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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

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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,

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 $\log y = \log b + \alpha \log x$. 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	
Pyttel et al. (2019)					X			X		X	
Pretzsch et al. (2015)	X					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
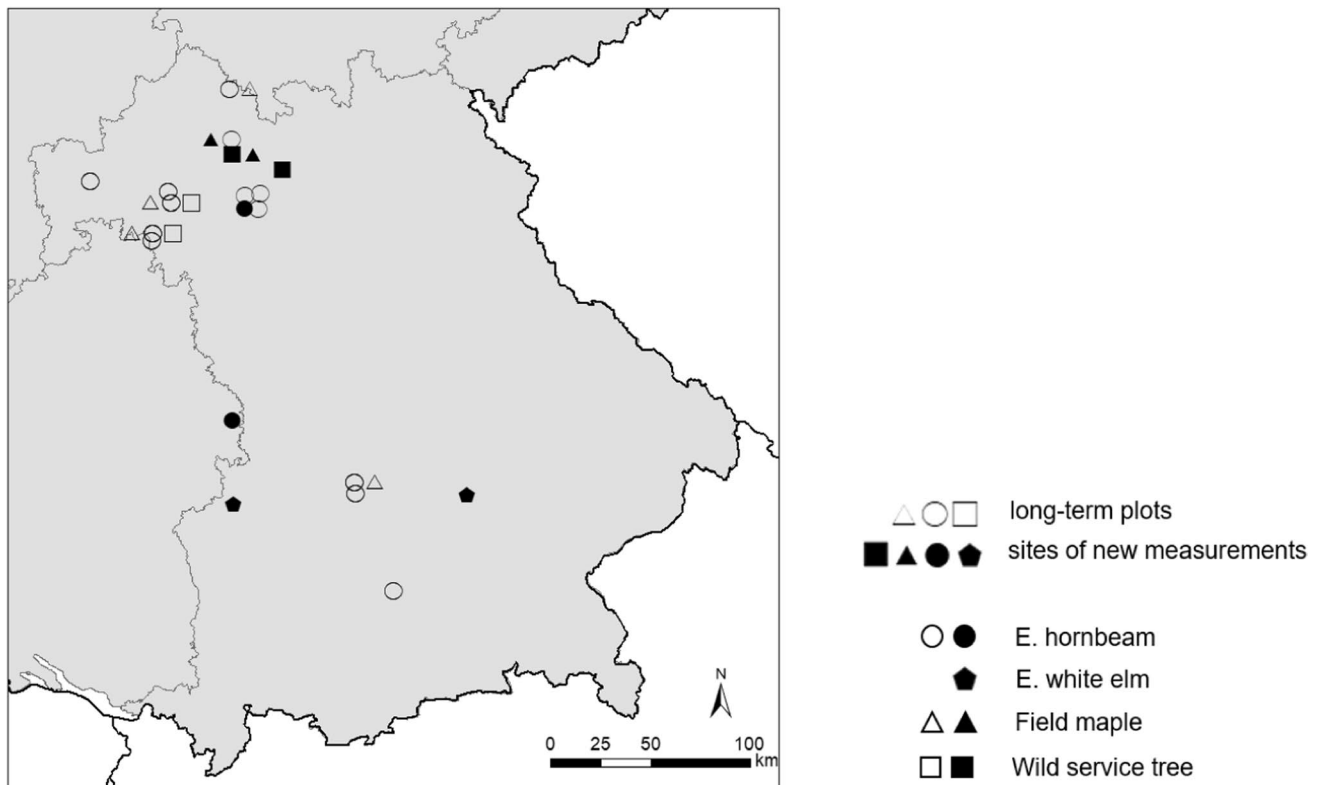

Fig. 1 Locations of seven research sites sampled in winter 2020/2021 and the long-term plots used in this study

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)	Mean annual temperature (°C)
	(1991–2020)	(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 ($cr = \sqrt{(r_N^2 + r_{NE}^2 + \ldots + r_{NW}^2/8)}$). 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
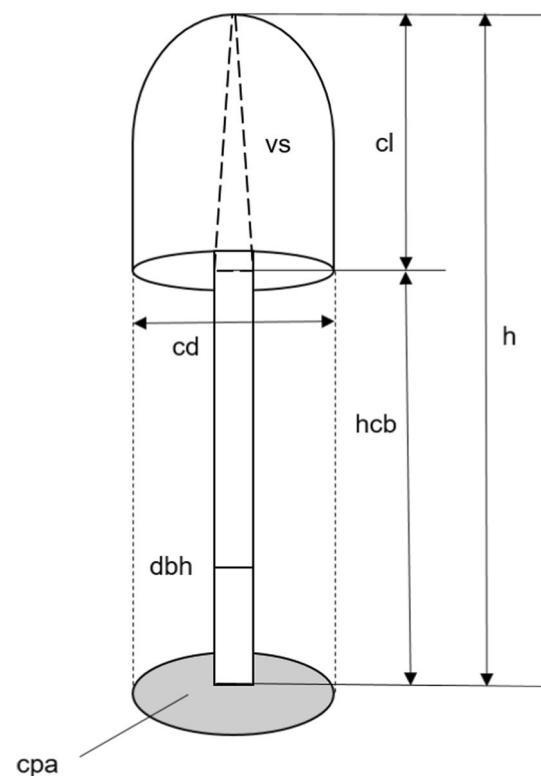

Fig. 2 Tree parameters used in this analysis: crown length (cl), crown diameter (cd), crown projection area (cpa), diameter at breast height (dbh), height of crown base (hcb), height (h), stem volume (vs)

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 dMI = P/(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.

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

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

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

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

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 [m²]	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 [m²]	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 [m²]	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 [m²]	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 [m²]	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 [m²]	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 m² 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.

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

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
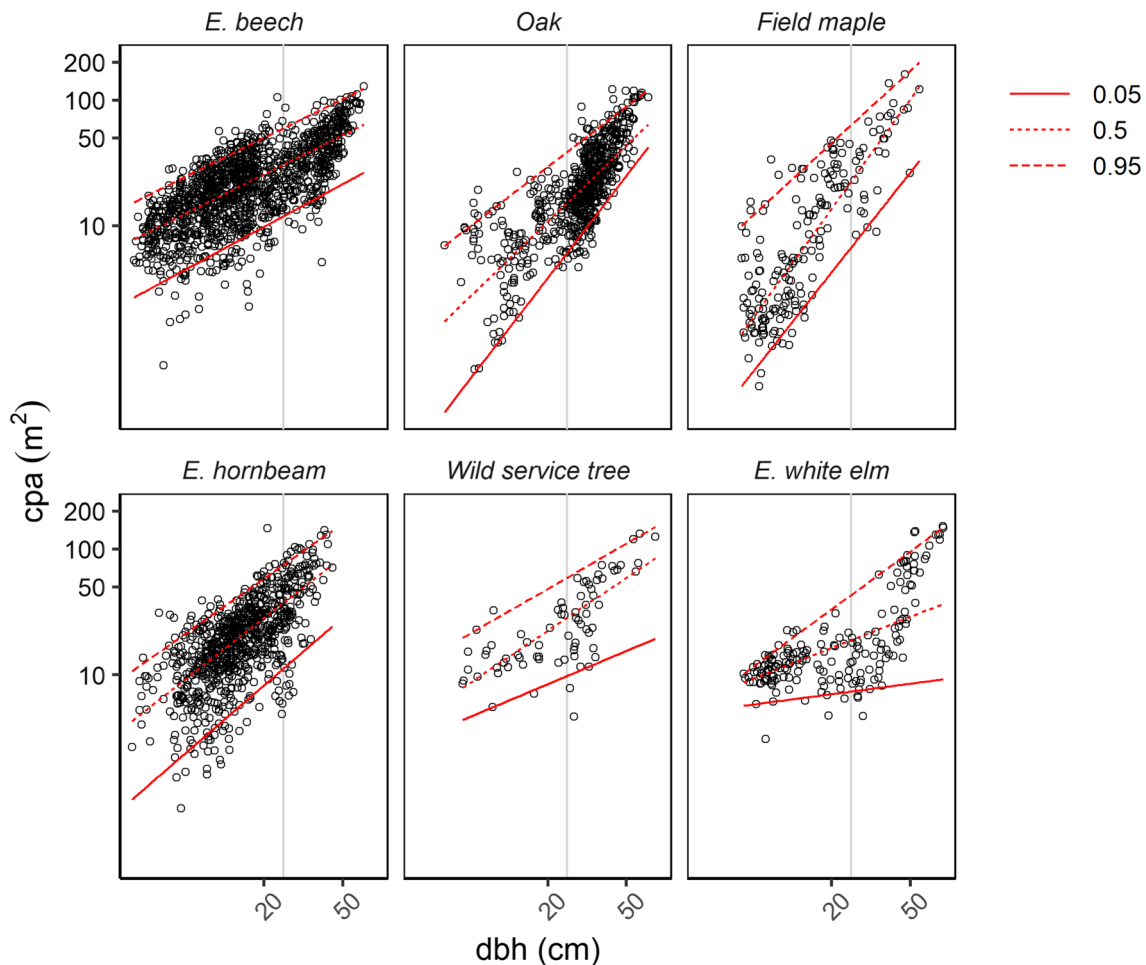
Fig. 3 Allometric relationships between dbh and cpa, for European hornbeam, European white elm, field maple, wild service tree, European beech and oak. The upper line represents the 0.95-quantile, the lower line the 0.5-quantile-regression. At 25 cm, a reference line has been inserted for better orientation. 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
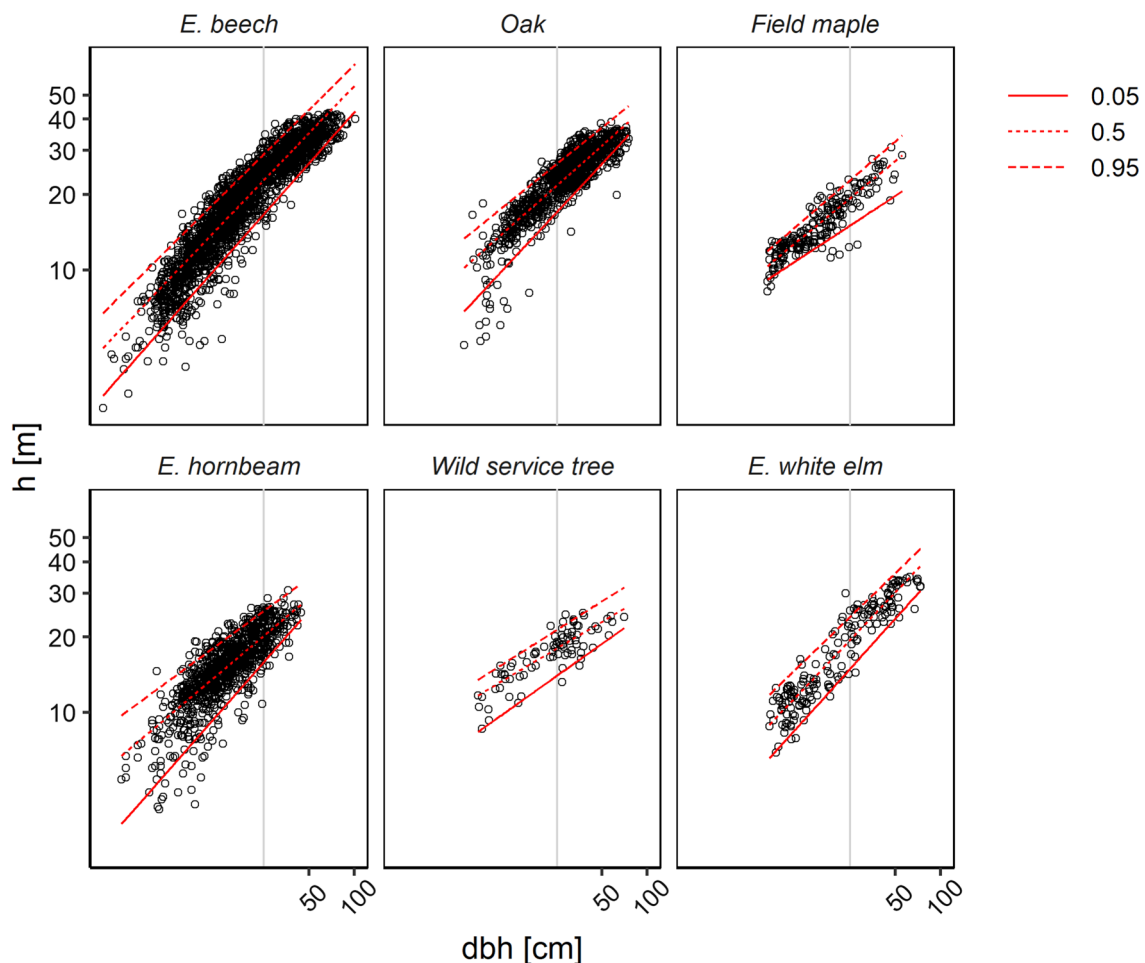
Fig. 4 Allometric relationships between stem diameter (*d*) and height (*h*), for European hornbeam, European white elm, field maple, wild service tree, European beech and oak.The upper line represents the 0.95-quantile, the lower line the 0.5-quantile-regression. At 25 cm, a reference line has been 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.
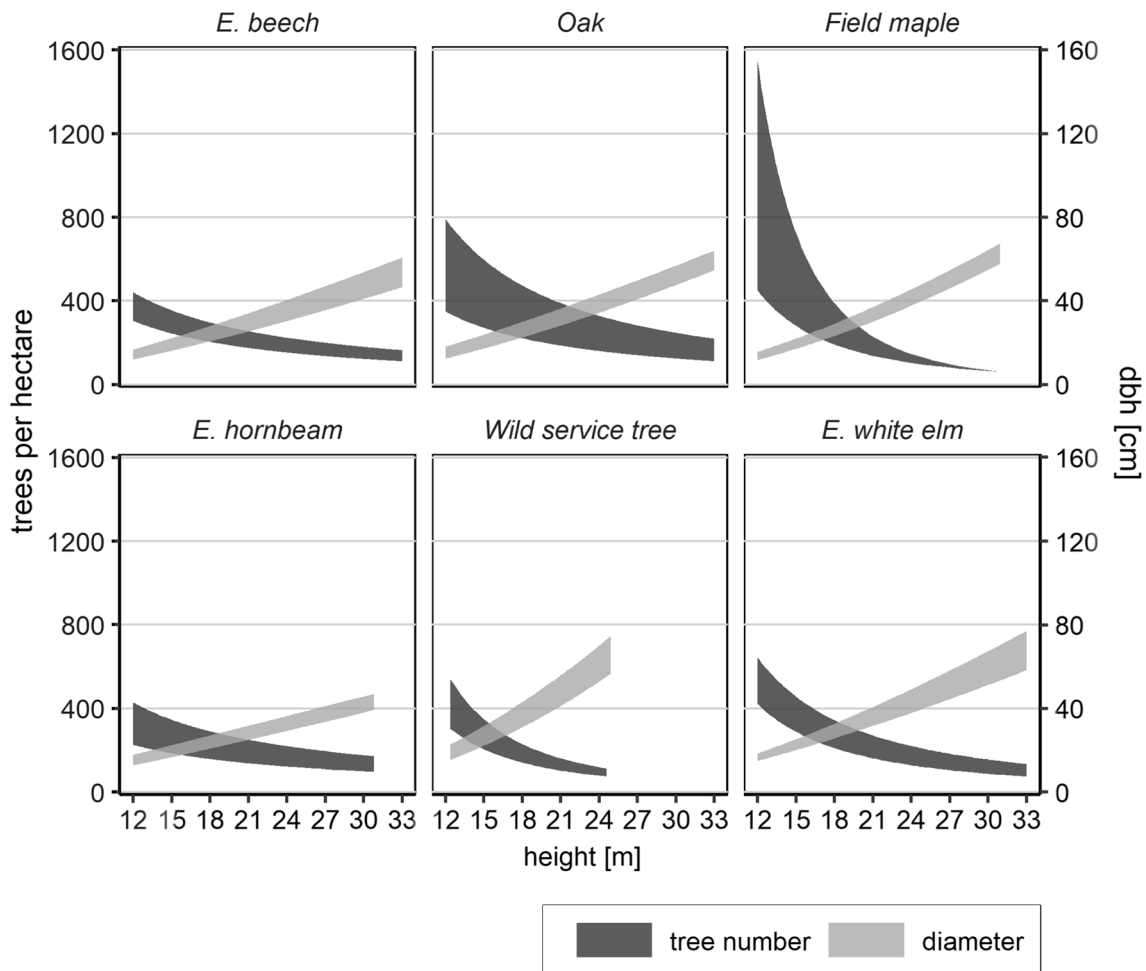
Fig. 5 Range of maximal tree numbers per hectare and dbh over tree height (*m*). Calculated based on the 0.75 and 0.95 quantiles of the cpa-h and dbh-h allometry. Statistical parameters can be found in supplementary Table S2. The units for the tree numbers per hectare are displayed on the left y-axis, 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.

Declarations

Conflict of interest No conflicts of interest were identified.

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