

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 may considerably vary depending on phylogeny, life strategies, growth conditions and ontogeny. We hypothesized that in multilayered 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 forming 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. In contrast, the response of morphological traits on competition was stronger in light adapted than in shade tolerant species. The crown width to crown length ratio was not associated with light demand. Except for the different allocation pattern of ash, between-species differences in the slenderness ratio were insignificant. Allometry and sensitivity to competition was different in trees growing in the upper and lower stand layer. Our results show that the dichotomy of basic growth strategies of stress tolerance or stress avoidance is too simplistic and does not encompass social status and species-specific features such as apical control.

1. Introduction

Trees have evolved to build a diverse array of architectures to enable survival and reproduction under a variety of ecological conditions. Their morphological plasticity is a major strategy to mitigate resource limitation (Horn 1971). Tree architecture may be viewed as a result of multiple trade-offs, including lateral extension for light capture, maintenance of mechanical stability and hydraulic safety, and slow versus fast growth strategies (Ford 1992; Verbeeck et al. 2019). Long-living and large organisms such as trees have developed numerous mechanisms to modify their architecture in response to changes linked with intrinsic growth processes, disturbances occurring in their neighborhood and interactions with other organisms (Horn 1971). Tree longevity relies on vegetative vigor and disease resistance together with plastic crown branching and root readjustments (Piovesan and Biondi 2021). Trees may change the pattern of resource allocation and in the longer term also the structure of their organism to reduce self-shading and stem elongation requirements for leaf arrangement, maintain mechanical resistance and improve survival (Messier and Nikinmaa 2000; Hitsuma et al. 2015). The architecture of trees is a very plastic feature and may considerably vary depending on the conditions and environments in which trees grow (Seidel et al. 2011; Schröter et al. 2012). Therefore, scaling parameters may strongly vary and may not be centered on the values predicted by geometric or metabolic scaling theories (West et al. 2009; Pretzsch 2009).

It is well recognized that light availability exerts a decisive influence on the morphology of photosynthetic organs (Lang et al. 2010; Harja et al. 2012; Osada 2012). The morphology, inclination and spatial

distribution of leaves in tree crowns are linked with the light demand and successional status of tree species (Hagemeier and Leuschner 2019a). Short-lived pioneers that experience consistently high light levels display low plasticity, and shade tolerant species high plasticity, in leaf traits linked to photosynthetic capacity and carbon balance (Rozendaal et al. 2006). Shade tolerant species are capable of developing shade leaves adjusted to achieve a net carbon gain in low light conditions through reduced leaf construction and maintenance costs but increased leaf absorptance (Hagemeier and Leuschner 2019b). Such tree species produce larger total leaf areas than light adapted species due to the formation of extended leaf layers with low leaf mass area and nearly horizontal leaf orientation in the lower crown. Shade tolerant species benefit from investing in leaf area at low cost with a high leaf area/leaf mass ratio rather than from investing in durable leaves with a low leaf area/leaf mass ratio (Klooster et al. 2007).

The morphological and physiological differences between shade tolerant and light adapted species are reflected in divergent growth strategies developed to survive in forest ecosystems (Claveau et al. 2002; Franceschini and Schneider 2014). Light adapted species form elongated crowns with multiple leaf layers to optimize light interception under open canopy conditions. They have developed a strategy of escape which consists of minimizing light deficiency by allocation of 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). Although tree allometry is plastic rather than fixed and scaling parameters vary around predicted central tendencies, light adapted species are often taller for any given diameter (Hulshof et al. 2015). The pattern of development of their architecture favors 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 reported higher growth rates in light adapted than in shade tolerant species at both low and high light levels (Beaudet and Messier 1998; Poorter 1999). 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 ones 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 to horizontally expand their crowns and root systems. At low light levels this strategy manifests in the reduction of the slenderness ratio, formation of wide crowns and minimization of self-shading by decreasing the degree of spatial aggregation of foliage and branching frequency (Niinemets 2010; MacFarlane and Kane 2017).

Tree allometry and scaling parameters of crowns, stems and roots are also influenced by competitive interactions with neighboring trees (Vieilledent et al. 2010, Pretzsch and Dieler 2012, Barbeito et al. 2014; Forrester et al. 2017; Owen et al. 2021). Mixed-species forests frequently exhibit greater canopy packing than monocultures due to vertical stratification and considerably larger crowns (Jucker et al. 2015; Pretzsch 2019). Similarly, trees growing in mixed stands may show modified allometry and structural crown properties (Bayer et al. 2012; del Rio et al. 2019). Local tree species diversity usually has a positive

effect on crown volume, potentially driven by enhanced above-ground light capture (Pretzsch 2014; Kunz et al. 2019). Trees growing under strong competition in one-layered stands typically exhibit smaller crown projection areas, shorter crowns, greater height and lower taper for a given diameter (Assmann 1970; Pretzsch 2009). However, spatial relationships between trees in one-layered and multi-layered stands strongly differ. In the first case tree crowns concentrate in a single, typically densely-packed stand layer. This causes trees to be exposed to crowding, and their available growth area is strongly reduced by the crowns of neighboring trees (Canham et al. 2004). 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). Within homogeneously structured stands, crown abrasion through wind sway is also likely to spatially restrict lateral expansion (Meng et al. 2006). In multilayered stands the heights of neighboring 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 allometry and growth of trees growing under crowding in one-layered 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 multilayered forests is still fragmentary 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). This gap becomes particularly severe 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 decisive 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 the efficiency of space utilization (Ishii and Asano 2010; Pretzsch 2014; Jucker et al. 2015; Pretzsch et al. 2022). Thus, knowledge on the morphological properties of tree species growing in different light conditions is crucial for modeling and silvicultural regulation (Pretzsch 2019).

In this paper we analyzed allometric relationships for six tree species of different shade tolerance growing in multi-layered and multi-species stands. The light adapted species are represented here by alder *Alnus glutinosa* (L.) Gaertner, pedunculate oak *Quercus robur* L., and ash *Fraxinus excelsior* L., and the shade tolerant species by 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 depending on competition level. We hypothesized that 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, represented here by alder, oak and ash, respond to increasing competition with a stronger increase in height growth and height-to-diameter ratio and a stronger reduction of 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. Because we assume 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 hypothesized also that the allometry and response of morphological traits to competition level is different in trees growing in the lower and upper stand layer.

2. Methods

2.1. Study area 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 S1, online supplementary material), is a lowland flat area (185–220 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 and Pleistocene fluvioglacial and bottom moraine sediments 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 an 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 *Quercus robur* L., alder *Alnus glutinosa* (L.) Gaertner, hornbeam *Carpinus betulus* L., lime *Tilia cordata* Miller, ash *Fraxinus excelsior* L., European white elm *Ulmus laevis* Pall., 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 with an area of 0.64 ha (Table S1, online supplementary material). 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 layer, and an absence of tree stumps cut in the last 20 years. The field measurements comprised stem coordinates, tree heights (h), diameters at a height of 1.3 m (dbh), crown lengths (i.e. the vertical distance between the tree top and the height of the lowest part of the

compact, solidcrown 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 and not branch bases, i.e. 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, that is if sections without leaves were shorter than 2 m. Morphological parameters were determined to the nearest 10 cm. Crown radii 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 parameters and tree heights were determined in the leafless period (dead and live branches were distinguished based on the presence of buds).

Species compositions, stem numbers (236–583 ha⁻¹), basal areas (25.6–41.4 m² ha⁻¹) and stand volumes (302–577 m³ ha⁻¹) on sample plots are given in Table S1 (online supplementary material). The dbh distributions represent multi-modal, negative exponential or rotated sigmoid types (Bartkowicz and Paluch 2019). The largest oaks reach dbhs above 120 cm, ashes 100 cm, limes and elms 80 cm, and hornbeams and alders 60 cm. 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 – greater than 150 years (L. Bartkowicz, pers. comm.).

2.2. Data analysis

The analysis included six species which occurred on the sample plots with sufficient frequency. According to increasing shade-tolerance, these species may be ordered as follows: alder, oak, ash, elm, lime, hornbeam (Burschel and Huss 1997; Jaworski 2011). The set of morphological features comprised dbh, height and crown parameters: length, width and volume. Tree crowns were modelled exact to 10 cm³ 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 part was assigned to the more shade tolerant species, or – if both individuals represented the same species – to the tree with a lower d/ba ratio, where ba is basal area and d the horizontal distance between the given point and the stem basis of the respective tree.

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

$$CI_i = \sum (dbh_j rLAI_j) / (dbh_i (dist_{ij} + 1))$$

,

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 widths dependent on tree dbhs,

$b_0 \ln(Dbh_i) - b_1 + b_0 \ln(Dbh_j) - b_1$, with parameters $b_0=2,57$ and $b_1=1,97$ derived from the empirical data set. Because light is a primary driver of competitive interactions in forest communities, we used the relative species-specific leaf area index as a weighting factor to account for the different competitive power of trees species. Small trees of shade tolerant species growing in the neighborhood of a subject tree may have a disproportional impact on the morphological characteristics of its crown. Incorporation of the weighting factor closely related to species-specific foliage density, mimicked asymmetric competition between species of different light demand 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; Soudani et al. 2002; Stenberg et al. 1994; Šramek 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 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; hornbeam 1.00. For admixed species we used the following: pine 0.27; wild cherry 0.55; sycamore and Norway maple 0.73; bird cherry 0.91. To minimise border effects, only trees distanced by 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 more distanced from the border.

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 maximal tree height registered on the sample plot. Trees forming the upperstand layer were treated separately because for a long 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 (183–763 for single species) and 335 trees from the upper stand layer (20–140 for single species except for hornbeams) (Table S2, online supplementary material). Hornbeams are trees of a short stature and rarely reach heights above 27 m in the studied stands. Because of the small number of sampled trees 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 and crown lengths, widths and volumes) of the six species studied was tested by using general linear models with the species as the qualitative 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. Variation in morphological features and values of competition indices are displayed in Fig. S1-S5 (online supplementary material). Logarithm transformations of dbhs, crown widths and crown volumes were used to minimize heteroscedasticity and linearize the analysed relationships. The tested models had the general form

$$Y_i = b_0 + b_{1i}H + b_{2i}CI + e$$

where Y denotes a response variable, 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 ϵ is the model error. In particular, 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. Preliminary results showed that incorporation of non-linear relationships and plot-specific effects do not improve the model fit significantly. To test between-species differences in the slope parameters b_1 and b_2 , we applied Welch's tests 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) extended with several macros.

We also developed models which by means of an additional parameter took into account the interaction of tree height and competition level, that is, they assumed that the effect of competition alters with social position (tree height). Because the results indicated that this assumption is valid only for some species and some response variables and the predictive power of the models increased only insignificantly (by not more than 0.02 in terms of adjusted R^2 statistics), in this paper we refer to the results obtained for the simple models with only two independent variables, i.e. tree height and competition level.

3. Results

3.1. Diameter (dbh)

As may be judged on the basis of respective regression coefficients (Fig. 1a), in the lower stand layer the height-dbh relationship considerably differed between ash and the other species. 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. Among the species other than ash, the differences in dbhs of trees of comparable heights were insignificant (Fig. 1acd). In the upper stand layer, the height-dbh relationship was similar in ashes and the other species. Given comparable height and competitive pressure, in the upper stand layer elms and oaks had the largest dbhs and alders the smallest (Fig. 1cd).

The negative values of the regression coefficients (Fig. 1b) indicate that trees which grow under stronger competition generally have smaller dbhs and hence a greater slenderness ratio than trees which grow under weaker competition (Fig. 1cd). 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 competition level, although in a statistical sense the between-species differences were not always significant (Fig. 1b).

Small trees of all species growing in the lower stand layer allocated relatively less resources to dbh growth than to height growth compared to larger trees from the upper layer (Fig. 1a), but their diameter growth 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 maximal values at a height range of 15–20 m, depending on competition level (Fig. 2ab).

3.2. Crown length

The relative crown lengths well reflected the light demand of the studied species. The light adapted species alder and oak had shorter crowns than shade tolerant species (Fig. 2cd). Shade tolerant species growing in the lower and, less distinctly, also in the upper stand layer had longer crowns than light adapted species (Fig. 3acd).

In general, the crowns of trees growing in less competitive surroundings were longer than those of trees growing in more competitive surroundings (Fig. 3ef). 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 (Fig. 3b). We did not find consequent differences in the response to competition between trees from the lower and upper stand layers (Fig. 3b).

3.3. Crown width

The crown width to height ratio was greatest in small trees and decreased exponentially with tree height (Fig. 2ef). This indicates that crown widths increase at a slower rate than tree heights. 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. 4a). In the lower stand layer light adapted species alder, oak and ash had the most narrow crowns among the studied species (Fig. 4cd). In the upper stand layer, however, the ranking of the species changed and oaks and ashes had similarly wide crowns as shade tolerant lime or mid-tolerant elm (Fig. 4cd). 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 widths decreased with increasing competition (Fig. 4b). In the lower stand layer this effect was stronger in light adapted species than in shade tolerant species (Fig. 4bef), but in the upper layer this tendency was not discernible and we did not find statistically significant between-species differences (Fig. 4b).

The crown width to crown length ratio was affected by tree height, species and competition intensity (Fig. 5). This characteristic, however, were not a reflection of 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 hornbeams and elms the lowest (Fig. 5ab).

Depending on species and tree size, competition level exerted a different influence on the shape of crowns (Fig. 5cd). In general, taller trees growing in a more competitive neighborhood were characterized by lower values of the crown width-to-crown length ratio, i.e. they had less flat crowns. Nonetheless, this general response pattern was different in small oaks and less distinctly also in alders, in which we found increasing crown flattening with increasing competition level (Fig. 5c). Furthermore, we found no clear relationship between competition level and the crown width to crown length ratio in small hornbeams and elms (Fig. 5c).

3.4. Crown volume

In the lower stand layer the slope coefficients describing the relationship between tree height and crown volume clearly increased with species' shade tolerance (Fig. 6a). This denotes that shade tolerant trees growing in the lower stand layer formed much larger crowns than light adapted trees (Fig. 6cd). The difference between both groups of species increased with tree heights (Fig. 6cd). In the upper stand layer this ranking blurred, and light adapted species oak and ash had similar crown volumes as shade tolerant elms and limes (Fig. 6cd).

The negative values of the slope coefficients indicate that trees growing under stronger competition had smaller crowns (Fig. 6bcd). The response to competition was stronger in light adapted than in shade tolerant species and similarly stronger in tall trees than in short trees from the lower stand layer (Fig. 6ef).

4. Discussion

We hypothesized that light adapted species represent the strategy of stress avoidance (escape) and in reaction to increasing competition maintain their allocation of resources towards height growth and decrease self-shading by reducing crown width. In contrast, the strategy of shade tolerant species relies on decreasing the slenderness ratio and development of crowns of greater width, length and volume that are better adapted to greater light capture in shaded environments.

In general, the obtained results confirm the assumption that light demand is an important factor shaping allometric relationships and also survival rate in these two functional groups of species. The shade tolerant species were capable of tolerating much higher competitive pressure than 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 (Fig. S5, online supplementary material): alder 3.8, oak 4.7, ash 5.5, elm 5.7, lime 5.9 and hornbeam 6.7. A very similar ranking described crown lengths and crown volumes; at a given height the shade tolerant species growing in the lower stand layer had crowns of greater width, length and volume than the light adapted species. The lengths, widths and, in particular, volumes of the crowns increased divergently with tree height, i.e. at a lower rate in light adapted than in shade tolerant 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 may be explained by decreasing light availability with the depth of the forest canopy. Leaves and branches are abscised once they become a net carbon drain (Ackerly 1999; Poorter et al. 2012). Therefore, shade tolerant species are capable of maintaining branches located deeper in the forest canopy than light adapted species. The realized crown architecture is the result of accumulated stem and branch growth and losses (Mäkelä and Valentine 2006). In the studied stands we did not find any signs indicating intense disturbances over the last two to three decades, such as newly formed gaps or stumps of harvested large diameter trees. On this basis we assume that the stands cumulated their biomass in this period. Tree height, crown base height and lateral expansion of the crown are morphological features that are very sensitive to changes in local stand density (Juchheim et al.

2017; Georgi et al. 2018), so we assume that the registered crown characteristics well correspond with registered levels of competitive pressure.

A stronger response of the crown morphology of light adapted species to stress related to competition was also reported by Longuetaud et al. (2013), who found a stronger crown shape distortion in light adapted oak than in shade tolerant beech in oak-beech forests in France. Osada et al. (2004) obtained similar results in *Fagus crenata* and *Quercus crispula* forests in Japan. Dietze et al. (2008) also found that the crowns of shade tolerant species were wider and longer than those of light adapted species in their study conducted in hardwood forests in southeastern USA. Similarly, Sumida and Komiyama (1997) reported that relatively shade tolerant *Quercus mongolica*, *Acer sieboldianum* and *Magnolia obovata* developed wider crowns than light adapted *Betula platyphylla* and *B. maximowicziana*. Also, in northern hardwood forests in the USA, the ranking of species (*Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis* and *Fraxinus americana*) with respect to crown area to basal area ratio corresponded with their shade tolerance (Ray et al. 2011). Similar results were reported by Schmucker et al. (2022) for *Carpinus betulus*, *Sorbus torminalis*, *Ulmus laevis* and *Acer campestre*. However, a positive relationship between shade tolerance and crown width was not confirmed by Hemery et al. (2005) in their study, which took into account eleven tree species growing in the UK, and Thorpe et al. (2010), who analyzed the morphological features of mixed-species conifer forests with *Abies lasiocarpa*, *Pinus contorta* and *Picea glauca engelmannii* in British Columbia. Similarly, Iida et al. (2011) observed no effect of life-history strategy on crown depth and width allometries among 200 co-occurring species in Malaysia.

Allometric relationships may also be significantly affected by factors other than light demand. Research conducted in mixed-species broadleaved forests showed that in one-layered stands mechanistic interactions between tree crowns may play an important role (Hajek et al. 2015). In the literature attention is paid to mechanical wood properties (Dietze et al. 2008; Aiba and Nakashizuka 2009; Poorter et al. 2012); the greater they are the greater heights trees may reach and the wider and shorter crowns they may develop. 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 than, for example, limes. Thus, the allometric relationships in six species included in our study were largely driven by their light demand, this factor likely masked the effect of between-species differences in mechanical wood properties.

However, not all obtained results were concordant with the hypothesized traits of light adapted and shade tolerant species and the respective strategies of escape and persistence. In opposition 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 which grow under stronger competition generally had smaller dbhs and thus a greater height to dbh ratio than trees which grow under weaker competition. However, in the lower stand layer we found no clear

relationship between the response to competition and shade tolerance of tree species. In opposition to our results, increased allocation of resources towards height increment in light adapted species was reported by Dietze et al. (2008) in oak-hickory forests in southeastern USA, Aiba and Nakashizuka (2009) in multispecies oak-beech forests in Japan and Poorter et al. (2012) in beech-oak-pine forests from the Iberian peninsula. We attribute these dissimilarities to the fact that our stands were characterized by relatively high stand basal area and moderately closed canopies. As a consequence, the height growth of trees from the lower stand layer may strongly depend on available space and their chances of vertical expansion on the local configuration of competitors. This factor also might override species-specific effects linked to growth strategies.

Another allometric feature which 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 better correspond with the strategy of persistence assigned to shade tolerant species because this crown shape facilitates light capture and minimizes self-shading (Horn 1971; Niinemets 2010). This pattern of morphological response 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 oak had the most flattened crowns, mid shade tolerant ashes had the least flattened crowns and shade tolerant species showed intermediate properties. Thus, the registered crown width to crown length ratios did not reflect the light demand of the species.

Ash least of all fitted into the two growth hypothesized strategies. In the upper layer ashes formed moderately long but wide, large crowns like other light adapted species with strong wood. However, ashes growing in the lower stand layer were characterized by a high slenderness ratio that was significantly greater than that of all other species, and formed crowns as narrow as light adapted species and as long as shade tolerant species. Thus, in ash we found a separate growth strategy and not intermediate features of the two strategies hypothesized. Perhaps this divergence is linked with 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 with respect to vertical expansion was emphasized by Hein and Spiecker (2008). Similar properties are also exhibited by sycamore (Hein and Spiecker 2008; Petritan et al. 2009). This might suggest that morphological response is related not only to shade tolerance but also to species-specific apical control. Both features seem to be weakly correlated. Although many light adapted species often display strong apical dominance (e.g., poplars and alders), the opposite feature may characterize both shade tolerant (beech) and light adapted species (oak) (Szweykowska and Szweykowski 1996; Schütz 2003).

It is generally assumed that broadleaved trees develop relatively short and wide crowns when they reach the stand canopy (Blanchard et al. 2016). Indeed, in several instances we found significant divergences in the ranks of species growing in the lower and upper stand layer. This may suggest a different allometry of trees dependent on their social status. Dbhs and crown volumes were less closely related to tree heights in individuals from the upper stand layer than in individuals from the lower stand layer. However, the dbhs of trees from the upper stand layer were more sensitive to competition. We link these results with

more heterogeneous light conditions in the upper zone of the canopy, which favor variation in tree architecture (Juchheim et al. 2017; Georgi et al. 2018). In the lower stand layer competition is very intensive, and generally trees allocate more resources towards height growth than towards dbh growth and crown development (Messier and Nikinmaa 2000; Xiang et al. 2021). On the between-species level, these divergences were particularly striking in the slenderness ratio of ashes and in the crown widths and crown volumes of oaks and ashes. In the case of both characteristics, the ranks of these 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 seem to be linked solely 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 in oak and ash. It is likely that shade tolerant species form larger crowns already in the lower stand layer, and social advancement into the upper stand layer is associated with smaller changes in their architecture than in light adapted species.

5. Conclusions

The analyzed allometric relationships were species-specific and dependent on local density and species composition. We found that some crown parameters of trees growing in the lower stand layer were closely linked with the light demand of the studied six species. The lengths, widths and volumes of the crowns increased with tree 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, in opposition to our hypotheses, we found no relationship between shade tolerance and the crown width to crown length ratio. Moreover, we were not able to prove that in shaded environments light adapted species allocate greater resources towards height growth than towards dbh growth compared to shade tolerant species. Thus, the postulated dichotomy of growth strategies (escape versus persistence) seems too simplistic and does not encompass the growth pattern of some mid-tolerant species characterized by strong apical control, in our study represented by ash. The obtained results confirm that the allometry of trees growing in the upper and lower stand layers may considerably differ. Furthermore, shade tolerance seems to be a more crucial factor for allometric relationships in trees growing in the lower stand layer and shaded environments than in trees from the upper layer. In the latter case, phylogeny, which determines among others longevity, wood density and its mechanical properties, branching system, apical control, ability to form secondary modules from epicormic buds and resistance to damage, may be more important. In summary, we obtained a complex picture of allometric relationships which only partially fit into the one-dimensional gradient based on the light demand of tree species.

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 operations. The models reported in our study may help in the regulation of stand density and species composition to achieve a desired architecture of trees growing in uneven-aged deciduous forests. Their predictive power may further be enhanced by considering individual life histories and refining indicators of competitive pressure. One possible research direction is to separate effects attributable to 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.

Declarations

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Competing interests

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

Authors' contribution:

Leszek Bartkowicz and Jarosław Paluch conceived the ideas and designed methodology, Leszek Bartkowicz collected the data; Jarosław Paluch developed computer programs; Leszek Bartkowicz and Jarosław Paluch performed analyses; Leszek Bartkowicz and Jarosław Paluch wrote the manuscript; Leszek Bartkowicz and Jarosław Paluch gave final approval for submission.

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Figures

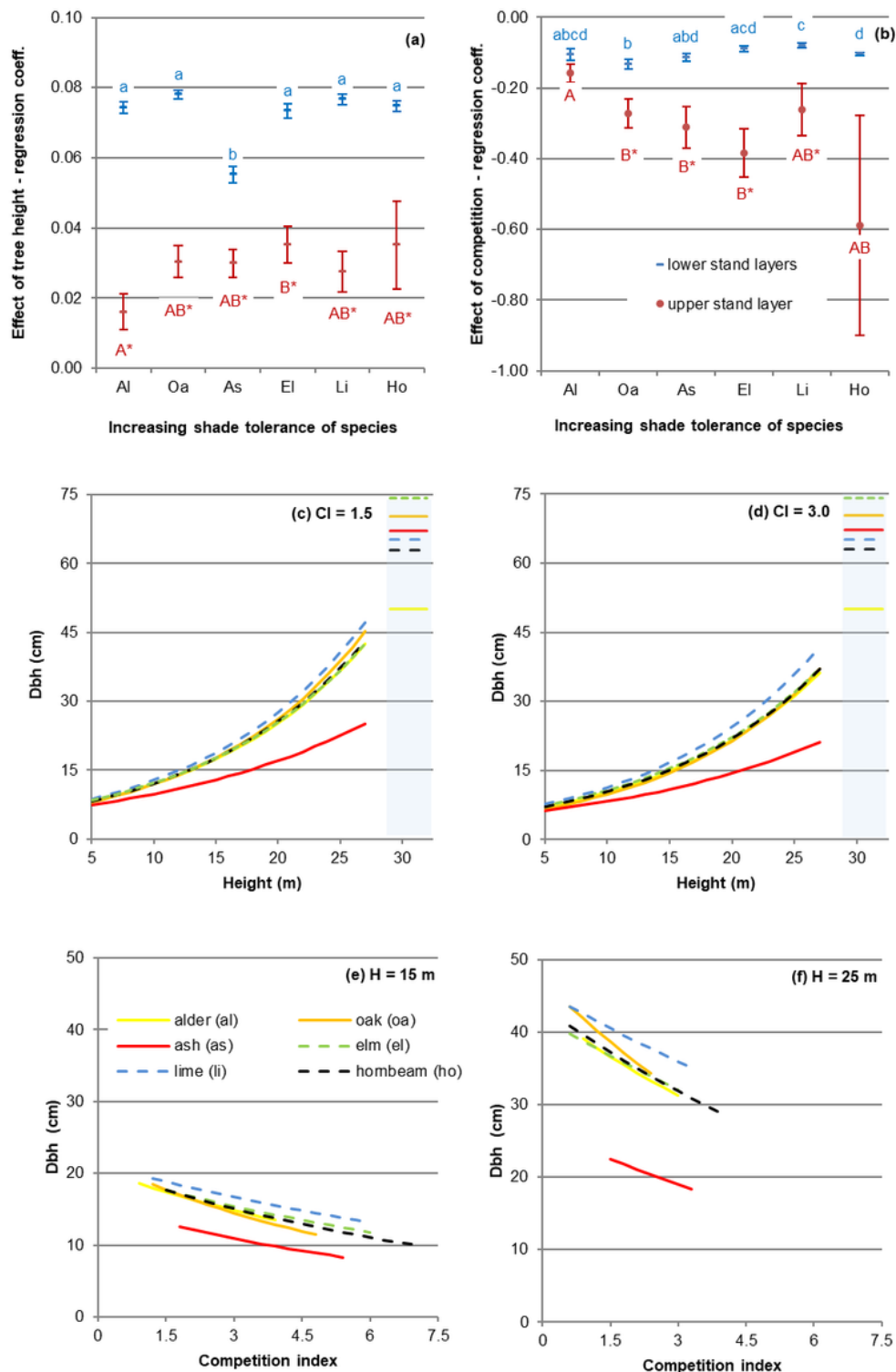


Figure 1

Relationships between tree height, competition intensity 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)** modelled dbhs at a given constant competition level (weaker competition CI=1.5, stronger competition CI=3.0) and changing tree heights; **(d)** modelled dbhs at a given constant height and changing competition level

Notes:

¹Species for which we did not find significant differences were marked by the same letters in Fig. **1ab**. 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 was marked by an asterisk added to the lower case letters. The values of the regression coefficients were given in Tables S3 and S4 (online supplementary material)

²Shaded areas in Fig. **1cd** contain parameters modelled for the upper layer trees growing under average competition pressure (height = 30 m, CI = 0.8)

³Species-specific ranges of competition intensity displayed in Fig. **1ef** correspond with the values observed in the studied stands

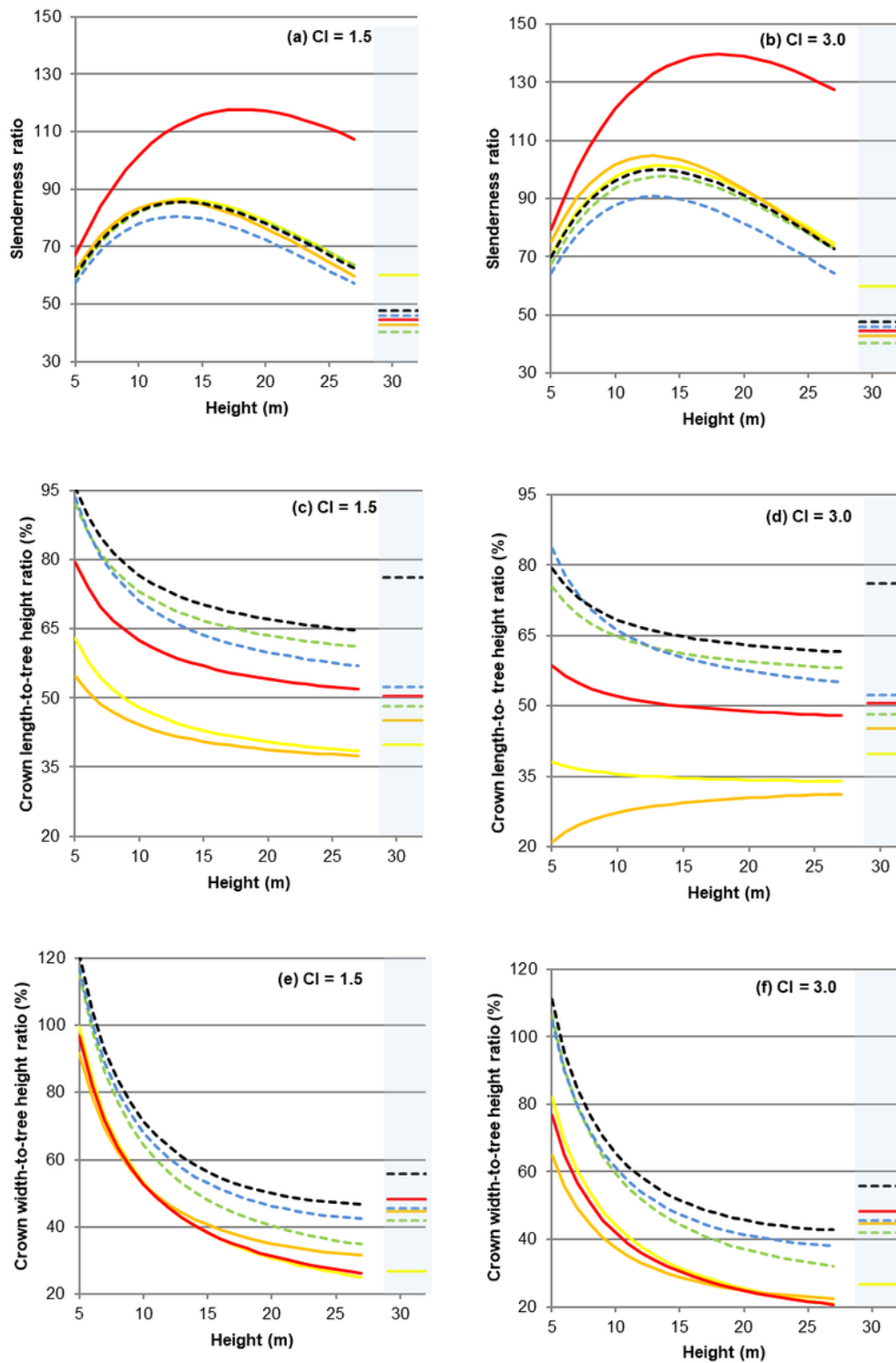


Figure 2

Height:dbh(slenderness) ratio (**ab**), crown length:tree height ratio (**cd**) and crown width:tree height ratio (**ef**) depending on tree height and competition level (CI).

Notes: ²Shaded areas in Fig.2**cd** contain parameters modelled for upper layer trees growing under average competition pressure (height = 30 m, CI = 0.8)

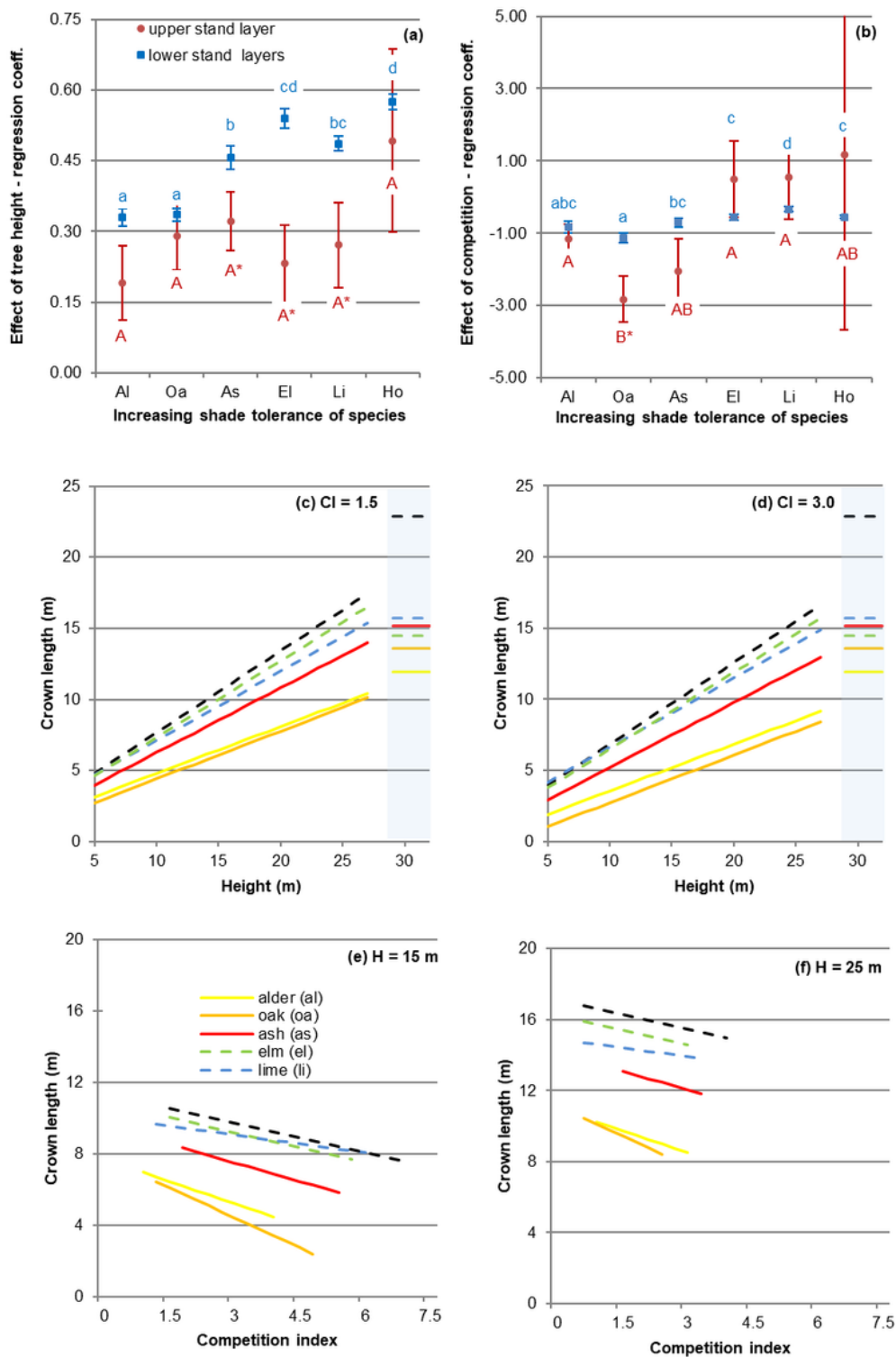


Figure 3

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); **(cd)** modelled crown lengths at a given constant competition level (weaker competition CI=1.5, stronger

competition CI=3.0) and changing tree heights; (ef) modelled crown lengths at a given constant height and changing competition level. Notesas perFig. 1

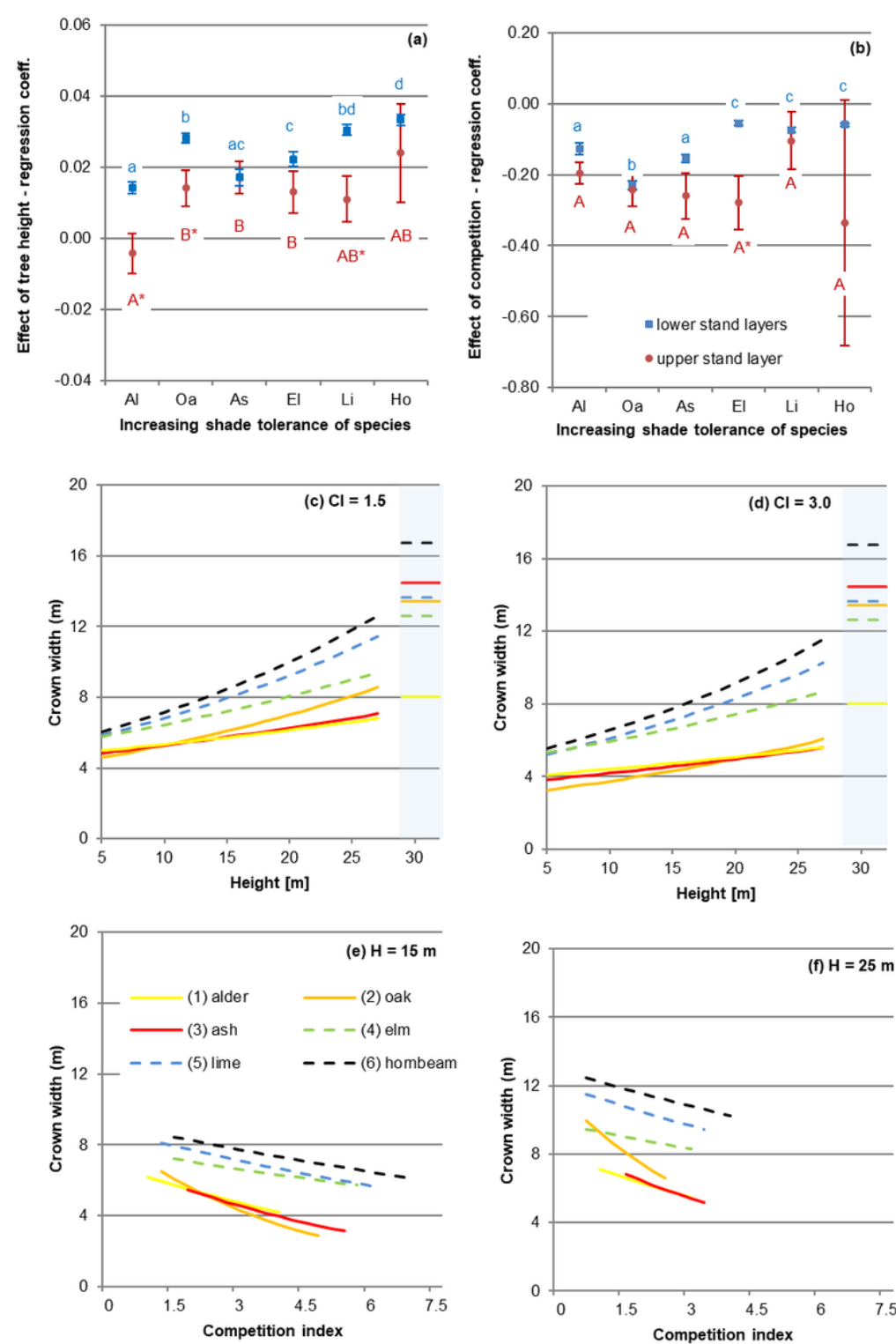


Figure 4

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); (cd) modelled crown widths at a given constant competition level (weaker competition CI=1.5, stronger competition CI=3.0) and changing tree heights; (ef) modelled crown widths at a given constant height and changing competition level. Notes as per Fig. 1

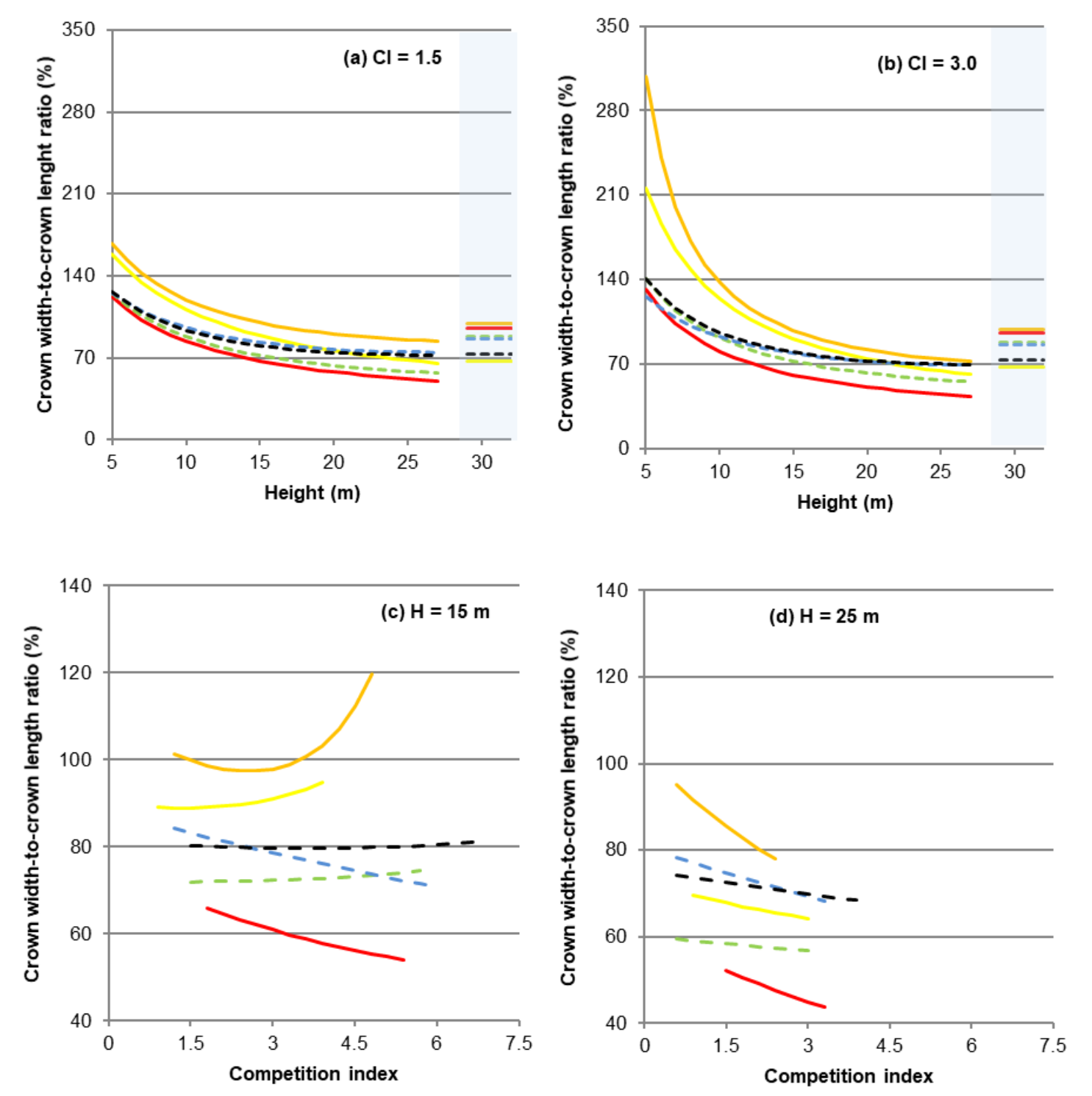


Figure 5

Relationships between tree height, competition intensity and crown width to crown length ratio: **(ab)** modelled ratios at a given constant competition level (weaker competition CI=1.5, stronger competition CI=3.0) and changing tree heights; **(cd)** modelled ratios at a given constant height and changing competition level

Notes: For comparison, values modelled for upper layer trees growing at an average intensity of competition (height = 30 m, CI = 0.8) are shown in the shaded areas **(ab)**

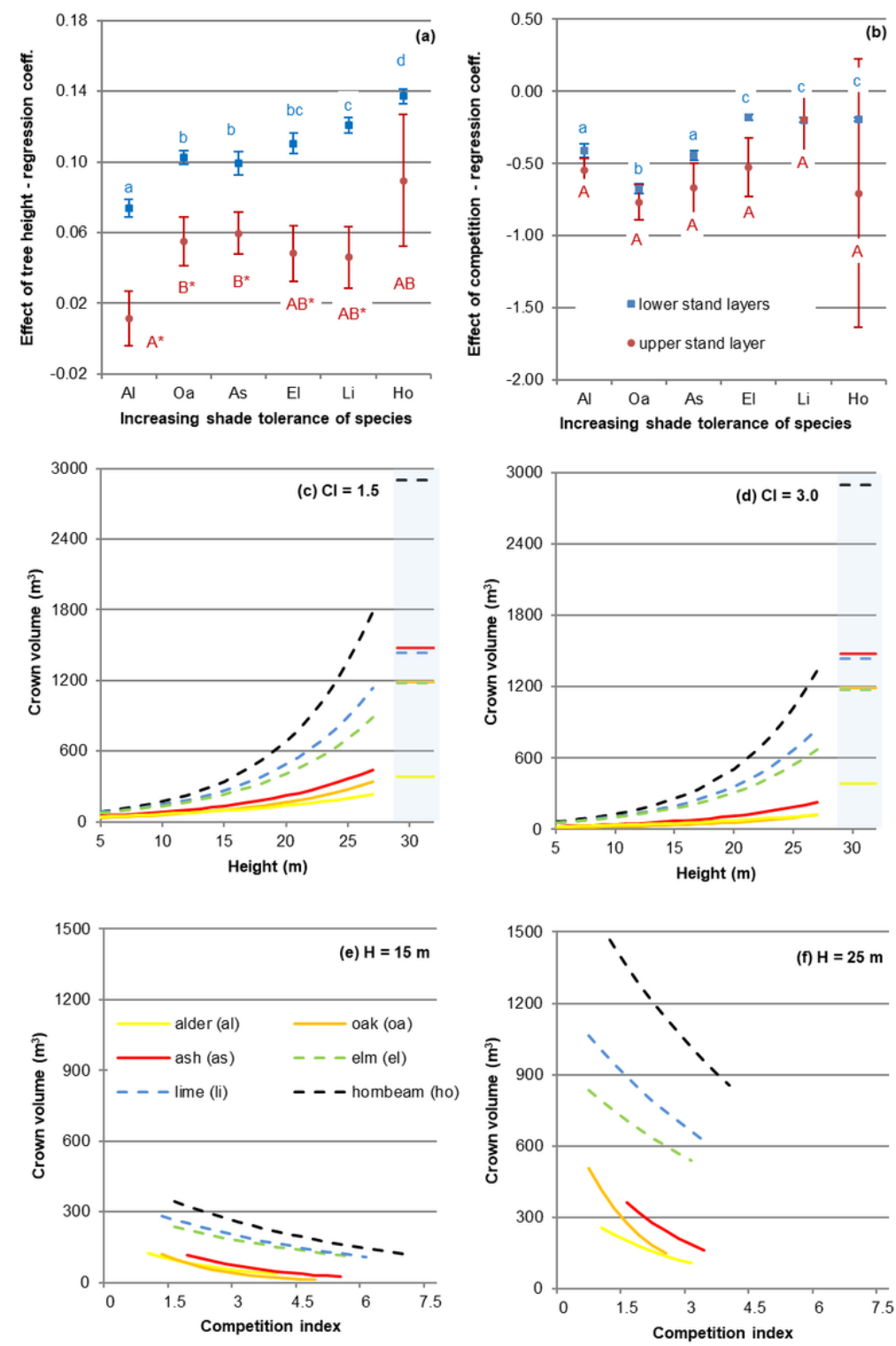


Figure 6

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); **(cd)** modelled crown volume at a given constant competition level (weaker competition CI=1.5, stronger competition CI=3.0) and changing tree heights; **(ef)** modelled crown widths at a given constant height and changing competition level. Notes as per Fig. 1

Supplementary Files

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