Technische Universität München
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Structure, growth and drought stress response of European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), true service tree (*Sorbus domestica* L.) and wild service tree (*Sorbus torminalis* (L.) Crantz)

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List of abbreviations

ACS	angle count sample
AIC	Akaike Information Criterion
cpa	crown projection area (m^2)
cl	crown length (m)
cd	crown diameter (m)
CI	Hegyi competition index
dbh	diameter at breast height (1.3 m) (cm)
DMI	De Martonne Aritidy Index
DED	Dutch elm disease
h	height (m)
hcb	height of crown base (m)
vs	stem volume (m^3)
SPEI	Standardised Precipitation Evapotranspiration Index
SMI	Soil Moisture Index
RWI	Ring-width index
Rt	Resistance
Rc	Recovery
Rs	Resilience

Abstract

The effects of climate change on Central European forests have become more evident in the last two decades. Current main tree species suffer from frequent and severe heat and drought events. Their share of forest area is decreasing, and there is an urgent need to adapt forests to the new climatic conditions. In this context, rare native tree species are increasingly considered promising alternatives and additions to the current main tree species in forests facing climate change. In the past, these species were often neglected in favour of fast-growing and economically more demanded species. Therefore, there was little engagement to examine the rare species and to improve their silvicultural concepts. However, it is necessary to know their growth patterns, drought tolerance, and space requirements for feasible management. This thesis investigated five rare native tree species (European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), wild service tree (*Sorbus torminalis* (L.) Crantz) and true service tree (*Sorbus domestica* L.)) concerning (I) their general allometric coefficients, space requirements and silvicultural treatment, (II) their general growth characteristics and yield levels on the single-tree level, and (III) their drought stress response. Throughout, results were compared to the more established oak (sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.)) and, besides true service tree, European beech (*Fagus sylvatica* L.). As they are well-known Central European tree species, a broad knowledge about their growth and drought response across wide geographical ranges is available. Bringing the results of European beech and oak in relation to the rare native species allows for categorising their growth and drought reaction and contextualising their performance.

To analyse European hornbeam, European white elm, field maple and wild service tree data from eight temporary research plots located on seven sites across south-eastern Germany was used, augmented by data from long-term plots. Using quantile regression, fundamental relationships between crown projection area and diameter and height and diameter were investigated. Subsequently, with a mixed-effect model, the dependence of crown allometry on different stand variables was detected. The derived maximum stem numbers per hectare for each species at different stand heights provide much-needed practical guidelines for forest managers. In the early stages of stand development, European white elm and field maple can be managed with higher stem numbers than European beech, similar to oak ones. European hornbeam and wild service tree require lower stem numbers, similar to European beech. However, the rare native tree species must be released from competitors during the first or second thinnings, as shade tolerance and competitiveness decrease with age. Furthermore, thinnings must be

performed at a higher frequency in stands with admixed European beech because of the specie‘s high shade tolerance. When properly managed, rare species can reach target diameters similar to oak and beech (Schmucker et al. 2022; see Chapter 3.1 and Appendix A).

Until now, the drought resistance of European hornbeam, European white elm, field maple, and wild service tree was mainly determined by observations of their natural distribution range and experiences of forest managers. Scientifically confirmed data was missing. This thesis used tree-ring data to evaluate species-specific growth characteristics and variability and quantify the reaction to single drought events, depending on the site and tree variables. The results show that besides European white elm, the rare species showed an overall lower annual growth with a higher growth variability than European beech and oak. However, especially field maple and wild service tree were better adapted to drought than European beech and partially even recovered better than oak. Combining the aspects of growth stability and drought tolerance, it can be concluded that rare native tree species are well suited as admixed species in future forest stands. European hornbeam is a suitable match for European beech on wetter sites, while field maple and wild service tree are a sensible complement for the climate-stable oak on drier sites (Schmucker et al. 2023; see chapters 3.2, 3.3 and Appendix B).

Among the species studied, the true service tree takes a special position. It is the rarest of the five species, with a very low occurrence in Central Europe. Due to its appealing flowers and fruits, it is of great interest for its use in forests and urban environments. This thesis used measurements from true service trees growing in forests and cities in Germany, southern Scandinavia, northern Italy, and Slovakia to determine the specie’s allometric relationships and space requirements. Additionally, tree cores from Germany and Slovakia and stem disks of a true service tree in Copenhagen were used to study growth patterns and drought stress response. The results indicated that true service tree and oak have similar growth patterns and space requirements. True service tree and oak had a fast growth in their youth, followed by a gradual reduction at later stages. The crown projection area of the true service tree was similarly influenced by competitors as that of oak, indicating a similar sensitivity towards competition. Likewise, similarities in growth response to drought and, hence, drought tolerance were identified. Due to their comparable growth pattern and drought tolerance, it was hypothesised that oak, in many regards, can be used as a model species for the management of true service tree (Schmucker et al. (in press); see chapters 3.1, 3.2, 3.3 and Appendix C).

Zusammenfassung

Die Auswirkungen des Klimawandels auf die Wälder in Mitteleuropa sind in den letzten beiden Jahrzehnten immer offensichtlicher geworden. Die derzeitigen Hauptbaumarten leiden unter häufigen und schweren Hitze- und Dürreperioden. Ihr Anteil an der Waldfläche nimmt ab, und es besteht ein dringender Bedarf, die Wälder an die neuen klimatischen Bedingungen anzupassen. In diesem Zusammenhang werden seltene heimische Baumarten zunehmend als vielversprechende Alternativen und Ergänzungen zu den derzeitigen Hauptbaumarten in Wäldern betrachtet. In der Vergangenheit wurden diese seltenen Arten oft zugunsten schnell wachsender und wirtschaftlich gefragterer Arten vernachlässigt. Daher gab es wenig Interesse, die Arten genauer zu untersuchen und ihre waldbaulichen Konzepte zu verbessern. Für eine angepasste Bewirtschaftung ist es jedoch notwendig, ihre Wachstumsmuster, Trockenheitstoleranz und Platzbedarf zu kennen. Diese Arbeit untersucht die fünf seltenen heimischen Baumarten Hainbuche (*Carpinus betulus* L.), Flatterulme (*Ulmus laevis* Pall.), Feldahorn (*Acer campestre* L.), Elsbeere (*Sorbus torminalis* (L.) Crantz) und Speierling (*Sorbus domestica* L.) in Bezug auf (I) ihre allgemeinen allometrischen Zusammenhänge, Platzbedarf und waldbauliche Behandlung, (II) ihre allgemeinen Wachstumsmerkmale und Ertragsniveaus auf Einzelbaumebene und (III) ihre Reaktion auf Trockenstress. Die Ergebnisse wurden mit den der etablierten Baumarten Eiche (Traubeneiche (*Quercus petraea* (Matt.) Liebl.) und Stieleiche (*Quercus robur* L.)) und, abgesehen vom Speierling, Rotbuche (*Fagus sylvatica* L.) verglichen. Diese Arten sind weit verbreitet in Mitteleuropa und es gibt umfangreiche Kenntnisse über ihr Wachstum und ihre Reaktion auf Trockenstress. Der Vergleich der Ergebnisse der Buche und der Eiche zu den seltenen heimischen Arten ermöglichen die Einordnung ihres Wachstums, ihrer Trockenstressreaktion und ihrer Leistungspotentials.

Für die Untersuchung von Hainbuche, Flatterulme, Feldahorn und Elsbeere wurden Daten von acht temporären Versuchsflächen an sieben Standorten in Südostdeutschland verwendet, ergänzt durch Daten von langfristigen Versuchsflächen. Unter Verwendung von Quantilregression wurden grundlegende Beziehungen zwischen Kronenprojektionsfläche und Durchmesser sowie Höhe und Durchmesser untersucht. Anschließend wurde mithilfe eines gemischten linearen Modells die Abhängigkeit der Kronenallometrie von verschiedenen Bestandesvariablen ermittelt. Die abgeleiteten maximalen Stammzahlen pro Hektar für jede Art bei verschiedenen Bestandeshöhen bieten dringend benötigte praktische Richtlinien für Forstleute. In den frühen Entwicklungsstadien können Flatterulme und Feldahorn mit höheren Stammzahlen bewirtschaftet werden als die Buche, ähnlich wie Eichen. Hainbuche und Elsbeere erfordern

niedrigere Stammzahlen, ähnlich wie die Buche. Die seltenen heimischen Baumarten müssen jedoch während der ersten oder zweiten Durchforstung von Konkurrenten befreit werden, da die Schattentoleranz und Konkurrenzstärke mit dem Alter abnehmen. Darüber hinaus müssen in Beständen mit beigemischter Buche aufgrund ihrer hohen Schattentoleranz die Durchforstungen in höherer Frequenz durchgeführt werden. Bei einer ordnungsgemäßer Bewirtschaftung können die seltene Arten ähnliche Zielstärken wie Eiche und Buche erreichen (Schmucker et al. 2022; siehe Kapitel 3.1 und Anhang A).

Bisher wurde die Trockentoleranz von Hainbuche, Flatterulme, Feldahorn und Elsbeere hauptsächlich durch Beobachtungen ihres natürlichen Verbreitungsgebiets und Erfahrungen von Forstleuten bestimmt. Wissenschaftlich gesicherte Daten fehlten. In dieser Arbeit wurden Jahrringdaten verwendet, um die artspezifischen Wachstumsmuster und ihre Variabilität zu bewerten, den Einfluss von Standort- und Baummerkmalen auf das jährliche Wachstum zu untersuchen und die Reaktion auf einzelne Dürreereignisse zu quantifizieren. Die Ergebnisse zeigen, dass die seltenen Arten im Vergleich zu Buche und Eiche insgesamt ein geringeres jährliches Wachstum mit höherer Variabilität aufwiesen. Allerdings waren insbesondere Feldahorn und Elsbeere besser an Trockenheit angepasst als die Buche und erholten sich teilweise sogar besser als die Eiche. Durch die Kombination von Wachstumsstabilität und der Trockenheitstoleranz kann geschlossen werden, dass seltene heimische Baumarten gut als Mischbaumarten in zukünftigen Waldbeständen geeignet sind. Die Hainbuche ergänzt gut die Buche auf frischen Standorten, während Feldahorn und Elsbeere eine sinnvolle Ergänzung zur klimastabilen Eiche auf trockeneren Standorten darstellen (Schmucker et al. 2023; siehe Kapitel 3.2, 3.3 und Anhang B).

Der Speierling nimmt unter den in dieser Arbeit untersuchten Arten eine Sonderstellung ein. Er ist die seltenste der fünf Arten mit einem sehr geringen Vorkommen in Mitteleuropa. Aufgrund seiner ansprechenden Blüten und Früchte ist er nicht nur für die Verwendung in Wäldern von großem Interesse, sondern auch in städtischen Umgebungen. In dieser Arbeit wurden Messungen von Speierlingen aus Wäldern und Städten in Deutschland, Südskandinavien, Norditalien und der Slowakei verwendet, um die allometrischen Beziehungen und Platzbedarf der Art zu bestimmen. Zusätzlich wurden Bohrkerne aus Deutschland und der Slowakei und Stammscheiben eines Speierlings aus Kopenhagen verwendet, um Wachstumsmuster und die Reaktion auf Trockenstress zu untersuchen. Die Ergebnisse zeigten, dass der Speierling und die Eiche ähnliche Wachstumsmuster und Platzbedarf aufweisen. Beide zeigten in ihrer Jugend ein schnelles Wachstum, gefolgt von einer allmählichen Reduzierung in späteren Stadien. Die

Kronenprojektionsfläche des Speierlings wurde ähnlich von Konkurrenten beeinflusst wie die der Eiche, was auf eine ähnliche Empfindlichkeit gegenüber Konkurrenz hinweist. Ebenso wurden Ähnlichkeiten in der Reaktion auf Trockenheit und somit in der Trockentoleranz festgestellt. Aufgrund ihres vergleichbaren Wachstumsmusters und ihrer Trockentoleranz wird angenommen, dass die Eiche in vielerlei Hinsicht als Modellart für die Bewirtschaftung des Speierlings verwendet werden kann (Schmucker et al. (in press); siehe Kapitel 3.1, 3.2, 3.3 und Anhang C).

Article Overview

This dissertation is a cumulative thesis based on three peer-reviewed articles. The following provides the original abstract, publication status, journal information, and author contributions. The articles are attached to this thesis in Appendix A-C or can be accessed via the DOI. Additionally, Appendix D provides a complete overview of contributions and other studies taken out in the framework of this thesis.

Article I

Crown allometry and growing space requirements of four rare domestic tree species compared to oak and beech: implications for adaptive forest management

Julia Schmucker, Enno Uhl, Mathias Steckel, Hans Pretzsch

Published in 2022 in the European Journal of Forest Research 141.4, 587-604

DOI: https://doi.org/10.1007/s10342-022-01460-w

Journal impact factor: 2.8 (2022)

Abstract: Rare domestic tree species are increasingly being viewed as promising alternatives and additions to current main tree species in forests facing climate change. For feasible management of these rare species, it is, however, necessary to know their growth patterns and space requirements. This information has been lacking in management and science up to now. Our study investigated the basic crown allometries of four rare domestic tree species (European hornbeam, European white elm, field maple and wild service tree) and compared them to the more established and assessable European beech and oak (sessile oak and pedunculate oak). For our analysis, we used data from eight temporary research plots located on seven sites across south-eastern Germany, augmented by data from long-term plots. Using quantile regression, we investigated the fundamental relationships between crown projection area and diameter, and height and diameter. Subsequently, we used a mixed-effect model to detect the dependence of crown allometry on different stand variables. We derived maximum stem numbers per hectare for each species at different stand heights, thus providing much-needed practical guidelines for forest managers. In the early stages of stand development, we found that European white elm and field maple can be managed with higher stem numbers than European beech, similar to those of oak. European hornbeam and wild service tree require lower stem numbers, similar to European beech. However, during first or second thinnings, we hypothesise that the rare domestic tree species must be released from competitors, as shade tolerance and competitiveness decrease with age. Furthermore, we argue that thinnings must be performed at a higher frequency in stands with admixed European beech because of the species' high shade tolerance. When properly managed, rare species can reach target diameters similar to oak and beech.

Individual contributions: Development and conceptual design of the research project: 15 %, Gathering, collection, acquisition or provision of data, software or sources: 95 %,

Analysis/evaluation or interpretation of data, sources and conclusions drawn from them: 90 %,
Drafting of the manuscript 95 %

Article II

Growth and drought reaction of European hornbeam, European white elm, field maple and wild service tree

Julia Schmucker, Enno Uhl, Gerhard Schmied, Hans Pretzsch

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Journal impact factor: 2.3 (2022)

Abstract: In our study, we assessed the growth and drought reaction of the four rare native tree species European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), and wild service tree (*Sorbus torminalis* (L.) Crantz). Based on tree-ring data, we (I) evaluated their species-specific growth characteristics and variability and examined the influencing site and tree characteristics on annual growth. (II) We quantified their reaction to single drought events, also depending on site and tree variables. (III) We compared our results to oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.). As they are well-known Central European tree species, there is a broad knowledge about their growth and drought response across wide geographical ranges available. Bringing the results of European beech and oak in relation to the rare native species allows us to categorise their growth and drought reaction and to contextualise their performance. Our results show, that besides European white elm, the rare species showed an overall lower annual growth with a higher variability than European beech and oak. However, especially field maple and wild service tree were better adapted to drought than European beech and partially even recovered better than oak. Combining the aspects of growth stability and drought tolerance, we conclude that rare native tree species are well suited as admixed species in future forest stands. European hornbeam is a suitable match for European beech on wetter sites, while field maple and wild service tree are a sensible complement for the climate-stable oak on drier sites.

Individual contributions: Development and conceptual design of the research project: 20 %, Gathering, collection, acquisition or provision of data, software or sources: 75 %, Analysis/evaluation or interpretation of data, sources and conclusions drawn from them: 90 %, Drafting of the manuscript: 95 %

Article III

Crown structure, growth, and drought tolerance of true service tree (*Sorbus domestica* L.) in forests and urban environments

Julia Schmucker, Jens Peter Skovsgaard, Enno Uhl, Hans Pretzsch

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True service tree (*Sorbus domestica* L.) is a rare native species of Central Europe. It grows well in dry and warm environments and may consequently be well adapted to the expected future climate further north. It is considered a potentially suitable species for climate change adaptation in forests and urban environments. In this study, we used total tree height, stem diameter, and crown dimensions from true service trees in Germany, southern Scandinavia, northern Italy, and Slovakia to determine the specie's allometric relationships and space requirements. Additionally, we used tree cores from Germany and Slovakia and stem disks of a true service tree in Copenhagen to study growth patterns and drought stress response. Throughout, we compared to oak (mainly *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) as common and well-studied species. Our results indicated that true service tree and oak have similar growth patterns and space requirements. True service tree and oak both had a fast growth in their youth, followed by a gradual reduction at later stages. The crown projection area of true service tree was similarly influenced by competitors as that of oak, indicating a similar sensitivity towards competition. Likewise, we identified similarities in growth response to drought and, hence, drought tolerance. Due to their comparable growth pattern and drought tolerance, we hypothesise that oak, in many regards, can be used as a model species for the management of true service tree.

Individual contributions: Development and conceptual design of the research project: 35 %, Gathering, collection, acquisition or provision of data, software or sources: 90 %, Analysis/evaluation or interpretation of data, sources and conclusions drawn from them: 90 %, Drafting of the manuscript: 90 %

1. Introduction

1.1 Motivation

In Central Europe, rare native tree species are increasingly considered promising alternatives and additions to the current main tree species in forests facing climate change. Especially European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus leavis* Pall.), field maple (*Acer campestre* L.), true service tree (*Sorbus domestica* L.) and wild service tree (*Sorbus torminalis* (L.) Crantz) seem to be auspicious species. In the past, they were often neglected in favour of fast-growing and economically more demanded species. Forest managers prioritised tree species that were easier to manage due to their higher competitive strength, yield, shade tolerance and lower susceptibility towards browsing. Most notably, European hornbeam, field maple and wild service tree, once important species of coppice forests (Bayerischer Forstverein 1997; Helfrich and Konolw 2010; Pyttel et al. 2013; Unrau et al. 2018), lost their relevance with the shift towards high forest systems combined with longer rotation cycles. The habitat of European white elm, a species of riparian systems, decreased due to a land use change and straightening of watercourses. In the past, the wood of native broadleaved species was often used for specific products or uses that lost their importance or got substituted by other materials. The low use of native tree species in European silviculture and the loss of their natural habitat has resulted in a small occurrence and great rarity. Today, those tree species predominantly grow on sites with extreme conditions, under special protection or, in the case of the European hornbeam, as an understorey species for promoting the production of high-quality oak timber (Bartsch et al. 2020). Under these conditions, they can not reach their full growth potential and are often considered minor species, only growing in the second layer of a stand.

Therefore, current scientific research on alternative tree species mainly focuses on a few non-native species which seem particularly economically promising (Burkardt et al. 2019; del Río et al. 2019; Thurm et al. 2017). However, compared to native species, species from other regions or continents have many disadvantages. Their exposure to pests, wood quality, and influence on other ecosystem services are widely unexplored (Castro-Díez et al. 2019; Matevski and Schuldt 2021; Sapsford et al. 2020). Furthermore, they are possibly not adopted by native flora and fauna and are potentially invasive. Non-native species might especially be maladapted to colder winter temperatures and late frost events, which are also expected to increase in the future (Kreyling et al. 2015; Vitasse et al. 2019; Zohner et al. 2020). Much time-consuming and elaborate research must be done for non-native species to clarify all the potential risks. Given the rapidly progressing climate change, the time for this research is often not given. For native species, all the above points are widely known (Castro-Díez et al. 2019; Matevski and Schuldt 2021; Sapsford et al. 2020). Because of their geographical origin in Central Europe, they are genetically adapted to the ecosystem and its climate conditions (Kreyling et al. 2015). An immediate increased cultivation would be possible and low in risks, considering the consequences for the ecosystem. However, there are still considerable gaps in knowledge regarding the specific structure, growth and drought tolerance of European hornbeam, European white elm, field maple, true service tree and wild service tree in Central Europe, although these information are urgently needed to manage forest trees and trees in urban environments.

Knowledge about tree structure and the relationships between tree and crown variables provide an understanding of the growing space requirements of a tree species. Appropriate degrees of thinning on different sites and removal of adjacent trees can be elaborated by knowing those space requirements. Then, the optimal number of trees per hectare leads to an ideal use of the site's productive potential. In urban environments, the space occupation of the very limited space can be optimally calculated. Only species-appropriate silviculture, considering the growing-space requirements, can prevent a demixing to the detriment of the rare species (Pretzsch et al. 2021). Because of the close linkage between site- and species-specific conditions, the tree- and crown structure furthermore provide a magnitude of insights into growth characteristics. They can be used as an indicator to assess other ecological and economic aspects such as productivity (Pretzsch 2021b), carbon stocks and ecosystem services (Chave et al. 2014; Forrester et al. 2017a; Henry et al. 2013).

Tree structure is often assessed by allometric relationships. Comparing static ratios of tree characteristics of different groups (e.g. tree species or stands with different silvicultural treatments) is usually not purposeful, as the values underlie an allometric drift and differences and, therefore, often result from size differences (Pretzsch 2010a). The true divergence between groups becomes apparent only through allometric ratios, adjusted for size differences. Some theories state that there are universal allometric exponents for many anatomical and physiological relationships (e.g. metabolic rate, population density, self-thinning line and life span, relations between trunk and crown dimensions) in plants (Enquist et al. 1998; Enquist et al. 2009; L. H. Reineke 1933; Mäkelä and Valentine 2006; West et al. 1997; West et al. 2009; Yoda 1963). In the context of these theories, differences between groups are related to the size only. However, many studies rejected the universal validity of allometric exponents (Harper 1977; Pretzsch 2010a, 2014; Pretzsch and Biber 2005). They state that there are inter- (Pretzsch 2006; Pretzsch and Dieler 2012; Purves et al. 2007) and intra-specific (del Río et al. 2019; Dieler and Pretzsch

2013; Duursma et al. 2010; Pretzsch and Mette 2008) differences in allometry. Therefore, the research on the allometric relation on the species level is essential.

A tree's slenderness, described by its height-diameter ratio (h/d), can be used as a measure of the stability of a collective (Pretzsch 2019b). Lower h/d-values are associated with a longer crown, lower centre of gravity and a better-developed root system (Wang et al. 1998). The h/d-allometry can even be a proxy for wood properties (Øvrum 2013). By using h/d models, the costly and erroneous measurement of tree heights in inventories can be scaled down to the height measurement of only a few trees and the diameter measurement of the remaining trees (Bronisz and Mehtätalo 2020; MacPhee et al. 2018; Sharma et al. 2019). The allometric relationship between height and diameter is also a more reliable indicator of the stability of a collective than the static ratio (Pretzsch 2019b). Even more expressive is the examination of crown allometry. Crown variables are reliable indicators for tree health (Assman 1970; Zarnoch et al. 2004), vigour, growing stage, stability and production efficiency (Pretzsch and Schütze 2005). Crown size (determined by crown surface, crown projection area, crown length and crown width) is closely correlated with absorbed photosynthetic active radiation (APAR) (Binkley et al. 2013; Forrester et al. 2012) and leaf area (Forrester et al. 2013). When measuring crown parameters, they can be used as a proxy for leaf area and light interception (Pretzsch 2014). Additionally, crown sizes correlate with the growth of biomass or other parts of the tree, making them predictors for tree growth and to be used in biomass models (Sharma et al. 2017). Crown allometry and especially the allometries of crown projections area are crucial indicators for a tree's fitness and, thereby, also for its competitiveness and ability to occupy space (Pretzsch 2010a, 2019b). This, in turn, also affects the structure and dynamics of the whole stand (Enquist et al. 1998), e.g. by the self-thinning rule that takes effect (White et al. 2007; Yoda 1963). Crown projection area again is determined by the length of branches and, therefore, wood density (Kuprevicius et al. 2013). Higher wood density means less swinging and less abrasion of branches when contacting branches of neighbouring crowns (Juchheim et al. 2017; Putz et al. 1984). Higher wood density, therefore, results in longer branches and bigger crowns, especially in older stands (Hajek et al. 2015; Pretzsch 2019b). Crown and stem morphology also provide insight into wood quality (Rais et al. 2021). With the generated allometric functions forest functioning, fundamental morphological and physiological tree variables can be predicted (Forrester et al. 2017b).

For weighing out different species against each other and choosing sensible species for cultivation, it is, furthermore, necessary for forest managers to assess the potential growth of the species, as reliable and stable growth is an essential economic characteristic of tree species. A tree's growth during and after drought thereby represents a particular case of growth patterns. By addressing it, one can assess the species's drought tolerance. This is especially important, as the effects of climate change on temperate forests have become more evident in the last two decades. Central Europe has experienced several severe drought summers in recent years with high temperatures and low precipitation (Buras et al. 2020). The successive hot and dry summers caused damages and drought stress in significant parts of Germany, affecting stands of coniferous trees planted in monocultures in non-adequate sites as well as current main species that were previously assumed to be drought tolerant (Bundesministerium für Ernährung und Landwirtschaft 2021; Schuldt et al. 2020; Thurm et al. 2018). Persistent climatic changes will increase current issues and will further enhance the risk of growth decline, forest mortality (Allen et al. 2010; Allen et al. 2015; Senf et al. 2020), and diminish forest productivity (Rita et al. 2020), diversity, and carbon storage (Pilli et al. 2022). The composition of Central European forests is expected to change due to different drought resistance of tree species. The share of current main tree species in forest area will further decrease, and there is an urgent need to adapt forests to the new climatic conditions to maintain their functions in the future. It is also crucial to further evaluate the potential of rare native tree species to cope with climate change to develop adapted management strategies for Central European forests. Hence, more information on the drought response patterns of these species is urgently needed.

1.2 State of knowledge

Structure and allometric relationships of the species dealt with in this thesis are widely unknown. Studies addressing the height-diameter relationship of the species mostly include them as part of many species and focus on the general influence of ecological factors as climate (Fortin et al. 2019 for European hornbeam, field maple and wild service tree) or competition on the allometry (Forrester et al. 2017b for European hornbeam) rather than providing basic allometric equations. Only for wild service tree there is a height-diameter equation available (Pyttel et al. 2013). Kausch-Blecken von Schmeling (2000) and Skovsgaard and Graversgaard (2013) published some basic height-diameter and age-height relationships for true service tree. Cisneros et al. (2006) and Coello et al. (2013) published recommendations for stand density and potential target diameters, however, without presenting their underlying methodology. Concerning the crown structure, crown plasticity based on crown radius and centricity of rare species was addressed by Longuetaud et al. (2013), who found a high plasticity of European hornbeam and plasticity in the middle field for wild service tree and field maple. Allometric relations between crown projection area and diameter of European hornbeam were also addressed in Pretzsch et al. (2015), however with a focus on city trees. For true service, so far, only Paganová et al. (2015) described different types of crown shapes for true service trees in urban environments in Slovakia. Studies on general allometric relationships, also in forests, are scarce. Other allometric relationships for the species were addressed as biomass equations of European hornbeam based on its diameter (Forrester et al. 2017a; Suchomel et al. 2012). Only for field maple recommendations on stem numbers per hectare exist, however, not differentiating between different species of the genus "maple" (Klädtke and Abetz 2010). For European white elm, there is no information existing at all.

Basic functions aimed at competitiveness and direct space requirements of the rare native tree species are still missing. There are no precise specifications or references to tree spacing requirements for European hornbeam, European white elm, true service tree, wild service tree or field maple, even in many silvicultural guidelines.

Besides structure and allometric relationships, the general growth patterns of the species dealt with in this thesis are also widely unknown. Only for European hornbeam, a yield table for Northern Germany exists (Lockow 2009). For wild service tree, Pyttel et al. (2013) used stem analysis to determine annual increments and deduced age-height curves. Other than that, no knowledge about the species' growth exists. Several current research projects throughout Europe address rare native tree species, mainly in the context of provenance trials to test their adaptivity to climate change. For instance, of the species treated in this work, the wild service tree is included in Swiss planting trials (Frei et al. 2018) and together with field maple, among others, as part of a study to examine the reforestation of former vineyards in South-western Germany (Kunz and Bauhus 2015). Research has also been carried out to define the genetic provenances of the wild service tree in Southern Germany (Kavaliauskas et al. 2021). Similar projects for white elm and field maple are planned or in operation. Liesebach et al. (2021) propose establishing additional provenance trials for field maple and wild service tree in Germany. For true service tree experiments have been planted in Denmark and Sweden to observe the survival, growth and health of different provenances (Jansson 2017; Skovsgaard et al. 2017; Skovsgaard and Graversgaard 2013), likewise in Slovakia (Bakay and Rovná 2021) and Italy (Piagnani et al. 2018). Concerning its growth, most available studies focus on young trees, typically seedlings or saplings and generally cover only the first few years of growth (Kunz et al.

2016; Paganová et al. 2014). In general, to the author's best knowledge, there are no long-term experimental plots of the rare species in Europe to deal with growth or yield.

Concerning the drought tolerance of the rare species dealt with in this thesis, studies of adult trees are currently scarce and their detailedness differs between species. Often, the literature is based on observations of the natural distribution range or green-house experiments with seedlings. Mature European hornbeams were found to withstand severe and short droughts due to a relatively stable sap flow under stress conditions (Leuzinger et al. 2005). Seedlings, however, showed a high drought sensitivity, but also a high capacity to recover (Beloiu et al. 2020). Also Scharnweber et al. (2020) found a strong growth decline of mature European hornbeams after the drought of 2019. Knowledge about the drought tolerance of European white elm is mainly derived by its current distribution range that covers climates from dry and cool to warm and moist (Collin and Bozzano 2015). This range is expected to stay (Koch et al. 2022) or even expand (Thurm et al. 2018) in central Europe under predicted climate change scenarios. A study on sapling did not find an influence of mild drought stress does not have an influence on morphological traits (Black-Samuelsson et al. 2003). However, drought reactions may highly vary between different provenances (Black-Samuelsson et al. 2003; Venturas et al. 2015). Leonova et al. (2022) found that European white elm, similar to oak, can maintain or enlarge the amount of fine root biomass under drought conditions. Also for field maple the current distribution range is often used to assess a high drought tolerance, as it is favouring a mild climate with low autumn precipitation and does not occur in regions with high precipitation (Coudun et al. 2006). In a previous study field maple showed a high drought tolerance, even exceeding that of oak (Kunz et al. 2018). In a greenhouse experiment, seedlings were found to have a high drought resistance (Kunz et al. 2016), which could however not be confirmed under field conditions where a high mortality and low recovery was noted (Beloiu et al. 2020). In general, field maple is expected to be well adapted to future climate change scenarios (Walentowski et al. 2014). Also the wild service tree is currently growing in warm and dry parts of Europe (Rasmussen and Kollmann 2004) which are regions that correspond to future climate conditions in Central Europe. This adaptation makes the wild service tree a promising tree species under climate change conditions (Walentowski et al. 2014). A recent study noticed a higher drought tolerance than European beech, but not than oak (Kunz et al. 2018). Seedlings are sensitive to drought, but recover quickly afterwards (Kunz et al. 2016). Also descriptions of the drought tolerance and heat sensitivity of true service tree are often based on observations and considerations of the current range of distribution (e.g., Cisneros et al. 2006; Coello et al. 2013; Gonin et al. 2013; Rueda Salgueiro et al. 2006) rather than on experimental evidence or other quantitative indicators. However, due to the use of the true service tree for fruit production, its range of distribution is highly influenced by human activity (Drapier 1993; Kausch-Blecken von Schmeling 2000; Skovsgaard and Graversgaard 2013), resulting in potentially biased interpretations and conclusions. So far, only two dendroecological studies of adult trees have been carried out and with contrasting results: Kunz et al. (2018) found the drought tolerance of true service tree to be marginally lower than that of oak, while Camarero et al. (2023) found it to be marginally higher. In general, most studies are based on experiments with seedlings or young plants or simulations (e.g. Kunz et al. 2016; Thurm et al. 2018; Varol et al. 2022). In summary, the current study situation and literature indicates a high drought tolerance of the five species, which is, however, by far not fully explored and needs further research.

1.3 Outline and objective

The overarching objective of this thesis was to get closer insights into the structure, growth, and drought tolerance of the rare native species European hornbeam, European white elm, field maple, true service tree and wild service tree. These information enable forest managers to carefully select site-adequate tree species and to manage them to fully utilise their potential.

Tree structure was assessed through allometric relationships between crown and stem variables, making it possible to deduce information about space requirements and ecological characteristics of the species. For this, data from measurements of crown and stem variables of the rare species collected in Southeast Germany was used. For European hornbeam additional data from Poland was included, for true service tree measurements form Scandinavia, Slovakia and Northern Italy. Insights into general growth characteristics were obtained by analysing tree ring data from extracted tree cores of single trees. Growth was assessed both as increment over time and growth variability displayed by the Gini-coefficient. Finally, predictions of the species' drought tolerance were made by further examining the growth data with a focus on the increment before, during and after selected drought years. To make results for the rare species easier accessible for forest managers and forest scientists, they were compared to European beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) in this thesis. Data of these species was collected with the same methods from trees in close vicinity to the rare species. European beech and oak are the dominant deciduous tree species in central Europe (Meyer et al. 2020), so their growth and drought reactions are already well-studied and widely known. Therefore, they are well-suited indicator species for the characterisation of the five rare species treated in this thesis.

As studies about the structure and growth of European hornbeam, European white elm, field maple, true service tree and wild service tree are scarce (see chapter 1.2), this thesis provides urgently needed information for forest managers and scientists. Furthermore, the results of this work provide a useful basis for further research on the topic of rare native tree species.

These objectives can be summarised in the following three questions that provide the framework of the thesis:

Q1: What are the general allometric coefficients of the five rare native tree species, what are their space requirements, and which silvicultural treatment can be derived from this?

Q2: What are the species' general growth characteristics and yield levels on the single-tree level?

Q3: How do the species respond to drought events?

Figure 1 gives an overview of the three questions and their connection.

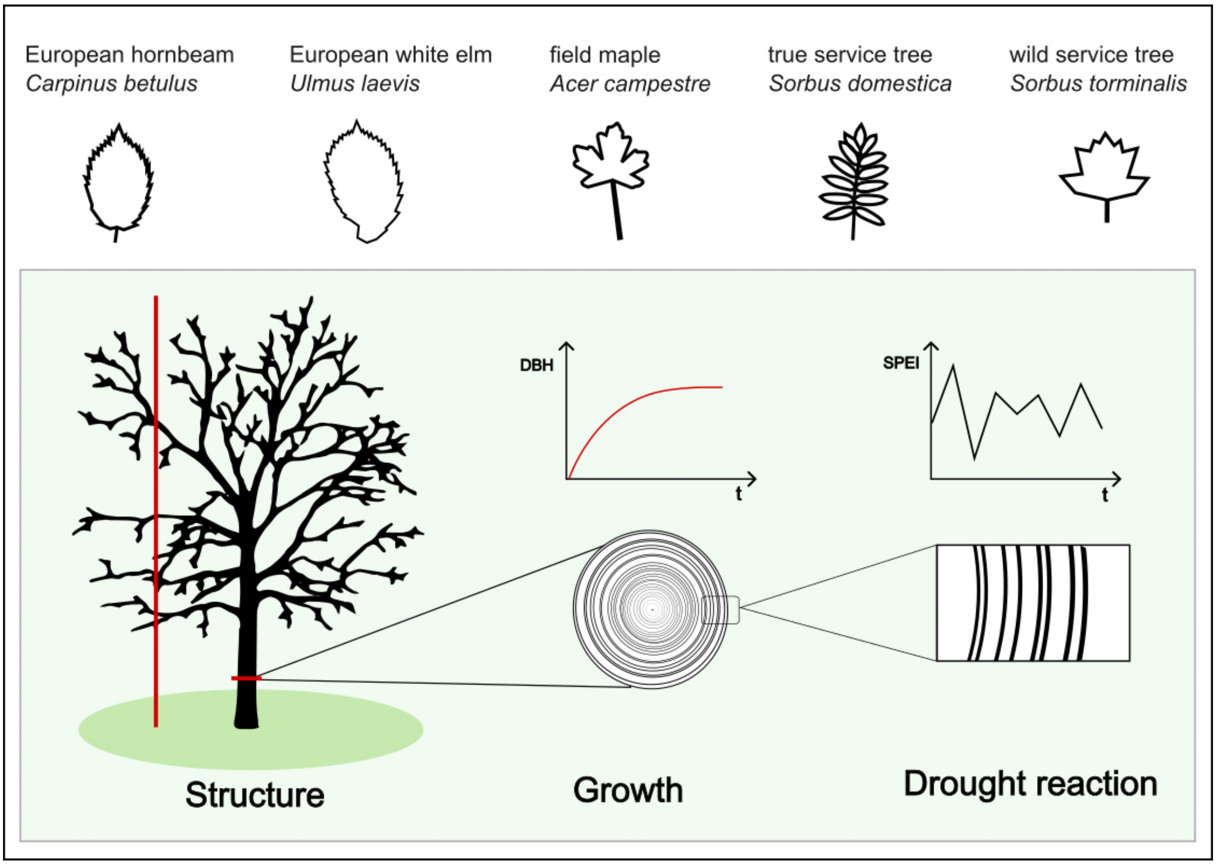

Figure 1 General framework of the cumulative thesis.

2. Material and Methods

2.1 Material

2.1.1 Study sites and measurements

Article 1: Allometry and growing space requirements of European hornbeam, European white elm, field maple and wild service tree

Data from experimental plots in Bavaria, Germany, was used to analyse the allometric relationships of European hornbeam, European white elm, field maple and wild service tree (Article I). The primary data source was measurements from temporary plots of the species. These plots were specifically established in stands with a large proportion of the target species. For each species, two plots on each of two sites were established (Figure 2).

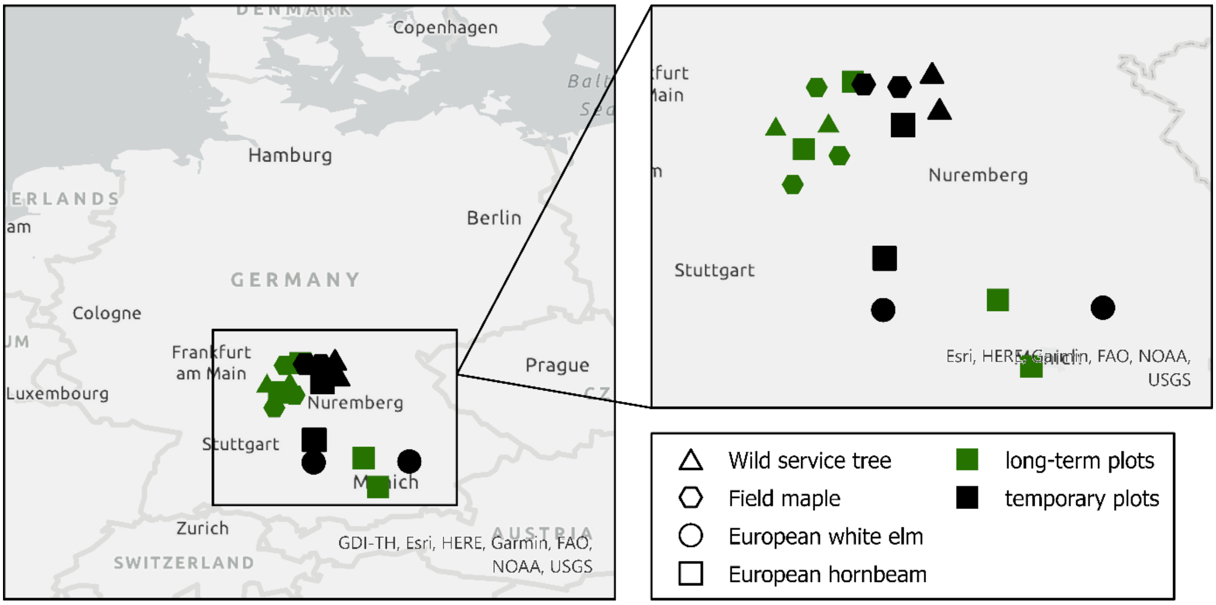

Figure 2 Geographic location of the experimental plots used in the study. The shape of the symbols refers to the tree species, and the colour refers to the plot type: Green symbols refer to the long-term experimental plots, and black symbols refer to newly established plots for the study.

Trees were measured in two different aged stands on each site to cover as broad an age spectrum as possible (Figure 3). Trees were measured within the borders of newly established plots in areas with a high proportion of the species under scrutiny, favouring mono-specific stands where possible. Also, data from 15 oaks or European beeches was collected, depending on the occurrence at each plot. No distinction was made between sessile and pedunculate oak. Both species were grouped as oak. The oak and beech trees were preferably of the same age (according to information of the management plan) or had a similar diameter and grew under the same site conditions as the targeted rare species. Data were collected in winter 2020/2021. The data was extended with measurement from the network of long-term experimental plots maintained by the Chair of Forest Growth and Yield Science at the Technical University of Munich, Germany. Although no specific experimental plots are dedicated to observing European hornbeam, field maple and wild service tree, single individuals often occur on the plots. European white elm is not distinguished explicitly in the database, only as *Ulmus* spec., and could, therefore, not be used. Furthermore, measurements of all European beeches and oak trees on the long-term plots containing the rare native species studied were included. Both the data sources included trees with a minimum diameter of 7 cm at a height of 1.30 m. The mean temperature and precipitation on the plots can be obtained from Table 1.

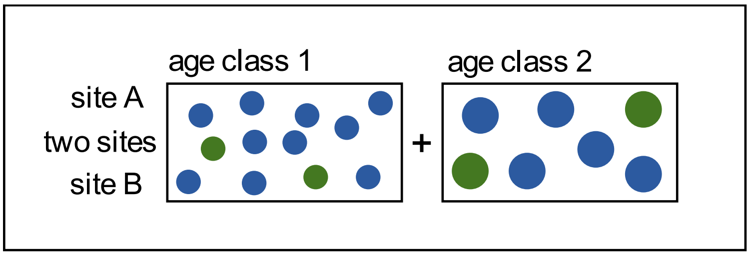

Figure 3 Experimental design of the temporary plots. The black boxes stand for the almost pure stands of the target species. Blue circles represent the target species, and green circles represent single trees of admixed species.

Table 1 Annual precipitation (mm) and mean temperature (°C) of plots used in Article I . Location numbers refer to long-term yield plots.

Location	Annual precipitation sum (mm) (1991 – 2020)	Mean annual temperature (°C) (1991 – 2020)
Schweinfurt (SCH)	736.3	8.9
Sailershausen (SAI)	663.9	9.5
Baunach (BAU)	744.6	9.1
Ebrach (EBR)	765.8	8.6
Wallerstein (WAL)	786.8	8.9
Offingen (OFF)	753.5	9.2
Freising (FRS)	708.9	9.4
102	629.6	9.9
105	714.8	9.4
106	679.4	9.6
132	706.4	9.0
133	762.6	8.6

140	1043.3	9.1
638	688.1	9.2
640	814.3	8.3
648	627.9	9.0
801	979.5	8.9
803	717.7	9.1
804	754.1	9.0
832	746.4	9.2
851	777.8	9.1
852	901.1	7.7

Tree height (h), crown base height (cbh) (height of the first primary branch with leaves), and diameter at breast height (dbh) using a girth tape for all sample trees were measured. Furthermore, the crown radii (cr) in all cardinal and sub-cardinal directions were measured using the vertical sighting method (Pretzsch 2019a; Preuhsler 1981; Röhle 1986). The crown projection area (cpa) was obtained from the eight radii measurements via a periodic spline function interpolating the distances at 40 equally spaced points. The crown radius was calculated as the quadratic mean of all the radii (r) measured ($cr = \sqrt{r_N^2 + r_{NE}^2 + \cdots + r_{NW}^2}\ / \ 8$). The exact location and relation between the variables can be obtained from Figure 4.

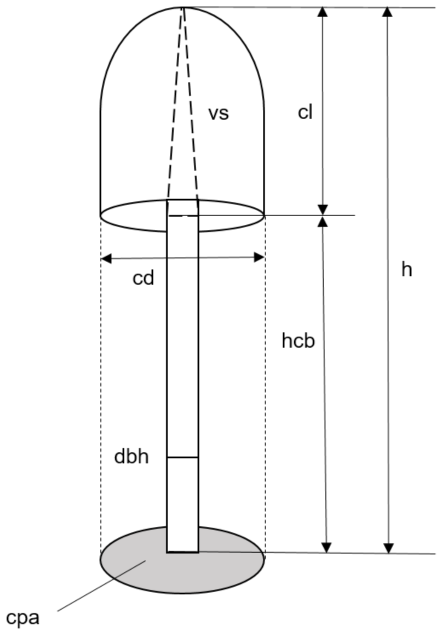

Figure 4 Tree variables used in this analysis: crown length (cl), crown diameter (cd), crown projection area (cpa), diameter at breast height (dbh), height of crown base (hcb), height (h), stem volume (vs)

The single tree's surrounding basal area was used to measure competition. It was obtained using the angle count sampling (ACS) by Bitterlich (1952). On the temporary plots, it was conducted for each tree at the plot, using a relascope. The surrounding basal area for the long-term experimental plots was calculated using the diameters and distances between trees obtained by their spatial coordinates. The social status index described by Fortin et al. (2019), calculated by dividing the tree's height by the stand's quadratic mean height, was used to account for a tree's social status.

An overview of the measured variables can be obtained from Table 2.

Table 2 Overview of the main tree variables used in this study grouped by species. n = sample size, min = minimum value, max = maximum value, mean = mean value, h = height, dbh = diameter at breast height, cpa = crown projection area.

species	**variable**	**min**	**max**	**mean**	**n**
European hornbeam	dbh [cm]	7.00	44.30	15.79	1057
	cpa [m^2]	0.87	146.78	24	810
	h [m]	4.10	30.80	15.78	1057
European white elm	dbh [cm]	7.20	73.60	25.83	183
	cpa [m^2]	3.09	151.28	25.84	182
	h [m]	6.90	34.77	18.94	183
field maple	dbh [cm]	7.00	55.70	17.61	220
	cpa [m^2]	0.53	160.60	18.06	190
	h [m]	8.20	30.90	15.62	220
wild service tree	dbh [cm]	7.40	70.10	25.91	86
	cpa [m^2]	4.65	132.9	32.30	75
	h [m]	8.60	24.90	17.70	86
European beech	dbh [cm]	7.10	102.10	23.27	2276
	cpa [m^2]	0.78	128.91	25.88	1355
	h [m]	2.80	42.30	20.59	2276
oak	dbh [cm]	7.00	75.20	31.56	1140
	cpa [m^2]	0.72	121.74	25.41	677
	h [m]	5.00	39.00	24.13	1140

Article 2: Growth and drought reaction of European hornbeam, European white elm, field maple and wild service tree

For the analysis of growth and drought reaction, tree cores were used, obtained from single trees of temporary experimental in Bavaria, and additional stands Poland (Figure 5). For each species, tree cores from trees in two stands on two different sites in Bavaria were taken in the winter of 2020/2021. For wild service tree on the second site, only cores of one stand could be extracted. European hornbeam was also sampled in two stands in eastern and central Poland, respectively. In total, the selected rare species were sampled in 17 stands on nine sites. All stands were undergoing regular silvicultural treatment in the past. As all stands were even-aged, the two stands per site covered a dbh range per species. The two stands per site were chosen as close to each other as possible to ensure similar site conditions. In each stand, 15–20 trees were sampled, covering the whole diameter spectrum of the stand. Trees were randomly selected, however, not standing directly next to each other. Depending on the occurrence, additional 10–15 European beech or oak trees or both were sampled (in total, 105 European beeches and 107 oaks). They were chosen to grow in the direct vicinity of each stand with the sampled rare species and within a similar species composition, past treatment, age and site conditions. There was no differentiation between sessile oak and pedunculate oak when selecting oaks. Tree-ring data from two existing experimental plots of European beech that were in close vicinity to the plots with rare species were additionally included (Schmied et al. 2023). The basal area values included in Tables 2 and 3 were determined by doing an angle count sample at each cored tree. The selected European beech, field maple, oak and wild service tree sites were located in their core distribution area in Europe. The two European hornbeam sites in Poland showed lower precipitation rates than the German sites. Both sites of European white elm were located on sites with relatively high precipitation compared to the rest of the European white elm's distribution range (Figure 6).

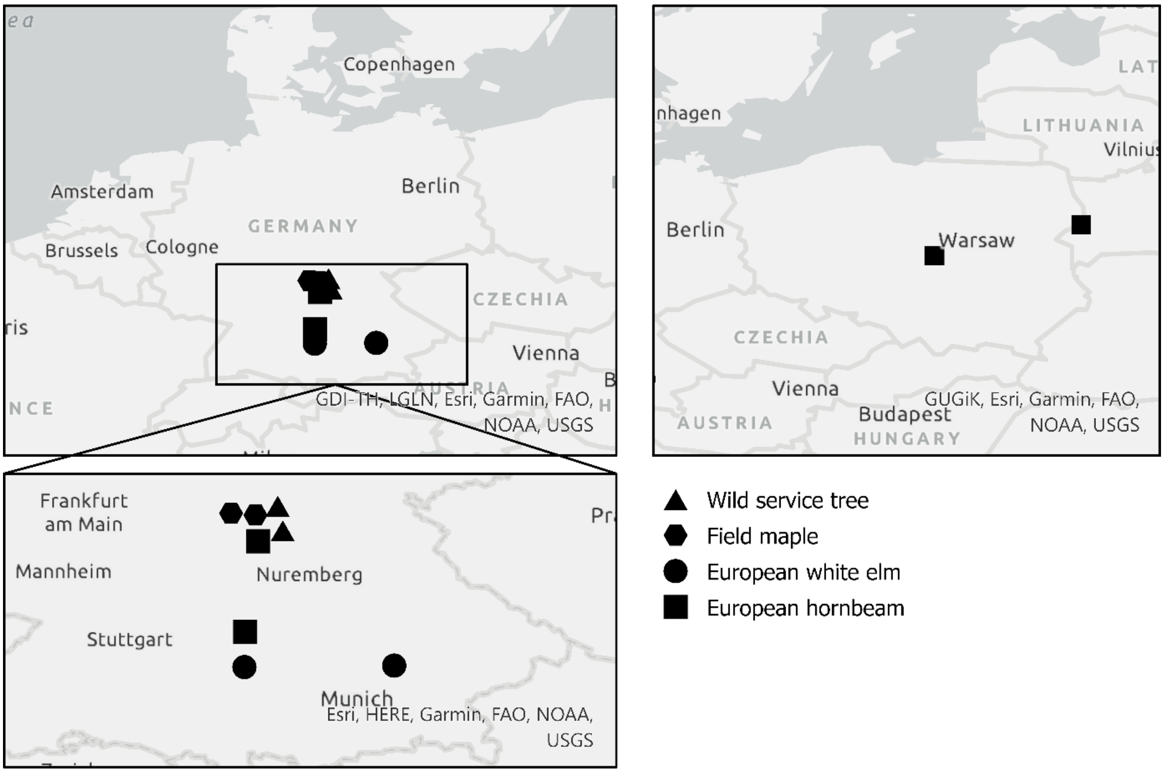

Figure 5 Geographic location of the experimental plots used in the study

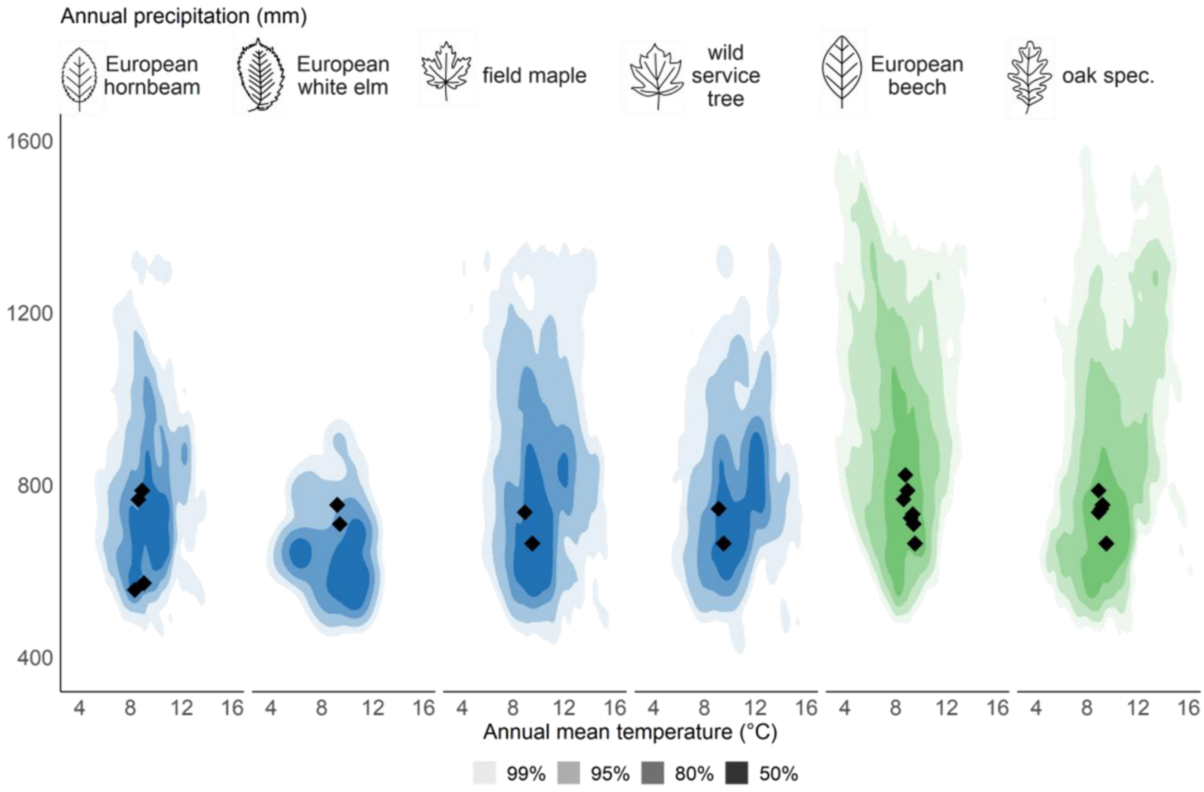

Figure 6 Climate space diagram showing the location of sampled stands (black squares) in the species` distribution range (Mauri et al. 2017) based on annual mean temperature and precipitation (DWD Climate Data Center). Coloured areas show the classified density distribution of species occurrences.

Table 3 Information about the stands of rare native tree species used. Coordinates of each stand, mean, max and min dbh of sampled trees, mean basal area per hectare (BA), age per plot and information about soil type and texture and the average De Martonne index (DMI) averaged over the last 30 years. N sampled refers to the number of trees we collected cores from, the number in brackets refers to the number of trees of which we could use the cores for measurements

Site	Code	Stand	Coordinates WGS84 (lat, lon)	Species	N sampled (useable)	*dbh* [cm]			Age	BA [m^2/ha]	Soil type	Soil texture	DMI
						Mean ± SD	Max	Min					
Ebrach	EBR	1	49.82647442, 10.53185277	European hornbeam	15 (15)	12.81 ± 2.84	16.2	7.3	48	35.95	Cambisol	loam	40.7
		2	49.82079687, 10.50741329	European hornbeam	15 (15)	24.1 ± 6.49	34.5	10.7	105	25.01	Cambisol	sand	41.9
Wallerstein	WAL	1	48.86604417, 10.3974315	European hornbeam	15 (15)	25.82 ± 5.39	33.9	14.5	105	38.32	Cambisol/Leptosol/Stagnosol	clay	41.0
		2	48.89506442, 10.33643931	European hornbeam	16 (16)	22.26 ± 3.99	30.8	15	60	24.35	Cambisol/Leptosol/Stagnosol	loam	39.9
Bialowieza	BIA	1	52.695104, 23.842052	European hornbeam	20 (19)	27.59 ± 4.09	36.3	20.2	95	32.43	Brunic arenosol	sand	31.3
Rogow	ROG	1	51.860028, 19.870768	European hornbeam	20 (20)	25.51 ± 3.19	21.8	20.1	75	26.66	Luvisol	loam	29.3
Offingen	OFF	1	48.4930946, 10.38870031	European white elm	15 (12)	11.19 ± 1.35	14.3	9.4	8	19.21	Fluvisol	sand	38.7
		2	48.49201022, 10.38738316	European white elm	15 (11)	54.95 ± 9.67	73.2	40	90	36.86	Fluvisol	sand	38.7
Freising	FRS	1	48.50358428, 11.97072302	European white elm	15 (14)	31.93 ± 9	45.7	18.2	56	34.15	Fluvisol	loam	36.1
		2	48.50876362, 11.97562965	European white elm	16 (16)	33.51 ± 9.03	47.5	18.3	60	19.23	Fluvisol	Sand	37.6
Schweinfurt	SCH	1	50.11861244, 10.28173906	Field maple	15 (15)	30.36 ± 5.78	49.7	19.1	55	37.83	Cambisol	Silt	38.5
		2	50.13765167, 10.28047059	Field maple	16 (16)	13.57 ± 1.48	17.5	11.4	40	26.35	Cambisol	Silt	36.1
Sailerhausen	SAI	1	50.06424136, 10.44109035	Field maple	15 (13)	38.78 ± 8.64	55.7	19.9	90	25.65	Vertisol / Leptosol	Clay	38.6
		2	50.06140085, 10.44188777	Field maple	15 (11)	20.6 ± 4.31	29	13.2	52	27.56	Leptosol	Clay	33.9
		3	50.03816495, 10.40565929	Wild service tree	15 (13)	39.45 ± 9.04	58.4	28.2	85	17.42	Pelosol	Silt	37.3
		4	50.06728171, 10.43006179	Wild service tree	16 (16)	13.26 ± 5.54	24.3	7.3	45	22.00	Pelosol	Silt	38.6
Baunach	BAU	1	49.99296123, 10.78056017	Wild service tree	15 (12)	24.49 ± 7.65	34.7	6.8	90	24.15	Cambisol	clay	40.4

Table 4 Information about the stands of European beech and oak used. Coordinates of each stand, mean, max and min dbh of sampled trees, mean basal area per hectare (BA), age per plot and information about soil type and texture and the average De Martonne index (DMI) averaged over the last 30 years. N sampled refers to the number of trees we collected cores from, the number in brackets refers to the number of trees of which we could use the cores for measurements. Stands from additional experimental plots used in Schmied et al. (2023) are labelled as "additional stand"

Site	Code	Stand	Coordinates WGS84 (lat, lon)	Species	*n* sampled (useable)	*dbh* [cm]			age	BA [m^2 / ha]	Soil type	Soil texture	De Martone Index
						Mean ± SD	Max	Min					
Ebrach	EBR	1	49.82647442, 10.53185277	European beech	15 (12)	12.81 ± 3.62	18.5	7.1	45	34.67	Cambisol	loam	40.7
		2	49.82079687, 10.50741329	European beech	15 (15)	41.65 ± 7.13	55.3	29.5	105	26.78	Cambisol	sand	41.9
Wallerstein	WAL	1	48.86604417, 10.3974315	Oak spec	10 (6)	51.71 ± 5.48	59.5	45.9	115	32.50	Cambisol/Leptosol/ Stagnosol	clay	41.0
		2	48.89506442, 10.33643931	European beech	10 (7)	28.37 ± 6.76	40.5	21.1	65	23.0	Cambisol/Leptosol/ Stagnosol	loam	39.9
Offingen	OFF	1	48.4930946, 10.38870031	Oak spec	15 (14)	8.83 ± 1.37	11.6	6	8	12.6	Fluvisol	sand	38.7
		2	48.49201022, 10.38738316	Oak spec	15 (12)	34.03 ± 6.4	47.1	16.3	112	17.33	Fluvisol	sand	38.7
Freising	FRS	1	48.50358428, 11.97072302	European beech	15 (14)	18.31 ± 3.88	26.7	12.8	45	21.27	Fluvisol	loam	36.1
Schweinfurt	SCH	1	50.11861244, 10.28173906	oak spec	15 (14)	28.79 ± 3.06	34.1	23.8	65	35.6	Cambisol	Silt	38.5
		2	50.13765167, 10.28047059	Oak spec	18 (18)	14.35 ± 3.35	22.9	10.6	35	21.5	Cambisol	Silt	36.1
Sailerhausen	SAI	1	50.07325, 10.43116	European beech	15 (15)	43.56 ± 4.47	49.8	32.4	100	42.6	Vertisol / Leptosol	Clay	37.7
		2	50.06140085, 10.44188777	European beech	15 (12)	20.04 ± 3.88	26.1	13.4	60	34.73	Leptosol	Clay	33.9
		3	50.03816495, 10.40565929	Oak spec	15 (14)	42.05 ± 4.94	53.8	34.3	121	32.07	Pelosol	Silt	37.3
		4	50.06728171, 10.43006179	Oak spec	15 (15)	18.93 ± 5.61	28.9	7.3	50	23.38	Pelosol	Silt	38.6
Baunach	BAU	1	49.99296123, 10.78056017	Oak spec	15 (14)	39.27 ± 6.19	53	29.8	155	23.34	Cambisol	clay	40.4
Additional beech stands			49.96712, 9.755348	European beech	15 (15)	40.02 ± 6.24	55.1	30.9	110	37.8	Cambisol	Silt	38.0
			48.45696, 10.06725	European beech	15 (15)	55.68 ± 5.79	65.2	44.8	125	42.1	Cambisol	Silt	43.9

A Haglöf increment corer with a diameter of 5 mm was used to collect tree cores. Two cores per tree at breast height (*dbh*, 1.30 m) were extracted, one from the northern and one from the eastern cardinal direction. This minimised the influence of reaction wood induced by the main wind direction from SW and allowed a better representation of overall growth (Pretzsch et al. 2013; Speer 2010). Since wild service tree and European white elm are scarce species with valuable timber, cores could only be extracted at a height of 30 cm due to forest owner preferences. For easy handling and measurement, the increment cores were glued on wooden boards and subsequently sanded with increasingly finer abrasive paper from 400 to 800 grit to enhance the visibility of tree-ring borders. Measurements were taken to the nearest 1/100 mm using a digital positioning table (Kutschenreiter and Johann; Digitalpositiometer, Biritz and Hatzl GmbH, Austria).

Visual cross-dating was performed based on common matching patterns of wide and narrow rings (Schweingruber 1988; Speer 2010). Afterwards, the crossdating was statistically verified using the dplR package in R (Bunn 2010).

Due to the low visibility of the tree rings of European hornbeam, an alternative method was used to measure this species. After sanding, the cores were photographed using the microscopic camera of a Lignostation (Rinntech) with a resolution of 1/10 mm. The resulting photographs were imported into Adobe Photoshop (version 22). Using a high pass filter with a radius of 40 pixels, a linear light blending mode and changing the displayed colour spectrum, tree-ring borders were easier to detect. More compact wood sections appeared more yellow, less compact sections were more blueish. The resulting photos were imported into the Lignovision software (Rinntech, version 1.37). Here, tree rings were marked, measured, and visually crossdated.

During the measurement and crossdating process, several cores had to be rejected due to the extremely weak visibility of tree rings, making it impossible to measure and cross-date the cores. The final number of cores per plot used in this study can be found in Tables 2 and 3.

Article 3: Crown structure, growth, and drought tolerance of true service tree (Sorbus domestica L.) in forests and urban environments

True service trees were measured in four regions in Central Europe: southern Scandinavia, northern Franconia in Germany, western Slovakia and the province of Bolzano in South Tyrol, Italy (Figure 7). The occurrences in Germany and Slovakia lay within the core distribution range or true service tree (Caudullo et al. 2017). The Scandinavian trees were growing outside the core range but in regions where the climate is expected to shift towards warmer temperatures and more drought, similar to the species' current distribution (Skovsgaard and Graversgaard 2013). Climatic conditions in South Tyrol were similar to those of the core distribution range. A broad overview of the growth of true service tree under different climatic conditions could be given by covering both core populations and marginal individuals. In Scandinavia and South Tyrol, all known individual trees were measured. In Germany and Slovakia, stands with a relatively high proportion of true service trees were selected, and individual trees across the range of size classes were measured. The measurements in Germany and Scandinavia took place during spring 2022. Trees in South Tyrol were measured during winter 2022, and trees in Slovakia during spring 2023. On each site, additional oaks with a similar dbh (diameter at 1.30 m above ground level) in close vicinity to the true service tree but without crown contact were measured. The measured trees included individuals growing in forest stands, urban environments, and parks. In contrast to forest stands, urban environments and parks were defined as locations within cities and locations where trees were standing in a continuous grass cover without a closed canopy. This included city parks, arboreta, and "Castelfeder"-nature reserve in South Tyrol, where trees stood in extensively managed meadows or between vineyards.

All trees were measured for total height (h), dbh, crown length (cl = total tree height minus height above ground level of the lowest living branch (excluding epicormic branches)) and crown radius (cr = distance from the centre of the stem to the point of projection of the crown periphery, as measured at ground level) in eight cardinal directions. For single trees in South Tyrol, however, the crown projection was only measured in four directions (due to the inaccessibility of some trees standing close to steep slopes). Crown projection area (cpa) was derived based on mean cr:

$$cpa = cr_{mean}^{2} * \pi \tag{1}$$

Trees taller than approximately 8-9 m were measured for height by using a Haglöf Vertex 4 and trees of lower height by using a telescopic height pole, cr was measured using a tape measure or a Haglöf Vertex 4, and dbh was measured using a tape measure. Furthermore, the distance and diameter of surrounding trees with a diameter larger than 5 cm within a radius corresponding to one third of the height of the true service tree were measured. The competition status of each tree was assessed based on the Hegyi competition index (CI) (Hegyi 1974). CI was calculated using the following equation:

$$CI_i = \sum_{j=1}^{n} \frac{d_j}{d_i * dist_{ij}} \tag{2}$$

with $i \neq j$, where di is the diameter of the central tree, dj is the diameter of the competitor, and distij is the distance between the central tree and the competitor. The measurements are summarized in Table 1.

Increment cores were collected at the stands in Germany and two locations in Slovakia. The cores were taken at 1.30 m above ground level in Gerolzhofen and 0.3 m in Zellingen and Slovakia, using a Haglöf increment corer in both cases. The oaks at each site were also cored. Two cores per tree were taken, one from the north and one from the east. In April 2022, a true service tree in Copenhagen was felled. The tree was located next to a bitumen road near the strait of Øresund and was open-grown (hence, without competition from other trees). After cutting the tree, five cross-sectional stem discs were collected (at 0.3 m, 2.0 m, 4.0 m, 6.0 m and 8.0 m above ground level, respectively). As the main stem was branching out at a height of 1.4 m, the largest of the multiple stems above this point was selected for disc extraction. In October 2013, the stem of a true service tree in the park in Alnarp, Sweden, was measured. The upper part of the stem had broken off during a recent windstorm. The entire stem was measured at intervals of 25-50 cm up to 10 m above ground level. Stem volumes were derived based on these measurements, and stem profiles were sketched based on measurements at 1-2 m intervals (to ‘smoothen out’ irregularities in the stem profile). The stem volume of the main axis of the trees was calculated based on the length and mid-diameter of each stem section, assuming a cylindric form of each section. The volume of all sections was added up to the total stem volume.

Figure 7 Locations of trees and stands measured for this investigation.

2.1.2 Meteorological data

In *Articles I, II* and *III,* climate data from the German Weather Service (DWD) was used (Deutscher Wetterdienst 2021). Monthly mean, maximum, minimum temperature (T) and precipitation (P) data were derived from an extrapolated 1 × 1 km grid. For the sites in Poland (*Article II*), Slovakia and Scandinavia (*Article III*), additional climate data from the Climate Research Unit (CRU) was used (Harris et al. 2020), for plots in Italy (*Article III*) data from the climate stations in Auer and Meran Gratsch. The data is accessible through the open data portal of South Tyrol (https://data.civis.bz.it/).

Using the climate data, the De Martonne aridity index (DMI) (Martonne 1926) was calculated for each site, using the formula $DMI = P/(T + 10)$, where P is the sum of annual precipitation in mm and T the annual mean temperature in °C. The DMI was averaged over the last 30 years for a general characterisation of the site aridity.

For the assessment of drought years (*Article I and II*), the standardised precipitation evaporation index (SPEI) (Vicente-Serrano et al. 2010) was used. This multiscalar index includes precipitation, temperature and potential evapotranspiration (calculated using the Hargreaves equation (Droogers and Allen 2002; Hargreaves 1994)) and is suitable for evaluating drought. To compare the fit of different time spans, the SPEI for 3, 6, and 12 months and its seasonal averages for spring (March, April, May), summer (June, July, August), autumn (September, October, November), winter (December, January, February) and the vegetation period (March to September) were used.

For the sites located in Germany in *Article II*, additionally, the soil moisture index (SMI) (Helmholtz Centre for Environmental Research 2021; Samaniego et al. 2013; Zink et al. 2016) was obtained from the Helmholtz Centre for Environmental Research (Helmholtz Centre for Environmental Research 2021; Zink et al. 2016). The SMI is an index scaled between 0 and 1 describing the soil moisture compared to a long-term expected value. It uses interpolated climate data and implements it into the hydrological model system mHM (Kumar et al. 2013; Samaniego et al. 2010) to simulate soil moisture at 4 × 4 km resolution. In this paper, the data of the total soil column (1.8 m) from 1951 to 2020 was used in a monthly resolution.

2.2 Methods

2.2.1 Quantile regression (*Articles I and III*)

In *Articles I* and *III*, key figures for tree size dependent space requirements were developed based on evaluating allometric relationships. These relationships can be expressed by the allometric formula $y = a * x^{\propto}$ (Huxley and Teissier 1936). Here, x and y represent measurements of the respective tree organs, while b and α represent allometric constants. The formula is often used in log-transformed notation $\ln(y) = \ln(a) + \propto \ln(x)$. The allometric exponent α can be seen as a distribution coefficient between the trait measurements x and y (Pretzsch 2010b). Theoretic approaches assume that there are fixed, generalised allometric exponents describing the allometric relationships between tree variables under ideal growing conditions (e.g., 2/3 for the h-d-relationship and 4/3 for the cpa-d-relationship) (West et al., 1997; Enquist et al., 1998). In reality, allometric exponents often deviate from these ideal values and depend on site and growing conditions (del Río et al. 2019; Forrester et al. 2017b; Fortin et al. 2019; Poorter et al. 2012). The resulting species-specific variation of the allometric exponent can be interpreted as an allometric corridor (Fahrmeir et al. 2013). The width, course, and upper and lower limits of this corridor allow for conclusions regarding the ecological characteristics of a given species.

The allometric corridor was displayed by fitting a quantile regression to different conditional quantiles of the log-transformed h-d and cpa-d relationships. The 0.05 and 0.95 quantiles were chosen to represent the lower and upper border of the corridor, and the 0.5 quantiles to represent the typical median relationship. Each quantile represents different growing situations and the respective shift in resource allocation. The 0.05 quantile describes the growing situation in which a tree allocates its resources in favour of dbh growth vs h or cpa growth (e.g., with low lateral competition or under a canopy of taller trees). The 0.95 quantile describes the opposite, i.e., a decreased dbh growth compared to h or cpa, as is the case for crowns of open-grown trees with few or no competitors, as we often find them in urban environments (c.f. *Article III*). It is assumed that these two quantiles represent the extreme growth forms of a tree species. Below or above them, dieback of the tree is expected, e.g., due to light deficiency. In *Article I* the cpa-h and dbh-h allometry were used to deduce growing space requirements and target diameters for specific heights (c.f. Chapter 2.2.2). The confidence intervals for each regression model were calculated by rank inversion (Koenker 2005).

2.2.2 Deducing stem numbers per hectare for different heights (*Article I*)

In silvicultural guidelines, the treatment of forest stands is often based on a stand's top height. It is an easy variable to measure, an indicator for the site index and only little affected by thinnings (Pretzsch 2019a). Thinnings usually start at the height of 12–14 m and are carried out in intervals that correspond to a height growth of 3 m (Klädtke and Abetz 2010; Landesbetrieb HessenForst 2016; Ministerium für Umwelt, Landwirtschaft, Natur- und Verbraucherschutz NRW 2019; Schleswig-Holsteinische Landesforsten AöR and Nordwestdeutsche Forstliche Versuchsanstalt 2021). Therefore, in this thesis, maximum stem numbers per hectare were derived for every tree species based on top heights starting from 12 m and going to a maximum of 30 m (or the end of the fitted data). This guaranteed easy application in practice and a smooth fit to existing management guidelines.

In the first step, a quantile regression on the 0.75 and 0.95 quantiles of the cpa-h-allometry was fitted. The two quantiles cover the most vital trees of a certain height with the highest space requirement. As a next step, the area of 10,000 m^2 (1 ha) was divided by the resulting values of each curve to obtain a range of stem numbers per hectare.

Furthermore, the 0.75 and 0.95 quantiles of the dbh-h allometry were calculated to retrieve a range of target diameters for each height. The resulting ribbon describes the targeted diameter development of the stand.

2.2.3 Analysis of growth and drought reaction (*Articles II and III*)

Analysis of tree-ring data

Tree-ring data were detrended using a 30-year spline with a 50% frequency cutoff (Cook 1992; Cook and Peters 1997; Klesse 2021). This smoothens the age-trend-related low-frequency variation in the series while retaining the high-frequency and inter-annual variation. The detrending procedure resulted in dimensionless ring-width indices (RWI) (c.f. Figure 8 for European hornbeam, European white elm, field maple, true service tree, oak and European beech).

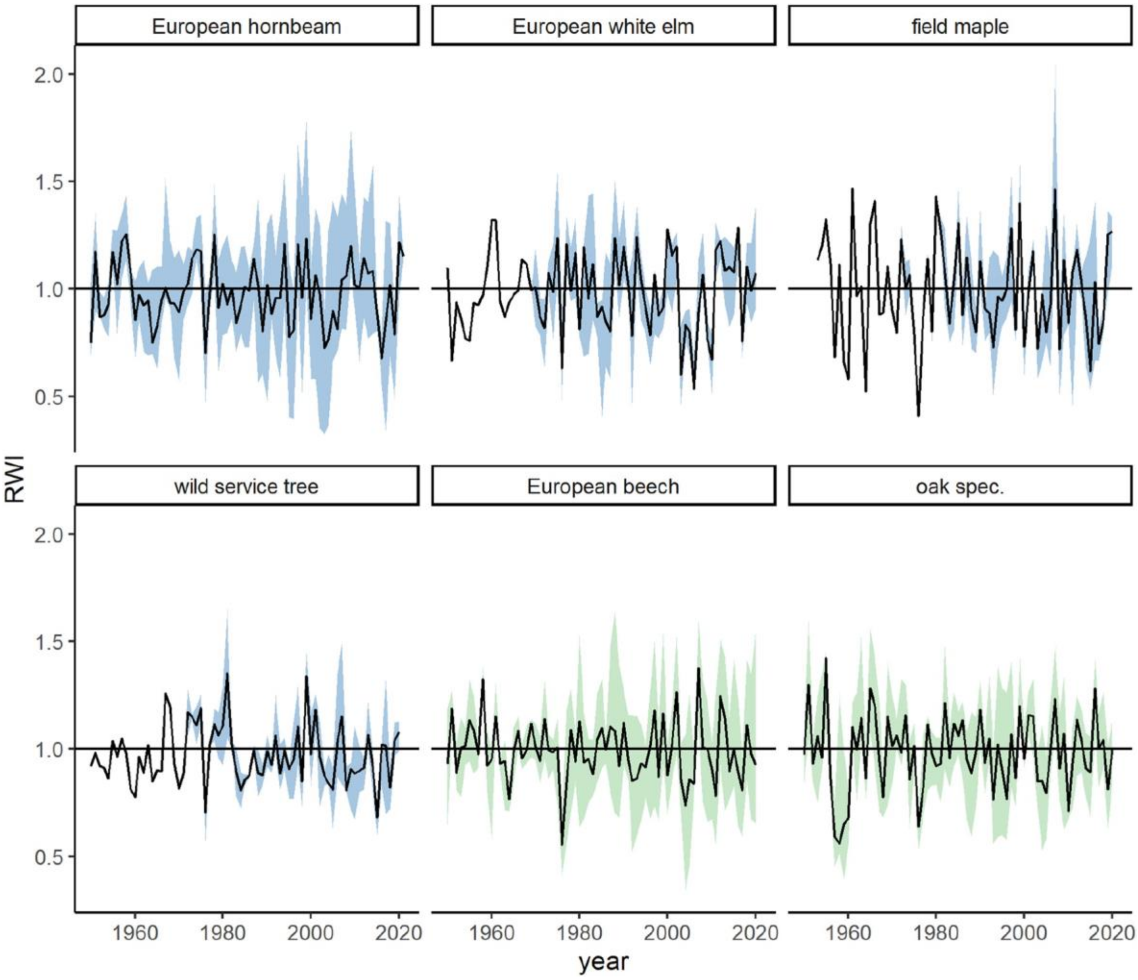

Figure 8 Species-specific chronologies of RWI. The black line refers to the mean chronology per species over all stands, and the ribbon refers to the minimum and maximum stand-specific chronology values for each year.

Next, the two measurements were averaged for each tree, using Tukey's bi-weight robust mean and average RWI chronologies were built for each site (Cook 1992). Finally, the RWI of each site were transformed into respective average chronologies. Years with measurements from less than five trees were truncated. The chronologies' quality was assessed using common dendroecological key figures (interseries correlation, signal-to-noise ratio, mean gleichläufigkeit and subsample signal strength).

For true service tree, the tree-ring data from the stem disks of the tree in Copenhagen were used to reconstruct the three-dimensional stem development. The height development was reconstructed using a standard interpolation method from the data obtained from different stem heights (Carmean 1972; Newberry 1991). Diameters between the stem disks were estimated by linear interpolation between tree-rings. Here, all values refer to under-bark diameters.

Variability of growth and influence of site and tree variables (Article II)

The Gini coefficient was used to assess the dispersion of the tree-ring series, calculated from the detrended year ring widths, as proposed by Biondi and Qeadan (2008). The Gini coefficient is a frequently used data variability index covering all lags in a tree-ring series. To test differences between the species-specific Gini coefficients, the detrended tree-ring data was pooled for each species and bootstrapped 95% confidence intervals were calculated (Dixon et al. 1987).

Selection of drought years

One single drought index was identified to select drought years. Requirements of this index were a reliable identification of drought, a high spatial resolution, and a high correlation with tree growth over all species and stands. Therefore, a bootstrapped Pearson's correlation was calculated between all climate variables, drought indices, and species-specific site chronologies. Monthly values and seasonal means were used for all variables and indices. For precipitation, the values for the corresponding seasons were summed up. To calculate average site-overarching coefficients for each tree species, the correlation coefficients were transformed using Fisher's z scores to avoid underestimations due to skewed distributions (Silver and Dunlap 1987) and subsequently averaged.

In *Article II*, chronologies of young European white elm and oak of stand OFF1 were excluded from the analysis of climate growth relationships and the analysis of drought reaction due to the short time period covered.

Of the climate data available for this thesis, SMI and SPEI were the most reliable drought indices (Schwarz et al. 2020). Combining both temperature and precipitation makes them more suitable for determining drought years than indices only considering one of the variables (Zscheischler and Seneviratne 2017). While SMI included soil data, SPEI was available in a higher spatial resolution and for all European locations.

For European hornbeam, European white elm, field maple and wild service tree (*Article II*), the seasonal SPEI3 for summer ($\mathrm{SPEI3}_{\mathrm{summer}}$) showed the highest correlation and lowest inter-stand variation over all species and stands and was used in further analysis. Drought years selected with this index are also resembling future climatic conditions when drought events will mainly happen in summer but also in spring months (Cook et al. 2020; Ionita et al. 2020; Ionita and Nagavciuc 2021), as it includes mainly summer data but due to its 3-month frame also spring months. Furthermore, SPEI3 is a suitable index as it targets short-term extreme events and seasonal precipitation changes and is widely used to assess drought in forest ecosystems (Bachmair et al. 2018; Dell'Oro et al. 2020; Obladen et al. 2021; Spinoni et al. 2017). Drought year identification was based on classifications by Slette et al. (2019). All years with $\mathrm{SPEI3}_{\mathrm{summer}} \leq -1$ were considered as potential drought years. The three driest years of the time covered by the chronology of each stand were chosen from these years.

For true service tree (*Article III*), drought year selection was based on SPEI12 for July. This index had a high correlation with annual growth over all locations. It also includes the previous year's drought conditions and reflects the two peak increment growth of true service tree throughout the vegetation period (Camarero et al. 2023). For each location of true service tree, drought years from 1965 onwards were selected. Following the classifications of Slette et al. (2019), all years with a SPEI12 in July of less than -1.5 (categories severely dry and extremely dry) were selected.

Reaction to single drought events

For the selected drought years, the indices of resistance (*R*t), recovery (*R*c) and resilience (*R*s) (Lloret et al. 2011) were calculated to quantify growth responses towards droughts. These indices are commonly used in dendroecological studies (Schwarz et al. 2020). They are calculated as ratios between the growth in a period before (PreDr), during (Dr), and after drought (PostDr):

$$Rt = Dr \;/\; PreDr \tag{3}$$

$$Rc = PostDr \;/\; Dr \tag{4}$$

$$Rs = PostDr \;/\; PreDr \tag{5}$$

The indices were calculated with pre- and post-drought periods of 2, 3 and 5 years, as recommended by Schwarz et al. (2020). However, there was no evident difference between different periods. Therefore, a pre - and post-drought period of 2 years was chosen, as this period restricts the influence of other effects like mast years or defoliation by insects (Bottero et al. 2021; Schwarz et al. 2020) and also allowed the inclusion of the recovery values of 2018 in the study.

To detect significant differences between the median values of the species for each Lloret index, a Wilcoxon rank-sum test with Bonferroni correction and a p-value of 0.05 was applied for European hornbeam, European white elm, field maple, wild service tree, oak and European beech, as the assumption of normal distribution of the samples could not be accepted for all species. For true service tree, the hypothesis of different mean values of resistance, recovery and resilience compared to oak was based on bootstrapping (n = 1000) the differences in mean and confidence intervals of 95 %.

As proposed by Schwarz et al. (2020), the species-specific relationship between resistance and recovery was compared to the "line of full resilience". This line was derived from the relation between recovery, resilience and resistance when the resilience values are set to 1:

$$Rc = Rs \,/\, Rt \tag{6}$$

$$Rc = 1 \,/\, Rt \tag{7}$$

The species-specific relationship follows a power-function with the following formula:

$$Rc = \mathrm{a} * Rt^{b} \tag{8}$$

The line of full resilience shows a tree's hypothetical recovery values to reach to fully obtain its pre-drought growth level (full resilience) for each resistance value. By observing the deviation and progression of the species-specific curve compared to the line of full resilience, we can rank and summarise the growth responses to drought and assess the recovery potential of the species.

To detect differences in the relationships of recovery and resistance between the European hornbeam, European white elm, field maple, wild service tree, oak and European beech, Eq. 8 was linearised by using a logarithmic transformation and the species were included as a linear term:

$$\log(Rc) = \log(\mathrm{a}) + b * \log(Rt) + species \tag{9}$$

Post hoc comparisons of coefficient combinations were performed using the glht function from the *multcomp* package (Hothorn et al. 2015) to evaluate differences in the progression of the curve of full resilience between species.

2.2.4 Mixed linear model (*Articles I, II, and III*)

Mixed linear models were applied for a more detailed examination of the species' allometric relationships (*Articles I and III*), growth and drought reaction (*Articles II and III*) and their dependence on site and stand variables. The data set of the studies included multiple observations of tree variables of trees on different plots. Moreover, some of these plots were located at the same sites. These dependency structures were considered by applying random intercepts on plot and site level (*Article I*), plot and type level (*Article III*) and tree level (*Article II*).

To assess the cpa of the rare species (*Article I*), the following global model was applied:

$$\ln\left(cpa_{ijk}\right) = a_0 + a_1 * \ln\left(dbh_{ijk}\right) + a_2 * DMI_{ij} + a_3 * ACS_{ijk} + a_4 * social\ status_{ijk} + a_5 * \ln\left(dbh_{ijk}\right) * DMI_{ij} + a_6 * \ln\left(dbh_{ijk}\right) * ACS_{ijk} + a_7 * \ln\left(dbh_{ijk}\right) * social\ status_{ijk} + a_8 * DMI_{ij} * ACS_{ijk} + a_9 * DMI_{ij} * social\ status_{ijk} + Plot_{ij} + Site_j + \varepsilon_{ij} \qquad (10)$$

where DMI represents the average Martonne index of 1991–2020, 'ACS' the local stand basal area and 'social status' the social status index.

The full model was stepwise reduced by eliminating non-significant effects and re-fitted following a procedure suggested by Zuur et al. (2009). The more complex elements (interactions) were removed first, and non-significant effects were retained when they were also part of a significant interaction.

To consider the influence of climate and competition on the crown size of true service tree (*Article III*) and to test species-specific differences between oak and true service tree, a linear mixed model based on the following equation was applied:

$$\ln\left(cpa_{ij}\right) = a_0 + a_1 * \ln\left(dbh_{ij}\right) + a_2 * CI_{ij} + a_3 * DMI_{ij} + a_4 * species_{ij} + a_5 * type_i + a_6 * CI_{ij} * species_{ij} + plot_i + \varepsilon_{ij} \qquad (11)$$

where CI refers to Hegyi's competition index, and plot is the random intercept on the plots. The factor variable 'type' refers to the tree's location in a park or a forest setting. It was included in the model to account for variability in management and overall growing conditions in urban environments and forests over the whole lifespan of the trees.

The variables used in the models were scaled to the standard deviation and centred around the mean to enhance comparability and comprehensibility (Schielzeth 2010).

In *Article II*, the sensitivity of annual growth to tree and site variables was modelled for each species with the following global model:

$$\ln\left(annual\ growth_{pti}\right) = a_0 + a_1 * \ln\left(dbh_{pti}\right) + a_2 * SPEI3_{tp} + a_3 * DMI_p + a_4 * \ln(dbh)_{pti} * SPEI3_{pt} + a_5 * \ln\left(dbh_{pti}\right) * DMI_p + a_6 * SPEI3_{pti} * DMI_p + b_i + \varepsilon_{itp} \tag{12}$$

An autoregressive correlation structure was included to consider autocorrelation between consecutive tree-ring measurements (Pinheiro and Bates 2000; Venables and Ripley 2002).
The model for the assessment of the effect of site and tree variables on the drought response of rare native species was as follows:

$$\ln\left(Lloret\ index_{itp}\right) = a_0 + a_1 * \ln\left(dbh_{itp}\right) + a_2 * SPEI3_{tp} + a_3 * DMI_p + a_4 * \ln(\mathrm{dbh}_{itp}) * SPEI3_{tp} + a_5 * \ln\left(dbh_{itp}\right) * DMI_p + a_6 * SPEI3_{tp} * DMI_p + b_i + \varepsilon_{itp} \tag{13}$$

In both equations, *t* referred to the year, p to the plot, i to the random intercept on tree level and SPEI3 to the SPEI3summer. a_0, a_1, a_2, a_3, a_4, a_5 and a_6 were regression coefficients and ε_{itp} the normally distributed error term. The b_i variable respected the nested data structure on the annual and tree level. Lloret index refers to the indices of resistance, recovery and resilience.

The global models were stepwise reduced using the Akaike Information Criterion (AIC). The DMI was removed from the model for European white elm, as both sites showed very similar values (36.11 and 38.68). The predictive variables were scaled and centred to enhance the comparability and comprehensibility of variables and their influence on the response variable (Schielzeth 2010).

In all cases (Eq. 10-13), the model assumptions of homoscedasticity and normality of residuals were checked visually using qq-plots and by plotting residuals vs. fitted values. The plots showed no violation of model assumptions.

2.2.5 Statistical software

All analyses were conducted in R (R Core Team 2022) using Rstudio (Posit team 2022). For the calculation of SPEI, the *SPEI* package (Beguería et al. 2014), described in (Beguería and Vicente-Serrano 2017) was used. For the analysis of tree-ring data the packages *dplR* (Bunn 2010; Bunn et al. 2021) and *pointRes* (van der Maaten-Theunissen et al. 2015; van der Maaten-Theunissen et al. 2021) were used. Climate growth relationships were calculated using the *treeclim* package (Zang and Biondi 2015). For fitting quantile regression, the *quantreg* package was applied (Koenker 2020).

Data exploration was conducted using the protocol of Zuur et al. (2010). Linear mixed-effect models were fitted using *lme4* (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). Interactions were displayed using *sjPlots* (Lüdecke 2021). The package *multcomp* (Hothorn et al. 2015) was used for general linear hypothesis testing, and for calculating the Gini coefficient, the package *DescTools* (Signorell 2022).

3 Results

3.1 Allometric relationships of rare native species (*Articles I and III*)

3.1.1 Basic allometric relations

Cpa-d allometry

European hornbeam, European white elm, field maple and wild service tree

Figure 9 displays the 0.05, 0.5 and 0.95 quantile regression curve of the cpa-dbh-allometry of European hornbeam, European white elm, field maple, wild service tree, European beech and oak. The 0.05 quantile represents trees with relatively small crowns with little space for expansion. In contrast, the 0.95 quantile shows trees with larger crowns, dominating trees or solitary trees (Pretzsch et al. 2015). The 0.95 quantile, therefore, has a major significance in calculating the space requirements of the tree species.

The α-values of the 0.05 quantile range from 0.21 for white elm to 2.04 for oak. For the 0.95 quantile α-values from 0.78 (European beech) to 1.45 (field maple) could be observed. Wild service tree, and especially European white elm, showed higher α-values for the 0.95 than for the 0.05 quantile, resulting in diverging curves for larger diameters. The morphological variability of the crown increased for larger diameters. The opposite course could be observed for field maple and oak. Both species had higher α-values for their 0.05 than for their 0.95 quantiles and, therefore, a narrower cpa-range for high dbh-values than for lower ones. European hornbeam and beech showed similar values for the 0.05 and 0.95 quantiles, resulting in almost parallel curves.

When looking at the α-values of the 0.5-quantile, European beech had an α-value of 0.78. For European white elm, the α-value was even smaller (0.62). These values implied a negative allometric relation ($\alpha < 1$) between cpa and dbh. Wild service tree had an α-value of 1.06, showing an almost isometric relation ($\alpha = 1$). The a-values of the 0.5- quantile ranged from -3.93 (field maple) to 0.94 (European white elm). European white elm and beech were the only species with positive values, the other species had negative values or, in case of wild service tree, close to 0 (-0.05). By combining a and α-values, crown expansion strategies for the species could be deduced. Field maple, oak and hornbeam with low a and high α-values are associated with initially smaller crowns extending to larger ones in later growth, compared to the crown size of other species at the same age. As indicated by the 0.95 and 0.05-quantile, the morphological variation in crown sizes of oak and field maple increased much more than in the case of hornbeam. European white elm with high a and low α-values appears to be a species with a large crown both in young and mature age. However, the results of the 0.95 and 0.05 quantiles implied a large span of crown sizes for higher diameters. European beech and wild service tree showed similar behaviour.

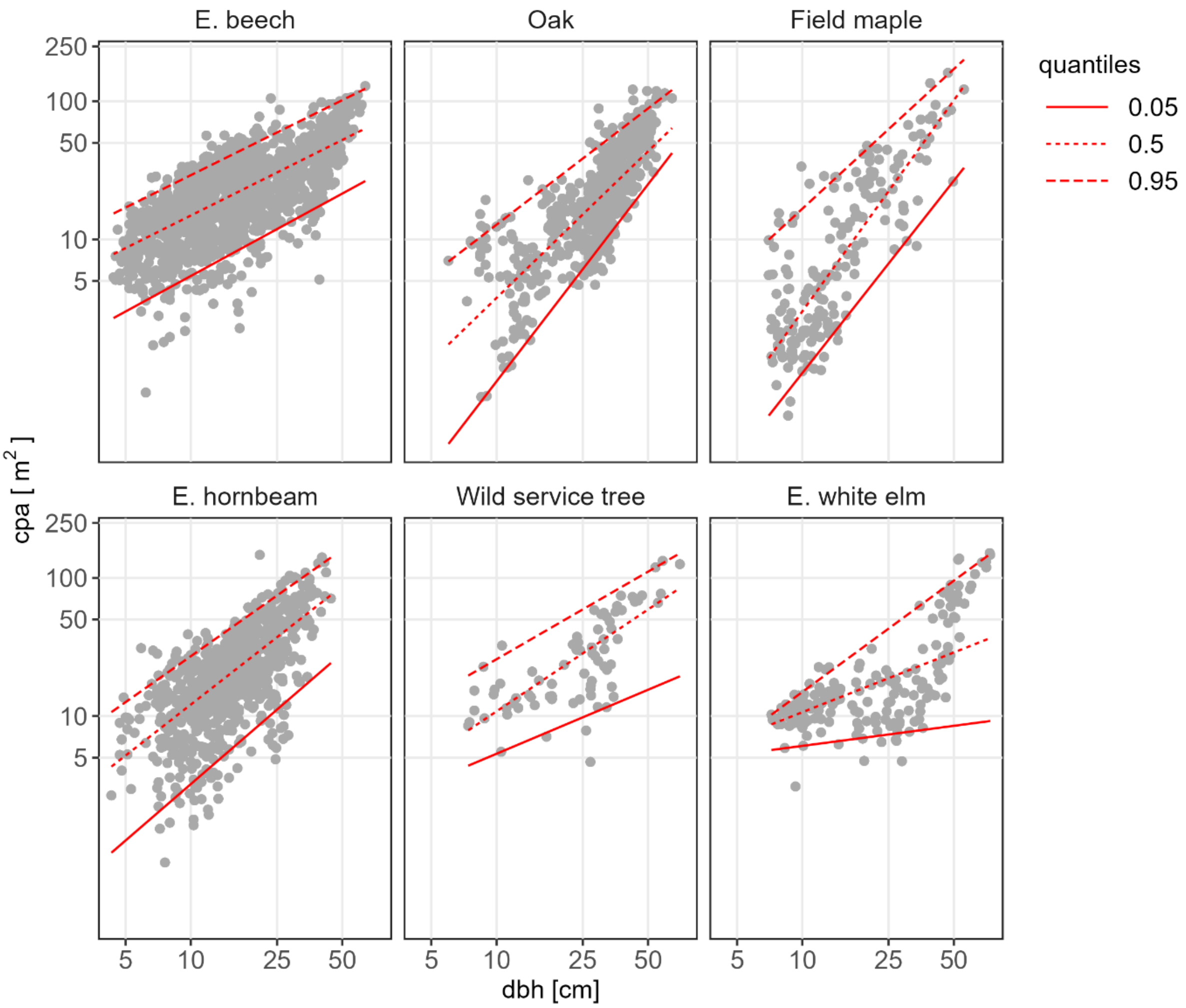

Figure 9 Allometric relationships between dbh and cpa for European hornbeam, European white elm, field maple, wild service tree, European beech and oak. The upper line represents the 0.95-quantile, the middle line the 0.5-quantile and the lower line represents the 0.05-quantile regression.

True service tree

The intercepts of the 0.95 and the 0.5 quantiles were smaller for oak than for true service tree. The values for the allometric exponent, however, were larger. In the 0.05 quantile, the intercept was smaller for true service tree, and the allometric exponent was larger than for oak. Overall, the two species behaved similarly.

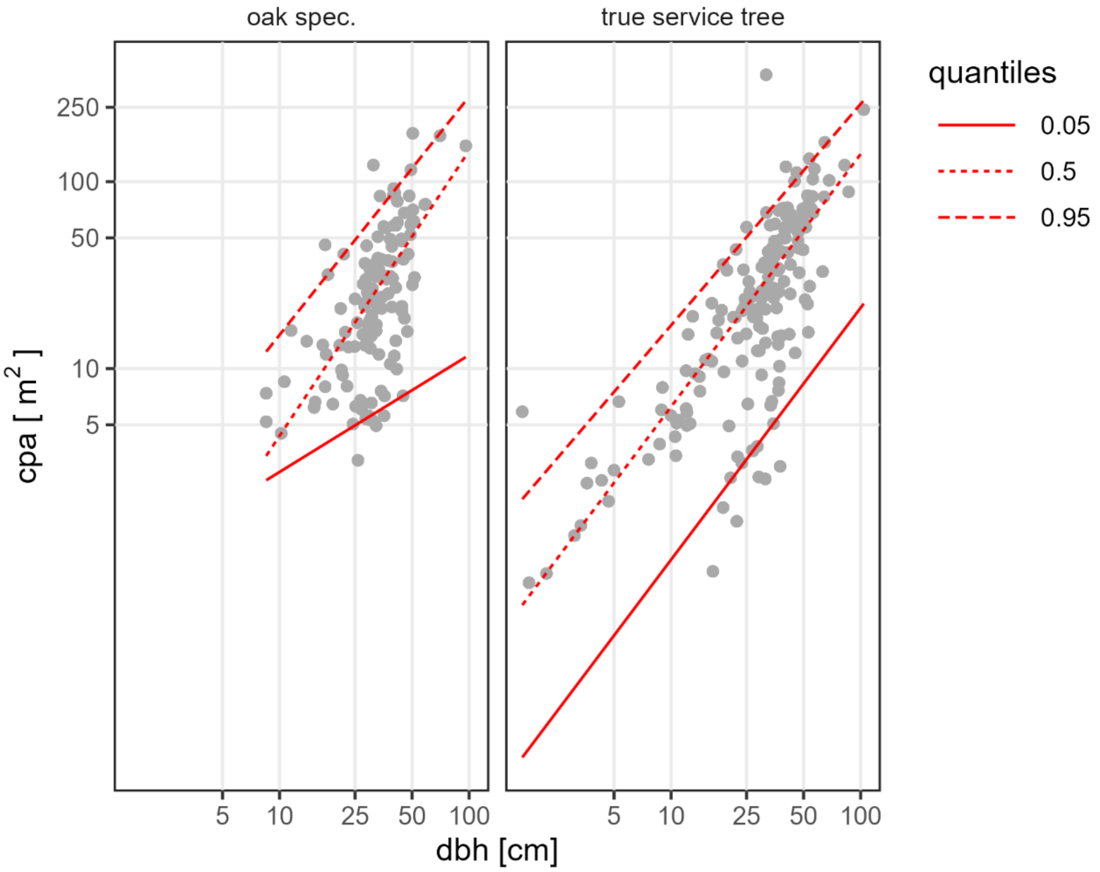

Figure 10 Allometric relationships between dbh [cm] and cpa [m2] for true service tree and oak. The upper line represents the 0.95-quantile, the middle line the 0.5-quantile-regression and the lowest line the 0.05.

H-d allometry

European hornbeam, European white elm, field maple and wild service tree

Figure 11 displays the results of the quantile regression analysis between height and diameter for the six tree species used in *Article I*. For the 0.05 quantile, the α-values ranged from 0.39 (field maple) to 0.68 (European hornbeam). The 0.95 quantile covered values from 0.38 (wild service tree) to 0.59 (European beech). All α-values were smaller than 1, indicating a negative allometric relationship. The distance between the 0.05 and 0.95 quantiles got narrower, with higher dbh values for all species besides field maple. The difference between the a-values of the 0.05 and 0.95 quantiles was the smallest for field maple (1.45 and 1.43) and the highest for European hornbeam (0.576 and 1.823), indicating a generally narrow height level range for field maple.

The α-value of wild service tree is the smallest of all species (0.36). Conversely, European white elm had the highest α-value (0.63), similar to European beech (0.62), although with a lower a-value (1.12 for European beech and 0.95 for European white elm).

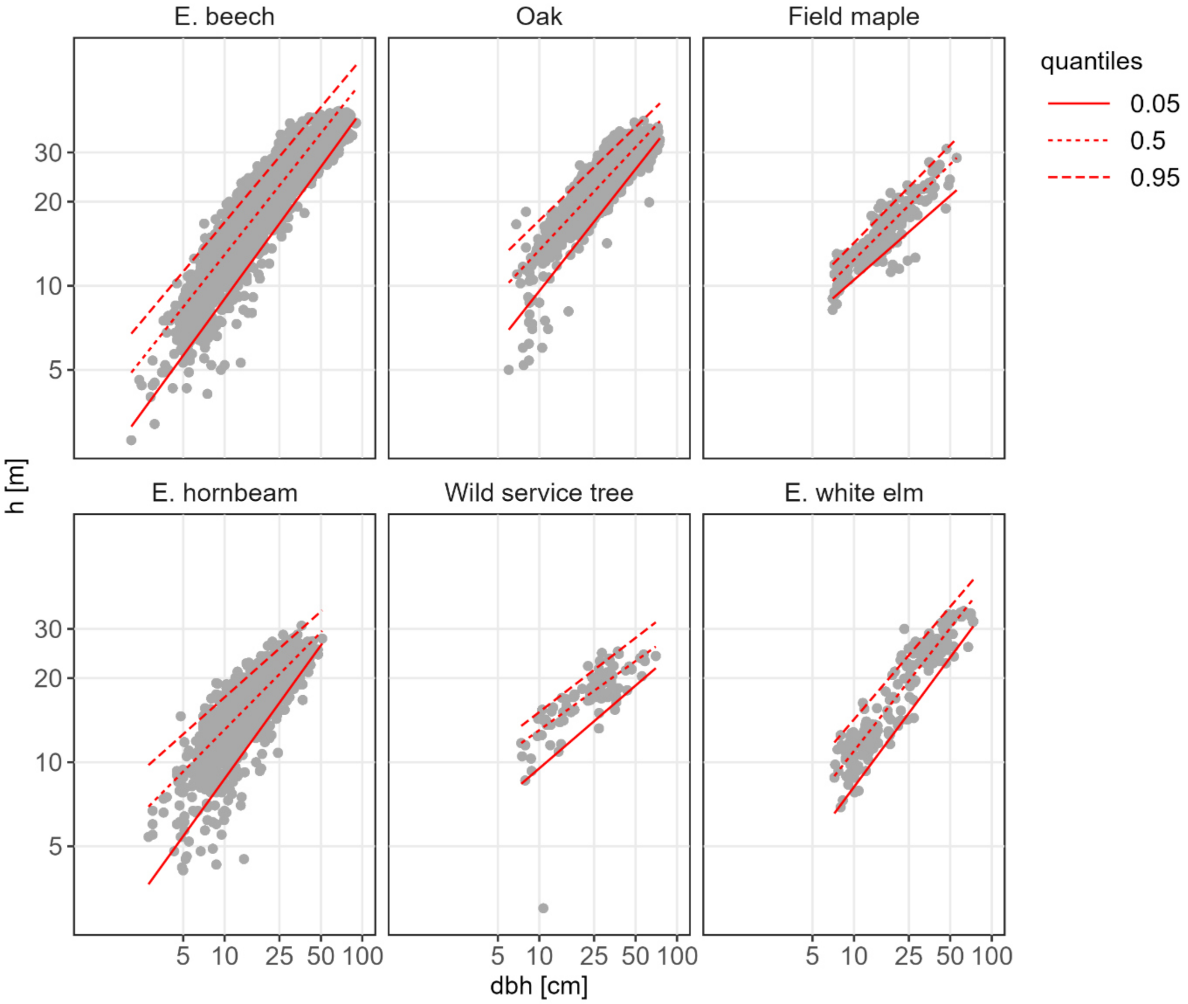

Figure 11 Allometric relationships between stem diameter (d) and height (h) for European hornbeam, European white elm, field maple, wild service tree, European beech and oak. The upper line represents the 0.95-quantile, the middle line the 0.5-quantile and the lower line represents the 0.05-quantile regression.

True service tree

For true service tree, the fitting of quantile regressions resulted in the curves displayed in Figure 12. True service tree and oak had similar ranges for the exponent and intercept of the h-d relationship. The values of the allometric exponent for true service tree ranged between 0.48 and 0.58. Especially for the 0.95 quantile, both species' intercept and allometric exponent values were similar or identical. For the 0.5 quantiles, only the intercepts differed, but marginally. For the 0.05 quantile, the values for oak were larger than for true service tree.

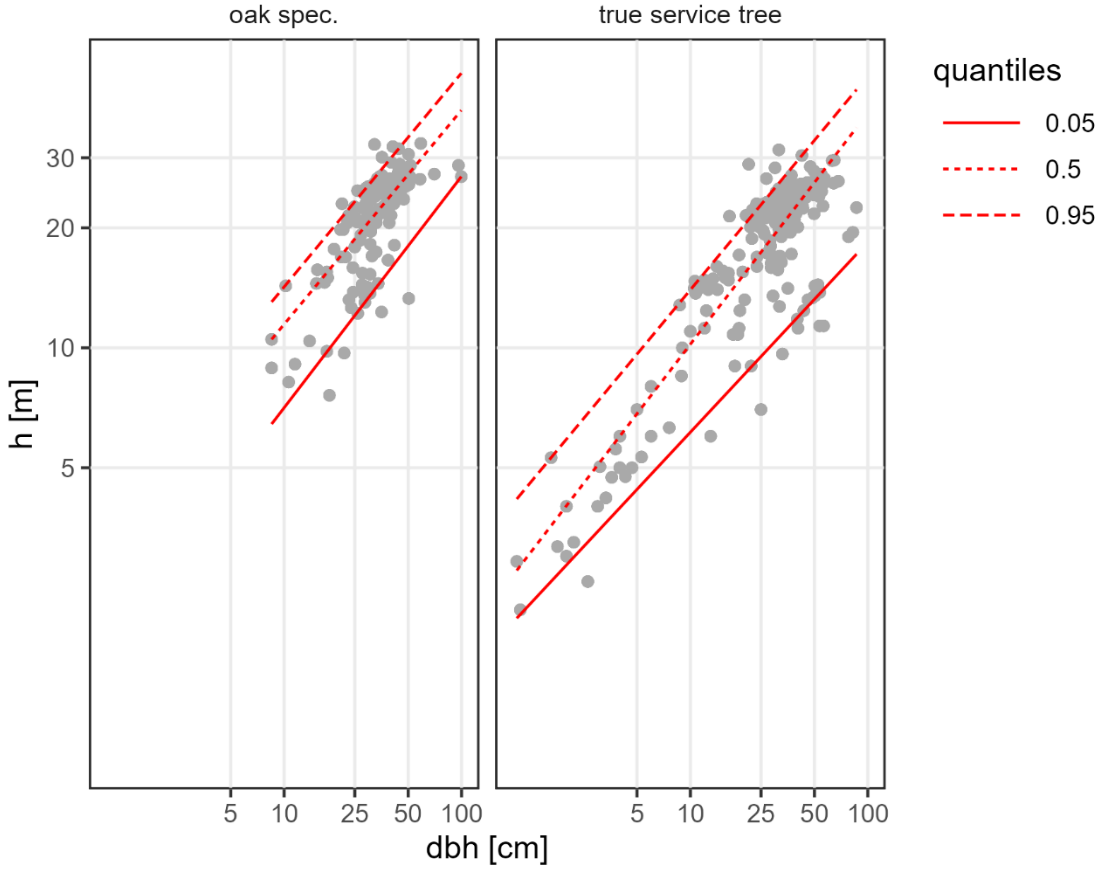

Figure 12 Allometric relationships between dbh [cm] and h [m] for true service tree and oak. The upper line represents the 0.95-quantile, the middle line the 0.5-quantile-regression and the lowest line the 0.05 quantile.

3.1.2 Stem shape of true service tree

The true service trees in Copenhagen and Alnarp had a somewhat pyramidical stem profile. Stem increment mainly occurred on the lower parts of the stem, up to a height of 2 m. The annual radius increment in the upper parts of the stem was much lower, resulting in a highly tapered stem (Figure 13). The total volume of the stem in Copenhagen was 0.77 m^3 and of the stem in Alnarp 2.38 m^3.

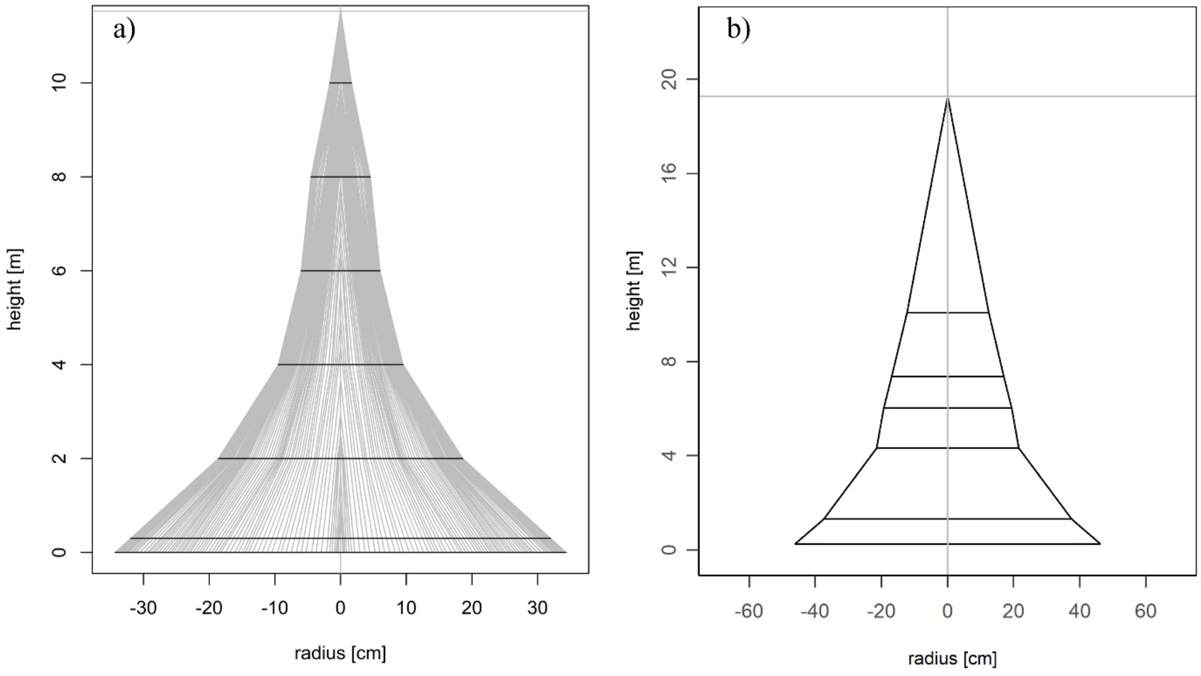

Figure 13 Stem diagram based on the stem analysis of a true service tree in Copenhagen (a) and sec-tion-wise diameter measurements of a tree in Alnarp (b). Black lines refer to the height of stem disks taken; grey lines show the annual increment.

3.1.3 Influence of site conditions and competition on crown allometry

European hornbeam, European white elm, field maple and wild service tree

The model selection based on the global model resulted in the model equations described in Table 5. In the case of European hornbeam, cpa was significantly influenced by dbh, DMI, the tree's social status and the interaction between diameter and DMI ($p < 0.01$). The crowns of trees in the lower stand layers were wider than those of trees of the same diameter in the upper layer. Overall, the site water supply increased the cpa, although the effect was more pronounced in smaller trees, as indicated by the significant interaction term.

For European white elm, the final model kept the local stand basal area and social status as predictors. Furthermore, the interaction between both variables proved significant ($p < 0.01$). Generally, higher social status and competition meant a decrease in cpa. The significant interaction term indicated a more substantial negative effect of competition on the cpa of trees with a low social status. In contrast, increased competition had a negligible effect on trees in the higher stand layers.

The social status and its interaction with the dbh were retained as the most important variables influencing the cpa of field maple. A high social status was overall connected to a decrease in the cpa. However, due to the significant interaction term between dbh and social status, it could be observed that the cpa of trees with a lower social status increased less with a higher dbh than those of trees with high social status.

The model reduction of the wild service tree resulted in a model with the competition and interaction between it and the diameter as significant variables ($p < 0.01$). As implied by the significant interaction term of diameter and competition, an increase in cpa with higher diameter was especially pronounced for trees with low competition.

For the European beech model, all the variables and the significant interactions between dbh and social status, ACS and Martonne index, and the interaction between Martonne index and social status were kept in the final model. A good water supply positively affected the cpa, which was especially pronounced for trees with higher diameters. An increase in the competition was connected to smaller crowns overall. However, this effect was less pronounced at higher diameters. Concerning the social status, wider crowns for trees in upper layers were observed. However, this effect was insignificant ($p > 0.05$). Nevertheless, the significant interaction term between social status and dbh indicated a higher increase in the cpa with increasing dbh for trees in lower stand layers. A more pronounced effect of water supply could also be observed for these trees.

For oak, the surrounding basal area, the social status and the interaction between both as variables were included in the final model. Overall, high competition and social status resulted in a smaller cpa. The negative effect of competition was especially powerful for trees in lower stand areas.

Table 5 Results of fitting the global model (Eq. 10) to the data. Variables not mentioned in the table were not included.

European hornbeam	Fixed Effects	Parameter	Estimate	Standard Error	p
	Intercept	a0	-3.08	1.03	0.004
	log(dbh)	a1	2.36	0.30	0.000
	Martonne	a2	0.09	0.03	0.002
	social status	a4	-1.33	0.14	0.000
	log(dbh) x Martonne	a5	-0.03	0.01	0.001
	Random Effects	**Parameter**		**Standard deviation**	
	Plot	Plotij		0.12	
	Site	Sitej		0.34	

European white elm	**Fixed Effects**	**Parameter**	**Estimate**	**Standard error**	**p**
	Intercept	a0	0.89	0.62	0.276
	log(dbh)	a1	1.05	0.10	0.000

	ACS	a3	-0.03	0.01	0.003
	social status	a4	-1.17	0.31	0.000
	ACS x social status	a10	0.03	0.01	0.006
	Random Effects	**Parameter**		**Standard deviation**	
	Plot	Plotij		0.24	
	Site	Sitej		0.70	
Field maple	**Fixed Effects**	**Parameter**	**Estimate**	**Standard error**	**p**
	Intercept	a0	3.69	1.23	0.003
	log(dbh)	a1	-0.09	0.46	0.848
	social status	a4	-4.84	1.30	0.000
	log(dbh) x social status	a7	1.50	0.46	0.001
	Random Effects	**Parameter**		**Standard deviation**	
	Plot	Plotij		0.28	
	Site	Sitej		0.66	
Wild service tree	**Fixed Effects**	**Parameter**	**Estimate**	**Standard error**	**p**
	Intercept	a0	-3.09	0.97	0.003
	log(dbh)	a1	1.97	0.29	0.000
	ACS	a3	0.13	0.04	0.002
	log(dbh) x ACS	a6	-0.04	0.01	0.001
	Random Effects	**Parameter**		**Standard deviation**	
	Plot	Plotij		0.09	
	Site	Sitej		0.49	
European beech	**Fixed Effects**	**Parameter**	**Estimate**	**Standard error**	**p**
	Intercept	a0	1.46	0.68	0.033
	log(dbh)	a1	0.14	0.35	0.683
	Martonne	a2	0.00	0.01	0.825
	ACS	a3	-0.02	0.01	0.005
	social status	a4	0.12	0.58	0.842
	log(dbh) x Martonne	a5	0.02	0.01	0.01
	log(dbh) x ACS	a6	0.01	0.00	0.004
	log(dbh) x social status	a7	0.22	0.06	0.000
	Martonne x social status	a9	-0.05	0.01	0.000
	Random Effects	**Parameter**		**Standard deviation**	
	Plot	Plotij		0.32	
	Site	Sitej		0.00	
Oak	**Fixed Effects**	**Parameter**	**Estimate**	**Standard error**	**p**
	Intercept	a0	-2.58	0.40	0.000

log(dbh)	a1	2.29	0.09	0.000
ACS	a3	-0.04	0.01	0.001
social status	a4	-1.53	0.30	0.000
ACS x social status	a10	0.03	0.01	0.007

Random Effects	**Parameter**	**Standard deviation**
Plot	Plotij	0.44
Site	Sitej	0.38

True service tree

For true service tree, the linear mixed model (Eq. 11) detected a significant effect of dbh, competition and location type on cpa. Crown size increased with lower competition and was generally bigger in parks than in forests. There were no significant differences in crown size and sensitivity towards competition between species.

Table 6 Parameter estimates for Eq. 11. df = degrees of freedom

		Estimate	Standard Error	df	statistic	p-value
	Fixed Effects					
	(Intercept)	2.41	0.15	29.92	15.71	0.00
	ln dbh	1.12	0.07	329.83	16.19	0.00
	CI	-0.18	0.06	332.52	-3.22	0.00
	Species: true service tree	0.08	0.06	319.57	1.34	0.18
	Type: park	1.09	0.32	32.89	3.35	0.00
	DMI	0.01	0.06	34.67	0.23	0.82
	CI: true service tree	0.02	0.06	323.91	0.33	0.74
	Random effects					
plot	sd__(Intercept)	0.66				
Residual	sd__Observation	0.53				

3.1.4 Maximum tree numbers and diameter development

The calculation of maximum tree numbers resulted in the curves displayed in Figure 14. The range of the diameter values represents the 75-95 % of the biggest trees in a stand, which are considered the most vital and economically interesting ones. The range of stem numbers per hectare is derived from the 75 and 95% values of the cpa-h allometry. The 3 m height steps on the x-axis represent thinning intervals. The diameter curve shows the species-specific potential diameter development in the corresponding height. These target diameters can be obtained when the tree number per hectare lies within the associated tree number range. High tree numbers correspond with smaller crowns, and lower numbers correspond with wider crowns.

Field maple can be managed with the highest stem numbers per hectare at early height stages, resulting in a broad corridor. After that, the corridor becomes narrower, beginning at a height of 15 m. The development of the target diameters resembles that of oak. The tree number ranges of European beech and European hornbeam show a similar course, while European hornbeam diameters are lower than those of European beech. Wild service tree shows a steep increase in diameter with a simultaneous decrease in stem number per hectare, resulting in target diameters above 60 cm at the height of 24 m. The diameter development and the tree numbers per hectare of European white elm resemble those of oak, though with larger diameters at great heights.

At a height of 15 m, for instance, European beech can reach diameters from 16.2 - 22.1 cm, European hornbeam similarly from 16.8 – 22.4 cm, oak from 17.3 – 22.1 cm and field maple from 17.1 – 22.1 cm. Of all species, wild service tree and European white elm show the largest diameters for this height (22.2 – 31.6 cm for wild service tree and 20.2 – 25.4 cm for European white elm). To achieve these target diameters, European beech should have a cpa of 27.6 – 40.2 m^2, resulting in 248 - 362 trees per hectare. The space requirement of European hornbeam is slightly higher in this height (cpa of 28.8 – 53.8 m^2 and 186 - 347 trees per hectare). While having similar target diameters, the size-related cpa range of field maple has a lower limit than oak (13.8 – 35.6 m^2 for field maple vs. 16.7 – 36.7 m^2 for oak). Therefore, up to 723 field maples and only 273 – 599 oaks have space on one hectare. The wild service tree needs a cpa of 28.6 – 48.6 m2 to reach the target diameter. This results in maximum stem numbers of 205 – 349. European white elm needs a cpa of 21.9 – 34.7 m^2 and 288 – 456 trees per hectare.

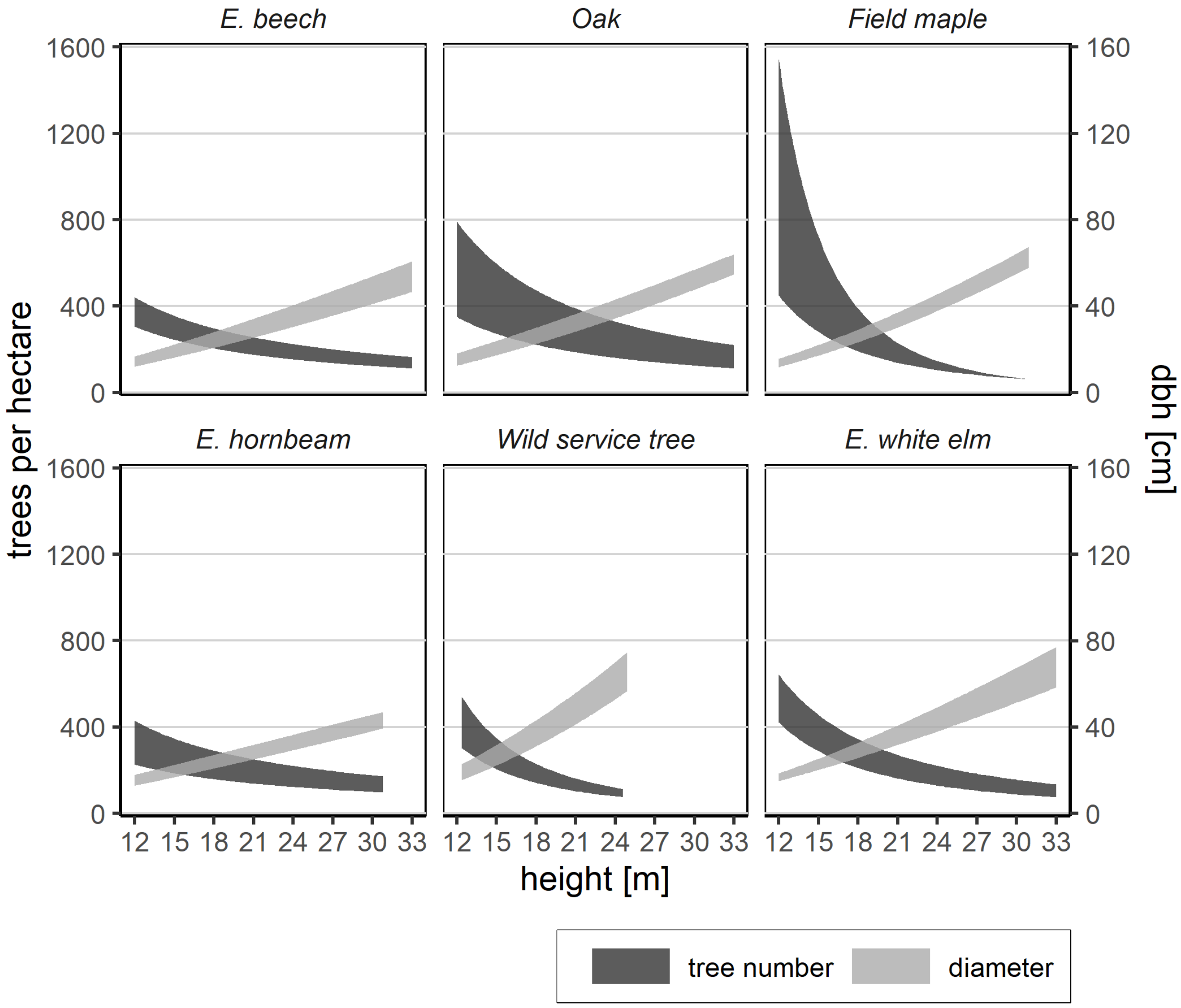

Figure 14 Range of maximal tree numbers per hectare and dbh over tree height., calculated based on the 0.75 and 0.95 quantiles of the cpa-h and dbh-h allometry. The units for the tree numbers per hectare are displayed on the left y-axis, and the diameter units are shown on the secondary y-axis on the right.

3.2 Growth and growth variability

3.2.1 Growth rates and growth variability (*Articles II and III*)

European hornbeam, European white elm, field maple and wild service tree

The basic tree-ring values for European hornbeam, European white elm, field maple, wild service tree, European beech and oak can be obtained from Table 7. European white elm showed the highest maximal tree-ring widths of all species and the highest standard deviation. This resulted in a substantial variability of diameters at a given age (Figure 15). Compared to the other tree species, the tree-ring widths of European hornbeam did not vary much between different sites and stands. The dbh-age curves of the trees both on the plots located in Germany and the plots located in Poland were very similar. While the mean tree-ring widths of wild service tree remained under the level of European beech and oak, its maximum tree-ring width showed a higher value than oak and European beech.

Table 7 Mean year ring width, standard deviation, maximum and minimum year ring widths per species.

species	**Tree-ring width [mm]**			
	mean	sd	max	min
European beech	1.97	0.89	7.72	0.01
oak spec.	1.81	1.06	8.81	0.16
European hornbeam	1.4	0.76	6.18	0.06
European white elm	2.43	2.1	15.11	0.01
field maple	1.7	0.93	6.18	0.18
wild service tree	1.46	1.22	9.87	0.01

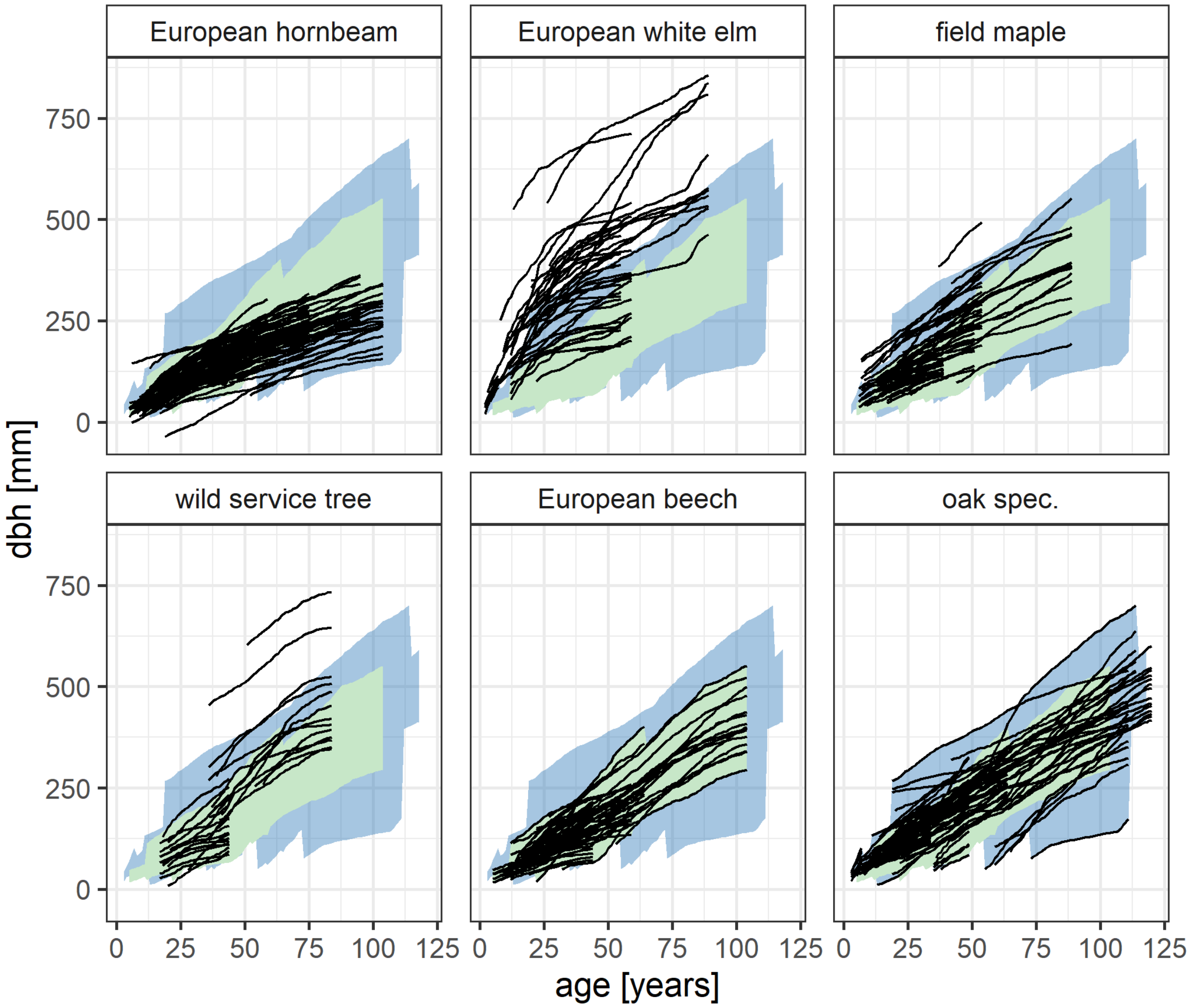

Figure 15 Species-specific diameter growth of trees over age for European hornbeam, European white elm, field maple, wild service tree, European beech, and oak. In the background, the ranges of the diameter growth over age for European beech (green) and oak (blue) are displayed.

The growth variability of detrended tree rings was higher for the rare species than for European beech and oak (Figure 16). Here, European white elm showed the highest Gini coefficient and European beech the lowest. Confidence intervals of European white elm, field maple and wild service tree were wider than for European beech, oak and European hornbeam. Reasons for that are different sample sizes and also a higher sample variability, pointing again to the higher variation of growth of Euorpean white elm and wild service tree.

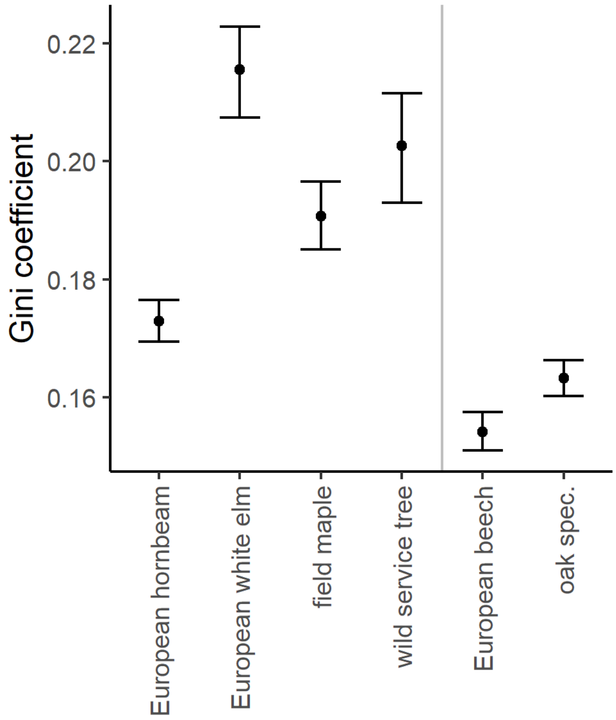

Figure 16 Gini coefficients computed on detrended tree-ring chronologies per species with bootstrapped 95% confidence intervals.

True service tree

True service trees and oak in Germany and Slovakia showed similar growth patterns over the period of measurements (Figure 17), with mostly lower annual increments for higher dbhs.

The height-age curve derived from stem analysis of a tree in Copenhagen (Figure 18 a) indicated fast growth until around 20-22 years of age. Subsequently, growth slowed down, and the curve flattened. The transition from fast to slow height growth was rather abrupt, and the growth rate was constant in these two phases. In contrast, the growth of dbh was almost linear until around 50 years and only slowed down considerably at about 70 years (Figure 18 b).

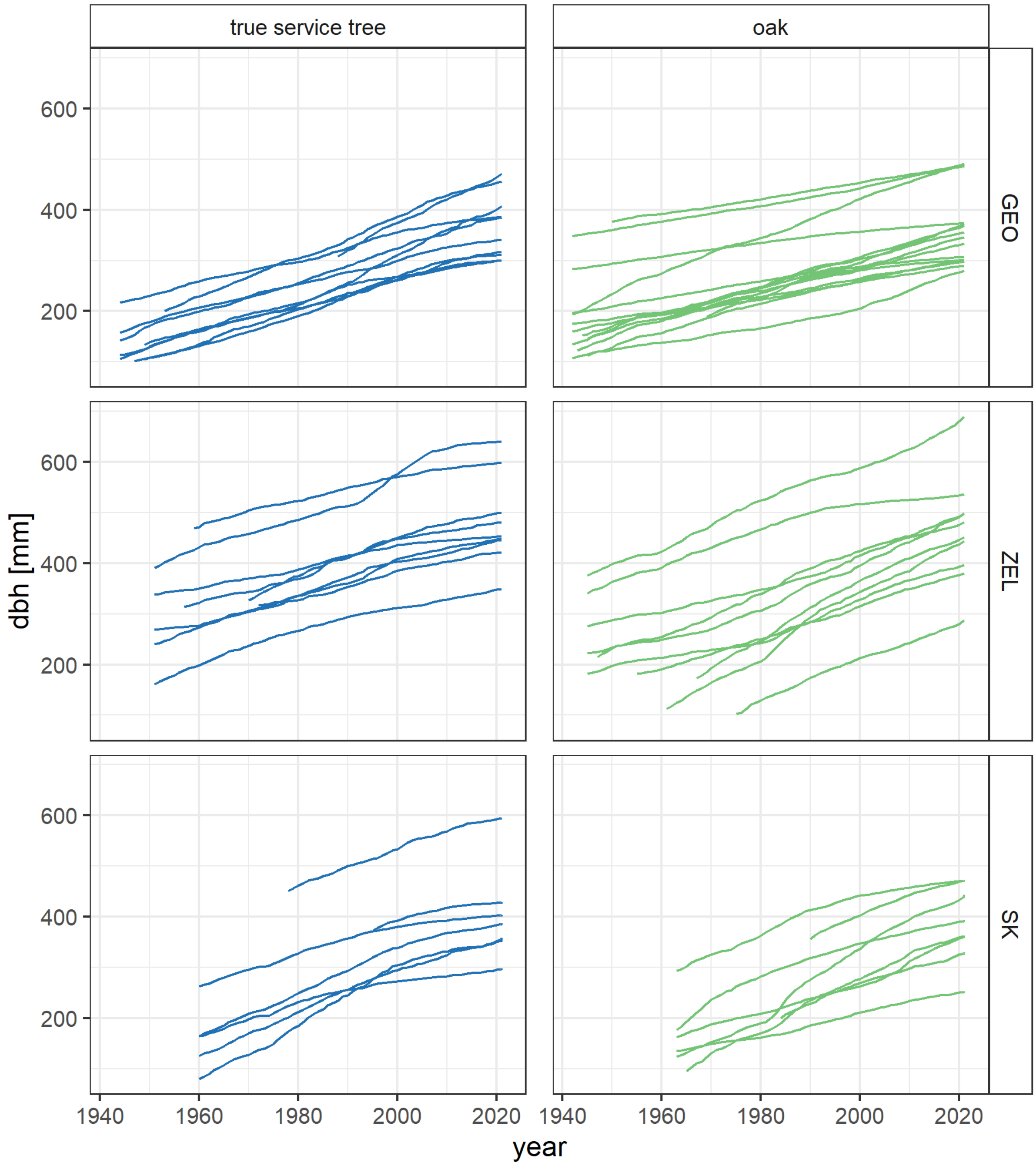

Figure 17 Species-specific diameter growth of trees over the calendar year for true service tree and oak. Legend: GEO = Gerolzhofen, ZEL = Zellingen, SK = Slovakia.

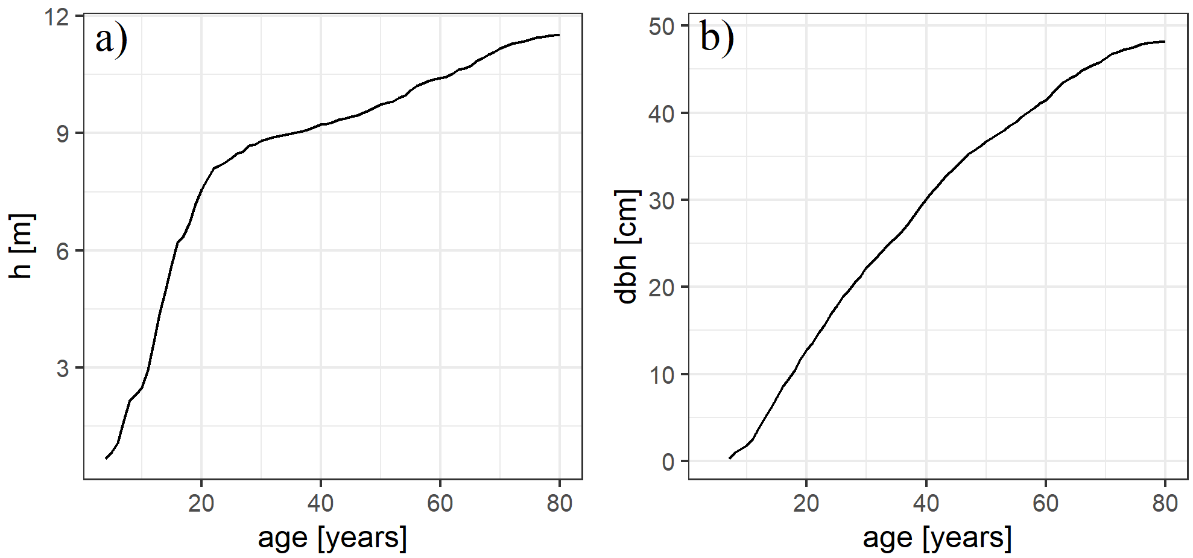

Figure 18 Height-age curve (a) and diameter-age curve (b) derived from a stem analysis of a true service tree in Copenhagen.

3.2.2 Effect of site and tree variables on annual growth (*Article II*)

The fit and reduction of the global model (Eq. 12) to the data of each species resulted in species-specific models. The annual growth of all species was significantly affected by dbh, annual SPEI and, where applicable, the DMI. Significant differences in annual growth between sites with poor and better water supply could be observed for European beech, European hornbeam, field maple, wild service tree, and oak. On very dry sites, the annual growth decreased for bigger trees. On better sites, however, this decrease was weaker for field maple and wild service tree or did not happen at all for European beech, European hornbeam, and oak. Here, even an increase in annual growth for bigger dbhs could be observed. For European beech and field maple the reaction on annual weather conditions, displayed by the SPEI, differed between sites. For these species, the increase of annual growth as a reaction to high SPEI values was higher on good sites than on very dry sites. All other species did not show a difference in their response between sites. However, higher SPEI values generally led to higher annual growth. European white elm and European hornbeam showed a higher sensitivity and increase in annual growth towards wetter years for thinner trees.

3.3 Drought stress response

3.3.1 Resistance, resilience, and recovery

European hornbeam, European white elm, field maple and wild service tree

The species could be sorted by their median values for the index of resistance in the following order: Field maple (0.61) < European hornbeam (0.73) < wild service tree (0.74) < oak (0.76)

< European beech (0.79) < European white elm (0.92) (Figure 19). After testing the hypothesis of equal medians, it could be differentiated between three groups: field maple with low resistance values, oak and European hornbeam with a middle position and European white elm with the highest resistance values. European beech and wild service tree took an intermediate position between European hornbeam and European white elm.

The median recovery values were ranked as follows: European white elm (1.05) < oak (1.13) < European hornbeam and wild service tree (1.18) < European beech (1.20) < field maple (1.63). There were no significant differences between medians after testing for equal means. Only field maple showed a significantly higher recovery value than the other species.

Median resilience values followed the subsequent order: oak (0.86) < wild service tree, European white elm and European hornbeam (0.90) < European beech (0.94) < field maple (1.02). No significant difference could be observed between the median of oak and field maple. For all other species the hypothesis of equal medians could not be rejected.

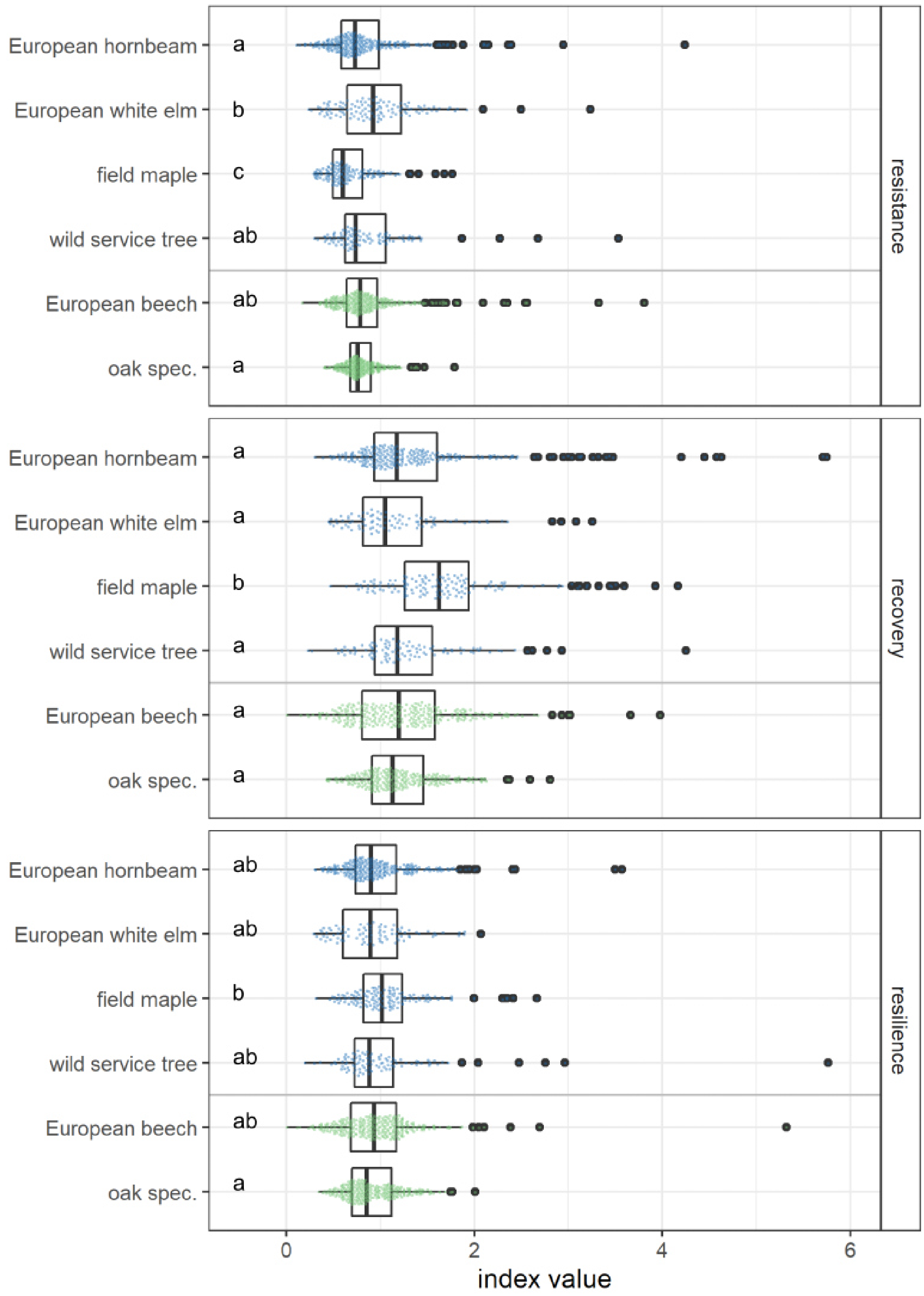

Figure 19 Index values of the Lloret indices of recovery, resilience and resistance for European beech, European hornbeam, European white elm, field maple, oak, and wild service tree. Significant differences ($p < 0.05$) between the medians of the index value per species, determined by a Wilcoxon rank-sum test with Bonferroni correction, are displayed with letters.

Figure 20 shows the relationship between recovery and resistance of the species and the theoretical line of full resilience. European hornbeam, field maple and European beech already showed a very close fit to the line of full resilience for very low resistance values. Field maple and wild service tree intersected the full-resilience line even for lower resistance values than the other species. The model intercept of European beech was significantly higher ($p < 0.05$) than that of wild service tree, European hornbeam, and field maple. Also, field maple showed a significantly higher intercept than oak. For resistance values above 1, field maple, oak and wild service tree showed the highest positive deviation from the line of all species.

In general, three primary curve shapes could be observed. On the one hand, European hornbeam and European beech showed a good fit to the line of full resilience for all resistance values. On the other hand, European white elm, wild service tree and oak showed a negative deviation from the line for low resistance values but, especially for wild service tree, with an early intersection and a subsequent clear positive divergence. Field maple, as the only species, shows a good fit on the line of full resilience for low resistance values and exceeding for high resistance values.

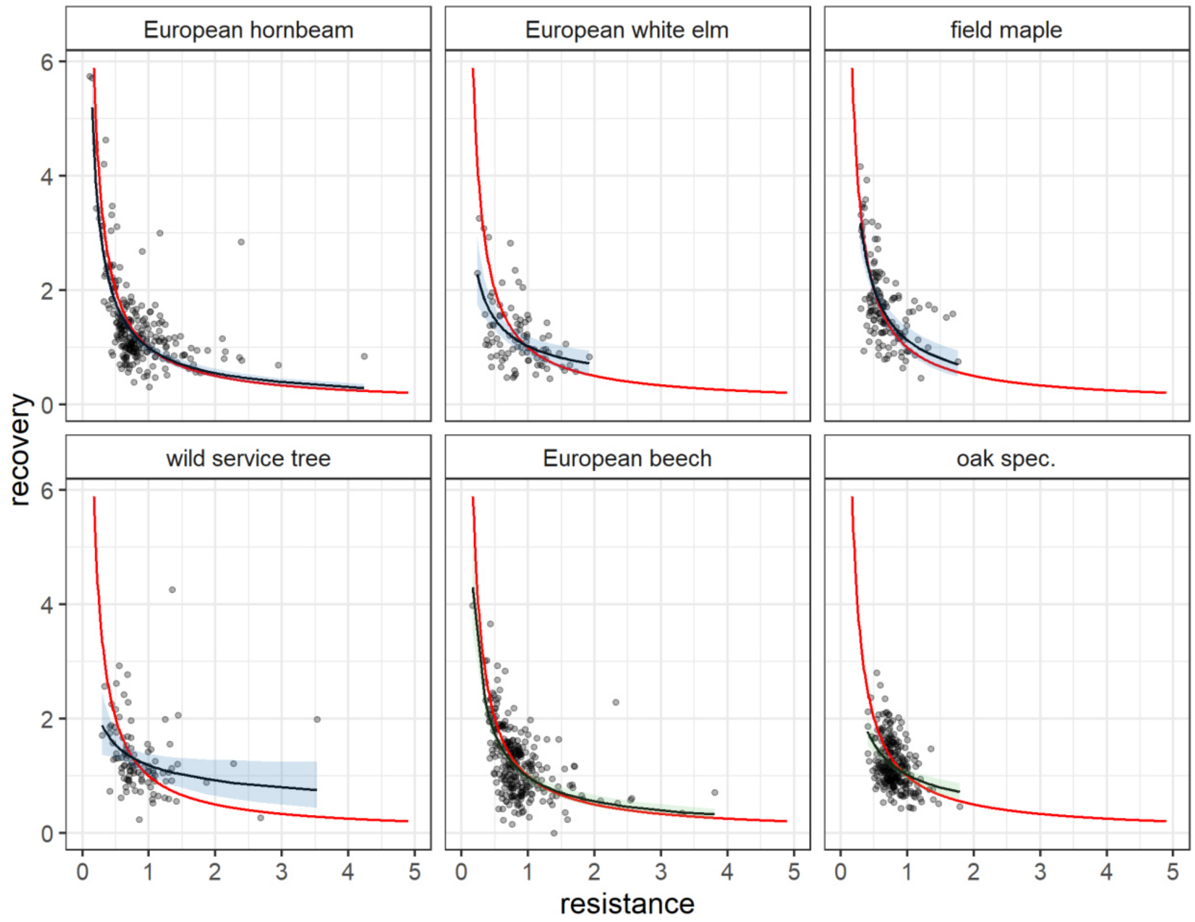

Figure 20 Species-specific relationship between resistance and recovery (black line (see Eq. 8) with confidence bands calculated with a bootstrap with 1000 iterations, the red line (see Eq. 7) represents the theoretical line of full resilience.

True service tree

The hypothesis of equal means could not be rejected when looking at the species-specific indices of resistance, recovery, and resilience for true service tree and oak (Figure 21). Comparing the lines of full resilience (Figure 22), both species had a similar drought response. For lower resistance values, both species were lying under the line of full resilience but intersecting it already at a resistance value below 1. After that, the curves for both species proceeded above the line of full resilience.

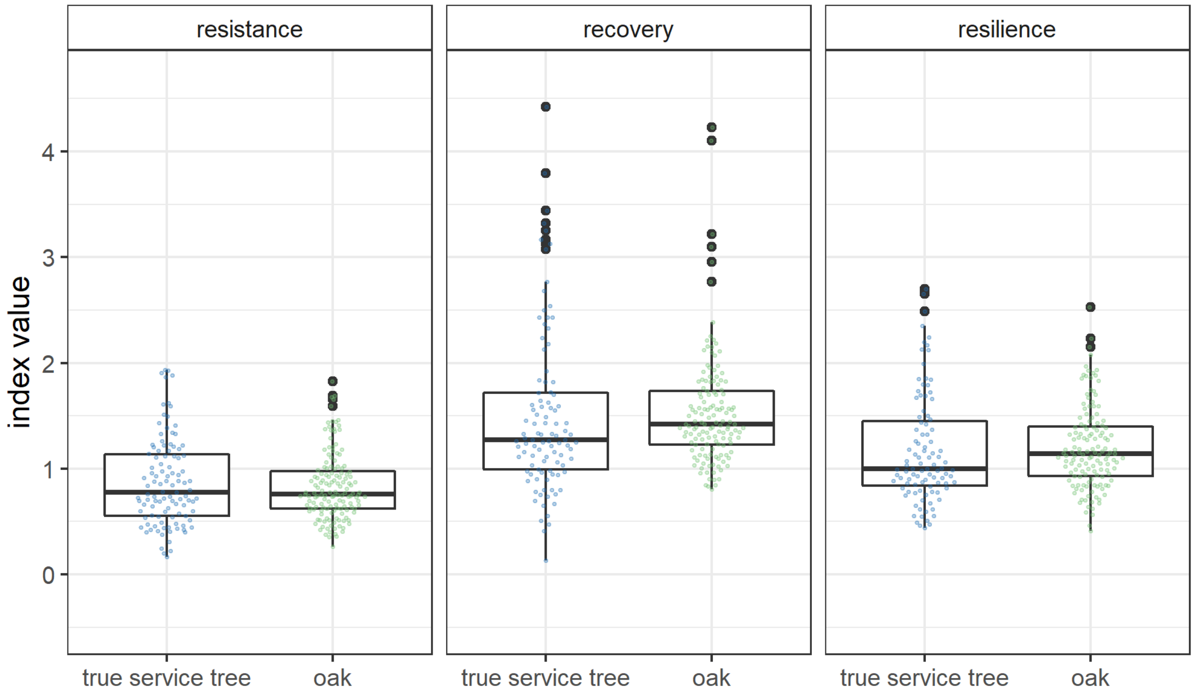

Figure 21 Boxplots showing the values of the Lloret indices of recovery, resilience and resistance for true service tree and oak.

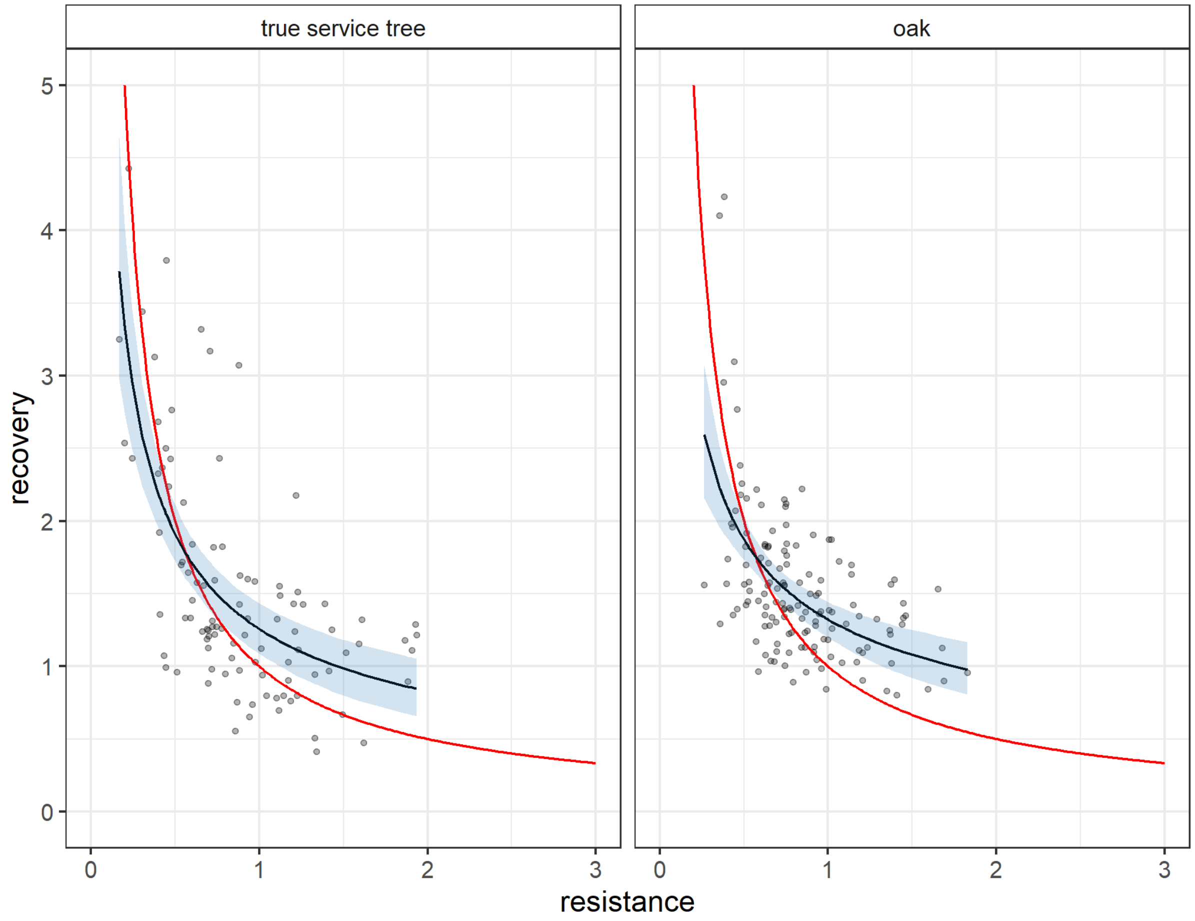

Figure 22 Species-specific relationship between resistance and recovery (black line with confidence bands calculated in a bootstrap with 1000 iterations), the red line represents the theoretical line of full resilience.

3.3.2 Effect of site and tree variables on drought stress response

Concerning the drought reaction, significant influences of tree size, drought severity and overall site conditions could be observed. However, the expression of the effects strongly differed between species.

The resilience of European hornbeam, European white elm and field maple was significantly affected by the severity of the drought year, displayed by the SPEI values. Field maple and European white elm were more resilient after milder drought years, while European hornbeam showed an opposite reaction. For field maple this effect was especially visible on sites with a lower DMI, while on sites with more favourable climatic conditions, the resilience was similar over different drought intensities. Also, for European beech and oak an influence of the long-term climatic conditions of the site, displayed by the DMI, and a significant influence of the dbh could be observed. For European beech, the resilience values were higher on sites with higher water supply and for thinner trees. For oak, the higher resilience of thin trees was only observed on sites with a high DMI. On sites with a lower DMI, trees of all diameters showed similar resilience values. Notable is that for wild service tree, there were no significant effects of any variable.

Concerning the resistance, a significant influence of the SPEI values of the drought year was observed for all species besides wild service tree. For oak, European white elm and field maple, less severe drought years led to higher resistance values. European beech showed low resistance values in very dry years on sites with a low DMI, while the resistance of European hornbeams increased with more severe droughts on those sites. Concerning the effect of tree size on the resistance, European beech showed a higher resistance in bigger trees on sites with a high DMI and thinner trees on sites with a low DMI. Again, it is notable that no significant effect of any variable could be found for wild service tree.

The tree size did not significantly affect the recovery of European white elm, field maple, and wild service tree. Oak recovered better for thinner trees. Thinner European hornbeams showed a better recovery on favourable sites than bigger trees, while on sites with a low DMI, no such size effect could be observed. The opposite could be observed for European beech, with better recovery of thin trees on sites with a low DMI and bigger trees on sites with a high DMI. This significant influence of the climate conditions on the sites could also be observed for oak and field maple. Field maple and European beech showed generally higher recovery values on sites with low water supply and less severe drought years. On more favourable sites, this effect was reversed. The recovery values of oak generally increased with a higher DMI. Wild service tree and European white did not show a significant effect of diameter, site and SPEI on their recovery.

In summary, European beech was highly susceptible to severe droughts on sites with a low DMI, while oak was more stable, especially on good sites and over different tree sizes. Among the rare native species, field maple again stuck out with high robustness towards drought, even on very dry sites and towards severe drought. European hornbeam reacted similarly like European beech, however, with a higher tolerance towards severe droughts and more constant over different tree sizes. For wild service tree, the data showed a stable drought reaction without any influence of site and tree variables. European white elm showed a particularly high capacity towards mild droughts.

3.4 Comparison between true service tree and oak

Throughout this thesis, the true service tree was compared to oak, a well-known and studied species frequently used in forest and urban environments. The true service tree commonly grows in oak stands in its natural distribution range. The comparison of both species makes it easy to assess the characteristics of true service tree, and forest and city tree guidelines of oak can easily be adjusted for true service tree.

Combining this thesis's results and observations from the literature, the differences between oak and true service tree in allometry, growth and drought response can be resumed in the following overview:

	True service tree	**Oak**
h-d allometry	Similar for both species, but a steeper increase for oak at the 0.05 quantile. Essentially identical height growth for both species.	
cpa-d allometry	Similar for both species, but a steeper increase for the true service tree at the 0.05 quantile. Larger crown size for smaller trees of true service tree; otherwise, similar space requirements.	
Sensitivity to competition	Our analysis: no significant difference between species. Literature: higher sensitivity of true service tree	
Growth	Both species: fast height growth in youth, which later decreases, in line with Skovsgaard and Graversgaard (2013).	
Drought tolerance	Our analysis: similar drought tolerance. Literature: oak is less drought tolerant (Camarero et al. 2023) or more (Kunz et al. 2016; Kunz et al. 2018)	
aboveground CO2 storage	Age 50: 1.51 tons (Orlandi et al. 2022)	Age 46+: 1.18 tons of carbon (Weissert et al. 2017), equals 4.33 tons of CO2
PM10 uptake	1.16 g/m2 (Orlandi et al. 2022) - 1.01 g/m^2 (Fares et al. 2020)	0.7 g/m^2 (Fares et al. 2020)

4 Discussion

4.1 Allometric relationships of rare native species (*Articles I and III*)

4.1.1 Basic allometric relationships

European hornbeam, European white elm, field maple and wild service tree

When comparing the α-values of the cpa-d and the h-d allometry of European hornbeam, European white elm, field maple, wild service tree, European beech and oak to the generalised ideal allometric values (Niklas 1994; West et al. 2009), interspecific variation and divergence from the general values could be observed. Only the exponents of the 0.5 quantile of European hornbeam were lying within a close range to the ideal 4/3 of the cpa-d allometry (Niklas 1994), followed by oak (1.52) and wild service tree (1.06). The values of European beech and European white elm were far smaller, and the value of field maple was higher. In the case of field maple, this could indicate a high light demand, while European beech and European white elm can grow with smaller crowns.

A broad range of cpa values at a given dbh indicates a high morphological variability. This high crown variability is mainly observed in the literature for long-living tree species, often for more shade-tolerant tree species rather than for short-living species that demand much light (Pretzsch 2014). In this thesis, the morphological variability appeared to vary within the developmental stages of a tree. A relatively higher cpa expansion with increasing diameter growth, as identified for field maple, is a strategy observed in light-limited trees to cope with this limitation (Comeau and Kimmins 1989; Kimmins 1997). Concerning the 0.05 and 0.95 quantiles of the tree species, the widening corridor of European white elm and wild service tree with higher diameters indicates their potential to survive even in lower stand layers with suppressed crowns. Conversely, the narrowing cpa range of field maple and oak implies an increasing sensitivity against competition and suppression and a decreasing shade tolerance with higher age.

Compared to the ideal allometric exponent of 2/3 for the dbh-h-allometry (Niklas 1994), most α-values of the 0.5 quantile were similar and within a specific allometric corridor. Only the exponents of the wild service tree were lower. Lower values than 2/3 can be interpreted as relatively lower height development with increasing diameter growth. This behaviour is mainly observed for trees that follow a stabilisation strategy with reduced height growth compared to diameter growth. Values higher than 2/3, as for European beech and European white elm, can be interpreted as a survival strategy with an enhanced height growth to outcompete neighbours in the competition for light (Pretzsch 2009). The similar alpha-values of the 0.5 quantile of the two species show that European white elm can keep up with the height growth of European beech. With a specific lead in height, European white elm can even outcompete European beech in terms of height growth.

As the data did not follow a real-time series of measurements but is instead a combination of data from different stands, it was impossible to include past competition, mixture or provenance in the thesis. As these variables strongly influence allometry (Forrester et al. 2018; Genet et al. 2011; Pretzsch 2021b; Pretzsch and Schütze 2005), the present deviations of the allometric exponent from the generalised exponents could also be attributed to the trees' behaviour to provenance and site conditions. Furthermore, not all trees could be measured in pure stands. Wild service tree and true service tree were so rare that there were only mixed stands for older age classes. Finally, the overall sample size may have an impact on the results. With increasing measurements, the numbers could continue approaching the ideal allometric exponents.

True service tree

The exponents of the h-d relationship for both oak and true service tree were lower than the expected general exponent of 2/3. In contrast, the exponents of the cpa-d relationships were not significantly different from the assumed 4/3 (West et al. 1999). It is therefore recommended to use the species-specific exponents from this thesis for the h-d relationship to avoid an overestimation of height. For assessing crown sizes, the 4/3 exponent can be applied.

The parameters of the h-d relationship of oak and true service trees had similar values for the 0.95 and 0.5 quantiles. So, city planners and foresters can rely on their experience with oak to assess the potential height of true service trees. Concerning the crown development, the crown projection area of true service trees in the 0.95 quantile was slightly higher than for oaks. The quantile is associated with city trees, as these trees are often growing as essentially solitary trees and represent an exceptional case along the competition gradient. The higher space requirements should be considered in urban planning. For the 0.05 quantile, true service tree had smaller crown sizes for small dbh values than oak. However, this reversed with increasing dbh. Following the classification of Pretzsch et al. (2015), the true service tree has the same crown type as black locust (*Robinia pseudoacacia* L.) and European hornbeam (*Carpinus betulus* L.). When free from competition, these species form large crowns and further increase their crown size with bigger diameters. Given the same diameter, this results in a larger space requirement than other species but also creates larger shading areas that can have a cooling effect in urban areas. However, a study on the closely related Sorbus arnoldiana (Rahman et al. 2015) indicares a relatively low shading intensity.

Compared to the results of other scientists, this thesis found a large similarity between true service tree and oak, even when comparing across different regions in Europe. Kausch-Blecken von Schmeling (2000) published h-d values of true service trees in south German forests that are very similar to the results of this thesis. He also described maximum heights up to 34 m for true service tree. The highest tree in this dataset was a Slovakian tree with a height of 31.4 m. In German forest stands, there were several trees with a height of 29 m. Also, crown diameters of more than 20 m (Paganová et al. 2015; Skovsgaard and Graversgaard 2013) could be confirmed, as observed for a tree in Slovakia. Turrientes et al. (2009) examined young service tree in a dry climate (precipitation < 500 mm) and found a mean height of 2.3 m (min. 0.8 m, max. 4.7 m) and a mean diameter of 1.2 cm after six years. According to this thesis's allometric equations, a diameter of 1.2 cm results in a median height (0.5 quantile) of 2.99 m for the 0.95 quantile in 4.6 m and the 0.05 quantile in 2.24 m. Especially for the 0.95 quantile, the models indicated a very close fit to their measurements. The mean value of Turrientes et al. (2009) is most immediate to the 0.05 quantile, which can be attributed to the very dry conditions.

4.1.2 Stem taper and stem volume of true service tree

The stem profiles derived from section diameters and tree-ring analysis indicate that open-grown true service tree may have a particular stem taper that differs from other tree species. When comparing the actual stem volume of the two trees in Copenhagen and Alnarp to the total stem volume calculated by functions for other broadleaved tree species, it was found that available functions substantially overestimated the stem volume of true service tree. The best matching function was one by Hillebrand (1998) for rowan (*Sorbus aucuparia* L.), which overestimated volume 'only' by 33-35 %. A function by Kahle (2004) for wild service tree overestimated volume by around 100 %, and functions for European beech and pedunculate oak by Hagberg and Matérn (1975) and oak by Petersen et al. (2003) overestimated by 30-79 %. It should be cautioned, however, that these functions were not calibrated on trees with a dbh and height similar to those of the two true service trees used in this thesis, or such dbh-h combinations were on the edge of the calibration range. Moreover, open-grown trees, not least trees growing in a special environment such as in the city, may deviate in growth pattern and growth allocation from those within a forest. Nevertheless, the stem volume measurements indicate the potential need for a species-specific stem volume function for true service tree.

When comparing the allometric exponents to the ones of other rare native tree species studied in this thesis, the allometric exponent of true service tree for the cpa-d ratio was generally higher than the ones of other rare species, except field maple. True service tree showed the closest similarities to European hornbeam among the other rare species. Compared to the related wild service tree, higher exponent values of true service tree could be observed throughout all quantiles.

4.1.3 Influence of size and site variables on crown allometry

European hornbeam, European white elm, field maple and wild service tree

The crown size can indicate a tree's fitness, competitiveness and ability to occupy space (Pretzsch 2010a, 2019b). Additionally, the crown size (determined by crown surface, cpa, cl and crown width) correlates with the absorbed photosynthetic active radiation (APAR) (Binkley et al. 2013; Forrester et al. 2012) and leaf area (Forrester et al. 2013). Therefore, crown parameters can be used as a proxy for leaf area and light interception (Pretzsch 2014), and species that maintain a large crown in lower stand layers can be rated relatively shade-tolerant and competitive. This ability was observed for European hornbeam, European white elm and field maple, European beech and oak. However, the ability to form large crowns in lower stand layers decreased at higher diameters for field maple. It can be concluded that field maple has a certain tolerance against shade in younger stages, which in older stages decreases. Then, a higher sensitivity towards competition could be observed for field maple. White elm and oak could maintain the ability to form larger crowns in stands with low side pressure, even at lower stand layers. More shade-tolerant species like European beech and European hornbeam may only increase their crown expansion slowly with higher competition. Still, they can therefore also survive in lower stand layers in more suppressed conditions.

Based on the findings, the crown development of wild service trees appears to benefit from low competition, particularly in larger diameter ranges. This also matches the findings of Pyttel et al. (2019), who observed an increase in diameter growth and the densification of crowns for wild service trees released from suppression. The wild service tree appears to tolerate more competitors in lower diameter ranges.

European beech is a very competitive and shade-tolerant species that could develop large crowns, even in deeper stand layers and under high competition, especially at higher diameters. It can, therefore, easily dominate the canopy space, particularly on sites with a good water supply. When rare species, especially more light-demanding species like field maple or less competitive species than European beech, like white elm and wild service tree, are mixed with beech, constant and strict management operations are needed to promote the rare species. Even in older stands, regular and careful interventions are still essential for managing light availability. In general, competition is an important factor in crown development (Hasenauer and

Monserud 1996). For all species applied, the higher the competition, the more it determined crown growth above all other influencing variables. However, in this thesis, it was only possible to include the current situation of measurement of the competition rather than a value describing it over the whole lifetime of the tree, which could show different results.

Under less favourable growing conditions, tree growth focuses on root growth rather than crown expansion to maintain the water and nutrient supply (Comeau and Kimmins 1989; Kimmins 1997). This effect could explain the pattern observed in European hornbeam, where smaller trees exhibited much smaller crowns under dry conditions than under moister ones. Moreover, the species mixture in a stand could influence the crown allometry. This was not included in this thesis and needs to be the subject of further research.

True service tree

The linear mixed model (Eq. 11) indicated that crowns of true service tree in parks are larger than those in forests, all else being equal. This may be attributed to the negligible competition in parks throughout the entire lifetime of solitary trees, as also reflected by the Hegyi-index. Difficult growing conditions due to soil compaction or possible underground constructions did not negatively influence true service tree. As all true service trees in urban environments used in this study were growing in park-like conditions with some grass around them, it did not include street trees growing in heavily sealed or paved soil.

There was no difference in crown size between oak and true service tree and no difference in the influence of competition between the two species. This corroborates the results from the quantile regression analysis. It can be concluded that the growing space requirements, growth and competitive power of true service tree are similar to those of oak.

4.1.4 Maximum tree numbers and diameter development

The maximal tree numbers in Figure 14 can be used as reference values for silvicultural management. The numbers are favourable for management aimed at lower stem numbers and maximised tree diameter increment. The diameter range gives target values for the stand development. When the diameters of a forest stand of a certain height are lower than the suggested values of the curve, the stem number per hectare can be lowered so that the individual trees can develop wider crowns and again approach the target range of diameter growth.

All the species studied are within a similar range regarding maximum stem numbers. For earlier developmental stages, however, field maple, wild service tree and white elm can all be managed with higher stem numbers per hectare than beech and slightly higher numbers than oak.

Hornbeam lies in a similar range to European beech. In later thinnings for maple, wild service tree and European white elm, more or more substantial management interventions are necessary to lower the stem numbers. Despite being often perceived as only additional or serving species, rare deciduous species can develop target diameters comparable to oak and beech.

4.2 Growth and Growth Variability

European hornbeam, European white elm, field maple and wild service tree

Concerning the age-growth relationships, the rare species' growth lay within the growth range of European beech and oak on the same sites. When comparing the growth of European hornbeam with existing yield tables for northern Germany (Lockow 2009), sites in Germany reached a site index of II.5 (site WAL) and II (site EBR). Both sites in Poland reached a site index of II.25 despite their lower DMI. For all stands, the mean diameters were higher than those specified by the yield table. This indicates that the validity of the yield table of Lockow (2009) might be regionally limited to stands in northern Germany with their specific climatic and soil conditions. On other sites, the yield table may underestimate the actual growth of European hornbeam. The similar growth patterns of European hornbeam in Poland and Germany underline its high ecological amplitude. Even in eastern Poland, under climate conditions limiting the distribution range of European beech, the European hornbeam shows high growth rates.

For wild service tree, the annual increments were similar to the ones observed by Pyttel et al. (2013). They also observed very low annual increments, which they explained by the high shade tolerance of wild service tree and its ability to even survive under strong suppression. This indicates that some of the wild service trees used in the study might have been suppressed in the past or growing under much competition. This also explains the high variation in the dbh-age curves shown in Figure 4, where some trees had much higher diameters for a given age than others.

In general, European beech and oak grew more stable overall sites. The missing significant difference in annual growth between sites with different DMI of oak in the linear mixed model is another indication of the lower climatic sensitivity of oak in comparison to European beech (Scharnweber et al. 2011). The maximum tree ring widths of the rarer species show they can reach high year ring widths under suitable conditions and with proper silvicultural management. Combined with the results of the model assessing the sensitivity on site variables, it can be assumed that the high Gini coefficients of rare species are also connected to a high susceptibility to favourable years. Apparently, the species can quickly implement good annual growing conditions in annual growth. The high Gini coefficients may also be related to a different silvicultural treatment of the species in the past. European hornbeams are often used as a so called “serving” tree species in oak stands for the shading of stems and the prevention of the development of secondary branches. A higher growth can be provoked after a release of suppression by the extraction of the canopy. However, this again underlines that with enough growing space, high year ring widths of the rare species are possible.

The lower sensitivity to drier years of trees with a smaller dbh could be related to their smaller height and thus the lower gravimetric potential they have to overcome to transport water in the tree trunk and the higher stomatal conductance and sensitivity that make smaller trees less prone to transpirational stress (Grote et al. 2016; Ryan et al. 2006; Ryan and Yoder 1997). The decline in growth with an increasing tree size on dry sites can be traced back to a typical age effect and the culmination of growth already at lower diameters on poorer sites. The decrease of annual growth in field maple and wild service tree, even on better sites, indicates that both species culminate earlier in their growth than European beech and oak. Again, it also indicates a different silvicultural treatment of the species in the past. The increase of growth with higher diameters on better sites for European beech, oak and European hornbeam points to a release from suppression or competition at higher ages. Outstanding is the high potential of annual growth of European white elm. Especially on good sites and in young stands this species can easily obtain year ring widths of more than 1 cm.

True service tree

Due to its rarity in cities, forests, and landscapes alike, the stem analysis of Copenhagen's felled true service tree is unique. Even if there was only one sample tree, it provided the unprecedented possibility of insights into the specie’s growth in an urban environment. The tree germinated around 1943, was planted at its permanent location in December 1948 and was cut in April 2022 at an age of approximately 80 years. As the tree was growing next to a road and 350 m northwest of a power plant that was coal-fired until 1985, it was directly exposed to air pollution. The diameter increment, however, stayed stable over time. It only decreased during the last ten years, possibly relating mainly to the inherent age decline. In line with these observations, Orlandi et al. (2022) found that the ability of true service tree to absorb PM10 is above average. Height growth culminated at the age of 20-22 years. Subsequently, it still increased, but at a lower rate. This may be attributed to the species-specific growth characteristics of true service tree, as Skovsgaard and Graversgaard (2013) indicated. Based on a simple model calibrated on empirical observations, they more specifically stated that the height development of true service tree is characterised by fast or even very fast growth in youth, followed by a gradual decline and later a final stagnation, much like the height development of oak. For oak, it is known that this decreased growth steadily can go on for a long time.

The investigation could not examine the long-term growth trend of true service tree. Unfortunately, age determination for tree cores was impossible as it was impossible to reach the pith of the cored trees. However, the diameter growth curves indicate a steady growth over multiple years. Similar growth patterns could be observed when comparing the dbh curves derived from the tree cores from oak. This indicates that oak and true service tree share this characteristic of long-term, steady growth. Moreover, true service trees can grow to a very old age of several hundred years, similar to oak, again indicating similar growth patterns.

4.3 Drought stress response (*Articles II and III*)

4.3.1 Resistance, resilience, and recovery

European hornbeam, European white elm, field maple and wild service tree

There were few significant differences between species when comparing the Lloret indices of all species, not considering site and tree variables. Nevertheless, it was noticeable that field maple showed especially high values of recovery and resilience, however, with low resistance values. The resistance values of European beech being higher than the ones of field maple contradicts the results of Kunz et al. (2016), who had reverse findings. This could be due to a different selection of drought years and stands in both studies and the missing consideration between resistance and recovery values (Schwarz et al. 2020). However, when combining resistance and recovery values and comparing them with the line of full resilience, field maple and wild service tree stick out as drought tolerant species. Wild service tree due to its capability to surpass the line of full resilience for milder droughts and field maple for both its high recovery values in years with low resistance and its good performance after milder drought. This again matches the findings of Kunz et al. (2016). It once more shows the importance of combining both resistance and recovery rather than looking at the single indices when evaluating the drought tolerance of different species. Thereby, it can be considered that species with high resistance values often showed low recovery values and vice versa, as, after a substantial decline, there is naturally a stronger potential for recovery. Species with higher recovery values for lower resistance values, such as wild service tree and field maple, can recover more easily even in years with a strong growth decline. Oak showed better overall resistance to drought than the rare species, however, in severe drought years field maple and wild service tree seem to be better adapted.

The good recovery of oak and European white elm in years with milder drought can be attributed to their wood anatomy. In contrast to the other species considered in this study, oak and elm are ring-porous species. They are less sensitive to climate and drought than diffuse-porous species (Elliott et al. 2015) as they produce larger earlywood vessels where most of the hydraulic transport occurs (Hacke and Sauter 1996; Zimmermann 1983). After a drought event, they can, therefore, recover more quickly as larger vessels are already produced at the start of the next growing season. Diffuse porous species must use their smaller vessels created throughout the previous growing period. Embolised conduits can be repaired by refilling them (Hacke and Sauter 1996). Furthermore, the results correspond to the findings of Leonova et al. (2022), who found an increased fine root growth of European white elm during drought. This also leads to an enhanced growth during the next growing season.

True service tree

Overall, the results match the findings of other studies on true service tree. While the true service tree was found to be as drought tolerant as oak in this thesis, Camarero et al. (2023) found it even more drought tolerant than Mediterranean oaks. In their study, true service tree showed a better recovery after drought events, mainly to short drought events between 2-7 months. Carried out in Spain, their study indicated that the growth of true service tree was influenced primarily by dry spring conditions. Apparently, the species has a second peak of increment growth after the summer months, which is an advantage compared to oak. Therefore, the divergent results of the two studies might be attributed to different climatic conditions in Spain. Another study on tree rings of older trees (Kunz et al. 2018) did not suggest better drought tolerance of true service tree as compared to oak. However, combining the results of this thesis, covering locations both in Germany and Slovakia and one tree in Copenhagen, and the results of Camarero et al. (2023), covering locations in Spain, it is reasonable to assume that in most cases, the drought tolerance of the true service tree and oak are similar. Furthermore, it is generally recognised that most species of *Sorbus* have a good drought tolerance (wild service tree: Kunz et al. (2018), Schmucker et al. (2023); rowan (*Sorbus aucuparia* L.): Vogt (2001)).

4.3.2 Effect of site and tree variables on drought stress response (*Article II*)

Regarding the drought reaction, European hornbeam had a higher drought tolerance towards severe drought and on dry sites, as Leuzinger et al. (2005) observed. This could be explained by differences in their water consumption and stomatal regulation strategies, where European hornbeam follows a more isohydric behaviour (Köcher et al. 2009; Leuschner et al. 2019). In contrast to the results of this thesis, Scharnweber et al. (2020) observed a substantial growth decline for European hornbeam after two consecutive drought years. The drought tolerance of European beech and European hornbeam was similar in their study, with even a higher growth decline for European hornbeam. However, they suppose that a part of this growth decline can be attributed to the increased growth of roots in drought years as an adaptation strategy. This again matches the results where the higher resistance of European horn-beam towards severe drought could be observed for dry sites, where the European hornbeam might already be adapted to drought events. There was a high resilience and very high recovery towards milder droughts for field maple on very dry sites. Field maple recovered very well on more favourable sites after severe drought events. This one more time points out the high drought tolerance of the species and its high potential on dry sites. As Kunz et al. (2018) already studied, field maple is a highly drought-tolerant species with a high potential under climate change. Beloiu et al. (2022) found a low recovery and increased mortality after drought for field maple saplings, while Kunz et al. (2016) found much younger seedlings to be highly drought-resistant. This indicates that the initial drought resistance of the species may decrease with age. However, the high mortality after drought events may lead to a natural selection of trees with a higher drought resistance and, therefore, an adaptation to drought. At the same time, it may result in a higher drought tolerance of surviving trees due to an acclimation effect after the drought event (Kozlowski and Pallardy 2002). This again results in a higher drought tolerance of mature trees. It could not be differentiated between different climatic site conditions for European white elm, as the two sites had very similar DMI values. However, a high resistance against milder drought could be observed. Although more detailed research is needed, this thesis confirms Walentowski et al.'s (2014) assumptions that European white elm could be a suitable species under drier climate conditions. Site variables did not influence the wild service tree's drought resilience, recovery, and resistance. This is also a sign of the high stability of wild service tree under different site conditions. On both sites, a good recovery after mild droughts could be found, which was already observed by Kunz et al. (2016) for seedlings.

However, oak could cope better with drought on wetter sites, showing higher resistance values for large trees and a faster recovery of small trees on dry sites. This can be attributed to the weaker stomatal control of photosynthesis of small oak trees (Zang et al. 2012). In the study, there was no dependence of drought tolerance of European beech on climatic site conditions. On wetter sites, the tolerance of severe droughts was higher than on dry sites, while the tolerance towards mild droughts was lower. This higher susceptibility to mild drought on sites with a good water supply has already been observed in other studies dealing with the growth of European beech towards its distribution margins (Cavin and Jump 2017; Muffler et al. 2020;

Weber et al. 2013). It might be the result of a phenotypical reaction (Cavin and Jump 2017; Leuschner 2020) to site conditions and an acclimatation after multiple drought years (Petrik et al. 2022). This could point to a more isohydric behaviour of trees on drier sites (Nguyen et al. 2017). The good recovery of beech in milder droughts on dry sites can be connected to the rapid recovery of leaf metabolism (Leuschner 2020). High recovery values on wet sites after droughts might be related to the stimulation of fine root growth, as observed for saplings of European beech (Zang et al. 2014).

4.4 Study limitations

This thesis's results show some limitations. By sampling two sites per species for European hornbeam, European white elm, field maple and wild service tree, a variety of different site conditions were covered. However, this was only sometimes possible, as the occurrence of the species was often limited to sites where European beech or coniferous species were not dominating. In the case of field maple and wild service tree, these were very dry sites, in the case of European white elm riparian forests. However, the selected stands were primarily located in the species' core distribution range, representing typical climatic conditions. Nevertheless, expanding the study area with more plots on the edges of the distribution range could be interesting for future studies.

Tree cores used in this thesis were partially taken of different stem heights. The expression of climate sensitivity decreases on lower parts of the stem (Hoffmann et al. 2018), which may lead to some inaccuracy when comparing values of stands with different retrieval heights. Furthermore, no dead trees were sampled, as initially proposed by Schwarz et al. (2020). So, climatic factors that might have a negative, even lethal, effect on tree growth were not assessed. The low mean-Gleichläufigkeit values of European white elm indicate that the growth of trees on the plots was not primarily limited by precipitation and evapotranspiration but rather by other site factors. As both sampled sites of European white elm were in riparian forests, the flooding regime and groundwater access could be factors deterring tree growth. This follows the critique of Schwarz et al. (2020) and Zang et al. (2020), who suggest including more soil parameters in studies. This was not possible for this study as, besides the SMI, no data on past soil moisture were available for those stands. The SMI, however, only has a resolution of 4 x 4 km, leading to imprecise results for the first stands.

In the study, it was not accounted for the fact that repeated drought events may influence the drought reaction of the species. Especially for younger stands, the selected drought years might be the first droughts that the trees were experiencing. However, as all species covered younger and older trees with a different number of past drought events, this effect was neglected in the analysis.

The study indicates that true service tree and oak are similar in sensitivity to competition from other trees. This implies that the low occurrence of true service tree is probably much influenced by human activity to promote high forest systems and fast-growing coniferous species (Drapier 1993; Kausch-Blecken von Schmeling 2000; Skovsgaard and Graversgaard 2013). However, the overall mortality of trees and the competition on moist sites was not studied. The study was limited to relatively dry and warm regions, where other species are generally less competitive.

5 Conclusion

In terms of management, the results of this thesis lead to recommendations for the silvicultural treatment of the species. In early developmental stages, the rare tree species can survive with small crown sizes and can be managed in higher stem numbers than European beech and oak. For later stages, however, the competitiveness and shade tolerance, especially of field maple, decreases and the space requirements increase. It is therefore recommended to perform thinnings aiming at the release of competition for the species starting at the latest at a height of 15 m, as already implemented in many silvicultural guidelines. These thinnings should be repeated regularly, particularly when there is a large mixing percentage of beech. Field maple has to be released from crown competition before reaching a diameter of 20 cm. Hornbeam can tolerate crown competition and more side pressure, making it a species lower in maintenance compared to the other species in the study. For European hornbeam and European beech, drought sensitivity increases with diameter. Therefore, an adjustment of target diameters might be considered. True service tree is recommended to be managed based on guidelines for oak in forest settings. In urban environments, height growth can be assessed based on nearby oak. The crown projection area of true service tree is, however, marginally larger than that of oak. Therefore, true service tree provides a correspondingly larger shading area than oak, however, with a potentially low intensity, as indicated by results of other *Sorbus* species with similar leaves.

Concerning their growth and drought tolerance, field maple, true service tree, and wild service tree turned out to be good options to enrich oak stands on sites where many very dry years are expected in the future. The proportions of the rare species on the mixture should increase with increasing drought potential. European hornbeam showed similar growth patterns and drought stress response as European beech, with a slightly smaller climate sensitivity and with a stable growth across different climate zones in Poland and Germany. Furthermore, the results showed a good resistance of European hornbeam against severe drought events. It is therefore recommended to use European hornbeam as a complementary species for enriching European beech stands. Also, oak stands with a slightly better water supply could be suitable for an admixture of European hornbeam.

The higher drought tolerance of younger trees of wild service tree, field maple and European white elm is especially important concerning the relative uncertainty of weather development in the next years. The results suggest that young stands with those species that were recently established or will be established in the following years can cope with a variety of different weather conditions and are, therefore, a low-risk option to sustain unstable stands on dry sites.

European white elm can be highly recommended as a species for riparian forest systems. Even if there was only a limited assertion of its behaviour under drought conditions, the results generally indicated a high drought tolerance, which implies suitability also on dry sites. European white elm is prone to the invasive Dutch elm disease (DED), but much less than other native elm species like wych elm (*Ulmus glabra* Huds.) (Jürisoo et al. 2019; Jürisoo et al. 2021). As common ash *(Fraxinus excelsior* L.) also suffers from ash dieback, European white elm remains a relatively stable species on floodplain sites, fulfilling ecological and economic functions. The high growth rates also make it an interesting species concerning forest carbon sequestration.

True service tree's drought tolerance and overall growth behaviour are similar to those of oak. In contrast to common belief, as indicated in the literature, no higher sensitivity to competition for true service tree than for nearby oak trees growing under similar conditions could be identified. Its growth characteristics, combined with its high drought tolerance, make the true service tree a promising admixed species in forest stands and urban environments. Due to its high susceptibility to fungal canker, limited cultivation is recommended, and further research on pathology and silviculture and their interactions stays important.

In general, rare native species are a promising option to enrich the species composition on dry sites and contribute to establishing climate-tolerant forest stands. However, with ongoing climate change, even those species will eventually reach the limits of their drought tolerance. Therefore, the fight against climate change remains the most critical factor in guaranteeing the stability of future forests.

6 Perspective

This thesis gives first insights into the growth and drought stress reaction of rare native tree species. However, many questions and fields remain unclear and should be further investigated. This mainly concerns the growth under different site conditions, genetics, pathology and silvicultural treatment, including regeneration and mixture, but also the design and methodology of future research.

Concerning tree structure, future research complementing the results of this thesis should focus on crown shape in higher layers, as regular allometric formulas based on dbh often fail to predict crown growth (Ishii et al. 2017). Also, the role of provenances and genetic diversity on crown structure remains to be determined, as does the crown development under different types and forms of mixture with other species. Depending on the competing tree species, different grades of overlapping crowns can be observed (Pretzsch 2014; Schütz 1989). This also affects the packing density of trees per area and, therewith, the area-related productivity. Productivity is not only important for economic decision-making and tree species selection but also necessary when considering the carbon sequestration capacity of a particular tree species or species mixture.

Regarding growth patterns and especially structure of trees, forest trees and city trees are often considered two different and clearly separable groups. In reality, trees in urban environments are only a special, extreme case within the possible range of competition, growing with little or no competition. Therefore, as done in this theses, it might be more purposeful to see the separation between urban and forest trees as a continuum, include both in studies dealing with tree structure and growth, and transfer new findings from one field to another. Especially for the research on rare native tree species this is a promising method to increase sample sizes and to study a broader range of sites.

Genetic provenances were not included in this study but may significantly impact growth allometry (Pretzsch 2021a), growth and drought stress response. Also, provenances from the species' whole distribution range, beyond the sites used in this thesis, should be included. Especially marginal provenances could be of great interest. In addition, more measurements could be performed along a broader range of site conditions and soils to uncover effects that might be masked by this study's relatively narrow climate range. As site conditions in this database were often very similar, the influence of environmental conditions could not be clarified entirely.

Data used in this thesis covered different ages and tree sizes, which, however, originated from different stands. Observations of the long-term growth of single trees and stands, starting from the planting and including mortality, still need to be included. Also, in this thesis, only growth and drought stress responses on the tree-level were studied. Patterns and growth on stand level could differ from these results.

In a silvicultural context, the contribution of rare broadleaved species to uneven-aged, structured forests or in a pioneer forest to reforestate clear-cutted or disturbed areas is of high interest and should be further investigated. In this context, it is also essential to focus on natural regeneration. The species treated in this thesis are currently mainly distributed by planting. However, natural regeneration or seed may also be valuable options with advantages concerning root development and adaptation to specific site conditions. Here, it is remarkable that the natural regeneration of true service tree is rarely observed in nature. Browsing, light regime and genetic constrictions are under suspicion to reduce the germination capacity and the growth of seedlings, but the actual reasons remain unclear. Experiments on different regeneration techniques and germination rates for all species are necessary to develop guidelines and avoid a demixing of stands.

Increasing the research on the species is necessary to clarify these growth-related questions. The establishment of long-term plots is crucial for getting valid results. Experiments should cover provenance and thinning trials and should be established systematically to cover different soil types and climates. Furthermore, different planting densities and thinning regimes should be addressed. The mixing effect of different admixed species should also be addressed in these trials, combined with different mixing types (e.g., group-, single or row-wise) to work out silvicultural treatment options for various site conditions and objectives.

Most of the tree-ring data used in this study was derived from tree cores taken at dbh height but partly also on tree base height. In agreement with forest owners, this was the only possible way to minimise wood devaluation. However, different extraction heights may also lead to diverging results. Also, forest owners often limited the sample size to a certain tree number per stand to avoid damaging too many trees. In the future, new, non-invasive techniques like mobile CT scanners could be used to collect data without damaging the tree. This would allow an increased sample size with more homogenous measurements.

Besides open questions on tree growth, forest pathology issues must be addressed. All of the species included in this study, besides European hornbeam, are affected by (invasive) pathogens that require further research (*Cryptostroma corticale* on field maple (Kespohl et al. 2022), *Neonectria ditissima* on true service tree and wild service tree (Keil 1996), partially Dutch elm disease on European white elm (Jürisoo et al. 2021). More research is required to better understand the mechanisms of these diseases and to find protective measures. Also, it remains unclear if different provenances and populations on specific site types are more susceptible towards the diseases. As climate change and globalisation are progressing, the appearance of new pests and pathogens becomes more probable and should be considered in research and management.

The shift of forest composition towards a higher proportion of broadleaved species will also change the structure of future wood supply. This sets a challenge for the wood industry in Central Europe, which was mainly focused on coniferous species in the past. Here, new potential applications for the wood of broadleaved species have to be examined. Furthermore, the industry has to adapt its methods and hardware to the characteristics of the rare species. For this, more research on wood properties and potential uses is needed.

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Appendix

A. Article I

Title: Crown allometry and growing space requirements of four rare domestic tree species compared to oak and beech: implications for adaptive forest management

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ORIGINAL PAPER

Crown allometry and growing space requirements of four rare domestic tree species compared to oak and beech: implications for adaptive forest management

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Abstract

Rare domestic tree species are increasingly being viewed as promising alternatives and additions to current main tree species in forests facing climate change. For a feasible management of these rare species, it is, however, necessary to know their growth patterns and space requirements. This information has been lacking in management and science up to now. Our study investigated the basic crown allometries of four rare domestic tree species (European hornbeam, European white elm, field maple and wild service tree) and compared them to the more established and assessable European beech and oak (sessile oak and pedunculate oak). For our analysis, we used data from eight temporary research plots located on seven sites across south-eastern Germany, augmented by data from long-term plots. Using quantile regression, we investigated the fundamental relationships between crown projection area and diameter, and height and diameter. Subsequently, we used a mixed-effect model to detect the dependence of crown allometry on different stand variables. We derived maximum stem numbers per hectare for each species at different stand heights, thus providing much-needed practical guidelines for forest managers. In the early stages of stand development, we found that European white elm and field maple can be managed with higher stem numbers than European beech, similar to those of oak. European hornbeam and wild service tree require lower stem numbers, similar to European beech. However, during first or second thinnings, we hypothesise that the rare domestic tree species must be released from competitors, as shade tolerance and competitiveness decrease with age. Furthermore, we argue that thinnings must be performed at a higher frequency in stands with admixed European beech because of the species' high shade tolerance. When properly managed, rare species can reach target diameters similar to oak and beech.

Keywords Allometry · Growing space · Acer campestre · Carpinus betulus · Sorbus torminalis · Ulmus laevis

Introduction

In Central Europe, the range of tree species covers more than 40 native tree species that are adapted to a broad range of site and climatic conditions (Fitschen and Hecker 2017; Roloff and Bärtels 2018). However, forestry and forest science have in the past mainly focused on a few main tree species, such as the Scot's pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. H. Karst), European beech (*Fagus sylvatica* L.) or oak species (*Quercus petraea* L., *Quercus robur* L.). In contrast, less frequent domestic tree species, such as European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), and the wild service tree (*Sorbus torminalis* (L.) Crantz) have received only a little attention. Presumably because the main species were less prone to risks and relatively easy to manage. Most notably, European hornbeam,

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field maple and wild service tree, once important species of coppice forests (Pyttel et al. 2013; Bayerischer Forstverein 1997; Helfrich and Konolw 2010; Unrau et al. 2018), lost their relevance with the shift towards high forest systems combined with longer rotation cycles. Forest managers prioritised tree species that were easier to manage due to their higher competitive strength, yield and shade tolerance. European white elm, naturally a tree species of the hardwood floodplains and highly specialised in surviving long periods of flooding, lost large parts of its natural habitat due to the human-induced reduction in floodplains (Schindler et al. 2021). Furthermore, the European white elm has suffered from the invasive Dutch elm disease (DED) in recent years, although not as much as other European elm species (Jürisoo et al. 2019). The moderate use of rare domestic tree species in European silviculture, and the loss of their natural habitat, has resulted in low occurrence and great rarity. Today rare domestic tree species predominantly grow on sites with extreme site conditions, under special protection or, in the case of the European hornbeam, as an understorey species for promoting the production of high-quality oak timber (Bartsch et al. 2020). Against the backdrop of climate change and its detrimental effects on the growth and vitality of well-established main tree species like the European beech and Norway spruce (Schuldt et al. 2020; Thurm et al. 2018), rare domestic tree species are gaining importance as potential substitute species for the establishment of future forest stands. This approach is supported by initial studies indicating a high drought tolerance of field maple and the wild service tree (Kunz et al. 2016, 2018). Walentowski et al. (2014) anticipate that both species are exceptionally well adapted to warmer and drier climates, as predicted for Central Europe (IPCC 2021). European hornbeam is also considered to tolerate single years of severe drought (Leuzinger et al. 2005). Thurm et al. (2018) studied possible distribution ranges and productivity of European tree species in times of climate change, concluding that, unlike European beech and Norway spruce, the potential distribution area of European white elm will expand. Also it shows a high growth performance under different climate change scenarios. Moreover, rare domestic tree species included in this study have high economic and ecological values. The wild service tree is of particular ecological interest as its fruits and flowers provide a valuable food source for insects and mammals (Werres 2018). European white elm could substitute common ash (*Fraxinus excelsior* L.), which is currently suffering from ash dieback in large parts of its distribution range, on wet and floodplain sites and would thus make an important contribution to keeping these specialized ecosystems intact (Müller-Kroehling 2019). In contrast to non-domestic species, European hornbeam, European white elm, field maple and wild service tree have adapted to the forest ecosystem of Central Europe and their climate conditions (Kreyling et al. 2015) and can be cultivated without the elusive disadvantages of introducing non-domestic species, such as the uncertainty regarding exposure to pests, as well as economic utility, potential invasiveness and adoption by local flora and fauna (Sapsford et al. 2020; Castro-Díez et al. 2019; Matevski and Schuldt 2021; Vor et al. 2015).

Several current research projects throughout Europe address rare domestic tree species, mostly in the context of provenance trials to test their adaptivity to climate change. For instance, of the species treated in this study, the wild service tree is included in Swiss planting trials (Frei et al. 2018) and together with field maple, among others, as part of a study to examine the reforestation of former vineyards in South-western Germany (Kunz and Bauhus 2015). Research has also been carried out to define genetic provenances of the wild service tree in Southern Germany (Kavaliauskas et al. 2021). Similar projects for white elm and field maple are planned or in operation. Liesebach et al. (2021) propose establishing additional provenance trials for field maple and wild service tree in Germany. However, there are no long-term experimental plots of the species in Europe to deal with growth or yield.

Despite an increasing scientific interest in these species and a high practical relevance for the establishment of climate smart forests, only very little is known about those species' growth, yield, tree morphology and growing conditions. However, this knowledge is essential to assist forest managers in sustainably select and manage tree species that will endure in times of climate change. This makes it all the more important to generate and provide knowledge for the silvicultural management of rare domestic tree species.

One key piece of information needed to manage a forest is the growing space requirement of the tree species in question. Appropriate degrees of thinning and removal of adjacent trees can be elaborated through by knowing the growing space requirements of tree species on different sites. The optimal number of trees per hectare leads to an ideal use of the site's productive potential. Even less experienced private forest owners, or forest managers who have had little contact with these tree species in the past, can gain a simple understanding of thinning severity and space requirements from specific numbers. Only by providing species-appropriate silviculture and growing space management can a demixing to the detriment of the rare species be prevented (Pretzsch et al. 2021).

In this study, the development of key figures for tree size-dependent space requirements is based on the evaluation of allometric relationships. Most relations between a tree's stem and crown parameters underlie allometric growth functions (Pretzsch 2010, 2019b; Gayon 2000). That implies that they do not follow a linear growth process but the changes in relative dimensions of tree organs are correlated with changes in overall size (Gayon 2000). Only when looking at these underlying, species-specific relations, can we find true divergences that are not masked by differences in size. When modelling allometric relations, the allometric formula $y = b * x^{\alpha}$ is most commonly applied (Huxley 1932; Teissier 1934). Here, x and y represent measurements of the respective tree organs, while b and α represent allometric constants. Often, the formula is also used in log-transformed notation $\log y = \log b + \propto \log x$. The allometric exponent α can be seen as a distribution coefficient between the trait measurements x and y (Pretzsch 2010). Some theories state that universal allometrical exponents exist for many anatomical and physiological relationships (e.g. metabolic rate, population density, self-thinning line and life span, relations between trunk and crown dimensions) in plants (West et al. 1997; Enquist et al. 1998; Yoda 1963; West et al. 2009; L. H. Reineke 1933; Enquist et al. 2009; Mäkelä and Valentine 2006). Conversely, other studies have rejected the universal validity of allometric exponents (Harper 1977; Pretzsch and Biber 2005; Pretzsch 2010, 2014). There may, for example, be inter-specific (Pretzsch and Dieler 2012; Purves et al. 2007; Pretzsch 2006; Poorter et al. 2003; Dahlhausen et al. 2016; Antos et al. 2010) and intra-specific differences (Dieler and Pretzsch 2013; Pretzsch and Mette 2008; Duursma et al. 2010; del Río et al. 2019) in allometry. Furthermore, allometric factors may also be determined by factors other than size, for example environmental conditions (Poorter et al. 2012; Wang et al. 1998; Fortin et al. 2019), tree species diversity (Forrester et al. 2017a), competition (del Río et al. 2019; Pretzsch 2019b) or species diversity (Pretzsch 2010, 2014). Therefore, universal factors appear useful for rough calculations, but species-specific factors provide a more accurate perspective on size relations for more detailed analysis (Pretzsch and Dieler 2012; Niklas 2004). The specific space requirements can be determined through the allometry of, for instance, the height and diameter or height and crown projection area.

Unfortunately, there is little knowledge regarding the space requirements and allometry of the four rare domestic tree species analysed in this study (Table 1). At the same time, there are many publications dealing with the allometric relations of the main tree species (e.g., Scot´s pine (Hynynen 1995; Mäkelä and Valentine 2006; Sharma et al. 2017), European beech (Dieler and Pretzsch 2013; Juchheim et al. 2017; Longuetaud et al. 2013; Sharma et al. 2018), Norway spruce (Mäkelä and Valentine 2006; Sharma et al. 2018), Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Curtis 1967; Thurm et al. 2017; Thurm and Pretzsch 2016) and oak (del Río et al. 2019; Longuetaud et al. 2008, 2013). Most publications based on inventory data do not cover rare domestic tree species due to underrepresentation or because of grouping of deciduous tree species. Basic functions aimed at competitiveness and direct space requirement are still missing. There are

Table 1 Literature overview of relevant publications on the topic of allometry or space requirements of E. hornbeam, E. white elm, field maple and wild service tree. A cross represents the coverage of the topic within the publication, a cross in parentheses indicates partial coverage (e.g. mentioning a group name like "maple" but not specifically field maple)

	E. hornbeam	E. white elm	Field maple	Wild service tree	h/d	Cpa /Cr	Crown length	Plasticity	Biomass	Space requirements	Tree number/ha
Fortin et al. (2019)	X		X	X	X						
Forrester et al. (2017b)	X								X		
Forrester et al. (2017a)	X				X	X	X				
Suchomel et al. (2012)	X								X		
Longuetaud et al. (2013)	X		X	X				X			
MLUK Brandenburg (2009)	X								X		
Klädtke and Abetz (2010)			(X)							X	X
Pyttel et al. (2019)					X			X		X	
Pretzsch et al. (2015)	X					X				X	

no precise specifications or references to tree spacing requirements of European hornbeam, European white elm, wild service tree or field maple, even in many silvicultural guidelines.

Therefore, the objective of this study was to improve the knowledge base in terms of the allometric relationships of European hornbeam, European white elm, field maple, and wild service tree. To make the findings more accessible and put them in a more familiar context, we always compared the resulting numbers with those for European beech and oak.

To address the research objective, we:

(i) Analyse the allometric relations and functions of European hornbeam, European white elm, field maple and wild service tree and compare them to European beech and oak.
(ii) Show how the individual tree allometry depends on the site and competition.
(iii) Derive species specific growing space requirements and provide recommendations for silvicultural operations at different heights.

Materials and methods

Data

We measured European hornbeam, European white elm, field maple and wild service tree at different locations in southeast Germany to evaluate crown allometry. We first screened inventory data on the Bavarian state forest to find suitable stands. Next, we contacted local forest authorities in regions with a high abundance of the relevant species to get more information on possible stands and inspected them on site. Eventually we selected two sample sites for each species (Fig. 1). We measured trees in two different aged stands on each site to cover as wide an age spectrum as possible. Trees where measured within the borders of newly established plots. We chose areas with a high proportion of the species under scrutiny as plot positions, favouring mono-specific stands where possible. Admixed trees of other species inside the plots covered in this study were also measured and included in the data. We also collected data of 15 oaks or European beeches, depending on the occurrence at each plot. No distinction was made between sessile and pedunculate oak. Both species were grouped together as oak. The oak and beech trees were preferably of the same age

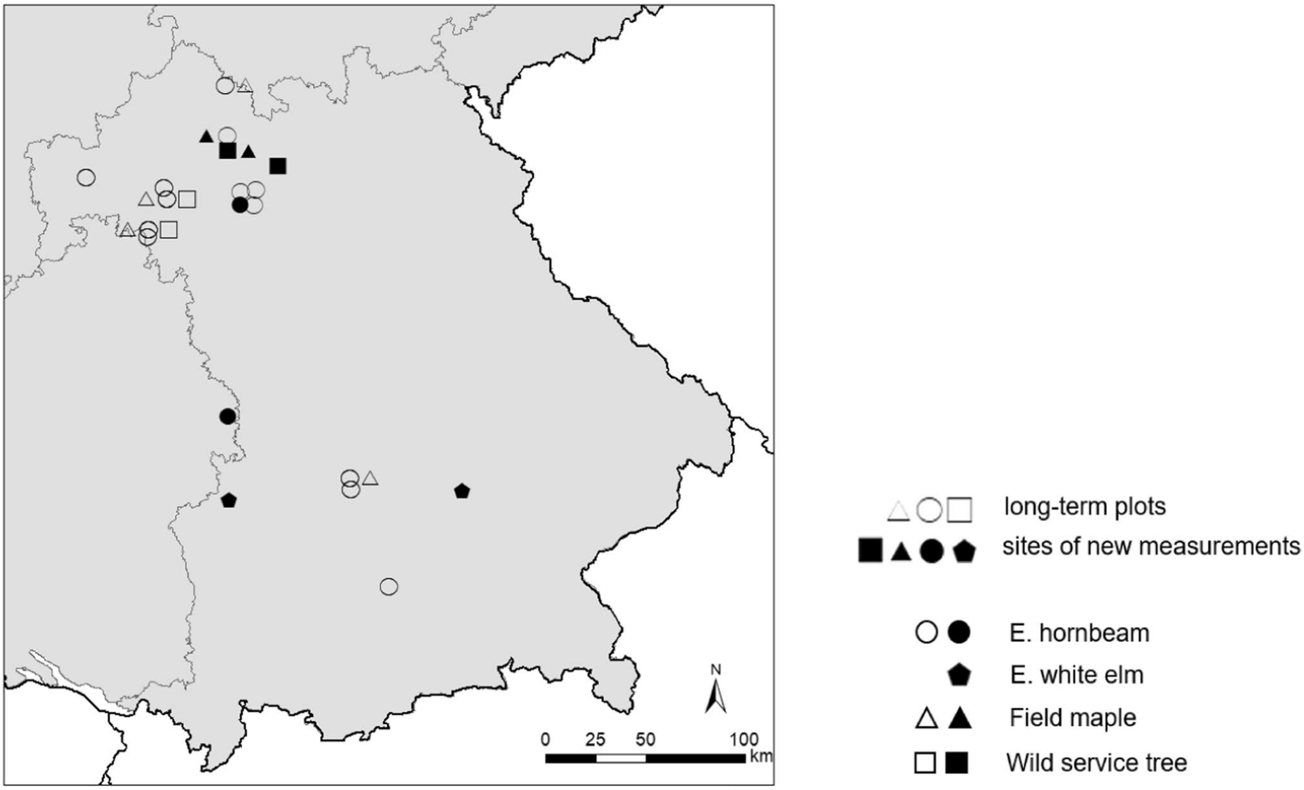

Fig. 1 Locations of seven research sites sampled in winter 2020/2021 and the long-term plots used in this study

Table 2 Climate data on sites investigated. The data was obtained using DWD grid data (Deutscher Wetterdienst 2021). Location numbers refer to long term yield plots

Location	Mean annual precipitation (mm) (1991–2020)	Mean annual temperature (°C) (1991–2020)
Schweinfurt (SCH)	736.3	8.9
Sailershausen (SAI)	663.9	9.5
Baunach (BAU)	744.6	9.1
Ebrach (EBR)	765.8	8.6
Wallerstein (WAL)	786.8	8.9
Offingen (OFF)	753.5	9.2
Freising (FRS)	708.9	9.4
102	629.6	9.9
105	714.8	9.4
106	679.4	9.6
132	706.4	9.0
133	762.6	8.6
140	1043.3	9.1
638	688.1	9.2
640	814.3	8.3
648	627.9	9.0
801	979.5	8.9
803	717.7	9.1
804	754.1	9.0
832	746.4	9.2
851	777.8	9.1
852	901.1	7.7

(according to information of the management plan) or had a similar diameter and grew under the same site conditions as the targeted rare species. Data were collected in winter 2020/2021.

Data from a network of long-term experimental plots maintained by the Chair of Forest Growth and Yield Science at the Technical University of Munich, Germany, formed another component of the database. Data from these plots had already been used in different publications (Pretzsch and Biber 2005; Pretzsch and Schütze 2005; Pretzsch 2010; Pretzsch et al. 2019) regarding other species. Although there are no specific experimental plots dedicated to observing European hornbeam, field maple and wild service tree, single individuals often occur on the plots. European white elm is not distinguished explicitly in the data base, only as *Ulmus* spec. and therefore could not be used. We filtered the data for the species investigated and selected the latest measurements of the trees for our analysis. Furthermore, we also included all European beeches and oak trees on the long-term plots containing the rare domestic species studied, besides white elm, to compare the data with measurements of oak and European beech trees on similar sites. All the data sources included trees with a minimum diameter of 7 cm at a height of 1.30 m. The sample sizes per tree species, site and data source can be found in S3 and S4, the climatic conditions in Table 2.

Tree parameters

We measured tree height, crown base height (height of the first primary branch with leaves), and diameter at breast height (DBH), using a girth tape for all sample trees. Furthermore, we measured the crown radii in all cardinal and sub-cardinal directions using the vertical sighting method (Pretzsch 2019a; Preuhsler 1981; Röhle 1986).

The crown projection area was obtained from the eight-radii measurements via a periodic spline function interpolating the distances at 40 equally spaced points (R package "sp" (Pebesma and Bivand 2005; Bivand et al. 2013)). The crown radius was calculated as the quadratic mean of all the radii measured ($\mathrm{cr} = \sqrt{(r_N^2 + r_{\mathrm{NE}}^2 + \ldots + r_{\mathrm{NW}}^2/8}$). The exact location and relation between the parameters can be obtained from Fig. 2, the parameter abbreviations from Table 3.

We used the surrounding basal area of the single tree as a measurement of competition. It was obtained using the angle

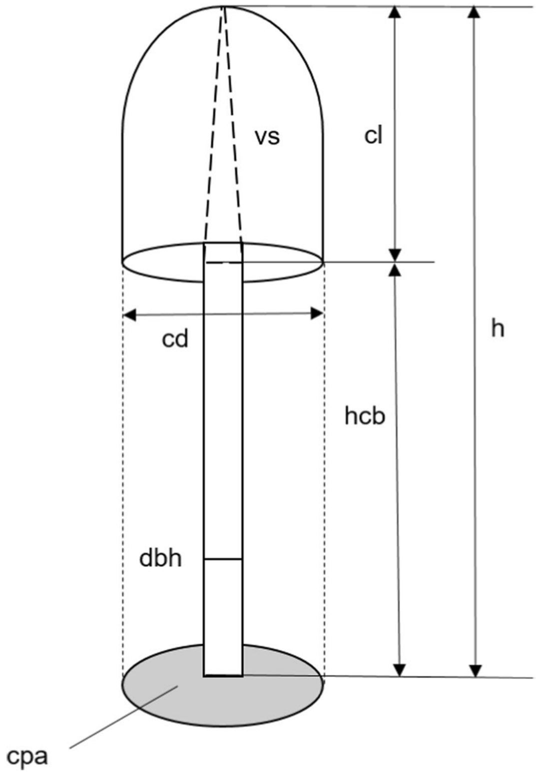

Fig. 2 Tree parameters used in this analysis: crown length (cl), crown diameter (cd), crown projection area (cpa), diameter at breast height (dbh), height of crown base (hcb), height (h), stem volume (vs)

Table 3 List of parameter abbreviations

Parameter	Abbreviation
Crown length	cl
Crown projection area	cpa
Diameter at breast height	dbh
Height	h
Crown diameter	cd
Crown radius	cr

count sampling by Bitterlich (1952). While making our own measurements, we conducted the angle count sampling for each tree at the plot, using a relascope. We calculated the surrounding basal area for the long-term experimental plots by using the diameters and distances between trees obtained by their spatial coordinates.

We used the social status index described by Fortin et al. (2019) to take the social status of a tree into account. This is calculated by dividing the tree's height by the stand's quadratic mean height.

We used the Martonne index (Martonne 1926) as a well-known index for aridity for modelling the climatic site conditions (Pretzsch et al. 2020; Bielak et al. 2014; Pardos et al. 2021). The Martonne index considers both the annual mean temperature and precipitation and is calculated with the formula $\mathrm{dMI} = \mathrm{P}/(\mathrm{T}+10)$, with P being the precipitation in mm and T being the temperature in °C. We used the climate data of the German Weather Service (DWD) for the period 1990–2020 (CDC; CDC) as input data. The data are available as an interpolated grid with a 1×1 km resolution. We extracted the data for the coordinates of each plot, calculated the index and subsequently derived an average value over the whole period.

Statistics

All analyses were conducted in R (R Core Team 2020) using RStudio (RStudio Team 2020) and packages from the tidyverse (Wickham et al. 2019). We used ggplot2 (Wickham 2016) for graphics and the quantreg package (Koenker 2020) for fitting quantile regressions. Data exploration was conducted using the protocol of Zuur et al. (2010). All the fitted models were subject to the usual visual residual diagnostics. The residuals were plotted against the fitted values for all models. In no case did the plots suggest any violation of variance homogeneity. Likewise, the normality of errors was verified by making normal q-q plots of the residuals. We used the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) packages to fit the mixed-effect models. Interactions were displayed using sjPlots (Lüdecke 2021).

Quantile regression

We chose quantile regression to examine general allometric relationships. We can fit regression models to different conditional quantiles of the response variable with this technique. This is useful, as allometric relations of individual trees often occur inside a corridor or range of values rather than being represented by one single model (Fahrmeir et al. 2013). Quantile regression has the advantages that it is distribution-free, more flexible for covariate effects and less sensitive to extreme values (Fahrmeir et al. 2013). We fitted the 95%, the 50% and the 5% quantile for the cpa-dbh (Eq. 1) and h–d-allometry (Eq. 2). We chose these two allometric relations as they were the most accessible and most significant for growth and space requirements. Other tree parameters, such as the height of the crown base or crown radius, were well correlated with height and cpa. We used the cpa-h and dbh-h allometry (Eqs. 3 and 4) to deduce growing space requirements and target diameters for specific heights.

$$\ln(\mathrm{cpa}) = a + \alpha * \ln(\mathrm{dbh}) \tag{1}$$

$$\ln(h) = a + \alpha * \ln(\mathrm{dbh}) \tag{2}$$

$$\ln(\mathrm{cpa}) = a + \alpha * \ln(h) \tag{3}$$

$$\ln(\mathrm{dbh}) = a + \alpha * \ln(h) \tag{4}$$

We used a subsample from our dataset consisting of the trees for which each model's respective parameters were available. The exact subsample sizes per tree species, and data source of model 1 and 3 can be found in table S3, of model 2 and 4 in Table 4.

The confidence intervals for the regression models were calculated by rank inversion method (Koenker 1994).

Mixed linear model

Then, we made a more detailed examination of the cpa-d-allometry and its dependence on site and stand characteristics.

The data set of our study includes multiple observations of tree allometry parameters of trees on different plots. Moreover, some of these plots are located at the same site. We applied a mixed-effect model with plot and site as a random intercept to take this dependency structure of the data into account. We created the following global models based on the logarithmic allometric formula, containing all the variables and the interactions between them:

Table 4 Overview over the main tree parameters used in this study grouped by species

Species	Variable	Min	Max	Mean	*n*
European hornbeam	dbh [cm]	2.8	44.3	15.793	1057
	cpa [m^2]	0.87	146.775	24	810
	h [m]	4.1	30.8	15.781	1057
European white elm	dbh [cm]	7.2	73.6	25.828	183
	cpa [m^2]	3.09	151.28	25.84	182
	h [m]	6.9	34.77	18.935	183
Field maple	dbh [cm]	7	55.7	17.607	220
	cpa [m^2]	0.53	160.6	18.062	190
	h [m]	8.2	30.9	15.617	220
Wild service tree	dbh [cm]	7.4	70.1	25.912	86
	cpa [m^2]	4.65	132.9	32.303	75
	h [m]	8.6	24.9	17.699	86
European beech	dbh [cm]	2.1	102.1	23.267	2276
	cpa [m^2]	0.778	128.907	25.879	1355
	h [m]	2.8	42.3	20.586	2276
Oak	dbh [cm]	6	75.2	31.562	1140
	cpa [m^2]	0.723	121.739	25.409	677
	h [m]	5	39	24.131	1140

n sample size; *min* minimum value; *max* maximum value; *mean* mean value; *h* height; *dbh* diameter at breast height; *cpa* crown projection area

variable to measure, an indicator for the site index and only little affected by thinnings (Pretzsch 2019a). Thinnings usually start at a height of 12–14 m and are carried out in intervals that correspond to a height growth of 3 m (Schleswig–Holstein LF, and NWFVA 2021; Hessen-Forst 2016; Ministerium für Umwelt, Landwirtschaft, Natur- und Verbraucherschutz NRW 2019; Klädtke and Abetz 2010). We, therefore, derived maximum stem numbers per hectare for every tree species based on top heights starting from 12 m going to a maximum of 30 m (or the end of the fitted data). This guarantees easy application in practice and a smooth fit to existing management guidelines.

In a first step, we fitted a quantile regression on the 0.75 and 0.95-quantiles of the cpa-h-allometry (Eq. 3). The 95%-quantile includes the most vital trees of a certain height with the most significant space requirement, the 0.75%-curve still includes vital trees and trees with smaller crowns. As a next step, we divided 10.000 m^2 by the resulting values of each curve to obtain the stem numbers per hectare.

Furthermore, we calculated the 75% and 95%-quantile of the dbh-h allometry (Eq. 4) to retrieve a range of target diameters for each height. The resulting curve describes the targeted diameter development of the stand.

$$\begin{aligned}\ln\left(\mathrm{cpa}_{\mathrm{ijk}}\right) = {} & a_0 + a_1 \times \ln\left(\mathrm{dbh}_{\mathrm{ijk}}\right) + a_2 \times \mathrm{Martonne}_{\mathrm{ij}} + a_3 \times \mathrm{ACS}_{\mathrm{ijk}} + a_4 \times \text{social status}_{\mathrm{ijk}} \\ & + a_5 \times \ln\left(\mathrm{dbh}_{\mathrm{ijk}}\right) \times \mathrm{Martonne}_{\mathrm{ij}} + a_6 \times \ln\left(\mathrm{dbh}_{\mathrm{ijk}}\right) \times \mathrm{ACS}_{\mathrm{ijk}} \\ & + a_7 \times \ln\left(\mathrm{dbh}_{\mathrm{ijk}}\right) \times \text{social status}_{\mathrm{ijk}} + a_8 \times \mathrm{Martonne}_{\mathrm{ij}} \times \mathrm{ACS}_{\mathrm{ijk}} + a_9 \times \mathrm{Martonne}_{\mathrm{ij}} \times \text{social status}_{\mathrm{ijk}} \\ & + a_{10} \times \mathrm{ACS}_{\mathrm{ijk}} \times \text{social status}_{\mathrm{ijk}} + \mathrm{Plot}_{\mathrm{ij}} + \mathrm{Site}_j + \varepsilon_{\mathrm{ij}}\end{aligned} \tag{5}$$

where Martonne represents the average Martonne index of 1990–2020, 'ACS' the local stand basal area and 'social status' the social status index.

The full model (Eq. 5) was stepwise reduced by eliminating non-significant effects and re-fitted following a procedure suggested by Zuur et al. (2009). The more complex elements (interactions) were removed first, and non-significant effects were retained when they were also part of a significant interaction. The sample sizes and stand characteristics used in the model can be found in Tables S4 and S5.

Deducing the growing space requirements for different heights

In silvicultural guidelines, the treatment of forest stands is often based on a stand's top height as it is an easy

Results

Basic allometric relations

Cpa-d-allometry

In Fig. 3, we show the 0.05, 0.5 and 0.95 quantile regression curve of the cpa-dbh-allometry of European hornbeam, European white elm, field maple, wild service tree, European beech and oak as described in Eq. 1. The 0.05 quantile represents trees with rather small crowns, without much space for expansion. In contrast, the 0.95 quantile shows trees with larger crowns, dominating trees or solitary trees (Pretzsch et al. 2015). The 0.95 quantile therefore has a major significance in calculating the space requirements of the tree species.

The α-values of the 0.05 quantile range from 0.208 for white elm to 2.042 for oak. For the 0.95 quantile, we can

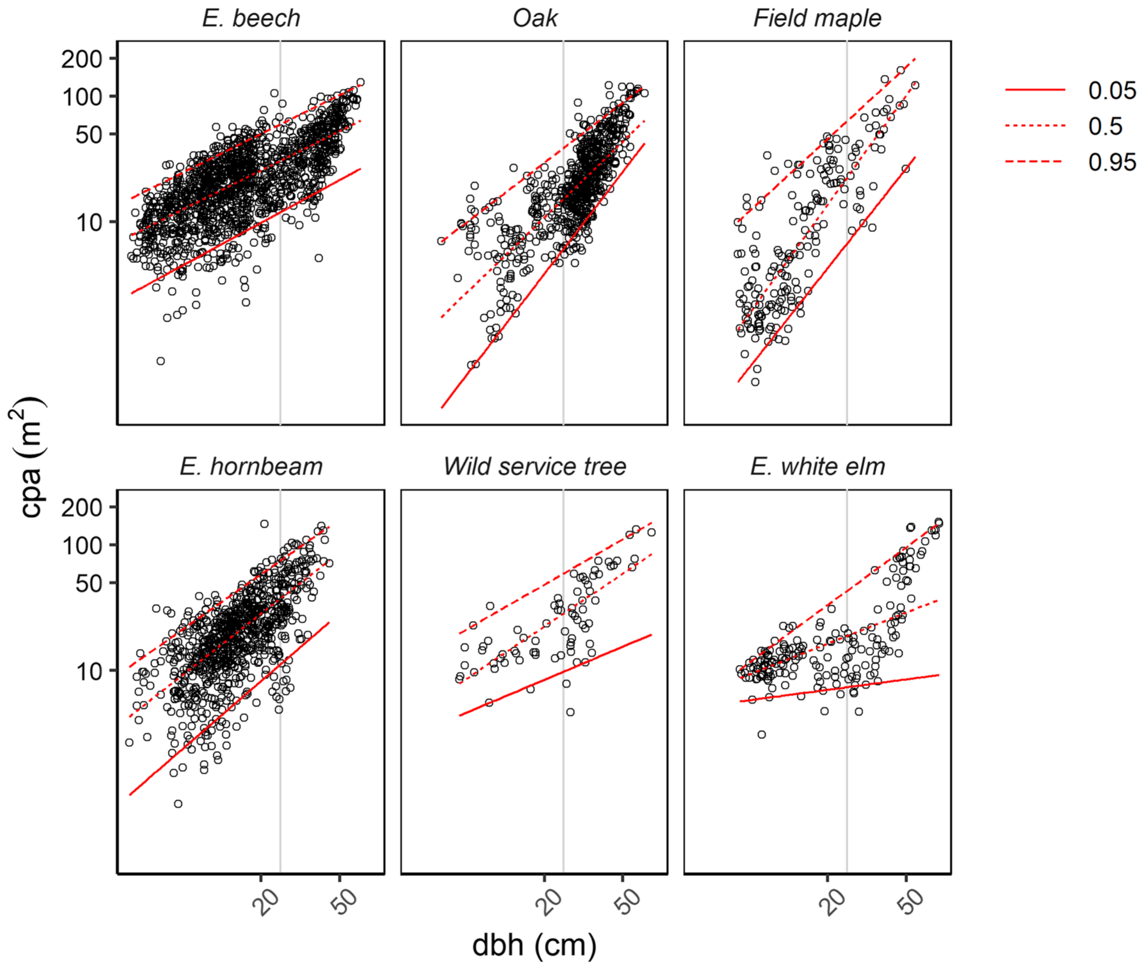

Fig. 3 Allometric relationships between dbh and cpa, for European hornbeam, European white elm, field maple, wild service tree, European beech and oak. The upper line represents the 0.95-quantile, the lower line the 0.5-quantile-regression. At 25 cm, a reference line has been inserted for better orientation. The statistical characteristics are shown in supplementary Table S1

observe α-values from 0.778 (European beech) to 1.447 (field maple). Wild service tree, and especially European white elm, shows higher α-values for the 0.95 than for the 0.05 quantile, resulting in diverging curves for larger diameters. The morphological variability of the crown increases for larger diameters. The opposite course can be observed for field maple and oak. Both species have higher α-values for their 0.05 than for their 0.95 quantile and therefore a narrower cpa-range for high dbh-values than for lower ones. European hornbeam and beech show very similar values for the 0.05 and 0.95 quantile resulting in almost parallel curves.

When looking at the α-values of the 0.5-quantile, we can observe an α-value of 0.783 for European beech. This implies a negative allometric relation ($\alpha < 1$) between cpa and dbh. For European white elm, the α-value is even smaller (0.619) also indicating a negative allometry. Wild service tree has an α-value of 1.055 showing an almost isometric relation ($\alpha = 1$). The a-values of the 0.5- quantile are ranging from −3.933 (field maple) to 0.942 (European white elm). European white elm and beech are the only species with positive values, the other species have negative values or, in case of wild service tree close to 0 (−0.048). By the combination of a and α-values, we can deduce crown expansion strategies for the species. Field maple, oak and hornbeam with low a and high α-values are associated with initially smaller crowns extending to larger ones in later growth, compared to the crown size of other species at the same age. As indicated by the 0.95 and 0.05-quantile, the morphological variation in crown sizes of oak and field maple increases much more than in the case of hornbeam. European white elm with high a and low α-values appears to be a species a large crown both in young and mature age. Additionally, however, the results of the 0.95 and 0.05 quantile imply a large span of

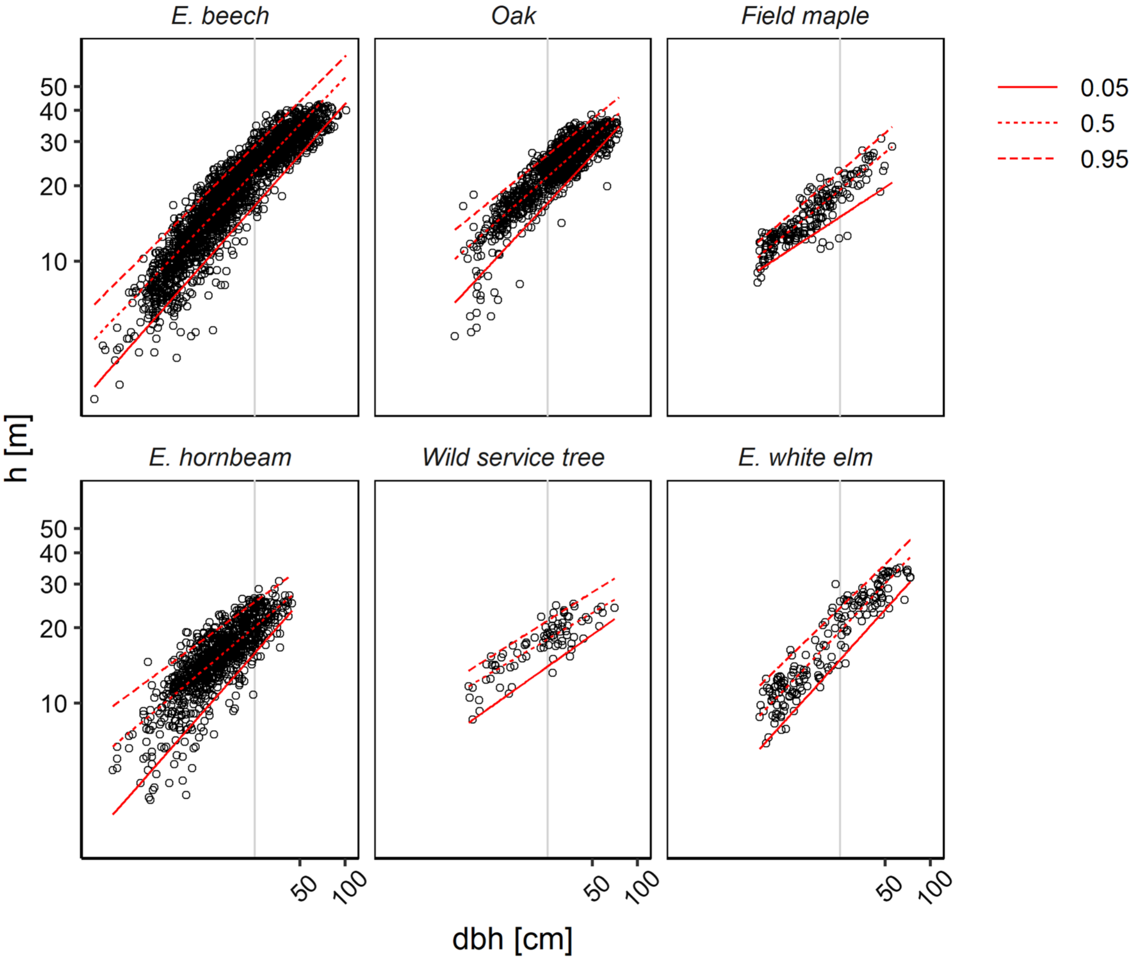

Fig. 4 Allometric relationships between stem diameter (*d*) and height (*h*), for European hornbeam, European white elm, field maple, wild service tree, European beech and oak.The upper line represents the 0.95-quantile, the lower line the 0.5-quantile-regression. At 25 cm, a reference line has been inserted for better orientation. The statistical characteristics are shown in supplementary Table S1

crown sizes for higher diameters. European beech and wild service tree show a similar behaviour.

Height-diameter allometry

In Fig. 4, we show the results of the quantile regression analysis calculated with Eq. 2. For the 0.05 quantile, the α-values range from 0.392 (field maple) to 0.68 (European hornbeam). The 0.95 quantile covers values from 0.38 (wild service tree) to 0.59 (European beech). All α-values are smaller than 1, indicating a negative allometric relationship with a height increment of less than 1% for a 1% increase of diameter. The distance between the 0.05 and 0.95 gets narrower with higher dbh values for all species, besides field maple. The difference between the a-values of the 0.05 and 0.95 is smallest for field maple (1.452 and 1.429) and the highest for European hornbeam (0.576 and 1.823), indicating a generally narrow height level range for field maple.

The *α*-value of wild service tree is the smallest of all species (0.355), resulting in a shallow growth pattern. Conversely European white elm has the highest α-value (0.629) similar to European beech (0.624), although with a lower a-value (1.119 for European beech and 0.945 for European white elm).

Influence of site conditions and competition on the cpa

The model selection based on the global model in Eq. 5 resulted in the models described in Table 5. Plots displaying the interactions for each model can be found in the supplements (Figs. S1–S9).

In the case of European hornbeam, cpa was significantly influenced by dbh, Martonne index, the tree's social status and interaction between diameter and Martonne index ($p < 0.01$). The crowns of trees in the lower stand layers were wider than those of trees of the same diameter in the

Table 5 Results of fitting the global model (Eq. 3) to the data

European hornbeam				
Fixed effects	Parameter	Estimate	Standard Error	*p*
Intercept	a0	− 3.075	1.034	0.004**
log(dbh)	a1	2.361	0.303	0.000***
Martonne	a2	0.087	0.027	0.002**
social status	a4	− 1.332	0.136	0.000***
log(dbh) x Martonne	a5	− 0.025	0.008	0.001**
Random effects		Parameter		Standard deviation
Plot		Plotij		0.123
Site		Sitej		0.335
European white elm				
Fixed effects	Parameter	Estimate	Standard error	*p*
Intercept	a0	0.889	0.623	0.276
log(dbh)	a1	1.047	0.104	0.000***
ACS	a3	− 0.03	0.01	0.003**
social status	a4	− 1.167	0.308	0.000***
ACS x social status	a10	0.027	0.01	0.006**
Random effects	Parameter			Standard deviation
Plot	Plotij			0.243
Site	Sitej			0.696
Field maple				
Fixed effects	Parameter	Estimate	Standard error	*p*
Intercept	a0	3.688	1.233	0.003**
log(dbh)	a1	− 0.089	0.462	0.848
social status	a4	− 4.844	1.295	0.000***
log(dbh) x social status	a7	1.504	0.46	0.001**
Random effects	Parameter			Standard deviation
Plot	Plotij			0.277
Site	Sitej			0.662
Wild service tree				
Fixed effects	Parameter	Estimate	Standard error	*p*
Intercept	a0	− 3.092	0.965	0.003**
log(dbh)	a1	1.966	0.285	0.000***
ACS	a3	0.126	0.038	0.002**
log(dbh) x ACS	a6	− 0.043	0.012	0.001***
Random effects	Parameter			Standard deviation
Plot	Plotij			0.087
Site	Sitej			0.486
European beech				
Fixed effects	Parameter	Estimate	Standard error	*p*
Intercept	a0	1.464	0.683	0.033*

Table 5 (continued)

European beech

Fixed effects	Parameter	Estimate	Standard error	p
log(dbh)	a1	0.143	0.349	0.683
Martonne	a2	− 0.003	0.014	0.825
ACS	a3	− 0.024	0.008	0.005**
social status	a4	0.115	0.578	0.842
log(dbh) x Martonne	a5	0.02	0.008	0.01**
log(dbh) x ACS	a6	0.009	0.003	0.004**
log(dbh) x social status	a7	0.221	0.06	0.000***
Martonne x social status	a9	− 0.048	0.013	0.000***

Random effects	Parameter	Standard deviation
Plot	Plotij	0.317
Site	Sitej	0.000

Oak

Fixed effects	Parameter	Estimate	Standard error	p
Intercept	a0	− 2.582	0.401	0.000***
log(dbh)	a1	2.288	0.092	0.000***
ACS	a3	− 0.035	0.011	0.001**
social status	a4	− 1.531	0.299	0.000***
ACS x social status	a10	0.025	0.009	0.007**

Random effects	Parameter	Standard deviation
Plot	Plotij	0.438
Site	Sitej	0.375

‘$*$’, ‘$**$’ and ‘$***$’ indicate $p<0.05$, 0.01 and 0.001, respectively. The parameters of the individual models correspond to the parameters of Eq. 5. Parameters not mentioned in the table were not included. Sample sizes are listed in supplementary Table S5

upper layer. Overall, the site water supply increased the cpa, although the effect was more pronounced in smaller trees, as indicated by the significant interaction term.

For European white elm, the final model kept the local stand basal area and social status as predictors. Furthermore, the interaction between both variables proved significant ($p<0.01$). Generally, higher social status and competition meant a decrease in cpa. The significant interaction term indicated a stronger negative effect of competition on the cpa of trees with a low social status, whereas an increase in competition only had a small effect on trees in the higher stand layers.

We retained the social status and its interaction with the dbh as the most important variables influencing the cpa of field maple. A high social status was overall connected to a decrease in the cpa. However, due to the significant interaction term between dbh and social status, we could observe that the cpa of trees with a lower social status increased less with a higher dbh than those of trees with high social status.

The model reduction of the wild service tree resulted in a model with the competition and interaction between it and the diameter as significant variables ($p<0.01$). As implied by the significant interaction term of diameter and competition, an increase in cpa with higher diameter was especially pronounced for trees with low competition.

For the European beech model, we kept all the variables and the significant interactions between dbh and social status, ACS and Martonne index, and the interaction between Martonne index and social status. A good water supply had a positive effect on the cpa, which was especially pronounced for trees with a higher diameter. An increase in the competition was connected to smaller crowns overall. However, this effect was less pronounced at higher diameters. In relation to the social status, we observed wider crowns for trees in upper layers, however, this effect was insignificant ($p>0.05$). Nevertheless, the significant interaction term between social status and dbh indicated a higher increase in the cpa with increasing dbh for trees in lower stand layers.

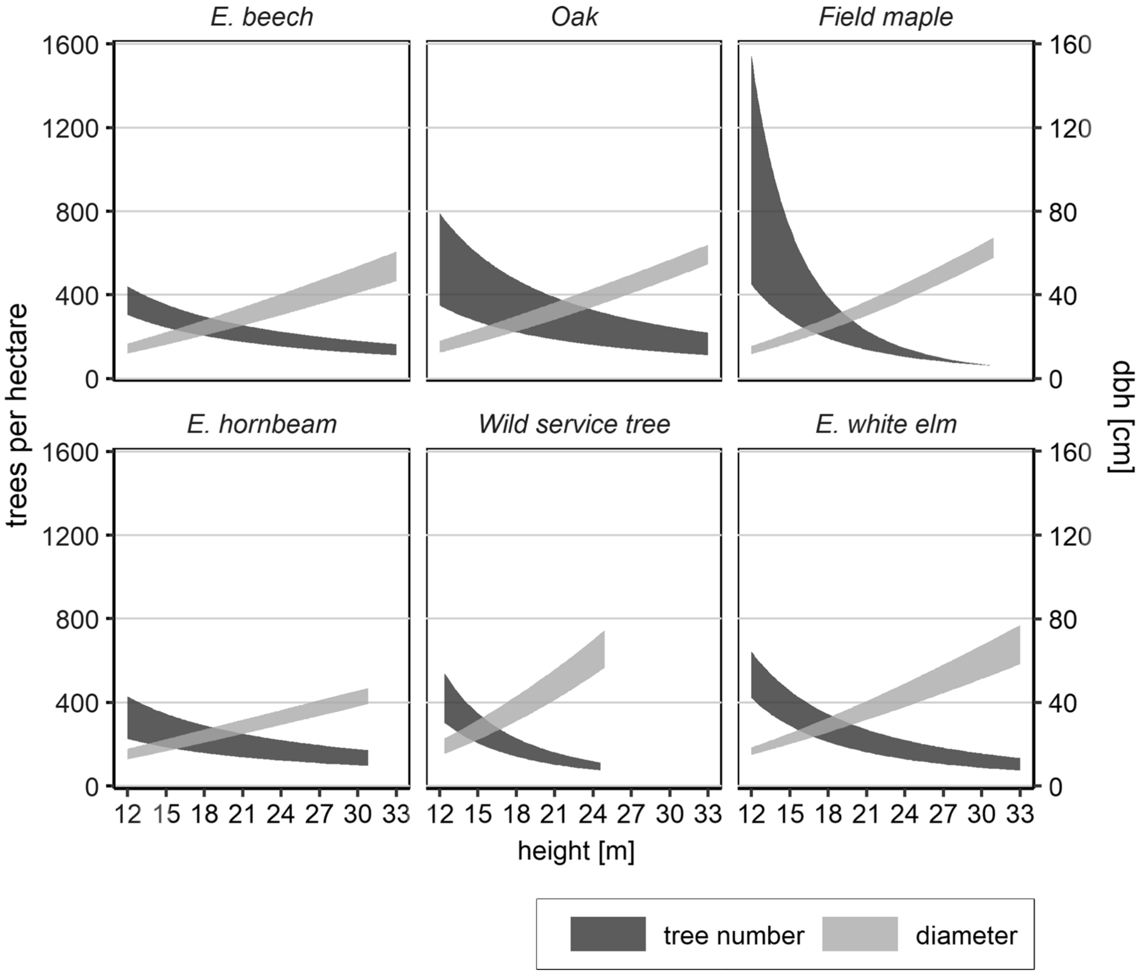

Fig. 5 Range of maximal tree numbers per hectare and dbh over tree height (*m*). Calculated based on the 0.75 and 0.95 quantiles of the cpa-h and dbh-h allometry. Statistical parameters can be found in supplementary Table S2. The units for the tree numbers per hectare are displayed on the left y-axis, the dimeter units are displayed on the secondary y-axis on the right

A more pronounced effect of water supply could also be observed for these trees.

For oak, we kept the surrounding basal area, the social status and the interaction between both as variables. Overall, high competition and social status resulted in a smaller cpa. The negative effect of competition was especially powerful for trees in lower stand areas.

Maximum tree numbers per hectare

The calculation of maximum tree numbers resulted in the curves displayed in Fig. 5. The range of the diameter values represents the 75–95% biggest trees in a stand which are considered as the most vital and economical interesting ones. The range of stem numbers per hectare is derived by the 75 and 95% values of the cpa-h allometry. The 3 m height steps on the x-axis represent thinning intervals. The diameter curve shows the species-specific potential diameter development in the corresponding height. These target diameters can be obtained when the tree number per hectare lies within the associated tree number range. High tree numbers correspond with smaller crowns, lower numbers with wider crowns.

Field maple can be managed with the highest stem numbers per hectare at early height stages, resulting in a broad corridor. After that, the corridor becomes narrower, beginning at the height of 15 m. The development of the target diameters resembles that for oak. The tree number ranges of European beech and European hornbeam show a similar course, while European hornbeam diameters are lower than those of European beech. Wild service tree shows a steep increase in diameter with a simultaneous decrease in stem number per hectare, resulting in target diameters above 60 cm at the height of 24 m. The diameter development and the tree numbers per hectare of European white elm resemble those for oak, though with larger diameters at great heights.

At a height of 15 m, for instance, European beech can reach diameters from 16.2 to 22.1 cm, European hornbeam similarly from 16.8 to 22.4 cm, oak from 17.3 to 22.1 cm and field maple from 17.1 to 22.1 cm. Of all species, wild service tree and European white elm show the largest diameters for this height (22.2–31.6 cm for wild service tree and 20.2–25.4 cm for European white elm). To achieve these target diameters, European beech should have a cpa of 27.6–40.2 m^2, resulting in 248–362 trees per hectare. The space requirement of European hornbeam is slightly higher in this height (cpa of 28.8–53.8 m^2 and 186–347 trees per hectare). While having similar target diameters, the size related cpa range of field maple has a deeper lower limit than the one of oak (13.8–35.6 m^2 for field maple vs. 16.7–36.7 m^2 for oak). Therefore, up to 723 field maples and only 273–599 oaks have space on one hectare. The wild service tree needs a cpa of 28.6–48.6 m^2 to reach the target diameter. This results in maximum stem numbers of 205–349. European white elm needs a cpa of 21.9–34.7 m^2 and 288–456 trees per hectare. If forest managers observe diameters lower than the ones in the dbh guide curve for the corresponding height, they should lower the stem number per hectare in the next thinning until it lies within the recommended stem number range. In case the stem number is already inside the range, they should orient themselves towards the lower end of the scale.

Discussion

Allometry of rare domestic tree species

When comparing the α-values of the cpa-d and the h–d-allometry of hornbeam, white elm, field maple, wild service tree, beech and oak to the generalised ideal allometric values (Niklas 1994; West et al. 2009), we can see an interspecific variation and divergence from the general allometric values.

When comparing the α-values with the ideal allometric exponent of 4/3 concerning the cpa-d allometry (Niklas 1994) for the 0.5 quantile, only the value of European hornbeam ($\alpha = 1.226$) lies within a close range. The next closest values are oak (1.518) and wild service tree (1.055). The values of European beech and European white elm are far smaller, the value of field maple higher. A relatively higher cpa expansion with increasing diameter growth, as identified for field maple, is a strategy observed in light limited trees to cope with this limitation (Comeau and Kimmins 1989; Kimmins 1997). In case of field maple, this could indicate a high light demand, while European beech and European white elm are able to increase their diameter with comparably smaller cpa.

Compared to the ideal allometric exponent of 2/3 according to the elastic similarity model for the dbh-h-allometry (Niklas 1994), most α-values of the 0.5 quantile are similar and within a specific allometric corridor. Only the α–value of wild service tree is far lower (0.355).

Lower values than 2/3, as observed for European hornbeam, field maple, oak and wild service tree, can be interpreted as relatively lower height development with increasing diameter growth. This behaviour is mostly observed for trees that follow a stabilisation strategy with reduced height growth in comparison to diameter growth. Values higher than 2/3, as for European beech and European white elm, can be interpreted as a survival strategy with an enhanced height growth to outcompete neighbours in the competition for light (Pretzsch 2009). The similar alpha-values of the 0.5 quantile of the two species show that European white elm can keep up with the height growth of European beech. With a certain lead in height, European white elm can even outcompete European beech in terms of height growth.

However, as our data do not follow a real-time series of measurements but is instead a combination of data from different stands, we could not include past competition, mixture or provenience in our study. As allometry is strongly influenced by these variables (Forrester et al. 2018; Pretzsch and Schütze 2005; Genet et al. 2011; Pretzsch 2021b) the present deviations of the allometric exponent from the generalised exponents could also be attributed to the trees' behaviour to provenience and site conditions. Furthermore, not all trees could be measured in pure stands. The wild service tree was so rare that we could only find mixed stands for older age classes. Finally, also the overall sample size may have an impact on the results. With an increasing amount of measurements, the numbers could continue to approach the ideal allometric exponents.

A broad range of cpa values at a given dbh indicates a high morphological variability. This high crown variability is mainly observed in the literature for long-living tree species, often for more shade-tolerant tree species rather than for short living species that demand much light (Pretzsch 2014). In our study, the morphological variability appears to vary within the developmental stages of a tree (Fig. 3). Concerning the 0.05 and 0.95 quantiles of the tree species, the widening corridor of European white elm and wild service tree with higher diameters indicates their potential to survive even in loser stand layers with suppressed crowns. Conversely, the narrowing cpa-range of field maple and oak implies an increasing sensitivity against competition and suppression, as well as a decreasing shade tolerance with higher age.

Impact of tree-, stand and site- characteristics on crown allometry

For the tree species investigated in our study, different parameters impacted their cpa. We observed larger crowns in trees growing in lower stand layers for European hornbeam, European white elm and field maple, European beech and oak. This is a behaviour often observed when light limitation forces tree to expand their access to light (van Hees and Clerkx 2003; Hofmann and Ammer 2008). Supressed trees have a tendency to increase their crown expansion compared to their diameter growth to obtain enough light (Comeau and Kimmins 1989; Kimmins 1997). For light demanding tree species like field maple, the shift to a higher crown expansion compared to diameter growth might already happen with low competition. More shade tolerant species like European beech and European hornbeam may only increase their crown expansion slowly with higher competition, but can therefore also survive in lower stand layers in more supressed conditions.

The crown size can be used to indicate a tree's fitness, competitiveness and ability to occupy space (Pretzsch 2010, 2019b). Additionally, the crown size (determined by crown surface, cpa, cl and crown width) is closely correlated to absorbed photosynthetic active radiation (APAR) (Binkley et al. 2013; Forrester et al. 2012) and leaf area (Forrester et al. 2013). When measuring crown parameters, we can, therefore, use them as a proxy for leaf area and light interception (Pretzsch 2014). Therefore, species that can maintain a large crown in lower stand layers can be rated as relatively shade-tolerant and competitive. For field maple, the ability to form large crowns in lower stand layers decreases at higher diameters. It has a certain tolerance against shade before this stage. White elm and oak can maintain the ability to form larger crowns in stands with low side pressure, even at lower stand layers. The higher the competition becomes, the more it determines crown growth above all other influencing variables.

Under less favourable growing conditions, tree growth focusses on root growth rather than on crown expansion to maintain the supply of water and nutrients (Comeau and Kimmins 1989; Kimmins 1997). This effect could explain the pattern observed in European hornbeam, where smaller trees exhibited much smaller crowns under dry conditions compared to moister ones. Moreover, the species mixture in a stand could have an influence on the crown allometry. This factor was not included in our study and needs to be the subject of further research.

Based on our findings, the crown development of wild service trees appears to benefit from low competition, particularly in larger diameter ranges. This also matches the findings of Pyttel et al. (2019), who observed an increase in diameter growth and the densification of crowns for wild service trees released from suppression. The wild service tree appears to tolerate more competitors in lower diameter ranges. Competition is generally an important factor in crown development (Hasenauer and Monserud 1996). However, it was not a significant parameter for most species in this study. It is difficult to make a general statement as we could only include the current situation of measurement of the competition rather than a value describing it over the whole lifetime of the tree.

European beech is a very competitive and shade-tolerant species that can develop large crowns, even in deeper stand layers and under high competition, especially with higher diameters. It can easily dominate the canopy space, particularly on sites with a good water supply. When rare species, especially light-demanding species like field maple or less competitive species like white elm and wild service tree, are mixed with beech, constant and strict management operations are needed in favour of the rare species. Even in older stands, constant and careful interventions are still essential for managing light availability.

Maximum tree numbers and curve of diameter development

The maximal tree numbers shown in Fig. 5 can be used as reference values for silvicultural management. The numbers are favourable for management aimed at lower stem numbers and maximised tree diameter increment. The diameter range gives target values for the stand development. When the diameters of a forest stand of a certain height are lower than the suggested values of the curve, the stem number per hectare can be lowered, so that the individual trees can develop wider crowns and can again approach the target range of diameter growth.

All the species studied are within a similar range in terms of maximum stem numbers. For earlier developmental stages, however, field maple, wild service tree and white elm can all be managed with higher stem numbers per hectare than beech and slightly higher numbers than for oak. Hornbeam lies in a similar range to beech. In later thinnings for maple, wild service tree and elm more or stronger management interventions are necessary to lower the stem numbers. Despite often being perceived as being only additional or serving species, rare deciduous species can develop target diameters comparable to oak and beech.

Conclusions

European hornbeam, white elm, field maple and wild service tree can play an important role in future forests. In early developmental stages, they are relatively shade tolerant and can be managed in higher stem numbers than beech and oak. For later stages, however, the competitiveness and shade tolerance, especially of field maple, decreases and the space requirements increase. We therefore recommend to perform thinnings aiming on release of competition for the species starting latest at a height of 15 m, as already implemented in many silvicultural guidelines. These thinnings should be repeated regularly in particular when there is a large mixing percentage of beech. Field maple additionally has to be released from crown competition before it reaches a diameter of 20 cm. Hornbeam can tolerate crown competition and more side pressure, making it a species lower in maintenance compared to the other species in the study.

Future research could focus on crown shape in higher layers. As regular allometric formulas based on DBH often fail to predict the crown growth (Ishii et al. 2017). Furthermore, genetic provenances were not included in this study but may significantly impact growth allometry (Pretzsch 2021a). In addition, more measurements could be performed along a broader range of sites to uncover effects that might be masked by the relatively narrow climate range in this study. As site conditions in this database were often very similar, the influence of environmental conditions could not be clarified entirely. Therefore, systematic provenance and thinning trials are essential for future research.

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Author's contribution JS collected and analysed data and wrote the manuscript; EU supervised data collection, analysis and writing process; MS supervised data collection and contributed to manuscript writing; HP initiated the study and supervised the whole data collection, analysis and writing process.

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Data availability Data are available from the corresponding author if reasonably requested.

Declarations

Conflict of interest No conflicts of interest were identified.

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B. Article II

Title: Growth and drought reaction of European hornbeam, European white elm, field maple and wild service tree

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ORIGINAL ARTICLE

Growth and drought reaction of European hornbeam, European white elm, field maple and wild service tree

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Abstract

Key message **Considering their drought tolerance and growth characteristics, rare native tree species are well-suited admixed species for the development of climate-stable forests in Central Europe.**

Abstract In our study, we assessed the growth and drought reaction of the four rare native tree species European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), and wild service tree (*Sorbus torminalis* (L.) Crantz). Based on tree-ring data, we (I) evaluated their species-specific growth characteristics and variability and examined the influencing site and tree characteristics on annual growth. (II) We quantified their reaction to single drought events, also depending on site and tree variables. (III) We compared our results to oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.). As they are well-known Central European tree species, there is a broad knowledge about their growth and drought response across wide geographical ranges available. Bringing the results of European beech and oak in relation with the rare native species, it allows to categorise their growth and drought reaction and to contextualise their performance. Our results show, that besides European white elm, the rare species showed an overall lower annual growth with a higher variability than European beech and oak. However, especially field maple and wild service tree were better adapted to drought than European beech and partially even recovered better than oak. Combining the aspects of growth stability and drought tolerance, we conclude that rare native tree species are well suited as admixed species in future forest stands. European hornbeam is a suitable match for European beech on wetter sites, while field maple and wild service tree are a sensible complement for the climate stable oak on drier sites.

Keywords Rare native tree species · Drought · Growth · Variability

Introduction

In recent years, Central Europe has experienced several severe drought summers with high temperatures and low precipitation (Buras et al. 2020). Climate change projections for Central and Northern Europe predict even drier and hotter climate conditions in the future, with more frequent, severe and prolonged droughts (Cook et al. 2020; Eyring et al. 2016; Ionita and Nagavciuc 2021; Spinoni et al. 2019; Zscheischler and Seneviratne 2017). The associated consequences for forest ecosystems are substantial. Persistent climatic changes enhance the risk of growth decline, forest mortality (Allen et al. 2010, 2015; Senf et al. 2020), and diminish forest productivity (Rita et al. 2020), diversity, and carbon storage (Pilli et al. 2022). Recent droughts in Central European forests have caused canopy damages (Beloiu et al. 2022; Buras et al. 2020; Philipp et al. 2021; Sturm et al. 2022; Thonfeld et al. 2022) resulting in reduced crown size and height growth (Jacobs et al. 2021). The composition of Central European forests is expected to change in future due to different drought resistance of tree species. The introduction and promotion of alternative admixed species is a viable option to increase forest stability (Sturm et al. 2022). In this context, non-native tree species, as western hemlock (*Tsuga heterophylla* (Raf.) Sarg), northern red oak (*Quercus rubra* L.) or

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sweet chestnut (*Castanea sativa* Mill.), that are expected to be well adapted to hot summer temperatures and drought seem to be promising and recommended for an increased cultivation (Bolte et al. 2009; Hoffmann et al. 2018; Pötzelsberger et al. 2020). However, non-native species might be maladapted to colder winter temperatures and late frost events, which are also expected to increase in the future (Kreyling et al. 2015; Vitasse et al. 2019; Zohner et al. 2020). Therefore, native and drought resilient species may be a more reasonable alternative to complement present prevailing species. Other than for non-native species, they exhibit less uncertainties concerning the exposure to pests, adoption by local fauna, the potential use of their wood and their influence on other ecosystem services (Castro-Díez et al. 2019; Matevski and Schuldt 2021; Sapsford et al. 2020).

Among native species, especially European hornbeam (*Carpinus betulus* L.), European white elm (*Ulmus laevis* Pall.), field maple (*Acer campestre* L.), and wild service tree (*Sorbus torminalis* (L.) Crantz) seem to be promising options for admixture in Central European forests. The distribution range of European hornbeam is mainly determined by annual mean and winter temperature of the region (Varol et al. 2022). It tolerates annual mean temperatures up to 15 °C, which qualifies it for the use in Central European silviculture, where its future distribution range is considered to still be congruent to its present one (Koch et al. 2022). In the strictly preserved zone of Bialowieza national park, it even increased its share in the tree species composition in the last decades (Brzeziecki et al. 2018, 2020). Severe and short droughts can be withstood by European hornbeam due to a relatively stable sap flow under stress conditions (Leuzinger et al. 2005). Seedlings, however, were found to show a high drought sensitivity, but also a high capacity to recover (Beloiu et al. 2020). In addition, Scharnweber et al. (2020) found a strong growth decline of mature European hornbeams after the drought of 2019. Overall, detailed studies about the drought tolerance of adult trees of European hornbeam are currently scarce.

European white elm is a tree species of riparian forests with a current distribution range that covers climates from dry and cool to warm and moist (Collin and Bozzano 2015). It is expected to keep (Koch et al. 2022) or even expand (Thurm et al. 2018) this distribution range in central Europe under predicted climate change scenarios, especially where a decline of current dominant species is observed. At the same time, European white elm is able to maintain a high growth performance under different climatic scenarios (Thurm et al. 2018). Mild drought stress does not have an influence on morphological traits of its saplings (Black-Samuelsson et al. 2003). However, drought reactions may highly vary between different provenances (Black-Samuelsson et al. 2003; Venturas et al. 2015). Leonova et al. (2022) found that European white elm, similar to oak, can maintain a constant amount of fine root biomass under drought conditions and can even enlarge it during drought.

Field maple favours a mild climate with low autumn precipitation and occurs within the entire temperate climate zone, except high mountain areas, regions with high precipitation (e.g. the British Isles) and the Mediterranean (Coudun et al. 2006). In a previous study, field maple showed a high drought tolerance, even exceeding that of oak (Kunz et al. 2018). In a greenhouse experiment, seedlings were found to have a high drought resistance (Kunz et al. 2016), which could, however, not be confirmed under field conditions where a high mortality and low recovery was noted (Beloiu et al. 2020). In general, field maple is expected to be well adapted to future climate change scenarios (Walentowski et al. 2014).

Wild service tree is currently growing in warm and dry parts of Europe (Rasmussen and Kollmann 2004) which are regions that correspond to future climate conditions in Central Europe. This adaptation makes the wild service tree a promising tree species under climate change conditions (Walentowski et al. 2014). A recent study noticed a higher drought tolerance than European beech, but not than oak (Kunz et al. 2018). Seedlings are sensitive to drought, but recover quickly afterwards (Kunz et al. 2016).

General growth patterns of the species are widely unknown. Only for European hornbeam, a yield table for Northern Germany exists (Lockow 2009). For wild service tree, Pyttel et al. (2013) used stem analysis to determine annual increments and deduced age-height and height-diameter curves. In other studies, rare species are often aggregated in categories as “other hard wood species”. For weighing out different species against each other and choose sensible species for cultivation, it is, however, important for forest managers to assess the potential growth of the species. It is also crucial to further evaluate the potential of rare domestic tree species to cope with climate change to develop adapted management strategies for Central European forests. Hence, more information on drought response patterns of these species is urgently needed. Most studies addressing the drought sensitivity of rare species are based on experiments with seedling or young plants or simulations (e.g. Kunz et al. 2016; Thurm et al. 2018; Varol et al. 2022). Studies using data from older trees are underrepresented. However, not only drought tolerance is an important characteristic of tree species for forest managers, but also a reliable and stable growth with economic potential.

To make our results for the rare species easier to access for forest managers and forest scientists, we compare them to European beech (*Fagus sylvatica* L.) and oak (*Quercus* *robur* L., *Quercus petraea* (Matt.) Liebl.). As these are the dominant deciduous tree species in central Europe (Meyer et al. 2020), their growth and drought reactions are already well studied and widely known. European beech shows pronounced growth declines in large parts of is distribution range as a reaction to recent drought events (Leuschner 2020; Schuldt et al. 2020). Although it has been found to have the potential to genetically adapt to increasing drought stress (Petrik et al. 2022; Pfenninger et al. 2021), a declined growth and distribution range are anticipated, especially at its drier and warmer distribution limits (Del Martinez Castillo et al. 2022; Muffler et al. 2020). Pedunculate oak and sessile oak show a higher drought tolerance than European beech (Mette et al. 2013; Meyer et al. 2020) and are expected to show stable growth even under drier and hotter conditions. However, a decrease in sap flow rates and canopy conductance were observed in response to extreme drought events (Süßel and Brüggemann 2021). These negative effects of extreme drought on the ecophysiological processes of oaks can be mitigated by mixing with other species, e.g. European beech or Scot's pine (Steckel et al. 2020; Stimm et al. 2021). In general, oak and European beech show different drought reactions (Scharnweber et al. 2011; van der Werf et al. 2007), with higher stability of oak (Kasper et al. 2022) and also a higher resistance and resilience towards drought (Meyer et al. 2020).

In our study, we used tree-ring data to:

(I) Assess the dendrometric growth characteristics of European hornbeam, European white elm, field maple, and wild service tree and the overall variability of growth, depending on site and tree variables. We hypothesise that there are species-specific growth characteristics and differences in the influence of site conditions.

(II) Quantify and compare the species' reaction to single drought events. We hypothesise that the species show differences in their resistance and resilience towards drought and their recovery after drought events. We further hypothesise that the species-specific drought reactions are influenced by the individual tree size and site-specific climate conditions.

(III) Compare the growth characteristics and drought reaction of the four rare native tree species with the well-studied European beech and oak which themselves differ in their growth and reaction to drought. We hypothesise that rare species show generally a smaller annual growth than European beech and oak and that they are at least as drought tolerant as European beech.

Materials

Sites and sample tree selection

For each species, we took tree cores from trees in two stands on two different sites in South-Eastern Germany in winter 2020/2021. Except for wild service tree for which on the second site, we only took cores in one stand. For European hornbeam, we additionally sampled trees of two stands located in eastern and central Poland, respectively. In total, we sampled the selected rare species in 17 stands on 9 sites (Fig. 1). We selected stands where the species grew in large proportions to reflect mono-specific or only slightly mixed conditions. The sites per species ideally covered different site conditions. However, due to the rarity of the species the desired variation in growing conditions could not be always realised. Therefore, the two sites of field maple and European white elm did not differ strongly in site conditions. All stands were undergoing regular silvicultural treatment in the past. As all stands were even-aged, the two stands per site covered a *dbh*-range per species (Table 1). The two stands per site were chosen as close to each other as possible to ensure similar site conditions.

In each stand, we sampled 15–20 trees, covering the whole diameter spectrum of the stand. Trees were randomly selected, however, not standing directly next to each other. Depending on the occurrence, additional 10–15 European beech or oak trees or both were sampled (in total 105 European beeches and 107 oaks). They were chosen to grow in the direct vicinity of each stand with the sampled rare species and within a similar species composition, past treatment, age and site conditions (Table 2). When selecting oaks, we did not differentiate between sessile oak and pedunculate oak. We additionally included tree-ring data from two existing experimental plots of European beech that were in close vicinity to the plots with rare species (Schmied et al. 2023). The values of basal area included in Tables 1 and 2 were determined doing an angle count sample at each cored tree.

The selected sites for European beech, field maple, oak and wild service tree were located in their core distribution area in Europe. The two European hornbeam sites in Poland showed lower precipitation rates than the German sites. Both sites of European white elm were located on sites with a rather high precipitation compared to the rest of the European white elm's distribution range (Fig. 2).

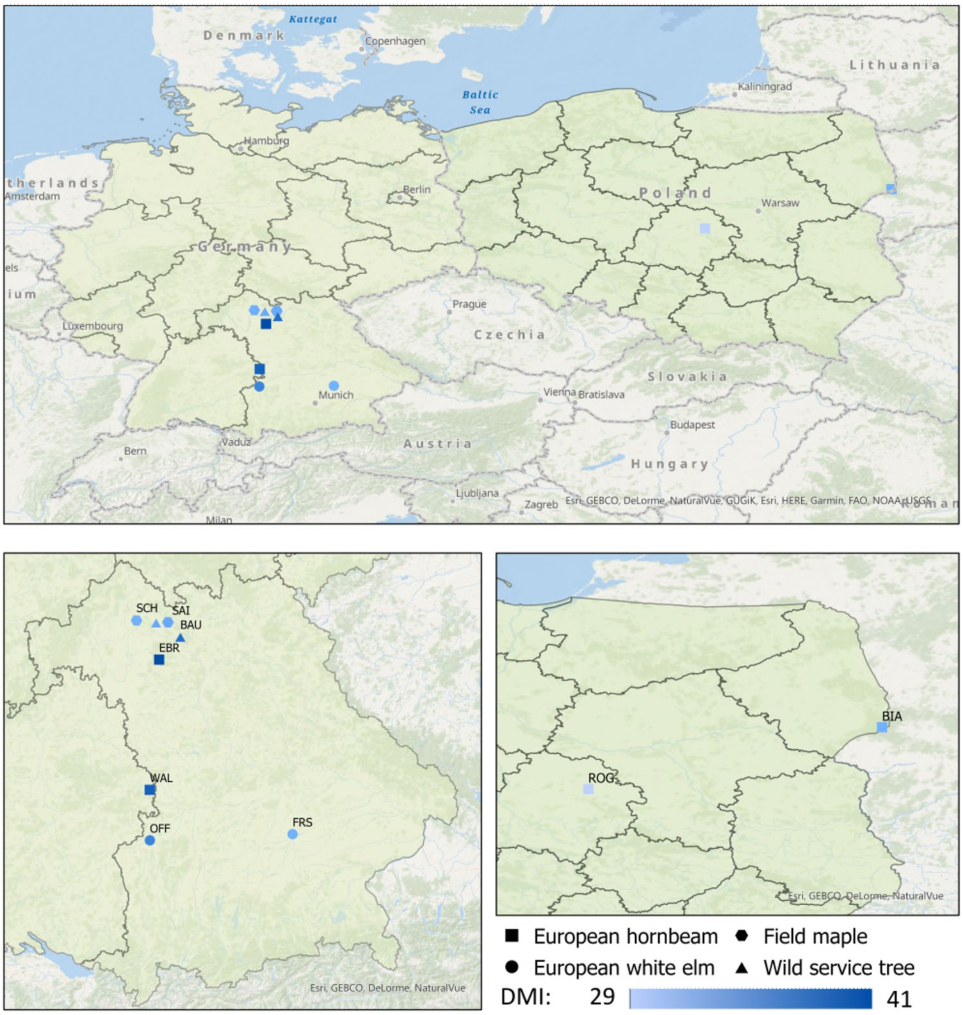

Fig. 1 Locations of research sites in Germany and Poland sampled in winter 2020/2021. The different shades of blue refer to the averaged De Martonne Index values from 1991 to 2020

Climate data

For the sites located in Germany, we used data of monthly mean, maximum and minimum temperature and precipitation derived from a 1 × 1 km grid of the German weather service (DWD) (DWD Climate Data Center 2022a; b). For the sites in Poland, we used climate data of the Climate Research Unit (CRU) (Harris et al. 2020).

Using the temperature and precipitation data, we calculated the standardised precipitation evaporation index (SPEI) for each stand (Vicente-Serrano et al. 2010). The SPEI is a multiscalar drought index which combines precipitation and temperature data and is a well performing and frequently used index in studies which evaluate the impact of drought on forest growth (Bhuyan et al. 2017; Ionita and Nagavciuc 2021; Skiadaresis et al. 2019; Vicente-Serrano et al. 2012). For the potential evapotranspiration, that is included in the index, we were using the Hargreaves equation (Droogers and Allen 2002; Hargreaves 1994). We calculated the SPEI for periods of 3, 6, 10 and 12 months to also cover lagged climate-induced growth reactions.

To characterise the long-term climatic conditions on a site, we used the De Martonne aridity index (DMI) (Martonne 1926), based on the reference period of 1991–2020. The index is calculated as $\mathrm{DMI} = P/(T + 10)$ with P being the sum of annual precipitation and T the annual mean temperature. For a general characterisation of sites, the DMI is more suitable than the SPEI, as the SPEI is a standardised index that approaches zero for long-term means.

For the sites located in Germany, we also used the soil moisture index (SMI) (Helmholtz Centre for Environmental Research 2021; Samaniego et al. 2013; Zink et al. 2016) obtained from the Helmholtz Centre for Environmental Research (Helmholtz Centre for Environmental Research 2021; Zink et al. 2016). The SMI is an index scaled between 0 and 1 describing the soil moisture in comparison to a long-term expected value. It uses interpolated climate data and implements it into the hydrological model system mHM (Kumar et al. 2013; Samaniego et al. 2010) to simulate soil moisture at a resolution of 4 × 4 km. In this paper, we used

Table 1 Information about the stands of rare native tree species used. Coordinates of each stand, mean, max and min *dbh* of sampled trees, mean basal area per hectare (BA), age per plot and information about soil type and texture and the average De Martonne index (DMI) averaged over the last 30 years. *N* sampled refers to the number of trees we collected cores from, the number in brackets refers to the number of trees of which we could use the cores for measurements

Site	Code	Stand	Coordinates WGS84 (lat, lon)	Species	*N* sampled (useable)	*dbh* [cm]			Age	BA [m^2/ha]	Soil type	Soil texture	DMI
						Mean ± SD	Max	Min					
Ebrach	EBR	1	49.82647442, 10.53185277	European hornbeam	15 (15)	12.81 ± 2.84	16.2	7.3	48	35.95	Cambisol	loam	40.7
		2	49.82079687, 10.50741329	European hornbeam	15 (15)	24.1 ± 6.49	34.5	10.7	105	25.01	Cambisol	sand	41.9
Wallerstein	WAL	1	48.86604417, 10.3974315	European hornbeam	15 (15)	25.82 ± 5.39	33.9	14.5	105	38.32	Cambisol/Leptosol/Stagnosol	clay	41.0
		2	48.89506442, 10.33643931	European hornbeam	16 (16)	22.26 ± 3.99	30.8	15	60	24.35	Cambisol/Leptosol/Stagnosol	loam	39.9
Bialowieza	BIA	1	52.695104, 23.842052	European hornbeam	20 (19)	27.59 ± 4.09	36.3	20.2	95	32.43	Brunic arenosol	sand	31.3
Rogow	ROG	1	51.860028, 19.870768	European hornbeam	20 (20)	25.51 ± 3.19	21.8	20.1	75	26.66	Luvisol	loam	29.3
Offingen	OFF	1	48.4930946, 10.38870031	European white elm	15 (12)	11.19 ± 1.35	14.3	9.4	8	19.21	Fluvisol	sand	38.7
		2	48.49201022, 10.38738316	European white elm	15 (11)	54.95 ± 9.67	73.2	40	90	36.86	Fluvisol	sand	38.7
Freising	FRS	1	48.50358428, 11.97072302	European white elm	15 (14)	31.93 ± 9	45.7	18.2	56	34.15	Fluvisol	loam	36.1
		2	48.50876362, 11.97562965	European white elm	16 (16)	33.51 ± 9.03	47.5	18.3	60	19.23	Fluvisol	Sand	37.6
Schweinfurt	SCH	1	50.11861244, 10.28173906	Field maple	15 (15)	30.36 ± 5.78	49.7	19.1	55	37.83	Cambisol	Silt	38.5
		2	50.13765167, 10.28047059	Field maple	16 (16)	13.57 ± 1.48	17.5	11.4	40	26.35	Cambisol	Silt	36.1
Sailerhausen	SAI	1	50.06424136, 10.44109035	Field maple	15 (13)	38.78 ± 8.64	55.7	19.9	90	25.65	Vertisol / Leptosol	Clay	38.6
		2	50.06140085, 10.44188777	Field maple	15 (11)	20.6 ± 4.31	29	13.2	52	27.56	Leptosol	Clay	33.9
		3	50.03816495, 10.40565929	Wild service tree	15 (13)	39.45 ± 9.04	58.4	28.2	85	17.42	Pelosol	Silt	37.3
		4	50.06728171, 10.43006179	Wild service tree	16 (16)	13.26 ± 5.54	24.3	7.3	45	22.00	Pelosol	Silt	38.6
Baunach	BAU	1	49.99296123, 10.78056017	Wild service tree	15 (12)	24.49 ± 7.65	34.7	6.8	90	24.15	Cambisol	clay	40.4

Table 2 Information about the stands of European beech and oak used. Coordinates of each stand, mean, max and min *dbh* of sampled trees, mean basal area per hectare (BA), age per plot and information about soil type and texture and the average De Martonne index (DMI) averaged over the last 30 years. *N* sampled refers to the number of trees we collected cores from, the number in brackets refers to the number of trees of which we could use the cores for measurements. Stands from additional experimental plots used in Schmied et al. (2023) are labelled as "additional stand"

Site	Code	Stand	Coordinates WGS84 (lat, lon)	Species	*n* sampled (useable)	*dbh* [cm]			age	BA [m^2 / ha]	Soil type	Soil texture	De Martone Index
						Mean ± SD	Max	Min					
Ebrach	EBR	1	49.82647442, 10.53185277	European beech	15 (12)	12.81 ± 3.62	18.5	7.1	45	34.67	Cambisol	loam	40.7
		2	49.82079687, 10.50741329	European beech	15 (15)	41.65 ± 7.13	55.3	29.5	105	26.78	Cambisol	sand	41.9
Wallerstein	WAL	1	48.86604417, 10.3974315	Oak spec	10 (6)	51.71 ± 5.48	59.5	45.9	115	32.50	Cambisol/Leptosol/ Stagnosol	clay	41.0
		2	48.89506442, 10.33643931	European beech	10 (7)	28.37 ± 6.76	40.5	21.1	65	23.0	Cambisol/Leptosol/ Stagnosol	loam	39.9
Offingen	OFF	1	48.4930946, 10.38870031	Oak spec	15 (14)	8.83 ± 1.37	11.6	6	8	12.6	Fluvisol	sand	38.7
		2	48.49201022, 10.38738316	Oak spec	15 (12)	34.03 ± 6.4	47.1	16.3	112	17.33	Fluvisol	sand	38.7
Freising	FRS	1	48.50358428, 11.97072302	European beech	15 (14)	18.31 ± 3.88	26.7	12.8	45	21.27	Fluvisol	loam	36.1
Schweinfurt	SCH	1	50.11861244, 10.28173906	oak spec	15 (14)	28.79 ± 3.06	34.1	23.8	65	35.6	Cambisol	Silt	38.5
		2	50.13765167, 10.28047059	Oak spec	18 (18)	14.35 ± 3.35	22.9	10.6	35	21.5	Cambisol	Silt	36.1
Sailerhausen	SAI	1	50.07325, 10.43116	European beech	15 (15)	43.56 ± 4.47	49.8	32.4	100	42.6	Vertisol / Leptosol	Clay	37.7
		2	50.06140085, 10.44188777	European beech	15 (12)	20.04 ± 3.88	26.1	13.4	60	34.73	Leptosol	Clay	33.9
		3	50.03816495, 10.40565929	Oak spec	15 (14)	42.05 ± 4.94	53.8	34.3	121	32.07	Pelosol	Silt	37.3
		4	50.06728171, 10.43006179	Oak spec	15 (15)	18.93 ± 5.61	28.9	7.3	50	23.38	Pelosol	Silt	38.6
Baunach	BAU	1	49.99296123, 10.78056017	Oak spec	15 (14)	39.27 ± 6.19	53	29.8	155	23.34	Cambisol	clay	40.4
Additional beech stands			49.96712, 9.755348	European beech	15 (15)	40.02 ± 6.24	55.1	30.9	110	37.8	Cambisol	Silt	38.0
			48.45696, 10.06725	European beech	15 (15)	55.68 ± 5.79	65.2	44.8	125	42.1	Cambisol	Silt	43.9

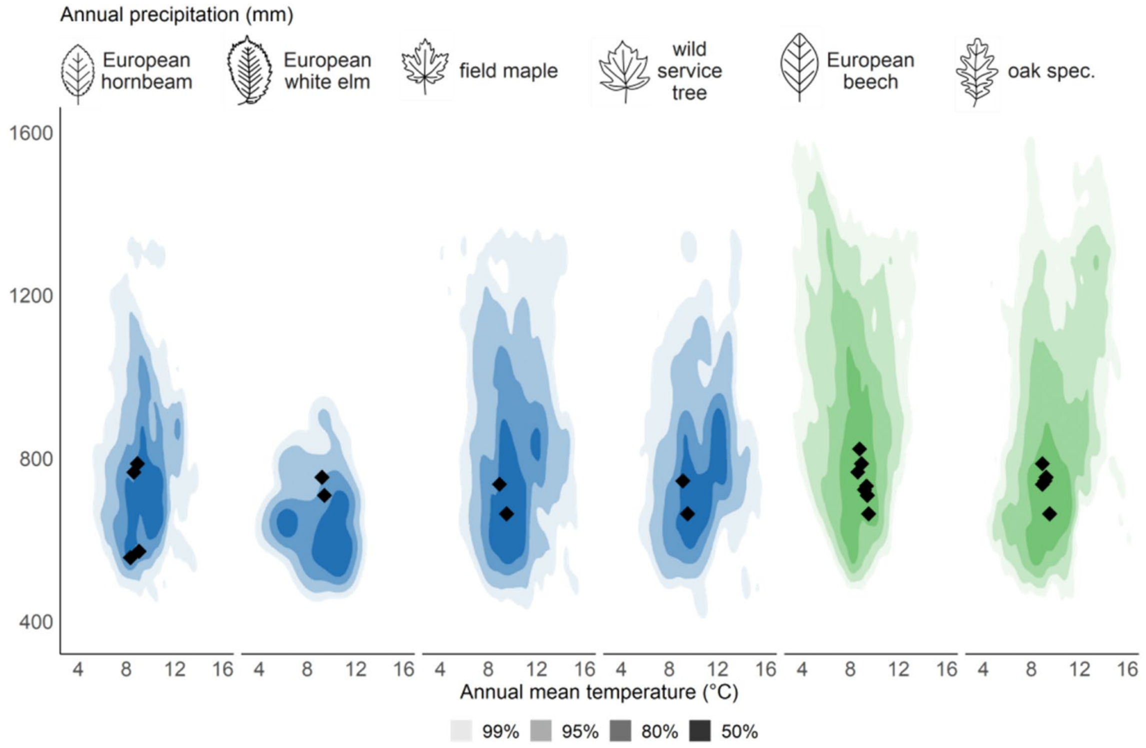

Fig. 2 Climate space diagram showing the location of sampled stands (black squares) in the species' distribution range (Mauri et al. 2017) based on annual mean temperature and precipitation (DWD Climate Data Center 2022a). Coloured areas show the classified density distribution of species occurrences. A version containing the names of Table 1 can be found in the supplementary material

the data of the total soil column (1.8 m) from 1951 to 2020 in a monthly resolution.

Sample and data preparation

For the collection of tree cores, we used a HAGLÖF increment corer with a diameter of 5 mm. We extracted two cores per tree at breast height (*dbh*, 1.30 m), one from northern and one from eastern cardinal direction. This minimised the influence of reaction wood induced by the main wind direction from SW and allowed a better representation of overall growth (Pretzsch et al. 2013; Speer 2010). Since wild service tree and European white elm are very rare species with valuable timber, we were only able to extract cores at a height of 30 cm due to forest owner preferences.

For an easy handling and measurement, we glued the increment cores on wooden boards and subsequently sanded with increasingly finer abrasive paper from 400 to 800 grit to enhance the visibility of tree-ring borders. Measurements were taken to the nearest 1/100 mm using a digital positioning table (Kutschenreiter and Johann; Digitalpositiometer, Biritz and Hatzl GmbH, Austria). Visual crossdating was performed based on common matching patterns of wide and narrow rings (Stokes and Simley 1996; Schweingruber et al. 1990; Speer 2010). Afterwards, we statistically verified crossdating using the dplR package in R (Bunn 2010).

Due to the low visibility of the tree rings of European hornbeam, we used an alternative method for measurements of this species. After sanding, the cores were photographed using the microscopic camera of a Lignostation (Rinntech) with a resolution of 1/10 mm. The resulting photographs were imported into Adobe Photoshop (version 22). Using a high pass filter with a radius of 40 pixels, a linear light blending mode and changing the displayed colour spectrum, tree-ring borders were easier to detect. More compact wood sections appeared more yellow, less compact section more blueish. The resulting photos were then imported into the Lignovision software (Rinntech, version 1.37). Here, tree rings were marked, measured, and visually crossdated.

During the measurement and crossdating process, we had to reject several cores due to an extremely weak visibility of tree rings that made it impossible to measure and crossdate the cores. The final number of cores per plot used in this study can be found in Tables 1 and 2.

Methods

Selection of drought years

For the selection of single drought years, we identified one single drought indicator. Requirements of this index were a reliable identification of drought, a high spatial resolution, and a high correlation with tree growth over all species and stands. Therefore, we calculated bootstrapped Pearson's correlation between all climate variables and drought indices and our species-specific site chronologies. For all variables and indices, we used monthly values as well as seasonal means for spring (March–May), summer (June–August), autumn (September–November), winter (December–February of the following calendar year) and the vegetation period (April–September). For precipitation, we summed up the values for the corresponding season.

To calculate average site-overarching coefficients for each tree species, we transformed the correlation coefficients using Fisher's *z* scores to avoid underestimations due to skewed distributions (Silver and Dunlap 1987) and averaged them. After the calculation, they were back-transformed. Chronologies of young European white elm and oak of stand OFF1 were excluded from the analysis of climate growth relationships, as well of the analysis of drought reaction due to the short time-period covered. Coefficients of correlations for all sites and species can be obtained from the supplements (Figs. S1 and S2).

Of the climate data available for this study, SMI and SPEI were the most reliable drought indices (Schwarz et al. 2020). As they combine both temperature and precipitation, they are more suitable to determine drought years than indices only considering one of the variables (Zscheischler and Seneviratne 2017). While SMI also includes soil data, SPEI was available in a higher spatial resolution. The seasonal SPEI3 for summer ($\mathrm{SPEI3}_{\mathrm{summer}}$) showed the highest correlation and lowest inter-stand variation for all species and stands and was used in further analysis. Drought years selected with this index are also resembling future climatic conditions, where drought events will mainly happen in summer, but also in spring months (Cook et al. 2020; Ionita et al. 2020; Ionita and Nagavciuc 2021), as it includes mainly summer data but due to its 3-month frame also spring months. Furthermore, SPEI3 is a suitable index as it is targeting short-term extreme events and seasonal precipitation changes and is widely used to assess drought in forest ecosystems (Bachmair et al. 2018; Dell'Oro et al. 2020; Obladen et al. 2021; Spinoni et al. 2017).

Drought year identification was based on classifications by Slette et al. (2019). We considered all years with $\mathrm{SPEI3}_{\mathrm{summer}} \leq -1$ as potential drought years. From these years, we chose the three driest years of the time covered by the chronology of each stand separately (Supplements Table S2).

Analysis of tree-ring data

Tree-ring data were detrended using a 30-year spline with a 50% frequency cutoff (Cook 1992; Cook and Peters 1997; Klesse 2021). This spline smoothes low-frequency variation in the tree-ring series which are associated with management (e.g. due to thinnings) and age trends. Inter-annual variability and high-frequency variation, however, are still preserved. The detrending procedure resulted in dimensionless ring-width indices (RWI) (see Fig. 3).

For the two cores of each tree, the mean value per year was calculated using a Tukey's biweight robust mean. Finally, we transformed the RWI of each site into respective average chronologies. Years with measurements from less than 5 trees were truncated. In addition, we calculated the subsample signal strength (SSS) (Wigley et al. 1984) for each plot and year covered by the data. The SSS (Wigley et al. 1984) is a value quantifying the correlation between a subsample of time series and a larger sample and is an indicator for the strength of representation of the larger sample by the smaller subsample (Buras 2017). Years in a chronology with a SSS smaller than 0.85 were truncated, following the recommendations of Wigley et al. (1984). The quality of the chronologies was furthermore assessed by using common dendroecological key figures. The values can be obtained from Supplementary Table S1.

Variability of growth and influence of site and tree variables

To assess the dispersion of tree-ring series, we used the Gini coefficient, calculated from the detrended year ring widths, as proposed by Biondi and Qeadan (2008). The Gini coefficient is a frequently used index of data variability, covering all lags in a tree-ring series. To test differences between the species-specific Gini coefficients, we pooled the detrended tree-ring data for each species and calculated bootstrapped 95% confidence intervals (Dixon et al. 1987).

To assess the sensitivity of annual growth on tree and site variables, we fitted a mixed effects model for each tree species. For the evaluation of annual drought conditions, we used the $\mathrm{SPEI3}_{\mathrm{summer}}$. The global model was fitted using the following formula:

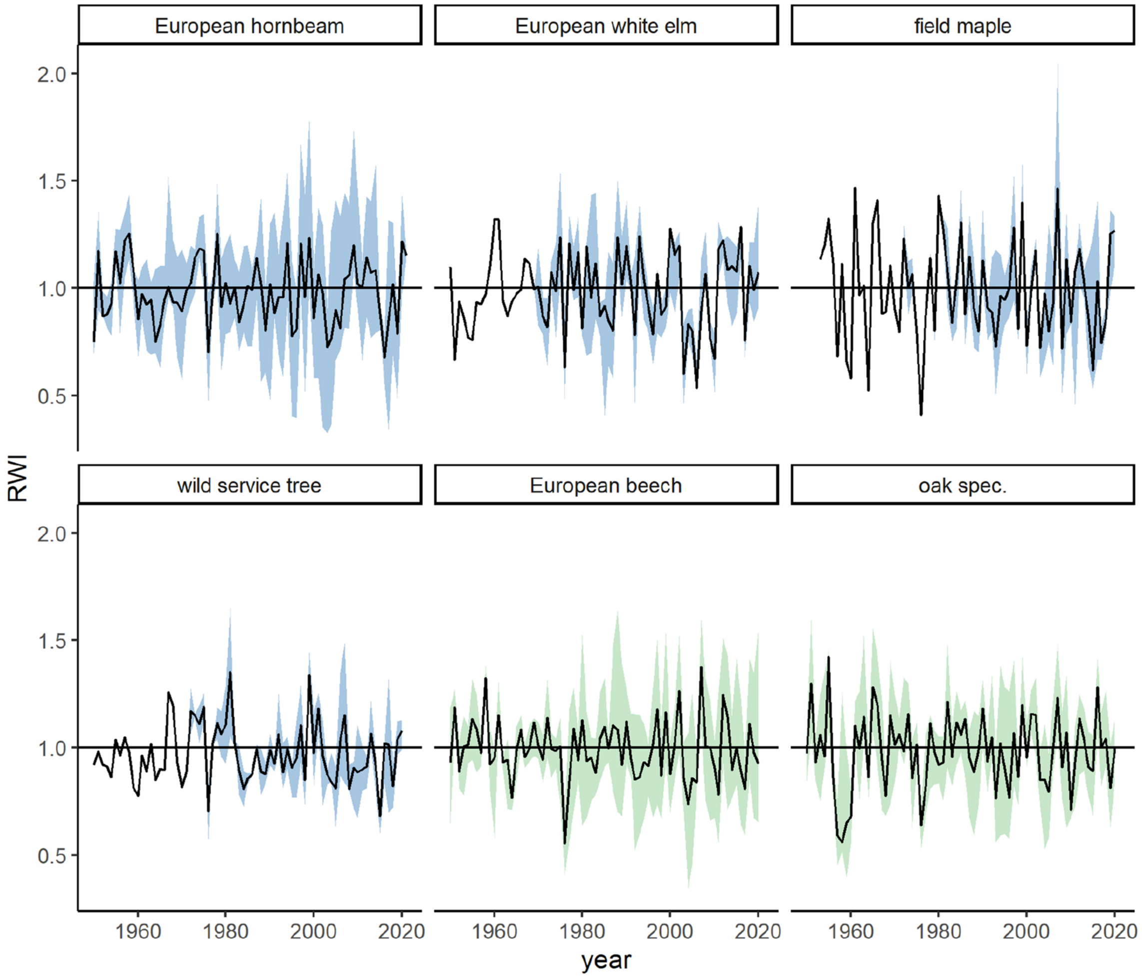

Fig. 3 Species-specific chronologies of RWI. The black line refers to the mean chronology per species over all stands, the ribbon refers to the minimum and maximum stand-specific chronology values for each year

$$\begin{aligned}\log(\text{annual growth}) = {} & a_0 + a_1 * \log(dbh_t) + a_2 * \text{SPEI3}_t + a_3 \\ & * \text{DMI} + a_4 * \log(\text{dbh}_t) * \text{SPEI3}_t + a_5 * \log(\text{dbh}_t) \\ & * \text{DMI} + a_6 * \text{SPEI3}_t * \text{DMI} + b_i + \varepsilon_{it},\end{aligned} \tag{1}$$

where t referred to the year and i to the random intercept on tree level and a_0, a_1, a_2, a_3, a_4, a_5 and a_6 were regression coefficients and ε_{it} the normally distributed error term. The b_i variable respected the nested data structure on tree level. To consider the presence of an autocorrelation between consecutive tree-ring measurements, we included an autoregressive correlation structure (Pinheiro and Bates 2000; Venables and Ripley 2002).

The model assumptions of homoscedasticity and normality of residuals were checked visually using qq-plots and by plotting residuals vs. fitted values. The plots showed no violation of model assumptions.

The global model was then stepwise reduced using the Akaike Information Criterion (AIC). For European white elm, we additionally removed the DMI from the model, as both sites showed very similar values (36.11 and 38.68). We scaled and centred the predictive variables to enhance the comparability and comprehensibility of variables and their influence on the response variable (Schielzeth 2010). A summary of the unstandardised input variables can be found in supplementary table S3.

Analysis of drought reaction

Reaction to single drought events

For the selected drought years, we subsequently calculated indices of resistance (R_t), recovery (R_c) and resilience (R_s) according to Lloret et al. (2011) to quantify growth responses towards droughts. These indices are commonly used in dendroecological studies (Schwarz et al 2020). They are calculated as ratios between the growth in a period before (PreDr), during (Dr), and after drought (PostDr):

$$R_{\mathrm{t}} = \mathrm{Dr} / \mathrm{PreDr} \tag{2}$$

$$R_{\mathrm{c}} = \mathrm{PostDr}/\mathrm{Dr} \tag{3}$$

$$R_{\mathrm{s}} = \mathrm{PostDr}/\mathrm{PreDr}. \tag{4}$$

We chose variable pre- and post-drought periods of 2, 3 and 5 years as recommended by Schwarz et al. (2020). However, we could not find an evident difference between different periods. We decided to use a pre- and post-drought period of 2 years, as this period restricts the influence of other effects like mast years or defoliation by insects (Bottero et al. 2021; Schwarz et al. 2020) and also allowed us to include the recovery values of 2018 in our study.

To detect significant differences between the median values of the species for all Lloret indices, we used a Wilcoxon rank-sum test with Bonferroni correction and a p value of 0.05, as the assumption of normal distribution of the samples could not be accepted for all species.

As proposed by Schwarz et al. (2020), we also compared our species-specific relationship between resistance and recovery to the "line of full resilience". This line is derived by the relation between recovery, resilience and resistance (5), when the resilience values is set to 1 (6):

$$R_{\mathrm{c}} = R_{\mathrm{s}}/R_{\mathrm{t}}. \tag{5}$$

$$R_{\mathrm{c}} = 1/R_{\mathrm{t}} \tag{6}$$

The species-specific relationship follows a power-function with the following formula:

$$R_{\mathrm{c}} = a * R_{\mathrm{t}}^{\mathrm{b}} \tag{7}$$

The line of full resilience shows the hypothetical recovery values a tree needs to reach to fully obtain its pre-drought growth level (full resilience) for each resistance value. By observing the deviation and progression of the species-specific curve in comparison to the line of full resilience, we can rank and summarise the growth responses to drought and assess the recovery potential of the species.

To detect differences in the relationships of recovery and resistance between the species, we linearized formula (7) by using a logarithmic transformation and included the species as a linear term:

$$\log\left(R_{\mathrm{c}}\right) = \log(a) + b * \log\left(R_{t}\right) + \text{ species.} \tag{8}$$

We performed post hoc comparisons of coefficient combinations using the glht function from the multcomp package (Hothorn et al. 2015) to evaluate differences in the progression of the curve of full resilience between species.

Effect of site and tree variables on drought response

To assess the dependency of resilience, resistance and recovery on site variables and diameter, we fitted mixed effect models for every species, following the same approach as for the model of annual growth sensitivity.

This resulted in the following global models:

$$\begin{aligned}\log(\text{resilience}) = {} & a_0 + a_1 * \log(\mathrm{dbh}_t) + a_2 * \mathrm{SPEI3}_t \\ & + a_3 * \mathrm{DMI} + a_4 * \log(\mathrm{dbh}_t) * \mathrm{SPEI3}_t \\ & + a_5 * log(\mathrm{dbh}_t) * \mathrm{DMI} + a_6 * \mathrm{SPEI3}_t \\ & * \mathrm{DMI} + b_i + \varepsilon_{it}\end{aligned} \tag{9}$$

$$\begin{aligned}\log(\text{recovery}) = {} & a_0 + a_1 * \log(\mathrm{dbh}_t) + a_2 * \mathrm{SPEI3}_t \\ & + a_3 * \mathrm{DMI} + a_4 * \log(\mathrm{dbh}_t) * \mathrm{SPEI3}_t \\ & + a_5 * \log(\mathrm{dbh}_t) * \mathrm{DMI} \\ & + a_6 * \mathrm{SPEI3}_t * \mathrm{DMI} + b_i + \varepsilon_{it}\end{aligned} \tag{10}$$

$$\begin{aligned}\log(\text{resistance}) = {} & a_0 + a_1 * \log(\mathrm{dbh}_t) + a_2 * \mathrm{SPEI3}_t \\ & + a_3 * \mathrm{DMI} + a_4 * \log(\mathrm{dbh}_t) * \mathrm{SPEI3}_t \\ & + a_5 * \log(\mathrm{dbh}_t) * \mathrm{DMI} + a_6 * \mathrm{SPEI3}_t \\ & * \mathrm{DMI} + b_i + \varepsilon_{it},\end{aligned} \tag{11}$$

where t referred to the year and i to the random intercept on tree level and a_0, a_1, a_2, a_3, a_4, a_5 and a_6 were regression coefficients and ε_{it} the normally distributed error term. $\mathrm{SPEI3}_t$ stands for the SPEI3 of summer months of the year t. The b_i variable represented the random intercept on tree level. The model's explanatory variables were stepwise reduced, resulting in the model with the lowest AIC.

The model assumptions of homoscedasticity and normality of residuals were again checked visually using qq-plots and by plotting residuals vs. fitted values. The plots showed no violation of model assumptions.

Statistical software

All analyses in our study were carried out using R, version 4.2.1 (R Core Team 2022). For calculating SPEI values, we used the SPEI package (Beguería and Vicente-Serrano 2017), described in Beguería et al. (2014). For detrending, the calculation of descriptive statistics and chronology building of tree-ring data, we used the R package dplR (Bunn 2010; Bunn et al. 2021) and pointRes (van der Maaten-Theunissen et al. 2015, 2021). Climate growth relationships were calculated using the treeclim package (Zang and Biondi 2015). Linear mixed effect model were fitted using lme4

(Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). For general linear hypothesis testing, we used the package multcomp (Hothorn et al. 2015), and for the calculation of the Gini coefficient, the package DescTools (Signorell 2022).

Results

Growth rates and growth variability

The basic tree-ring values for all species can be obtained from Table 3. European white elm showed the highest maximal year ring widths of all species, with also the highest standard deviation. This resulted in a strong variability of diameters at a given age (Fig. 4). Compared to the other tree species, the tree-ring widths of European hornbeam did not vary much between different sites and stands. The *dbh*-age curves of the trees were very similar. This applied to both the plots located in Germany and the plots located in Poland. While mean tree-ring widths of wild service tree remained under the level of European beech and oak, its maximum tree-ring width showed a higher value than oak and European beech.

The growth variability of detrended tree rings was higher for the rare species than for European beech and oak (Fig. 5). Here, European white elm showed the highest Gini coefficient, European beech the lowest.

Table 3 Mean year ring width, standard deviation, maximum and minimum year ring widths per species

species	Year ring width [mm]			
	Mean	SD	Max	Min
European beech	1.97	0.89	7.72	0.01
Oak spec	1.81	1.06	8.81	0.16
European hornbeam	1.4	0.76	6.18	0.06
European white elm	2.43	2.1	15.11	0.01
Field maple	1.7	0.93	6.18	0.18
Wild service tree	1.46	1.22	9.87	0.01

Effect of site and tree variables on annual growth

The fit and reduction of the global model (Eq. 1) resulted in the species-specific models displayed in Supplementary Table S4.

The annual growth of all species was significantly affected by *dbh*, annual SPEI and, was applicable, by the DMI. For European beech, European hornbeam, field maple, wild service tree and oak we could observe significant differences in annual growth between sites with poor and better water supply. On very dry sites, the annual growth decreased for bigger trees. On better sites, however, this decrease was

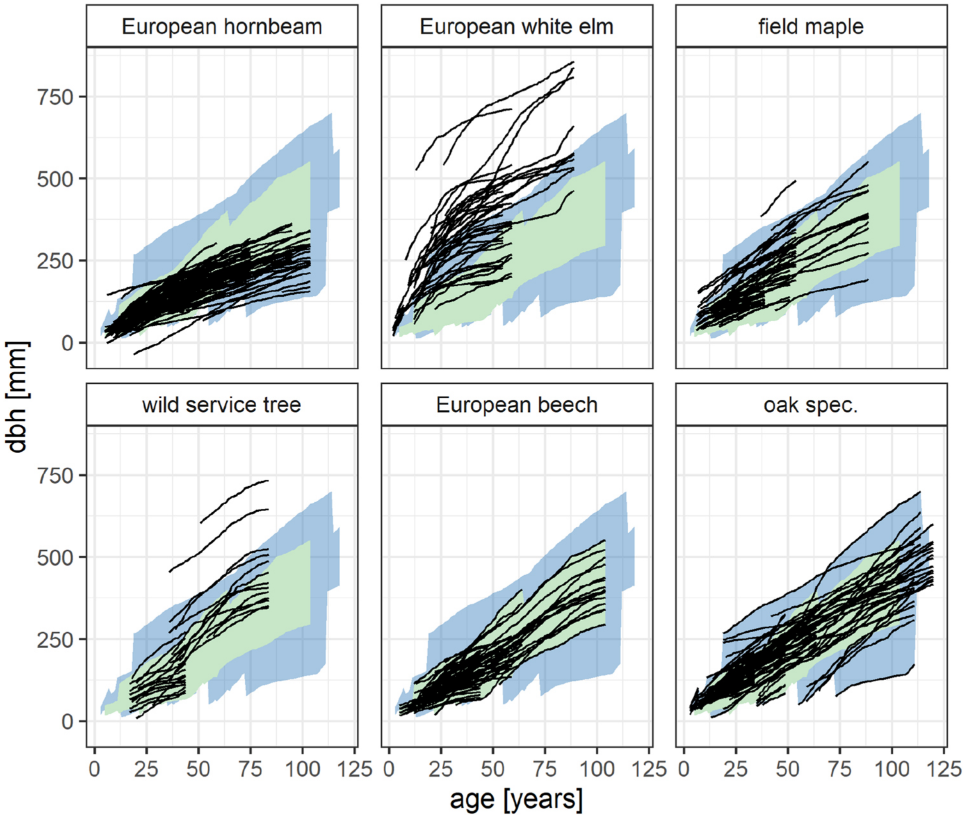

Fig. 4 Species-specific diameter growth of trees over age for European hornbeam, European white elm, field maple, wild service tree, European beech, and oak. In the background, the range of the diameter growth over age for European beech (green) and oak (blue) are displayed

weaker for field maple and wild service tree or did not happen at all for European beech, European hornbeam, and oak. Here, we could even observe an increase in annual growth for bigger *dbh*s. For European beech and field maple also, the reaction on annual weather conditions, displayed by the SPEI, differed between sites. For these species, the increase of annual growth as a reaction to high SPEI values was higher on good sites than on very dry sites. All other species did not show a difference in their reaction between sites. However, higher SPEI values generally led to a higher annual growth. European white elm and European hornbeam showed a higher sensitivity and increase in annual growth towards wetter years for thinner trees.

Species-specific drought reaction

Resistance, resilience, and recovery towards drought

We could sort the species by their median values for the index of resistance in the following order: Field maple (0.61) < European hornbeam (0.73) < wild service tree (0.74) < oak (0.76) < European beech (0.79) < European white elm (0.92) (Fig. 6). After testing the hypothesis of equal medians, we could differ between three groups: field maple with low resistance values, oak and European hornbeam with a middle position and European white elm with the highest resistance values. European beech and wild service tree took an intermediate position between European hornbeam and European white elm.

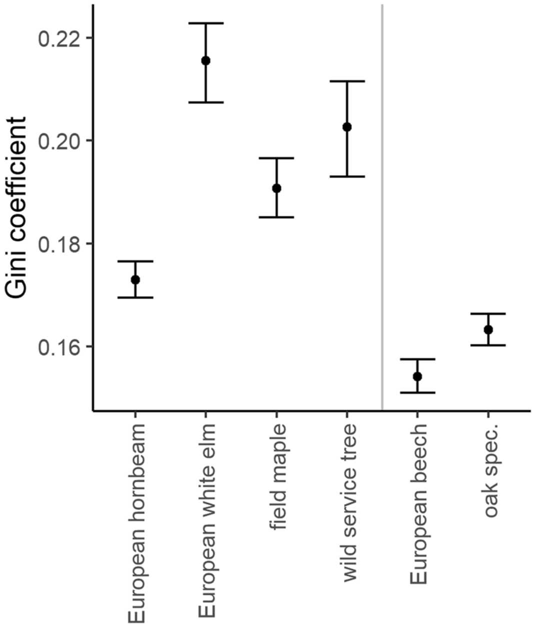

Fig. 5 Gini coefficients computed on detrended tree-ring chronologies per species with bootstrapped 95% confidence intervals

The median recovery values were ranked as follows: European white elm (1.05) < oak (1.13) < European hornbeam and wild service tree (1.18) < European beech (1.20) < field maple (1.63). Overall, after testing for equal means, we could not find significant differences between medians. Only field maple showed a significant higher recovery value than the other species.

Median resilience values followed the subsequent order: oak (0.86) < wild service tree, European whit elm and European hornbeam (0.90) < European beech (0.94) < field maple (1.02). Between the median of oak and field maple, we could observe a significant difference. For all other species, the hypothesis of equal medians could not be rejected.

Figure 7 shows the relationship between recovery and resistance of the species and the theoretical line of full resilience. European hornbeam, field maple and European beech already showed a very close fit to the line of full resilience for very low values of resistance. Field maple and wild service tree intersected the full-resilience line even for lower resistance values than the other species. The model intercept of European beech was significantly higher ($p < 0.05$) than the one of wild service tree, European hornbeam, and field maple. In addition, field maple showed a significant higher intercept than oak. For resistance values above 1, field maple, oak and wild service tree showed the highest positive deviation from the line of all species.

In general, we could observe three major curve shapes. European hornbeam and European beech on the one hand showed a good fit to the line of full resilience for all resistance values. On the other hand, European white elm, wild service tree and oak showed a negative deviation from the line for low resistance values but, especially for wild service tree, with a an early intersection and a subsequent clear positive deviation. Field maple, as the only species, shows both a good fit on the line of full resilience for low resistance values and its exceeding for high resistance values.

Influence of site and tree size on drought reaction

Concerning the drought reaction, we could observe significant influences of tree size, drought severity and overall site conditions. However, the expression of the effects strongly differed between species.

The resilience of European hornbeam, European white elm and field maple was significantly affected by the severity of the drought year, displayed by the SPEI values. Field maple and European white elm were more resilient after milder drought years, while European hornbeam showed an opposite reaction. For field maple, this effect was especially visible on sites with a lower DMI, while on sites with more favourable climatic conditions, the resilience was similar over different drought intensities. In addition, for European beech and oak, we could observe an influence of the long-term

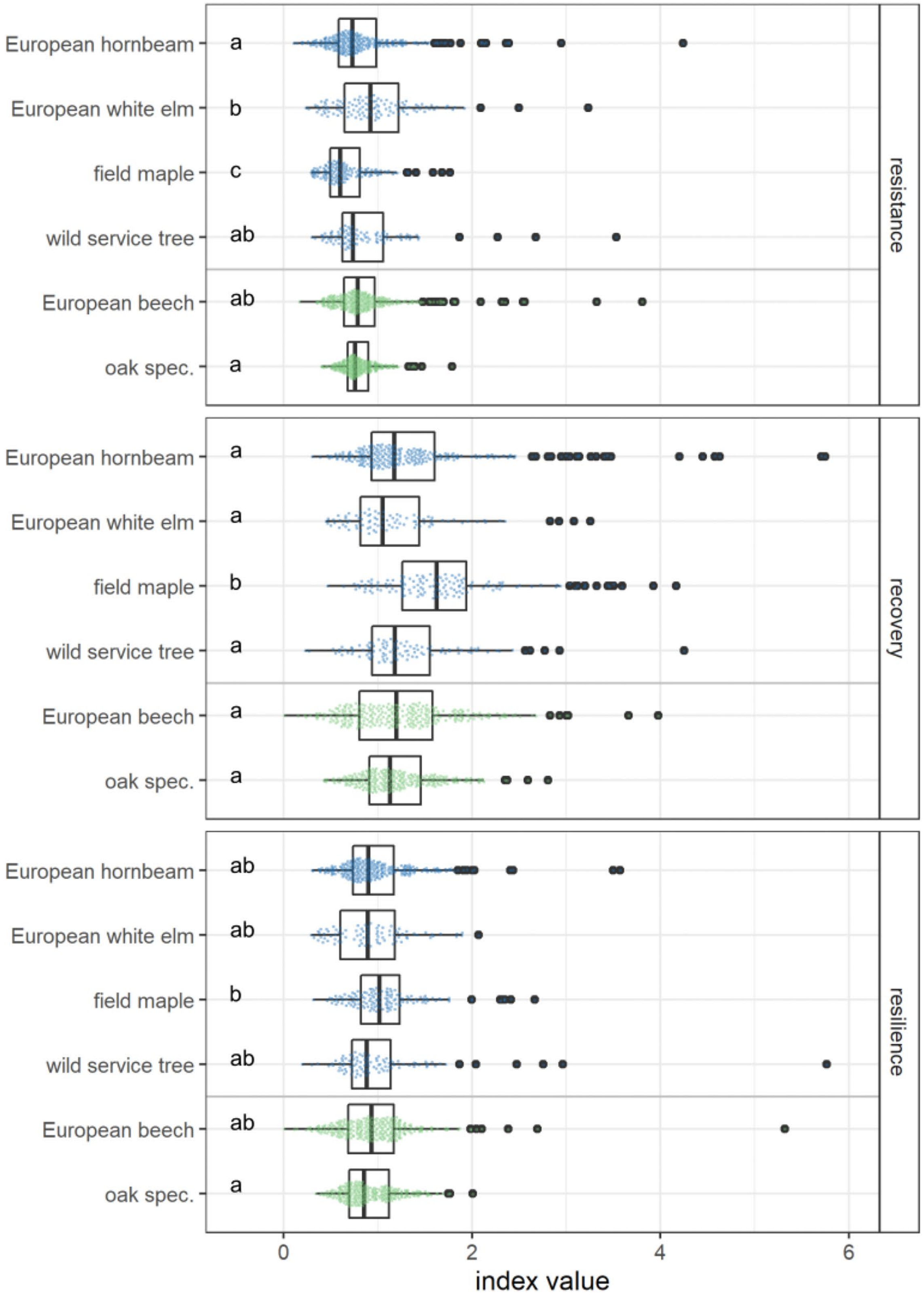

Fig. 6 Index values of the Lloret indices of recovery, resilience and resistance for European beech, European hornbeam, European white elm, field maple, oak, and wild service tree. Significant differences ($p < 0.05$) between the medians of the index value per species, determined by a Wilcoxon rank-sum test with Bonferroni correction, are displayed with letters

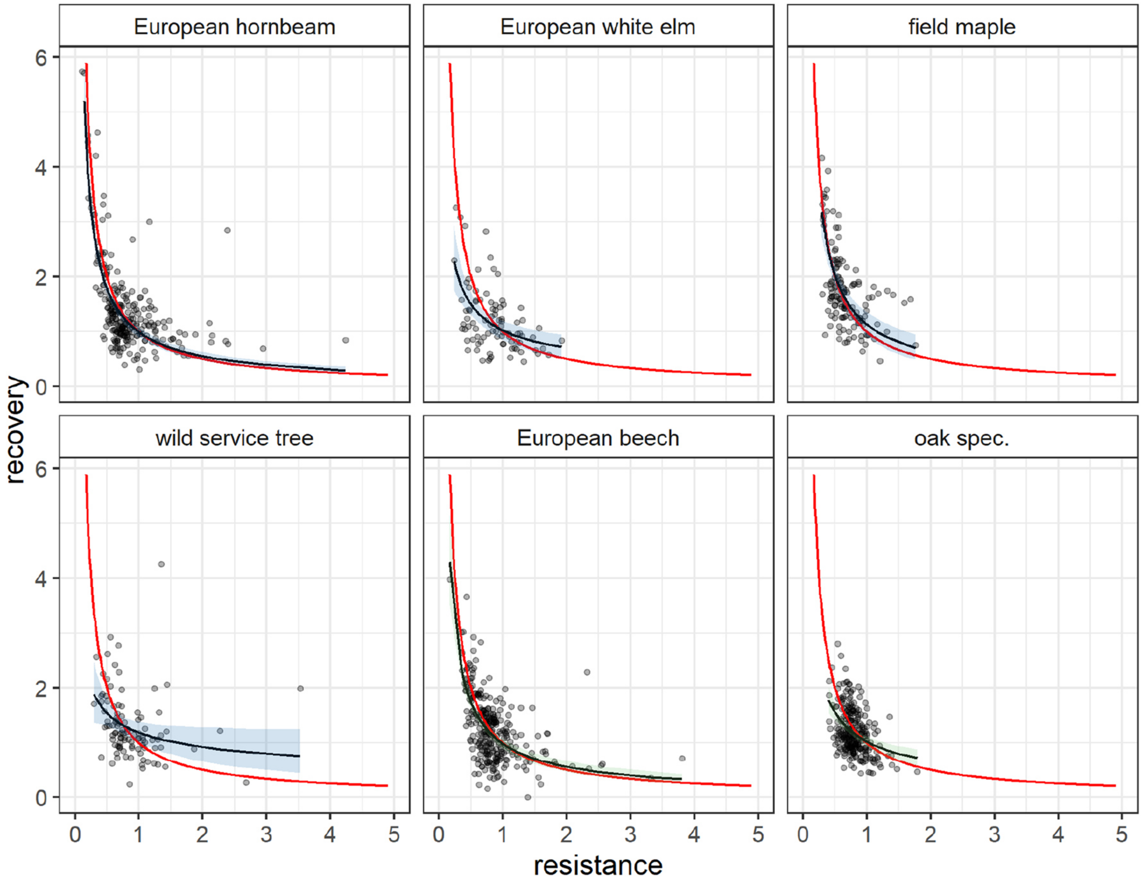

Fig. 7 Species-specific relationship between resistance and recovery (black line (see Eq. 7) with confidence bands calculated with a bootstrap with 1000 iterations), the red line (see Eq. 6) represents the theoretical line of full resilience

climatic conditions of the site, displayed by the DMI, and a significant influence of the *dbh*. For European beech, the resilience values were higher on sites with higher water supply and for thinner trees. For oak, we could observe the higher resilience of thin trees only on sites with a high DMI. On sites with a lower DMI trees of all diameters showed similar resilience values. Notable is, that for wild service tree, we could not find a significant effect of any variable.

Concerning the resistance, we could observe a significant influence of the SPEI values of the drought year for all species beside wild service tree. For oak, European white elm and field maple, a less severe drought led to higher resistance values. European beech showed low resistance values in very dry years on sites with a low DMI, while the resistance of European hornbeams increased with more severe droughts on those sites. Concerning the effect of tree size on the resistance European beech showed a higher resistance in bigger trees on sites with a high DMI and thinner trees on sites with a low DMI. Again, it is notable that for wild service tree, we could not find a significant effect of any variable.

The tree size did not have a significant influence on the recovery of European white elm, field maple, and wild service tree. For oak, we could observe a better recovery for thinner trees. Thinner European hornbeams showed a better recovery on favourable sites than bigger trees, while on sites with a low DMI no such size effect could be observed. For European beech, we could observe the opposite, with a better recovery of thin trees on sites with a low DMI and of bigger trees on sites with a high DMI. This significant influence of the climate conditions on the sites could also be observed for oak and field maple. Field maple and European beech showed generally higher recovery values on sites with low water supply and less severe drought years. On more favourable site, this effect was reversed. The recovery values of oak generally increased with a higher DMI. Wild service tree and European white did not show a significant effect of diameter, site and SPEI on their recovery.

In summary, we could observe a high susceptibility to severe drought for beech on sites with a low DMI, while oak was more stable, especially on good sites and over different tree sizes. Among the rare native species, field maple again stuck out with a high robustness towards drought, even on very dry sites and towards severe drought. European hornbeam reacted similarly as European beech, however, with a higher tolerance towards severe droughts and more constant over different tree sizes. For wild service tree, our data showed a stable drought reaction without any influence of site and tree variables. European white elm showed a particularly high tolerance towards mild droughts.

Discussion

Growth rates and growth variability

Concerning the age-growth relationships, we could observe that the growth of the rare species is within the growth range of European beech and oak on the same sites. When comparing the growth of European hornbeam with existing yield tables for northern Germany (Lockow 2009), sites in Germany reached a site index of II.5 (site WAL) and II (site EBR). Both sites in Poland reached a site index of II.25, despite their lower DMI. For all stands, the mean diameters were higher than the diameters specified by the yield table. This indicates that the validity of the yield table of Lockow (2009) might be regionally limited to stands in northern Germany with their specific climatic and soil conditions. On other sites, the yield table may underestimate the actual growth of European hornbeam. The similar growth patterns of European hornbeam in Poland and Germany underline its high ecological amplitude. Even in eastern Poland, under climate conditions that are limiting the distribution range of European beech, the European hornbeam shows high growth rates.

For wild service tree, the annual increments were similar to the ones observed by Pyttel et al. (2013). They also observed very low annual increments which they explained by the high shade tolerance of wild service tree and its ability to even survive under strong suppression. This indicates that some of the wild service trees used in our study might have been suppressed in the past or growing under a lot of competition. This also explains the high variation in the *dbh*-age curves showed in Fig. 4, where some trees had much higher diameters for a given age than others.

In general, European beech and oak grew more stable over all sites. The missing significant difference in annual growth between sites with different DMI of oak in the linear mixed model is another indication of the lower climatic sensitivity of oak in comparison to European beech (Scharnweber et al. 2011). The maximum tree-ring widths of the rarer species show, that under good conditions and with proper silvicultural management, they can reach high year ring widths. Combined with the results of the model assessing the sensitivity on site variables, we can see that the high Gini coefficients of rare species are also connected to a high susceptibility of the species to favourable years. Apparently, the species can easily implement good annual growing conditions in annual growth. The high Gini coefficients may also be related to a different silvicultural treatment of the species in the past. European hornbeams are often used as a so called “serving” tree species in oak stands for the shading of stems and the prevention of the development of secondary branches. After a release of suppression by the extraction of the canopy, a higher growth can be provoked. However, this again underlines that with enough growing space high year ring widths of the rare species are possible.

The lower sensitivity to drier years of trees with a smaller *dbh* that we observed could be related to their smaller height and thus the lower gravimetric potential they have to overcome to transport water in the tree trunk and the higher stomatal conductance and sensitivity that make smaller trees less prone to transpirational stress (Grote et al. 2016; Ryan et al. 2006; Ryan and Yoder 1997). The decline in growth with an increasing tree size on dry sites can be traced back to a typical age effect and the culmination of growth already at lower diameters on poorer sites. The decrease of annual growth in field maple and wild service tree even on better sites indicates that both species culminate earlier in their growth than European beech and oak. Again, it also indicates a different silvicultural treatment of the species in the past. The increase of growth with higher diameters on better sites for European beech, oak and European hornbeam points to a release from suppression or competition in higher ages. Outstanding is the high potential of annual growth of European white elm. Especially on good sites and in young stands, this species can easily obtain year ring widths of more than 1 cm.

Drought reaction

When comparing the Lloret indices of all species, not considering site and tree variables, we could not find many significant differences between species. Nevertheless, it was noticeable that field maple showed especially high values of recovery and resilience, however, with low resistance values. The resistance values of European beech being higher than the ones of field maple is contradicting the results of Kunz et al. (2016) who had reverse findings. This could be due to a different selection of drought years and stands in both studies and also the missing consideration between resistance and recovery values (Schwarz et al. 2020). However, when combining resistance and recovery values and comparing them with the line of full resilience, field maple and wild service tree stick out as drought tolerant species. Wild service tree due to its capability to surpass the line of full resilience for milder droughts and field maple for both its high recovery values in years with low resistance and its good performance after milder drought. This again matches the findings of Kunz et al. (2016). It once more shows the importance of rather combining both resistance and recovery than looking at the single indices when evaluating the drought tolerance of different species. Thereby, it can be considered that species with high resistance values were often showing low recovery values and vice versa, as after a strong decline, there is naturally a stronger potential for recovery. Species with higher values of recovery for lower resistance values, as wild service tree and field maple, can recover more easily even in years with a strong growth decline. Oak showed better overall resistance to drought than the rare species, however, in severe drought years field maple and wild service tree seem to be better adapted.

The good recovery of oak and European white elm in years with milder drought can be attributed to their wood anatomy. In contrast to the other species considered in this study, oak and elm are ring porous species. They are less sensitive to climate and drought than diffuse-porous species (Elliott et al. 2015) as they produce larger early wood vessels in which then the majority of the hydraulic transport takes place (Hacke and Sauter 1996; Zimmermann 1983). After a drought event, they can, therefore, recover more quickly as larger vessels are already produced at the start of the next growing season. Diffuse porous species must use their smaller vessels, created throughout the previous growing period. Embolised conduits can be repaired by refilling them (Hacke and Sauter 1996). Furthermore, our results correspond to the findings of Leonova et al. (2022), who found an increased fine root growth of European white elm during drought. This also leads to an enhanced growth during the next growing season.

Influence of size and site variables

Regarding the drought reaction, we could observe a higher drought tolerance of European hornbeam towards severe drought and on dry sites, as already observed by Leuzinger et al. (2005). This could explained by differences in their water consumption and stomatal regulation strategies, where European hornbeam follows a more isohydric behaviour (Köcher et al. 2009; Leuschner et al. 2019). In contrast to our results, Scharnweber et al. (2020) observed a strong growth decline for European hornbeam after two consecutive drought years. The drought tolerance of European beech and European hornbeam was similar in their study, with even a higher growth decline for European hornbeam. However, they suppose that a part of this growth decline can be attributed to an increased growth of roots in drought years as an adaptation strategy. This again matches our results where the higher resistance of European hornbeam towards severe drought could be observed for dry sites, where the European hornbeam might already be adapted to drought events. For field maple on very dry sites, we could observe a high resilience and very high recovery towards milder droughts. On more favourable sites field maple also recovered very well after severe drought events. This one more time points out the high drought tolerance of the species and its high potential on dry sites. As already studied by Kunz et al. (2018), field maple is a highly drought tolerant species with a high potential under climate change. Beloiu et al. (2022) found a low recovery and high mortality after drought for field maple saplings, while Kunz et al. (2016) found much younger seedlings to be highly drought resistant. This indicates that the initial drought resistance of the species may decrease with age. However, the high mortality after drought events may lead to a natural selection of trees with a higher drought resistance and, therefore, an adaptation to drought. At the same time, it may result in a higher drought tolerance of surviving trees due to an acclimation effect after the drought event (Kozlowski and Pallardy 2002). This again results in a higher drought tolerance of mature trees. For European white elm, we could not differentiate between different climatic site conditions, as the two sites had very similar DMI values. However, we could observe a high resistance against milder drought. Although more detailed research is needed, our study confirms the assumptions of Walentowski et al. (2014), that European white elm could be a suitable species under drier climate conditions. Site variables did not have any influence on drought resilience, recovery, and resistance of wild service tree. This is also a sign of the high stability of wild service tree under different site conditions. On both sites, we could find a good recovery after mild droughts, which was already observed by Kunz et al. (2016) for seedlings.

Oak could cope better with drought on wetter sites, however, showing higher resistance values for large trees and a faster recovery of small trees on dry sites. This can be attributed to the weaker stomatal control on photosynthesis of small oaks trees (Zang et al. 2012). In our study, we could observe the dependence of drought tolerance of European beech on climatic site conditions. On wetter sights, the tolerance of severe droughts was higher than on dry sites, while the tolerance towards mild droughts was lower. This higher susceptibility to mild drought on sites with a good water supply was already observed in other studies dealing with the growth of European beech towards its distribution margins (Cavin and Jump 2017; Muffler et al. 2020; Weber et al. 2013). It might be the result of a phenotypical reaction (Cavin and Jump 2017; Leuschner 2020) to site conditions and an acclimation after multiple drought years (Petrik et al. 2022). This could point to a more isohydric behaviour of trees on drier sites (Nguyen et al. 2017). The good recovery of beech in milder droughts on dry sites can be connected to the rapid recovery of leaf metabolism (Leuschner 2020).

High recovery values on wet sites after droughts might be related to the stimulation of fine root growth, as observed for saplings of European beech (Zang et al. 2014).

Study limitations

Our study results show some limitation as tree cores were partially taken of different stem heights. The expression of climate sensitivity decreases on lower parts of the stem (Hoffmann et al. 2018) which may lead to some inaccuracy when comparing values of stands with different retrieval height. Furthermore, we did not sample dead trees as proposed by Schwarz et al. (2020). Therefore, we were not able to assess climatic factors that might have a very negative, even lethal, effect on tree growth. The low mean-Gleichläufigkeit values of European white elm indicate that the growth of trees on the plots was not primarily limited by precipitation and evapotranspiration, but rather by other site factors. As both sampled sites of European white elm were in riparian forests, the flooding regime and groundwater access could be factors determining tree growth. This follows the critique of Schwarz et al. (2020) and Zang et al. (2020), who suggest including more soil parameters in studies. For our study this was not possible, as, besides the SMI, no data on past soil moisture were available for those stands. The SMI, however, only has a resolution of 4 × 4 km, which again leads to imprecise results for our forest stands.

By sampling two sites per species, we tried to cover a variety of different site conditions. However, this was not always possible, as the occurrence of our species was often limited to sites where European beech or coniferous species were not dominating. These were, in case of field maple and wild service tree, very dry sites, in case of European white elm riparian forests. However, as seen in Fig. 2, our selected stands were located mostly in the core distribution range of the species and thereby represent typical climatic conditions. Nevertheless, an expansion of the study area with more plots on the edges of the distribution range could be interesting for future studies.

In our study, we did not account for the fact that repeated drought events may influence the drought reaction of the species. Especially for younger stands, the selected drought years might be the first droughts that the trees were experiencing. However, as all species covered younger and older trees with a different number of past drought events, we decided to neglect that effect in our analysis.

Conclusion: implications for silviculture

Even if European beech shows a certain drought resistance on sites with a good water supply and during mild droughts, it is generally displaying a high sensitivity towards drought. This points out a possible limitation on its occurrence and cultivation. Even on more favourable sites, the risk of drought events will increase in the future. As other rare species were more resistant towards drought on these sites, they could increase their shares in the species composition while the share of European beech might decrease.

Oak turned out to be a stable species, even under dry conditions. Comparably high increments combined with a high drought resistance make it a solid basis for future forest stands. For sites were in the future many very dry years are expected, wild service tree and field maple are good options to enrich these stands. These two species are very well adapted to drought and can keep up with oak with their ability in transforming good weather conditions into annual growth. The proportions of mixture should increase with increasing drought potential.

Concerning the drought sensitivity and growth, European hornbeam showed overall a similar behaviour as European beech, however, with a slightly smaller climate sensitivity and a stable growth even over different climate zones in Poland and Germany. Furthermore, our results show a good resistance against severe drought years. We, therefore, recommend European hornbeam as a complementary species for the enrichment of European beech stands. As for both species drought sensitivity increased with diameter, an adjustment of target diameters might be considered. In addition, oak stands with slightly better water supply could be suitable for an admixture of European hornbeam.

The higher drought tolerance of younger trees of wild service tree, field maple and European white elm is especially important concerning the relative uncertainty of weather development in the next years. Our results suggest that young stands with those species, that were recently established or will be established in the next years, can cope with a variety of different weather conditions and are, therefore, a low-risk option to sustain unstable stands on dry sites.

European white elm can be highly recommended as a species for riparian forest systems. Even if we could only get a limited assertion of its behaviour under drought conditions, our results generally indicate a high drought tolerance which implies a suitability also on dry sites. European white elm is prone to the invasive Dutch elm disease (DED), but much less than other native elm species like wych elm (*Ulmus glabra* Huds.) (Jürisoo et al. 2019, 2021). As common ash (*Fraxinus excelsior* L.) is also suffering from ash dieback, European white elm remains as a relatively stable species on floodplain sites, fulfilling both ecological and economical functions. The high growth rates also make it an interesting species concerning the carbon sequestration in forests.

In general, rare native species are a promising option to enrich the species composition on dry sites and to contribute to the establishment of climate tolerant forest stands. However, with ongoing climate change, even those species will eventually reach the limits of their drought tolerance. Therefore, the fight against climate change stays the most important factor to guarantee the stability of future forests.

Author contribution statement JS collected and analysed data and wrote the manuscript; GS supervised the tree-ring analysis and manuscript writing process; EU supervised data collection, analysis and writing process; HP initiated the study and supervised the whole data collection, analysis and writing process.

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Data availability The materials described in the manuscript including all relevant raw data will be freely available upon request from the corresponding author.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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C. Article III

Title: Crown structure, growth, and drought tolerance of true service tree (Sorbus domestica L.) in forests and urban environments. Urban Forestry and Urban Greening.

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Crown structure, growth, and drought tolerance of true service tree (*Sorbus domestica* L.) in forests and urban environments

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Author contributions

JS – investigation, formal analysis, methodology, writing - original draft, JPS – investigation, writing - review & editing, supervision, EU – conceptualisation, supervision, funding acquisition, methodology, writing – review & editing, HP – conceptualisation, supervision, methodology, writing – review & editing

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Highlights

- True service tree and oak have a similar growth pattern
- The crown size of open-grown true service tree is slightly larger than that of oak
- True service tree and oak are equally sensitive to competition
- True service tree and oak are equally drought tolerant

Abstract

True service tree (*Sorbus domestica* L.) is a rare native species of Central Europe. It grows well in dry and warm environments and may consequently be well adapted to the expected future climate further north. It is considered a potentially suitable species for climate change adaptation in forests and urban environments. In this study, we used total tree height, stem diameter, and crown dimensions from true service trees in Germany, southern Scandinavia, northern Italy, and Slovakia to determine the specie's allometric relationships and space requirements. Additionally, we used tree cores from Germany and Slovakia and stem disks of a true service tree in Copenhagen to study growth patterns and drought stress response. Throughout, we compared to oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.), as common and well-studied species. Our results indicated that true service tree and the two oak species have similar growth patterns and space requirements. True service tree and oak both had a fast growth in their youth, followed by a gradual reduction at later stages. The crown projection area of true service tree was similarly influenced by competitors as that of oak, indicating a similar sensitivity towards competition. Likewise, we identified similarities in growth response to drought and, hence, drought tolerance. Due to their comparable growth pattern and drought tolerance, we hypothesise that oak, in many regards, can be used as a model species for the management of true service tree.

Keywords

Allometry, crown size, drought response, drought tolerance, stem form

1 Introduction

As a xerophilic species with a core distribution in the south and south-east of Europe, the true service tree *(Sorbus domestica* L.) is considered a potentially suitable species for climate change adaptation in forests and urban environments. Even if there is still a debate to which extent the species is native to Central Europe (Rueda Salgueiro et al., 2006; George et al., 2016; Špíšek et al., 2018; Špíšek et al., 2022), it fits in very well in native forest ecosystems in this region. In contrast to many other forest tree species, the true service tree is pollinated by insects and its fruits are considered of high ecological value. Furthermore, its conspicuous flowers add to the aesthetics of urban environments and forest settings (Kausch-Blecken von Schmeling, 2000) and, depending of management practice, true service tree may contribute to the production of highly valuable timber (Coello et al., 2013; Piagnani et al., 2018).

The true service tree is rarely used in cities and forests as managers generally prioritise tree species that are easier to manage due to their higher competitive strength, yield, and shade tolerance. Moreover, planted individuals of true service tree are very susceptible to *Neonectria ditissima,* which causes an uncurable canker and may lead to complete dieback (Keil, 1996). Naturally regenerated individuals of true service tree are scarce, and natural regeneration is generally absent (BLE, 2013). As a reflection of this rareness, the literature on true service tree (supplements tables 1-3) includes little quantitative information on ecological and silvicultural characteristics. Concerning the crown allometry, so far, only Paganová et al. (2015) described different types of crown shapes for true service trees in urban environments in Slovakia. Studies on general allometric relationships, also in forests, are scarce. Kausch-Blecken von Schmeling (2000) and Skovsgaard and Graversgaard (2013) published some basic height-diameter and age-height relationships. Cisneros et al. (2006) and Coello et al. (2013) published recommendations for stand density and potential target diameters, however, without presenting their underlying methodology.

Most studies on tree growth focus on young trees, typically seedlings or saplings and generally cover only the first few years of growth (Paganová et al., 2014; Kunz et al., 2016). Other than that, there are only a few experimental plots including true service tree. In Germany, a provenance trial across several states, is no longer active (Tabel et al., 2001). In Denmark and Sweden, experiments have been planted to observe the survival, growth and health of different provenances (Skovsgaard and Graversgaard, 2013; Jansson, 2017; Skovsgaard et al., 2017), likewise in Slovakia (Bakay and Rovná, 2021) and Italy (Piagnani et al., 2018).

Descriptions of the drought tolerance and heat sensitivity of true service tree are often based on observations and considerations of the current range of distribution (e.g., Cisneros et al., 2006; Rueda Salgueiro et al., 2006; Coello et al., 2013; Gonin et al., 2013) rather than on experimental evidence or other quantitative indicators. However, due to the use of the true service tree for fruit production, its range of distribution is highly influenced by human activity (Drapier, 1993; Kausch-Blecken von Schmeling, 2000; Skovsgaard and Graversgaard, 2013), resulting in potentially biased interpretations and conclusions. So far, only two dendroecological studies of adult trees have been carried out and with contrasting results: Kunz et al. (2018) found the drought tolerance of true service tree to be marginally lower than that of oak, while Camarero et al. (2023) found it to be marginally higher.

In summary, the site-specific growth characteristics, drought tolerance and allometric relationships of true service tree are essentially unknown, or at least, unquantified. Such information is needed to derive relevant management prescriptions, spacing requirements throughout the lifetime of individual trees and the selection of tree species for specific locations. Especially in cities, where space is often limited and claimed by many stakeholders, accurate information about the crown allometry and growth patterns may be crucial. Also, the shading and cooling potential of the species can be assessed based on the crown allometry, as the crown size is highly related to a tree’s photosynthetic active radiation (APAR) and leaf area (Binkley et al., 2013; Forrester et al., 2017b). In this context, addressing the crown dimensions of solitary or so-called open-grown trees is essential as trees in cities generally grow with no or only a few competitors. In forests, the knowledge of allometric relationships enables the manager to assess the space requirements of a species throughout the rotation and, in turn the need for release from competitors and plan and the weight and frequency of thinning operations. Knowledge of the height development pattern aids the selection of suitable species mixtures and their suitable management. The assessment of the drought response aids in the assessment of need for maintenance by, for example, watering during drought periods in urban environments and of the overall suitability of true service tree for cities and forests under climate change conditions.

The objective of the study presented here was to quantify the crown size and the growth of true service tree subjected to different degrees of inter-tree competition. Data was collected along a north-south gradient in Italy, Slovakia, Germany, Denmark, Sweden and Norway. The response to drought was analysed based on stem cores from true service trees in Germany and Slovakia and stem discs from a city tree in Copenhagen, Denmark. Throughout, the measurements and growing patterns of true service tree were compared to sessile oak (*Quercus petraea* (Matt.) Liebl) and pedunculate oak (*Quercus robur* L.), from here on referred to as 'oak' growing nearby under similar conditions. The tow oak species are well-known across most of Europe (Mölder et al., 2019), both in forests and cities and their growth and response to drought have been quantified and modelled in great detail (Mette et al., 2013; Pretzsch, 2019; Meyer et al., 2020; Stimm et al., 2022). This makes it easy for landscape, forest, park and city tree managers to compare and assess our results and put them in the context of their local circumstances. Knowing the similarities and differences between oak and true service tree, forest and city tree guidelines of oak can easily be adjusted for true service tree.

Our study addressed and quantified the following topics:

1. Allometric relationships of the crown and stem of true service tree.
2. Site-specific growth patterns of true service and their response to drought.
3. A comparison of these characteristics to those of oak.
4. The suitability of true service tree for urban environments and forests under climate change, interpreted based on these quantitative indicators.

2 Materials and Methods

Sites

We measured true service trees in four regions in Central Europe: southern Scandinavia, northern Franconia in Germany, western Slovakia and the province of Bolzano in South Tyrol, Italy (Figure). The occurrences in Germany and Slovakia are within the core distribution range or true service tree (Caudullo et al., 2017). The Scandinavian trees were growing outside the core range but in regions where the climate is expected to shift towards warmer temperatures and more drought, similar to the species' current distribution (Skovsgaard and Graversgaard, 2013). Climatic conditions in South Tyrol are similar to those of the core distribution range. By covering both core populations and marginal individuals, we could give a broad overview of the growth of true service tree growing under different climatic conditions. In Scandinavia and South Tyrol, we measured all individual trees we could find. In Germany and Slovakia, local forest authorities provided maps with the locations of single trees. Based on those, we selected stands with a relatively high proportion of true service tree and measured individual trees across the range of size classes. The measurements in Germany and Scandinavia took place during spring 2022. Trees in South Tyrol were measured during winter 2022, and trees in Slovakia during spring 2023. On each site, we additionally measured oaks. Selection criteria were a similar dbh (diameter at 1.30 m above ground level) as the true service trees and a position in close vicinity to the true service tree, but without crown contact. The oaks were chosen to grow within a similar species composition, with a similar past treatment, age and under similar site conditions.We measured trees growing in forest stands, urban environments, and parks. In contrast to forest stands, we defined urban environments and parks as locations within cities and locations where trees were standing in a continuous grass cover without a closed canopy. This included city parks, arboreta, and "Castelfeder"-nature reserve in South Tyrol, where trees stood in extensively managed meadows or between vineyards. The type of locations, the annual mean temperature, the precipitation sum, and the number of trees measured per site can be found in the supplements.

Field measurements

All trees were measured for total height (h), dbh, crown length (cl = total tree height minus height above ground level of the lowest living branch (excluding epicormic branches)) and crown radius (cr = distance from the centre of the stem to the point of projection of the crown periphery, as measured at ground level) in eight cardinal directions. For single trees in South Tyrol, however, we only measured the crown projection in four directions (due to inaccessibility of some trees standing on steep slopes). Crown projection area (cpa) was derived based on mean cr as cpa = $cr_{mean}^2 \cdot \pi$.

Trees taller than approximately 8-9 m were measured for height by using a Haglöf Vertex 4 and trees of lower height by using a telescopic height pole, cr was measured using a tape measure or a Haglöf Vertex 4, and dbh was measured using a tape measure. Furthermore, we measured the distance and diameter of surrounding trees with a diameter larger than 5 cm within a radius corresponding to one third of the height of the true service tree. The competition status of each tree was assessed based on the Hegyi competition index (CI) (Hegyi, 1974). CI was calculated using the following equation:

$$CI_i = \sum_{j=1}^{n} \frac{d_j}{d_i * dist_{ij}} \quad (1)$$

with $i \neq j$, where d_i is the diameter of the central tree, d_j is the diameter of the competitor, and $dist_{ij}$ is the distance between the central tree and the competitor. The measurements are summarized in Table 1.

At the stands in Germany and at two locations in Slovakia, we also collected increment cores. The cores were taken at 1.30 m above ground level in Gerolzhofen and at 0.3 m in Zellingen and Slovakia, in both cases using a Haglöf increment corer. The oaks at each site were also cored. We took two cores per tree, one from the north and one from the east. In April 2022, we felled a true service tree in Copenhagen. The tree was located next to a bitumen road near the strait of Øresund and was open-grown (hence, without competition from other trees). After cutting the tree, we collected five cross-sectional stem discs: (at 0.3 m, 2.0 m, 4.0 m, 6.0 m and 8.0 m above ground level, respectively). As the main stem was branching out at a height of 1.4 m, we selected the largest of the multiple stems above this point for disc extraction. In October 2013, we measured the stem of a true service tree located in the park in Alnarp, Sweden. The upper part of the stem had broken off during a recent wind-storm. The entire stem was measured at intervals of 25-50 cm up to 10 m above ground level. Stem volumes were derived based on these measurements, and stem profiles were sketched based on measurements at 1-2 m intervals (to 'smoothen out' irregularities in the stem profile).

Meteorological data

For the locations in Slovakia and Scandinavia, we extracted monthly precipitation sums and temperature data (mean, maximum and minimum) from extrapolated grids of the Climate Research Unit (CRU) for the years from 1901 to 2021 (Harris et al., 2020). For the two locations in Germany, we used the grid data of the German Weather Service (DWD) (DWD Climate Data Center, 2022). For locations in Italy, we used data from the climate station in Auer for Neumarkt, Castelfeder and Montan and data from the station Meran Gratsch for Gargazon and Burgstall. The data is accessible through the open data portal for climate data of South Tyrol (https://data.civis.bz.it/). The De Martonne aridity index (DMI) (Martonne, 1926) was calculated for each site, using the formula $DMI = P/(T + 10)$, where P is the sum of annual precipitation and T the annual mean temperature. For a general characterisation of local aridity, we averaged the DMI from 1992 to 2021.

For the assessment of drought years, we used the standardised precipitation evaporation index (SPEI) (Vicente-Serrano et al., 2010). This multiscalar index includes both precipitation and temperature and is, therefore, suitable for assessing drought. The SPEI includes the potential evapotranspiration, which we calculated using the Hargreaves equation (Hargreaves, 1994; Droogers and Allen, 2002). To compare the fit of different time spans, we calculated the SPEI for 3, 6, and 12 months and calculated seasonal averages for spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February).

Tree ring measurements

Each increment core was dried, glued onto a wooden board and sanded with increasingly finer abrasive paper from 800 to 4000 grits, thereby improving the visibility of tree-ring borders. Likewise, each stem disc was grinded and measured from north and east directions from bark to pith. We measured tree-rings to the nearest 0.001 mm using a digital positioning table (Kutschenreiter and Johann; Digitalpositiometer, Biritz and Hatzl GmbH, Austria). The resulting curves underwent a visual crossdating where years of common growth over all curves were used as reference (Speer, 2010). The cross-dating was then statistically verified using the dplR package in R (Bunn, 2008, 2010; Bunn et al., 2022).

Allometry

The relationships between h and dbh and between cpa and dbh of a tree were described basd on the classical model for allometric relationships: y = a $*$ x^{α} (Huxley, 1932; Teissier, 1934), where x and y are measurements of tree organs and a and α are allometric constants. We used the log-transformed version ln y = ln a + α ln x. The exponent α describes the allocation of resources between x and y. Theoretic approaches assume that there are fixed, generalised allometric exponents describing the allometric relationships between tree variables under ideal growing conditions (e.g., 2/3 for the h-d-relationship and 4/3 for the cpa-d-relationship) (West et al., 1997; Enquist et al., 1998). In reality, allometric exponents often deviate from these ideal values and depend on site and growing conditions (Poorter et al., 2012; Forrester et al., 2017; Del Río et al., 2019; Fortin et al., 2019). The resulting species-specific variation of the allometric exponent can be interpreted bas on the relationship between two variables in an allometric corridor (Pretzsch, 2010). The width, course, and upper and lower limits of this corridor allow for conclusions regarding the ecological characteristics of a given species.

We displayed the allometric corridor by fitting a quantile regression to different conditional quantiles of the log-transformed h-d and cpa-d relationships. We chose the 0.05 and 0.95 quantiles to represent the lower and upper border of the corridor and the 0.5 quantiles to represent the typical median relationship. Each quantile represents different growing situations and the respective shift in resource allocation, as reflected in quantile-specific. The 0.05 quantile describes the growing situation in which a tree allocates its resources in favour of diameter growth vs h or cpa growth (e.g., with low lateral competition or under a canopy of taller trees). The 0.95 quantile describes the opposite, i.e., a decreased diameter growth compared to h or cpa, as is the case for crowns of open-grown trees with few or no competitors, as we often find them in urban environments. We assume that these two quantiles represent the extreme growth forms of a tree species. Below or above them, we can expect a dieback of the tree, e.g., due to light deficiency.

We calculated the confidence intervals for each regression models by rank inversion (Koenker, 2005).

To consider the influence of climate and competition on crown size and to test spcies-specific differences between oak and true service tree, we extended the allometric formula to a linear mixed model based on the following equation:

$$\ln(cpa) = a_0 + a_1 * \ln\left(dbh_{ij}\right) + a_2 * CI_{ij} + a_3 * DMI_{ij} + a_4 * species_{ij} + a_5 * type_i + a_6 * CI_{ij} * species_{ij} + plot_i + \varepsilon_{ij} \qquad (2)$$

where CI refers to Hegyi’s competition index, type refers to the tree's location in a park or a forest setting, and plot is the random intercept on the plots as defined in Table 1.

The variables used in the model were scaled to the standard deviation and centred around the mean to enhance comparability and comprehensibility (Schielzeth, 2010). The factor variable type was included in the model to account for variability in management and overall growing conditions in urban environments and forests over the whole lifespan of the trees. It refers to the classification of trees into forest or park trees (Supplementary Table S4).

The model assumptions of homoscedasticity and normality of residuals were checked visually based on qq-plots and by plotting standardized residuals vs. fitted values. The plots indicated no violation of model assumptions.

Stem volume of the main axis of the trees, was calculated based on the length and mid-diameter of each stem section, assuming a cylindric form of each section. The volume of all sections was added up to the total stem volume.

Growth and drought stress response

Tree ring analysis

We detrended the tree-ring data to remove age- and management-related trends from the curves. Detrending was carried out based on a 30-year spline with a 50 % frequency cut-off (Cook, 1990; Cook and Peters, 1997; Klesse, 2021). This smoothens the age-trend-related low-frequency variation in the series while retaining the high-frequency and inter-annual variation. The result of the detrending were dimensionless ring-width indices (RWI).

Next, we averaged the two measurements for each tree, using Tukey's bi-weight robust mean and built average RWI chronologies for each site (Cook, 1990). The respective chronologies were truncated for years with measurements of less than 5 trees. To assess the quality of the tree-ring series, we calculated common dendroecological statistics (interseries correlation, signal-to-noise ratio, mean gleichläufigkeit and subsample signal strength; see supplementary table S1).

The tree-ring data from the stem disks of the tree in Copenhagen were used to reconstruct the three-dimensional stem development. The height development was reconstructed using a standard interpolation method from the data obtained from different stem heights (Carmean, 1972; Newberry, 1991). Diameters between the stem disks were estimated by linear interpolation between tree-rings. Here, all values refer to under-bark diameters.

Selection of drought years

We evaluated climate-growth relationships of the tree-ring chronologies of oak and true service tree to determine which climatic variables were most influential on growth. As climate variables, we used the monthly precipitation and temperature, the monthly SPEI3, SPEI6, and SPEI12, and the seasonal means of all variables. Subsequently, we calculated bootstrapped Pearson's correlation coefficients between the variables and the species-specific site chronologies, using a stationary bootstrap (Politis and Romano, 1994)with 1000 samples. We also calculated correlation coefficients over all sites for each species by transforming the correlation coefficients using Fisher's z scores (Silver and Dunlap, 1987), averaging them and finally back-transforming them (see Table S2).

We selected drought years by using the SPEI12 for July. This index had a high correlation with annual growth for both species over all stands. It also includes the previous year's drought conditions and reflects the two peaks of increment growth of true service tree throughout the vegetation period (Camarero et al., 2023).

For each location we selected drought years from 1965 onwards (see Table S3). Following the classifications of Slette et al. (2019), we selected all years with a SPEI12 in July of less than -1.5 (categories severely dry and extremely dry).

Quantifying the drought stress response

Drought stress tolerance was assessed through indices of resistance (Rt), recovery (Rc) and resilience (Rs) (Lloret et al., 2011), calculated as follows:

$$Rt = Dr / PreDr$$

$$Rc = PostDr / Dr$$

$$Rs = PostDr / PreDr$$

where Dr is the growth in the drought year, PreDr is the growth in a period before the drought and PostDr is the growth in a period after the drought year.

The hypothesis of different mean values of resistance, recovery and resilience between oak and true service tree was based on bootstrapping (n = 1000) the differences in mean and confidence intervals of 95 %.

Following the recommendations of Schwarz et al. (2020), we compared different periods before and after drought (2, 3 and 5 years) to choose the most reliable one. As we found no evident differences between periods, we selected a pre- and post-drought period of two years, thereby, limitng the influence of other events affecting the growth of trees.

In addition to the original Lloret indices, we calculated the so-called line of full resilience (Schwarz et al., 2020). This line indicates the level of recovery a tree would have to reach to obtain its pre-drought growth level.

The line is derived by putting recovery, resilience and resistance in relation to each other and setting the resilience to 1:

$$Rc = Rs / Rt$$

$$Rc = 1 / Rt$$

The species-specific relationship follows a power function with the following formula:

$$Rc = a * Rt^{b}$$

Statistical software

All statistical analyses were carried out using R (R Core Team, 2022) and R Studio (Posit team, 2022) using the packages of the tidyverse (Wickham et al., 2019). Quantile regressions were calibrated in the package quantreg (Koenker, 2022) and mixed-effect models in the packages lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017).

Results

Allometry of crown and stem

The fitting of quantile regressions resulted in the curves displayed in Figure 3 and Figure . We could observe similar values for true service tree and oak for both the height-diameter (h-d) and cpa-diameter relationships (Table 2). The h-d relationship values of the allometric exponent for true service tree ranged between 0.48 and 0.58. Especially for the 0.95 quantile, both species' intercept and allometric exponent values were similar or identical. For the 0.5 quantiles, only the intercepts differed, but marginally. For the 0.05 quantile, the values for oak were larger than for true service tree.

For the cpa-d relationship, the intercepts of the 0.95 and the 0.5 quantiles were smaller for oak than for true service tree. The values for the allometric exponent, however, were larger. In the 0.05 quantile the intercept war smaller for true service tree and the allometric exponent larger than for oak.

The trees in Copenhagen and Alnarp, clearly had somewhat pyramidical stem profile. Stem increment mainly occurred on the lower parts of the stem, up to a height of 2 m. The annual radius increment in the upper parts of the stem was much lower, resulting in a highly tapered stem (Figure). The total volume of the stem in Copenhagen was 0.77 m^3 and of the stem in Alnarp 2.38 m^3.

The linear mixed model (Equation 2) detected a significant effect of dbh, competition and location type on cpa (Table 3). There were no significant differences of crown size and sensitivity towards competition between species.

Growth and drought stress response

Growth

True service trees and oak in Germany and Slovakia showed similar growth patterns over the period of measurements (Figure 5) with mostly lower increments for higher dbhs.

The height-age curve derived from stem analysis of a tree in Copenhagen (Figure 6 a) indicates fast growth until around 20-22 years of age. Subsequently, growth slowed down and the curve flattened. The transition from fast to slow height growth was rather abrupt and the growth rate was essentially constant in each of these two phases. In contrast, the growth on dbh was almost linear until around 50 years and only slowed down considerably at around 70 years (Figure 6 b).

Drought stress response

When looking at the species-specific indices of resistance, recovery, and resilience (Figure 7), we could not reject the hypothesis of equal means. Comparing the line of full resilience (Figure 8), we found a similar drought response in both species. For lower resistance values, both species were lying under the line of full resilience but intersecting it already at a resistance value below 1. After that, the curves for both species were proceeding above the line of full resilience.

Comparison to oak

Combining our results and observations from the literature, we can summarise the differences between oak and true service tree in allometry, growth and drought response in the following overview:

	True service tree	**Oak**
h-d allometry	Similar for both species, but a steeper increase for oak at the 0.05 quantile. Essentially identical height growth for both species.	
cpa-d allometry	Similar for both species, but a steeper increase for true service tree at the 0.05 quantile. Larger crown size for smaller trees of true service tree; otherwise, similar space requirements.	
Sensitivity to competition	Our analysis: no significant difference between species. Literature: higher sensitivity of true service tree	
Growth	Both species: fast height growth in youth, which later decreases, in line with Skovsgaard and Graversgaard (2013).	
Drought tolerance	Our analysis: similar drought tolerance. Literature: oak less drought tolerant (Camarero et al., 2023) or more (Kunz et al., 2016; Kunz et al., 2018)	
aboveground CO2 storage	Age 50: 1.51 tons (Orlandi et al., 2022)	Age 46+: 1.18 tons of carbon (Weissert et al., 2017), equals 4.33 tons of CO2

PM10 uptake	1.16 g/m2 (Orlandi et al., 2022) - 1.01 g/m^2 (Fares et al., 2020)	0.7 g/m^2 (Fares et al., 2020)

Discussion

Allometry of crown and stem

Quantile regression

The exponents of the h-d relationship for both oak and true service tree were lower than the expected general exponent of 2/3, while the exponents of the cpa-d relationships were not significant different from the assumed 4/3 (West et al., 1999). We therefore recommend using the species-specific exponents from our study for the h-d relationship to avoid an overestimation of height. For assessing crown sizes the 4/3 exponent can be applied.

The parameters of the h-d relationship of oak and true service trees had similar values for the 0.95 and 0.5 quantiles. So, city planners and foresters can rely on their experience with oak to assess the potential height of true service trees. Concerning the crown development, the crown projection area of true service trees in the 0.95 quantile was slightly higher than for oaks. The quantile is associated with city trees, as these trees are often growing as essentially solitary trees and represent an exceptional case along the competition gradient. The higher space requirements should be considered in urban planning. For the 0.05 quantile, true service tree had smaller crown sizes for small dbh values than oak. However, this reversed with increasing dbh. Following the classification of Pretzsch et al. (2015), the true service tree has the same crown type as black locust (*Robinia pseudoacacia* L.) and European hornbeam (*Carpinus betulus* L.). These species form large crowns when free from competition and further increase their crown size with bigger diameters. Given the same diameter, this results in a larger space requirement than for other species but also creates larger shading areas that can have a cooling effect in urban areas. A study dealing with the closely related *Sorbus arnoldiana* (Rahman et al., 2015), however, indicates a rather low shading intensity.

In comparison to results of other scientists, we found a large degree of similarity, even when comparing across different regions in Europe. Kausch-Blecken von Schmeling (2000) published h-d values of true service trees in south German forests that are very similar to our results. He also described maximum heights of up to 34 m for true service tree. The highest tree in our dataset is a Slovakian tree with a height of 31.4 m. In German forest stands, we found several trees with a height of 29 m. We could also confirm the existence of crown diameters of more than 20 m (Skovsgaard and Graversgaard, 2013; Paganová et al., 2015), as observed for a tree in Slovakia. Turrientes et al. (2009) examined young service tree in a dry climate (precipitation < 500 mm) and found a mean height of 2.3 m (min. 0.8 m, max. 4.7 m) and a mean diameter of 1.2 cm after 6 years. According to our allometric equations, a diameter of 1.2 cm results in a median height (0.5 quantile) of 2.99 m for the 0.95 quantile in 4.6 m and the 0.05 quantile in 2.24 m. Especially for the 0.95 quantile, our models indicated a very close fit to their measurements. The mean value of Turrientes et al. (2009) is closest to our 0.05 quantile, which can be attributed to the very dry conditions.

When comparing the allometric exponents to the ones of other rare native tree species, as studied by Schmucker et al. (2022), we could see that the allometric exponent of true service tree for the cpa-d ratio was generally higher than the ones of other rare species, expect field maple (*Acer campestre* L.). True service tree showed the closest similarities to European hornbeam among the other rare species. Compared to the related wild service tree (*Sorbus torminalis* (L.) Crantz), we could observe higher values of true service tree throughout all quantiles.

Stem taper and stem volume

The stem profiles derived from section diameters and tree-ring analysis indicate that open-grown true service tree may have a particular stem taper that differs from that of other tree species. When comparing the actual stem volume of the two trees in Copenhagen and Alnarp to total stem volume calculated by functions for other broadleaved tree species, we found that available functions substantially overestimated the stem volume of true service tree. The best matching function was one by Hillebrand (1998) for rowan (*Sorbus aucuparia* L.) which overestimated volume ‘only’ by to 33-35 %. A function by Kahle (2004) for wild service tree overestimated volume by around 100 %, and functions for European beech and pedunculate oak by Hagberg and Matérn (1975) and for oak by Petersen et al. (2003) (cf. (Tarp-Johansen et al., 1997) overestimated by 30-79 %. It should be cautioned, however, that these functions were not calibrated on trees with a dbh and height similar to those of our two true service trees, or such dbh-h combinations were on the edge of the calibration range. Moreover, open-grown trees, not least trees growing in a special environment such as in the city, may deviate in growth pattern and growth allocation from those within a forest. Nevertheless, our stem volume measurements indicate the potential need for a species-specific stem volume function for true service tree.

Influence of competition and climate on crown size

Our linear mixed model (Eq. 2) indicated that crowns in parks are larger than those in forests, all else being equal. This may be attributed to the negligible competition in parks throughout the entire lifetime of solitary trees, as also reflected by the Hegyi-index. Difficult growing conditions due to soil compaction or possible underground constructions did not seem to negatively influence true service tree. As all trees in urban environments used in our study were growing in park-like conditions with some grass around them, we did not include street trees growing in heavily sealed or paved soil.

We found no difference in crown size between oak and true service tree and no difference in the influence of competition between the two species. This corroborates our results from the quantile regression analysis. We therefore conclude that the growing space requirements, growth and competitive power of true service tree are similar to those of oak. Our study indicates that true service tree and oak are similar in sensitivity to competition from other trees. This implies that the low occurrence of true service tree is probably much influenced by human activity to promote high forest systems and fast-growing coniferous species (Drapier, 1993;

Kausch-Blecken von Schmeling, 2000; Skovsgaard and Graversgaard, 2013). However, we did not study the overall mortality of trees and the competition on moist sites. Our study was limited to relatively dry and warm regions, where other species are generally less competitive.

Growth and drought stress response

Due to its rarity in cities, forests, and landscapes alike, the stem analysis of the felled true service tree in Copenhagen is rather unique. Even if we only have one sample tree, it gave us the unprecedented possibility of insights into the specie's growth in an urban environment. The tree germinated around 1943, was planted at its permanent location in December 1948 and was cut in April 2022 at an age of approximately 80 years. As the tree was growing next to a road and 350 m northwest of a power plant that was coal-fired until 1985, it was directly exposed to air pollution. Diameter increment, however, stayed stable over time. It only decreased during the last 10 years, possibly relating mainly to the inherent age decline. In line with these observations, Orlandi et al. (2022) found that the ability of true service tree to absorb PM10 is above average. Height growth culminated at the age of 20-22 years. Subsequently, it still increased, but on a lower rate. This may possibly be attributed to the species-specific growth characteristics of true service tree, as also indicated previously by Skovsgaard and Graversgaard (2013). Based on a simple model calibrated on empirical observations, they more specifically stated that the height development of true service tree is characterized by fast or even very fast growth in youth, followed by a gradual decline and later a final stagnation, much like the height development of oak. For oak, it is known that this decreased growth steadily can go on for a long time.

In our investigation, the long-term growth trend of true service tree could not be examined. Unfortunately, age determination for tree cores was impossible as we could not reach the pith of the trees that were cored. However, the diameter growth curves indicated a steady growth over multiple years. We observed similar growth patterns when comparing the dbh curves derived by the tree cores from oak. This indicates that oak and true service tree, in fact, share this characteristic of long-term, steady growth. Moreover, true service trees can grow to a very old age of several hundred years, similar to oak, again indicating similar growth patterns.

Overall, our results match the findings of other studies on true service tree. While we found the true service tree to be as drought tolerant as oak, Camarero et al. (2023) found it even more drought tolerant than Mediterranean oaks. In their study, true service tree showed a better recovery after drought events and mainly so to short drought events between 2-7 months. Carried out in Spain, their study indicated that the growth of true service tree was influenced mainly by dry spring conditions. Apparently, the species has a second peak of increment growth after the summer months which is an advantage compared to oak. Therefore, the divergent results of the two studies might be attributed to different climatic conditions in Spain. Another study on tree rings of older trees (Kunz et al., 2018) did not suggest better drought tolerance of true service tree as compared to oak. However, combining the results of our study, covering locations both in Germany and Slovakia and one tree in Copenhagen, and the results of Camarero et al. (2023), covering locations in Spain, it is reasonable to assume that in most cases, the drought tolerance of the true service tree and oak are similar. Furthermore, it is generally recognized that most species of *Sorbus* have a good drought tolerance (wild service tree: Kunz et al. (2018), Schmucker et al. (2023); rowan (*Sorbus aucuparia* L.): Vogt (2001)). The similar growth patterns over all survey sites show the potential of true service tree to adapt to different climatic conditions. In light of climate change, planting of true service trees in urban areas and forests is a feasible option. However, due to the remaining uncertainty regarding the susceptibility to pests, a selected and careful cultivation is indicated.

Both allometric analysis and analysis of tree-ring data fulfilled all statistical requirements and showed meaningful significances that led to new insights. Despite its rarity we were able to measure true service trees at different locations and under different growing conditions. To our best knowledge, the study provides the most extensive empirical coverage of the true service tree so far.

Conclusions

True service tree's drought tolerance and overall growth behaviour are similar to those of oak. In contrast to common belief, as indicated in the literature, we could not identify a higher sensitivity to competition for true service tree than for nearby oak trees growing under similar conditions. In forest settings, we recommend managing true service tree based on guidelines for oak. In urban environments, height growth can be assessed based on nearby oak. The crown projection area of true service tree is, however, marginally larger than that of oak. Therefore, true service tree provides a correspondingly larger shading area than oak, however, with a potentially low intensity, as indicated by results of other *Sorbus* species with similar leaves. Its growth characteristic, combined with its high drought tolerance make the true service tree a promising admixed species in forest stands and for urban environments. Due to its high susceptibility to fungal canker, we still recommend a limited cultivation. We highly encourage further research on pathology, especially with a focus on the influence of a changing climate on pathogens and potential prevention methods. Furthermore, controlled plantings under different climatic conditions that allow the observation of growth from a young age are required to study the influence of climate on the growth, distribution range and ecosystem services of the true service tree.

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Tables

Table 1 Mean values of measured variables by country.

	species	dbh [cm] ± sd	h [m] ± sd	cpa [m2] ± sd	n_{comp}	CI	n_{cores}
D	oak	34.08 +- 12.28	22.68 +- 4.35	36.98 +- 30.41	12.05	1.98	26
	true service tree	33.09 +- 15.23	21.08 +- 4.68	38.42 +- 30.81	11.74	2.09	19
DK	oak	37.97 +- 31.33	15.18 +- 6.61	89.27 +- 73.37	0.00	0.00	0
	true service tree	20.93 +- 28.72	8.25 +- 4.94	40.61 +- 25.55	3.75	0.46	1
IT	oak	23.89 +- 9.18	11.79 +- 2.95	29.27 +- 25.55	5.00	1.05	0
	true service tree	23.65 +- 11.29	12.69 +- 4.64	26.5 +- 25.46	4.75	1.24	0
SK	oak	35.46 +- 6.68	23.34 +- 4.62	21.47 +- 17.87	11.21	1.77	0
	true service tree	34.53 +- 11.34	21.96 +- 4.28	30.47 +- 50.29	9.10	1.49	0
N	true service tree	23.5 +- 2.12	8 +- 1.41	50.2 +- 9.74		0.00	0
S	true service tree	9.5 +- 4.95	6	19.03		0.00	0

Table 2 Parameter estimates for the quantile regression models describing the relationship between h and dbh and between cpa and dbh.

model	**quantile**		**true service tree**		**oak spec.**	
			a	**α**	**a**	**α**
ln(cpa) = a + α * ln(d)	0.5	estimate	-1.28	1.35	-2.04	1.52
		conf. low	-1.78	1.28	-3.22	1.19
		conf.high	-1.07	1.47	-0.91	1.85
	0.95	estimate	0.11	1.18	-0.22	1.27
		conf.low	-0.51	0.84	-0.78	0.81
		conf.high	1.32	1.36	1.44	1.55
	0.05	estimate	-3.15	1.35	-0.41	0.63
		conf.low	-9.97	0.57	-9.16	0.05
		conf.high	-0.69	3.00	1.20	3.05
ln(h) = a + α * ln(d)	0.5	estimate	0.99	0.58	1.20	0.54
		conf.low	0.81	0.55	0.88	0.43
		conf.high	1.09	0.63	1.66	0.63
	0.95	estimate	1.40	0.54	1.42	0.54
		conf.low	1.37	0.04	0.89	0.19
		conf.high	3.57	0.55	3.30	0.70
	0.05	estimate	0.72	0.48	0.62	0.58
		conf.low	0.31	0.47	-0.01	0.45
		conf.high	0.76	0.56	0.91	0.68

Table 3 Parameter estimates for Equation 2. df = degrees of freedom

		Estimate	Standard Error	df	statistic	p-value
	Fixed Effects					
	(Intercept)	2.41	0.15	29.92	15.71	0.00
	ln dbh	1.12	0.07	329.83	16.19	0.00
	CI	-0.18	0.06	332.52	-3.22	0.00
	Species: true service tree	0.08	0.06	319.57	1.34	0.18
	Type: park	1.09	0.32	32.89	3.35	0.00
	DMI	0.01	0.06	34.67	0.23	0.82
	CI: true service tree	0.02	0.06	323.91	0.33	0.74
	Random effects					
plot	sd__(Intercept)	0.66				
Residual	sd__Observation	0.53				

Figures

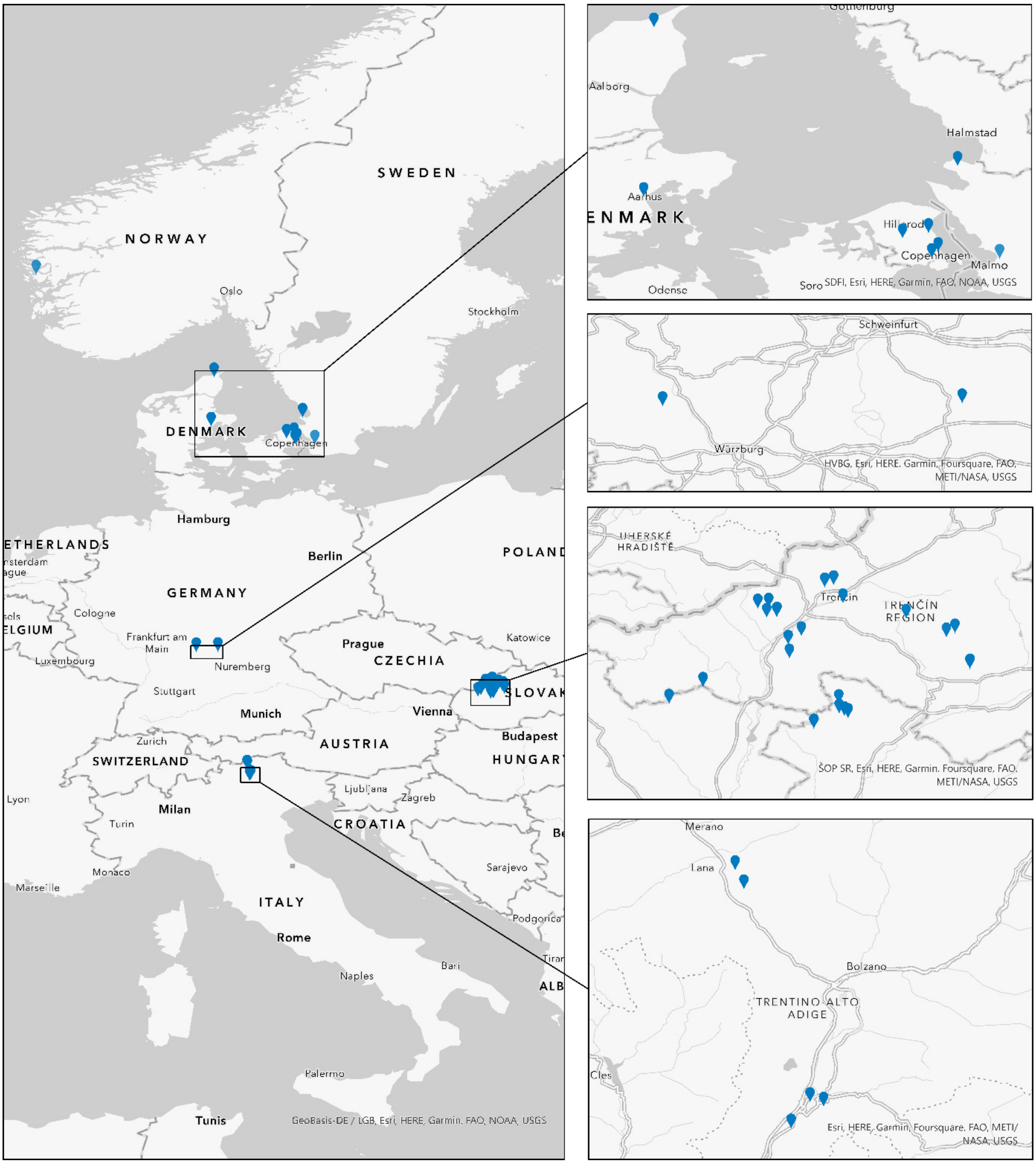
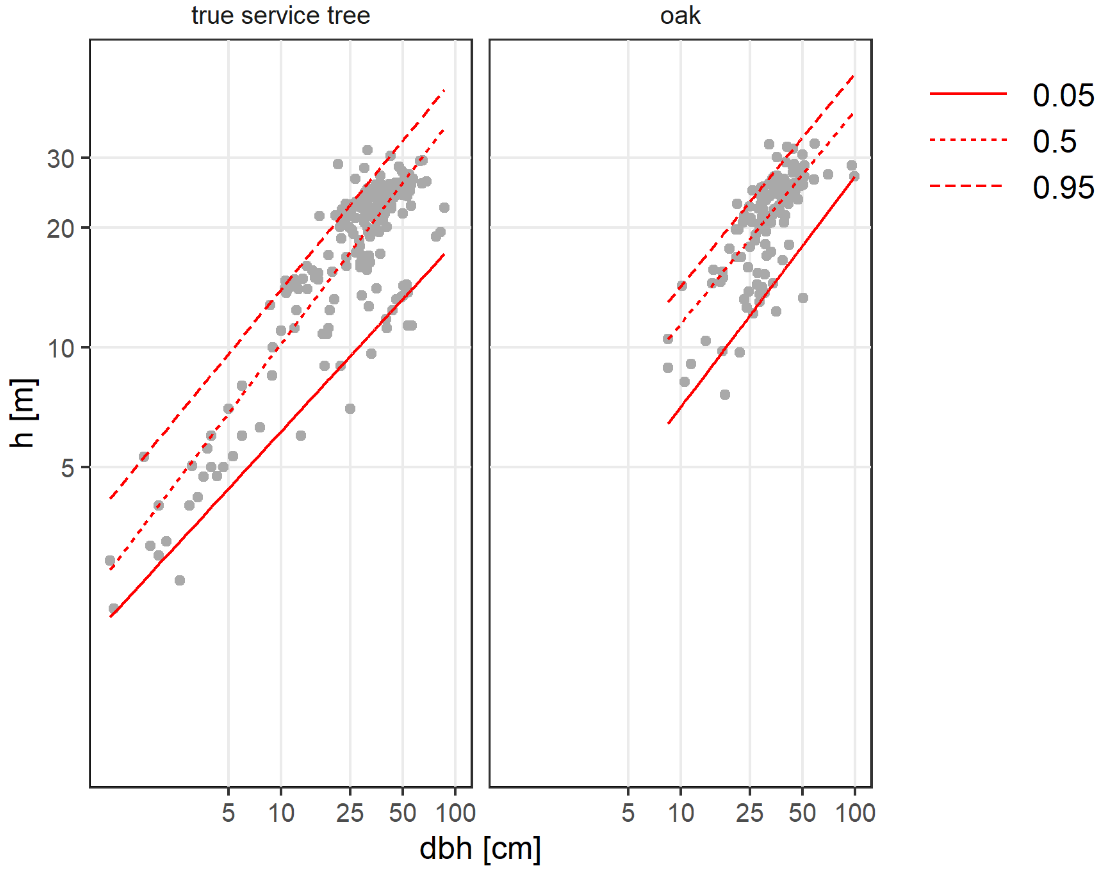
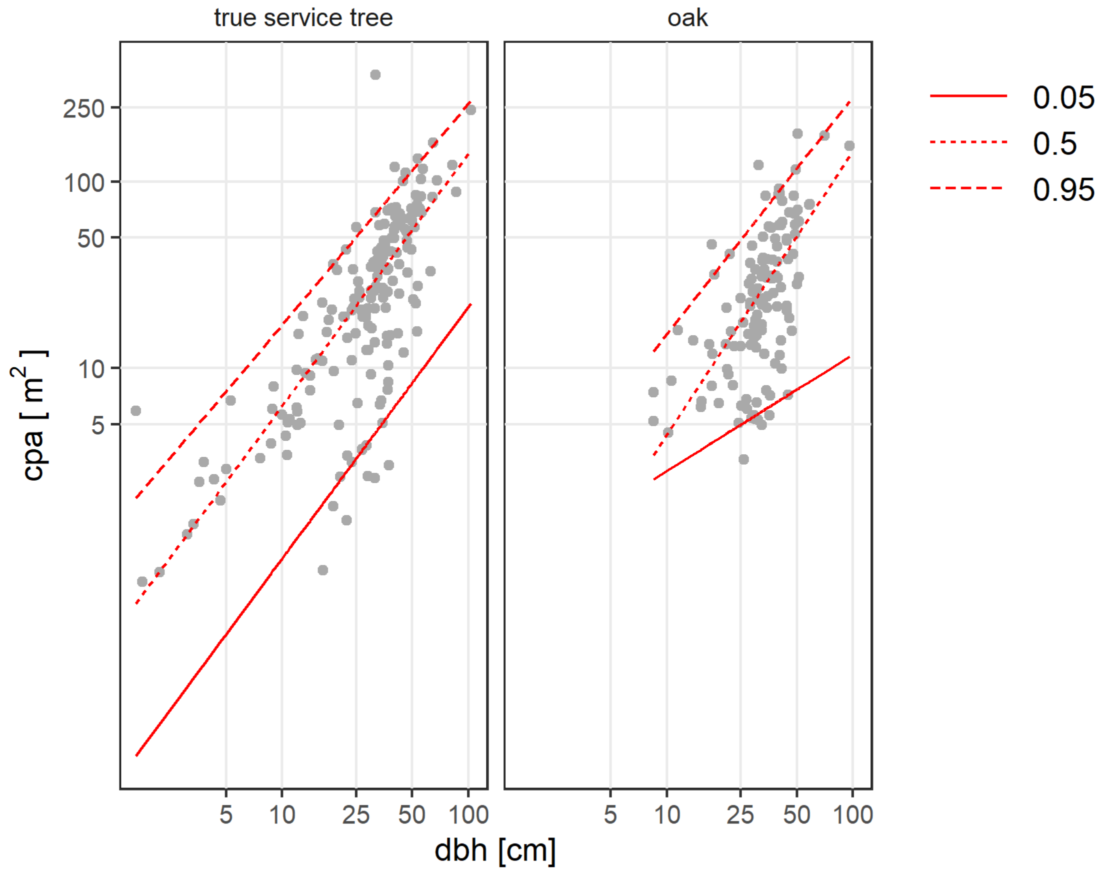


Figure 1



737

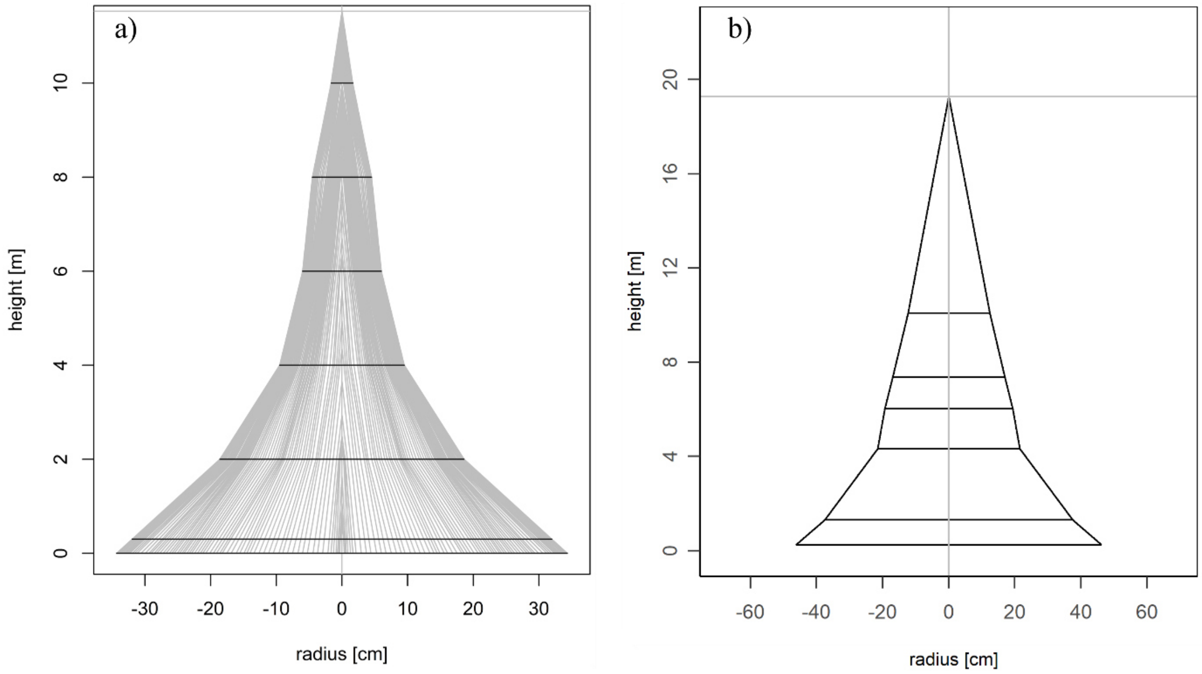
738 **Figure 2**



739

740 **Figure 3**

741



742

743 **Figure 4**

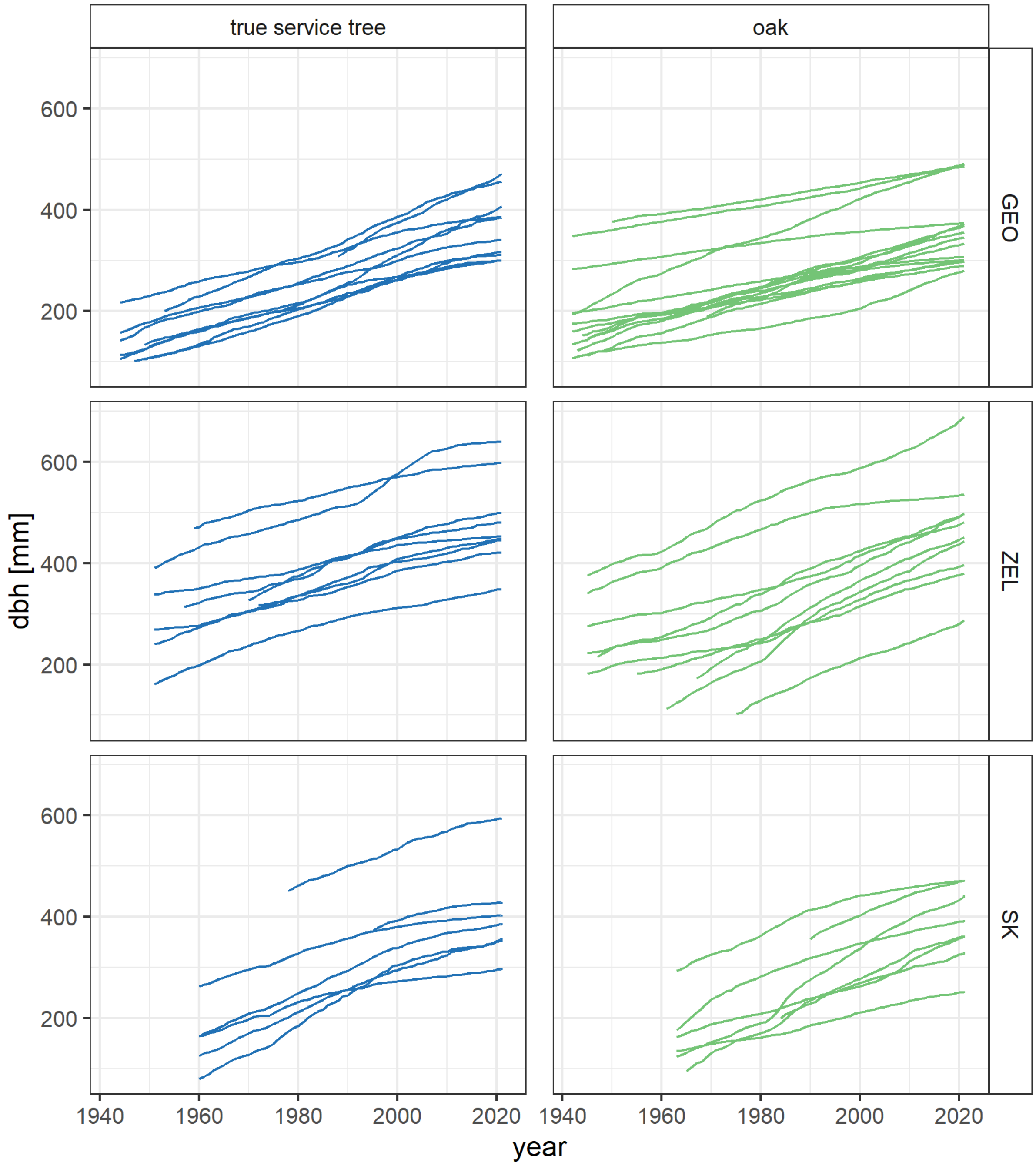
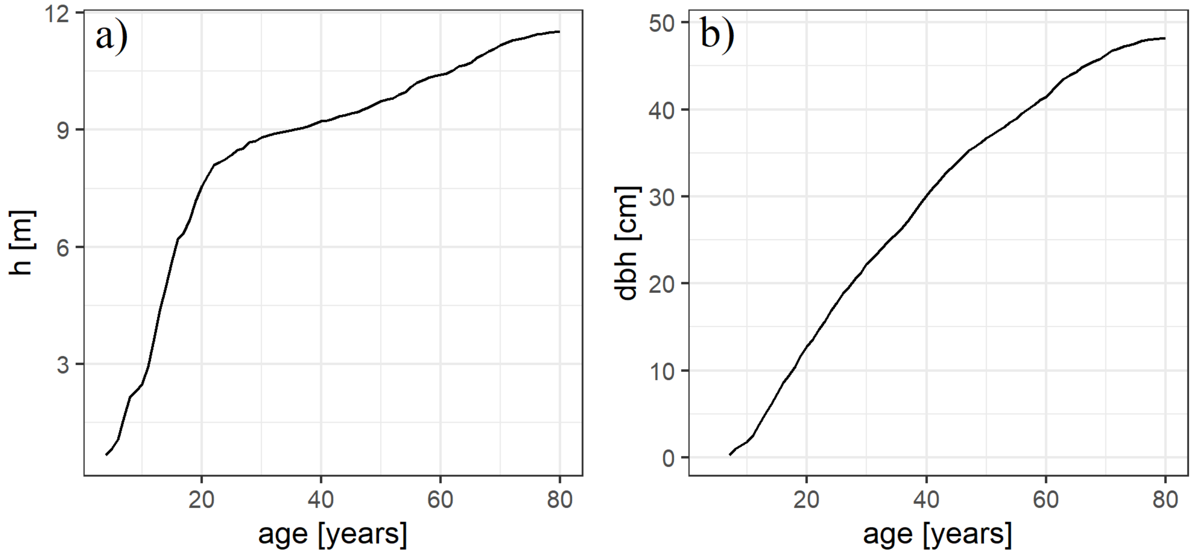

true service tree
oak
GEO
ZEL
SK
dbh [mm]
600
400
200
1940
1960
1980
2000
2020
year

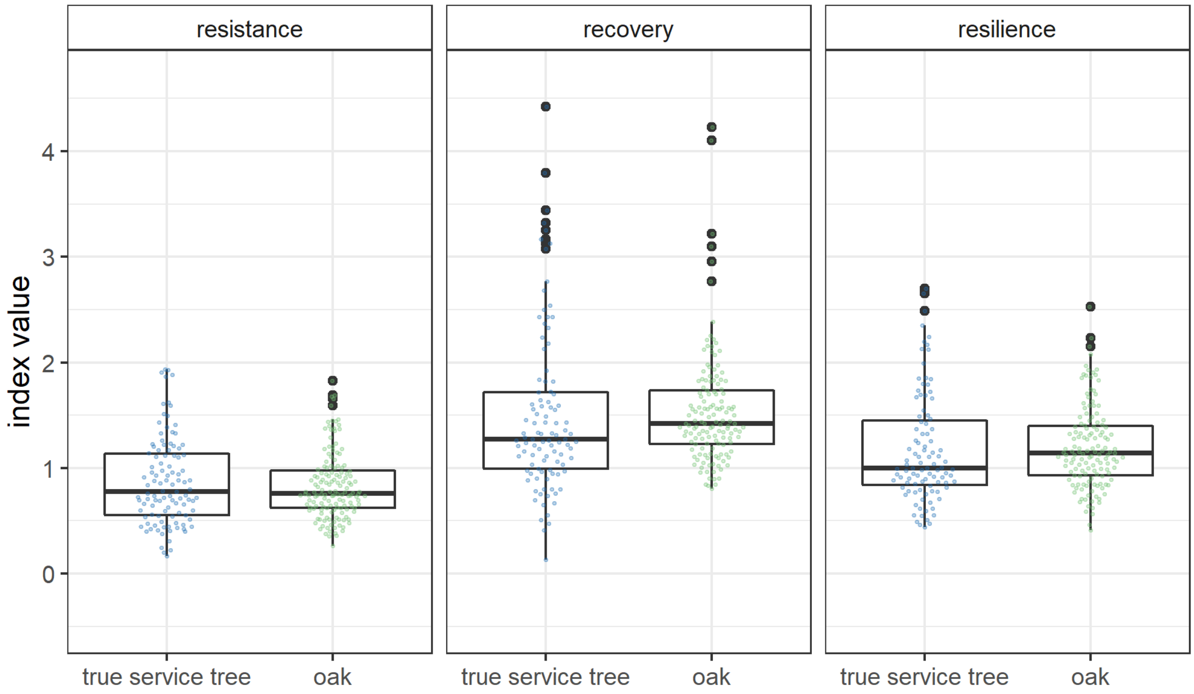
Figure 5

746



747 **Figure 6**

748



749

750 **Figure 7**

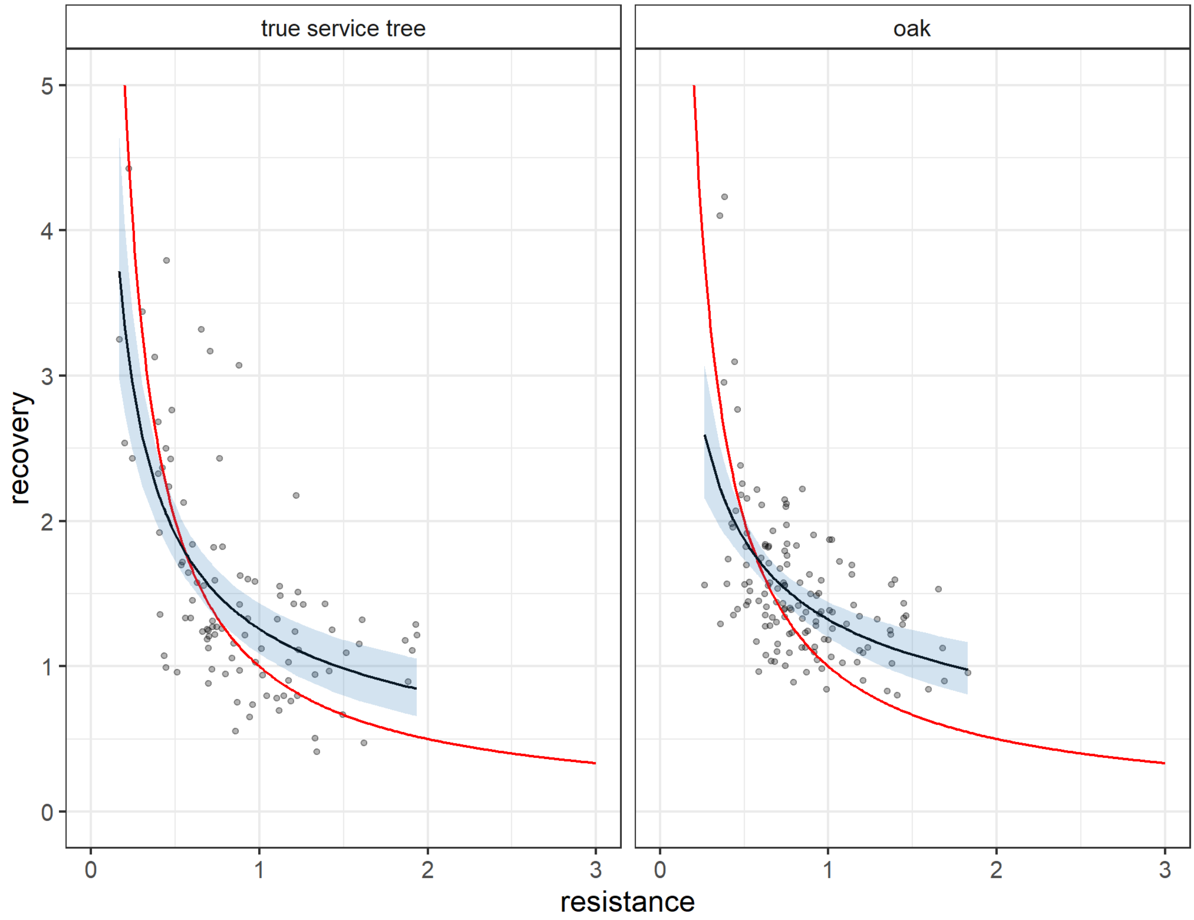


Figure 8

Figure captions

Figure 1 Locations of trees and stands measured for this investigation.

Figure 2 Allometric relationships between dbh [cm] and h [m] for true service tree and oak. The upper line repre-sents the 0.95-quantile, the middle line the 0.5-quantile-regression and the lowest line the 0.05 quantile (parameter estimates in Table 2).

Figure 3 Allometric relationships between dbh [cm] and cpa [m2] for true service tree and oak. The upper line represents the 0.95-quantile, the middle line the 0.5-quantile-regression and the lowest line the 0.05 quantile (parameter estimates in Table 2).

Figure 4 Stem diagram based on the stem analysis of a true service tree in Copenhagen (a) and section-wise diameter measurements of a tree in Alnarp (b). Black lines refer to the height of stem disks taken; grey lines show the annual increment.

Figure 5 Species-specific diameter growth of trees over age for true service tree and oak. Legend: GEO = Gerolzhofen, ZEL = Zellingen, SK = Slovakia.

Figure 6 height-age curve (a) and diameter-age curve (b) derived from a stem-analysis of a true service tree in Copenhagen.

Figure 7 Boxplots showing the values of the Lloret indices of recovery, resilience and resistance for true service tree and oak. The lower and upper hinges represent the 25th and 75th percentiles, the horizontal line the median. The upper and lower whisker extend from the hinges to the values closest to a multiple of 1.5 of the interquantile range. All data beyond the whiskers are displayed as outlier points.

Figure 8 Species-specific relationship between resistance and recovery (black line with confidence bands calcu-lated in a bootstrap with 1000 iterations), the red line represents the theoretical line of full resilience.

D. List of Publications

Publication list of the three articles included in this thesis.

Schmucker, J., Uhl, E., Steckel, M., & Pretzsch, H. (2022). Crown allometry and growing space requirements of four rare domestic tree species compared to oak and beech: implications for adaptive forest management. European Journal of Forest Research, 141(4), 587-604. https://doi.org/10.1007/s10342-022-01460-w

Schmucker, J., Uhl, E., Schmied, G. & Pretzsch, H. (2023). Growth and drought reaction of European hornbeam, white elm, field maple and wild service tree. Trees 37, 1515-1536. https://doi.org/10.1007/s00468-023-02441-1

Schmucker, J., Skovsgaard, J.P., Uhl, E., Pretzsch, H. (2023). Crown structure, growth, and drought tolerance of true service tree (Sorbus domestica L.) in forests and urban environments. Urban Forestry and Urban Greening. https://doi.org/10.1016/j.ufug.2023.128161

List of further publications published in peer-reviewed and non-peer-reviewed journals during the period of this thesis:

Willim, K., Ammer, C., Seidel, D., Annighöfer, P., **Schmucker, J.,** Schall, P., & Ehbrecht, M. (2022). Short-term dynamics of structural complexity in differently managed and unmanaged European beech forests. Trees, Forests and People, 8, 100231. https://doi.org/10.1016/j.tfp.2022.100231

Schmied, G., Pretzsch, H., Ambs, D., Uhl, E., **Schmucker, J.,** Fäht, J., Biber, P., Hoffmann, Y., Šeho, M., Mellert, K., Hilmers, T. (2023). Rapid beech decline under recurrent drought stress: Individual neighbourhood structure and soil properties matter. Forest Ecology and Management, Volume 545, 121305, https://doi.org/10.1016/j.foreco.2023.121305

Biber, P., Grigolato, S., **Schmucker, J**., Uhl, E., Pretzsch, H. (2023). care4cmodel: Carbon-Related Assessment of Silvicultural Concepts. R package version 1.0.0, https://CRAN.R-project.org/package=care4cmodel