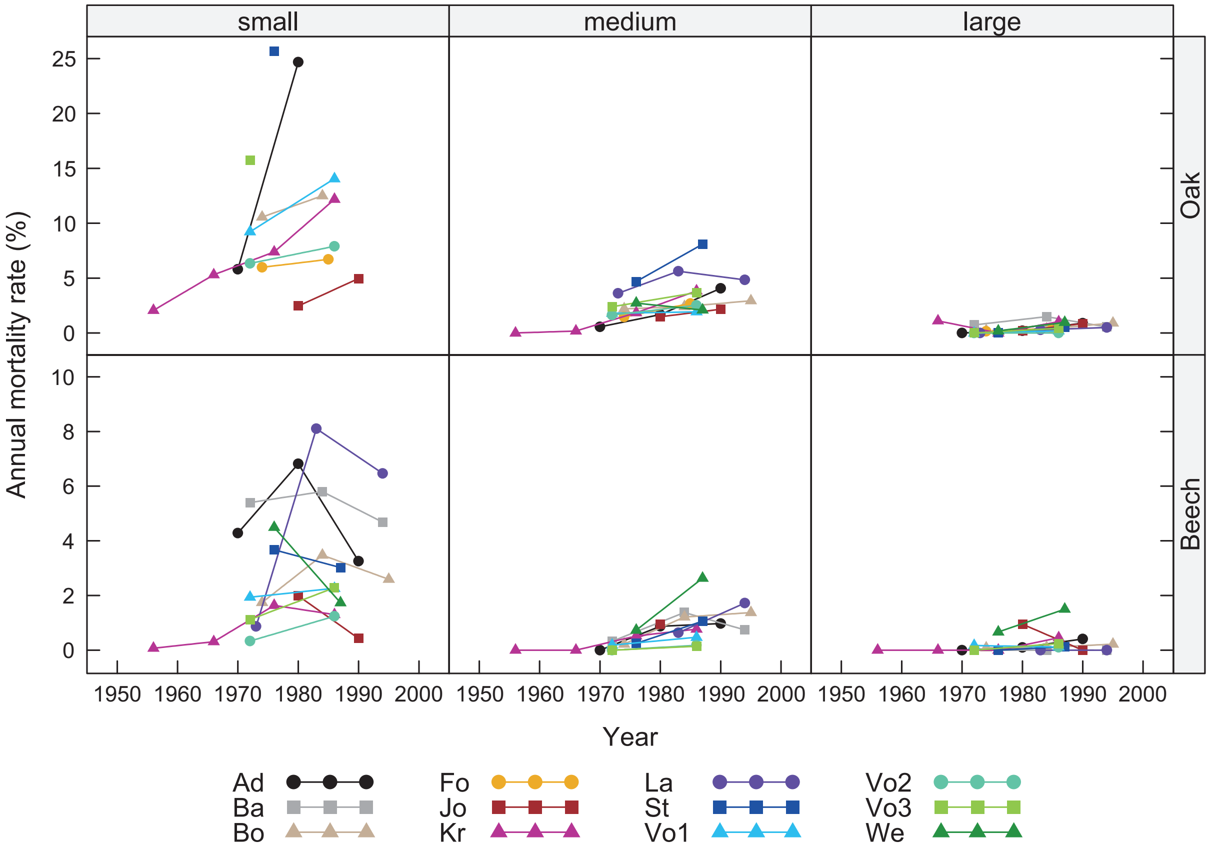


Figure 4. Annual mortality rates of small, medium and large oak and beech trees plotted against the years at the beginning of the corresponding periods. ‘Small’, ‘medium’ and ‘large’ refer to the diameter ranges of the smallest, medium and largest third of all trees over the complete investigated period within the particular sites (site abbreviations according to Table 1). For intervals in which the number of living trees at the beginning (N_0) was < 10, mortality rates were not calculated, which resulted in some mortality rates being unconnected in the figure. Please note the varying y-axis scales.

Drivers of oak and beech mortality

Based on the Akaike weights, model 7 clearly described the mortality rates of beech best, whereas for oak several models (models 6, 13 and 15) described the mortality rates similarly well (Table 2).

DBH reached a relative importance of 100% for describing both oak and beech mortality rates (Table 3), reflecting the fact that all candidate models without DBH had an Akaike weight of 0% (Table 2). The correlation between DBH and mortality was negative (for a detailed model outcome see Appendix S4), indicating consistently decreasing mortality rates with increasing DBH. The decrease in mortality with increasing DBH was significant ($P < 0.001$) for both oak and beech, although more pronounced for oak (Fig. 5, Appendix S4).

The relative importance of PG was 92% for beech, whereas it was almost 30% lower for oak. PG was positively correlated with mortality (Appendix S4), indicating higher mortality during more humid periods relative to the mean conditions of the individual sites. Beech had a higher effect size and a higher significance than oak (Fig. 5, Appendix S4).

BA reached a relative importance of 84% for describing oak mortality but only 29% for describing beech mortality. It was not included in the best-fitting beech model, whereas a significant positive correlation with mortality was found in the best-fitting oak model (Appendix S4). Thus, oak mortality was generally higher in stands with higher stand basal area (Fig. 5).

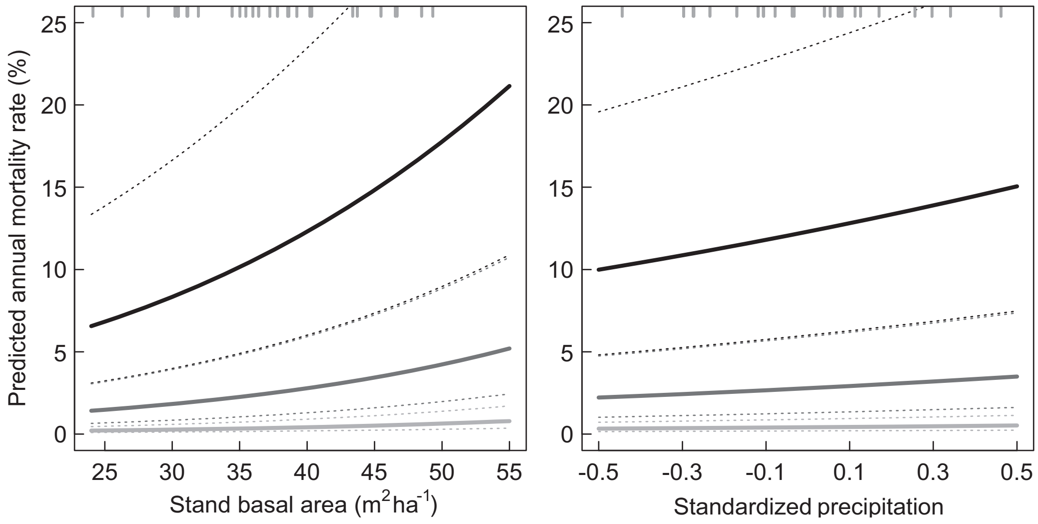
SL was not included in the best-fitting models for either oak or beech (Table 2). Thus, it showed by far the lowest relative importance of all explanatory variables (38% for oak and 25% for beech, Table 3).

Table 3. Relative importance of variables for oak and beech mortality. The relative importance of the explanatory variables diameter at breast height (DBH), slope (SL), stand basal area (BA) and standardized precipitation (PG) is defined as the sum of the Akaike weights of those models, in which the variables occur (Burnham & Anderson 2002; Akaike weights according to Table 2).

	Oak	Beech
DBH (%)	100	100
SL (%)	38	25
BA (%)	84	29
PG (%)	63	92

The fixed effects of the best-fitting oak model fitted the observed mortality rates better than those of the best-fitting beech model (see Appendix S5). For both species, the inclusion of a random effect clearly improved model predictions. Residual diagnostics based on deviance residuals did not show any undesirable patterns for either the oak or the beech model. Furthermore, leaving out individual sites in the model did not affect the results for beech and generally not for oak. However, leaving out Krummenlinden or Strassberg slightly changed the order of the relative importance of PG, BA and SL for oak, whereas DBH reached 100% of relative importance in every case.

a) Oak model 13



b) Beech model 7

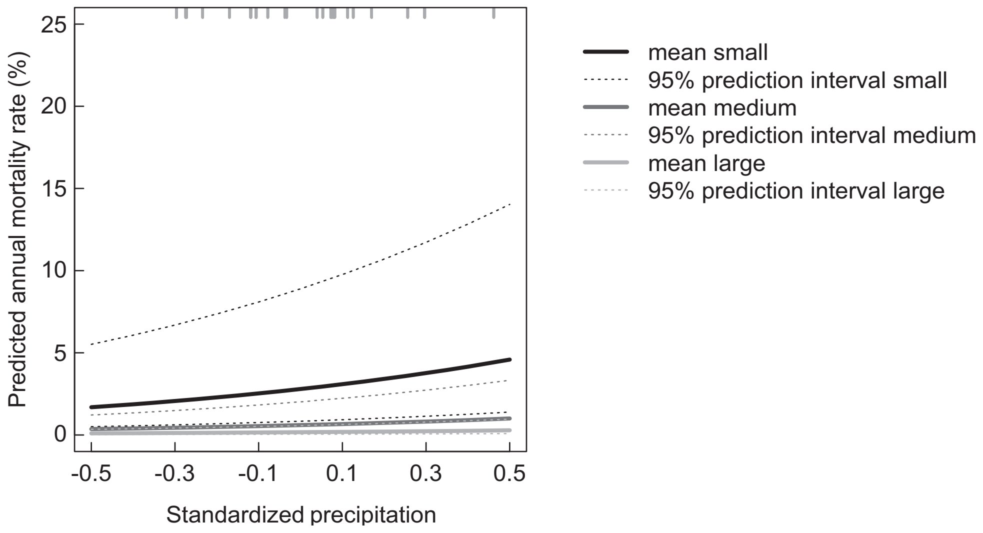


Figure 5. Best-fitting models for (a) oak and (b) beech. Mortality estimates are plotted against the included explanatory variables per DBH class (small, medium, large). For oak, stand basal area and standardized precipitation were kept constant within the visualization of the other variable (stand basal area = 40 m^2ha^{-1}, standardized precipitation = 0). Observed values of the explanatory variables are indicated with a rug plot (top of the panels).

Discussion

Development of stand structure

The analysis of repeated inventory data from 12 oak–beech stands in Swiss forest reserves revealed shifts in the DBH distributions and IVs during the past 50 yrs, indicating that the species composition underwent considerable changes, leading to an increased abundance of beech compared to oak. A change in the proportions of the two tree species is particularly evident from the increasing relative frequency of beech in the small diameter classes over time. Similar shifts in the DBH distribution of shade-tolerant tree species compared to shade-intolerant tree species were found in other naturally developing forests, e.g. in an old-growth oak forest in the USA (Parker et al. 1985) and in several forest types in the Białowieża National Park in Poland (Bernadzki et al. 1998). Among our sites, the only exceptions were Les Follatères and Josenwald, where no trend towards increased beech dominance was found, probably because the dry conditions of these forests lie outside the range of strong competitiveness of beech (Ellenberg & Klötzli 1972).

The more pronounced decrease in stem density for oak and the opposite trends in the IVs of oak and beech at many of our study sites further indicate an increasing dominance of beech, which coincides with developments in other natural forests throughout Europe (Koop & Hilgen 1987; Emborg et al. 2000). However, some abrupt changes in stem density, basal area and IVs are likely due to changes in the inventoried area (cf. Table 1).

Stand basal area of most forests studied here increased substantially after management had been abandoned. In the last inventory, stand basal area reached or even exceeded values observed in old-growth beech forests (Commarmot et al. 2005). This finding may be interpreted as a further indicator for the development towards more natural stand structures (cf. Heiri et al. 2009). Particularly in stands with a strong increase in stand basal area at earlier inventories, this development may already be further advanced. The observed changes in stem density and basal area of oak and beech indicate that stand basal area increased due to radial growth rather than due to additional trees (for details cf. Appendix S2). Furthermore, the decrease in tree numbers suggests that mortality plays a crucial role in these forests.

Mortality patterns

The decrease in relative oak abundance is consistent with their higher mortality rates compared to beech. The generally higher mortality for oak than for beech is in accordance with findings from southern France (Kunstler et al. 2005), but contrasts with observations from Austria (Monserud & Sterba 1999); however, both of these studies included mainly managed forests, and the former was located in a warmer area with drier summers resulting in reduced comparability. The decrease in relative oak abundance became more evident over time, which is further indicated by the significantly higher increase in mortality for oak than for beech.

Mortality rates of both oak and beech were, compared to results from other studies in Europe, higher in the small DBH class but similar in the large DBH class (Monserud & Sterba 1999; Mountford et al. 1999). Mortality rates of the medium DBH class were comparably high for oak but not for beech. Annual mortality rates of oak and beech did not exceed 2% in Austria (Monserud & Sterba 1999) and 4.5% in the United Kingdom (Mountford et al. 1999), whereas values ≥ 5% were frequent for small and medium-sized oak and small beech trees in our study. These high mortality rates are probably due to the absence of management in our sites, at least compared to the observations in Austria (Monserud & Sterba 1999).

Drivers of oak and beech mortality

Observed mortality rates were described fairly accurately by the variables included in the statistical models, although better for oak than for beech. Predictions based on DBH, BA and PG achieved a Pearson correlation of 0.77 with observed oak mortality, whereas beech mortality showed a correlation of 0.67 with predictions based on DBH and PG. Bearing in mind how many complex and interacting factors have been supposed to influence mortality (cf. Franklin et al. 1987), this model performance is relatively high.

Mortality rates consistently decreased with increasing DBH for both oak and beech. Similar patterns were found in a variety of managed (Monserud & Sterba 1999; Adame et al. 2010) and natural forests (Lorimer et al. 2001; Coomes & Allen 2007). They were mostly interpreted as a result of competitive self-thinning, in which smaller trees compete less successfully for light than larger trees (Adler 1996; Reynolds & Ford 2005; Coomes & Allen 2007). In our data, this effect was more pronounced for oak, which coincides with its higher demand for light compared to beech (Ellenberg & Leuschner 2010). Additionally, several studies suggested a U-shaped relationship between DBH and mortality, indicating that mortality increases for the largest trees as a result of senescence and disturbance (Goff & West 1975; Lorimer et al. 2001; Coomes & Allen 2007; Lines et al. 2010; Hurst et al. 2011). However, in the present study, trees larger than 50 cm were rare and sites with documented stand-wide disturbances were excluded, hence this supposed increase in mortality rates could not be evaluated here.

Oak mortality was considerably higher in stands with higher BA, whereas beech mortality remained unaffected. This difference can be used to explain the observed shift in relative abundance from oak towards the more shade-tolerant beech, as stand basal area consistently increased over time at most sites. The increasing stand basal area has likely enhanced competitive pressure and thus the struggle for light (cf. Heiri et al. 2009), leading to increasing mortality rates of the light-demanding oak, whereas the shade-tolerant beech was less affected. Stand basal area has previously been discussed as a driver of species-specific tree mortality (Fridman & Ståhl 2001; Klos et al. 2009; Lines et al. 2010), however, differential responses of European oak and beech species have not been shown to date.

Climate variability affected mortality rates by slightly increasing beech and oak mortality during more humid periods. Since PG did not systematically increase over time, a spurious correlation due to a simultaneous increase in stand basal area is unlikely. However, PG did not explain much of the observed variability in mortality rates, especially not for oaks. The small positive effect of PG on mortality seems rather unexpected because precipitation is usually assumed to be a limiting factor in the Swiss lowlands (Ellenberg & Leuschner 2010) and particularly under severe drought, tree mortality is assumed to increase (Allen et al. 2010). Thus, under conditions of limited precipitation, more humid periods are expected to enhance growing conditions and consequently reduce mortality. However, an indirect effect possibly led to an increased mortality of weakened trees, because trees tend to enlarge leaf area during humid periods (Jose & Gillespie 1997; Dobbertin et al. 2010). Vigorous trees may have benefited from increased leaf area as they could absorb more light, whereas smaller and weakened trees, which did not reach the canopy or did not develop a full crown, may have suffered from reduced light availability below and within the main canopy. This explanation is in line with the observation that especially the mortality of small trees increased with PG.

Current and future roles of oak and beech in near-natural forests

The present study indicates that tree size, stand basal area and precipitation explain a large amount of the mortality in Central European oak–beech forests that are developing towards more natural states. Therefore, the observed mortality patterns may be interpreted as combined effects of stand structures and climate. Furthermore, differences in relative competitiveness are likely to have caused higher mortality of oak compared to beech, especially in stands with high stand basal area.

A possible climate-induced relative benefit of the drought-tolerant oak has not been detected in our data set, although it has been suggested as an emerging pattern for Central Europe (Brzeziecki et al. 1995; Wohlgemuth et al. 2006). Moreover, if the trend of increasing stand basal area holds, oak may further be outcompeted by beech. However, this effect is likely to decelerate by the time when stand basal area is close to its maximum.

The effects of stand structure and climate on mortality were analysed collectively for the three oak species. These species are likely to respond somewhat differently to climate variations; for example, *Q. petraea* copes with a fairly large amplitude of moisture conditions whereas *Q. robur* is more adapted to moist soils and *Q. pubescens* performs best under dry conditions (Ellenberg & Leuschner 2010). Thus, further studies based on single oak species would be desirable to yield more differentiated insights regarding the effects of climate variability on oak mortality. Unfortunately, this was not possible in our case since the three species are not consistently distinguished in the inventory data. Yet, the three oak species are far more light-demanding and thus less competitive in dense canopies than beech (Ellenberg & Leuschner 2010). Therefore, our finding regarding increased oak mortality due to increased competitive pressure is likely to be representative for a wide range of oak–beech forests in Central Europe.

The shift from oak towards increased beech dominance indicates a development towards proximity to natural conditions, since site conditions in most investigated forests are more favourable for beech than for oak. The formerly high proportion of oaks largely resulted from human facilitation (Ellenberg & Leuschner 2010) and has consequently been decreasing in the course of the development towards natural conditions. Due to the high importance of oaks for many associated species (Ranius & Jansson 2000; Bernicchia et al. 2008; Bertiller & Müller 2010), this replacement is likely to entail a variety of ecological consequences for the affected forests, including a loss of biodiversity. Thus, in order to maintain the current proportion of oaks and to prevent the loss of the associated diversity in European forests, management needs to create favourable conditions for oaks, especially by reducing competitive pressure.

Up to half a century of natural succession was covered in the forest reserve data set, reflecting a time span matched in only a few other studies on natural forest dynamics (e.g. Parker et al. 1985; Bernadzki et al. 1998; Mountford et al. 1999). Despite this long record, the results presented here are capturing a fairly short time period of both tree life and forest succession. In addition, it should be kept in mind that only undisturbed sites were included in our study. Disturbances may initiate pulses of oak regeneration (cf. Mountford et al. 1999), and thus in the longer term the currently observed decline of oak may be reversed e.g. by more frequent disturbances such as windstorms or forest fires under a warmer and drier climate. However, many Central European forests have experienced widespread oak decline for the last ca. 15 yrs, often accompanied by infections of pathogenic fungi (Thomas et al. 2002). Even though Swiss forests seem to have been unaffected so far (Engesser 2005), it cannot be ruled out that oaks in Switzerland are on the verge of a similar decline. The continued monitoring of forest reserves will improve our understanding of the differential responses of oak and beech to a changing climate and to disturbances.

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References

Aas, G. 1998. Morphologische und ökologische Variation mitteleuropäischer *Quercus*-Arten: Ein Beitrag zum Verständnis der Biodiversität. Libri botanici 19, IHW-Verlag, Eching bei München, DE.

Adame, P., del Río, M. & Cañellas, I. 2010. Modeling individual-tree mortality in Pyrenean oak (*Quercus pyrenaica* Willd.) stands. Annals of Forest Science 67: article 810. Available at: http://www.afs-journal.org/10.1051/forest/2010046 [EDP Sciences].

Adler, F.R. 1996. A model of self-thinning through local competition. Proceedings of the National Academy of Sciences, USA 93: 9980–9984.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H.T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660–684.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajączkowski, J. & Żybura, H. 1998. Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. Journal of Vegetation Science 9: 229–238.

Bernicchia, A., Benni, A., Venturella, G., Gargano, M.L., Saitta, A. & Gorjón, S.P. 2008. Aphyllophoraceous wood-inhabiting fungi on *Quercus* spp. in Italy. Mycotaxon 104: 445–448.

Bertiller, R. & Müller, R. 2010. Biodiversität im Eichenwald. pro-Quercus; Bundesamt für Umwelt BAFU [Merkblatt 05], Bern, CH.

Bigler, C. & Bugmann, H. 2003. Growth-dependent tree mortality models based on tree rings. Canadian Journal of Forest Research 33: 210–221.

Brang, P., Commarmot, B., Rohrer, L. & Bugmann, H. 2008. Monitoringkonzept für Naturwaldreservate in der Schweiz. Available at: http://www.wsl.ch/publikationen/pdf/8555.pdf [Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL; ETH Zürich, Professur für Waldökologie].

Brang, P., Heiri, C. & Bugmann, H. (eds.). 2011. Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt, Bern, CH.

Brzeziecki, B., Kienast, F. & Wildi, O. 1993. A simulated map of the potential natural forest vegetation of Switzerland. Journal of Vegetation Science 4: 499–508.

Brzeziecki, B., Kienast, F. & Wildi, O. 1995. Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. Journal of Vegetation Science 6: 257–268.

Bugmann, H. 1997. Sensititvity of forests in the European Alps to future climatic change. Climate Research 8: 35–44.

Burnham, K.P. & Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York, NY, US.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R. & Zingg, A. 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest, Snow and Landscape Research 79: 45–56.

Coomes, D.A. & Allen, R.B. 2007. Mortality and tree-size distributions in natural mixed-age forests. Journal of Ecology 95: 27–40.

Dobbertin, M., Eilmann, B., Bleuler, P., Giuggiola, A., Graf Pannatier, E., Landolt, W., Schleppi, P. & Rigling, A. 2010. Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. Tree Physiology 30: 346–360.

Eastaugh, C. 2008. Adaptations of forests to climate change: a multidisciplinary review. International Union of Forest Research Organizations [IUFRO Occasional Paper 21], Vienna, AT.

Ellenberg, H. & Klötzli, F. 1972. Waldgesellschaften und Waldstandorte der Schweiz. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 48: 589–930.

Ellenberg, H. & Leuschner, C. 2010. Vegetation Mitteleuropas mit den Alpen, 6th ed. Ulmer, Stuttgart, DE.

Emborg, J., Christensen, M. & Heilmann-Clausen, J. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 126: 173–189.

Engesser, R. 2005. Die Krankheiten der Eiche. In: Bonfils, P., Horisberger, D. & Ulber, M. (eds.) Förderung der Eiche: Strategie zur Erhaltung eines Natur- und Kulturerbes der Schweiz. pp. 28–30. proQuercus; Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern, CH.

FAO. 1998. World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome, IT.

Franklin, J.F., Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. BioScience 37: 550–556.

Fridman, J. & Ståhl, G. 2001. A three-step approach for modelling tree mortality in Swedish Forests. Scandinavian Journal of Forest Research 16: 455–466.

Goff, F.G. & West, D. 1975. Canopy–understory interaction effects on forest population structure. Forest Science 21: 98–108.

Heiri, C., Wolf, A., Rohrer, L. & Bugmann, H. 2009. Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. Ecological Applications 19: 1920–1934.

Hurst, J.M., Allen, R.B., Coomes, D.A. & Duncan, R.P. 2011. Size-specific tree mortality varies with neighbourhood crowding and disturbance in a montane *Nothofagus* forest. PLoS One 6: e26670. Available at: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0026670 [Public Library of Science].

Johnson, J.B. & Omland, K.S. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101–108.

Jose, S. & Gillespie, A.R. 1997. Leaf area–productivity relationships among mixed-species hardwood forest communities of the central hardwood region. Forest Science 43: 56–64.

Kissling, P. 1980. Clef de détermination des chênes médioeuropéens (*Quercus* L.). Berichte der Schweizerischen Botanischen Gesellschaft 90: 29–44.

Klos, R.J., Wang, G.G., Bauerle, W.L. & Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecological Applications 19: 699–708.

Koop, H. & Hilgen, P. 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecology and Management 20: 135–150.

Kunstler, G., Curt, T., Bouchaud, M. & Lepart, J. 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. Canadian Journal of Forest Research 35: 1657–1668.

Leibundgut, H. 1984. Unsere Waldbäume. Verlag Huber, Frauenfeld, CH.

Lines, E.R., Coomes, D.A.& Purves, D.W. 2010. Influences of forest structure, climate and species composition on tree mortality across the eastern US. PLoS One 5: e13212. Available at: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0013212 [Public Library of Science].

Lorimer, C.G., Dahir, S.E. & Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. Journal of Ecology 89: 960–971.

Monserud, R.A. & Sterba, H. 1999. Modeling individual tree mortality for Austrian forest species. Forest Ecology and Management 113: 109–123.

Mountford, E.P., Peterken, G.F., Edwards, P.J. & Manners, J.G. 1999. Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Plant Ecology, Evolution and Systematics 2: 223–272.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter III, R.T., Gehring, C.A. & Whitham, T.G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology 93: 1085–1093.

Muir, G., Fleming, C.C. & Schlötterer, C. 2000. Species status of hybridizing oaks. Nature 405: 1016.

OcCC. 2008. Das Klima ändert - was nun? Der neue UN-Klimabericht (IPCC 2007) und die wichtigsten Ergebnisse aus Sicht der Schweiz. Organe consultatif sur les changements climatiques OcCC, Bern, CH.

Parker, G.R. & Leopold, D.J. 1983. Replacement of *Ulmus Americana* L. in a mature east-central Indiana wood. Bulletin of the Torrey Botanical Club 110: 482–488.

Parker, G.R., Leopold, D.J. & Eichenberger, J.K. 1985. Tree dynamics in an old-growth, deciduous forest. Forest Ecology and Management 11: 31–57.

Peterken, G.F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, UK.

Ranius, T. & Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85–94.

Reynolds, J.H. & Ford, E.D. 2005. Improving competition representation in theoretical models of self-thinning: a critical review. Journal of Ecology 93: 362–372.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A. & Appenzeller, C. 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427: 332–336.

Sheil, D. & May, R.M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. Journal of Ecology 84: 91–100.

Slik, J.W.F. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. Oecologia 141: 114–120.

Thomas, F.M., Blank, R. & Hartmann, G. 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. Forest Pathology 32: 277–307.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science 323: 521–524.

Wallnöfer, S. & Hotter, M. 2008. Syntaxonomy and site ecology of mixed oak forest communities in the Inner and Intermedial Alps of Tyrol (Austria). Botanica Helvetica 118: 21–43.

Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B 365: 2019–2024.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35: 1–22.

Wohlgemuth, T., Bugmann, H., Lischke, H. & Tinner, W. 2006. Wie rasch ändert sich die Waldvegetation als Folge von raschen Klimaveränderungen? In: Wohlgemuth, T. (ed.) Forum für Wissen 2006. pp. 7–16. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf, CH.

Wolf, A., Møller, P.F., Bradshaw, R.H.W. & Bigler, J. 2004. Storm damage and long-term mortality in a semi-natural, temperate deciduous forest. Forest Ecology and Management 188: 197–210.

Wunder, J., Brzeziecki, B., Żybura, H., Reineking, B., Bigler, C. & Bugmann, H. 2008. Growth–mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. Oikos 117: 815–828.

Wunder, J., Reineking, B., Matter, J.-F., Bigler, C. & Bugmann, H. 2007. Predicting tree death for *Fagus sylvatica* and *Abies alba* using permanent plot data. Journal of Vegetation Science 18: 525–534.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY, US.

Supporting information

Appendix S1. Location of the study sites in Switzerland.

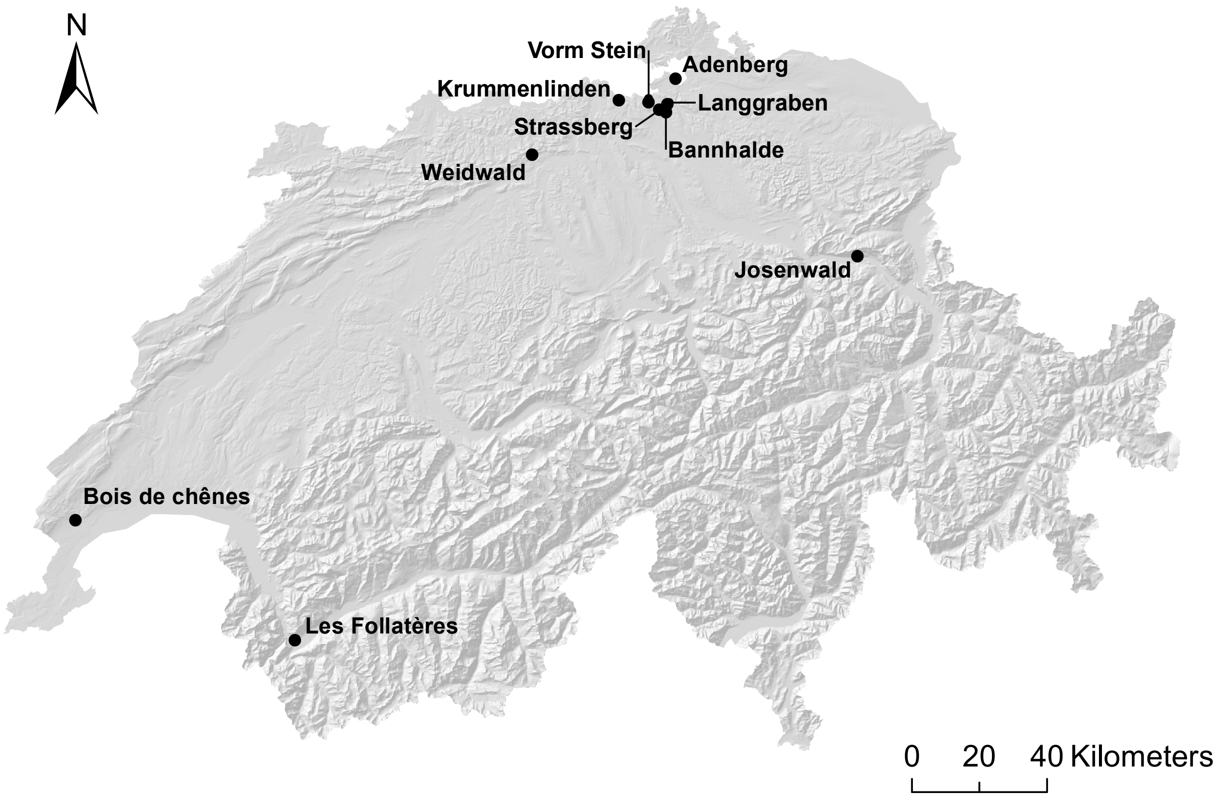


Figure S1. Location of the study sites in Switzerland.

Appendix S2. Development of stem densities.

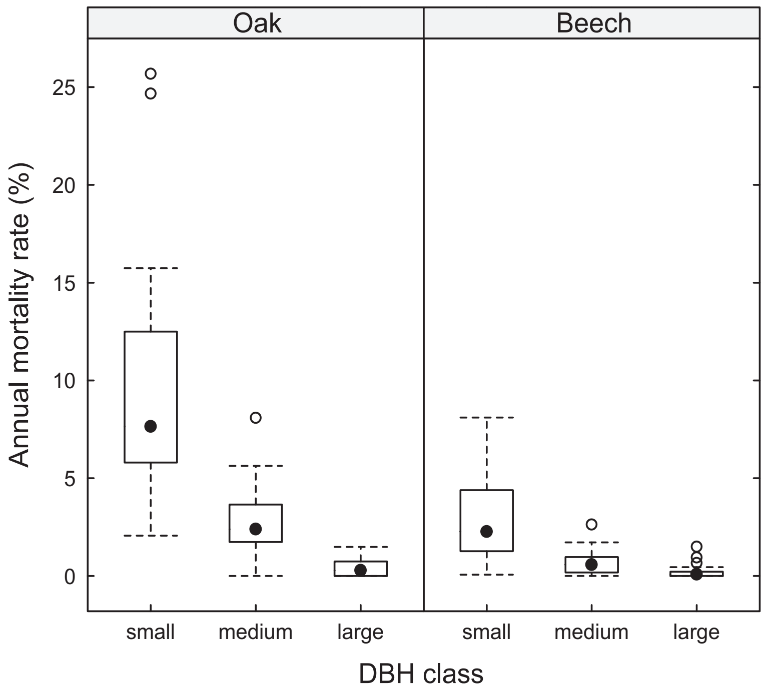
Table S2. Development of stem densities for oak, beech and the combination of oak and beech. Changes in stem densities over time are indicated as the percentage relative to the first inventory (Inv.). For the combination of oak and beech, absolute stem densities (stems ha^{-1}) are indicated in brackets, whereas separate absolute stem densities for oak and beech are shown in Figure 3.

Site	Oak					Beech					Oak + Beech				
	Inv. 1	Inv. 2	Inv. 3	Inv. 4	Inv. 5	Inv. 1	Inv. 2	Inv. 3	Inv. 4	Inv. 5	Inv. 1	Inv. 2	Inv. 3	Inv. 4	Inv. 5
Adenberg	100%	90%	76%	58%		100%	75%	51%	42%		100% (761)	77% (589)	55% (422)	45% (342)	
Bannhalde	100%	91%	72%	66%		100%	71%	52%	48%		100% (457)	74% (340)	56% (255)	51% (233)	
Bois de Chênes	100%	52%	44%	36%		100%	102%	89%	80%		100% (720)	83% (596)	72% (516)	63% (453)	
Les Follatères	100%	90%	79%			*	*	*			100% (1048)	90% (945)	79% (828)		
Josenwald	100%	92%	70%			100%	108%	119%			100% (853)	93% (795)	73% (626)		
Krummen-linden	100%	89%	76%	59%	43%	100%	107%	133%	123%	118%	100% (431)	99% (427)	107% (460)	94% (404)	84% (362)
Langgraben	100%	46%	40%	37%		100%	1174%	738%	577%		100% (610)	159% (970)	110% (671)	88% (535)	
Strassberg	100%	52%	29%			100%	79%	62%			100% (1476)	66% (972)	46% (677)		
Vorm Stein 1	100%	87%	70%			100%	140%	120%			100% (628)	118% (738)	99% (619)		
Vorm Stein 2	100%	121%	87%			100%	88%	85%			100% (759)	101% (770)	86% (654)		
Vorm Stein 3	100%	73%	56%			100%	100%	93%			100% (538)	88% (473)	76% (410)		
Weidwald	100%	85%	71%			100%	89%	73%			100% (432)	87% (376)	72% (312)		

* Since no beech trees were recorded in Les Follatères in the first inventory campaign, relative percentages are not indicated.

Appendix S3. Relationship between possible explanatory variables and annual mortality rates.

a) Diameter at breast height (DBH)



b) Slope

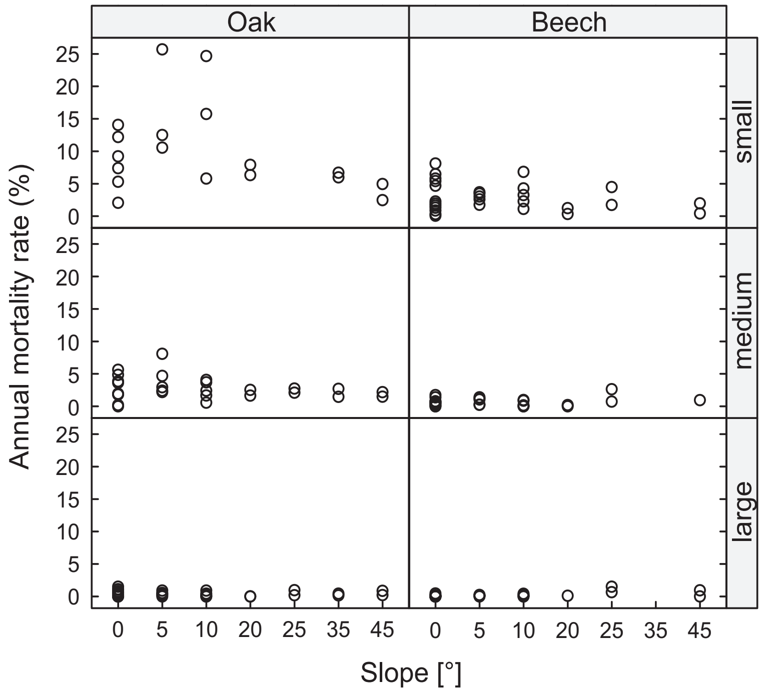
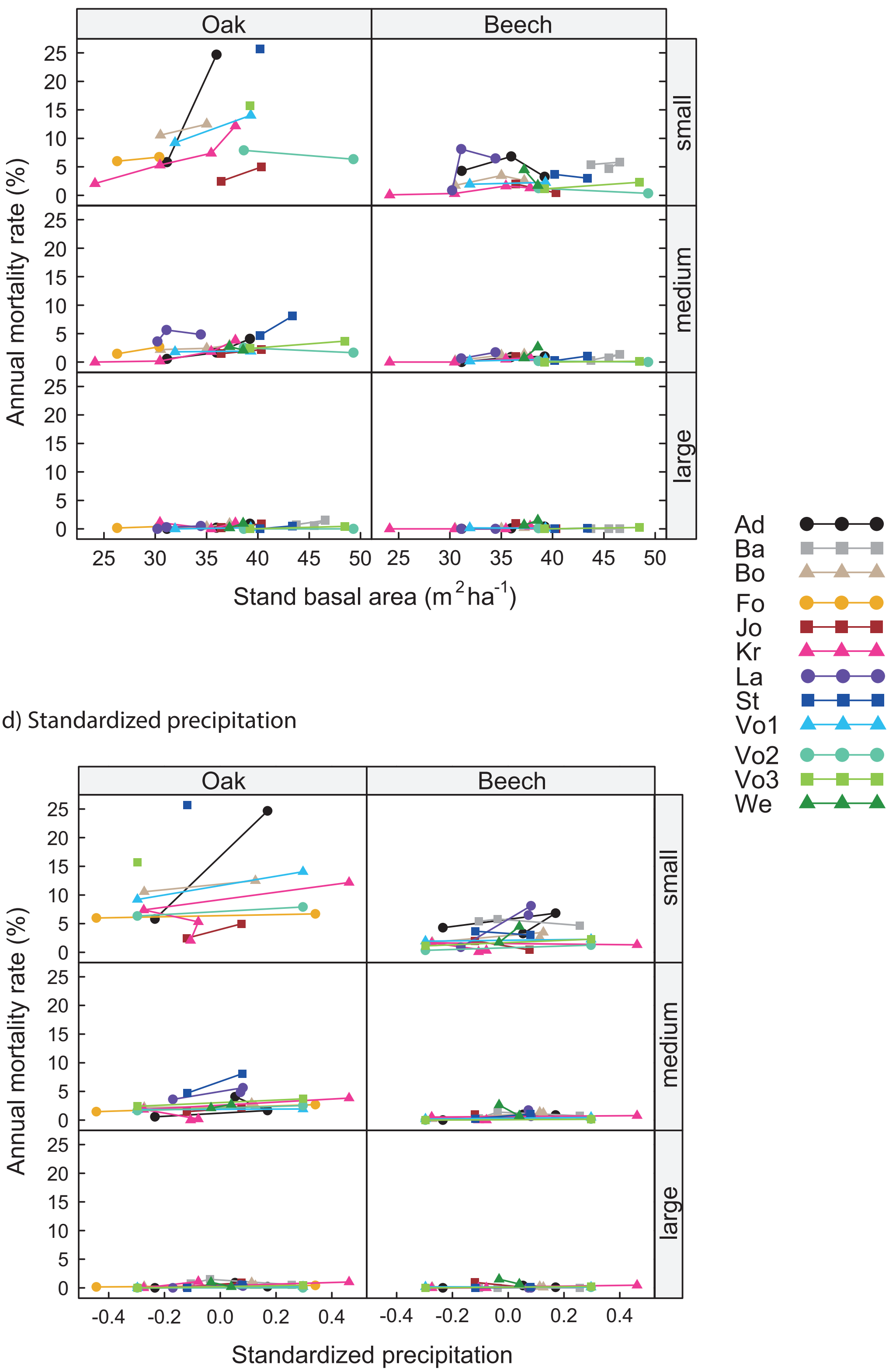


Figure S3. Annual mortality rates of oak and beech vs. the explanatory variables (a) diameter at breast height (DBH) class, (b) slope, (c) stand basal area, and (d) standardized precipitation. Lines indicate the chronological sequence. Abbreviations for sites are according to Table 1.

c) Stand basal area



d) Standardized precipitation

Figure S3. Continued.

Appendix S4. Coefficients of the best-fitting mortality models according to Akaike weights.

Table S4. Coefficients of the best-fitting mortality models according to Akaike weights for oak and beech. Model numbers and abbreviations of variables may be found in Table 2.

Species	Model		Intercept	DBH		BA	PG	Random intercept (standard deviation)
				medium	large			
Oak	13	Coefficient	-3.69	-1.59	-3.52	0.04	0.47	0.40
		(± standard error)	(± 0.72)	(± 0.12)	(± 0.22)	(± 0.019)	(± 0.28)	
		p-value	< 0.001	< 0.001	< 0.001	0.027	0.093	
Beech	7	Coefficient	-3.55	-1.55	-2.82		1.03	0.62
		(± standard error)	(± 0.21)	(± 0.17)	(± 0.36)		(± 0.36)	
		p-value	< 0.001	< 0.001	< 0.001		0.004	

Notes: Since the variable DBH was defined as a factor, a coefficient was fitted for both the medium and large DBH classes with the smallest DBH class as base level.

Appendix S5. Performance of the best-fitting models.

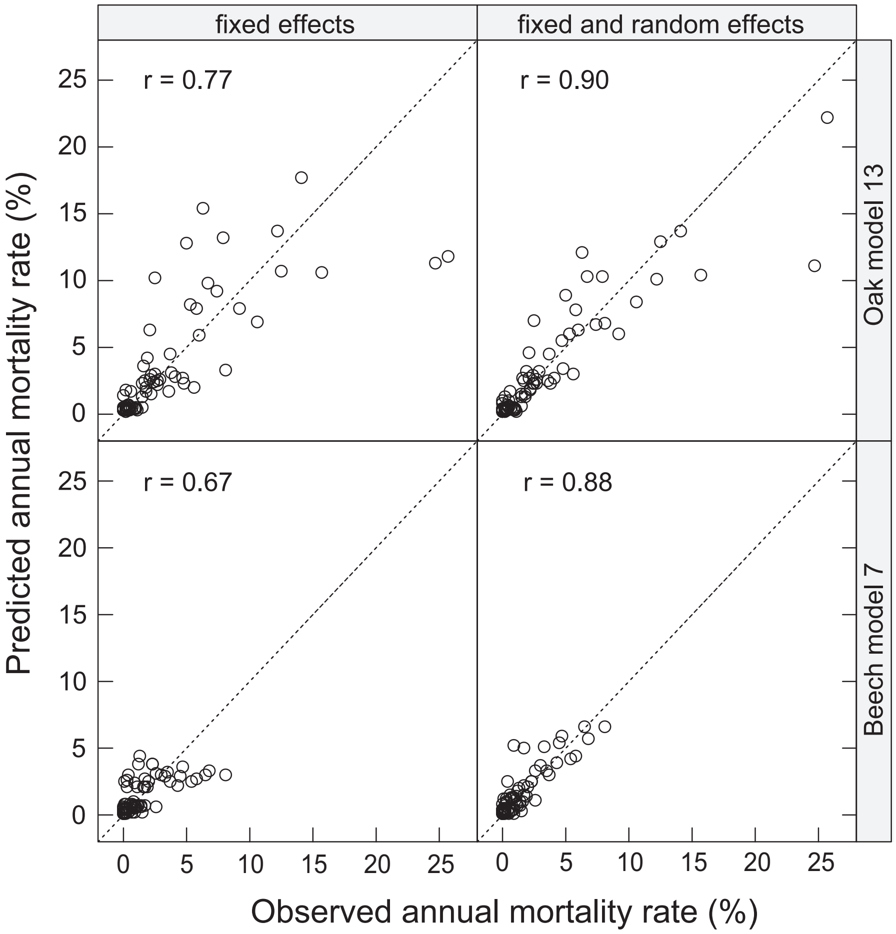


Figure S5. Performance of the best-fitting models for oak (model 13) and for beech (model 7). Predicted annual mortality rates are plotted versus observed values for oak (above) and beech (below). Mortality rates were fitted using fixed effects only (left), vs. both fixed and random effects (right). The Pearson correlation coefficient r was calculated between predicted and observed annual mortality rates.

Chapter II

Annual growth responses of oaks to temperature, precipitation and a drought index along a gradient of soil moisture in Swiss forest reserves

Brigitte Rohner, Harald Bugmann, Christof Bigler

Abstract. Tree rings have often been used to identify growth responses to climate, with response functions being a standard method. Growth responses of oaks are especially important since oaks play a key role in the conservation of biodiversity and in the adaptation of European forests to climate change. For many studies dealing with the ecological role of oak, knowledge on the relationships between climate and growth is a prerequisite. To lay the groundwork for the subsequent chapter of this thesis, we focus here on climate-growth responses of oaks in Swiss forest reserves. The main goal was (1) to identify the most important climatic drivers for oak growth in Central Europe, and (2) to assess the variability of the climate-growth relationships along a gradient of soil moisture. As climate variables we considered monthly mean temperatures, monthly precipitation, and a monthly atmospheric drought index that combines temperature and precipitation. The time span from June of the previous year until September of the current year was investigated as potentially influencing tree-ring widths. In general, more significant response coefficients were found for precipitation than for temperature, with precipitation of the current summer months resulting in the highest positive coefficients. The drought index revealed very similar response patterns compared to precipitation. Positive responses to precipitation and to the drought index in June were identified along the whole gradient of soil moisture, whereas for other months more positive responses were found at sites with comparably dry soil conditions. These results indicate that, although oaks are known to survive in fairly dry environments, they show reduced growth during dry summers, particularly if they are growing on dry soils. Since summers in Central Europe are expected to become dryer under climate change, future oak growth may be reduced compared to the past. From a methodological point of view, we suggest focusing on either precipitation or drought indices over the summer months as explanatory climate variables in future empirical studies on growth variability of Central European oaks.

Introduction

Besides regeneration and mortality, growth is the most important driver of tree population dynamics. Therefore, various measures of tree growth such as height and diameter increment have been a focus in forest science for a long time. In particular, the annual diameter growth in form of tree rings has received high attention, since tree rings proved to be useful for reconstructing climate parameters (Büntgen et al. 2011), for identifying growth reactions after disturbances (Black and Abrams 2003) and for relating growth responses to climate variability (Rozas 2005).

Understanding climate-growth relations of oak species is especially important because a large potential in the adaptation of European forests to climate change is ascribed to oaks due to their comparably high drought tolerance (Peñuelas and Boada 2003; Weber et al. 2007). In addition, oaks play a crucial role in biodiversity conservation. Oaks feature the highest number of associated species of all Central European tree species, covering a variety of organisms ranging from fungi (Bernicchia et al. 2008) to insects (Ranius and Jansson 2000) and birds (Caprio et al. 2009). Predicting oak growth depending on environmental variables and age is therefore an important task, with which we deal in the next chapter of this thesis. However, this task requires well-founded knowledge on the growth response of oaks to climate.

For analysing the influence of climate variability on tree-ring widths, statistical methods have been established already in the 1930s (Diller 1935; Fritts et al. 1971; Blasing et al. 1984). Since then, two types of statistical analyses between climate variables and tree-ring indices have been proposed: correlations vs. response functions. While correlation functions are based on univariate estimations of Pearson correlations, response functions are based on multivariate principal components regression (Fritts et al. 1971; Biondi and Waikul 2004). Compared to correlation functions, response functions have the advantage of taking the multicollinearity among the climate variables into account. Since significance levels of response coefficients turned out to be biased due to the omission of the principal components with the lowest amount of information, bootstrapped confidence intervals (cf. Efron and Tibshirani 1993) have become more important (e.g. Biondi and Waikul 2004). Over the past decade, correlation and response functions with bootstrapped confidence intervals have been used in a variety of studies concerning climate effects on tree growth (e.g. Lebourgeois et al. 2004; Zang et al. 2011; Michelot et al. 2012). Thus, they have evolved into the standard procedures to identify climate signals in tree-ring series.

Tree-ring widths of the most widespread European temperate oaks (*Quercus petraea*, *Quercus robur*) have been shown to be strongly related to climate variability in the summer months (Lebourgeois et al. 2004; Friedrichs et al. 2008; Zang et al. 2011; Michelot et al. 2012). For *Q. petraea*, the summer months of the current year are most important (Friedrichs et al. 2008; Michelot et al. 2012), whereas for *Q. robur*, the climate variability in the previous year shows additional effects (Friedrichs et al. 2008). In general, tree-ring widths were shown to be positively related to precipitation (Friedrichs et al. 2008; Zang et al. 2011; Michelot et al. 2012), whereas mostly negative, but rarely significant correlations were found with temperature (Friedrichs et al. 2008; Michelot et al. 2012). Several attempts have been made to determine the combined effect of temperature and precipitation on tree-ring widths of oaks by calculating correlation and response functions for various drought indices, which consistently revealed increased tree-ring growth in years with humid summers (Lebourgeois et al. 2004; Friedrichs et al. 2008; Michelot et al. 2012).

Although first insights about how climate variability may affect oak growth have already been gained, most previous studies have focussed on dominant trees in managed forests (e.g. Zang et al. 2011; Michelot et al. 2012). Therefore, little is known about whether these findings are also valid for co-dominant and suppressed trees, as they are common in unmanaged forest reserves like the ones studied in this thesis. Furthermore, previous studies about growth responses to climate were usually conducted at individual sites, which entails uncertainty about how robust the identified responses are along environmental gradients.

Therefore, in this chapter we address three main questions based on tree-ring series of more than 300 oaks, covering suppressed, co-dominant and dominant trees from 11 unmanaged forest sites along a gradient of soil moisture in Switzerland:

1) How are temperature and precipitation from the previous and the current year related to tree-ring widths of oaks?
2) How do these relationships change when combining temperature and precipitation in an atmospheric drought index?
3) How do the growth responses to temperature, precipitation and the atmospheric drought index change along a gradient of soil moisture?

Material and Methods

Study sites and tree species

All study sites belong to the Swiss forest reserve network, which consists of 49 unmanaged forests located all over Switzerland (for details see Brang et al. 2011; Rohner et al. 2012a). The network is a joint project by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), ETH Zurich, and the Swiss Federal Office for the Environment (FOEN). The establishment of the first reserves dates back to the late 1940s, but most forests had not been managed for several decades before their integration into the network (Leibundgut 1957; Brang et al. 2011). In permanent plots within the reserves, inventories have been repeated every 8-12 years. For the present study, we selected the same reserves as study sites as in the other chapters of this thesis (Rohner et al. 2012a; Rohner et al. 2012b).

All of them contained at least 10% *Quercus* species in the last inventory (calculated as [relative density + relative basal area] / 2 x 100; Parker and Leopold 1983) and only reserves with at least three inventories were considered. The eleven selected reserves comprise a total area of more than 600 ha (cf. Rohner et al. 2012b) and represent a wide range of climatic conditions and site characteristics (Table 1, Figure 1).

We collectively analyzed the three most frequent oak species in Switzerland (*Q. petraea*, *Q. robur*, *Q. pubescens*, referred to as 'oaks'), because they overlap in their morphological attributes, which makes a reliable discrimination of the species problematic (Aas 1998; Kissling 1980). In addition, the three oak species are known to hybridize, thus entailing uncertainty about whether they are different species at all (Kissling 1980; Aas 1998; Muir et al. 2000).

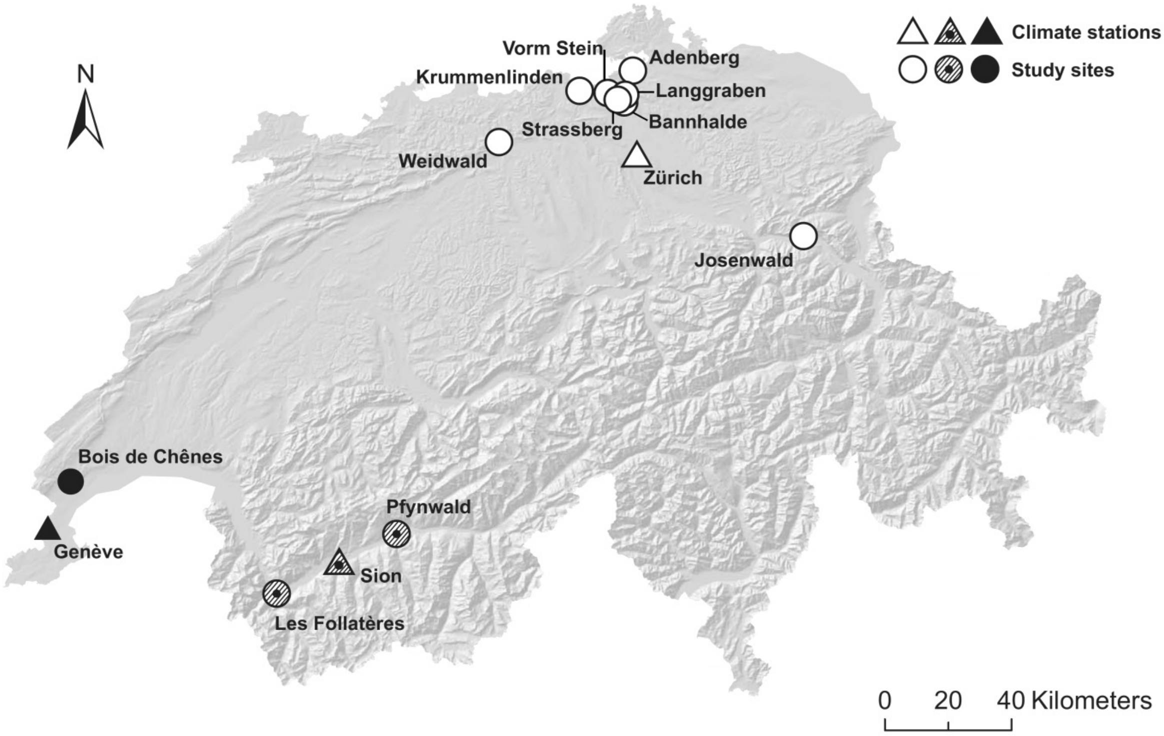


Figure 1. Location of the study sites and the climate stations in Switzerland. The symbol-filling style indicates for which study sites data from the particular climate stations were used. © swisstopo.

Tree-ring sampling and preparation

Tree-ring sampling was conducted in summer 2009 and 2010. We selected 30 or 31 oaks per site, leading to a total of 333 sampled oaks. The oaks were selected in such a way that the sample in every reserve represented the DBH distribution determined in the last inventory. Thus, not only dominant but also co-dominant and suppressed oaks were included in the sample. From every oak, one increment core was taken parallel to the contour line at 1.2 m above ground.

Table 1. Detailed information about the study sites and the preparation of the tree-ring chronologies. For elevation and slope, the range represented in the sample is shown. Phyto-sociological associations are indicated according to Ellenberg and Klötzli (1972), soil types are based on the FAO-system (FAO, 1998). The study sites are ordered according to increasing soil moisture. Parts of this table are published in Rohner et al. (2012a).

Site	Coordinates (northing, easting)	Elevation (m a.s.l.)	Water holding capacity[a]	Slope (°)	Mean summer drought index[b]	Main soil type	Main phyto-sociological association	Mean correlation of tree-ring series	Years used in statistical analysis
Pfynwald	46° 17' 36'' 7° 33' 48''	570-605	3	13 – 38	-147	Regosol	*Erico-Pinetum silvestris*	0.52	1969-2008
Les Follatères	46° 7' 39'' 7° 4' 26''	685-870	2	5 – 36	-9	Leptosol	*Arabidi turritae-Quercetum pubescentis*	0.57	1884-2008
Josenwald	47° 8' 5'' 9° 15' 19''	480-520	1	28 – 42	255	Leptosol	*Teucrio-Quercetum,* *Asperulo taurinae-Tilietum*	0.62	1911-2008
Weidwald	47° 24' 47'' 7° 59' 33''	610-640	3	6 – 36	37	Leptosol	*Asperulo taurinae-Tilietum,* *Cardamino-Fagetum,* *Seslerio-Fagetum*	0.69	1866-2008
Strassberg	47° 31' 55'' 8° 29' 40''	465-475	4	6 – 31	24	Cambisol	*Galio odorati-Fagetum*	0.59	1934-2008
Bois de Chênes	46° 26' 17'' 6° 13' 33''	500-520	5	0 – 15	-36	Cambisol	*Carici Fagetum caricetosum montanae, Aro-Fagetum*	0.55	1873-2008
Langgraben	47° 32' 49'' 8° 31' 36''	420	4	0	-10	Luvisol	*Galio odorati-Fagetum luzuletosum* *(Galio silvatici-Carpinetum)*	0.67	1913-2008
Vorm Stein	47° 33' 7'' 8° 27' 13''	475-495	4	0 – 27	33	Luvisol	*Galio odorati-Fagetum,* *Pulmonario-Fagetum melittetosum*	0.63	1916-2008
Adenberg	47° 36' 50'' 8° 33' 40''	490-530	5	0 – 17	-4	Cambisol	*Galio odorati-Fagetum*	0.66	1892-2008
Bannhalde	47° 31' 28'' 8° 31' 15''	425	5	0 – 14	-5	Cambisol	*Galio odorati-Fagetum*	0.65	1866-2008
Krummenlinden	47° 33' 27'' 8° 20' 8''	545-555	6	0	42	Cambisol	*Galio odorati-Fagetum luzuletosum*	0.59	1908-2008

[a] Categories indicate the following values: 1: < 15 l/m^2; 2: 15-30 l/m^2; 3: 30-45 l/m^2; 4: 45-60 l/m^2; 5: 60-100 l/m^2; 6: > 100 l/m^2.

[b] The summer drought index is calculated as the sum of precipitation minus potential evapotranspiration from May to July. The mean was calculated over the years 1960-2006.

The core samples were cut with a microtome (Gärtner and Nievergelt 2010) and prepared with chalk to enhance the visibility of the ring boundaries. We used a Lintab 5 measuring system and the TSAP-Win software (RINNTECH, Heidelberg, Germany) to measure the ring widths. Site-level crossdating was performed both visually based on pointer years and quantitatively using the software COFECHA (Holmes 1983). Nine oaks had to be excluded from the study because crossdating was not possible. Mean correlations of the remaining tree-ring series are shown in Table 1. The crossdated tree-ring series were detrended by a smoothing spline with a rigidity of 0.67 × series length, and a residual chronology per site was built (Figure 2) using the package *dplR* (Bunn 2008) in the statistical computing environment R (R Development Core Team 2010).

Climate data

Homogeneous monthly temperature means and precipitation sums since 1864 were taken from climate stations operated by MeteoSwiss (Begert et al. 2005). For every study site, data from the nearest climate station were used (Figure 1). Temperature and precipitation data were further combined in a monthly atmospheric drought index, calculated as precipitation minus potential evapotranspiration (Thornthwaite 1948; Bigler et al. 2006). The monthly potential evapotranspiration was calculated based on day length (estimated on the basis of the latitude according to Forsythe et al. 1995) and monthly temperature means using a modified Thornthwaite (1948) method (Willmott et al. 1985).

Statistical analysis

To identify the influence of monthly temperature means, precipitation and the drought index on the residual tree-ring chronologies, response functions were calculated at the site level. Climate variables from June of the previous year until September of the current year were considered as potentially influencing radial growth, which is in accordance with Weber et al. (2007) and Zang et al. (2011). The previous year was considered because its climate influences the amount of stored resources and the formation of buds, which can have a strong influence on tree-ring growth in the current year. The response functions were calculated based on a principal component regression (cf. Fritts et al. 1971; Fritts 1976). The confidence intervals of the response coefficients were estimated based on bootstrap simulations (cf. Efron and Tibshirani 1993) with 1000 repetitions. For calculating the response functions as well as the corresponding confidence intervals, we used the DendroClim2002 software (Biondi and Waikul 2004). The range of years used for these calculations is shown in Table 1 for every study site.

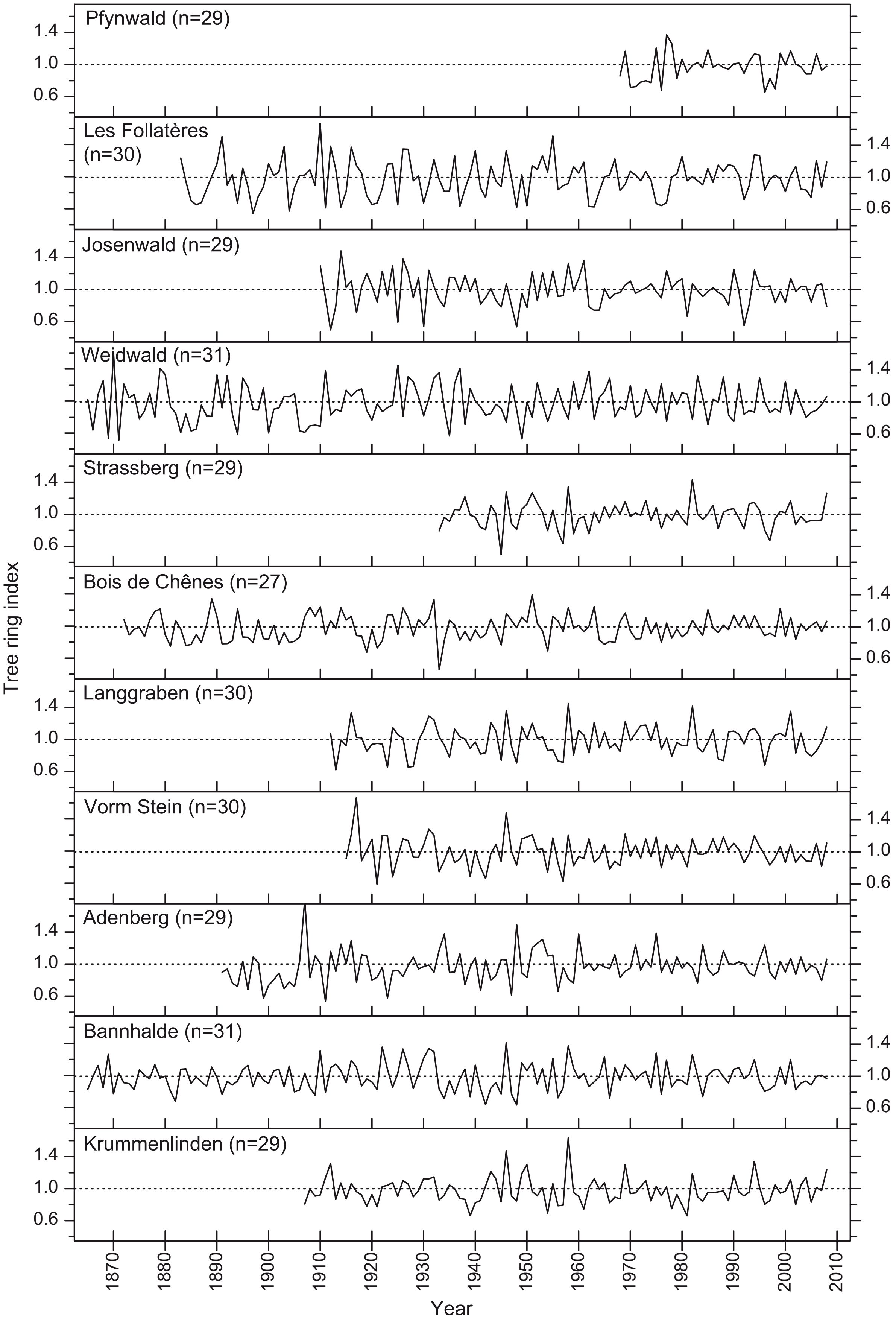


Figure 2. Residual chronologies. The residual chronology of every study site is shown for the time span used in the statistical analysis (see Table 1). The number of trees used to build the respective chronology is indicated by n (the chronology is not shown for years with a sample size < 5 trees since they were not used in the analysis). The study sites are ordered according to increasing soil moisture.

To identify patterns of growth responses among the different study sites, we compared the response coefficients along a gradient of soil moisture. For assessing the soil moisture of the particular sites, we considered (1) the water holding capacity taken from the soil suitability map of Switzerland (Bundesamt für Raumplanung (EJPD) et al. 1980), (2) the mean slope, which was determined for every tree during the field work by assessing the local topography within a radius of ca. 10 m (see Table 1), and (3) the mean atmospheric summer drought index, which was calculated analogously to the drought index used for the response functions, however, based on a different data source, i.e. temperature and precipitation data that were spatially interpolated on the basis of the DAYMET model (Thornton et al. 1997). From these interpolated data, we calculated the sum of the drought indices from May to July and averaged them over the available time period (1960-2006) separately for every study site. We used the spatially interpolated climate data rather than the homogenized data from the climate stations because a site-specific measure for the general summer drought conditions was needed for the soil moisture ranking (please note: we did not use the interpolated data for calculating the response functions because of the shorter available timeframe). For ranking the study sites according to their soil moisture, we determined their mean rank over the three considered characteristics (see Table 2).

Table 2. Ranking of the study sites according to their soil moisture. As indicators of soil moisture, we considered the water holding capacity, the mean slope and the mean atmospheric summer drought index. The absolute values of the considered criteria are shown in Table 1.

Site	Rank of individual indicators			Mean rank	Final rank
	Water holding capacity	Slope	Mean summer drought index		
Pfynwald	3	3	1	2.3	1
Les Follatères	2	1	4	2.3	1
Josenwald	1	1	11	4.3	3
Weidwald	3	3	9	5	4
Strassberg	5	5	7	5.6	5
Bois de Chênes	8	7	2	5.6	5
Langgraben	5	9	3	5.6	5
Vorm Stein	5	5	8	6	8
Adenberg	8	7	6	7	9
Bannhalde	8	9	5	7.3	10
Krummenlinden	11	9	10	10	11

Results

Effects of temperature and precipitation on tree-ring widths

For all study sites, the response coefficients of temperature and precipitation are shown in Figure 3. The current year showed more significant coefficients than the previous year for both temperature (9 vs. 6 coefficients) and precipitation (13 vs. 8 coefficients). Only few significant coefficients were found for temperature and precipitation in the winter months. In general, more significant response coefficients were found for precipitation than for temperature (21 vs. 15 coefficients).

The precipitation sums of June of the current year showed significant positive response coefficients at eight of the eleven study sites (Figure 3). At Vorm Stein, current June precipitation had a marginally significant positive coefficient, whereas even a negative coefficient was found at Weidwald. At three of the eight sites with a significant positive response to June precipitation, further significant positive coefficients were found for precipitation in either April or May of the current year. In addition, nine study sites showed positive but insignificant response coefficients for precipitation in July. Although not significant, precipitation at Pfynwald showed positive coefficients for all months of the current year except September. In addition to the responses of the current year, precipitation in June or July of the previous year was significantly negatively related to the tree-ring index at three study sites.

In contrast to precipitation, temperature in June of the current year showed negative response coefficients at all sites except Weidwald, although only three of them were significant (Figure 3). In addition, four sites showed significant positive responses to temperature in May. Furthermore, the temperature in June of the previous year had positive coefficients at all sites except Weidwald, being significant at four of them. In general, a tendency of opposite patterns of temperature and precipitation coefficients was evident during the summer months.

Relations between the drought index and tree-ring widths

The combined consideration of temperature and precipitation via the drought index revealed very similar response coefficients compared to precipitation (Figure 3). The same eight sites that showed significant positive coefficients for precipitation in June of the current year also showed significant positive coefficients for the drought index in June of the current year. Again, at nine study sites we found positive coefficients for the drought index in July of the current year. As for both temperature and precipitation, the drought index only showed few and scattered significant coefficients during winter. Regarding the previous year, negative responses to the drought index of June were found at most sites – similar as for precipitation. In general, most of the study sites showed positive coefficients for the drought index over large parts of the investigated time span.

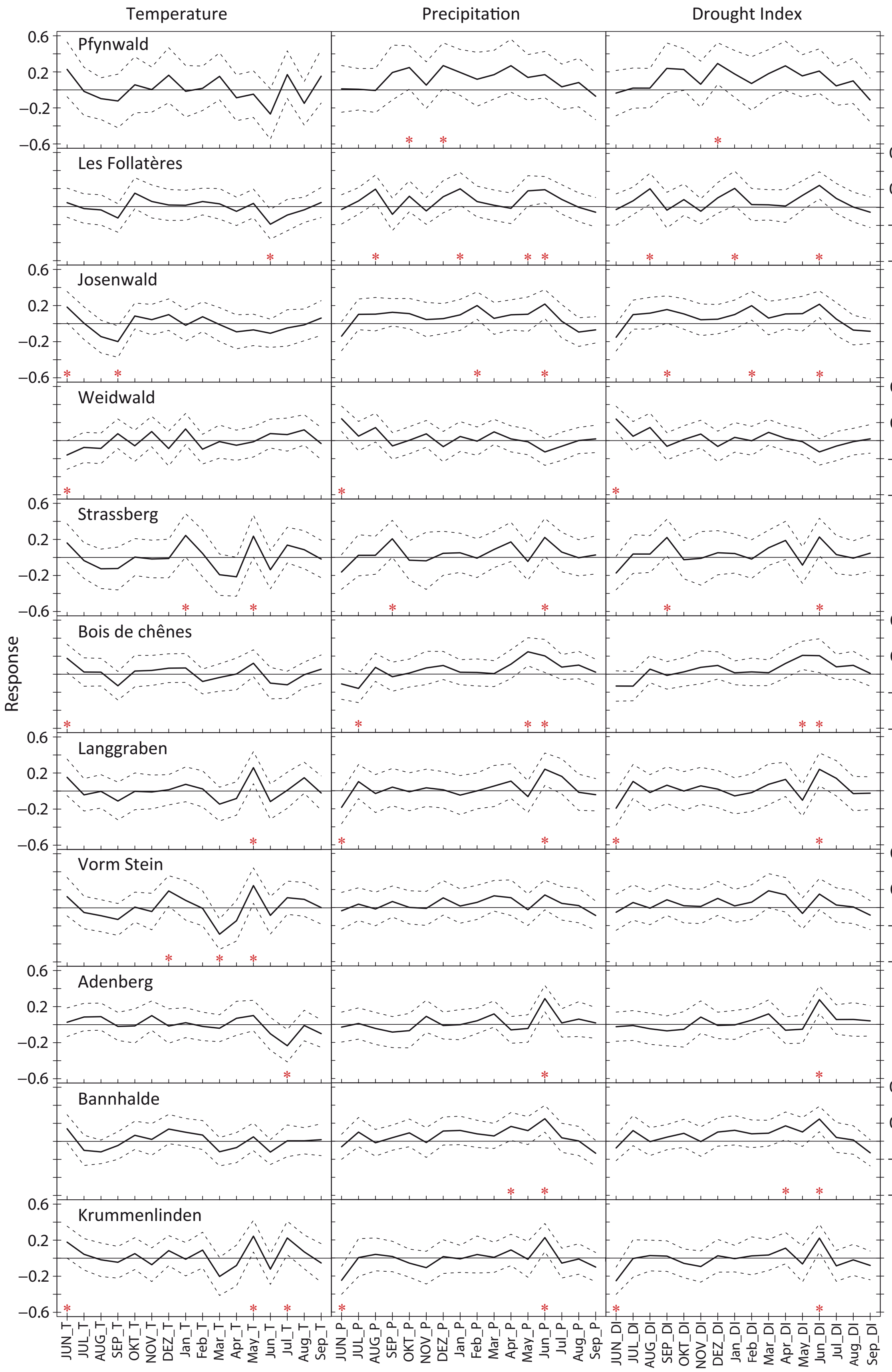


Figure 3. Response coefficients of monthly temperature means (T, left panels), monthly precipitation sums (P, middle panels) and monthly atmospheric drought index (DI, right panels) with residual tree-ring chronologies from all study sites. The 95% confidence interval is indicated by the dashed lines. Red asterisks indicate significant (P < 0.05) response coefficients. Months of the previous year are indicated in capital letters, months of the current year in lower case letters. The study sites are ordered according to increasing soil moisture.

Growth responses to climate variables along a gradient of soil moisture

The driest soil conditions considering water holding capacity, slope and mean summer drought index were ascribed to the study sites in the southern part of Switzerland (canton of Valais, Table 2). At the other end of the soil moisture gradient, the flat study sites in the northern lowlands were assessed as providing the moistest soil conditions.

For temperature, trees growing under mesic to moist soil conditions generally showed stronger positive responses in May of the current year than trees growing under drier soil conditions (Figure 4a). In addition, the strongest negative responses to current June temperatures were found in the study sites with the driest soil conditions. However, the identified tendency towards positive responses to temperatures in June of the previous year was identified along the whole gradient of soil moisture.

The positive response coefficients for precipitation in current June were identified irrespective of soil moisture (Figure 4b). However, in general, a higher number of positive responses to precipitation were found in study sites with drier soil conditions. Especially for previous autumn and winter, many significant positive coefficients were found under dry soil conditions, whereas no significant coefficient was found under moist soil conditions. Regarding precipitation in May, the response coefficients showed a decreasing tendency with increasing soil moisture.

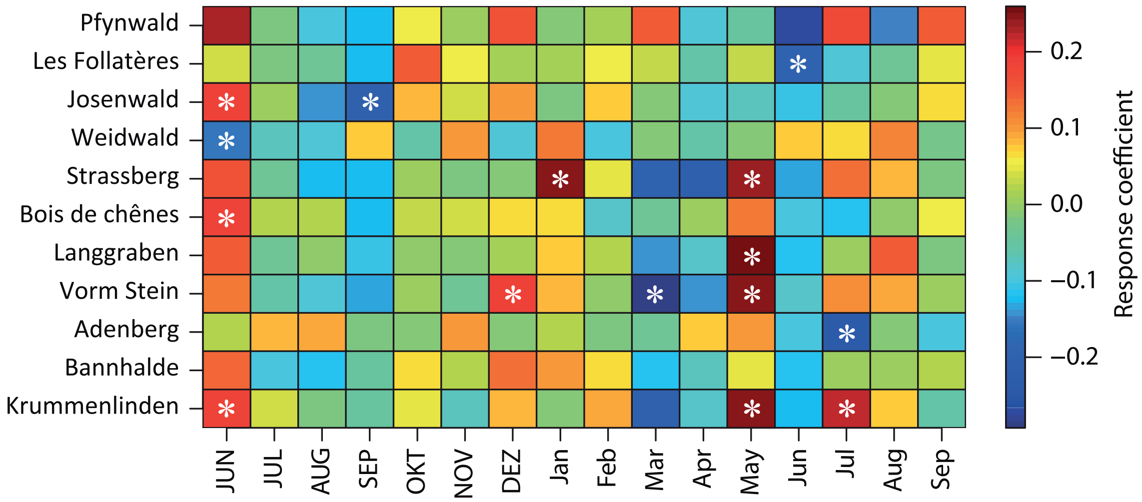
The higher number of positive responses at drier soil conditions also became apparent for the drought index (Figure 4c). Furthermore, the tendency of decreasing response coefficients in May with increasing soil moisture seemed to be even slightly stronger for the drought index than for precipitation. However, the positive response to drought in June of the current year was identified along the whole gradient of soil moisture.

Discussion

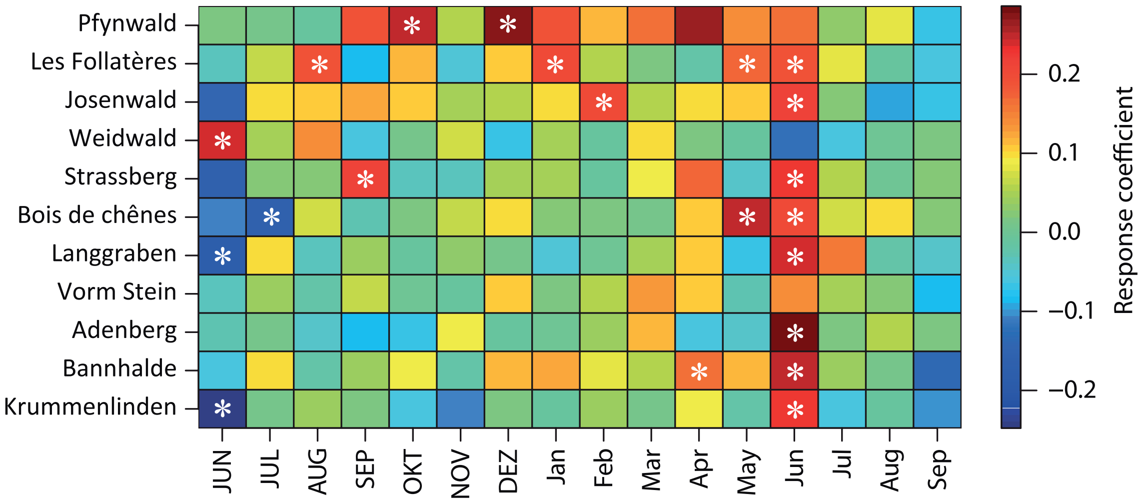
Effects of temperature and precipitation on tree-ring widths

The effects of climate variability on tree-ring widths that we identified in this study are largely supported by previously published results from other Central European oak forests. One of the most noticeable dependency in our data was the positive effect of current summer precipitation on tree-ring indices, which is in accordance with findings for *Q. petraea* in France (Michelot et al. 2012), for *Q. robur* in Germany (Zang et al. 2011) and for both species in Great Britain (Pilcher and Gray 1982). The general tendency of precipitation being positively related to radial growth of oaks, but temperature showing weaker negative or varying effects, was already described by Friedrichs et al. (2008) and Michelot et al. (2012). Similar results were also found by Vogel and Schweingruber (2001) for oaks in Switzerland, although their results cannot be directly compared to ours since they were based on the 'Gleichläufigkeit' measure (Eckstein and Bauch 1969) rather than on response functions.

a) Temperature



b) Precipitation



c) Drought index

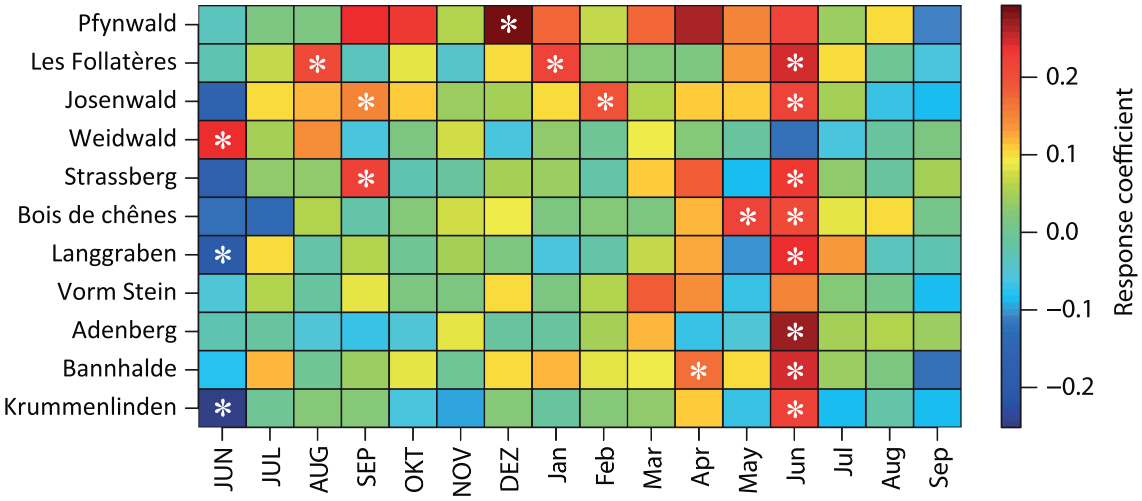


Figure 4. Response coefficients along the gradient of soil moisture. The response coefficients for (a) temperature, (b) precipitation and (c) the atmospheric drought index are shown for all study sites, which are ordered according to increasing soil moisture. Significant response coefficients are indicated by asterisks. Months of the previous year are written in capital letters and months of the current year are written in lower case letters.

The stronger responses to precipitation than to temperature reflect the fact that precipitation acts as the main limiting factor for trees in the European lowlands (Ellenberg and Leuschner 2010), with temperature showing a less pronounced gradient across the sites we investigated. Our study showed that particularly precipitation in June and the adjacent months limits oak growth in Switzerland. This clearly illustrates the role of summer drought caused by a lack of precipitation. The opposite response coefficients for temperature and precipitation indicate that this summer drought stress may even be intensified if low precipitation coincides with high temperature, which is a likely consequence of increased evapotranspiration under higher temperatures.

Relations between the drought index and tree-ring widths

The combination of temperature and precipitation in a drought index enables the interpretation of the combined effect of these two variables on growth, confirming the interpretations established separately for temperature and precipitation, i.e. increased tree-ring growth in years with comparably humid summers. The fact that the drought index in June had the highest effect further emphasizes that drought stress during the summer months acts as a crucial limiting factor for oak growth in Central Europe. Similar results based on the same drought index were described by Lebourgeois et al. (2004), although they identified May instead of June as the most important month. In addition, reduced oak growth due to summer drought has also been shown based on other measures of drought, e.g. the Palmer Drought Severity Index (Friedrichs et al., 2008) and the water balance calculated with the model BILJOU© (Granier et al. 1999; Michelot et al. 2012).

Three physiological processes have mainly been discussed to cause reduced growth during extraordinarily dry periods (cf. Kaufmann 1990). Firstly, trees may close their stomata as a consequence of loss of turgor under reduced water supply (Zweifel et al. 2006). Consequently, net CO_2 assimilation is reduced, and thus fewer carbon resources are available for growth. Secondly, shedding of foliage and twigs may occur in response to water stress, leading to a reduced photosynthetic capacity of the crown (Kaufmann 1990; Rust and Roloff 2004). Thirdly, severe droughts are expected to cause dieback of roots, which in turn reduces the absorption of soil water (Kaufmann 1990). We assume that a combination of these three processes led to the drought-related growth reductions we identified for oak, probably depending on the severity and duration of the particular drought events. While the closure of stomata is an immediate reaction to water stress, shedding of foliage and dieback of roots usually occur after severe longer-lasting drought periods (Kaufmann 1990). However, whether these explanations also apply to the trees studied here remains speculative since no information on physiological properties (e.g. crown transparency) was available.

Growth responses to climate variables along a gradient of soil moisture

The strongest response we detected, i.e. reduced growth during dry summers, was observed along the entire gradient, indicating that oak growth is sensitive to dry summer conditions no matter how dry soil conditions are on an absolute level. This is in line with similar results from a variety of forests in France (Michelot et al. 2012), Germany (Friedrichs et al. 2008; Scharnweber et al. 2011; Zang et al. 2011) and Switzerland (Vogel and Schweingruber 2001). Furthermore, Scharnweber et al. (2011) identified a strong response of oak growth to summer drought irrespective of the position along a precipitation gradient. These findings indicate that oak growth reduction during dry summers is a general feature in Central Europe.

However, some differing responses along the soil moisture gradient were identified. For example, more significant positive responses to drought were found at sites with drier soil conditions, i.e. growth is reduced more strongly if dry episodes occur at sites with generally dry soil conditions. For this effect, especially the previous year turned out to be important. Reduced growth in response to dry conditions during the previous late summer and autumn is likely to be a consequence of reduced storage of resources at the end of the growing season, which may hinder growth at the beginning of the subsequent growing season. This is in line with Zweifel et al. (2006) who showed that early growth of *Q. pubescens* depends entirely on internal storage of carbon. Our results indicate that this effect is more important at sites with generally dry soil conditions. To answer the question whether this difference is due to a higher proportion of earlywood at sites with drier soil conditions, intra-annual growth variability along a soil moisture gradient would need to be investigated.

A further difference along the soil moisture gradient concerned the growth response to dry winters and early springs, i.e. dry winter and early spring conditions resulted in reduced oak growth under dry but not under moister soil conditions. This result is likely connected to soil water storage. Since sites ranked at the dry end of the soil moisture gradient generally have a low water holding capacity (Table 2), oaks from these sites may struggle more intensively with drought after dry winters and springs because soil water supply is drawn down more quickly than at sites with a high water holding capacity. This effect may also explain the stronger growth reduction in response to drought in May on dry compared to moist soils.

Perspectives

Our study shows that oak growth is susceptible to summer drought, although oaks are known to be fairly drought tolerant (Ellenberg and Leuschner 2010). Since we focussed on growth rather than mortality, our results do not contradict the general drought tolerance ascribed to oaks – they rather indicate that, although oaks are able to survive under rather dry conditions, their growth may still be reduced. Such potential growth reductions should be taken into account in studies dealing with future oak growth. Concerning the potential of oaks in the adaptation of European forests to climate change, climate responses should be investigated relatively to competing tree species. Regarding growth, relative benefits have been discussed compared to *Pinus sylvestris* in the southern part of Switzerland (Weber et al. 2007) and to *Fagus sylvatica* in Germany (Scharnweber et al. 2011). However, concerning mortality, no benefit has been identified recently compared to *F. sylvatica* in Switzerland due to high competitive pressure (Rohner et al. 2012a).

The fact that previously identified effects of climate variability on tree-ring widths of oaks were confirmed by our study indicates that these general patterns are valid for a broad range of Central European oak forests. The present data set covers decades of natural tree development that was protected from any kind of human interventions. Thus, the described responses to climate variability can be assumed to be independent of human (i.e. management) activities. Furthermore, our results indicate that these patterns are valid not only for dominant trees (cf. Lebourgeois et al. 2004; Friedrichs et al. 2008; Zang et al. 2011; Michelot et al. 2012), but also for trees in all other canopy positions. We therefore suggest to focus on either precipitation or drought indices during the summer months as explanatory climate variables in further empirical studies on Central European oak growth.

For calculating the response functions, we used a dataset of climate variables that covers an extraordinarily long time span. Due to the attempts to homogenize the measured climate variables over the whole time span, this dataset is very reliable (Begert et al. 2005). However, these homogenized long-term climate data are only available at twelve climate stations in Switzerland. Thus, some of the study sites are located within quite different topographic settings in considerable distance from these climate stations. Therefore, spatially interpolated climate data, which have the potential to take into account also the local topography, may lend themselves to more accurate results in further studies about the impacts of climate on tree growth.

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References

Aas, G. (1998) Morphologische und ökologische Variation mitteleuropäischer *Quercus*-Arten: Ein Beitrag zum Verständnis der Biodiversität. Libri botanici 19. IHW-Verlag, Eching bei München.

Begert, M., Schlegel, T. & Kirchhofer, W. (2005) Homogeneous temperature and precipitation series of Switzerland from 1864-2000. International Journal of Climatology 25: 65-80.

Bernicchia, A., Benni, A., Venturella, G., Gargano, M. L., Saitta, A. & Gorjón, S. P. (2008) Aphyllophoraceous wood-inhabiting fungi on *Quercus* spp. in Italy. Mycotaxon 104: 445-448.

Bigler, C., Bräker, O. U., Bugmann, H., Dobbertin, M. & Rigling, A. (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9: 330-343.

Biondi, F. & Waikul, K. (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30: 303-311.

Black, B. A. & Abrams, M. D. (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecological Applications 13: 1733-1749.

Blasing, T. J., Solomon, A. M. & Duvick, D. N. (1984) Response functions revisited. Tree-Ring Bulletin 44: 1-15.

Brang, P., Heiri, C. & Bugmann, H. (2011) Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt, Bern.

Bundesamt für Raumplanung (EJPD), Bundesamt für Landwirtschaft (EVD) & Bundesamt für Forstwesen (EDI) (1980) Bodeneignungskarte der Schweiz. Grundlagen für die Raumplanung. Eidgenössische Drucksachen- und Materialzentrale, Bern.

Bunn, A. G. (2008) A dendrochronology program library in R (dplR). Dendrochronologia 26: 115-124.

Büntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., Kaplan, J. O., Herzig, F., Heussner, K.-U., Wanner, H., Luterbacher, J. & Esper, J. (2011) 2500 years of European climate variability and human susceptibility. Science 331: 578-582.

Caprio, E., Ellena, I. & Rolando, A. (2009) Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy. Landscape Ecology 24: 65-76.

Diller, O. D. (1935) The relation of temperature and precipitation to the growth of beech in northern Indiana. Ecology 16: 72-81.

Eckstein, D. & Bauch, J. (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwissenschaftliches Centralblatt 88: 230-250.

Efron, B. & Tibshirani, R. J. (1993) An introduction to the bootstrap. Chapman & Hall, New York.

Ellenberg, H. & Klötzli, F. (1972) Waldgesellschaften und Waldstandorte der Schweiz. Mitteilungen der Schweizerischen Anstalt für das Forstliche Versuchswesen 48: 589-930.

Ellenberg, H. & Leuschner, C. (2010) Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart.

FAO (1998) World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome.

Forsythe, W. C., Rykiel Jr., E. J., Stahl, R. S., Wu, H. & Schoolfield, R. M. (1995) A model comparison for daylength as a function of latitude and day of year. Ecological Modelling 80: 87-95.

Friedrichs, D., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B. & Löffler, J. (2008) Complex climate controls on 20th century oak growth in Central-West Germany. Tree Physiology 29: 39-51.

Fritts, H. C. (1976) Tree rings and climate. Academic Press, London.

Fritts, H. C., Blasing, T. J., Hayden, B. P. & Kutzbach, J. E. (1971) Multivariate techniques for specifying tree-growth and climate relationships and for reconstructing anomalies in paleoclimate. Journal of Applied Meteorology 10: 845-864.

Gärtner, H. & Nievergelt, D. (2010) The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia 28: 85-92.

Granier, A., Bréda, N., Biron, P. & Villette, S. (1999) A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecological Modelling 116: 269-283.

Holmes, R. L. (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43: 69-78.

Kaufmann, M. R. (1990) Ecophysiological processes affecting tree growth: water relationships. In: Process modeling of forest growth responses to environmental stress (eds R. K. Dixon, R. S. Meldahl, G. A. Ruark & W. G. Warren). Timber Press, Portland, Oregon.

Kissling, P. (1980) Clef de détermination des chênes médioeuropéens (*Quercus* L.). Berichte der Schweizerischen Botanischen Gesellschaft 90: 29-44.

Lebourgeois, F., Cousseau, G. & Ducos, Y. (2004) Climate-tree-growth relationship of *Quercus petraea* Mill. stand in the Forest of Bercé (‘Futaie des Clos’, Sarthe, France). Annals of Forest Science 61: 361-372.

Leibundgut, H. (1957) Waldreservate in der Schweiz. Schweizerische Zeitschrift für Forstwesen 108: 417-421.

Michelot, A., Bréda, N., Damesin, C. & Dufrêne, E. (2012) Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. Forest Ecology and Management 265: 161-171.

Muir, G., Fleming, C. C. & Schlötterer, C. (2000) Species status of hybridizing oaks. Nature 405: 1016.

Parker, G. R. & Leopold, D. J. (1983) Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of the Torrey Botanical Club 110: 482-488.

Peñuelas, J. & Boada, M. (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology 9: 131-140.

Pilcher, J. R. & Gray, B. (1982) The relationships between oak tree growth and climate in Britain. Journal of Ecology 70: 297-304.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, http://www.R-project.org.

Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85-94.

Rohner, B., Bigler, C., Wunder, J., Brang, P. & Bugmann, H. (2012a) Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. Journal of Vegetation Science 23: 892-905.

Rohner, B., Bugmann, H. & Bigler, C. (2012b) Estimating the age-diameter relationship of oak species in Switzerland using nonlinear mixed-effects models (submitted to European Journal of Forest Research).

Rozas, V. (2005) Dendrochronology of penduculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. Annals of Forest Science 62: 209-218.

Rust, S. & Roloff, A. (2004) Acclimation of crown structure to drought in *Quercus robur* L. – intra- and inter-annual variation of abscission and traits of shed twigs. Basic and Applied Ecology 5: 283-291.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C. & Wilmking, M. (2011) Drought matters - declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. Forest Ecology and Management 262: 947-961.

Thornthwaite, C. W. (1948) An approach toward a rational classification of climate. Geographical Review 38: 55-94.

Thornton, P. E., Running, S. W. & White, M. A. (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. Journal of Hydrology 190: 214-251.

Vogel, R. B. & Schweingruber, F. H. (2001) Centennial variability of tree-ring width of spruce, fir and oak in relation to climate in Switzerland for the last 450 years. Dendrochronologia 19: 197-209.

Weber, P., Bugmann, H. & Rigling, A. (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. Journal of Vegetation Science 18: 777-792.

Willmott, C. J., Rowe, C. M. & Mintz, Y. (1985) Climatology of the terrestrial seasonal water cycle. Journal of Climatology 5: 589-606.

Zang, C., Rothe, A., Weis, W. & Pretzsch, H. (2011) Zur Baumarteneignung bei Klimawandel: Ableitung der Trockenstress-Anfälligkeit wichtiger Waldbaumarten aus Jahrringbreiten. Allgemeine Forst- und Jagdzeitung 182: 98-112.

Zweifel, R., Zimmermann, L., Zeugin, F. & Newbery, D. M. (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. Journal of Experimental Botany 57: 1445-1459.

Chapter III

Estimating the age-diameter relationship of oak species in Switzerland using nonlinear mixed-effects models

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Abstract. Diameter growth plays a key role in forest dynamics, yet little attention has been paid to quantifying tree age-diameter relationships. Predicting diameter growth of oaks is especially important due to their role in nature conservation and adaptive forest management under climate change. Thus, we (1) identified environmental variables that shape age-diameter relationships of oaks and (2) quantified the accuracy of predictions (root mean square error between predictions and observations) based on these variables. We determined the age-diameter relationship of 243 oaks (*Quercus* spp.) growing in Switzerland by using tree-ring samples. Nonlinear mixed-effects models based on a modified Chapman-Richards equation were fitted with environmental variables included as covariates. The fixed effects elevation, slope and water holding capacity were most important in shaping the age-diameter relationships. Lower elevations, steeper slopes, north-facing aspects, higher water holding capacities and moister summers resulted in larger maximum diameters. Predictions based on the fixed effects reached a high accuracy for 75% of the oaks; the inclusion of random effects increased model accuracy for 86% of the trees. These results suggest that runoff plays a key role for the age-diameter relationships, accompanied by limiting temperature effects at higher elevations. The fixed effects explained variability in site quality, whereas the random effects included tree-specific deviations from expected age-diameter relationships due to e.g. neighborhood effects.

Keywords: Chapman-Richards growth equation; diameter growth; model averaging; *Quercus* spp.; tree age.

Introduction

Tree growth is a key driver of forest dynamics. Therefore, identifying the environmental influences that determine tree growth is central for (1) an improved understanding of the abiotic and biotic growth-limiting factors such as climate (Fritts 1976); (2) quantifying qualitatively well-known processes influencing tree growth such as release effects following disturbances (Black and Abrams 2003); (3) developing models of tree growth that can be implemented in succession models (cf. Bugmann 2001); and (4) forecasting future growth, e.g. concerning expected timber yield (Hall and Clutter 2004). Thus, understanding the processes that operate on tree growth is crucial from the point of view of ecology, forest science and forest management.

Estimating tree growth has been a focus of scientific research for a long time. First attempts emerged in the form of yield tables in the early 19th century (Tesch 1981; Weiskittel et al. 2011). The use of nonlinear growth equations gained popularity in the mid-20th century, when e.g. the equation by von Bertalanffy (1957) and its generalization by Chapman-Richards (Richards 1959) were established. Subsequently, continuous progress in statistical techniques led to the widespread use of regression methods for estimating tree growth (Tesch 1981). Recent developments have been dominated by increasing computing power, which opened the way for both simulation modelling and sophisticated empirical techniques such as mixed-effects models (Weiskittel et al. 2011).

To date, many empirical growth models have been developed to estimate the age-height relationship (e.g. Fang and Bailey 2001; Nothdurft et al. 2006), whereas the age-diameter relationship has attracted less attention. The focus on tree height may originate from traditional yield and site considerations, because height growth is a useful proxy of site productivity (Tesch 1981). However, a tree's diameter at breast height (DBH) is an equally fundamental variable in forestry. For instance, several silvicultural characteristics including basal area or standing crop are calculated based on DBH measurements, and DBH distributions may be used to infer the successional phase of a forest (Heiri et al. 2009). In addition, growth models based on DBH may reach a higher applicability in practice since the DBH of a tree is easier to measure than its height.

Diameter growth has often been modelled empirically in relation to tree height (e.g. Adame et al. 2008), but less frequently in relation to age. The few models available for the age-DBH relationship are typically based on linear relationships (Martin-Benito et al. 2011), which restricts their applicability to the range of observed ages and diameters (cf. Pinheiro and Bates 2000). Promising nonlinear modelling approaches have attracted attention in recent times (Crecente-Campo et al. 2010; Subedi and Sharma 2011). However, empirical modelling of growth curves – for height as well as for diameter – has often focussed on curve fitting, whereas ecological influences determining the shape of the growth curves have not often been considered. Thus, imposing linear relationships and mere curve fitting have limited the generality of many findings achieved so far.

A high potential for studying the development of DBH with age lies in the use of tree-ring data, since they allow for reconstructing the age-DBH relationship retrospectively at an annual resolution. While tree-ring data are ideally suited for the model fitting step to calibrate age-DBH relationships based on environmental influences, applications of such models may also involve repeated DBH measurements e.g. from forest inventories to estimate future growth of the inventoried trees.

Identifying environmental influences that affect the growth of oak is especially important due to their potential role in the adaptation of European forests to climate change (e.g. Weber et al. 2007) and their high ecological value, e.g. with respect to insect and bird diversity, which has been shown to be closely related to tree size (Caprio et al. 2009; Ranius and Jansson 2000). However, the age-DBH relationship of oak has attracted only little attention so far.

Therefore, the present study aims at (1) identifying the ecological influences that underlie the age-DBH relationships of oaks across a large environmental gradient, and (2) predicting the age-DBH relationship using nonlinear mixed-effects models with covariates. For these purposes, we investigated the growth curves of more than 240 oaks from 10 unmanaged forest reserves in Switzerland. The models were fitted to tree-ring data covering ages up to 270 years. We focussed on two main questions:

1) What environmental variables are important for shaping the age-DBH relationship of oak?
2) How accurate are estimations of the age-DBH relationship based on these variables?

Material and Methods

Study sites and tree species

Study sites were selected within oak forests belonging to the Swiss forest reserve network (http://www.waldreservate.ch), which is jointly managed by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), ETH Zurich, and the Swiss Federal Office for the Environment (FOEN; for details see Brang et al. 2011; Rohner et al. 2012). From this network, we selected those reserves that contained a minimum of 10% *Quercus* species in the last inventory, calculated as the importance value ([relative density + relative basal area] / 2 x 100; Parker and Leopold 1983). The composition of further tree species within the selected reserves differs strongly, ranging from mainly *Pinus sylvestris* in south-western Switzerland to mainly *Fagus sylvatica* in northern Switzerland. Additionally, only reserves with at least three inventories were considered. These criteria were met by eleven reserves, from which we excluded one located in the south-west of Switzerland (Les Follatères); the extreme site conditions (south-facing aspect, steep slopes, shallow soils) in combination with the continental climate led to implausible model predictions for some trees (i.e. negative diameter growth). The remaining ten study sites cover more than 140 km of latitude and 230 km of longitude and represent a wide range of oak habitats varying in climatic conditions and site characteristics (Table 1).

The most frequent oak species in Switzerland are *Q. petraea*, *Q. robur* and *Q. pubescens,* with relative stem numbers of 61%, 24% and 15%, respectively (National Forest Inventory; Brändli 2010). We sampled and analyzed these oak species collectively (referred to as 'oak') because (1) the discrimination of the species in the field (i.e. without subsequent genetic analyses) is not reliable due to overlapping morphological attributes (Aas 1998); (2) the species also overlap in their physiological attributes (Kleinschmit and Kleinschmit 2000), thus we did not expect fundamentally different growth responses to environmental variables, especially not for *Q. petraea* and *Q. robur*; (3) the three species are genetically not completely isolated because all of them tend to hybridize, leading to controversies whether they are different species at all (Muir et al. 2000). As a consequence, oak species are often not discriminated in large-scale monitoring (cf. Rohner et al. 2012) and in practical applications such as Payment for Ecosystem Services schemes (e.g. Bolliger et al. 2008), i.e. efforts towards a distinct analysis may have hindered its application.

Data collection and preparation

Field methods

Field work was conducted in summer 2009 and 2010. We selected a total of 303 oaks comprising 30-31 living individuals per site, with the sample being representative of the DBH distribution recorded in the last inventory campaign. From every selected tree, one increment core was taken parallel to the contour line. Since this study was conducted within forest reserves, only one core per tree was taken to minimize the impact on the cored trees. We cored at 1.2 m above ground to avoid an impact on stem geometry at 1.3 m above ground, where DBH is measured in the inventory campaigns.

For every cored tree, we recorded site characteristics, i.e. elevation, slope and aspect (Table 1). Slope and aspect (both in degrees) were determined based on the local topography within a radius of ca. 10 m. The azimuth of the aspect was converted into a north-south indicator (NSI) calculated as

$$\mathrm{NSI} = \cos(\mathrm{azimuth} / 360 \times 2\pi) \tag{1}$$

A NSI of -1 represents a south-facing aspect, whereas a NSI of 1 represents a north-facing aspect. For a slope of 0°, NSI was set to zero. NSI was included because we expected growth to be correlated with solar radiation and evapotranspiration, whereas we did not expect such a correlation for the east-west indicator.

Table 1. Characteristics of the study sites. For elevation, slope and the north-south indicator (NSI), the range represented in the tree sample is shown.

Site	Coordinates (northing, easting)	Reserve area (ha)	Elevation (m a.s.l.)	Slope (°)	NSI[a]	Water holding capacity[b]	Drought index[c] (mm)	Main soil type[d]	Main phyto-sociological association[e]	Reserve foundation (year)
Adenberg	47° 36' 50'' 8° 33' 40''	5	490-530	0 – 17	0.00 – 0.77	5	-4	Cambisol	*Galio odorati-Fagetum*	1970
Bannhalde	47° 31' 28'' 8° 31' 15''	2.5	425	0 – 14	-0.91 – 0.64	5	-5	Cambisol	*Galio odorati-Fagetum*	1972
Bois de Chênes	46° 26' 17'' 6° 13' 33''	83	500-520	0 – 15	-1.00 – 0.00	5	-36	Cambisol	*Carici Fagetum caricetosum montanae, Aro-Fagetum*	1969
Josenwald	47° 8' 5'' 9° 15' 19''	85	480-520	28 – 42	-1.00 – -0.42	1	255	Leptosol	*Teucrio-Quercetum,* *Asperulo taurinae-Tilietum*	1976
Krummen-linden	47° 33' 27'' 8° 20' 8''	3	545-555	0	0.00	6	42	Cambisol	*Galio odorati-Fagetum luzuletosum*	1955
Langgraben	47° 32' 49'' 8° 31' 36''	4.5	420	0	0.00	4	-10	Luvisol	*Galio odorati-Fagetum luzuletosum* *(Galio silvatici-Carpinetum)*	1972
Pfynwald	46° 17' 36'' 7° 33' 48'′	7	570-605	13 – 38	-1.00 – 0.97	3	-147	Regosol	*Erico-Pinetum silvestris*	1957
Strassberg	47° 31' 55'' 8° 29' 40''	6.5	465-475	6 – 31	-0.98 – 1.00	4	24	Cambisol	*Galio odorati-Fagetum*	1975
Vorm Stein	47° 33' 7'' 8° 27' 13''	10	475-495	0 – 27	-1.00 – 0.00	4	33	Luvisol	*Galio odorati-Fagetum,* *Pulmonario-Fagetum melittetosum*	1971
Weidwald	47° 24' 47'' 7° 59' 33''	5	610-640	6 – 36	-1.00 – -0.50	3	37	Leptosol	*Asperulo taurinae-Tilietum,* *Cardamino-Fagetum,* *Seslerio-Fagetum*	1963

[a] Calculated according to Eq. 1 (see text). A NSI of -1 represents a south-facing aspect, whereas a NSI of 1 represents a north-facing aspect. For slope = 0°, the NSI was set to zero.

[b] Categories indicate the following values: 1: < 15 l/m^2; 2: 15-30 l/m^2; 3: 30-45 l/m^2; 4: 45-60 l/m^2; 5: 60-100 l/m^2; 6: > 100 l/m^2.

[c] The drought index is calculated as the sum of precipitation minus potential evapotranspiration from May to July. Bigger values of the drought index indicate moister summers.

[d] Nomenclature based on the FAO system (FAO 1998).

[e] Indicated following Ellenberg and Klötzli (1972).

As an indicator of soil susceptibility to drought, water holding capacity was determined from the soil suitability map of Switzerland (Bundesamt für Raumplanung (EJPD) et al. 1980), where it is indicated in the following categories: < 15 l/m^2, 15-30 l/m^2, 30-45 l/m^2, 45-60 l/m^2, 60-100 l/m^2, > 100 l/m^2. For the statistical analysis, we transformed these categories into integers from 1 to 6 to reduce the number of coefficients to estimate, and thus to improve model convergence.

Laboratory analyses

We used standard dendrochronological methods to prepare and analyze the tree cores. The surface of the cores was cut with a microtome (Gärtner and Nievergelt 2010) and prepared with chalk. The ring widths were measured using a Lintab 5 measuring system in combination with the TSAP-Win software (RINNTECH, Heidelberg, Germany). In addition to visual crossdating based on pointer years, we used the software COFECHA to quantitatively crossdate the tree-ring series at the site level (Holmes 1983).

To determine the distance and number of missing rings between the pith and the first complete ring on the core, the graphical method developed by Rozas (2003) was used. This method is based on the convergence of xylem rays and therefore allows an accurate estimation also under eccentric growth, as is often the case for oak (Rozas 2003). We excluded trees from the study (1) when crossdating failed, (2) when the distance between the pith and the first complete ring could not be determined (e.g. because the missing distance was too large), (3) when the series had both > 15% missing rings and > 10 missing rings; and (4) when values were missing for site characteristics. In total, 47 trees (15.5%) had thus to be excluded.

Data preparation

DBH beneath the bark (DBH_{bb}) was estimated as 2 × (cumulative sum of ring widths + estimated missing distance to the pith). The age at a tree height of 1.2 m was approximated as the sum of measured rings and the estimated number of missing rings between the pith and the first complete ring on the core.

As a proxy for the climatic conditions at the different sites, we used a drought index calculated as precipitation minus potential evapotranspiration (PET, Bigler et al. 2006; Thornthwaite 1948). The underlying data for this calculation were monthly precipitation sums and temperature means from 1960–2006, which were spatially interpolated to a 1-ha grid in Switzerland based on the DAYMET model (Thornton et al. 1997) by the research unit Landscape Dynamics at WSL Birmensdorf. From these data, the drought index was determined for the sites shown in Table 1. We calculated PET based on day length (estimated according to Forsythe et al. 1995) and monthly temperature means using a modified Thornthwaite (1948) method (Willmott et al. 1985). We used the sum of drought index values from May to July because tree rings showed the highest correlation with climate data from this period (B. Rohner, *unpublished*).

Statistical analysis

Model formulation

The age-DBH_{bb} relationship of the sampled oaks was modelled using nonlinear mixed-effects models with covariates (Pinheiro and Bates 2000). As the nonlinear growth function, we used the Chapman-Richards function (Richards 1959) with an expected value parameterization for the asymptote (Fang and Bailey 2001; Hall and Clutter 2004):

$$\text{DBH}_{\text{bb}} = a \times ((1 - e^{-b \times \text{age}})/(1 - e^{-b \times x_0}))^c \tag{2}$$

where the parameter a represents estimated DBH_{bb} at age x_0, b is a slope parameter, and c defines the type of the curve (i.e. presence of an inflection point). The value x_0 was set to 1200 years, the maximum age reported for *Q. robur* (Godet 1986). The slope parameter b defines how fast a tree approaches its asymptotic diameter (Richards 1959). The asymptotic diameter ($\text{DBH}_{\text{bb\_asym}}$) can be calculated as (Fang and Bailey 2001):

$$\text{DBH}_{\text{bb\_asym}} = a \,/\, (1 - e^{-b \times x_0})^c \tag{3}$$

Initially, we had several other growth equations (e.g. von Bertalanffy, Gompertz, logistic growth; cf. Zeide 1993) taken into consideration, but the modified Chapman-Richards function clearly fitted the data best. We used the modified rather than the original Chapman-Richards growth equation because of improved convergence.

For all three parameters (a, b, c), we estimated fixed effects, whereas an additional random intercept for the parameter a was estimated at the tree level. The decision whether to include random effects for the particular parameters was based on the ratio between the standard deviation of the random effect and the corresponding parameter estimation in the initial model fits (Pinheiro and Bates 2000). This ratio was relatively high for a (0.3), but very low for b and c (both < 10^{-7}). The fixed effects for a and b were modelled as linear combinations of various covariates (Pinheiro and Bates 2000) with the tree-specific parameters in Eq. 2 estimated as

$$\vec{a} = \boldsymbol{X} \times \vec{\alpha} + \vec{r} \tag{4}$$

$$\vec{b} = \boldsymbol{Y} \times \vec{\beta} \tag{5}$$

where $\boldsymbol{X}$ and $\boldsymbol{Y}$ are matrices containing the covariates, $\vec{\alpha}$ and $\vec{\beta}$ are vectors representing the coefficients of the covariates, and $\vec{r}$ indicates the vector of the random intercepts for parameter a. No covariates for explaining parameter c were considered; although we expected the temporal development of competition to have the highest influence on c, we lacked the necessary data to reconstruct competition along time.

A set of 100 competing models was formulated with varying combinations of covariates included in $\boldsymbol{X}$ (Eq. 4) and $\boldsymbol{Y}$ (Eq. 5); a complete list of all considered models is shown in the Online Resource 1. All possible combinations among topographical variables (i.e. elevation, slope and the NSI), water holding capacity and drought index, and additional combinations with the interaction between water holding capacity and drought index were considered.

We included the interaction between water holding capacity and drought index because we expected a stronger effect of the drought index at sites with a low water holding capacity, and vice versa. No other interactions were included because no intensifying effect was expected among topographical variables and water holding capacity, and the interaction between topographical variables and the drought index would have entailed too many additional parameters to estimate, thus leading to convergence problems.

We randomly selected a total of 200 trees with 20 trees per study site to fit each of the 100 models, whereas the remaining 43 trees were subsequently used as independent data for model evaluation (13 trees had to be excluded due to convergence problems caused by almost linear growth curves). In the fitting procedure, we incorporated a first order autoregressive process to model the temporal autocorrelation of the residuals (Pinheiro and Bates 2000). In addition, all covariates were centred and scaled to avoid convergence problems and to achieve comparability among parameter estimates (means and standard deviations used for scaling and centring are shown in the Online Resource 2). All pairwise Pearson correlations between the covariates were < |0.6|, with the only exception of slope and water holding capacity (r = -0.8).

Model evaluation and averaging

We evaluated the models following an information-theoretic approach based on the Akaike Information Criterion (AIC, Burnham and Anderson 2002). Thus, we ranked all models according to their Akaike weights w_i, which are defined as

$$w_i = \left(e^{-\frac{1}{2}\Delta_i}\right) / \left(\sum_{i=1}^{100} e^{-\frac{1}{2}\Delta_i}\right) \tag{6}$$

with Δ_i being the difference in AIC between model i and the model with the lowest AIC (Burnham and Anderson 2002). The Akaike weight of a model may be interpreted as the probability that this model best describes the data at hand among the 100 models that we fitted (Johnson and Omland 2004).

Since several models reached a notable Akaike weight, and since quantitative prediction was the main goal of the study, multi-model inference was performed (Burnham and Anderson 2002; Johnson and Omland 2004). Thus, we averaged the model-specific vectors of coefficients $\vec{\alpha}_i$ over all models based on a weighting scheme representing the w_is, according to

$$\vec{\alpha}_{averaged} = \sum_{i=1}^{100} w_i \times \vec{\alpha}_i \tag{7}$$

and analogously for $\vec{\beta}_{averaged}$. When a covariate was not present in a model, its coefficient was set to zero (Burnham and Anderson 2002; Johnson and Omland 2004). The corresponding standard errors were averaged from the model-specific vectors of standard errors $\overrightarrow{se}_{\alpha,i}$ as

$$\overrightarrow{se}_{\alpha,averaged} = \sum_{i=1}^{100} \left(w_i \times \sqrt{\overrightarrow{se}_{\alpha,i}{}^2 + \left(\vec{\alpha}_i - \vec{\alpha}_{averaged}\right)^2} \right) \tag{8}$$

and analogously for $\overrightarrow{se}_{\beta,averaged}$. Only those models were considered in which the particular covariate was present, because setting the standard error to zero in models in which the corresponding covariate does not occur would bias the averaged standard error towards zero. Therefore, we linearly adjusted the w_is that they sum up to 100% when considering only those models in which the respective covariate was present. P-values could not be specified for the averaged coefficients; however, since the coefficients are assumed to be normally distributed, the interval ± 1.96 × $se_{averaged}$ can be used as an indicator of the significance. The goodness of the averaged model fit was quantified based on the root mean square error (RMSE) between the observed and predicted DBH_{bb}.

Model validation

The generality of the averaged model was evaluated by applying it to the 43 control trees, which had not been used for the model fitting procedure. Since no random effects had been estimated for these trees, their age-DBH_{bb} relationship was predicted based on the fixed effects of the averaged model only. Again, we calculated the RMSE between the observed and predicted DBH_{bb} to quantify the goodness of the prediction.

All statistical analyses were performed using the packages *nlstools* (Baty and Delignette-Muller 2011) and *nlme* (Pinheiro et al. 2011) in R, a language and environment for statistical computing (version 2.11.1, R Development Core Team 2010).

Results

Model evaluation and averaging

Nine models reached Akaike weights between 0.03% and 62%, the remaining 91 models had Akaike weights < 0.01% (Table 2, Online Resource 1). For describing the parameters a and b, the same three covariate combinations were present in the models with Akaike weights > 0.01%, i.e. (1) topography and water holding capacity; (2) topography, water holding capacity and drought index; and (3) topography, water holding capacity, drought index and the interaction between the water holding capacity and the drought index. Thus, topography and water holding capacity were present for both parameters a and b in every model with an Akaike weight > 0.01%.

Model averaging resulted in the coefficients and standard errors shown in Table 3. Parameter a was strongly negatively correlated with elevation, and strongly positively correlated with slope and water holding capacity. In addition, the NSI and the drought index showed a weakly positive correlation with a, but the interval ± 1.96 × $se_{covariate}$ included zero. By far the weakest correlation with parameter a was found for the interaction between water holding capacity and the drought index. For parameter b, all coefficients showed opposite algebraic signs compared to parameter a, with the intercept being the only exception (Table 3). In fact, the estimates of the parameters a and b were strongly negatively correlated (Pearson correlation coefficient = -0.94, see Online Resource 3).

Table 2. Models with Akaike weights > 0.01%. A complete list of all considered models is shown in the Online Resource 1.

Model number	Parameter a[a]				Parameter b[a]				Akaike weight (%)
	Topography[b]	Water holding capacity	Drought index	Interaction[c]	Topography[b]	Water holding capacity	Drought index	Interaction[c]	
50	×	×			×	×			0.03
53	×	×	×		×	×			0.59
55	×	×	×	×	×	×			0.6
77	×	×			×	×	×		4.06
80	×	×	×		×	×	×		1.23
82	×	×	×	×	×	×	×		1.43
95	×	×			×	×	×	×	62.2
98	×	×	×		×	×	×	×	22.27
100	×	×	×	×	×	×	×	×	7.6

[a] The parameters a (Eq. 4) and b (Eq. 5) are from the modified Chapman-Richards growth equation (Eq. 2; Fang and Bailey 2001; Hall and Clutter 2004; Richards 1959).

[b] Topography includes elevation, aspect and the north-south indicator.

[c] Interaction between water holding capacity and the drought index.

Table 3. Coefficients ± standard errors of the averaged model.

Parameter	Intercept	Topography			Water holding capacity	Drought index	Interaction[c]	Random intercept (standard deviation)
		Elevation	Slope	NSI[b]				
a[a]	67.52 ± 2.38	-19.31 ± 2.15	17.95 ± 3.20	2.36 ± 3.26	24.49 ± 3.12	0.83 ± 3.10	-0.083 ± 2.40	19.23
b[a]	0.0042 ± 0.00021	0.0013 ± 0.00012	-0.0015 ± 0.00016	-0.00034 ± 0.00015	-0.0017 ± 0.00021	-0.000069 ± 0.00024	-0.00022 ± 0.00011	
c[a]	0.86 ± 0.0070							

[a] The parameters are from the modified Chapman-Richards growth equation (Eq. 2; Fang and Bailey 2001; Hall and Clutter 2004; Richards 1959).

[b] North-south indicator; calculated according to Eq. 1 (see text).

[c] Interaction between water holding capacity and the drought index.

The averaged model predicted values of the parameter a between 14.3 and 109.1 for the trees used in the model selection procedure (Online Resource 3), which corresponds to the expected DBH_{bb} when oaks reach an age of 1200 years. For parameter b, values between 9.4×10^{-4} and 8.1×10^{-3} were predicted. DBH_{bb_asym} resulting from these parameter estimates (Eq. 3) covered a range between 14.3 cm and 148.3 cm, with 50% of the trees reaching a predicted DBH_{bb_asym} between 60 cm and 80 cm (Fig. 1).

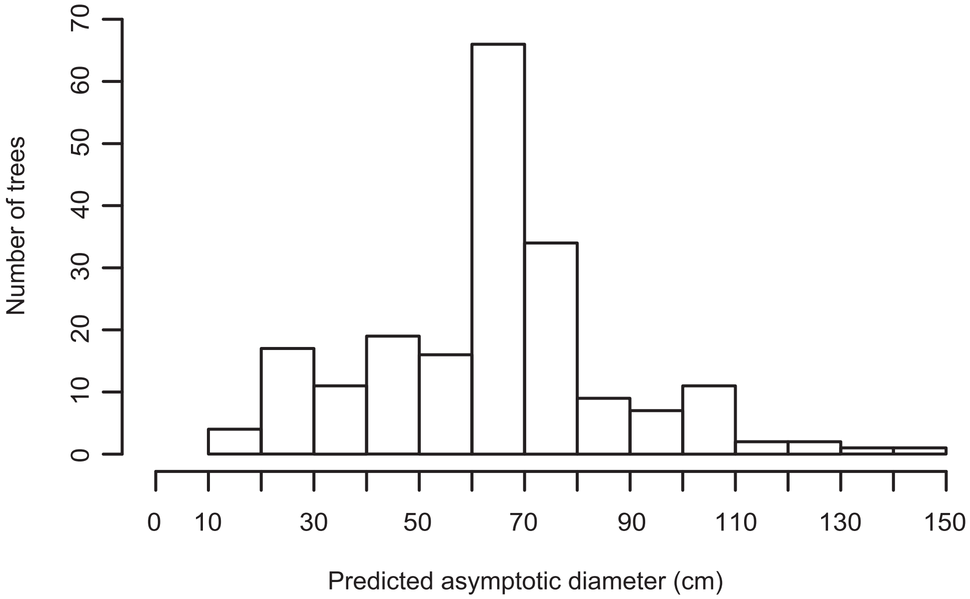

Figure 1. Predicted asymptotic diameters. The asymptotic diameter of every tree used for the model fitting procedure was calculated from the parameter estimation as a / $(1 - e^{-b \times x_0})^c$, where x_0 was set to 1200 years.

The age-DBH_{bb} curves that were predicted using the fixed effects of the averaged model fitted the observed curves of the trees included in the model fitting procedure fairly well (Fig. 2, for predictions of all trees see Online Resource 4). The RMSE was < 3 cm for 47% of the trees, and for 80% of the trees it did not exceed 6 cm. The inclusion of a random term reduced the RMSE for 86% of the trees (Fig. 2). This reduction was generally larger for trees whose predictions based on the fixed effects had a high RMSE. Those 14% of the trees for which the inclusion of a random term increased the RMSE had an RMSE < 6 cm based on the fixed effects only (Fig. 2).

Model validation

The application of the averaged model (Table 3) to the control trees revealed a similar distribution of the RMSE as for the trees used for model fitting (Fig. 3, model predictions for all control trees are shown in the Online Resource 5). Again, almost half of the trees (49%) had an RMSE < 3 cm between the observed and predicted DBH_{bb}, and a further 26% had an RMSE < 6 cm (Fig. 3). For some trees, the predictions fitted the observations fairly well until a certain age was reached, but abrupt growth changes subsequently led to an increasing divergence between the two curves (e.g. Fig. 3c and 3d).

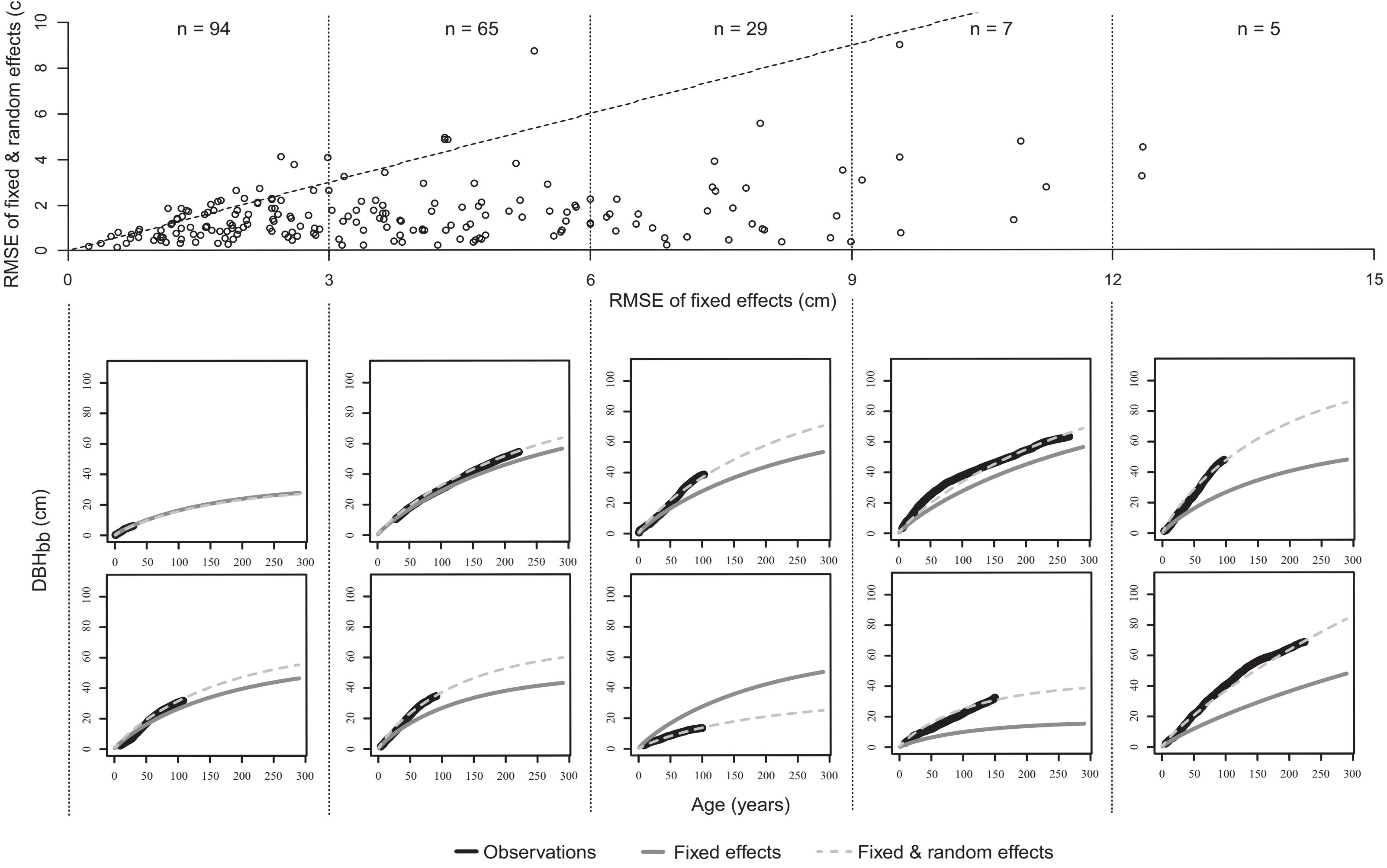

Figure 2. Accuracy of the averaged model (see Table 3). In the upper part, the root mean square error (RMSE) of the model fit based on the fixed effects is plotted against the RMSE of the model fit including both fixed and random effects. For all points below the dashed line, the inclusion of the random effect reduced the RMSE. Five classes were formed according to the RMSE based on the fixed effects (RMSE 0-3 cm, 3-6 cm, 6-9 cm, 9-12 cm, > 12 cm; indicated by vertical dotted lines), for which n indicates the number of trees in the corresponding class. Three trees outside the range of the graph are not shown (RMSE of the fixed effects: 16.2 cm, 19.3 cm, 21.1 cm). In the lower part, the model predictions are shown for the trees with the lowest (above) and highest (below) RMSE of the corresponding class, respectively. DBH$_{bb}$ indicates diameter beneath the bark at a height of 1.2 m. Predictions for all trees used in the model fitting procedure are shown in the Online Resource 4.

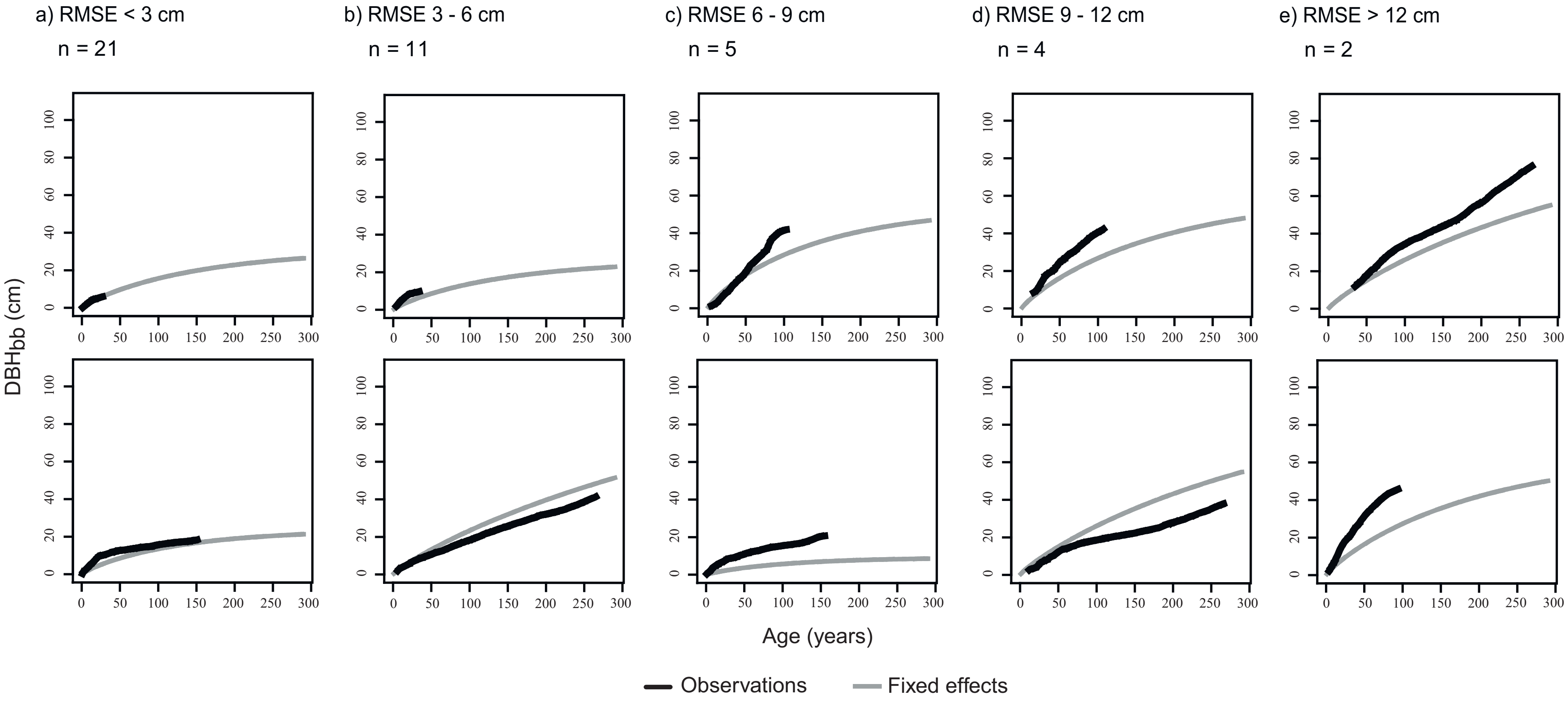

Figure 3. Application of the averaged model (see Table 3) to the control trees. The trees of the control sample were grouped according to the root mean square error (RMSE) the same way as the trees used for model fitting (a-e, see Fig. 2). For every group, n indicates the number of trees, and the model prediction is shown for the tree with the lowest (above) and the highest (below) RMSE. DBH_{bb} indicates the diameter at 1.2 m beneath the bark. Predictions for all control trees are shown in the Online Resource 5.

Discussion

Parameter estimation of the Chapman-Richards function

The use of nonlinear mixed-effects models for describing the age-diameter relationships of oaks in Switzerland resulted in accurate predictions and entailed several methodological advantages compared to alternative modelling approaches. First, the accuracy of the predictions is likely to result from the relatively flexible nonlinear Chapman-Richards growth equation. Second, this equation allows for projections outside the range of available data, e.g. for higher ages. Such projections are more reliable than those from *linear* mixed-effects models, e.g. polynomial models (Pinheiro and Bates 2000). Third, the Chapman-Richards growth equation has a biologically motivated background (Zeide 1993), which implies that estimating its parameters is equivalent to quantifying the ecological processes underlying the function (e.g. the growth constraint reflected in parameter a). Lastly, the inclusion of covariates allows for quantifying ecological influences on these processes.

The parameter c was estimated to be < 1, suggesting that the age-diameter relationship was most appropriately modelled without an inflection point. This contrasts von Bertalanffy's (1957) growth equation, where c equals 3 based on theoretical considerations. However, these considerations were mainly geared towards animal rather than plant growth. The shape of the growth curves of the individual trees likely depends on the competitive situation within their neighbourhood, with strong competition leading to flat sections in the growth curve and release from competition to steep parts of the curve. The estimation of a fixed c value for all trees in the sample neglects individual variation in the form of the growth curves possibly induced e.g. by suppression and release phenomena; therefore, this is likely to entail an increased RMSE for at least some trees in the sample. It would be possible to adjust the parameter c individually across time if the competitive situation of every tree could be reconstructed (cf. Weber et al. 2008), but due to the decay of dead trees this is feasible only for the past 10-20 years. Such an endeavor is not feasible in forest reserves because a dendrochronological analysis of all trees in the plot would be required.

The estimated values of $\text{DBH}_{\text{bb\_asym}}$ and the parameter a (DBH_{bb} at the age of 1200 years) seem rather low. However, representative reference values are rare and often speculative, since most trees are cut or die prior to reaching such high ages. Maximum diameters reported in the literature range between 250 and 300 cm for *Q. petraea*, 200 to 380 cm for *Q. robur*, and around 90 cm for *Q. pubescens* (cf. Bugmann 1994) and thus are considerably higher than those predicted by the averaged model, especially if we assume that *Q. pubescens* represents the lowest estimated $\text{DBH}_{\text{bb\_asym}}$. Furthermore, *Q. robur* trees with an age of only 250 to 450 years have been recorded with DBHs similar to or even exceeding the $\text{DBH}_{\text{bb\_asym}}$ estimated in the present study (Rozas 2005). An explanation for this discrepancy may be that reported maximum DBHs are likely to originate from exceptionally vigorous sites, whereas many dry sites with shallow soils were included in the present study. A difference of a few centimeters between DBH and DBH_{bb} due to the bark (bark thickness varied between 0.2 cm and 2.5 cm; B. Rohner, *unpublished*) provides another explanation. And finally, a further reason for the underestimation of the diameters in our model is the assumption of concentric growth, which is reflected in the fact that only one core per tree was sampled and the tree-ring widths were measured perpendicular to the ring boundaries. This assumption has been shown to be often violated for oaks (Rozas 2003) and to potentially bias long-term increment projections for both coniferous and deciduous tree species (Russell et al. 2011). Hence, for a sound comparison with DBH values measured by calliper, corrections of the DBH_{bb} related to bark thickness and eccentric growth would be necessary.

The estimated values of the slope parameter b need to be interpreted in combination with the corresponding values of a because they are strongly negatively correlated. This correlation likely results from annual diameter growth being restricted to a biologically plausible range. For example, if we compare two trees with an expected DBH_{bb_asym} of 15 cm vs. 150 cm, the same value of b for these two trees would imply the same time available for approaching DBH_{bb_asym} – this would likely entail implausible annual growth rates for either of them (for a visualization see Online Resource 6). This holds particularly true for oak, because a minimum tree-ring width is produced in most years (Rozas 2003). Accordingly, a lower value of b in combination with a higher value of a may still represent higher annual growth over a certain time span (see Online Resource 6). Hence, the slope parameter b does not have a consistent biological interpretation (cf. Richards 1959), and this is why we hereafter focus on parameter a.

Environmental variables shaping the age-diameter relationship

The estimated coefficients of several covariates for a indicate that, although water stress seems to be a key process limiting the age-DBH_{bb} relationship of oak, the amount of water being potentially present at a particular site is less important than the capability of retaining this amount. For instance, the highest correlation was found between parameter a and the water holding capacity, representing increasing DBH_{bb} at 1200 years with increasing water holding capacity. A likely explanation for this correlation is that trees on soils with a high water holding capacity experience prolonged water supply during dry periods, whereas tree growth on soils with a low water holding capacity may already be limited by drought early on in rainless periods. The water holding capacity has been shown to be important in the age-height relationship of various tree species in Europe, including *Q. petraea* (e.g. Piedallu et al. 2011), whereas influences on diameter growth have been found mainly in the context of annual increments (Weber et al. 2007). We are not aware of quantitative studies on possibly limiting effects on maximum tree diameter. The impact of the water balance on maximum diameter is further corroborated by the positive coefficient of the NSI, which indicates a higher DBH_{bb} at 1200 years on north-facing aspects, where lower evapotranspiration is expected. Although the positive correlation between parameter a and the drought index is weak, this relationship further supports the conclusion that water stress is limiting the maximum diameter of oak.

The comparably high negative correlation between elevation and DBH_{bb} at 1200 years may be indicative of frost conditions. Reduced tree dimension with increasing elevation due to temperature limitation is a well-known process that usually occurs at the upper end of a tree species' distribution range. The upper elevation limit of oaks in Central Europe is located at around 1000 m a.s.l. (Ellenberg and Leuschner 2010). The elevation gradient represented in our study thus covers a considerable amount of this distribution range. Lower temperatures at higher elevations may increase the risk of frost damage, for which oak is known to be susceptible (Ellenberg and Leuschner 2010). Furthermore, in the European Alps the length of the growing season decreases by seven days per 100 m of elevation gain (Gensler 1946). At higher elevations, these well-known effects of reduced temperature are likely to limit the maximum diameter of oak.

The positive effect of slope on parameter a indicates an increased DBH_{bb} of 1200 year old oaks on steeper slopes. This is rather unexpected as steep slopes are commonly associated with adverse growing conditions (e.g. Costa et al. 2008), e.g. due to high runoff and shallow soils. However, a geometrical effect may have caused increased asymptotic diameter values: the horizontal projection of a tree crown to the ground represents a larger area on steep compared to flat terrain. As a consequence, the root zone – and thus accessible water and nutrients – per tree may be larger on steeper slopes if identical soil depth is assumed. However, such a potential benefit has not been documented so far. Thus, the possibility that the positive coefficient for slope could be an artefact caused by the comparably high correlation with water holding capacity cannot be ruled out.

It is worth emphasising that our interpretations regarding the importance of water stress do not contradict the drought tolerance ascribed to oak. In fact, *Q. robur* and *Q. petraea* are able to grow under fairly dry conditions, although their optimum growth range lies in moist conditions, where they are usually suffering from high competition by more shade-tolerant species such as European beech (*F. sylvatica*; Ellenberg and Leuschner 2010). From this perspective, it is not surprising that reduced parameter values for a and associated DBH_{bb_asym} are predicted under drier conditions. Our model does not investigate *whether* oaks are able to grow, but it quantifies *how* they grow under specific conditions along an environmental gradient.

Accuracy and applicability of the age-diameter model

Although the present study generated an empirical growth model with possible applicability in a wide range of Central European oak forests, the simultaneous consideration of a south-facing *Q. pubescens* forest that is characterized by shallow soils located in the comparably dry Valais (Les Follatères) did not produce plausible results. This is likely due to the fact that Les Follatères covers the upper end of the elevation gradient (up to 870 m a.s.l.) as well as the lower end of the NSI (-1 to 0.71). Furthermore, Les Follatères has the second lowest water holding capacity (category 2, 15-30 l/m^2) among all study sites, only topped by Josenwald, where the drought index is higher (precipitation - PET from May to July = -9 mm at Les Follatères). Oaks from Les Follatères therefore struggle with adverse conditions, comparable to those in the Mediterranean area. The inability of the model to cope with such conditions indicates that its applicability to oaks from southern Europe is highly restricted.

The fixed effects of the averaged model reflected well the general variability in the age-diameter curves for the majority of the oaks in our sample. Since a broad range of growth-relevant site characteristics were represented by the fixed effects, they are likely to have captured site quality fairly well. The similar RMSE distributions of the model fitting and the control sample indicate that predictions from the averaged model are robust within the range of incorporated site characteristics. However, under specific site conditions, there is substantial variability in the age-diameter curves that cannot be explained by the fixed effects alone.

The inclusion of an additional random effect led to considerable improvement in the predictions for trees whose age-diameter relationship was captured only poorly by the fixed effects. In general, estimations based on both fixed and random effects fitted the observations very accurately. Similar improvements by adding random effects were found in a variety of empirical growth-modelling studies based on linear (Martin-Benito et al. 2011) and nonlinear relationships (Adame et al. 2008; Nothdurft et al. 2006; Subedi and Sharma 2011). However, tree-specific random effects are estimated during the fitting procedure, and are therefore not available for independent trees, even though it is exactly for those trees that model predictions would be most desirable. Our findings may thus be applied in two different contexts: (1) in the case of oaks for which only site information is available, the age-diameter relationship may be predicted based on the fixed effects alone; (2) in the case of trees for which additional tree-ring data or repeated diameter measurements are available, an analogue fitting procedure may be followed to base the predictions on both fixed and random effects.

The random effects in the present study accounted for individual deviations from expected site-specific age-diameter relationships that cannot be explained by the fixed effects. A considerable part of these deviations probably reflects variability in the competitive situation among individual trees as well as local nutrient availability. Growth effects caused by competition have not been included in the fixed effects because their reconstruction over longer time spans is a very cumbersome task (cf. Weber et al. 2008). However, efforts to solve this issue would be desirable, since the inclusion of information on the temporal development of the competitive situation in the fixed effects would be highly likely to improve the predictions based on the fixed effects alone.

Conclusion

Nonlinear mixed-effects models with covariates are a promising approach to model tree growth and specifically the age-diameter relationship of oak trees, because they are a flexible tool for the identification of environmental drivers acting on growth and for the prediction of tree growth. The model that we derived indicates that water runoff in combination with frost damage and a restricted length of the growing season towards the upper elevation limit are crucial factors shaping the age-diameter relationship of oak. Predictions based on the fixed effects of the model are fairly accurate, and the accuracy can be increased considerably by including an additional tree-specific random effect. The present findings can be used in future attempts to predict oak growth in Central Europe, be it for purposes of biodiversity conservation or for adaptive management strategies under climate change.

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References

Aas G (1998) Morphologische und ökologische Variation mitteleuropäischer *Quercus*-Arten: Ein Beitrag zum Verständnis der Biodiversität. Libri botanici 19. IHW-Verlag, Eching bei München

Adame P, del Río M, Cañellas I (2008) A mixed nonlinear height-diameter model for pyrenean oak (*Quercus pyrenaica* Willd.). For Ecol Manag 256:88-98

Baty F, Delignette-Muller ML (2011) nlstools: tools for nonlinear regression diagnostics. R package version 0.0-11

Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9:330-343

Black BA, Abrams MD (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecol Appl 13:1733-1749

Bolliger M, Schnidrig R, Stadler B (2008) Fachspezifische Erläuterungen zur Programmvereinbarung im Bereich Waldbiodiversität. In: Handbuch NFA im Umweltbereich. Bundesamt für Umwelt BAFU, Bern

Brändli U-B (ed) (2010) Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf; Bundesamt für Umwelt BAFU, Bern

Brang P, Heiri C, Bugmann H (2011) Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt, Bern

Bugmann H (2001) A review of forest gap models. Clim Change 51:259-305

Bugmann HKM (1994) On the ecology of mountainous forests in a changing climate: a simulation study. Dissertation, ETH Zurich

Bundesamt für Raumplanung (EJPD), Bundesamt für Landwirtschaft (EVD), Bundesamt für Forstwesen (EDI) (1980) Bodeneignungskarte der Schweiz. Grundlagen für die Raumplanung. Eidgenössische Drucksachen- und Materialzentrale, Bern

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York

Caprio E, Ellena I, Rolando A (2009) Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy. Landsc Ecol 24:65-76

Costa A, Madeira M, Oliveira ÂC (2008) The relationship between cork oak growth patterns and soil, slope and drainage in a cork oak woodland in Southern Portugal. For Ecol Manag 255:1525-1535

Crecente-Campo F, Soares P, Tomé M, Diéguez-Aranda U (2010) Modelling annual individual-tree growth and mortality of Scots pine with data obtained at irregular measurement intervals and containing missing observations. For Ecol Manag 260:1965-1974

Ellenberg H, Klötzli F (1972) Waldgesellschaften und Waldstandorte der Schweiz. Mitt Schweiz Anst Forstl Versuchswes 48:589-930

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen, 6th ed. Ulmer, Stuttgart

Fang Z, Bailey RL (2001) Nonlinear mixed effects modeling for slash pine dominant height growth following intensive silvicultural treatments. For Sci 47:287-300

FAO (1998) World Reference Base for Soil Resources. Food and Agriculture Organization of the United Nations, Rome

Forsythe WC, Rykiel Jr EJ, Stahl RS, Wu H, Schoolfield RM (1995) A model comparison for daylength as a function of latitude and day of year. Ecol Model 80:87-95

Fritts HC (1976) Tree Rings and Climate. Academic Press, London

Gärtner H, Nievergelt D (2010) The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia 28:85-92

Gensler GA (1946) Der Begriff der Vegetationszeit. Universität Zürich, Engadin Press, Samedan

Godet J-D (1986) Bäume und Sträucher: einheimische und eingeführte Baum- und Straucharten. Arboris-Verlag, Hinterkappelen-Bern

Hall DB, Clutter M (2004) Multivariate multilevel nonlinear mixed effects models for timber yield predictions. Biometrics 60:16-24

Heiri C, Wolf A, Rohrer L, Bugmann H (2009) Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. Ecol Appl 19:1920-1934

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull 43:69-78

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101-108

Kleinschmit J, Kleinschmit JGR (2000) *Quercus robur* - *Quercus petraea*: a critical review of the species concept. Glasnik Za Smske Pokuse 37:441-452

Martin-Benito D, Kint V, del Río M, Muys B, Cañellas I (2011) Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: Past trends and future perspectives. For Ecol Manag 262:1030-1040

Muir G, Fleming CC, Schlötterer C (2000) Species status of hybridizing oaks. Nature 405:1016

Nothdurft A, Kublin E, Lappi J (2006) A non-linear hierarchical mixed model to describe tree height growth. Eur J For Res 125:281-289

Parker GR, Leopold DJ (1983) Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bull Torrey Bot Club 110:482-488

Piedallu C, Gégout J-C, Bruand A, Seynave I (2011) Mapping soil water holding capacity over large areas to predict potential production of forest stands. Geoderma 160:355-366

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: linear and nonlinear mixed effects models. R package version 3.1-104.

Pinheiro JC, Bates DM (2000) Mixed-Effects Models in S and S-PLUS. Springer, New York

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, http://www.R-project.org

Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol Conserv 95:85-94

Richards FJ (1959) A flexible growth function for empirical use. J Exp Bot 10:290-300

Rohner B, Bigler C, Wunder J, Brang P, Bugmann H (2012) Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. J Veg Sci 23:892-905

Rozas V (2003) Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecol 167:193-212

Rozas V (2005) Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: establishment patterns and the management history. Ann For Sci 62:13-22

Russell MB, Weiskittel AR, Kershaw JA Jr (2011) Assessing model performance in forecasting long-term individual tree diameter versus basal area increment for the primary Acadian tree species. Can J For Res 41:2267-2275

Subedi N, Sharma M (2011) Individual-tree diameter growth models for black spruce and jack pine plantations in northern Ontario. For Ecol Manag 261:2140-2148

Tesch SD (1981) The evolution of forest yield determination and site classification. For Ecol Manag 3:169-182

Thornthwaite CW (1948) An approach toward a rational classification of climate. Geogr Rev 38:55-94

Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. J Hydrol 190:214-251

von Bertalanffy L (1957) Quantitative laws in metabolism and growth. Q Rev Biol 32:217-231

Weber P, Bugmann H, Rigling A (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. J Veg Sci 18:777-792

Weber P, Bugmann H, Fonti P, Rigling A (2008) Using a retrospective dynamic competition index to reconstruct forest succession. For Ecol and Manag 254:96-106

Weiskittel AR, Hann DW, John A. Kershaw J, Vanclay JK (2011) Forest Growth and Yield Modeling. Wiley-Blackwell, Chichester

Willmott CJ, Rowe CM, Mintz Y (1985) Climatology of the terrestrial seasonal water cycle. J Climatol 5:589-606

Zeide B (1993) Analysis of growth equations. For Sci 39:594-616

Supporting information

Online Resource 1

Table S1. Complete list of considered models. The parameters a and b are from the Chapman-Richards growth equation with an expected value parameterization for the asymptote (Eq. 2, Fang and Bailey 2001; Hall and Clutter 2004; Richards 1959). Models with an Akaike weight > 0.01% are shaded in grey. Topography includes elevation, aspect and the north-south indicator. 'Interaction' indicates the interaction between the water holding capacity and the drought index.

Model number	Parameter a				Parameter b				Akaike weight (%)
	Topography	Water holding capacity	Drought index	Interaction	Topography	Water holding capacity	Drought index	Interaction	
1									0
2	×								0
3		×							0
4			×						0
5	×	×							0
6	×		×						0
7		×	×						0
8	×	×	×						0
9		×	×	×					0
10	×	×	×	×					0
11					×				0
12						×			0
13							×		0
14					×	×			0
15					×		×		0
16						×	×		0
17					×	×	×		0
18						×	×	×	0
19					×	×	×	×	0
20	×				×				0
21		×			×				0
22			×		×				0
23	×	×			×				0
24	×		×		×				0
25		×	×		×				0
26	×	×	×		×				0
27		×	×	×	×				0
28	×	×	×	×	×				0
29	×					×			0
30		×				×			0
31			×			×			0
32	×	×				×			0
33	×		×			×			0
34		×	×			×			0

Table S1. Continued.

35	×	×	×			×		0
36		×	×	×		×		0
37	×	×	×	×		×		0
38	×						×	0
39		×					×	0
40			×				×	0
41	×	×					×	0
42	×		×				×	0
43		×	×				×	0
44	×	×	×				×	0
45		×	×	×			×	0
46	×	×	×	×			×	0
47	×				×	×		0
48		×			×	×		0
49			×		×	×		0
50	×	×			×	×		0.03
51	×		×		×	×		0
52		×	×		×	×		0
53	×	×	×		×	×		0.59
54		×	×	×	×	×		0
55	×	×	×	×	×	×		0.6
56	×				×		×	0
57		×			×		×	0
58			×		×		×	0
59	×	×			×		×	0
60	×		×		×		×	0
61		×	×		×		×	0
62	×	×	×		×		×	0
63		×	×	×	×		×	0
64	×	×	×	×	×		×	0
65	×					×	×	0
66		×				×	×	0
67			×			×	×	0
68	×	×				×	×	0
69	×		×			×	×	0
70		×	×			×	×	0
71	×	×	×			×	×	0
72		×	×	×		×	×	0
73	×	×	×	×		×	×	0
74	×				×	×	×	0
75		×			×	×	×	0
76			×		×	×	×	0
77	×	×			×	×	×	4.06
78	×		×		×	×	×	0
79		×	×		×	×	×	0
80	×	×	×		×	×	×	1.23
81		×	×	×	×	×	×	0

Table S1. Continued.

82	×	×	×	×	×	×	×		1.43
83	×					×	×	×	0
84		×				×	×	×	0
85			×			×	×	×	0
86	×	×				×	×	×	0
87	×		×			×	×	×	0
88		×	×			×	×	×	0
89	×	×	×			×	×	×	0
90		×	×	×		×	×	×	0
91	×	×	×	×		×	×	×	0
92	×				×	×	×	×	0
93		×			×	×	×	×	0
94			×		×	×	×	×	0
95	×	×			×	×	×	×	62.2
96	×		×		×	×	×	×	0
97		×	×		×	×	×	×	0
98	×	×	×		×	×	×	×	22.27
99		×	×	×	×	×	×	×	0
100	×	×	×	×	×	×	×	×	7.6

References

Fang Z, Bailey RL (2001) Nonlinear mixed effects modeling for slash pine dominant height growth following intensive silvicultural treatments. For Sci 47:287-300

Hall DB, Clutter M (2004) Multivariate multilevel nonlinear mixed effects models for timber yield predictions. Biometrics 60:16-24

Richards FJ (1959) A flexible growth function for empirical use. J Exp Bot 10:290-300

Online Resource 2

Table S2. Mean and standard deviation (SD) used for scaling and centring the covariates. No additional scaling and centring was done for the north-south indicator since it ranges between -1 and 1.

	Elevation (m a.s.l.)	Slope (°)	Water holding capacity	Drought index
Mean	500	11.7	4.2	21.7
SD	70	10.5	1.2	73.9

Online Resource 3

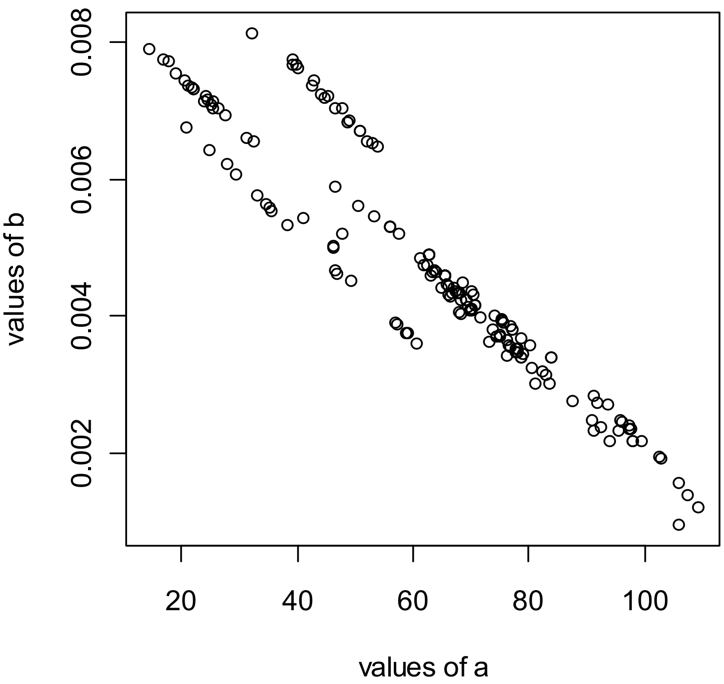


Figure S1. Correlation between the parameters a and b. The Pearson correlation coefficient is -0.94.

Online Resource 4

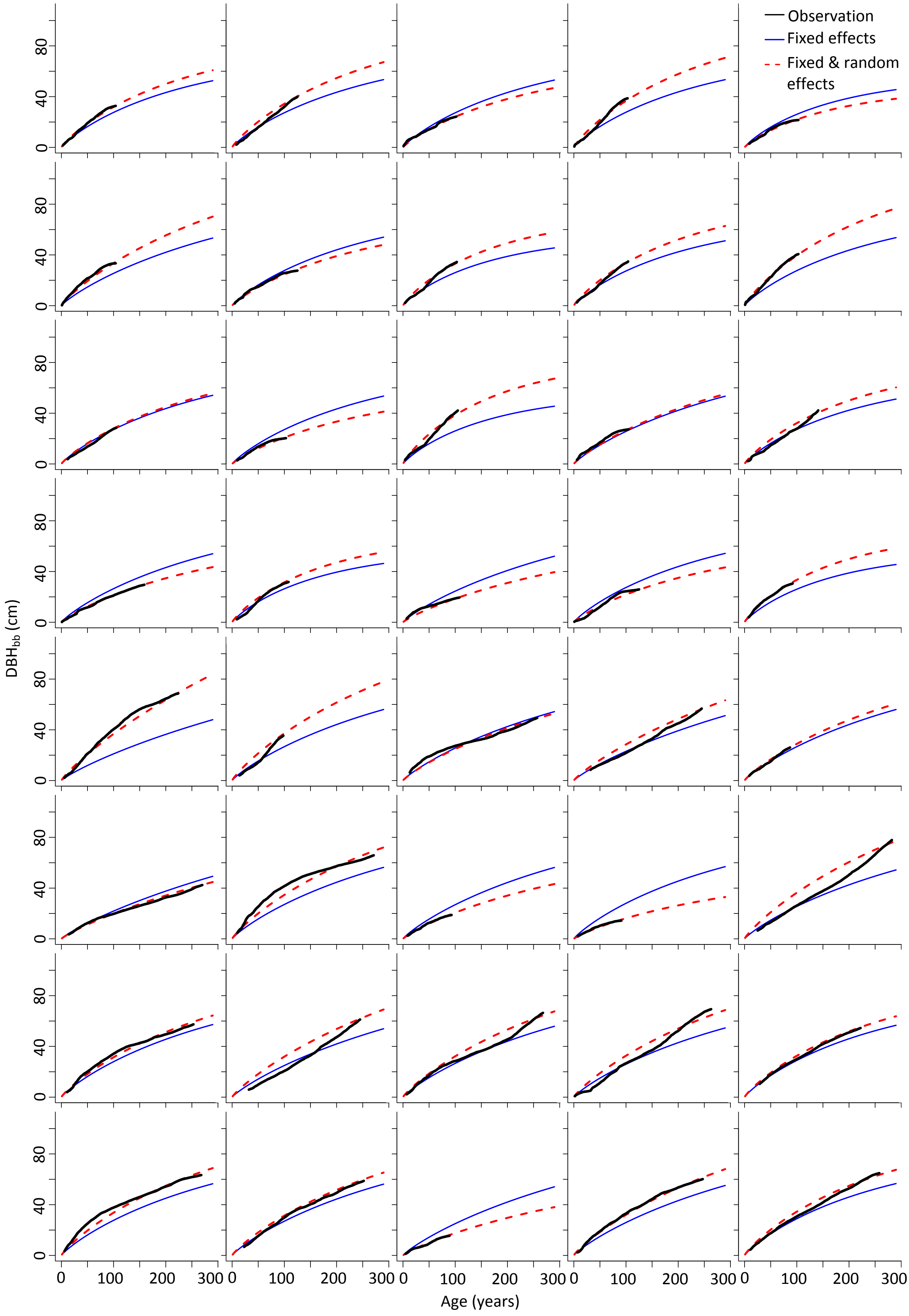


Figure S2. Predictions based on the averaged model for all trees used in the model fitting procedure. DBH$_{bb}$ denotes the diameter beneath the bark at 1.2 m above ground.

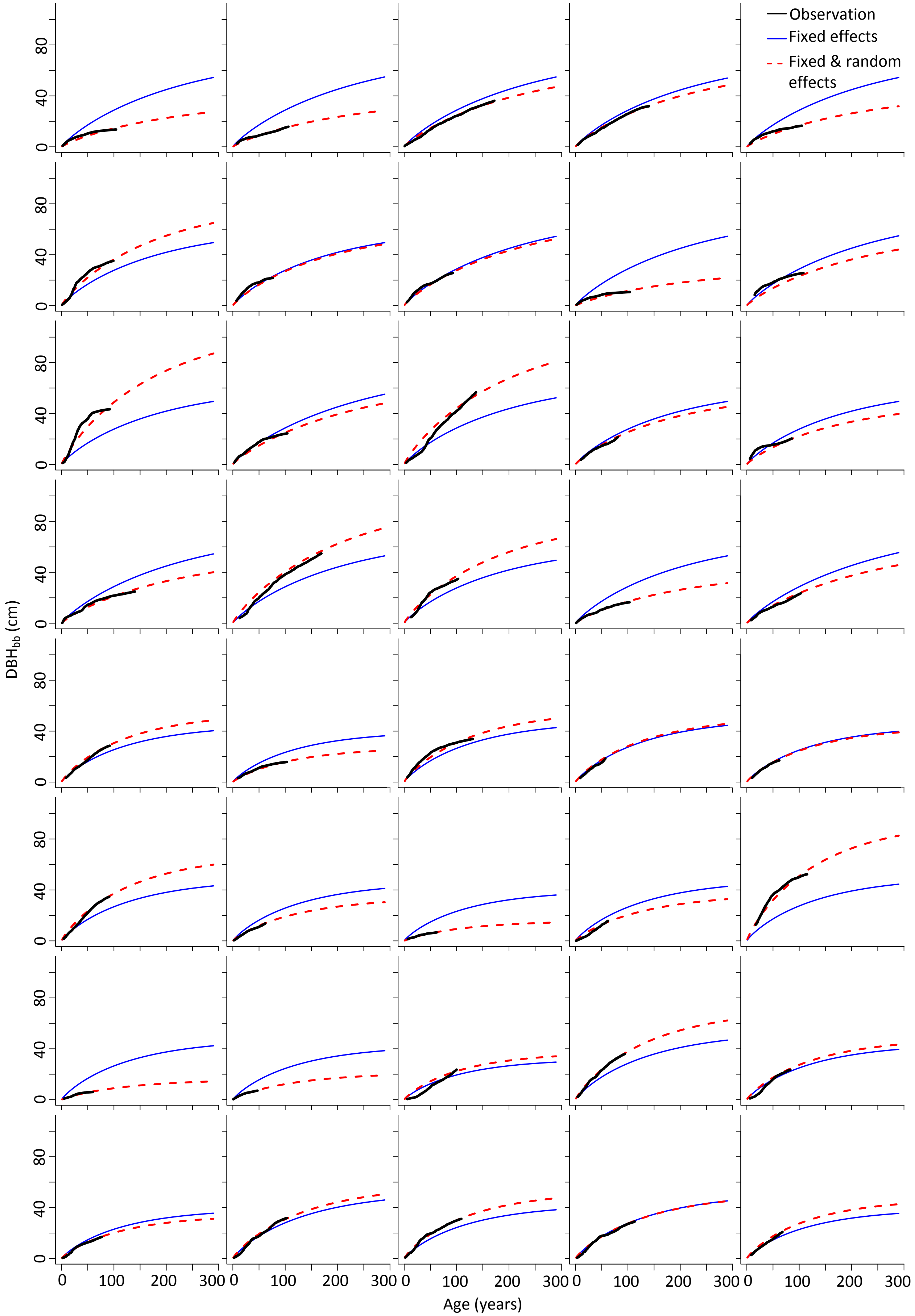
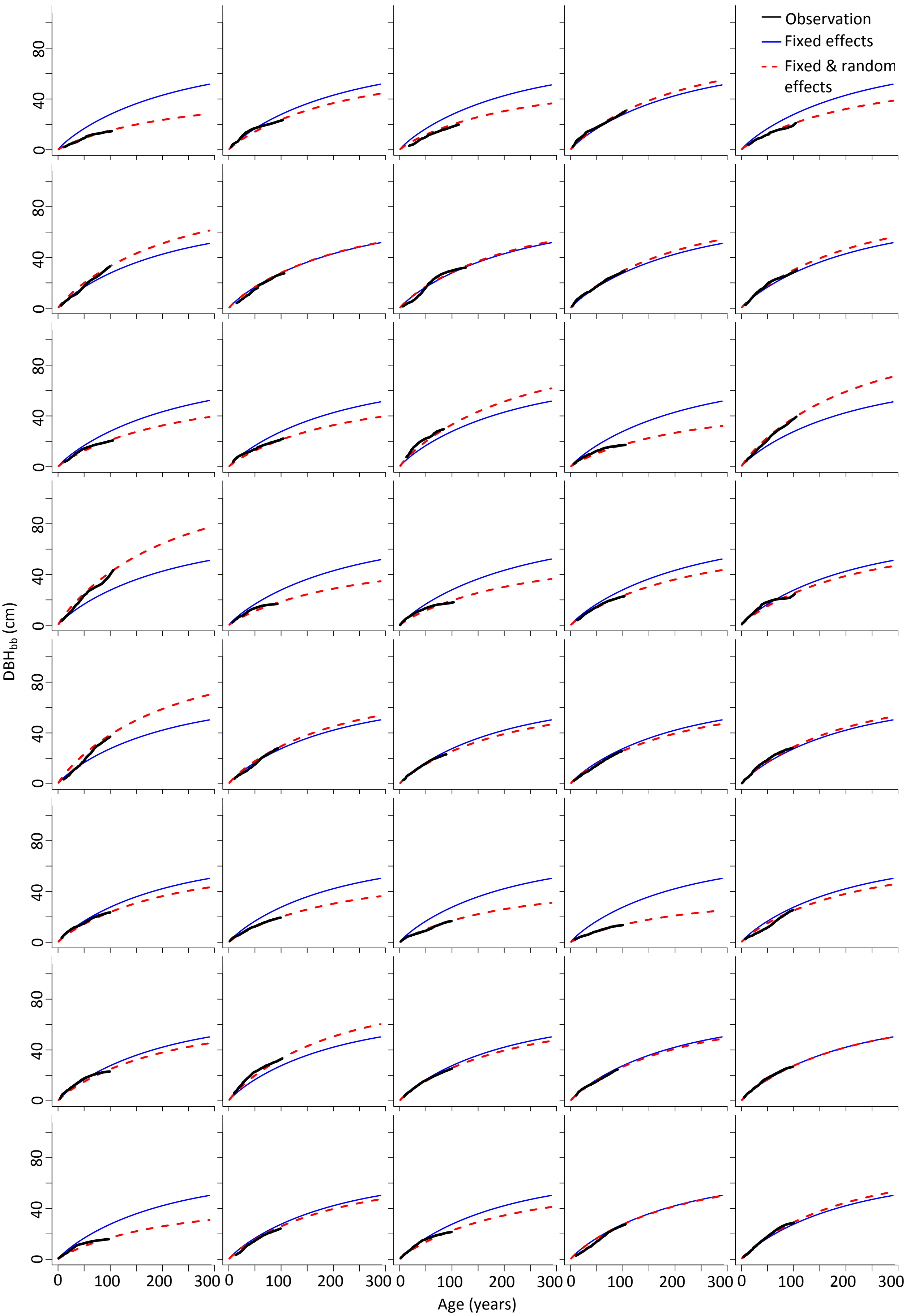


Figure S2. Continued.



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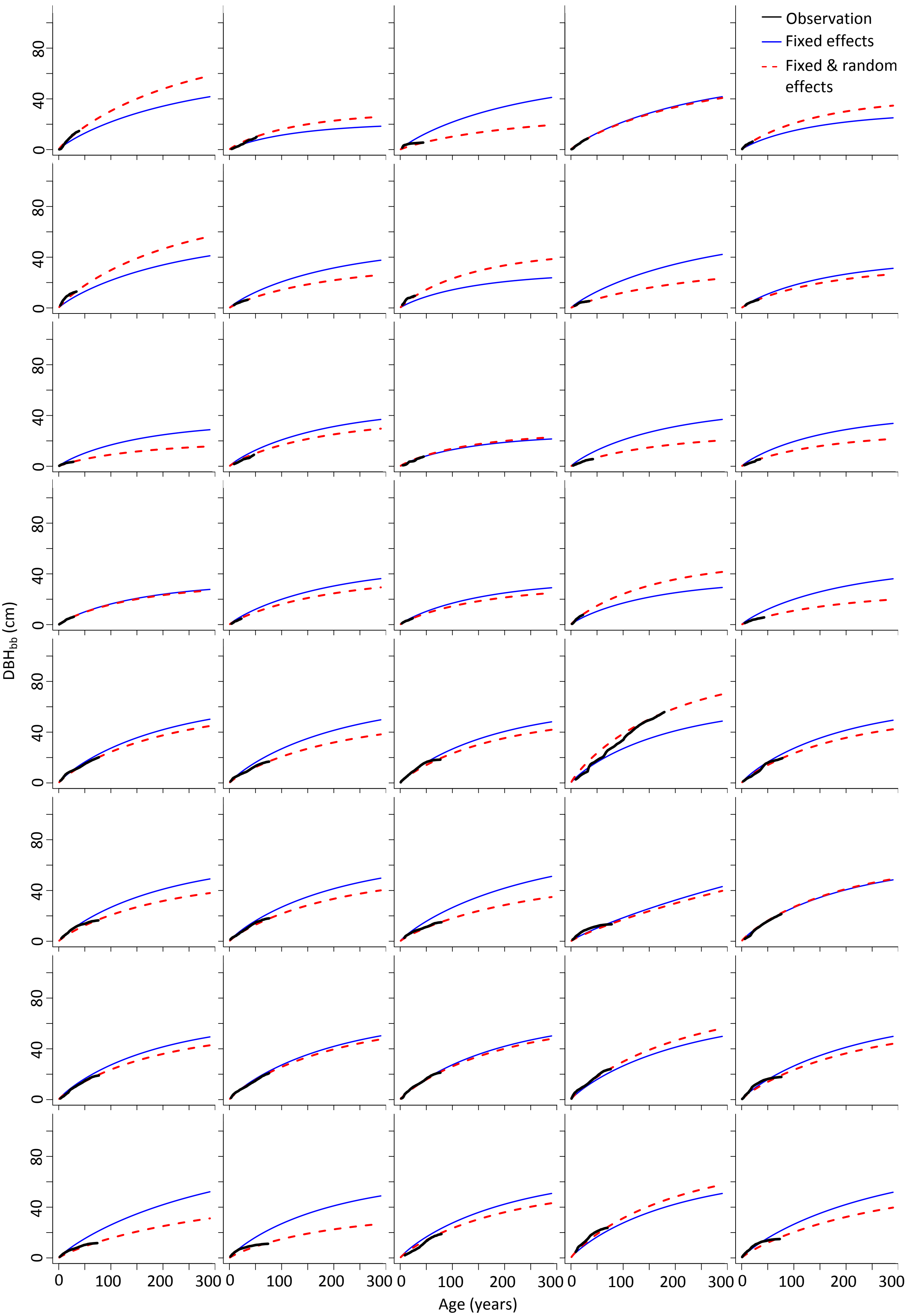

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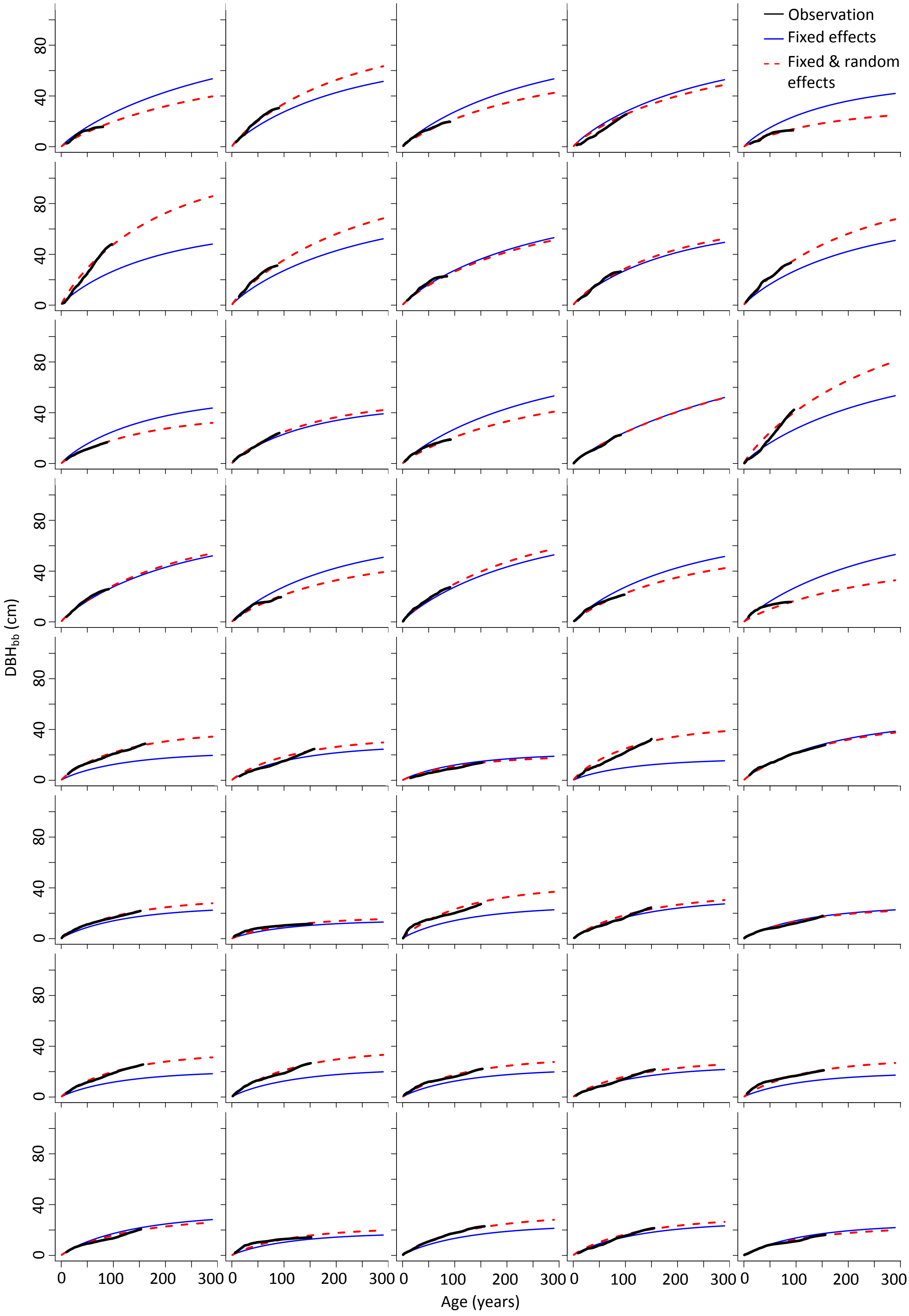

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Online Resource 5

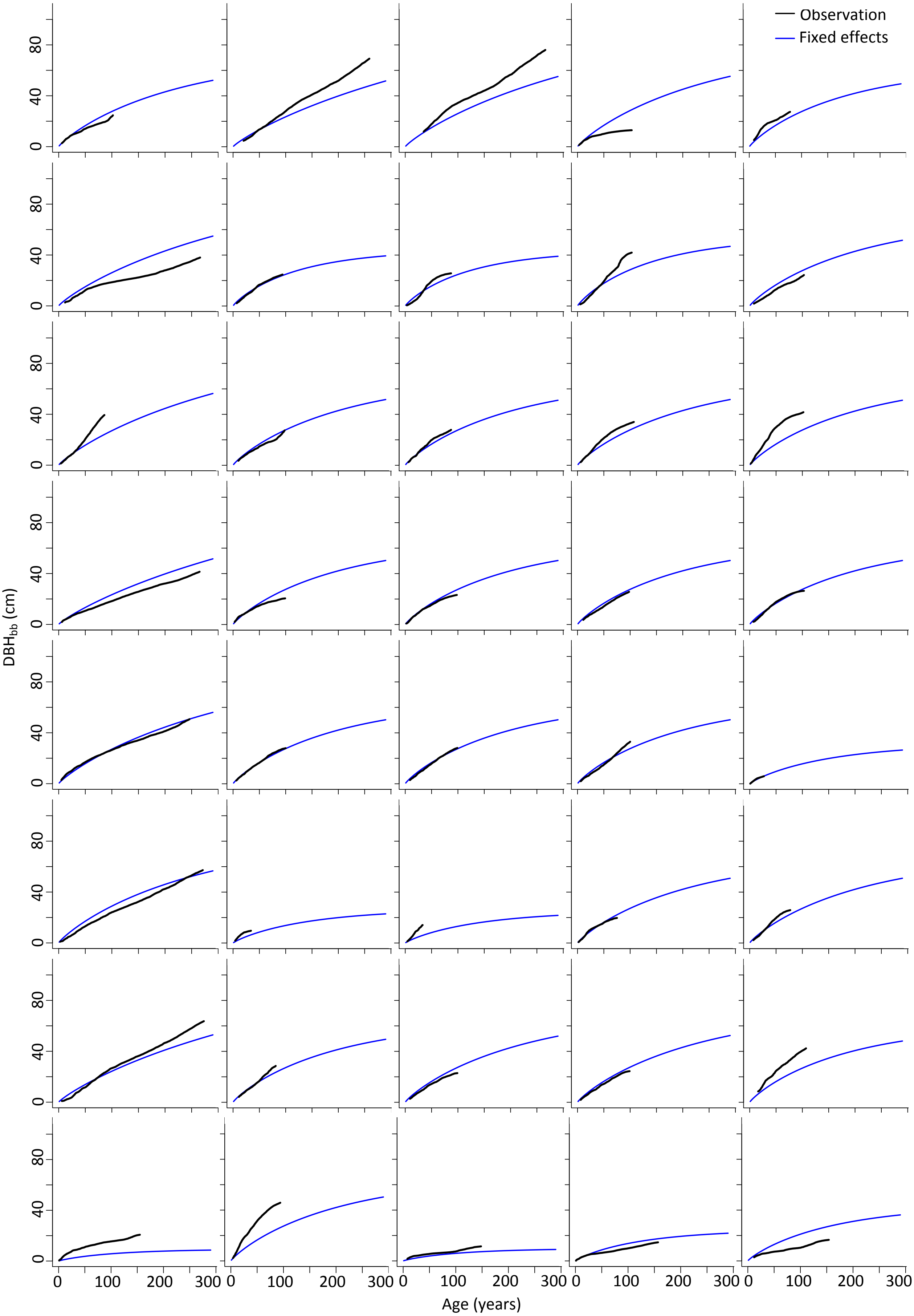


Figure S3. Predictions based on the averaged model for all control trees. DBH$_{bb}$ denotes the diameter beneath the bark at 1.2 m above ground.

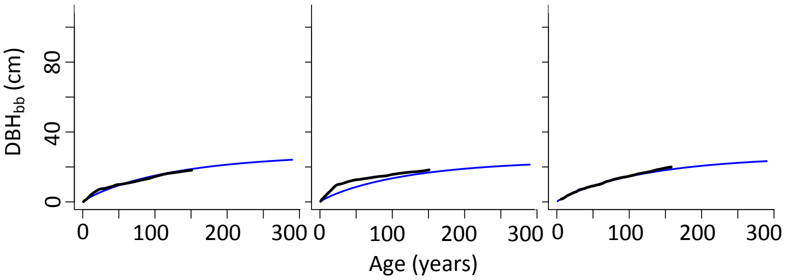


Figure S3. Continued.

Online Resource 6

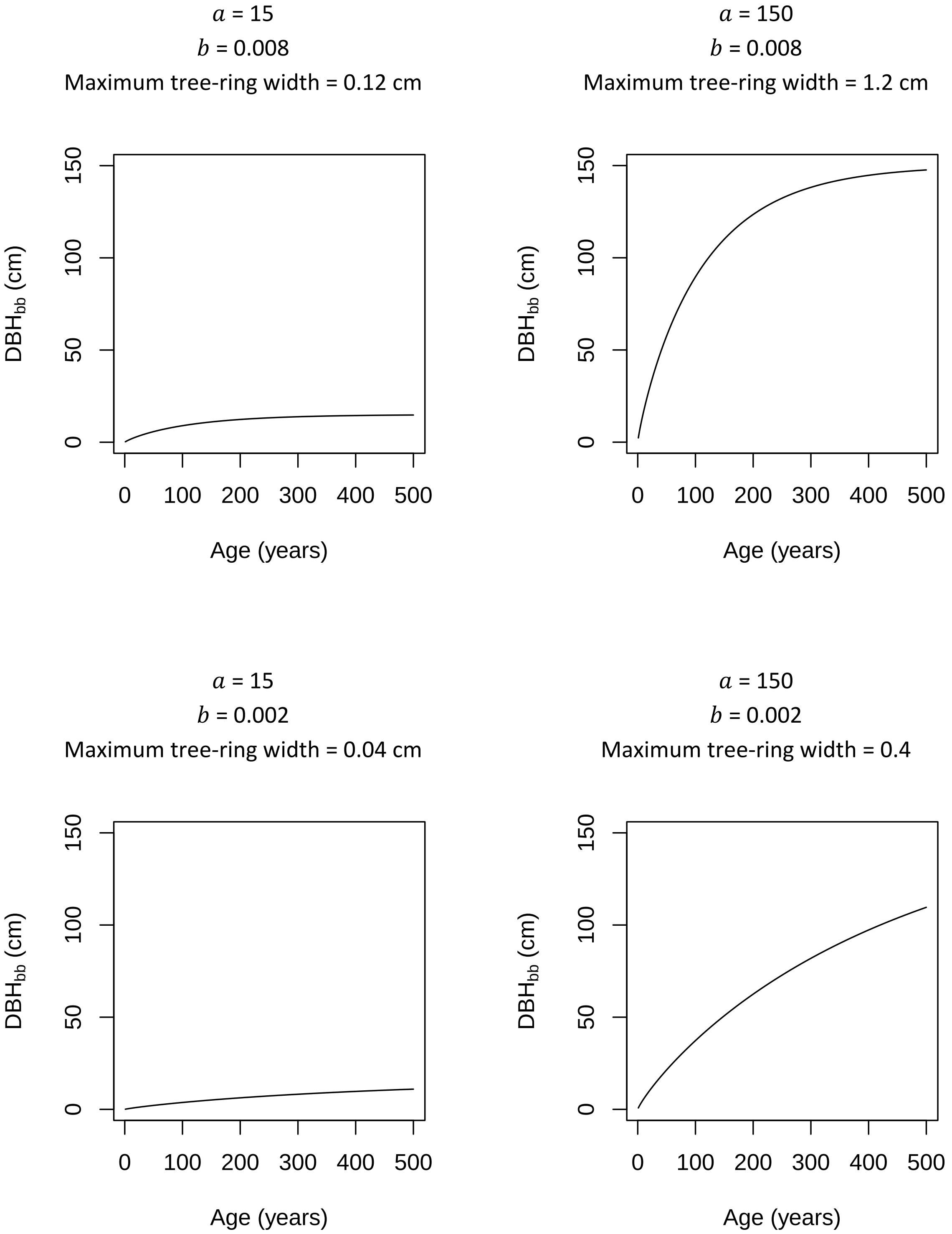


Figure S4. Visualization of varying combinations of the parameters a and b in the Chapman-Richards growth equation with an expected value parameterization for the asymptote (Eq. 2). In all visualizations, the parameter c was set to 0.863 as estimated in the averaged model (Table 3).

Chapter IV

Towards non-destructive estimation of tree age

Brigitte Rohner, Harald Bugmann, Christof Bigler

Methods in Ecology and Evolution (submitted)

Abstract

1. Accurate tree age information is required in many contexts ranging from nature conservation to forest science and management. Currently available methods for tree age estimation are either destructive or often inaccurate, the latter mostly because they do not tap the full potential of available data and knowledge on tree growth.

2. We compared two new approaches for tree age estimation based on nonlinear age-diameter relationships to a traditional polynomial approach. The nonlinear approaches were based on repeated diameter measurements. One of them included environmental covariates (slope, elevation, aspect, water holding capacity and a drought index) based on the fixed effects of a mixed-effects model. The accuracy of the approaches was evaluated for 243 oaks growing along an environmental gradient in Switzerland that comprised ages from 23 to 284 years. The potential of the nonlinear approach with covariates was assessed by additionally including the random effects of the mixed-effects model.

3. The nonlinear approach with covariates and the polynomial approach were of similar accuracy except for extreme sites, where the polynomial approach performed better. The nonlinear approach without covariates was least accurate. Additionally including the random effects in the nonlinear approach with covariates strongly improved the age estimations and reduced the relative errors below 40% for 98% of the trees.

4. Including repeated diameter measurements and environmental covariates led to similarly accurate age estimations as the traditional polynomial approach. However, the accuracy of the nonlinear approach with covariates has a high potential for further improvements. Additionally, the nonlinearity and the site information that is explicitly included allow for applications beyond the calibrated sites and ages. This transferability and the potential for extrapolation obviate the need for calibration in further applications, making it entirely non-destructive, which is a large advantage over the polynomial approach, which requires new fitting for new sites. Thus, the nonlinear approach with covariates is highly suitable e.g. in protected forests, where destructive age determination is not allowed.

Keywords: Age-diameter relationship; Age estimation; Chapman-Richards growth equation; dendrochronology; forest reserve; nonlinear mixed-effects model; *Quercus* spp.

Introduction

Knowledge of tree age distributions is important for several scientific and practical reasons. Tree age information is needed in many forest growth models as well as for projections of expected timber yield and carbon sequestration in forests (Hall & Clutter 2004; Thürig et al. 2005). Nature conservation relies on tree age information, e.g. because subsidies for the non-utilization of protected trees are often determined based on the age of the protected trees. Additionally, tree age is an indicator for a tree's ecological value, since structural diversity and the associated biodiversity generally increase with tree age (Michel & Winter 2009).

A range of methods have been developed to determine tree age. Identifying the number of annual growth rings proved to be an accurate method for trees in the temperate zone (Villalba & Veblen 1997; Wong & Lertzman 2001; Rozas 2003). However, such dendrochronological methods are invasive if based on increment cores and even destructive if based on stem cross sections. Therefore, dendrochronological age determination is not applicable in many cases, for example in the context of quality timber production or nature conservation. Non-invasive methods based on satellite data have evolved during the last decade, but have usually concentrated on stand rather than tree age (e.g. Sivanpillai et al. 2006). Alternative attempts have focussed on the relationship between tree diameter and tree age, which has usually been modelled empirically based on polynomials (Abrams 1985; Loewenstein, Johnson & Garrett 2000; Rozas 2003; Trotsiuk, Hobi & Commarmot 2012) although there is no biological motivation for using polynomials. In fact, these models, which are linear in their coefficients, are invalid outside the range of ages and diameters used for calibration (Pinheiro & Bates 2000; Rozas 2003). Furthermore, the age-diameter relationship is mostly tainted with high variability (Tyrrell & Crow 1994; Loewenstein, Johnson & Garrett 2000; Piovesan et al. 2005; Nagel, Levanic & Diaci 2007).

Various site and stand characteristics have been shown to influence tree growth and, consequently, the relationship between the diameter and age of trees. Regarding site characteristics, topographic attributes such as elevation, slope and aspect as well as soil properties such as water holding capacity are usually considered as key variables influencing tree growth (Parker 1982; Oberhuber & Kofler 2000; Rohner, Bugmann & Bigler 2012). Furthermore, tree growth responds sensitively to climatic conditions, i.e. temperature, precipitation or drought (Fritts 1976). Concerning stand characteristics, competition is thought to be the main growth-limiting feature (cf. Biging & Dobbertin 1995).

Although environmental variables have been shown to strongly influence tree growth, they have rarely been considered for tree age estimation (cf. Abrams 1985; Suarez et al. 2008). In fact, empirical age-diameter relations (e.g. polynomials) have often been calibrated for individual sites with rather homogeneous environmental conditions (e.g. Veblen 1986; Loewenstein, Johnson & Garrett 2000; Rozas 2003). Although being highly accurate for a specific site, such models are usually of limited generality and cannot be easily transferred to other conditions. Thus, including site characteristics in addition to diameter for the estimation of tree age should increase both its accuracy and generality.

Further potential to improve tree age estimation arises from repeated diameter measurements. In comparison to single diameter measurements, they provide additional, biologically relevant information in terms of the temporal development of diameter. The growth change within a sequence of repeated diameter measurements in combination with absolute diameter data might be used to infer the position of the sequence along a calibrated age-diameter curve. However, we are not aware of studies that have used this information to estimate tree age. Repeated diameter measurements are available for many forests all over the world, e.g. from national forest inventories or from monitoring in forest reserves (e.g. Brändli 2010; Brang, Heiri & Bugmann 2011). Such data sets often cover broad spatial and temporal ranges, and it would be desirable to use them to improve tree age estimations.

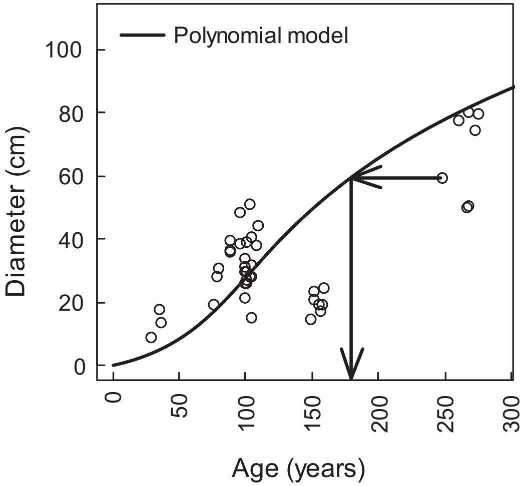
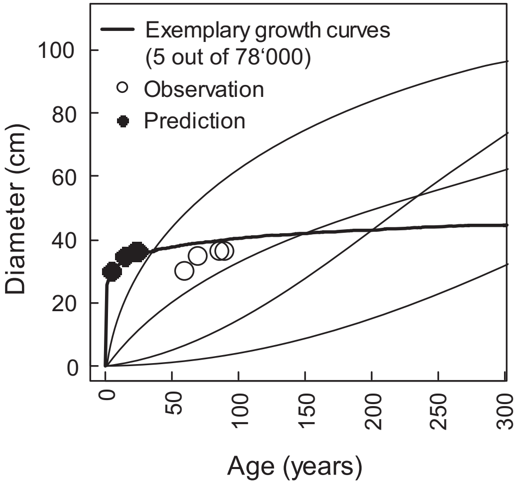
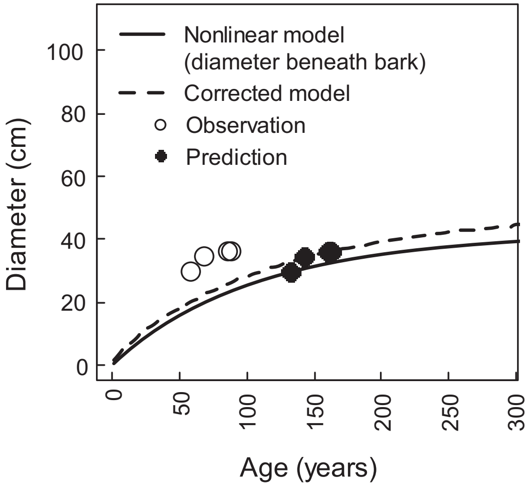
We compare a traditional polynomial approach with two new approaches for tree age estimation based on tree-specific nonlinear age-diameter relationships, which include repeated diameter measurements. The two nonlinear approaches differ insofar as one of them considers environmental influences on tree growth as covariates (Table 1). We focus on oak species in Switzerland because of their high conservation value and role in current Payment for Ecosystem Services (PES) schemes (Bolliger, Schnidrig & Stadler 2008). Our study aims at (1) comparing the accuracy of the age estimations arising from the three approaches for oaks in forest reserves along a large environmental gradient in Switzerland, and (2) quantifying the potential that lies in the nonlinear approach with covariates if knowledge about growth-influencing processes was increased. Based on up-to-date statistical methods, our study provides entirely new prospects for the long-standing need of accurate tree age estimation.

Methods

Study sites and tree species

All study sites belong to the Swiss forest reserve network, a joint project of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), ETH Zurich and the Swiss Federal Office for the Environment (for details see Brang, Heiri & Bugmann 2011; Rohner et al. 2012; Rohner, Bugmann & Bigler 2012). Hence, all forests considered in this study have not been managed for decades. We considered the same 10 study sites as in Rohner, Bugmann and Bigler (2012). All of the forests contain > 10% oak (calculated as the importance value = [relative density + relative basal area] / 2 x 100; Parker & Leopold 1983), whereas the composition of the further tree species differs strongly, ranging from *Pinus sylvestris*-dominated sites in the dry, inner-Alpine southwest of Switzerland to *Fagus sylvatica*-dominated sites under mesic conditions in northern Switzerland. Thus, the sites cover a wide variety of

Table 1. Overview of the approaches.

Approach	Polynomial	Nonlinear without covariates	Nonlinear with covariates
Repeated diameter measurements	No	Yes	Yes
Environmental influences on growth	No	No	Yes
Tree ring data needed for calibration	Yes	No	Yes
Visualization			

environmental conditions regarding topography, soil properties and climate (see Rohner, Bugmann & Bigler 2012) and represent a broad range of oak habitats in Central Europe.

The most frequent oak species in Switzerland is *Quercus robur* with 61%, followed by *Quercus petraea* with 24% and *Quercus pubescens* with 15% (based on stem numbers; Brändli 2010). *Q. petraea* and *Q. robur* overlap in many physiological and morphological attributes (Aas 1998). In addition, hybridization is frequent among the three species, leading to various intermediate forms (Kissling 1980; Aas 1998). Because a reliable distinction in the field is not feasible, we conducted the age estimation for the three oak species collectively.

Data collection and processing

Every forest reserve comprises permanent plots in which all trees are tagged individually. At regular intervals of 8-10 years, the diameter of all living tagged trees is recorded (cf. Brang, Heiri & Bugmann 2011). We considered the same sample of trees (total of 303 oaks) as in Rohner, Bugmann and Bigler (2012), where 30 – 31 tagged oaks per reserve had been selected according to the diameter distribution observed in the last inventory campaign. For every selected oak tree, a sequence of at least three diameter measurements was available from the inventory campaigns. One additional diameter measurement was collected during our field work.

The field work was conducted in summer 2009 and 2010 (for details see Rohner, Bugmann & Bigler 2012). To determine the age of the selected oaks, one increment core per tree was taken parallel to the contour line at 1.2 m above ground. The core samples were cut with a core microtome (Gärtner & Nievergelt 2010). Tree-ring widths were measured with a Lintab 5 measuring system using the software TSAP-Win (RINNTECH, Heidelberg, Germany) and cross-dated visually and quantitatively with the software COFECHA (Holmes 1983). For cores that missed the pith, the missed distance and the missed number of rings were determined according to the graphical method by Rozas (2003). The age at 1.2 m height of the individual oaks was approximated as the sum of the tree rings on the core and the estimated number of missed rings to the pith.

Subsamples for calibration and validation

After excluding some trees due to methodological difficulties, Rohner, Bugmann and Bigler (2012) eventually used 243 trees for estimating a nonlinear model that forms the basis of the nonlinear approach with covariates. In the development of their model, Rohner, Bugmann and Bigler (2012) divided the trees into a calibration subsample of 200 randomly selected trees (20 trees per reserve) and a validation subsample comprising the remaining 43 trees. In the present study, we used the same sample of calibration trees to achieve comparability among the approaches. Consequently, all age estimations were evaluated based on the same sample of validation trees. However, five calibration trees and one validation tree considered in Rohner, Bugmann and Bigler (2012) could not be used for the present study because these trees could not be assigned unequivocally to trees in the inventory data base. Thus, in the present study, we used 195 trees for calibration and 42 trees for validation purposes.

Polynomial approach

According to previous studies on tree age estimation (Loewenstein, Johnson & Garrett 2000; Rozas 2003; Trotsiuk, Hobi & Commarmot 2012), we considered first- to third-order polynomials for describing the relationship between diameter and age (Table 2). We did not include intercepts in the polynomials. All polynomials were fitted to the ages and diameters of the calibration trees in the year of the coring (2009/2010). For model selection, we compared both the adjusted R^2 and the Akaike weights w_i of the respective polynomials, which indicate the relative probability of the individual models to be best suited to describe the data at hand (Burnham & Anderson 2002); they are defined as

$$w_i = \left(e^{-\frac{1}{2}\Delta_i}\right) / \left(\sum_{i=1}^{n} e^{-\frac{1}{2}\Delta_i}\right) \qquad \text{(eqn 1)}$$

with Δ_i denoting the difference in AIC (Akaike Information Criterion) between model i and the model with the lowest AIC among all n considered models (Burnham & Anderson 2002). The polynomial with the highest adjusted R^2 and the highest w_i was used for estimating the age of the validation trees.

Table 2. Considered polynomials for modelling the relationship between diameter at breast height (DBH, in cm) and age.

Model number	Model structure	Akaike weight (%)*	Adjusted R^2
1	Age ~ DBH	0	0.92
2	Age ~ DBH + DBH^2	0	0.92
3	Age ~ DBH^2	0	0.71
4	Age ~ DBH + DBH^2 + DBH^3	0	0.93
5	Age ~ DBH + DBH^3	0	0.92
6	Age ~ DBH^2 + DBH^3	0	0.85
7	Age ~ DBH^3	0	0.46
8†	Age ~ DBH + DBH$^{1.5}$ + DBH^2	100	0.94

* Akaike weights indicate the relative probability of the individual polynomials for being best suited to describe the data at hand (see Equation 1, Burnham & Anderson 2002).

† Model structure according to Loewenstein, Johnson and Garrett (2000).

Nonlinear approach without covariates

The nonlinear approach without covariates was based on a modified Chapman-Richards growth function (Richards 1959; Fang & Bailey 2001; Hall & Clutter 2004), which is defined as

$$Diameter = a \times \left((1 - e^{-b \times age})/(1 - e^{-b \times x_0})\right)^c. \qquad \text{(eqn 2)}$$

In this function, parameter a represents the estimated diameter at age x_0, parameter b defines how fast the asymptotic diameter is approached, and parameter c defines the inflection point of the curve (Richards 1959). We set x_0 to 1200 years according to the maximum age reported for *Q. robur* (Godet 1986). By systematically varying the three parameters, a set of 78 000 growth curves was defined: parameter a was varied between 10 and 200 in steps of 5, parameter b between 0.0002 and 0.01 in steps of 0.0002, and parameter c between 0.1 and 4 in steps of 0.1. These ranges were motivated by the results of Rohner, Bugmann and Bigler (2012).

The age of the validation trees was estimated by individually determining the optimum position of their diameter sequences along the simulated 78 000 growth curves, which was identified by systematically fitting the diameter sequences to all positions along all growth curves and comparing the mean absolute error (MAE) of the fits. The fit with the lowest MAE was selected and the corresponding age was recorded as the age estimate for that particular tree (Table 1); the reason for using the MAE as the quality criterion is explained below. All age estimations were restricted to a maximum of 1000 years.

Nonlinear approach with covariates

The nonlinear approach with covariates was built on the model by Rohner, Bugmann and Bigler (2012), which is also based on the modified Chapman-Richards growth equation (Equation 2). However, in this model the parameters a and b were estimated separately for every tree as a function of the covariates slope, elevation, aspect, soil water holding capacity and a drought index. These covariates were used to reflect growth-influencing characteristics regarding topography, soil and climate. The model was fitted to data derived from the same core samples that were used for the age determination here, with diameters being approximated as diameter = 2 × (cumulative sum of tree-ring widths + estimated missed distance to the pith).

Slope, elevation and aspect were recorded for each tree during the field work; water holding capacity was estimated for individual study sites from the Swiss soil suitability map (Bundesamt für Raumplanung (EJPD), Bundesamt für Landwirtschaft (EVD) & Bundesamt für Forstwesen (EDI) 1980); and the drought index was calculated as precipitation minus potential evapotranspiration during summer (for details see Rohner, Bugmann & Bigler 2012). The model was designed as a mixed-effects model, i.e. fixed effects for the covariates and a random intercept per tree were estimated for the calibration trees. Random effects could be estimated for the calibration trees only; thus, the basis for the age estimation were the age-diameter curves predicted separately for every validation tree based on its environmental conditions, using the fixed effects of the model developed by Rohner, Bugmann and Bigler (2012; Table 1).

Before fitting the diameter sequences from the inventory campaigns, three corrections were made to achieve comparability with the diameters predicted by the model:

1) The model predicts diameters beneath the bark, whereas the diameters were measured with a calliper outside the bark during the inventories. We measured bark thickness when extracting the cores and applied a linear regression with the diameter measured at coring height as explanatory variable. Since diameter measurements with the calliper include the bark twice, the following correction resulted:
$\text{Diameter}_{\text{Correction\_1}} = \text{Diameter}_{\text{Model}} + 2 \times (0.3764 + 0.0120 \times \text{Diameter}_{\text{Model}})$.
2) The cores were taken 1.2 m above ground, whereas the diameter was measured 1.3 m above ground during the inventories. To overcome this discrepancy, we measured the diameters at both heights during field work and applied a linear regression, resulting in the following correction: $\text{Diameter}_{\text{Correction\_2}} = -0.2484 + 0.9957 \times \text{Diameter}_{\text{Correction\_1}}$.
3) Although eccentric growth is known to be frequent for oak (Rozas 2003), the model implies completely concentric growth since the tree rings are measured perpendicular to the boundaries and the diameters are approximated with the cumulative sum of the ring widths. Therefore, we modelled the difference between the bark- and height-corrected diameters derived from the tree rings and the measured diameters from the inventories with a linear regression, which resulted in the following correction:
$\text{Diameter}_{\text{Correction\_3}} = 0.5979 + 1.0765 \times \text{Diameter}_{\text{Correction\_2}}$.

All three steps were determined based on the calibration sample. They were finally combined to the aggregated correction formula $\text{Diameter}_{\text{Corrected}} = 1.1374 + 1.0976 \times \text{Diameter}_{\text{Model}}$, which was applied to modify all diameter predictions from the nonlinear model with covariates before using them for the age estimation.

For the age estimation of the validation trees, we fitted their diameter sequences to the corrected individual age-diameter curves predicted from the model. Similar to the previous approach, we restricted the growth curves to a maximum age of 1000 years. The best-fitting position of the diameter sequence along the corresponding growth curve was again identified by minimizing the MAE (Table 1). Several other quality criteria were initially considered (root mean square error, root mean square relative error, mean relative error), but the MAE resulted in the most accurate age estimations for the calibration sample. To achieve comparability, we used the MAE for both nonlinear approaches.

Comparison of the approaches

The accuracy of the age estimations derived from the three approaches (polynomial approach, nonlinear approach without covariates, nonlinear approach with covariates) was compared based on both absolute and relative errors between predicted and observed ages. The relative errors were defined as (observed age – predicted age) / observed age, with age in the year of coring used for the error calculation.

Potential of the nonlinear approach with covariates

The fixed effects in the nonlinear model represent known environmental influences on the age-diameter relationship (Rohner, Bugmann & Bigler 2012), whereas the random effects represent variability in the age-diameter relationship that cannot be explained by the considered covariates. It can be assumed that further research and additional data will provide improved knowledge regarding the determinants of the age-diameter relationship (e.g. when including competition). Thus, the proportion of explained variability in such models should increase in the future. Accordingly, more variability may be covered by fixed effects, entailing more accurate age estimations when using the nonlinear approach with covariates. To identify the maximum potential of this approach, we based the age estimations additionally on the fixed and the random effects of the nonlinear model with covariates, which reflects the assumption that all unexplained variability currently covered by the random effects may once be explained by the fixed effects. However, since random effects are only available for the calibration sample, this analysis could not be based on the validation sample. Instead, we estimated the ages of the calibration trees in this analysis, which is why the results are not directly comparable to the results from the three approaches above. The same procedure was followed for fitting the diameter sequences to the model predictions from the fixed and the random effects as described above for the fixed effects only.

All analyses were conducted in R, a language and environment for statistical computing and graphics (R Development Core Team 2010). For the development of the nonlinear model with covariates, the packages *nlstools* (Baty & Delignette-Muller 2011) and *nlme* (Pinheiro et al. 2011) were used. The *plotrix* package (Lemon 2006) was used for some visualizations.

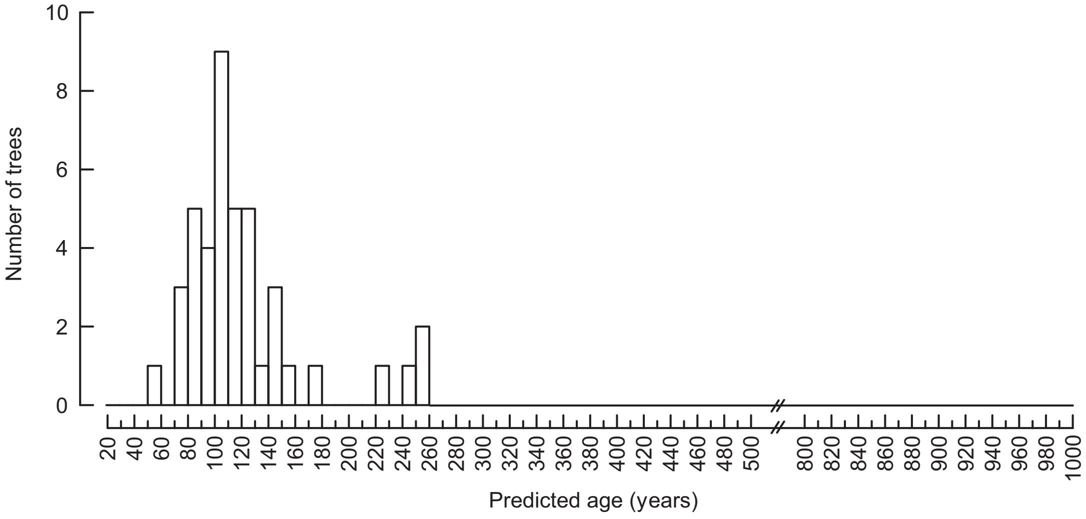
Results

Polynomial approach

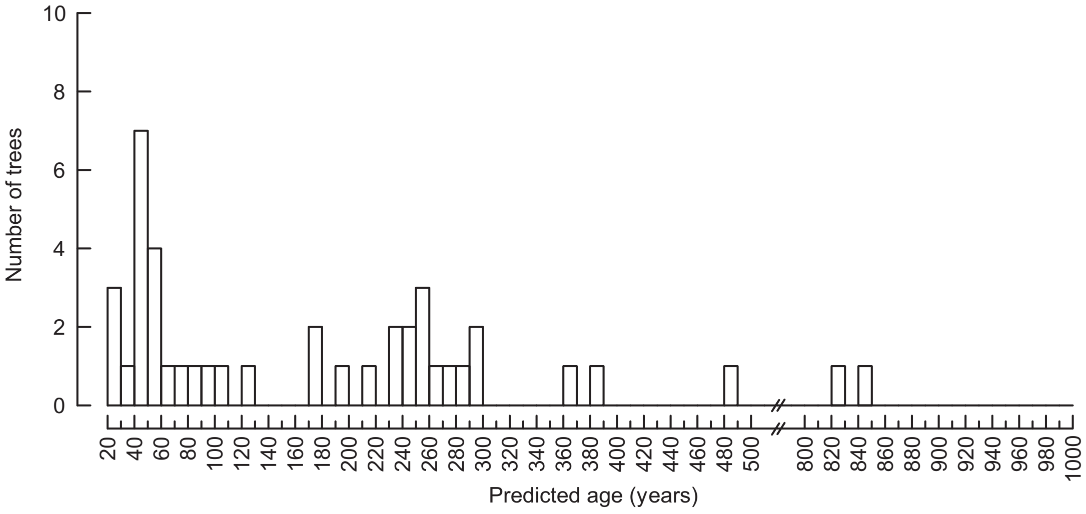
The second-order polynomial that additionally includes Diameter$^{1.5}$ best described the data of all polynomials that we considered (model 8 in Table 2). The adjusted R^2 (0.94) indicated a marginally better performance compared to some other polynomials, whereas the Akaike weights identified model 8 as being by far best suited to describe the data. The corresponding model formula was estimated as $\text{Age} = 11.67 \times \text{Diameter} - 2.3 \times \text{Diameter}^{1.5} + 0.15 \times \text{Diameter}^2$.

Based on this polynomial, all ages of the validation trees were predicted within a range of 40 to 260 years, with most predictions around 100 years (Fig. 1). The comparison of predicted vs. observed ages showed that the age of younger trees tended to be overestimated, whereas the age of older trees was somewhat underestimated (Fig. 2).

a) Polynomial approach



b) Nonlinear approach without covariates



c) Nonlinear approach with covariates

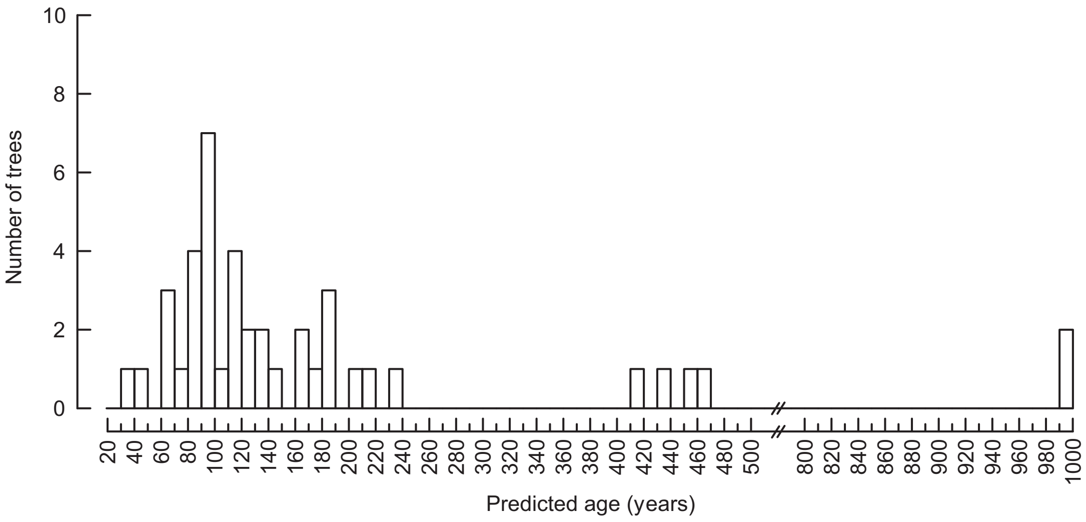


Figure 1. Distribution of the predicted ages based on (a) the polynomial approach, (b) the nonlinear approach without covariates and (c) the nonlinear approach with covariates. Please note the axis interruption between ages of 500 and 800 years.

The absolute error was less than 20 years for more than one third and less than 40 years for two thirds of the validation trees. For two trees, the predictions missed the observations by more than 100 years. Concerning relative errors, for 40% of the trees the model missed the observed ages by less than 20%, and for 70% of the trees by less than 40%. One tree had a relative error larger than 100%.

Nonlinear approach without covariates

The distribution of predicted ages from the nonlinear approach without covariates showed a peak at around 50 years and was generally flat over a wider range than the distributions from the other two approaches (Fig. 1). Except for two trees with age predictions higher than 800 years, all validation trees were predicted to be younger than 500 years. The comparison with observed ages revealed a rather random pattern for most predicted ages (Fig. 2).

Absolute errors were less than 20 years for 20% and less than 40 years for 40% of the trees. For 43% of the trees, the absolute error exceeded 100 years. The relative errors showed a similar pattern: for 20% of the trees, the model missed the observed age by less than 20%, and for 35% of the trees by less than 40%. For 30% of the trees, the relative error was larger than 100%.

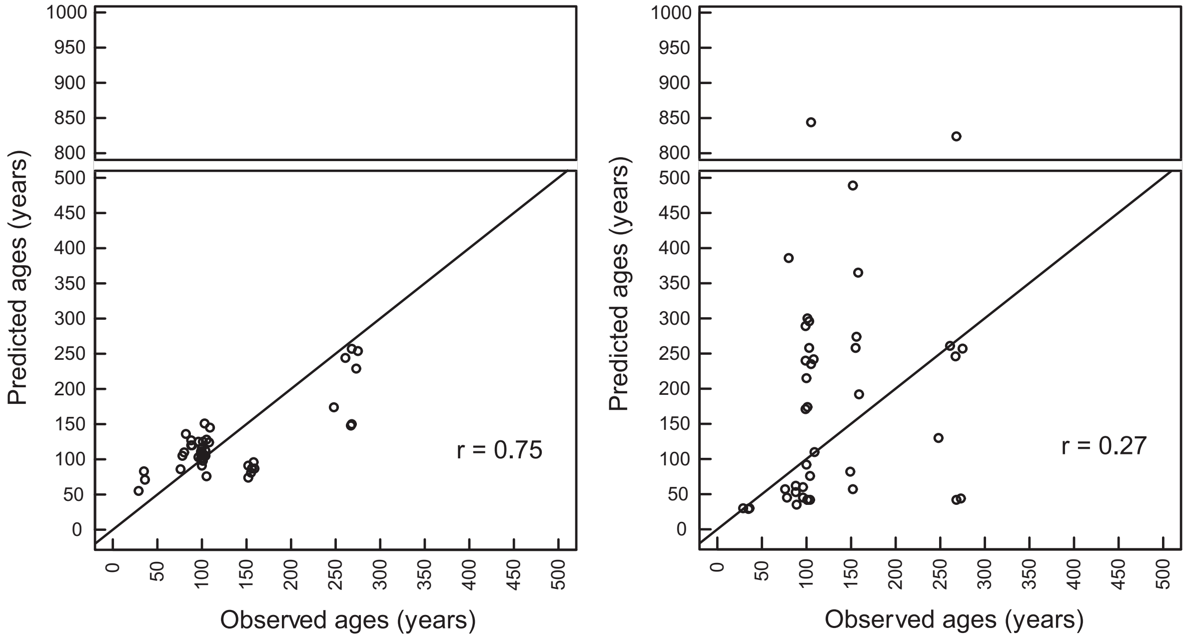
Nonlinear approach with covariates

The age predictions from this approach covered a similar range as those from the polynomial approach, except for four trees with predictions between 400 and 500 years and two trees with predictions at the upper end of the considered age range (Fig. 1). The age of most old and some medium-aged trees was overestimated considerably, whereas most young trees did not show a clear pattern of over- or underestimation (Fig. 2).

The absolute error of the age estimations based on the nonlinear approach with covariates was less than 20 years for 40% and less than 40 years for 70% of the validation trees. For six trees, the absolute error was more than 100 years, and for two of them more than 800 years. The relative error was less than 20% for 45% of the trees and less than 40% for 70% of the trees. Three trees had a relative error larger than 100%.

a) Polynomial approach

b) Nonlinear approach without covariates



c) Nonlinear approach with covariates

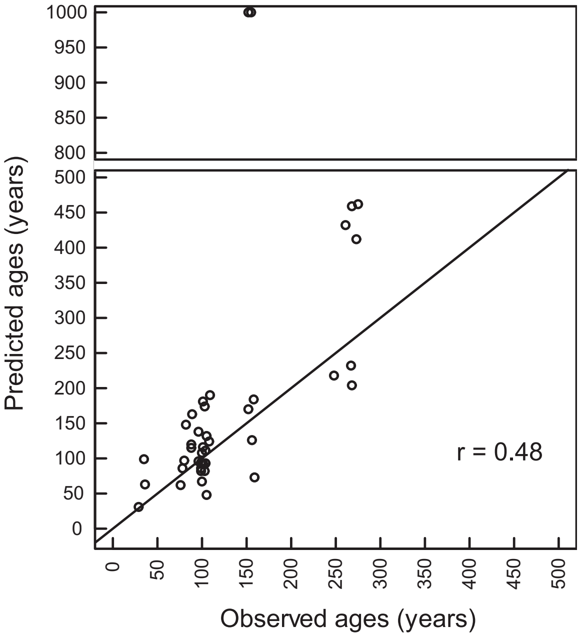


Figure 2. Accuracy of the predicted ages for (a) the polynomial approach, (b) the nonlinear approach without covariates and (c) the nonlinear approach with covariates. The Pearson correlation coefficient r is indicated for each approach.

Comparison of the approaches

Concerning both absolute and relative errors, the age predictions from the nonlinear approach without covariates were least accurate (Fig. 3). Predictions were strongly improved by including covariates in the nonlinear approach, except for two trees. Both nonlinear approaches showed a tendency towards overestimating the ages, whereas the polynomial approach had a slight tendency to underestimate the ages regarding absolute errors. Except for the two outliers, the nonlinear approach with covariates and the polynomial approach produced similarly accurate age predictions regarding relative errors. Regarding absolute errors, the polynomial approach clearly produced the most accurate age predictions.

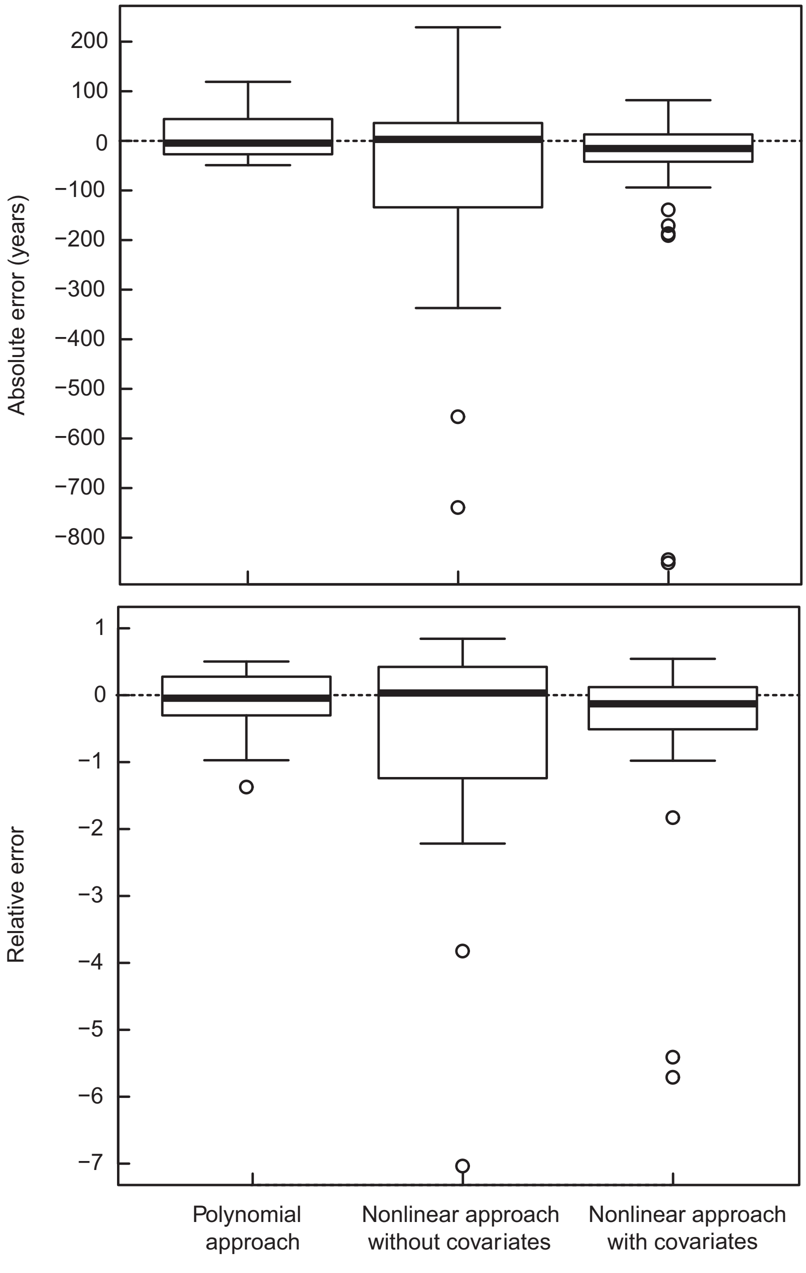
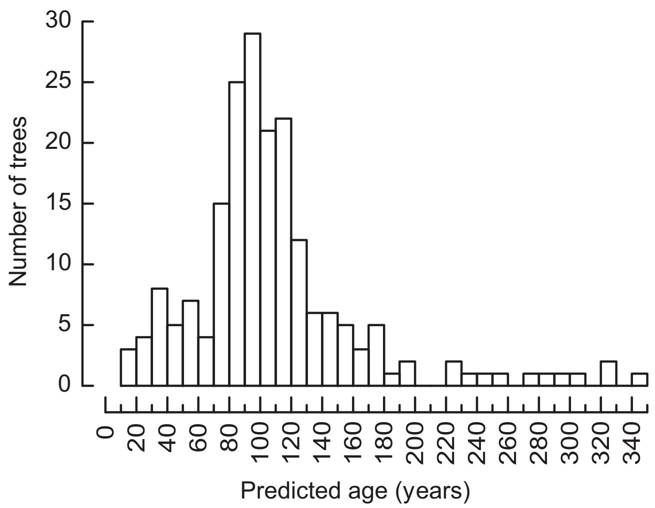


Figure 3. Absolute and relative errors of the predicted ages. The relative errors were calculated as (observed age - predicted age) / observed age.

Potential of the nonlinear approach with covariates

The age predictions based on the fixed and the random effects of the nonlinear model ranged between 10 and 350 years (Fig. 4a). The comparison of the predicted and the observed ages did not show any pattern of over- or underestimation (Fig. 4b). In general, these age predictions improved strongly compared to the nonlinear approach with covariates based on the fixed effects only (Fig. 4c). Concerning the absolute errors, half of the trees missed the observed age by less than 10 years, 75% of the trees by less than 20 years, and 92% of the trees by less than 40 years. The relative errors were below 10% for 48% of the trees, below 20% for 76% of the trees and below 40% for all but one tree.

a) Distribution of predicted ages



b) Observed vs. predicted ages

c) Absolute and relative errors

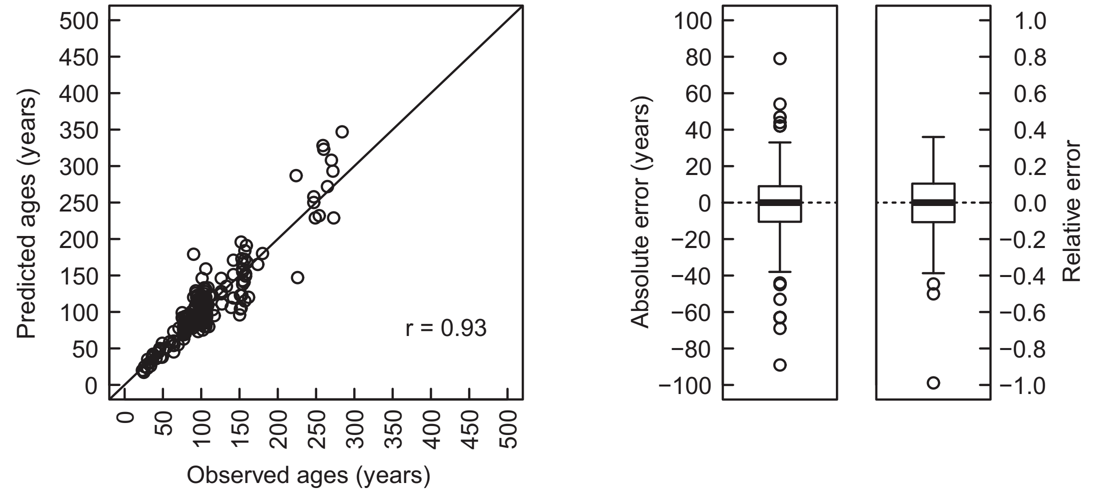


Figure 4. Theoretical accuracy of the nonlinear approach with covariates based on the fixed and the random effects. The Pearson correlation coefficient r is indicated in (b).

Discussion

In this study, we aimed to improve the accuracy and to broaden the applicability of statistically-based tree age estimation methods by including (1) repeated measurements that reveal diameter development over time, and (2) environmental covariates that reflect site-specific influences on tree growth.

Applicability of the three approaches

The nonlinear approaches have a higher applicability and generality compared to the polynomial approach due to their nonlinearity and the biologically motivated formulation of the underlying growth equation (cf. Zeide 1993). These features allow the approaches to be applied beyond the range of ages and diameters used for calibration (cf. Pinheiro & Bates 2000). This is a considerable advantage over the polynomial approach, because extrapolations from polynomials are often implausible beyond the calibrated range (Pinheiro & Bates 2000).

Strictly speaking, the polynomial approach and the nonlinear approach with covariates are not entirely non-invasive, since tree-ring data are needed for calibration. However, in the nonlinear approach with covariates, the calibration step can be skipped for further applications once a reliable model is available. Since environmental conditions are included explicitly, such transfers are likely to be more reliable than if a site-specifically calibrated polynomial was used. In contrast to the polynomial approach, the nonlinear approach with covariates thus has the potential for a completely non-invasive tree age estimation.

Accuracy of the three approaches

The traditional polynomial approach produced fairly accurate age estimations. In the best-fitting polynomial, diameter accounted for 94% of age variability, which is much more than reported in other empirical studies dealing with age-diameter relationships. For example, an R^2 between 40% and 60% was achieved by several polynomials fitted to data from an oak forest in the central United States, among them the polynomial used here (Loewenstein, Johnson & Garrett 2000). For a virgin beech forest in the Ukraine, a third-order polynomial reached an R^2 of 82% (Trotsiuk, Hobi & Commarmot 2012), whereas linear regressions showed an R^2 between 19% and 92% for beech and oak in Spain depending on the age cohort considered (Rozas 2003). The R^2 achieved in our study is particularly remarkable given the broad range of site conditions, which would rather give reason to expect a highly variable age-diameter relationship (cf. Abrams 1985; Piovesan et al. 2005; Suarez et al. 2008). Still, the model missed the true age of some trees by more than 100 years, caused by the fact that trees with similar diameters differed in age by up to 150 years. Such age differences are not exceptional and have been reported especially for old-growth forests (Piovesan et al. 2005; Trotsiuk, Hobi & Commarmot 2012). The well-established polynomial approach for tree age estimation may thus be characterized as being quite accurate, though prone to some uncertainty.

Solely considering repeated diameter measurements in the nonlinear approach, without taking into account environmental covariates, resulted in poorer age estimations compared to the polynomial approach. Despite the additional information in repeated diameter measurements, the age estimations were rather random and thus largely inaccurate. A possible reason for this inaccuracy is that growth variations over five to ten years, e.g. release effects (Black & Abrams 2003), are reflected as abrupt slope changes in the diameter sequences, and the fit procedure in the nonlinear approach without covariates is highly sensitive to such abrupt changes. Furthermore, the set of growth curves that we considered includes curves that have highly similar features over parts of their range, but these similar parts can be located at very different positions along time. Consequently, minor differences in the quality criterion may cause age estimations to differ by hundreds of years.

The inclusion of environmental covariates generally improved the age estimations strongly compared to the nonlinear approach without covariates. For some trees the estimation was highly accurate, whereas for some trees the method failed – ages at the upper limit of 1000 years were erroneously estimated. The nonlinear approach with covariates is highly sensitive if the underlying model predicts extremely flat age-diameter curves, which is the case mainly towards the extremes of the site conditions that we evaluated. For example, in Weidwald, where soils are shallow and slopes are steep (Rohner, Bugmann & Bigler 2012), the modelled asymptotic diameter for some trees was lower than the measured diameter data, resulting in the highest possible age being estimated. Thus, despite the additional information of repeated measurements and environmental covariates, the accuracy achieved by the traditional polynomial approach was matched, but not exceeded by the nonlinear approach with covariates.

Overall, the inclusion of additional information in tree age estimations yielded similarly accurate results as the polynomial approach for most trees, although at some sites it performed considerably worse. Importantly, the nonlinear approach without covariates proved useless due to its instability. Thus, if solely the accuracy of the age estimation at the investigated sites was considered and the advantages regarding general applicability were ignored, including additional information proved not to be worthwhile – at the current stage of development of the underlying nonlinear model with covariates – because too much variability in the age-diameter relationship remains unexplained.

Potential of the nonlinear approach with covariates

By taking into account the fixed and the random effects, we were able to illustrate that tree age estimations could be improved considerably if more accurate nonlinear models with covariates were available. In fact, the ages estimated using this approach reached an accuracy that is undisputed by any other non-destructive method suggested so far, including the traditional polynomial approach and multiple regressions (e.g. Matthes, Kelly & Larson 2008). On the basis of this high potential for improved accuracy, in combination with the possibility for sound extrapolation to older ages and for non-invasive transfers to further sites, we judge the potential of this approach as being quite high. This judgement is supported by the fact that the nonlinear approach with covariates already now reaches a similar accuracy as the polynomial approach for most trees.

The amount of variability explained by the covariates of the underlying model limits the accuracy of age estimations from the nonlinear approach with covariates. Therefore, attempts to increase the amount of explained variability by incorporating further covariates in nonlinear models would not only enhance our quantitative understanding of ecological relationships, but would also contribute to improved age estimations. On the one hand, such attempts could involve well-known processes such as competition for light, which was not included in the model that we used here simply due to methodological constraints (Rohner, Bugmann & Bigler 2012), although a substantial influence on the age-diameter relationship is expected (cf. Biging & Dobbertin 1995). On the other hand, further research on still poorly understood growth drivers such as belowground processes (Coomes & Grubb 2000; Heineman et al. 2011) are likely to contribute to further improve nonlinear growth models.

Application of the nonlinear approach with covariates for tree age estimations

Non-invasive methods for tree age estimations are important because the goals of forest management are often incompatible with the coring of trees, which has an impact on wood quality and possible negative consequences for other tree characteristics. Scientists and practitioners have debated intensively on possible impacts of tree coring such as the spread of pathogenic fungi (Hart & Wargo 1965) and reduced physical stability (Jaeger 1970). Although impacts on mortality have not been detected for conifers (van Mantgem & Stephenson 2004; Wunder et al. 2011), little is known about the susceptibility of deciduous trees, which generally seem to be more sensitive to injuries from coring (Jaeger 1970). These possible negative consequences in addition to the direct wood damage are underlying the widespread scepticism of forest owners and managers towards invasive methods, particularly in endangered and protected forests, even though the accurate determination of tree age is considered to be particularly important in such forests (Commarmot et al. 2005; Matthes, Kelly & Larson 2008; Suarez et al. 2008).

Provided that a reliable model is available, the nonlinear approach with covariates would not only be an accurate and widely applicable, but also a cheap substitute for destructive tree age estimations. Measuring the diameter of a tree is much faster than extracting an increment core and performing the associated laboratory work.

Accurate age estimations derived from the nonlinear approach with covariates have applications for various tasks that must be based on non-destructive methods. One example is the calculation of subsidies for the non-usage of protected trees (mostly oaks) in Central Europe (e.g. Kantonsforstamt St. Gallen 2003). Another application lies in the study of natural dynamics in virgin forests (cf. Commarmot et al. 2005), which may allow important conclusions to be drawn for close-to-nature forest management. In addition, the use of improved age estimations in forest growth models based on inventory data would entail more reliable projections e.g. regarding future forest dynamics and carbon sequestration (Thürig et al. 2005).

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References

Aas, G. (1998) Morphologische und ökologische Variation mitteleuropäischer *Quercus*-Arten: Ein Beitrag zum Verständnis der Biodiversität. Libri botanici 19. IHW-Verlag, Eching bei München.

Abrams, M.D. (1985) Age-diameter relationships of *Quercus* species in relation to edaphic factors in gallery forests in northeast Kansas. Forest Ecology and Management, 18, 181-193.

Baty, F. & Delignette-Muller, M.L. (2011) nlstools: tools for nonlinear regression diagnostics. R package version 0.0-11.

Biging, G.S. & Dobbertin, M. (1995) Evaluation of competition indices in individual tree growth models. Forest Science, 41, 360-377.

Black, B.A. & Abrams, M.D. (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecological Applications, 13, 1733-1749.

Bolliger, M., Schnidrig, R. & Stadler, B. (2008) Fachspezifische Erläuterungen zur Programmvereinbarung im Bereich Waldbiodiversität. Handbuch NFA im Umweltbereich. Bundesamt für Umwelt BAFU, Bern.

Brändli, U.-B. (ed) (2010) Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf; Bundesamt für Umwelt BAFU, Bern.

Brang, P., Heiri, C. & Bugmann, H. (2011) Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt, Bern.

Bundesamt für Raumplanung (EJPD), Bundesamt für Landwirtschaft (EVD) & Bundesamt für Forstwesen (EDI) (1980) Bodeneignungskarte der Schweiz. Grundlagen für die Raumplanung. Eidgenössische Drucksachen- und Materialzentrale, Bern.

Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2^{nd} edn. Springer, New York.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R. & Zingg, A. (2005) Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest, Snow and Landscape Research, 79, 45-56.

Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs, 70, 171-207.

Fang, Z. & Bailey, R.L. (2001) Nonlinear mixed effects modeling for slash pine dominant height growth following intensive silvicultural treatments. Forest Science, 47, 287-300.

Fritts, H.C. (1976) Tree Rings and Climate. Academic Press, London.

Gärtner, H. & Nievergelt, D. (2010) The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia, 28, 85-92.

Godet, J.-D. (1986) Bäume und Sträucher: einheimische und eingeführte Baum- und Straucharten. Arboris-Verlag, Hinterkappelen-Bern.

Hall, D.B. & Clutter, M. (2004) Multivariate multilevel nonlinear mixed effects models for timber yield predictions. Biometrics, 60, 16-24.

Hart, J.H. & Wargo, P.M. (1965) Increment borer wounds - penetration points for *Ceratocystis fagacerarum*. Journal of Forestry, 63, 38-39.

Heineman, K.D., Jensen, E., Shapland, A., Bogenrief, B., Tan, S., Rebarber, R. & Russo, S.E. (2011) The effects of belowground resouces on aboveground allometric growth in Bornean tree species. Forest Ecology and Management, 261, 1820-1832.

Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43, 69-78.

Jaeger, T.A. (1970) Increment borer damage and its control: a review of the literature. Publication No. 1270. Department of Fisheries and Forestry, Canadian Forestry Service, Ottawa, Ontario.

Kantonsforstamt St. Gallen (2003) Konzept Waldreservate Kanton St. Gallen (ed. T. Dietschi). Volkswirtschaftsdepartement des Kantons St. Gallen, St. Gallen.

Kissling, P. (1980) Clef de détermination des chênes médioeuropéens (*Quercus* L.). Berichte der Schweizerischen Botanischen Gesellschaft, 90, 29-44.

Lemon, J. (2006) Plotrix: a package in the red light district of R. R-News, 6, 8-12.

Loewenstein, E.F., Johnson, P.S. & Garrett, H.E. (2000) Age and diameter structure of a managed uneven-aged oak forest. Canadian Journal of Forest Research, 30, 1060-1070.

Matthes, U., Kelly, P.E. & Larson, D.W. (2008) Predicting the age of ancient *Thuja occidentalis* on cliffs. Canadian Journal of Forest Research, 38, 2923-2931.

Michel, A.K. & Winter, S. (2009) Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. Forest Ecology and Management, 257, 1453-1464.

Nagel, T.A., Levanic, T. & Diaci, J. (2007) A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slowenia. Annals of Forest Science, 64, 891-897.

Oberhuber, W. & Kofler, W. (2000) Topographic influences on radial growth of Scots pine (*Pinus sylvestris* L.) at small spatial scales. Plant Ecology, 146, 231-240.

Parker, A.J. (1982) The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography, 3, 160-168.

Parker, G.R. & Leopold, D.J. (1983) Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of the Torrey Botanical Club, 110, 482-488.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2011) nlme: linear and nonlinear mixed effects models. R package version 3.1-104.

Pinheiro, J.C. & Bates, D.M. (2000) Mixed-Effects Models in S and S-PLUS. Springer, New York.

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F. & Schirone, B. (2005) Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. Journal of Vegetation Science, 16, 13-28.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, http://www.R-project.org.

Richards, F.J. (1959) A flexible growth function for empirical use. Journal of Experimental Botany, 10, 290-300.

Rohner, B., Bigler, C., Wunder, J., Brang, P. & Bugmann, H. (2012) Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. Journal of Vegetation Science, 23, 892-905.

Rohner, B., Bugmann, H. & Bigler, C. (2012) Estimating the age-diameter relationship of oak species in Switzerland using nonlinear mixed-effects models (submitted to European Journal of Forest Research).

Rozas, V. (2003) Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecology, 167, 193-212.

Sivanpillai, R., Smith, C.T., Srinivasan, R., Messina, M.G. & Wu, X.B. (2006) Estimation of managed loblolly pine stand age and density with Landsat ETM+ data. Forest Ecology and Management, 223, 247-254.

Suarez, M.L., Renison, D., Marcora, P. & Hensen, I. (2008) Age-size-habitat relationships for *Polylepis australis*: dealing with endangered forest ecosystems. Biodiversity and Conservation, 17, 2617-2625.

Thürig, E., Kaufmann, E., Frisullo, R. & Bugmann, H. (2005) Evaluation of the growth function of an empirical forest scenario model. Forest Ecology and Management, 204, 51-66.

Trotsiuk, V., Hobi, M.L. & Commarmot, B. (2012) Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management, 265, 181-190.

Tyrrell, L.E. & Crow, T.R. (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology, 75, 370-386.

van Mantgem, P.J. & Stephenson, N.L. (2004) Does coring contribute to tree mortality? Canadian Journal of Forest Research, 34, 2394-2398.

Veblen, T.T. (1986) Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club, 113, 225-240.

Villalba, R. & Veblen, T.T. (1997) Improving estimates of total tree ages based on increment core samples. Ecoscience, 4, 534-542.

Wong, C.M. & Lertzman, K.P. (2001) Errors in estimating tree age: implications for studies of stand dynamics. Canadian Journal of Forest Research, 31, 1262-1271.

Wunder, J., Reineking, B., Hillgarter, F.-W., Bigler, C. & Bugmann, H. (2011) Long-term effects of increment coring on Norway spruce mortality. Canadian Journal of Forest Research, 41, 2326-2336.

Zeide, B. (1993) Analysis of growth equations. Forest Science, 39, 594-616.

Synthesis

This thesis aimed at assessing the natural potential of Central European oaks by investigating their growth and mortality in unmanaged forest reserves. Particular emphasis was placed on (1) the identification of environmental variables that influence oak growth and mortality, (2) the potential performance of oaks under climate change and without targeted facilitation, and (3) the development of a non-destructive method for tree age estimation. Keeping these key objectives in mind, the main insights from this thesis are synthesized first. Then, methodological considerations that span the entire thesis are summarized, and finally, an outlook on implications for forest management and on further research priorities is made.

Insights from this thesis

Drivers of oak growth and mortality

This thesis shows that oak growth in the Swiss forest reserves is to a large extent limited by drought. Their annual growth variability is heavily influenced by climatic conditions during the summer months, with dry summers leading to reduced growth, especially on dry soils (Chapter II). In addition, cumulative growth over the whole lifetime of the oaks is strongly affected by water availability (Chapter III). However, for this latter aspect, the site-specific capability to *retain* rainwater is more important than the amount of rainwater *per se*.

Regarding oak mortality, the strongest driver that I identified is tree size, with smaller oaks showing highest mortality rates (Chapter I). This represents a mortality process that is well-known as 'competitive self-thinning' (cf. General Introduction; Adler 1996). The second most important driver is stand basal area, indicating stand-scale competitive pressure. Further potential drivers of oak mortality that I considered, such as site characteristics (slope) and climate (precipitation) seem to have a weaker influence.

Overall, this thesis revealed that *growth* of oaks is strongly influenced by site characteristics and climate, whereas *mortality* is mainly driven by competition. The inversion of this conclusion holds true for mortality, i.e. site characteristics and climate only play a secondary role for oak mortality (Chapter I). However, concluding that competition does not affect oak growth would be inappropriate, because this relationship could not be addressed here due to the lack of long-term information on competition at the individual tree level. In fact, a considerable part of the unexplained growth variability that could not be addressed within this thesis is highly likely to result from differing competitive pressure (cf. Chapter III and Recommendations for further research, below).

The natural performance of oaks in Central Europe

Currently, there are two main contrasting hypotheses about the natural role of oaks in Central European forests. First, many oaks have been facilitated through human interventions (Bürgi 1999) and thus, if management was abandoned, they may largely disappear as a consequence of their lower competitiveness relative to other, more shade-tolerant species such as European beech (*Fagus sylvatica*; cf. Mühlethaler 2008). Second, the ongoing climate change – particularly increasing temperature and more frequent droughts – may invert the relative competitiveness in favour of the thermophile and drought-tolerant oaks (Weber et al. 2007; Contran et al. 2012). The results presented in this thesis tend to support the first hypothesis. In the absence of management, stand basal area increased within the investigated forests, which resulted in increased mortality rates for oak (Chapter I), whereas increasing stand basal area did not affect beech mortality. This pattern likely reflects the higher relative competitiveness of beech compared to oak due to its higher shade tolerance. A beneficial effect of climate change for oak has not been identified over the investigated time period within this thesis. Despite this support for the first hypothesis, it should be kept in mind that the last monitoring campaign dates back 10 to 15 years in most reserves (Chapter I). Thus, it cannot be ruled out that the relative competitiveness in Central European forests has started to shift in the meanwhile, or will do so in the near future. Furthermore, climate effects on mortality were investigated on a ca. decennial resolution. For additionally analyzing the effect of individual drought years, annual mortality rates would be required.

Regarding oak growth, my thesis indicates that considerable growth reductions are likely if summers become warmer and drier, which is expected under climate change. However, the observed negative correlation between drought and oak growth (Chapter II and III) does not contradict the drought tolerance ascribed to oaks. This correlation rather reflects the fact that oaks are able to grow under fairly dry conditions, although their optimum growth range tends to be in moist conditions (cf. Ellenberg 2009). Consequently, my results regarding reduced oak growth under water stress do not allow for ruling out a potential benefit of oak in a changing climate (since this would have required a simultaneous investigation of the competing species; see Recommendations for further research, below); the pattern I found only permits the conclusion that reduced growth compared to past decades may be expected.

Non-invasive tree age estimation for oak

Tree age information is often needed in scientific and practical applications that do not allow for the sampling of tree-ring information. My thesis contributes to identifying an alternative approach for tree age estimation that makes use of monitoring data alone and requires tree-ring information during an initial calibration stage only (Chapter IV). The resulting nonlinear and site-dependent age-diameter relationship allows the method to be applied also to other sites and to other ages than those considered during calibration. For most oaks, this new approach produced similarly accurate age estimations as the currently most often used method of fitting polynomials, which requires tree-ring data for calibration at every site and for every age range for which it is applied. The similar accuracy in combination with its potential for transfer and extrapolation make the new approach a promising alternative to the traditional method for tree age estimation.

However, since the new approach for tree age estimation does not exceed the accuracy of the traditional polynomial approach even though it includes additional information (i.e. repeated diameter measurements and site information), it could be argued that the traditional approach is more efficient. However, it should be kept in mind that further research is likely to considerably increase the accuracy of the newly developed method, whereas no such improvements are expected for the traditional approach. Additionally, irrespective of further improvements in accuracy, only the new approach opens the way for completely non-invasive age estimation.

Methodological aspects

Study sites

The Swiss forest reserve network, which includes all study sites of this thesis, owes its existence to the pioneering spirit of Prof. Leibundgut and the huge effort of all people having been involved in planning and conducting the monitoring campaigns since the early 1950s. Realizing this thesis within the framework of the reserve network entailed two major advantages:

(1) Within the reserves, forest dynamics proceed under the exclusion of human interventions. This fact has been a key precondition to assess the performance that can be expected from oaks under less intensive management, e.g. under close-to-nature management or under complete exclusion of management related to conservational goals. A major rationale behind the foundation of the Swiss forest reserve network was indeed the establishment of a scientific reference system for close-to-nature silviculture (Leibundgut 1993; Bugmann et al. 2011). A few comparable reserve networks exist in other countries such as in Slovakia (Korpeľ 1995), in the Czech Republic (Průša 1985), and the forest reserve Białowieża in Poland (Bernadzki et al. 1998). Thus, for my thesis, the Swiss forest reserve network provided a nearly unique opportunity to study forest dynamics unaffected by human interventions.

(2) The endeavour of Prof. Leibundgut to establish forest reserves in various forest types in Switzerland led to a highly diverse range of sites in the network. This high variability is a key advantage for studying how site characteristics influence tree growth and mortality, as done in Chapters I-III of this thesis. Furthermore, it formed the basis for a fairly broad application range of the method for tree age estimation that I developed in Chapter IV. However, although a considerable gradient of site characteristics is covered by the study

sites of this thesis, not the entire gradient is represented equally well. Forests with fairly moist and deep soils in the northern lowlands of Switzerland, where mainly beech occurs besides oak, tend to be overrepresented compared to mixed oak forests e.g. in the Jura Mountains or oak-pine forests in the dry inner-Alpine parts of Switzerland. This imbalance probably caused the age-diameter model developed in Chapter III to fail for oaks growing in the dry site Les Follatères, which is fairly far off climatically relative to the other study sites. A more balanced set of sites would have been beneficial from a statistical perspective; however, this would have required the inclusion of further – thus managed – forests, which was not considered for reasons of consistency and because of the unique advantages of unmanaged forests as explained above.

Tree species

The three most frequent oak species in Switzerland (*Q. petraea*, *Q. robur*, *Q. pubescens*) were analyzed collectively in all chapters of this thesis. From an ecological perspective, this combined consideration could be justified with their pronounced tendency to hybridize, which may even blur the boundaries of the species concept within the genus *Quercus* (Aas 1998; Kleinschmit and Kleinschmit 2000). Furthermore, all three oak species are described as being less competitive than their strongest opponent in the area of their optimum growth range (i.e. *F. sylvatica*; Ellenberg 2009). Consequently, comparable growth and mortality patterns are expected among the oaks in response to competitive pressure. However, considerable differences in ecological features among the three species have been described, e.g. related to drought tolerance (Ellenberg 2009). Therefore, especially regarding the influence of climate variables on growth and mortality, separate analyses of the three oak species would have been beneficial and could have revealed important insights. The reason why no species-specific analyses were conducted is partly of methodological nature: the oak species were not distinguished consistently during the monitoring campaigns, simply because a reliable distinction in the field based on morphological attributes alone is difficult. Although for chapters II – IV the identification of oak at the species level would have been theoretically possible during the field work (although time-consuming and expensive due to the necessity of genetic analyses), a retrospective determination of the oak species in the reserve data was clearly beyond the scope of my work, among others due to the progressing decay of oaks that died since the monitoring had started. Additionally, also in practical forest management, hybridization and ambiguous morphology of oak make the species identification difficult. Species-specific models for the age estimation would therefore likely have impeded their application in practice, rather than to facilitate it. For these reasons, the combined consideration of the three oak species was indeed appropriate for the purposes of this thesis, and species-specific analyses are left to other research projects (e.g. the project Querco at WSL Birmensdorf, see Contran et al. 2012; Fonti et al. 2012).

It should be kept in mind that with *Q. cerris* a further oak species exists at the boundary of its natural distribution in the southernmost part of Switzerland (cf. General Introduction). So far, this species has been restricted to eastern sub-Mediterranean areas due to its high sensitivity to late frost events (Ellenberg 2009). However, if summers become increasingly warmer in the course of climate change, it cannot be ruled out that *Q. cerris* will expand to the north of the Alps at some point. Unfortunately, within the Swiss forest reserve network *Q. cerris* does not have a sufficient abundance yet that would have allowed for a statistical analysis.

Data sources

The monitoring methods within the forest reserves have been applied consistently since the establishment of the network; this allows for comparing the monitoring data not only among sites but also over time. This consistency was a necessary precondition for investigating changes of stand structure and mortality patterns over time (Chapter I) as well as for the use of diameter sequences (Chapter IV). Despite the consistent monitoring procedure, the area of some investigated plots has changed considerably over the observed time span, which may have entailed biases in site-scale measures. Indeed, an abrupt change in stand basal area within one investigated plot was ascribed to a substantial expansion of the respective plot size (see Figure 2 in Chapter I). However, this case remained an exception, probably because the plots were explicitly defined in such a way that they were homogeneous with regard to site characteristics (cf. Matter 2004).

The length of the data series collected within the forest reserves is matched only by few forest-related data series worldwide (e.g. Korpeľ 1995; Bernadzki et al. 1998). The study of processes that operate as slowly as tree growth or occur as infrequently as tree mortality makes a long-term perspective an undisputable precondition. However, even though the monitoring data reflect an extraordinary foresight in the light of a scientific project (longer than a scientist’s career), the time span captured to date (maximum of ca. 50 years in just a few reserves) is still exceedingly short relative to a tree's natural life expectancy and the temporal scale on which forest dynamics proceed. Hence, when interpreting results derived from the monitoring data, it should be kept in mind that still only a small time slice of natural forest dynamics has been captured (cf. Discussion in Chapter I and the Outlook in this chapter). This fact underlines the importance of continuing the monitoring within the reserves in the long term.

The tree-ring data used in this thesis enhanced the time span of my investigations to the lifetime of the cored trees, which is considerably longer than the length of the monitoring data series in most cases (e.g. up to seven times longer in the forest reserve Bannhalde). Studying one tree generation may still be short, e.g. if changes in species composition are the main goal of investigation. However, the annually resolved tree-ring samples allowed me to quantify the influence of climate variability on oak growth (Chapter II). Since most of the cored trees had germinated before the foundation of the reserves, it cannot be ruled out that they experienced management impacts in their early days. Although such impacts cannot be reconstructed exactly, their bias is likely rather low because most reserves were established in forests in which the last interventions had taken place several decades earlier.

The tree-ring data were further used to reconstruct diameter increment with age (Chapter III). For this analysis, concentric growth had to be assumed, although it is known that oaks often show eccentric growth (Rozas, 2003). Variability in tree-ring widths caused by eccentric growth could have been taken into account if stem disks or multiple core samples per tree had been collected. However, felling trees to remove stem disks is certainly not appropriate within forest reserves. Furthermore, to minimize the impact on the investigated trees, I decided to take only one core per tree. Therefore, I deliberately renounced quantifying within-tree growth variability.

By combining monitoring data and tree-ring chronologies, this thesis brought together the two probably most comprehensive and most widely used data types in forest science. After having performed separate analyses, Chapter IV of this thesis explicitly focussed on the potential that lies in combining both data types. This combination aimed at developing a method for tree age estimation for which no further tree-ring information is needed. In contrast, a previous attempt that combined monitoring and tree-ring data focussed on the possibility of using both data types *together* for further estimations of tree age (Clark et al. 2007). In addition, completely different applications arising from a combined consideration are conceivable, e.g. an assessment how lagged growth responses to climatic events may influence diameter measurements in decennial monitoring.

Statistical analyses

In this thesis, a range of statistical methods was applied. While I used descriptive statistics to analyze stand structures in Chapter I, I modelled the mortality rates with generalized linear mixed-effects models. Chapter II identified annual growth responses based on a principle component regression, i.e. a multivariate method. In Chapter III, nonlinear mixed-effects models with covariates were fitted to describe age-diameter relationships, and an averaged model was then applied besides polynomials for the tree age estimation in Chapter IV. In addition, an information-theoretic approach was used for model selection in Chapter I and for model averaging in Chapter III. While detailed descriptions of these methods can be found in the respective chapters, this short overview illustrates that forest science has left behind a mainly observational character and increasingly uses sophisticated statistical methods (cf. Ellison and Dennis 2010). Accordingly, the choice of appropriate statistical methods and accounting for the corresponding pros and cons has been a crucial task in this thesis.

Mixed-effects models such as those fitted in Chapters I and III of the thesis have only recently gained importance in forest science, with early applications e.g. by Biging (1985) and Lappi and Bailey (1988). In contrast to traditional regression approaches that account just for fixed effects, mixed-effects models are able to take into account that many ecological data are grouped and that within-group measurements are often correlated (Pinheiro and Bates

2000). Accordingly, these models are an appropriate tool for studying longitudinal data, repeated measures and multilevel data such as those analyzed in this thesis, i.e. repeated measurements from trees (grouping level 1) within different reserves (grouping level 2). By taking into account the grouped structure of the data, mixed-effects models simultaneously estimate ‘fixed’ effects that are valid for all included units (e.g. tree populations in Chapter I) and ‘random’ effects that quantify the variability caused by the different groups of units (e.g. sites in Chapter I). By treating the groups as random effects, fewer parameters need to be estimated than if they were included as levels of a fixed factor or if separate models were fitted for every group, which is often done in traditional regression studies with just fixed effects. The associated saving of degrees of freedom is advantageous, especially because the (random) influence of the groups on the response variable is mostly not the key issue anyway.

Besides providing the appropriate model structure for dealing with grouped data as in Chapter I of the thesis, mixed-effects models further allowed for quantifying the unexplained variability in the age-diameter relationship among trees as discussed in Chapters III and IV. However, if mixed-effects models are used for predictions, the random effects are only applicable within the groups included in model fitting. Hence, variability that is not captured by the fixed effects is unpredictable for groups that have not been considered during model fitting, as it was the case for the validation trees in Chapters III and IV of this thesis. This restriction is mentioned only rarely in empirical studies based on mixed-effects models.

Model selection in Chapters I and III was based on an information-theoretic approach, which is explained in the respective chapters and in more detail in Burnham and Anderson (2002). For a long time, most statistical textbooks have proposed the use of stepwise comparisons of pairs of nested models – an approach that is based on null hypothesis testing (e.g. Stahel 2008). However, the information-theoretic approach has increasingly been applied in recent ecological studies due to four key advantages over traditional null hypothesis testing (cf. Johnson and Omland 2004): (1) the considered models do not need to be nested, (2) the selection is not based on an arbitrary threshold such as a P-value of 0.05; (3) instead of identifying one single ‘winner model’, all models are ranked according to their relative support by the data; and (4) if the relative support is similar among several models, model averaging with a weighting according to the particular relative support can be performed easily. In my thesis, the use of the information-theoretic approach for model selection has proved to be a good choice because the models developed in Chapters I and III were only partly nested, no model was clearly superior to the others (especially in Chapter I), and model averaging was beneficial for the predictions made in Chapter III.

In accordance with the use of recently developed statistical methods, the edge of current statistical knowledge and computing was touched at several points in this thesis. For example, the structure of the data analyzed in Chapters III and IV would have allowed for including environmental variables and random effects also for the parameters *b* and *c* as well as a second hierarchical level of random effects on the scale of the reserves. However, all attempts in doing so failed, because the currently available numerical algorithms did not converge. In addition, the way how temporal autocorrelation and overdispersion can be accounted in mixed-effects models (cf. Chapters I and III) is still intensively discussed (cf. Zuur et al. 2009).

Outlook

Recommendations for forest management

The maintenance of oak in Central European forests has increasing importance in nature conservation projects (e.g. Bonfils et al. 2005), since oaks feature a high associated biodiversity (Ranius and Jansson 2000; Barbier et al. 2008; Bernicchia et al. 2008; Caprio et al. 2009). The results in Chapter I of this thesis indicate that the complete protection of oak forests from management is likely counter-productive in the Swiss lowlands. Mixed deciduous forests released from management are expected to experience an increasing stand basal area, which likely entails increased oak mortality (cf. Chapter I). Therefore, in the context of nature conservation related to oaks, a combination of protection from management (i.e. restriction of cutting oaks) and targeted interventions for reducing competitive pressure is suggested. In Switzerland, this concept of forest reserves allowing for interventions with a specific purpose already exists under the name ‘Sonderwaldreservate’ (special forest reserves, Bundesamt für Umwelt 2005). My thesis provides the quantitative background that justifies the establishment of special forest reserves with respect to oak conservation.

Forest managers are faced with the task of assessing the future development of their forests, among others regarding future growth. Within this thesis, strong evidence was found that oaks show reduced growth both during dry years (Chapter II) and at sites prone to persistent water stress (Chapter III). Since drier and warmer conditions are expected with progressing climate change (Fischer 2011; Weigel and Fischer 2011), expecting growth rates as in the past is likely not realistic for the future. Despite the drought tolerance of oaks (cf. Ellenberg, 2009), forest managers are therefore recommended to lower their expectations regarding future oak growth, at least if competition remains unchanged.

In addition to forest reserves, the specific protection of groups of old oaks in Switzerland is a legal instrument at the cantonal level. For the resulting agreements, the age of the particular oaks plays a crucial role, on the one hand for the decision whether a group of oaks is a suitable target for protection, and on the other hand for the calculation of age-related subsidies that aim to compensate for the loss of timber revenue. In such applications, determining the age based on tree-ring samples is not optimal for financial and conservational reasons. The method for tree age estimation developed in Chapter IV of this thesis is suggested as an alternative. The further development of the underlying model and the inclusion of data from further sites are likely to improve the accuracy of the estimated ages – and consequently the acceptance that the method obtains. Increased accuracy may compensate for the fact that in many applications only one diameter measurement will be available (e.g. at the time the subsidies are determined). Therefore, I recommend further developing the model before it is applied in practice. In this improvement process, collaboration between forest science and practice would be desirable, e.g. to adapt the method to the demands of practitioners, or to share data about the age-diameter relationship from management plans and felled oaks.

Recommendations for further research

Specific recommendations for further research have been mentioned at several points in this thesis. However, I would like to particularly emphasize the following areas:

(1) *Further development of the nonlinear model with covariates:* As mentioned above, a further development of the nonlinear model with covariates to increase the amount of variability that is explained by the fixed effects would enhance its applicability for tree age estimation in practice (cf. Chapter IV). Improvements can be expected when including further environmental covariates such as nutrient availability (perhaps in a simple form such as site index) or the presence of pathogens. In addition, including covariates for the parameters that are currently modelled as being independent of site information would likely increase the performance of the model. A further feature whose inclusion is expected to considerably increase model performance is competition, which can be assumed to be time-varying. Moreover, at several points in this thesis, the potential for transfers and extrapolations of the nonlinear age estimation method has been suggested. A quantitative assessment of this potential would be highly desirable.

(2) *Competitive pressure on individual trees*: Competitive pressure on individual oaks could not be considered in this thesis although it has likely a strong influence on growth and mortality processes. Reconstructing the competitive situation around a tree over decades is impossible if no information about the location of individual trees, including now dead trees, is available. Although dendrochronology can help to reconstruct the competitive situation around individual trees (Weber et al. 2008), this is not possible over multiple decades due to the proceeding decay of dead trees. Since the reorganization of the Swiss forest reserve network in 2006, the exact location of all trees within the permanent plots is recorded. These spatially explicit data will allow for the identification of every tree’s individual neighbourhood at every monitoring campaign. In the long run, competitive pressure on the individual trees, e.g. calculated as distance-dependent competition indices (cf. Biging and Dobbertin 1995), can thus be included as an explanatory variable in individual-based models of tree growth and mortality.

(3) *Disturbances and regeneration*: Forest fires, storms and other natural events commonly known as disturbances can act as key drivers of forest dynamics through the initiation of successional phases related to tree mortality and subsequent regeneration. In this process, the tree species composition of the dying trees does not necessarily agree with the

species composition of the regeneration (cf. Parker and Leopold 1983), leading to compositional changes in the long term. For instance, disturbances that hit forests with dense canopies may enable the light-demanding oak to re-establish (cf. Mountford et al. 1999). However, broad-scale infestation of oaks with pathogenic fungi or insects may contribute to their disappearance from currently mixed stands (Thomas et al. 2002). Therefore, both disturbances and regeneration require intensive investigation before an overall assessment of the long-term natural potential of oaks in Central Europe is possible.

(4) *Management*: This thesis has explicitly aimed at excluding impacts of forest management on natural stand dynamics and has therefore been realized within unmanaged forest reserves. After having pointed out that the proportion of oak is likely to decrease in many Central European forests without targeted measures, and that growth reductions are expected with the progression of climate change, the next step could focus on the investigation of possible counteracting activities. Hence, comparing the influences of different management practices on growth and mortality of oaks could reveal highly relevant insights for both forest science and silviculture.

(5) *Further tree species*: While oak mortality was investigated in relation to the mortality of its strongest competitor beech (Chapter I), the growth analyses focussed on oak alone (Chapters II-III). For assessing how the identified growth patterns may be classified in relation to the growth patterns of competing species, the analyses performed in this thesis could be repeated for further common tree species in Central Europe. For example, the negative growth responses of oaks to drought that I found may be smaller than for less drought-tolerant tree species within the reserves (Weber et al. 2007). Furthermore, the suggested method for tree age estimation is not restricted to oaks. If relevant data were available, the method could easily be adopted for applications to other tree species by recalibrating the underlying model according to the methods described in Chapter III of this thesis.

(6) *Long-term effects of coring*: The cored oaks are individually tagged since they are located within permanent plots of the Swiss forest reserve network, which allows them to be traced in the future. Consequently, they provide a valuable basis for a long-term evaluation of the consequences of coring on the vitality of oaks. So far, only few studies have dealt with the long-term impacts of dendrochronological samplings on trees, and most of them focussed on conifers (van Mantgem and Stephenson 2004; Wunder et al. 2011). Therefore, such an investigation would significantly contribute to reducing the uncertainty related to the consequences of coring for deciduous trees. However, many cored oaks are located on permanent plots that were given up after the reorganization in 2006. To enable long-term recognition, the individual tags would need maintenance irrespective of the continuation of intensive monitoring.

(7) *Statistical developments*: The last recommendation may appear trivial at first sight: Forest scientists and ecologists are strongly encouraged to follow (if not actively advance)

developments in the fields of applied statistics and statistical computing (cf. Ellison and Dennis 2010). As pointed out above, complex statistical methods are increasingly applied in forest ecology. In fact, some methods used in this thesis were close to the limit of what is currently possible in statistical computing (e.g. convergence problems in Chapter III). An active tracking of statistical developments by forest scientists and ecologists is thus desirable for immediate implementation in forest science.

Conclusion

The study of monitoring data in my thesis revealed competition as the key driver of oak *mortality*, whereas strong effects of site characteristics and drought on oak *growth* were identified by analyzing tree-ring data. These findings indicate that for retaining the current proportion of oaks in Central European forests targeted management is needed. By combining monitoring and tree-ring data I developed a non-destructive method for tree age estimation, which is suggested to find application in the context of oak-related conservation.

References

Aas, G. (1998) Morphologische und ökologische Variation mitteleuropäischer *Quercus*-Arten: Ein Beitrag zum Verständnis der Biodiversität. Libri botanici 19. IHW-Verlag, Eching bei München.

Adler, F. R. (1996) A model of self-thinning through local competition. Proceedings of the National Academy of Sciences 93: 9980-9984.

Barbier, S., Gosselin, F. & Balandier, P. (2008) Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J. & Żybura, H. (1998) Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. Journal of Vegetation Science 9: 229-238.

Bernicchia, A., Benni, A., Venturella, G., Gargano, M. L., Saitta, A. & Gorjón, S. P. (2008) Aphyllophoraceous wood-inhabiting fungi on *Quercus* spp. in Italy. Mycotaxon 104: 445-448.

Biging, G. S. (1985) Improved estimates of site index curves using a varying-parameter model. Forest Science 31: 248-259.

Biging, G. S. & Dobbertin, M. (1995) Evaluation of competition indices in individual tree growth models. Forest Science 41: 360-377.

Bonfils, P., Horisberger, D. & Ulber, M. (2005) Förderung der Eiche. Strategie zur Erhaltung eines Natur- und Kulturerbes der Schweiz. Schriftenreihe Umwelt Nr. 383. proQuercus; Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern.

Bugmann, H., Commarmot, B., Meyer, P., Heiri, C., Wunder, J., Matter, J.-F. & Brang, P. (2011) Die Bedeutung von Naturwaldreservaten für die Forschung. In: Waldreservate. 50 Jahre Forschung in Schweizer Naturwäldern (eds P. Brang, C. Heiri & H. Bugmann), pp. 56-71. Haupt, Bern.

Bundesamt für Umwelt, Wald und Landschaft BUWAL (2005) Die Reservatstypen. Forstdirektion, Bern.

Bürgi, M. (1999) How terms shape forests: 'Niederwald', 'Mittelwald', and 'Hochwald', and their interaction with forest development in the Canton of Zürich, Switzerland. Environment and History 5: 325-344.

Burnham, K. P. & Anderson, D. R. (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Caprio, E., Ellena, I. & Rolando, A. (2009) Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy. Landscape Ecology 24: 65-76.

Clark, J. S., Wolosin, M., Dietze, M., Ibáñez, I., LaDeau, S., Welsh, M. & Kloeppel, B. (2007) Tree growth inference and prediction from diameter censuses and ring widths. Ecological Applications 17: 1942-1953.

Contran, N., Günthardt-Goerg, M. S., Kuster, T. M., Cerana, R., Crosti, P. & Paoletti, E. (2012) Physiological and biochemical responses of *Quercus pubescens* to air warming and drought on acidic and calcareous soils. Plant Biology (online). DOI: 10.1111/j.1438-8677.2012.00627.x.

Ellenberg, H. (2009) Vegetation ecology of Central Europe. Cambridge University Press, Cambridge.

Ellison, A. M. & Dennis, B. (2010) Paths to statistical fluency for ecologists. Frontiers in Ecology and the Environment 8: 362-370.

Fischer, A. M. (2011) Expected changes in extremes. In: Swiss climate change scenarios CH2011 (eds T. Corti, A. M. Fischer, A. Kress & P. Pall), pp. 47-55. C2SM; MeteoSwiss; ETH; NCCR Climate; OcCC, Zurich.

Fonti, P., Heller, O., Cherubini, P., Rigling, A. & Arend, M. (2012) Wood anatomical responses of oak saplings exposed to air warming and soil drought. Plant Biology (online). DOI: 10.1111/j.1438-8677.2012.00599.x.

Johnson, J. B. & Omland, K. S. (2004) Model selection in ecology and evolution. Trends in Ecology and Evolution 19: 101-108.

Kleinschmit, J. & Kleinschmit, J. G. R. (2000) *Quercus robur - Quercus petraea*: a critical review of the species concept. Glasnik Za Smske Pokuse 37: 441-452.

Korpeľ, Š. (1995) Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.

Lappi, J. & Bailey, R. L. (1988) A height prediction model with random stand and tree parameters: an alternative to traditional site index methods. Forest Science 34: 907-927.

Leibundgut, H. (1993) Europäische Urwälder: Wegweiser zur naturnahen Waldwirtschaft. Haupt, Bern.

Matter, J.-F. (2004) Waldreservate Professur Waldbau ETH-Zürich: Projekt-Dokumentation & Projekt-Stand. Unpublished report. Institut für Waldbau, ETH Zürich, Zürich.

Mountford, E. P., Peterken, G. F., Edwards, P. J. & Manners, J. G. (1999) Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Plant Ecology, Evolution and Systematics 2: 223-272.

Mühlethaler, U. (2008) Ein Plädoyer für die Eichenförderung. Schweizerische Zeitschrift für Forstwesen 159: 98-102.

Parker, G. R. & Leopold, D. J. (1983) Replacement of *Ulmus americana* L. in a mature east-central Indiana woods. Bulletin of the Torrey Botanical Club 110: 482-488.

Pinheiro, J. C. & Bates, D. M. (2000) Mixed-effects models in S and S-PLUS. Springer, New York.

Průša, E. (1985) Die böhmischen und mährischen Urwälder - ihre Struktur und Ökologie. Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prag.

Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85-94.

Rozas, V. (2003) Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecology 167: 193-212.

Stahel, W. A. (2008) Statistische Datenanalyse: Eine Einführung für Naturwissenschaftler. Friedrich Vieweg & Sohn Verlag, Wiesbaden.

Thomas, F. M., Blank, R. & Hartmann, G. (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. Forest Pathology 32: 277-307.

van Mantgem, P. J. & Stephenson, N. L. (2004) Does coring contribute to tree mortality? Canadian Journal of Forest Research 34: 2394-2398.

Weber, P., Bugmann, H., Fonti, P. & Rigling, A. (2008) Using a retrospective dynamic competition index to reconstruct forest succession. Forest Ecology and Management 254: 96-106.

Weber, P., Bugmann, H. & Rigling, A. (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. Journal of Vegetation Science 18: 777-792.

Weigel, A. P. & Fischer, A. M. (2011) Climate scenarios of seasonal means. In: Swiss climate change scenarios CH2011 (eds T. Corti, A. M. Fischer, A. Kress & P. Pall), pp. 29-39. C2SM; MeteoSwiss; ETH; NCCR Climate; OcCC, Zurich.

Wunder, J., Reineking, B., Hillgarter, F.-W., Bigler, C. & Bugmann, H. (2011) Long-term effects of increment coring on Norway spruce mortality. Canadian Journal of Forest Research 41: 2326-2336.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009) Mixed effects models and extensions in ecology with R. Springer, New York.

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