



Morphological plasticity of six tree species with different light demands growing in multi-layered deciduous forests in Central Europe

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Abstract

Tree allometry is a plastic feature, and scaling parameters can vary considerably depending on phylogeny, life strategies, growth conditions and ontogeny. We hypothesized that in multi-layered forests growing on rich sites and driven by stand dynamics without stand-replacing disturbances, light is a primary driver of allometric relationships and that the morphological plasticity of tree species is closely associated with their shade tolerance. We quantified and compared the morphological properties of six species that form a shade tolerance gradient: *Alnus glutinosa* (L.) Gaertner, *Quercus robur* L., *Fraxinus excelsior* L., *Ulmus laevis* Pall., *Tilia cordata* Miller and *Carpinus betulus* L. The relationships between tree height and local stand density as predictors and dbh, crown width, crown length and crown volume as response variables were characterized. We found that in the lower stand layer the values of crown parameters increased with tree height at a lower rate in light-adapted than in shade-tolerant species. Conversely, the response of morphological traits on competition was stronger in light-adapted species than in shade-tolerant species. The ratio of crown width-to-crown length was not associated with light demand. Apart from ash, which demonstrated a different allocation pattern, between-species differences in the slenderness ratio were insignificant. Allometry and sensitivity to competition varied in trees growing in the upper and lower stand layers. Our results indicate that the dichotomy of basic growth strategies of stress tolerance versus stress avoidance is overly simplistic and fails to consider social status and species-specific features such as apical control.

Keywords Tree architecture · Crown morphology · Slenderness ratio · Life strategy · Shade tolerance · Adaptive forestry

Introduction

The organization and functioning of multi-species communities is a major subject of research in plant ecology. In forest ecosystems, the successional status of species often provides the framework for such studies (Rameau et al. 1989). Pioneer species are well-adapted to intense disturbances, which reduce between-tree competition and release a considerable amount of resources, whereas late-successional species are better suited to stable environments. The co-existence of these two basic groups of species relies on the temporal

variability of the environment within a given disturbance regime (Pickett 1980; Frelich and Reich 1999).

The successional status of species is related to their ecological requirement and, in particular, to light demand. Typically, pioneer species are light demanding, whereas late-successional species are able to adapt to very low light intensity (Rameau et al. 1989). It is well recognized that light availability and the successional status of tree species exert a decisive influence on the morphology, inclination and spatial distribution of leaves in tree crowns (Lang et al. 2010; Harja et al. 2012; Osada 2012; Hagemeyer and Leuschner 2019a). Shade-tolerant species are capable of developing shade leaves, which achieve a net carbon gain in low light conditions through reduced leaf construction and maintenance costs, coupled with increased leaf absorptance (Hagemeyer and Leuschner 2019b). These species benefit from investing in leaf area at a lower cost, resulting in a high leaf area-to-leaf mass ratio (Klooster et al. 2007). Shade-tolerant trees produce larger total leaf areas per unit ground surface area (LAI) than light-adapted species due to the formation of

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extended leaf layers with low leaf mass and nearly horizontal leaf orientation in the lower crown (Cutini et al. 1998; Fang et al. 2019). Moreover, shade-tolerant species display high plasticity and pioneer species show low plasticity in leaf traits linked to photosynthetic capacity and carbon balance (Rozendaal et al. 2006).

The morphological and physiological differences between shade-tolerant and light-adapted species are reflected in divergent growth strategies (Claveau et al. 2002; Franceschini and Schneider 2014). Light-adapted species have developed a strategy of escape that consists of minimizing light deficiency by allocating resources towards rapid height growth and moving the foliage up into the upper canopy zone with better light accessibility (Valladares and Niinemets 2008; Poorter et al. 2012). They form elongated crowns with multiple leaf layers to optimize light interception under open canopy conditions. The pattern of development of their architecture favours greater efficiency in stem growth than in shape plasticity (Millet et al. 1999). At high light levels, light-adapted species typically exhibit higher growth rates than shade-tolerant species (Coates and Burton 1999; Gratzner et al. 2004), and some authors have reported higher growth rates in light-adapted species compared to shade-tolerant species at both low and high light levels (Beaudet and Messier 1998; Poorter 1999). Therefore, light-adapted species are often taller than shade-tolerant species for any given diameter (Hulshof et al. 2015). It may be expected that in response to shading, light-adapted trees strongly increase the slenderness (height-to-diameter) ratio of their stems and develop narrow crowns to minimize the self-shading effect and maintenance costs of non-photosynthesizing organs.

In contrast to light-adapted species, shade-tolerant species exhibit a strategy of persistence and stress tolerance. It has been posited that shade-tolerant tree species develop relatively shallow and flat crowns with a monolayer leaf arrangement to optimize light interception (Horn 1971). In shaded environments such tree species can decrease their height increment in favour of horizontally expanding their crowns and root systems. At low light levels this strategy results in a reduced slenderness ratio, the formation of wide crowns and minimization self-shading by decreasing the degree of spatial aggregation of foliage and branching frequency (Niinemets 2010; MacFarlane and Kane 2017).

It can be postulated that the growth strategies of escape and persistence are reflected in the allometry of trees, which, through scaling parameters, describe the proportions between the size of an organism and its organs (Ford 1992; Verbeeck et al. 2019). Nonetheless, the architecture of trees is a very plastic feature and can vary depending on the conditions and environments in which the trees grow (Seidel et al. 2011; Schröter et al. 2012). The allometry and scaling parameters of crowns, stems and roots are largely influenced by stand density and competitive interactions

with neighbouring trees (Vieilledent et al. 2010; Pretzsch and Dieler 2012; Barbeito et al. 2014; Forrester et al. 2017; Owen et al. 2021). Moreover, in mixed-species stands tree allometry can change depending on the local species composition (Bayer et al. 2013; del Río et al. 2019). Depending on their morphological and physiological properties (e.g. leaf area, leaf density, uptake of water and nutrients), tree species exert different competitive impacts on neighbouring trees and contribute differently to overall stand density (Pretzsch and del Río 2019). In relation to forest canopy characteristics, the leaf area index (LAI), which expresses the one-sided green leaf area per unit ground surface area, plays a crucial role (Cutini et al. 1998; Fang et al. 2019). This measure is closely related to light absorption by canopies formed by different tree species and, in mixed-species forests, can be used as a weighting factor describing above-ground light capture and competitive impact. Mixed-species forests frequently exhibit greater canopy packing than monocultures due to vertical stratification (Jucker et al. 2015; Pretzsch 2019). Local tree species diversity usually has a positive effect on total crown volume, potentially driven by enhanced above-ground light capture (Pretzsch 2014; Kunz et al. 2019).

The allometry of trees and growth strategies of tree species also depend on forest structure. The spatial relationships between trees in one-layered and multi-layered stands strongly differ. In the former, tree crowns are concentrated in a single, typically densely-packed stand layer. This causes trees to be exposed to crowding, and their available growth area is strongly limited by the crowns of neighbouring trees (Canham et al. 2004). Within homogeneously structured stands, crown abrasion through wind sway is also likely to spatially restrict lateral expansion (Meng et al. 2006). Trees in one-layered stands under intense competition typically exhibit smaller crown projection areas, shorter crowns, greater height and less taper for a given diameter (Assmann 1970; Pretzsch 2009). Under such conditions light capture may be increased by rapid height growth, moving the crown upwards and forming a monolayer type of crown architecture (Horn 1971). In multi-layered stands the heights of neighbouring trees usually strongly differ and their horizontal crown projections may overlap. The crowns of trees from the lower stand layer are typically suppressed from above but, in contrast to one-layered structures, frequently have more available area for lateral growth. In such a situation the allocation of resources in the lateral development of tree crowns may lead to greater light capture (Canham 1988). The growth conditions of trees growing under crowding in one-layered stands and under suppression and crowding in multi-layered stands may thus differ (Canham et al. 2004).

In contrast to one-layered stands (e.g., Hein and Spiecker 2008; Petritan et al. 2009; Bayer et al. 2013; Juchheim et al. 2017) or uneven-aged forests formed by economically important conifers (e.g., Jaworski and Paluch 1999; Grassi

and Giannini 2005; Stancioiu and O'Hara 2006; Vencurik et al. 2015; Brüllhardt et al. 2020) in which allometric relationships are well documented, in Europe knowledge on the morphological response of broadleaved species growing in mixed-species, uneven-aged and multi-layered forests is still fragmentary (Jucker et al. 2022) and mostly confined to the sapling stage of economically important tree species (e.g., Stancioiu and O'Hara 2006; Collet et al. 2011; Čater and Levanič 2013; Rozenbergar and Diaci 2014). This gap is particularly glaring because of the need to transform monocultures towards resilient ecosystems capable of adapting to rapid and ongoing climatic changes. Achieving this goal on rich sites necessitates the formation of forests of a diversified vertical structure and consideration of a wider range of tree species (Messier et al. 2013; Bravo-Oviedo 2018), including those which in the past were regarded as less economically important (Schmucker et al. 2022). The allometric relationships of tree organisms are critical for their resistance against wind, snow and ice (Gardiner et al. 2016; MacFarlane and Kane 2017). Crown parameters are basic indicators of vitality and health conditions (Roloff 1989). Moreover, they are closely linked with biomass increment and space utilization efficiency (Ishii and Asano 2010; Pretzsch 2014; Jucker et al. 2014; Pretzsch et al. 2022). Thus, knowledge on the morphological properties of tree species growing in different light conditions is crucial for modelling and silvicultural regulation (Pretzsch 2019).

In this paper we analysed the allometric relationships of six tree species with varying shade tolerance growing in multi-layered and multi-species stands. The light-adapted species studied here include alder *Alnus glutinosa* (L.) Gaertner, pedunculate oak *Quercus robur* L. and ash *Fraxinus excelsior* L., while the shade-tolerant species consist of European white elm *Ulmus laevis* Pall., lime *Tilia cordata* Miller and hornbeam *Carpinus betulus* L. We quantified and compared the allometric relationships driving the stem and crown morphology of these species under varying levels of competition. We hypothesized that (H1) the morphological plasticity of trees growing in the shaded environment of the lower stand layer is closely related to species-specific light demand. Specifically, we expected that light-adapted species respond to increasing competition with a stronger increase in height growth and height-to-diameter ratio and a more pronounced reduction in the widths, lengths and volumes of their crowns. In connection with this allocation pattern, we expected that at a similar competition level shade-tolerant species are smaller but have wider, longer and larger crowns, which are better adapted to low light intensities. Given our assumption that allometric relationships are differently influenced by tall competitors and shading from above (suppression) and lateral pressure exerted by trees of a similar social status (crowding), we also hypothesized (H2) that the allometry and response of morphological traits to

competition level is different in trees growing in the lower and upper stand layers.

Methods

Study area, sample plots and field measurements

The study area, located in southern Poland and confined by the geographic coordinates 50.007° N and 50.112° N and 20.352° E and 20.425° E (Table 1), is a flat lowland area (185 m a.s.l.) situated in the fork of the upper Vistula River and the Vistula's southern branch, the Raba River. The parent material consists of interspersed Holocene alluvial deposits on which Cambisols, Gleysols, Stagnosols and Phaeozems have developed (IUSS Working Group WRB 2015). The climatic conditions are typical for the nemoral zone with an increased influence of continental characteristics. The average annual temperature is 8 °C with annual precipitation of 650 mm, 60% of which occurs between May and October. The growing period with daily temperatures above 5 °C is about 230 days (Suliński 1981).

One remarkable feature of the studied stands is the occurrence of several species with varied light demand in different stand layers, as well as the vertical differentiation of stand structure at small spatial scales (Bartkiewicz and Paluch 2019). These mixed-species forests represent sub-continental lowland deciduous forests from the alliance *Carpinion betuli* and *Alno-Padion* (Matuszkiewicz 2001) and variously consist of the following species: oak, alder, hornbeam, lime, ash, European white elm, pine *Pinus sylvestris* L. (the only conifer species) and field elm *Ulmus minor* Miller (species are ranked by their descending proportion in the bulk volume of the stands).

The study was conducted on 17 square sample plots, each covering an area of 0.64 ha (Table 1). The sample plots were selected based on the following criteria: complex vertical stand structure, diversified species composition, the occurrence of tree species with different light demands in the upper and lower stand layers, and no evidence of trees cut in the last 20 years. Field measurements included stem coordinates, tree heights (H), diameters at a height of 1.3 m (DBH), crown lengths (defined as the vertical distance between the tree top and the height of the lowest part of the compact, solid crown with foliage), and crown radii determined in the four cardinal compass directions (N, E, S, W) for all live trees of DBH ≥ 7.0 cm. Crown length was defined by the distribution of leaves rather than the branch bases, meaning branches without leaves in their lowest part were not treated as crowns. Secondary branches formed from epicormic buds were included if the crown was continuous, i.e. if sections without leaves were less than 2 m apart. Morphological parameters were measured to the nearest 0.1 m. Crown radii

Table 1 Location and site characteristics of the sample plots

Plot no.	Location	Soil ^a	Forest assoc. ^b	Stem no. (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Volume (m ³ ha ⁻¹)	Canopy closure ^c (%)	Species composition ^d (%)						
								Al	Oa	As	El	Li	Ho	Others
1	50.093° N 20.364° E	1	1	450	35.5	471	67/94	–	13	–	–	30	50	7
								–	41	–	–	21	13	25
2	50.096° N 20.378° E	2	1	422	31.7	395	73/98	–	4	–	–	26	67	3
								–	26	–	–	39	17	18
3	50.088° N 20.364° E	4	1	448	28.9	358	49/98	–	6	1	–	17	76	–
								–	33	–	–	34	30	3
4	50.083° N 20.389° E	1	2	236	32.6	488	55/95	–	15	–	–	40	45	–
								–	54	–	–	16	30	–
5	50.086° N 20.388° E	1	2	248	30.4	430	47/95	–	11	–	2	48	38	1
								–	48	–	–	34	18	–
6	50.089° N 20.356° E	2	2	344	36.8	473	30/98	10	6	–	–	51	33	–
								18	33	–	–	27	22	–
7	50.007° N 20.418° E	1	2	253	25.6	345	20/89	2	70	–	–	17	6	5
								1	87	–	–	9	3	–
8	50.112° N 20.425° E	1	2	567	27.9	302	59/98	–	29	14	–	14	42	1
								–	65	7	–	17	9	2
9	50.110° N 20.373° E	2	2/3	500	35.6	527	54/99	–	16	10	–	2	71	1
								–	34	46	–	–	17	3
10	50.101° N 20.355° E	2	2/3	436	32.4	471	68/94	–	14	43	–	32	8	3
								–	42	39	–	12	4	3
11	50.109° N 20.352° E	2	2/3	373	30.6	477	39/93	4	19	48	8	–	–	21
								7	48	37	3	–	–	5
12	50.064° N 20.375° E	4	3	317	38.1	497	56/98	15	29	–	6	1	24	25
								14	61	–	6	–	14	5
13	50.103° N 20.381° E	1	3	286	35.8	518	62/93	13	20	4	38	4	20	1
								16	57	–	22	1	4	–
14	50.079° N 20.366° E	1	3	344	35.3	464	47/90	37	8	–	39	1	15	–
								36	19	–	35	–	10	–
15	50.079° N 20.375° E	1	3	278	41.4	577	68/93	50	4	–	23	8	12	3
								46	22	–	21	2	9	–
16	50.082° N 20.369° E	1	4	583	35.4	406	52/96	28	3	–	31	15	10	13
								52	11	–	21	8	5	3
17	50.008° N 20.417° E	1	4	305	33.5	464	37/89	54	27	–	–	2	7	10
								25	72	–	–	–	2	1

^aAccording to IUSS Working Group WRB (2015): 1—Stagnosol, 2—Mollic Cambisol, 3—Cambisol, 4—Gleysol

^bAccording to Matuszkiewicz (2001): 1—oak-hornbeam (*Tilio-Carpinetum typicum*), 2—oak-hornbeam—wet variant (*Tilio-Carpinetum stachyotosum*), 3—riparian forest (*Ficario-Ulmetum minoris*), riparian forest—wet variant (*Fraxino-Alnetum*)

^cRatio of horizontal crown projection area (without overlapping crowns)-to-ground area. Upper layer trees/all trees together. The method of toroidal shifts was used to mitigate border effects (Diggle 1983)

^dPer cent of stem number and basal area are given in the upper and lower row, respectively. Species are ordered according to increasing shade tolerance: Al—alder *Alnus glutinosa* (L.) Gaertner, Oa—oak *Quercus robur* L., As—ash *Fraxinus excelsior* L., Li—lime *Tilia cordata* Miller, Ho—hornbeam *Carpinus betulus* L., El—elms *Ulmus laevis* Pall. and *Ulmus minor* Miller, others: Scots pine, wild cherry, sycamore maple, Norway maple, bird cherry

were measured by a two-person team that first determined the cardinal directions using a compass and then projected the crown margins onto them using a spirit level. For better visibility, crown radii and tree heights were measured in the leafless period (dead and live branches were distinguished based on the presence of buds).

In the entire dataset, the species' percentages in the total stem number were as follows: hornbeam 34, oak 21, lime 17,

alder 12, ash 8, elm 7 and other minor species 1%. On the individual sample plots, the stem numbers ranged between 236 and 583 stems/ha, with a mean value of 376 stems/ha. The corresponding values for stand basal area were 25.6, 41.4 and 33.4 m² ha⁻¹, and for stand volume 302, 577 and 451 m³ ha⁻¹, respectively. Exact data on species compositions, stem numbers, basal areas, stand volumes and canopy closure are given in Table 1. The DBH distributions

represent multi-modal, negative exponential or rotated sigmoid types (Bartkiewicz and Paluch 2019). The stands are uneven-aged with age variation—estimated between 2000 and 2015 by counting the rings on stumps of the largest and smallest trees in the adjacent harvested stands—exceeding 150 years (unpublished data).

Data analysis

The analysis included six species, each represented by more than 50 individuals growing in different stand layers. According to increasing shade-tolerance, these species can be ordered as follows: alder, oak, ash, elm, lime and hornbeam (Burschel and Huss 1997; Jaworski 2011). The set of morphological features comprised DBH, height and crown parameters: length, width and volume. The models of tree crowns and stand canopy on the sample plots were modelled in a three-dimensional space with a $0.1 \times 0.1 \times 0.1$ m resolution (unit = 0.001 m^3) by using Visual Basic for Applications programming language. The models of tree crowns were modelled as four quarters of ellipsoids with the semi-axes corresponding to the crown lengths and crown radii measured in the field. It was assumed that tree crowns are widest at a relative crown length of 50%. If the tree crowns overlapped in the three-dimensional model of the stand canopy, the shared unit was assigned to the more shade-tolerant species, or—if both individuals represented the same species—to the tree with a lower $dist/BA$ ratio, where BA is basal area and $dist$ the horizontal distance between the given unit and the unit representing the stem basis of the respective tree.

The surroundings of trees were characterized by a competition index based on a formulation by Hegyi (Biging and Dobbertin 1995) modified by the authors:

$$CI_i = \sum (DBH_j rLAI_j) / (DBH_i (dist_{ij} + 1)),$$

where the summation is over all neighbours of the i th object tree, $rLAI$ is the relative species-specific leaf area index and $dist_{ij}$ is the horizontal distance between the i th object tree and its j th neighbour. All trees located within the zone of potential crown overlap were regarded as neighbours of the object tree i . This zone was defined as the sum of potential crown radii dependent on tree DBHs, $b_0 \ln(DBH_i) - b_1 + b_0 \ln(DBH_j) - b_1$, with parameters $b_0 = 2.570$ and $b_1 = 1.969$. The parameters were derived from the empirical dataset by fitting the function $y = b_0 \ln(x) - b_1$ to the 95th quantiles of the crown radii determined in 5-cm-wide DBH classes (Fig. S1, online supplementary material). Because light is a primary driver of competitive interactions in forest communities and light absorption is closely linked with LAI (Fang et al. 2019), we used the relative species-specific LAI as a weighting factor to account for the different competitive power of trees species. Small trees

of shade-tolerant species growing in the neighbourhood of a subject tree may have a disproportional impact on the morphological characteristics of its crown. The incorporation of a weighting factor, closely related to species-specific foliage density, mimicked asymmetric above-ground competition between species of different light demands and hence increased the sensitivity of the competition index to variation in local species composition both in horizontal and vertical mixtures. Based on the literature (Eliaš et al. 1989; Eschenbach and Kappen 1996; Čermak 1998; Šrámek and Čermak 2012), we assumed the following LAI values: alder 2.5, oak and ash 3.0, field and white elm 4.0, lime 5.0 and hornbeam 5.5. Given that hornbeam has the highest LAI among the considered six taxa, the relative values were as follows: alder 0.45, oak and ash 0.55, elm 0.73, lime 0.91 and hornbeam 1.00. For other minor species (with percentages of 0 to 5% in the stand basal areas, see Table 1), we used the relative values calculated on the basis of LAI values taken from the literature or assigned to species of similar light demand: Scots pine 0.27, wild cherry 0.55, sycamore and Norway maple 0.73, and bird cherry 0.91 (Stenberg et al. 1994; Soudani et al. 2002). To minimise border effects, only trees located more than 10 m from the nearest border of the sample plot were treated as object trees. In addition, we used a toroidal shifts method for quantification of local surroundings of trees farther away from the border (Diggle 1983).

The analysis was carried out separately for trees growing in the lower and upper stand layer. As a threshold value between these layers, we used a height equal to 80% of the maximum tree height registered on the sample plot. Given the large crowns of the largest trees on the sample plots, the threshold value used here resulted in a stratification very close to that recommended by Assmann (1970), which is based on a mean height of trees with a total horizontal crown projection of at least 1000 m^2 per ha and a threshold value the same as in our study, i.e. 80%. Trees forming the upper stand layer were treated separately because for a prolonged period, they have been growing without suppression by taller competitors in conditions similar to low-stocked one-layered stands, and their allometry may be different from that of trees growing in the lower stand layer. In total, the analysis included 1887 trees from the lower stand layer (166–763 for single species) and 335 trees from the upper stand layer (20–140 for single species except for hornbeams) (Table S1, online supplementary material). Hornbeams rarely reach heights above 27 m in the studied stands. Because of the small number of sampled hornbeams from the upper stand layer (only 6 individuals), results for this species were displayed only for completeness of illustration.

The effect of tree height and local competition on the morphological features (DBHs, crown lengths, widths and volumes, and crown width-to-crown length ratio) of the

six species studied was tested using general linear models (general multivariate regression models) with the species as the categorical variable. We used tree height and not DBH as a predictor variable because in multi-species stands this parameter directly describes the social status of trees. In preliminary analyses we also developed models which, by means of additional parameters, took into account plot-specific effects (stand basal area and plot code as a categorical variable) or the interaction of tree height and competition level.

Although our dataset was structured hierarchically, preliminary analyses showed that the effects attributed to the sample plot, soil and forest communities are insignificant compared to those related to local stand density and species composition, captured by the competition index used in the calculations. Therefore, the tested models incorporated only fixed effects and had the simple general form $Y_i = b_0 + b_1H + b_2CI + e$, where Y denotes a response variable of the i th species, H is tree height, CI is competition index, b_0 is a non-specific intercept, b_1 and b_2 are species-specific slope parameters describing the effect of height and competition, and e is the model error. Logarithm transformations of DBHs, crown widths and crown volumes were used to linearize the model and minimize heteroscedasticity. Considering the shape of the relationship, for the crown width-to-crown length ratio, the model was $Y_i = b_0 + b_1\ln H + b_2CI + e$. The slope parameters b_1 and b_2 were interpreted as quantities describing species-specific allometric relationships between tree height and response variables dependent on competitive pressure. To test between-species differences in the slope parameters b_1 and b_2 , we applied Welch's test with Holm-Bonferroni correction and a desired overall alpha level of 0.05 for multiple comparisons. In statistical computations we used Statistica software (ver. 13.3, Statsoft Inc., USA).

Results

Between-species variation in DBHs, heights and competition indices

On the sample plots the largest oaks, ashes and elms reached DBHs above 100 cm, limes 80 cm, and hornbeams and alders 60 cm (Table 2). The value of mean DBH was highest for oak (40.7 cm) and lowest for hornbeam (16.2 cm). The tallest trees were ashes (40.7 m), and the shortest were hornbeams (29.3 m). The maximum heights recorded for alders, oaks, elms and limes ranged between 32.2 and 34.8 m. Data on the variation in morphological characteristics of the individual species represented in the dataset are given in Table 2 and the online supplementary material (Table S2 and Fig. S2–S5). The shade-tolerant

species were capable of tolerating much higher competitive pressure than the light-adapted species. In terms of the competition index used in our study, the values of the 95th percentile registered for single species were as follows: alder 3.8, oak 4.7, ash 5.5, elm 5.7, lime 5.9 and hornbeam 6.7 (Table 2 and Table S2, Fig. S6, online supplementary material).

Because preliminary analyses showed that the incorporation of plot-specific effects, stand basal areas or the interactions of tree height and competition level into the models of DBHs and crown characteristics did not significantly improve their fits (by no more than 0.04 in terms of adjusted R^2 statistics, see Tables S3 and S4 in online supplementary material), below we refer to the results obtained for the simplest models based on tree height and competition level.

Effect of tree height and competition on DBH

Based on the respective regression coefficients, the relationship between height and DBH in the lower stand layer showed considerable differences between ash and the other species (Fig. 1a). Ashes allocated considerably more resources to height growth than to DBH growth, and at a given height had smaller DBHs and hence higher slenderness ratios than the other species (Figs. 1c, d; 2a, b). Among the species other than ash, the differences in DBHs of trees of comparable heights were not statistically significant (Fig. 1a, c, d). In the upper stand layer, the height-DBH relationship was similar in ashes and the other species (Fig. 1a, c, d). Given comparable height and competitive pressure, in the upper stand layer elms and oaks had the largest DBHs and alders the smallest (Fig. 1c, d).

The negative values of the regression coefficients indicate that trees growing under stronger competition generally have smaller DBHs and hence a greater slenderness ratio than trees growing under weaker competition (Fig. 1b). In the lower stand layer, this effect was not clearly correlated with the shade tolerance of the species; in the upper layer shade-tolerant species tended to exhibit a stronger response to the competition level, although in a statistical sense the between-species differences were not always significant (Fig. 1b, e, f).

Small trees of all species growing in the lower stand layer allocated relatively fewer resources to DBH growth than to height growth compared to larger trees from the upper layer, but the diameter growth of small trees was less sensitive to competition (Fig. 1b). Trees of a height of 10–15 m had the greatest slenderness ratio, except for ashes, in which this characteristic attained maximum values at a height range of 15–20 m, depending on the competition level (Fig. 2a, b).

Table 2 Variation in the analysed morphological features (trees from the upper and lower stand layers pooled together)

Characteristics		Alder	Oak	Ash	Elm	Lime	Hornbeam
Number of trees		283	376	190	203	401	769
DBH (cm)	Mean	35.5	40.7	20.9	22.8	24.5	16.2
	SD	12.3	25.3	23.2	20.2	15.9	11.4
	Min	7.5	7.5	7.0	7.0	7.0	7.0
	Max	68.5	148.5	112.5	108.5	85.0	64.5
Height (m)	Mean	24.0	22.5	19.0	16.7	17.4	14.7
	SD	5.0	7.0	7.1	6.3	6.3	4.5
	Min	6.6	3.5	9.2	6.2	3.8	4.3
	Max	32.2	34.8	40.7	33.0	32.6	29.3
Crown length (m)	Mean	9.2	9.1	9.2	9.6	10.2	9.1
	SD	3.0	4.2	4.1	4.3	4.2	4.0
	Min	1.5	1.0	2.1	1.2	1.1	1.0
	Max	18.3	23.1	24.1	18.6	23.5	25.0
Crown width (m)	Mean	6.6	8.7	6.2	7.3	8.2	7.7
	SD	1.6	4.3	4.1	2.6	2.9	2.8
	Min	2.5	2.3	1.8	3.4	2.1	3.0
	Max	12.0	22.6	24.2	21.6	20.7	18.8
Crown volume (m ³)	Mean	226	555	390	357	461	392
	SD	164	675	880	453	515	534
	Min	4	3	3	17	4	5
	Max	1030	4517	6133	4104	4051	3387
Height-to-DBH ratio (%)	Mean	73	69	129	94	83	108
	SD	18	26	40	30	25	32
	Min	41	21	30	29	23	33
	Max	141	141	214	159	158	215
Crown length-to-height ratio (%)	Mean	39	40	48	58	59	61
	SD	10	12	11	16	16	16
	Min	11	9	15	19	14	14
	Max	70	74	82	89	97	94
Crown width-to-tree height ratio (%)	Mean	29	38	31	46	50	55
	SD	9	13	9	13	14	16
	Min	12	14	13	23	23	21
	Max	95	114	71	104	112	125
Crown width-to-crown length ratio (%)	Mean	78	104	68	88	89	96
	SD	33	43	25	44	36	47
	Min	24	25	33	39	38	41
	Max	350	396	149	438	377	450
Competition index	Mean	1.75	2.79	1.41	3.18	2.92	3.90
	SD	0.74	1.26	0.87	1.78	1.75	1.84
	Min	0.43	0.39	0.23	0.36	0.43	0.46
	Max	4.78	7.50	5.90	9.92	10.46	11.72

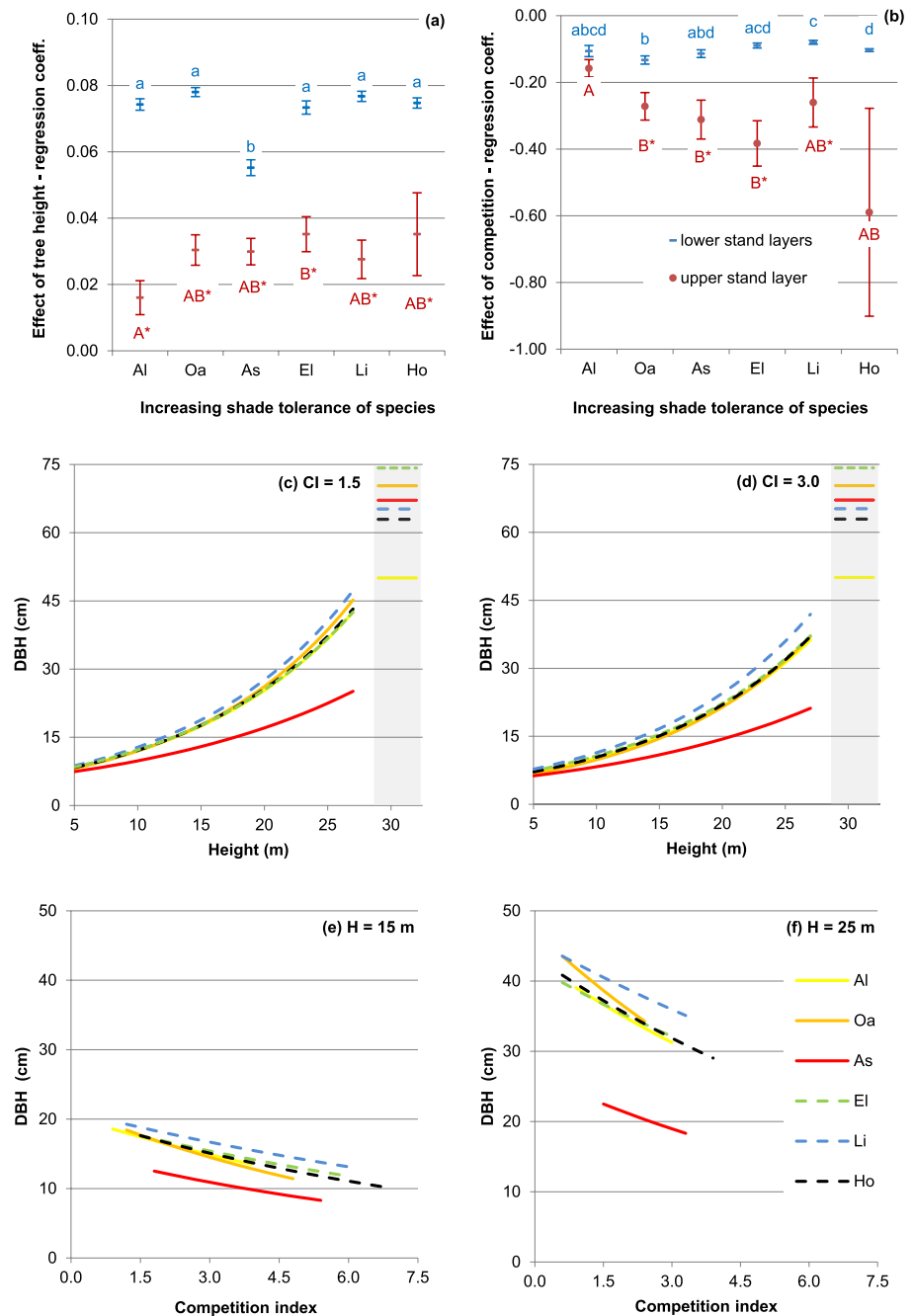
Tree species are ordered according to increasing shade tolerance

Effect of tree height and competition on crown length

Shade-tolerant species growing in the lower and, less distinctly, also in the upper stand layer had longer crowns than light-adapted species (Fig. 3c, d). In general, the crowns of trees growing in less competitive surroundings were longer

than those of trees growing in more competitive surroundings (Fig. 3e, f). The lower values of the respective regression coefficients show that the response of crown lengths to competition was stronger in light-adapted alders and oaks than in shade-tolerant limes and hornbeams. We did not find consequent differences in the response to competition between trees from the lower and upper stand layers

Fig. 1 Relationships between tree height (H), competition index (CI) and DBH: **a** regression coefficients describing species-specific relationships between height and DBH (\pm SE); **b** regression coefficients describing species-specific relationships between competition level and DBH (\pm SE); **c, d** modelled DBHs at a given constant competition level (weaker competition CI = 1.5, stronger competition CI = 3.0) and changing tree heights; **e, f** modelled DBHs at a given constant height (H = 15 or H = 25 m) and changing competition level. Notes: ¹Species for which we did not find significant differences were marked by the same letters in **ab**. Trees from the upper and lower stand layer are marked by upper case and lower case letters, respectively. If significant differences were found between trees of the same species from the upper and lower stand layer, this is marked by an asterisk added to the lower case letters. The values of the regression coefficients and the errors between empirical and modelled morphological characteristics are given in Tables S5–S7 (online supplementary material). ²Shaded areas in **cd** show DBHs modelled for the upper layer trees growing under average competition pressure (H = 30 m, CI = 0.8). ³Species-specific ranges of competition intensity displayed in **ef** correspond with the values observed in the studied stands. ⁴Species according to increasing shade tolerance: *Al* alder, *Oa* oak, *As* ash, *El* elm, *Li* lime, *Ho* hornbeam



(Fig. 3b). Also, the relative crown lengths well reflected the light demand of the studied species: the light-adapted species alder and oak had shorter crowns than the shade-tolerant species (Fig. 4a, b).

Effect of tree height and competition on crown width

In the lower stand layer, the slope coefficients for the height-to-crown width relationship attained the highest values for shade-tolerant species lime and hornbeam but

also for light-adapted oak (Fig. 5a). In the lower stand layer, light-adapted species alder, ash and oak had the narrowest crowns among the studied species. In the upper stand layer, however, oaks and ashes had similarly wide crowns as shade-tolerant limes or mid-tolerant elms (Fig. 5c, d). Thus, the crown widths of ashes and oaks growing in the lower and upper stand layers strongly differed; they were much wider in trees of dominant height and social position than in trees in the lower stand layer. The negative values of the slope coefficient for the crown width-competition level relationships indicate that crown

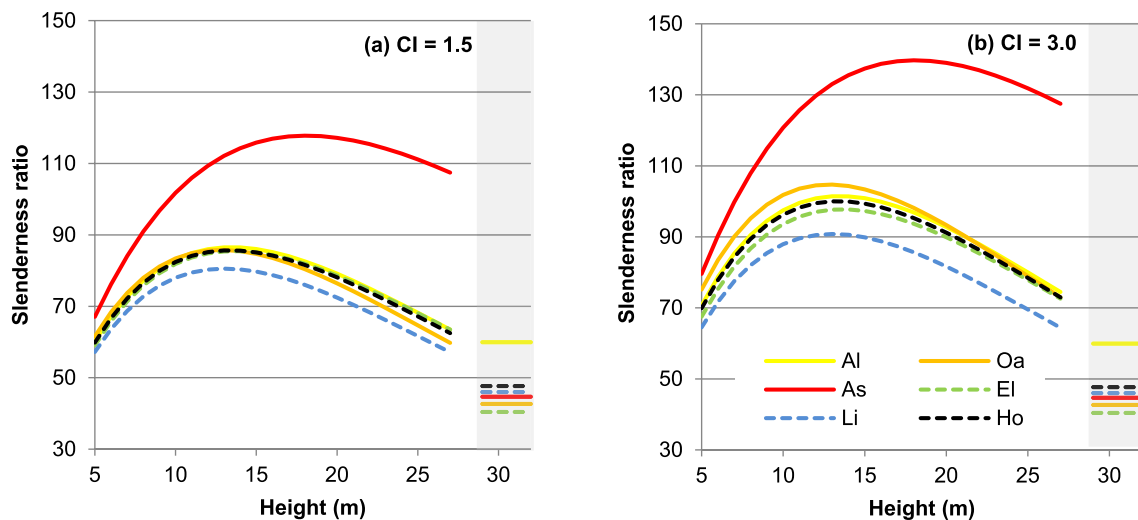


Fig. 2 Height to DBH (slenderness) ratio depending on tree height and competition level (CI). *Notes:* Shaded areas show the ratios modelled for upper layer trees growing under average competition pressure ($H = 30$ m, $CI = 0.8$)

widths decreased with increasing competition (Fig. 5b). In the lower stand layer, this effect was stronger in light-adapted species than in shade-tolerant species (Fig. 5b, e, f), but in the upper layer this tendency was not discernible and we did not find statistically significant between-species differences (Fig. 5b). The crown width-to-height ratio was greatest in small trees and decreased exponentially with tree height (Fig. 6a, b). This indicates that crown widths increase at a slower rate than tree heights.

The crown width-to-crown length ratio was affected by tree height, species and competition intensity (Fig. 7a, b). This characteristic, however, did not reflect the light demand of the species; in the lower stand layer, light-adapted alders and oaks had the most flattened crowns, mid shade-tolerant ashes had the least flattened crowns, and shade-tolerant species exhibited intermediate properties. In the upper stand layer, oaks and ashes had the highest crown width-to-crown length ratios, and alders and elms the lowest (Fig. 7c, d).

Depending on species and tree size, competition level exerted a different influence on the shape of crowns (Fig. 7b, e, f). In general, in the lower stand layer, taller trees growing in a more competitive neighbourhood were characterized by lower values of the crown width-to-crown length ratio, i.e. they had less flat crowns (Fig. 7e, f). Nonetheless, in the lower stand layer, we found no clear relationship between competition level and the crown width-to-crown length ratio in small alders, elms and hornbeams. In the upper stand layer, the relationships between tree size, competition level and the shape of crowns were weaker than in the lower stand layer and statistically not significant for the majority of the species (Fig. 7a, b).

Effect of tree height and competition on crown volume

In the lower stand layer, the slope coefficients describing the relationship between tree height and crown volume clearly increased with the shade tolerance of the species (Fig. 8a). This indicates that shade-tolerant trees growing in the lower stand layer formed crowns of a larger volume than light-adapted trees. The difference between both groups of species increased with tree heights (Fig. 8c, d). In the upper stand layer, this ranking became less distinct, and light-adapted species oak and ash had similar crown volumes as shade-tolerant elms and limes (Fig. 8c, d).

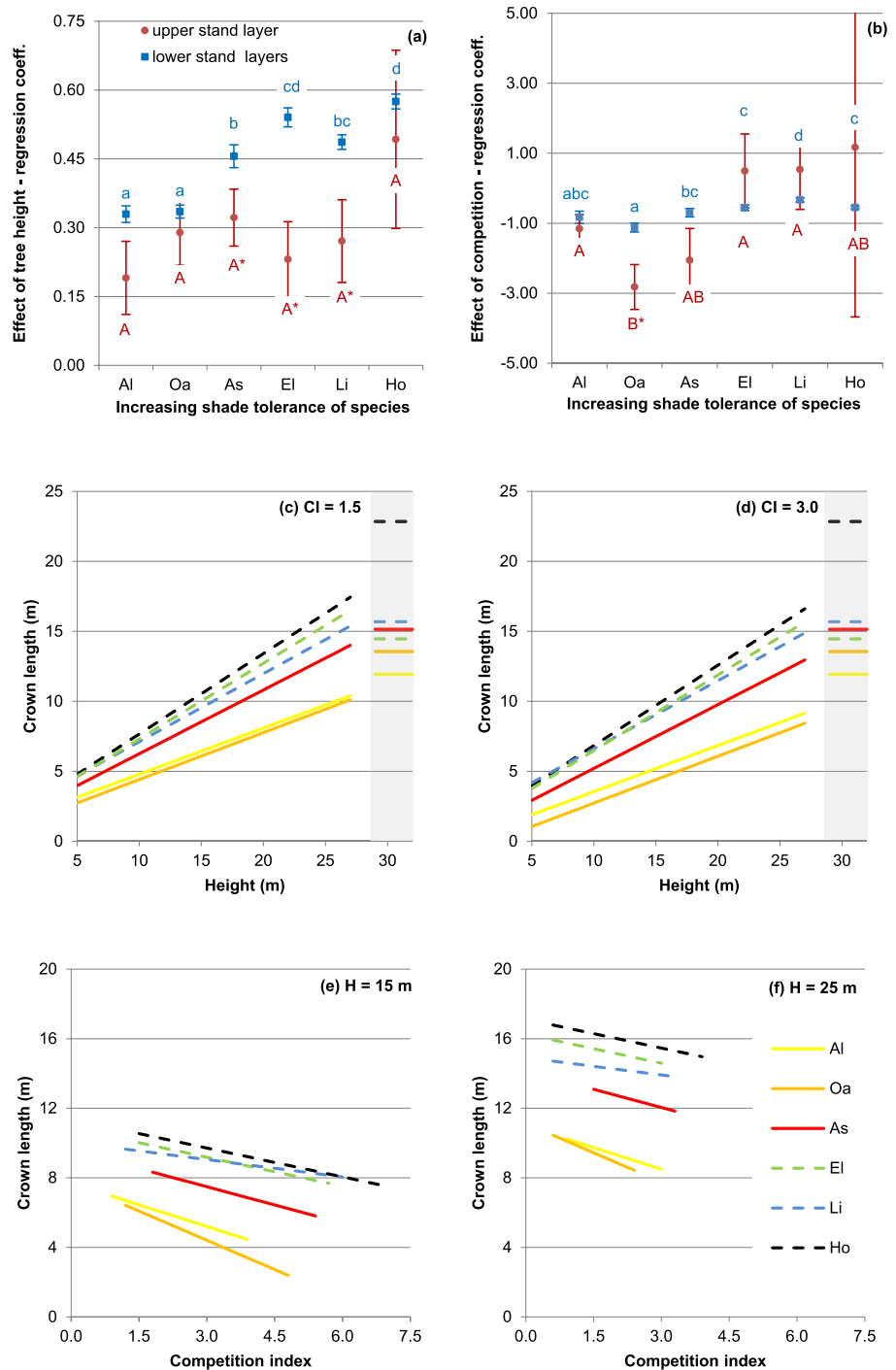
The negative values of the slope coefficients indicate that trees growing under stronger competition had smaller crowns (Fig. 8b). The response to competition was stronger in light-adapted species than in shade-tolerant species, and it was also stronger in tall trees compared to short trees in the lower stand layer (Fig. 8b, e, f).

Discussion

Results concordant with the hypothesized traits of light-adapted and shade-tolerant species

We hypothesized that light-adapted species adopt a strategy of stress avoidance (escape) and, in response to increasing competition, prioritize resource allocation towards height growth while reducing crown width to minimize self-shading. Conversely, shade-tolerant species are expected to decrease the slenderness ratio and develop wider, longer

Fig. 3 Relationships between tree height, competition intensity and crown length: **a** regression coefficients describing species-specific relationships between height and crown length (\pm SE); **b** regression coefficients describing species-specific relationships between competition level and crown length (\pm SE); **c, d** modelled crown lengths at a given constant competition level (weaker competition CI=1.5, stronger competition CI=3.0) and changing tree heights; **e, f** modelled crown lengths at a given constant height (H=15 or H=25 m) and changing competition level. Notes as per Fig. 1



and larger crowns that are better adapted for light capture in shaded environments. Overall, our results confirm that light demand is an important factor shaping allometric relationships in these two functional groups of species. Specifically, at a given height the shade-tolerant species growing in the lower stand layer had crowns of greater width, length and volume compared to the light-adapted species. The lengths, widths and, in particular, volumes of crowns increased at different rates with tree height, with shade-tolerant species

showing a steeper increase compared to light-adapted species. Moreover, in alders and oaks the response of the crown parameters to competition was generally stronger than in elms, limes and hornbeams, which also corroborates our working hypotheses.

The longer crowns of shade-tolerant species can be attributed to decreasing light availability with the depth of the forest canopy. As leaves and branches become a net carbon drain, they are shed by the tree (Ackerly 1999; Poorter

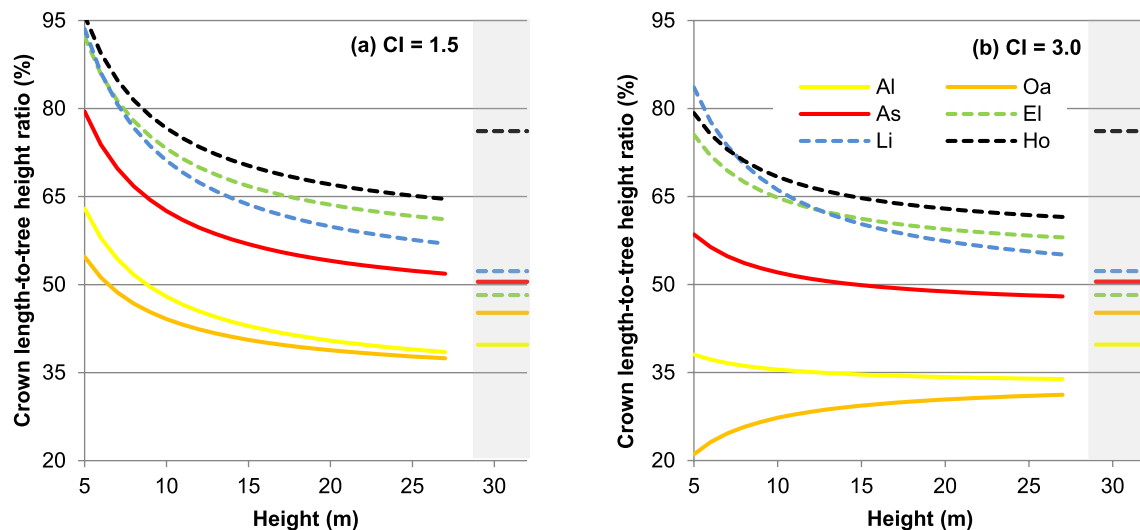


Fig. 4 Crown length-to-tree height ratio depending on tree height and competition level (CI). *Notes:* Shaded areas show the ratios modelled for upper layer trees growing under average competition pressure (height=30 m, CI=0.8)

et al. 2012). Therefore, shade-tolerant species are capable of maintaining branches located deeper within the canopy compared to light-adapted species. The overall crown architecture is the result of stem and branch growth and losses over time (Mäkelä and Valentine 2006). In the studied stands there were no evident signs of intense disturbances over the last two to three decades, such as newly formed gaps or stumps of harvested large-diameter trees, indicating a period of biomass accumulation. Tree height, crown base height and lateral crown expansion are morphological features that are highly sensitive to changes in local stand density (Juchheim et al. 2017; Georgi et al. 2018). Therefore, we can assume that the registered crown characteristics correspond well to the levels of competitive pressure observed in the stands.

Longuetaud et al. (2013) also found a stronger response in the crown morphology of light-adapted oak compared to shade-tolerant beech in oak-beech forests in France, indicating that light-adapted species exhibit greater crown shape distortion under competition related stress. Similar patterns in the crown morphology of light-adapted and shade-tolerant species have frequently been reported in mixed-species forests in the temperate zone (Sumida and Komiyama 1997; Osada et al. 2004; Dietze et al. 2008; Ray et al. 2011), including European species *Carpinus betulus*, *Sorbus torminalis*, *Ulmus laevis* and *Acer campestre* (Schmucker et al. 2022). However, there have been studies that did not confirm a positive relationship between shade tolerance and crown width and length (Hemery et al. 2005; Thorpe et al. 2010; Iida et al. 2011). The discrepancies in the results of these studies can be attributed to the fact that allometric relationships also are significantly influenced by factors other than light demand, such as phylogeny, wood density, branching

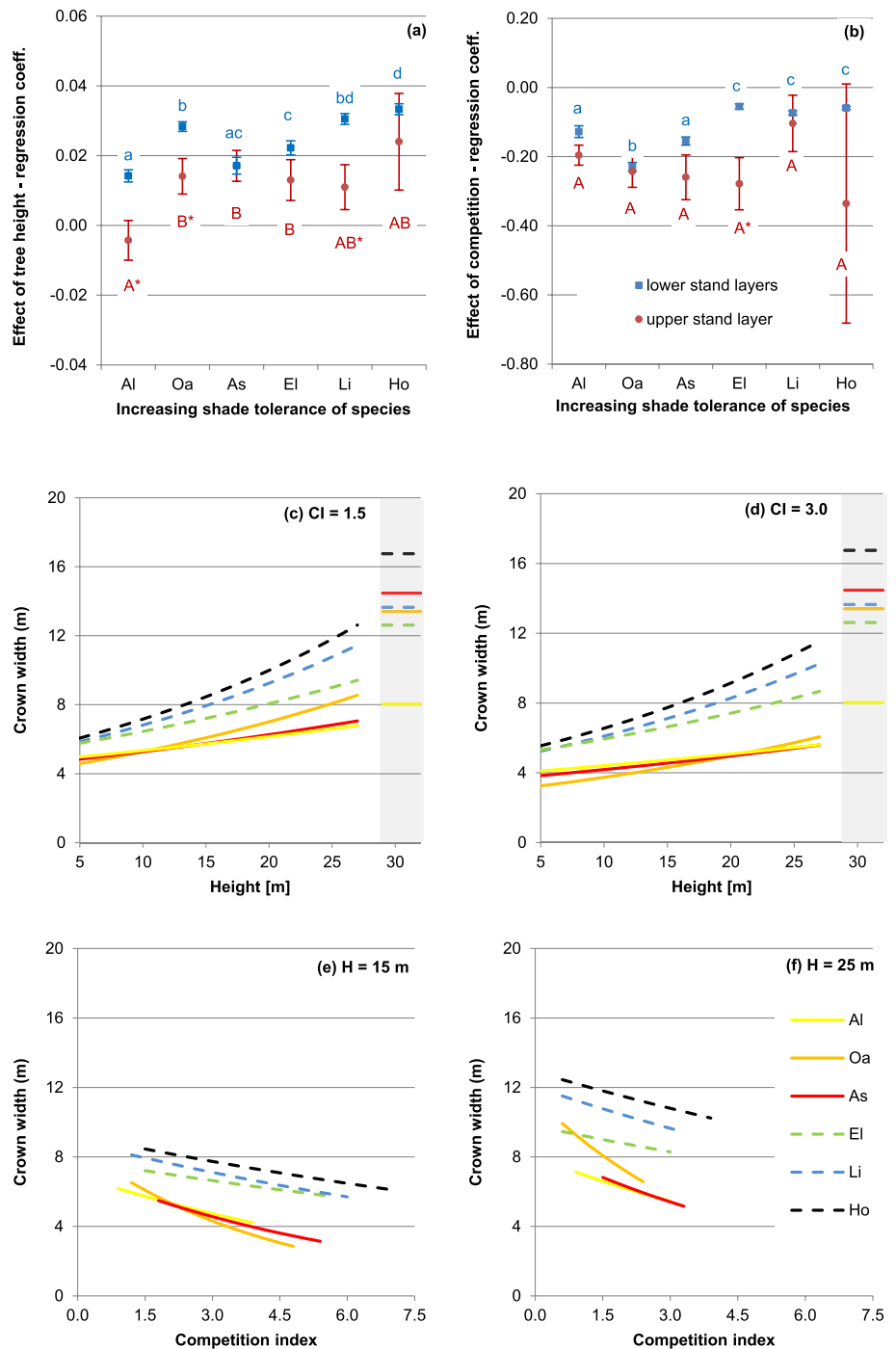
system and apical control, ability to form secondary modules from epicormic buds and resistance to damage, and mechanistic interactions between tree crowns (Hajek et al. 2015). Moreover, empirical material was collected on trees growing in different light environments, including isolated individuals in open areas (e.g., Hemery et al. 2005).

The literature also discusses the relationships between tree allometry and mechanical wood properties (Dietze et al. 2008; Aiba and Nakashizuka 2009; Poorter et al. 2012). In general, greater wood strength allows a tree species to reach greater heights and develop wider and shorter crowns. However, in the case of the species examined in our study, the ranking of the flexural (bending) strength of their wood is as follows: hornbeam (107 MPa), ash (99 MPa), oak (93 MPa), lime (90 MPa), elm (87 MPa) and alder (85 MPa) (Kotwica 2011; Lis and Lis 2013). This ranking does not clearly correspond with the light demand of the species or with the crown sizes of trees growing in the lower stand layer; oaks and ashes characterized by the high wood strength formed narrower crowns compared to limes.

Results not concordant with the hypothesized traits of light-adapted and shade-tolerant species

Not all of the results aligned with the hypothesized traits of light-adapted and shade-tolerant species and the respective strategies of escape and persistence. Contrary to our working hypothesis, which assumed a greater allocation of resources in height growth than DBH growth in light-adapted species, the differences in the slenderness ratio were insignificant (except for ash). Trees growing under stronger competition generally had smaller DBHs and thus greater height-to-DBH ratios than trees growing under weaker competition.

Fig. 5 Relationships between tree height, competition intensity and crown width: **a** regression coefficients describing species-specific relationships between height and crown width (\pm SE); **(b)** regression coefficients describing species-specific relationships between competition level and crown width (\pm SE); **c, d** modelled crown widths at a given constant competition level (weaker competition CI = 1.5, stronger competition CI = 3.0) and changing tree heights; **e, f** modelled crown widths at a given constant height (H = 15 or H = 25 m) and changing competition level. Notes as per Fig. 1



However, in the lower stand layer, we did not find a clear relationship between the response to competition and the shade tolerance of tree species. This contradicts findings from other regions of the world that have reported increased allocation of resources towards height increment in light-adapted species (Dietze et al. 2008; Aiba and Nakashizuka 2009; Poorter et al. 2012). We attribute these discrepancies to the relatively high stand basal area (between 25.6 and 41.4 m² ha⁻¹) and closed canopies (89–99%) in our stands.

As a consequence, the height growth of trees from the lower stand layer may strongly depend on available space and their ability to vertically expand in the presence of competitors. This factor also may override species-specific effects linked to growth strategies.

Another allometric feature that does not correspond with the light demand of tree species and our working hypotheses is the crown width-to-crown length ratio. We assumed that flat crowns would better correspond with the persistence

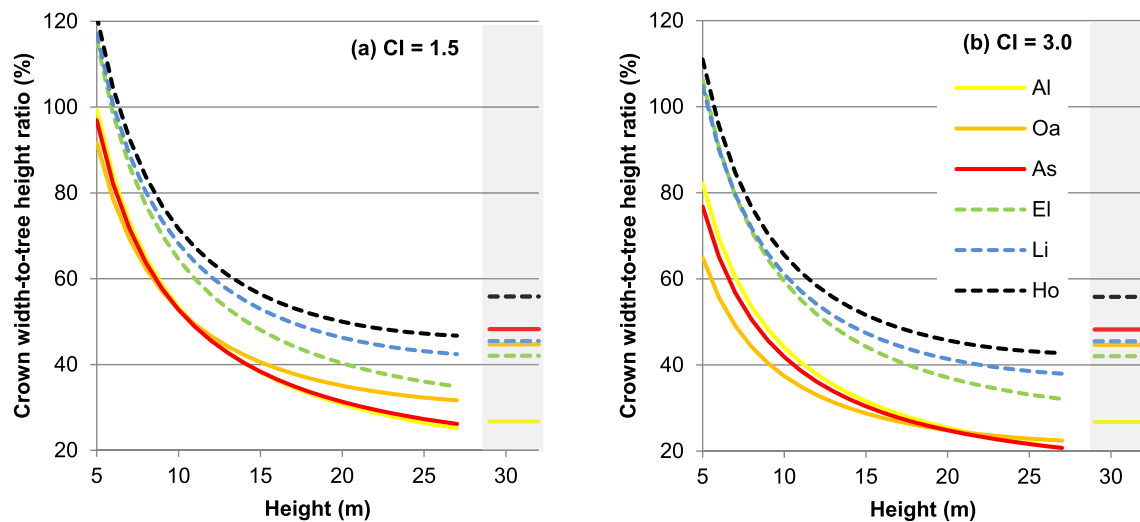


Fig. 6 Crown width-to-tree height ratio depending on tree height and competition level (CI). *Notes:* Shaded areas show the ratios modelled for upper layer trees growing under average competition pressure (height=30 m, CI=0.8)

strategy associated with shade-tolerant species because this crown shape facilitates light capture and minimizes self-shading (Horn 1971; Niinemets 2010). This morphological response pattern is well-documented in shade-tolerant conifers (Leibundgut 1945; Gratzner et al. 2004; Vencurik et al. 2015; Hitsuma et al. 2015). However, in the lower layer of the studied stands, light-adapted alders and oaks had the most flattened crowns, mid shade-tolerant ashes had the least flattened crowns and shade-tolerant species showed intermediate properties. A similar conclusion also applies to trees in the upper stand layer. Therefore, the observed crown width-to-crown length ratios do not reflect the light demand of the species.

Ash least of all fitted into the two hypothesized growth strategies. In the upper layer ashes formed moderately long but wide crowns, similar to other light-adapted species with strong wood. However, ashes growing in the lower stand layer had a high slenderness ratio, significantly greater than that of all other species. They formed crowns as narrow as light-adapted species and as long as shade-tolerant species. This indicates that ash exhibits a distinct growth strategy rather than intermediate features of the two hypothesized strategies. This divergence may be attributed to the strong apical control of this species. Broadleaf species tend to have weak apical control, which promotes branching (Wilson 2000) at the expense of the terminal growth of the main stem. However, the exceptional ability of ashes to vertically expand has been emphasized by Hein and Spiecker (2008). Similar properties are also exhibited by sycamore (Hein and Spiecker 2008; Petritan et al. 2009). This suggests that morphological response is not only related to shade tolerance but also to species-specific apical control, which are weakly correlated features. While many light-adapted species often

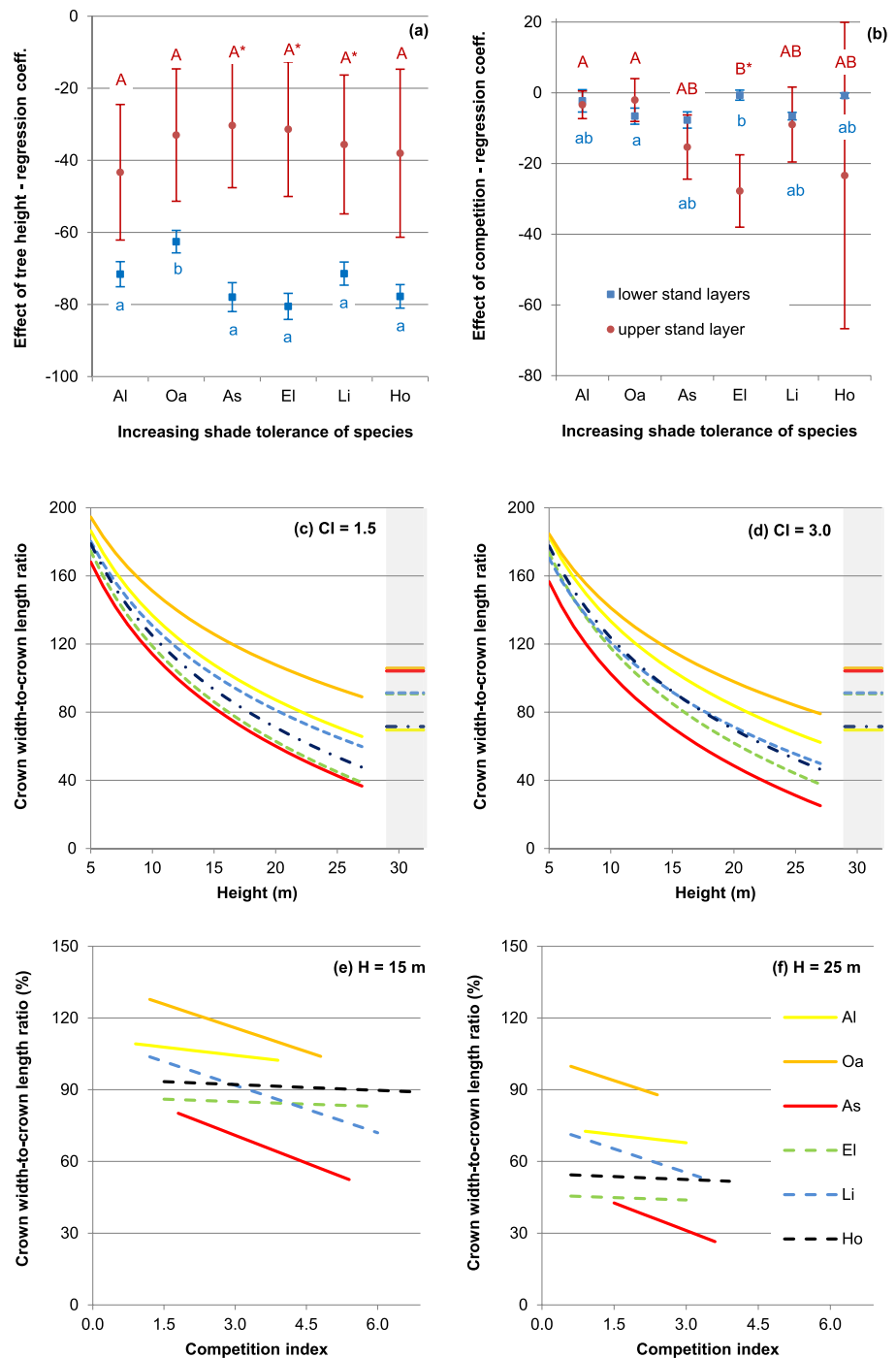
display strong apical dominance (e.g., poplars and alders), the opposite feature may characterize both shade-tolerant species (beech) and light-adapted species (oak) (Szwedkowska and Szweykowski 1996; Schütz 2003).

Lower versus upper layer trees

It is generally assumed that broadleaved trees develop relatively short and wide crowns when they reach the upper canopy layer (Blanchard et al. 2016). Indeed, the results obtained in our study demonstrate considerable differences in the allometry of trees growing in the upper and lower stand layers. DBHs and crown volumes were less closely related to tree heights in individuals from the upper stand layer compared to individuals from the lower stand layer. However, the DBHs of trees in the upper stand layer were more sensitive to competition. We attribute these findings to the more heterogeneous light conditions in the upper zone of the canopy, which promote greater variation in tree architecture (Juchheim et al. 2017; Georgi et al. 2018). In the lower stand layer, where competition is intense, trees generally allocate more resources to height growth than to DBH growth and crown development (Messier and Nikinmaa 2000; Xiang et al. 2021).

At the between-species level, the differences in the allometry of trees growing in the upper and lower stand layers were particularly striking for the slenderness ratio of ashes and for the crown widths and crown volumes of oaks and ashes. In the case of both characteristics, the rankings of these light-adapted species were low in trees from the lower stand layer and relatively high in trees from the upper stand layer. Although oak and ash are light-adapted species, the observed effect does not appear

Fig. 7 Relationships between tree height, competition intensity and crown width-to-crown length ratio: **a** regression coefficients describing species-specific relationships between height and crown width-to-crown length ratio (\pm SE); **b** regression coefficients describing species-specific relationships between competition level and crown width-to-crown length ratio (\pm SE); **c, d** modelled crown width-to-crown length ratio at a given constant competition level (weaker competition CI = 1.5, stronger competition CI = 3.0) and changing tree heights; **e, f** modelled crown width-to-crown length ratio at a given constant height (H = 15 or H = 25 m) and changing competition level. Notes as per Fig. 1

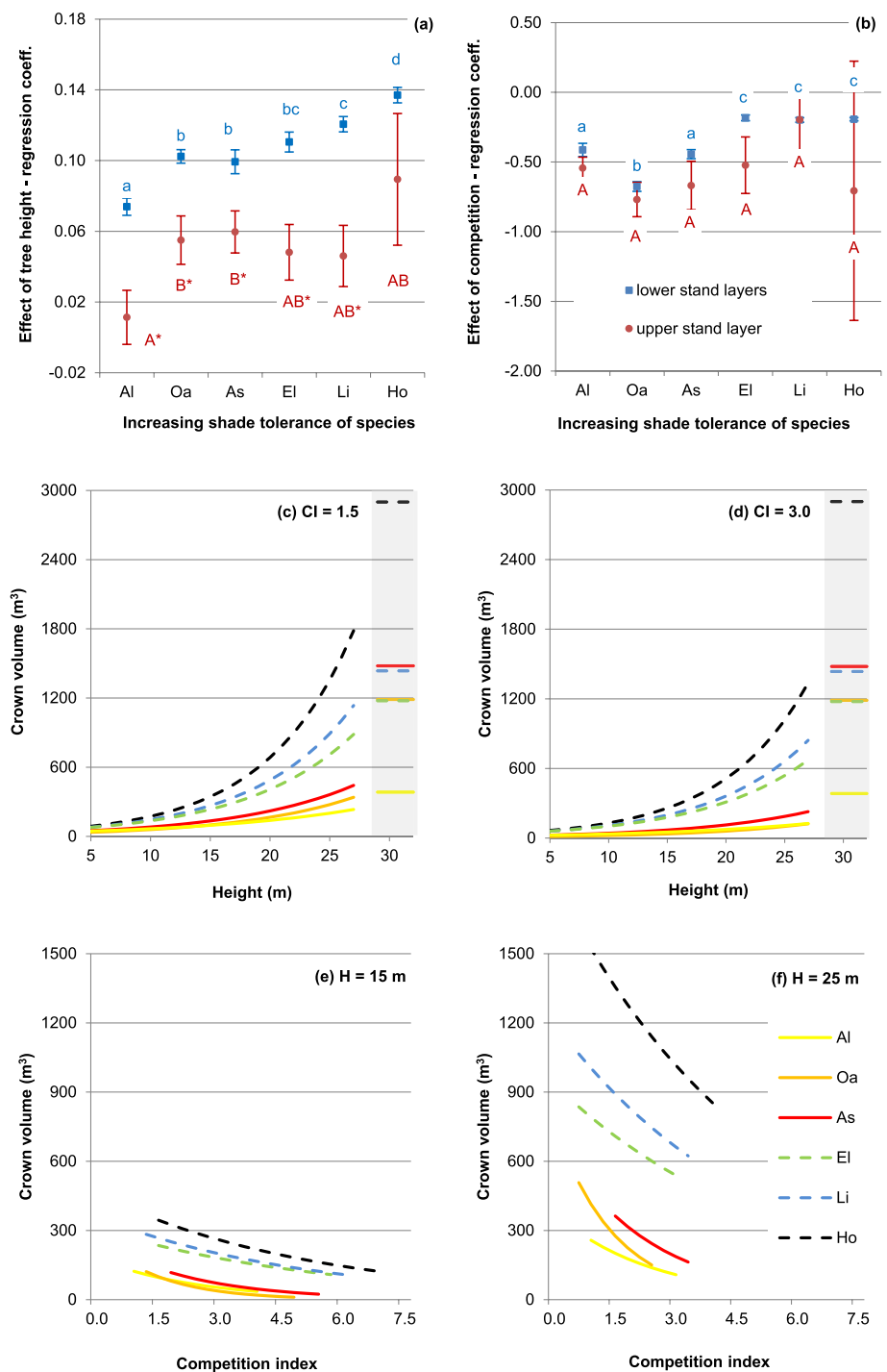


to be directly linked with this feature; in alder, a species with the greatest light demand among the studied six species, the allometry did not change as significantly as that in oak and ash. Therefore, the morphological response to advancing to the upper stand layer seems to be influenced by a broader set of factors, including phylogenetic factors such as wood properties, branching architecture, apical control, and the ability to form secondary modules from epicormic buds.

Conclusions

The analysed allometric relationships were found to be species-specific and dependent on local density and species composition. In accordance with hypothesis H1, we observed that the lengths, widths and volumes of the crowns of trees growing in the lower stand layer were closely related to the light demand of the six studied species. The lengths, widths and volumes of the crowns increased with tree

Fig. 8 Relationships between tree height, competition intensity and crown volume: **a** regression coefficients describing species-specific relationships between height and crown volume (\pm SE); **b** regression coefficients describing species-specific relationships between competition level and crown volume (\pm SE); **c**, **d** modelled crown volume at a given constant competition level (weaker competition CI = 1.5, stronger competition CI = 3.0) and changing tree heights; **e**, **f** modelled crown widths at a given constant height (H = 15 or H = 25 m) and changing competition level. Notes as per Fig. 1



height at a lower rate, and the response of these characteristics to competition was generally stronger in light-adapted species than in shade-tolerant species. However, contrary to hypothesis H1, we did not find a relationship between shade tolerance and the crown width-to-crown length ratio. Moreover, we were unable to confirm that light-adapted species allocate greater resources towards height growth than towards DBH growth in shaded environments compared to

shade-tolerant species. Nonetheless, despite the complex nature of the growth processes regulating tree architecture in the mixed-species, uneven-aged, broadleaved forests, we identified several allometric relationships that describe these processes. However, only a portion of the total variation in morphological characteristics can be directly attributed to the light demand of tree species. Furthermore, the postulated dichotomy of growth strategies (escape versus persistence)

appears overly simplistic and does not encompass the growth pattern of some mid-tolerant species, such as ash, characterized by strong apical control. Thus, the assumptions postulated by the hypothesis H1 were only partly confirmed.

As expected, the allometry and response of morphological traits to competition level differed between trees growing in the lower and upper stand layers (H2). The allometric relationships between DBH, crown sizes and heights were weaker in trees in the upper stand layer compared to those in the lower stand layer. Moreover, the role played by the light requirements of species seems to be less pronounced in trees in the upper stand layer than in the lower stand layer.

Relative crown length, crown size and slenderness ratio are important features of trees that are crucial for tree vitality, growth and mechanical stability. The development of these morphological characteristics is intentionally influenced by silvicultural practices. The models presented in our study can aid in regulating stand density and species composition to achieve a desired architecture of trees growing in uneven-aged deciduous forests. Their predictive power can be further enhanced by considering individual life histories and refining indicators of competitive pressure. One potential avenue for future research is to differentiate the effects of crowding and suppression, i.e. interactions between individuals from the same or different stand layers, and to consider mechanical interactions and species-specific apical control.

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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