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Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures

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ABSTRACT

Mixed-species forest stands are well explored in their favourable ecological, economical, and socio-economical functions and services compared with pure stands, but still poorly understood in their structure and functioning. Canopy structure and tree morphology affect the environmental conditions within the stand, the tree growth, and by this most forest functions and services. Here, I review how canopy structure and crown morphology in mixed stands can differ from pure stands and how this depends on the selection of tree species and interactions between them. The focus is on the macrostructure of canopy and crowns derived from the trees' positions, their convex crown hulls, and their space filling with branches.

In mixed canopies the sum of the crown projection area, but not the ground coverage by crowns, mostly exceeds pure stands due to multiple crown overlaps. The interspecific differences in crown shape and allometric scaling cause a 'selection effect' when complementary species are combined. In interspecific environment furthermore 'true mixing effects' like intraspecific shifts in size, shape, and inner space filling of crowns may occur. The much denser and more plastic canopy space filling in mixed stands may increase light interception, stand density, productivity, and growth resilience to disturbances. I discuss the relevance of interspecific interactions for forest management, model building, and theory development and draw perspectives of further research into stand canopy and crown structure.

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1. Introduction

Until the middle of the 20th century the strong influence of agronomics on forestry resulted in extensive mono-specific production systems. Since then, forest practice and forest science focused on more complex mixed-species stands (Puettmann et al., 2009). Evidence is growing that mixed-species forest stands can supply many ecological, economical and socio-cultural forest goods and services in a similar or even better way as far-from-nature monocultures (Gamfeldt et al., 2013). Tree species richness may trigger the variety of habitats and species diversity of other forest plants and animals (Gotelli and Colwell, 2001; Noss, 1990; Paillet et al., 2010), improve humus conditions and soil fertility (Binkley, 2003; Rothe and Binkley, 2001), the resilience to disturbances (Griess and Knoke, 2011), and the stand productivity (Morin et al., 2011; Piotta, 2007; Paquette and Messier, 2011). These advantages may be coupled with a depletion of soil water (Schume et al., 2004), loss of wood quality (Knoke and Seifert, 2008), increase of harvesting costs (Hanewinkel, 2001), or other drawbacks of mixed compared with pure stands. Some of the pros and cons may even change spatially (Forrester, 2013) and temporally (Lebourgeois et al., 2013; Río et al., 2014) depending on the prevailing site conditions. While research initially concentrated on comparing growth and yield between mixed and pure stands (Kelty, 1992; Pretzsch et al. 2010, 2013a and b), works by among others Forrester et al. (2006) and Rothe and Binkley (2001) gradually proceeded to analysing and understanding the mechanism behind mixing effects. Especially a better understanding of the species structural and functional traits and the dependency of these traits from the environmental conditions appears indispensable for developing new resource efficient multi-species production systems (Forrester, 2013; Richards et al., 2010).

Research into pure stands provides a wealth of knowledge about the interspecific variation of structural and functional traits (e.g., Augusto et al., 2002; Larcher, 2003; Purves et al., 2007). When cultivating tree species in mixture, complementary structural and functional traits can be useful for improving their resource efficiency and yield. Benefits can result among others from combining light demanding with shade tolerant species (Zöhner, 1969), shallow with deep rooting species (Schmid and Kazda, 2001, 2002), slim-crowned and height oriented with wide-crowned and more laterally expanding species (Pretzsch and Schütze, 2005, 2009), or nitrogen-fixing with non-nitrogen-fixing species (Forrester et al., 2006).

Further analyses in this paper will distinguish between 'selection effects' and 'true mixing effects'. Suppose species with complementary traits are mixed but each species sticks to its behaviour which is known from pure stands, the mixed stand provides hardly any surprises. In this case the performance of the mixed stand is equal to the weighted mean of the growth of the neighbouring pure stands. As this kind of mixing effect results from nothing more than selecting the species, it is called selection effect or 'additive effect' (Forrester, 2013; Kelty, 1992). A 'true mixing effect' in contrast means that the interspecific environment triggers species traits which go beyond their behaviour known from pure stands (Forrester, 2013). Compared with the restriction in pure stands, interspecific neighbourhood may trigger abilities of crown expansion and interlocking which the species acquired by their mutual co-evolution in the past, but which are rather irrelevant, undesired by forestry, or even unknown as long as the species grow in pure stands. However, when crowns and roots are let off the leash in mixed stands they may develop a behaviour not known from pure stands but highly relevant for understanding, modelling and predicting mixed stand dynamics. A synonymous term for the true mixing effect is 'multiplicative effect' (Kelty, 1992; Rothe, 1997, pp. 4, 150).

Because of their size, firm position, and longevity, tree crowns both reflect and determine many ecosystem characteristics, functions, and services (Franklin and Spies, 1991; Ishii et al., 2004; Ozanne et al., 2003). On the one hand the crown size indicates leaf area and reflects the light interception and growing conditions of individual trees within the stand (Assmann, 1970, pp. 111–122; Binkley et al., 2013). Thus crown and canopy structures reflect the individual trees' light interception (Sterba and Amateis, 1998; Webster and Lorimer, 2003). On the other hand crown morphology and the resulting canopy structure determines among others the within-stand environmental conditions, the stand productivity, stand stability and resilience, habitat structure, and even the aesthetic value of a stand.

By forming the local environmental conditions within the stand (e.g., interception of light and precipitation) the structure of the canopy and crowns is crucial for the feedback between structure → environment → growth which drives population dynamics (Fig. 1). By selecting two species with differing morphological traits the canopy structure is varied compared with pure stands. The modified structural pattern of the canopy can form interspecific environmental conditions which trigger 'true mixing effects' which go beyond the species' behaviour in pure stands. A result of the slow but continual feedback between structure, environment, and tree growth (bold arrows in Fig. 1) can be the morphological acclimation of the coexisting trees to their interspecific environment. This reflects that the crown morphology and resulting canopy structure which are in the focus of this review are both pivotal drivers and result of stand dynamics.

This review of canopy space filling and tree crown morphology in mixed stands is based on literature, own data of classical tree crown measurement on long-term experimental plots, and advanced measurements by terrestrial laser scanning (TLidar). The focus is on the macro-structure of canopy and crowns accessible by measuring the position (tree coordinates) and convex crown hull (tree height, height to the crown base, 8 crown radii) of individual trees in pure and mixed stands. Based on the degree of crown engagement and the degree of ground cover by crowns I first show how the canopy structure of mixed stands can differ from pure stands. Canopy space filling in mixed stands is determined by both the interspecific differences (selection effects) and the intraspecific variability of tree crown morphology (true mixing effects). Therefore the review continues with the interspecific differences in crown size and morphology. Subsequently the focus is on the intraspecific morphological shift which trees show when growing in mixed instead of pure stands. These emergent properties were hardly analysed so far and are essential for understanding, modelling, and developing efficient mixed species production systems. In the discussion I stress the relevance of knowledge of canopy structure and crown morphology for forest management

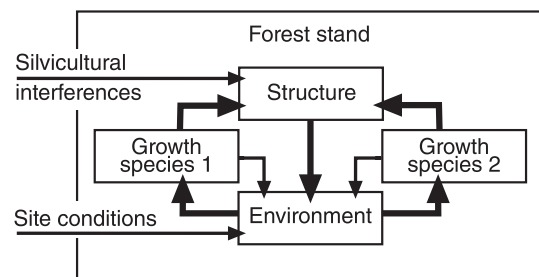


Fig. 1. Feedback loop between stand structure, environmental conditions, and tree growth in a two-species stand. The outer feedback loops structure → environment → growth → structure (bold arrows) are slow, the inner loops environment → growth → environment work faster. Further explanation given in the text.

and utilization, model building, theory development, and I draw perspectives of further research.

2. Canopy space filling and tree crown morphology

The following overview deals mainly with temperate forests where primarily light limits tree growth and the pre-emption of light by the tallest trees can result in a size-asymmetric competition (Schwinning and Weiner, 1998; Wichmann, 2002). Trees acclimate to size-asymmetric competition by morphological shifts in order to remedy the light limitation (Grams and Andersen, 2007). In pure stands, especially when rather homogeneous in genetics and tree size, all individuals compete with similar behaviour for the growing space and resources not sufficient for all. As the resource demands, physiological abilities and structural variability of the trees are similar to their competitors, canopy structure remains mostly homogeneous, competition rather size-asymmetric, and canopy depth low. In mixed stands, in contrast, the trees' elbowroom can be wider. If the crown shapes and the light ecology of the combined species complement each other, the trees might simply have more canopy space to occupy without mechanical abrasion or penetration of neighbouring crowns.

For this study I compiled 253 crown maps from 52 long-term experiments with a total of 187 plots in Germany with complete inventories of the individual tree crown projection areas for analysing the crown extension at tree level, the ground coverage by crowns at stand level, and the sum of the crown area. The crown measurements ($n = 35,728$ measured crowns) reach back to the 1950s and cover a broad range of tree species growing in pure and mixed stands (see Online Resource 1-Table 3).

Many studies show relatively close relationships between APAR and crown size, whether it is quantified in terms of leaf area, crown surface area, crown projection area, crown length, or crown width (Binkley et al., 2013; Forrester et al., 2012). These relationships will probably vary between species and growing conditions but as long as these are known, crown size characteristics should be a reasonable proxy for light interception. This is further indicated by studies showing that when trees increase their leaf area they often seem to simultaneously increase crown length or width rather than by increasing leaf area density. For example, Forrester et al. (2013) found that thinning, pruning and fertilizer application changed leaf area, crown length and width, but not leaf area density. As the crown projection area is much easier to measure at individual tree level and often available from past inventories of long-term plots, it can serve as a proxy for both leaf area and light interception. As crown morphology represents the holding fixture of leaves and the light interception, and canopy structure results from tree-tree interaction (Fig. 1), closer analysis of both may reveal species specific behaviour in mixed compared with pure stands.

2.1. Canopy space filling in mixed versus pure stands

The following analysis of the canopy space filling in mixed versus pure stands is based on combined measurement of tree positions and crown sizes (crown length and crown projection area) on long-term experimental plots. Among the various measures for assessing forest canopies (Jennings et al., 1999) the relative sum of crown projection area, RSCA, and relative ground cover by crowns, RGC, are of special interest. For detailed account of 8-radii-crown measurements see Pretzsch (2009, pp. 115–118).

RSCA is the ratio between the sum of the crown projection areas of a stand and the stand area multiplied by 100; i.e., $RSCA = 100$ would indicate that the sum of the crown projection areas and stand area are equal. $RSCA = 150$ means that the sum of the crown projection areas is higher than stand area and some parts of the

stand have multi-coverage. RGC indicates the ground cover by crowns when looking vertically from above. It is generally analysed by dot count analysis of crown maps: For that purpose a grid is laid over the crown map. RGC is obtained from the number of dot points covered by the crown, n , divided by the total number of grid dot points, p_{total} , multiplied by 100. $RGC = 100$ would indicate that the stand area is completely covered by crowns, $RGC = 80$ indicates that 20% is uncovered. RGC is equivalent to the "crown-free projection" (CFP) by Johansson (1985) who even developed the "vertical tube method" for its efficient measurement in forest stands.

For closer analysis of the canopy space filling I used 253 crown maps in pure ($n = 87$), 2-species ($n = 111$), and ≥ 3 -species ($n = 55$) mixed stands in Germany. All three groups comprise even-aged and uneven-aged stands of mainly Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* L.), sessile and common oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.), Scots pine (*Pinus sylvestris* L.), silver fir (*Abies alba* Mill.), and sycamore maple (*Acer pseudoplatanus* L.). The stands have a mean plot size of 0.30 ha and stand ages of 16–283 years. Their crown measurements from 1951–2013 were used for calculating the relative sum of crown projection area, RSCA, and relative ground cover by crowns, RGC. RSCA and RGC vary widely as the plots cover fully but also sparsely stocked stands. From plots with repeated crown surveys I included only those with ≥ 10 years between the successive inventories in order to avoid autocorrelation between the measurements.

The 95% and 75% percentile regression lines in Fig. 2a show that the sum of crown area amounts to 150 respectively 100% in pure stands and rises with species richness up to 220% respectively 180% (95% respectively 75% percentile). That means that in the fully stocked mixed stands tree species are so densely interlocked that the sum of the crown projection area can become more than twice the stand area. The relationship between ground coverage by crowns and tree species richness shown in Fig. 2b substantiates that in fully stocked mono- as well as poly-cultures mostly 5–10% of the stand area is even uncovered by crowns. Among other reasons, the frequently reported mechanical abrasion (Putz et al., 1984) resulting in crown shyness (Putz et al., 1984) may cause the 5–10% uncovered area in both pure and mixed stands. The wide variation of ground coverage below the ceiling line (95% respectively 75% quantile regression lines) can be attributed to the broad range of thinning grades included in the dataset of altogether 253 crown maps. The above finding that species richness may raise RSCA even when RGC is similar becomes even clearer in Fig. 2c. Especially in denser stands with $RGC > 80\%$ the RSCA is about 25% higher in 3-species stands compared with mono-cultures (upper versus lower line in Fig. 2c).

Studies in mixed species stands by Kennel (1965), Pretzsch (2009, pp. 267–269), and Preuhsler (1981) suggest that RSCA is often much higher than RGC due to up to 7-fold crown coverage especially in polycultures of species with complementary ecology. When studies which compare crown coverage between stands, count twice or more often covered areas only once they neglect that sum of the crown areas and all related advantages such as structural heterogeneity, growth and resilience may be underestimated (Assmann, 1970, pp. 102–107). Based on long-term experimental plots in Germany in pure and mixed stands of spruce and beech ($n = 110$) as well as oak and beech ($n = 74$) I closer analyse the phenomenon of multiple crown coverage. The crown measurements last from 1954 till present and cover stand ages between 26 and 207 years. In order to study the species specific coping with crowding only fully stocked and rather even-aged stands were included, in which all species were unthinned or just moderately thinned.

Table 1 shows that the relative canopy cover of the ground is on average only 64–83% in pure stands and 85–88% in mixture; i.e., in

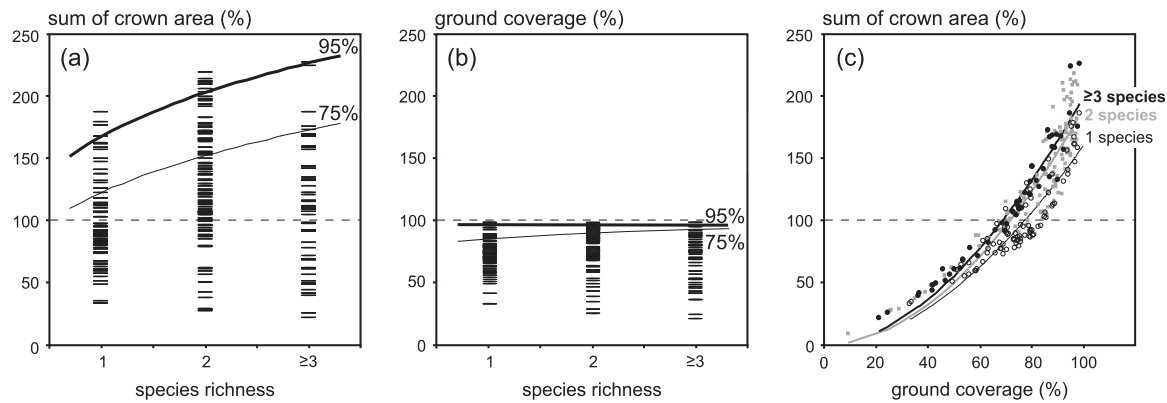


Fig. 2. Effect of species richness on relative sum of crown projection area, RSCA, and relative ground cover by crowns, RGC. (a) RSCA depending on tree species richness, (b) RGC depending on tree species richness, and (c) RSCA depending on RGC and tree species richness. Data base are 253 crown maps of 187 plots belonging to 52 long-term experiments in even-aged and uneven-aged stands in Germany with mean plot size 0.29 ha, earliest and latest survey 1951 respectively 2004, minimum and maximum stand age 16 respectively 283 years. The 95%- respectively 75%-quantile regression lines in Fig. 2a and b represent RSCA and RGC for fully respectively loosely stocked stands. The OLS regression lines in Fig. 2c represent the mean RSCA depending on RGC for ≥ 3 -, 2-, and 1-species stands (upper, middle, lower line, respectively) For further statistical characteristics see [Online Resource 2-Table 4](#).

Table 1
Relative ground cover by crowns (mean \pm standard error) in even-aged pure and mixed stands of Norway, European beech, and sessile oak based on crown maps of unthinned and moderately thinned stands. The uncovered and covered stand area adds up to 100%. In addition columns 5–8 give the percentage of onefold, two-folds and \geq three-fold crown cover and the relative sum of crown projection areas.

Species	stand type	n	ground cover		1-fold and multiple ground coverage			rel. sum of crown area (%)
			(%)	(%)	(%)	(%)	(%)	
Norway spruce	pure	32	77 \pm 2	23 \pm 2	64 \pm 1	12 \pm 2	1 \pm 1	91 \pm 4
European beech	pure	25	83 \pm 3	17 \pm 3	50 \pm 2	26 \pm 3	7 \pm 1	123 \pm 7
N. sp. & E. be.	mixed	53	88 \pm 1	12 \pm 1	48 \pm 2	30 \pm 1	10 \pm 1	138 \pm 4
Sessile oak	pure	22	64 \pm 4	36 \pm 4	50 \pm 2	12 \pm 3	2 \pm 1	81 \pm 7
European beech	pure	25	83 \pm 3	17 \pm 3	50 \pm 2	26 \pm 3	7 \pm 1	123 \pm 7
S. oak & E. be.	mixed	27	85 \pm 3	15 \pm 3	35 \pm 2	30 \pm 2	20 \pm 3	156 \pm 10

both kinds of stands a considerable portion is uncovered by crown projection area. Of special interest is that about 40–50% of the mixed stand ground area is covered more than onefold with crown projection area. The respective range in pure stands is 13–33%. The more multiple coverage in mixed versus pure stands is also reflected by a relative sum of crown area of 138–156% in mixed stands compared with 81–123% in pure stands. Beech achieves even in pure stands 83% crown cover with 33% more than onefold coverage, indicating its outstanding shade tolerance and crown plasticity.

Comparing pure and mixed stands regarding RSCA and RGC reveals the ‘over-packing’ of the canopy space of mixed stands compared with neighbouring pure stands. The term over-packing is used by analogy with over-yielding, which refers to the frequently observed superiority of mixed stands regarding productivity (Pretzsch, 2005; Vilà et al., 2005). Especially species combination with complementary light ecology as Norway spruce and European beech, respectively, sessile oak and European beech may lead to much denser and vertically layered canopies which in turn may cause higher light interception (Kelty, 2006; Morin et al., 2011) and overyielding (Bauhus et al., 2004; Pretzsch et al., 2010, 2013b) compared with mono-cultures.

Combination of species with different crown shapes and albedos may decrease the reflection and light loss at the upper canopy layer by 5–10%. Especially the rather notched canopies of conifers with light wells and low albedos reflect less light compared with deciduous forests (Otto, 1994, p. 213; Dirmhirn, 1964, p. 132).

Mixing of light demanding with shade tolerant species may increase the light interception due to complementary, species specific light compensation points (LCP) and light saturation points (LSP). Sessile and common oak represent light demanding species with both high light saturation ($LSP = 680 \mu\text{mol m}^{-2} \text{s}^{-1}$) and compensation points ($LCP = 17 \mu\text{mol m}^{-2} \text{s}^{-1}$) which can make the most of the light supply in upper canopy, but hardly survive in the deep shade like European beech (LCP and LSP for leaves and P_{max} according to Ellenberg and Leuschner, 2010, pp. 103–105). Beech combines a lower light saturation point ($LSP = 460 \mu\text{mol m}^{-2} \text{s}^{-1}$) with a lower light compensation point ($LCP = 13 \mu\text{mol m}^{-2} \text{s}^{-1}$) and is well equipped to forage for light beside or below oak or spruce (LSP respectively $LCP = 750$ and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$). The canopy space filling by species with complementary light ecology and their closer crown interlocking enables foraging full as well as weak light, a more complete light interception, and often results in a lower light intensity at the forest floor of mixed compared with pure stands (Mitscherlich, 1971, p. 82).

On top of this Kelty (1992) assumes a higher light use efficiency in mixed stands when crowns or branches of shade tolerant species replace more light demanding species, as the former may use the space more efficiently for growth. However, Reiter et al. (2005) showed exemplarily for spruce and beech that spruce reaches higher to the upper canopy and beech lower to the forest floor, but in the same zone they both have rather similar space use efficiencies in terms of carbon gain per tree crown volume.

Temporal and spatial resource use complementary may also occur in combined form, e.g., in mixed stands of Norway spruce

and European beech. In spring, before the leafing of beech, more intensive light can penetrate the stand and curtail the winter dormancy of spruce, thus prolonging its seasonal growth period which, per se, is longer than that of beech (Schober, 1950/1951). From this temporal niche complementary spruce may draw additional advantages in resource utilisation (Mitscherlich, 1952).

The shown complementary of tree species in space filling may also affect the re-closure of gaps in the canopy caused by disturbances. During stand development various kinds of disturbances (e.g., tree mortality due to competition, storm damage, bark beetle attacks, and thinnings) may cause openings in the canopy and gaps in the root space (Bauhus, 2009; Pretzsch et al., 2014). The following rough estimation for even-aged stands underlines the relevance of crown gap re-closure for the interspecific competition and stand productivity. The roughly 3% annual rate of tree loss due to mortality or thinning means that about 3% of the stand area are uncovered by drop out of trees. 3% of a hectare per year is equivalent to $300 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$. A continuation of this drop out process over a 100 years rotation period causes a transient gap area of about $30,000 \text{ m}^2$, i.e. 3.0 ha. With other words, a given growing area of a stand is repeatedly contested by neighbours, occupied by trees, released after mortality or thinning, and finally occupied by the most competitive neighbours. Starting with some thousand trees (when planted) or million trees (when naturally regenerated), occupation and reoccupation of growing area due to competition finally leaves just a few hundred trees per hectare (e.g., 50–100 trees per hectare in pure beech stands, 200–400 in pure spruce stands, about 100–300 trees in mixed stands of spruce and beech) at the rotation age. Again and again trees drop out, release space for the remaining neighbours, which occupy it the faster and completer the more plastic their crowns are.

The over-packing of mixed versus pure stand canopies can reduce canopy gaps and productivity losses caused by density reduction and stand fragmentation with increasing age. Based on the above-mentioned data of spruce and beech, Fig. 3a–c shows the change of RSCA in pure and mixed stands with progressing stand development (represented by the quadratic mean tree diameter, d_q , on the x-axis). Compared with the respective pure stands (100%-line) the mixture of spruce and beech results in RSCA values which start and remain much higher even in the advanced phase of stand development (Fig. 3c). Choi et al. (2001) found a similar trend in northern hardwood forests. It may result from gaps between trees which increase with age and need longer to be covered by crowns again. The relative ground coverage starts lower and can decrease below 80% in the pure stands (Fig. 3d and e) while it remains about 95% all over the stand development in the mixed stands (Fig. 3f).

At the stand level, multiple crown overlap, plastic crowns and quick gap occupation means resilience of productivity by reduction of uncovered ground. The shorter the period of time between opening of a gap till its closure by neighbouring trees, the higher the use of resources (light, water, nutrients) by stand members per time and unit area. The faster and wider a species' crown extension, the higher is its benefit from erratic gaps. Mixed stands with multiple crown overlap (Table 1 and Fig. 3) are less prone to deep-reaching and long-lasting canopy openings by natural (bark beetle attacks, windthrow, windbreak) or anthropogenic (thinning, regeneration cuts) disturbances. Especially in stands composed of light demanding and shade tolerant species any tree and productivity losses in the upper canopy can be mitigated by growth acceleration of more shade tolerant trees in a second or third canopy layer (Pretzsch, 2003).

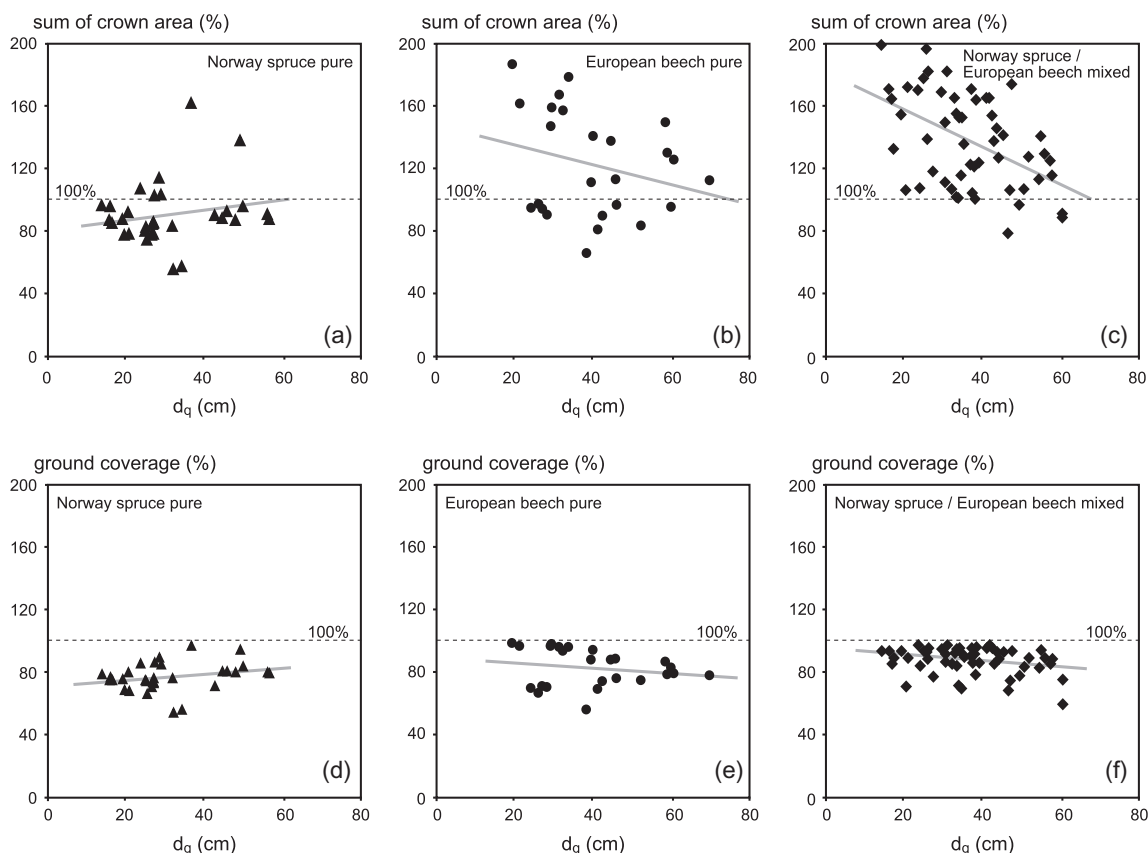


Fig. 3. Sum of crown projection area (%) and ground coverage (%) in even-aged pure and mixed stands of Norway spruce and European beech in dependence on quadratic mean diameter, d_q . Sample size from left to right $n = 32, 25,$ and 54 . For further statistical characteristics see [Online Resource 2-Table 4](#).

This considerably changes the relationship between stand density and net stand productivity. In pure stands this relationship follows a uni-modal shaped curve with a rather narrow saddle of maximum growth close to the maximum stand density (Assmann, 1970, pp. 227–235; Pretzsch, 2005) and degressive decrease of stand growth with reduction of stand density. In mixed stands with species which are complementary in light ecology and canopy space occupation, the relationship between stand density and productivity – known as curve by Langsaeter (1941) – can have a much broader saddle. Even when stand density in terms of stand basal area or standing volume is reduced by 20–50%, the productivity can remain rather constant, as crowns in lower layers compensate for the growth losses in higher layers (Mitscherlich, 1952; Pretzsch, 2005).

2.2. Interspecific difference of crown size

Combined cultivation of tree species with contrasting morphological traits, e.g., slim-crowned conifers with wide-crowned broadleaves, may result in canopy space filling and stand productivity differing from both species in pure stands. The difference is a mere proportional effect as long as the productivity of mixed stands is simply the weighted average of the respective monocultures. Beyond the selection effect mixing might trigger species interactions (see Section 2.3) so that the mixed stand exceeds or falls shorter than the weighted average of the respective monocultures. For differentiation between selection effects and true mixing effects, species specific morphological traits in pure stands need closer consideration.

In the following, tree morphology is quantified mainly by stem diameter at breast height, d , tree height, h , height to the crown base, h_{cb} , crown diameter, cd , crown projection area, cpa , and ratios between these variables. Species may differ in both in the crown size, y , at a given tree size, x , (shape and form) and/or in the differential of crown size with increasing size (scaling). Appropriate for comparing species' morphology is the allometric equation $\ln(y) = a + \alpha \times \ln(x)$ (or untransformed $y = a' \times x^\alpha$, $a' = e^a$). The allometric factor a , represents species shape and form, and can differ considerably between the species. Factor a represents a multiplicative effect of species on the crown expansion. The allometric exponent α represents how crown size scales to tree size (e.g., stem diameter) and reveals the exponential increase of the elbowroom of a species' crown with increasing size.

As crown projection area, cpa , scales non-isometric ($\alpha \neq 1$) to stem diameter, d , ($cpa \propto d^{\alpha_{cpa,d}}$ with $\alpha_{cpa,d} \cong 4/3$ for allometric ideal plants according to West et al. (2009)), and also to tree volume, v , ($cpa \propto v^{\alpha_{cpa,v}}$ with $\alpha_{cpa,v} \cong 1/2$ for allometric ideal plants according to West et al. (2009)) crown size and ratios between crown measures change nonlinearly during ontogeny with progressing tree size development (Pretzsch, 2010; West et al., 1997, 2009). When comparison of tree crown size within or between species neglect any differences in current tree size they run the risk to misconstrue simple size effects as changes in the allocation key and crown morphology. However, by comparing allometric crown size–tree size relationships any size effects are eliminated and true differences in crown shape and scaling can be revealed.

2.2.1. Interspecific variation of crown area and growing area requirement

Many studies provide evidence of species specific differences in tree crown size (Antos et al., 2010; Oldemann, 1990), morphology (Roloff, 2001; Zeide, 1998), and ratios between crown measures (Assmann, 1970, pp. 111–138) at a given time or state of development. How generic the tree crowns scale to tree size or tree mass, e.g., how their tree crown size changes with increasing tree size or tree mass, is still under debate. While allometric theory assumes

common species-overarching scaling relations between trunk and crown dimensions for the allometric ideal plant (Enquist et al., 2009), empirical studies provide evidence of interspecific (Pretzsch and Dieler, 2012; Purves et al., 2007) and intraspecific differences (Duursma et al., 2010; Dieler and Pretzsch, 2013; Pretzsch and Mette, 2008; Price et al., 2010) in allometric scaling of tree crowns. The scaling is relevant for understanding the expansion of a tree species with preceding size development, especially in mixed stands. Suppose a tree of species 1 is much more space consuming and expanding with increasing size than species 2, the initial mixing proportion and contributions to stand productivity will increase in favour of species 1. Species with similar crown allometry, in contrast, may rather keep to their initial role and mixing proportion.

For analysing the interspecific variation of tree stand area I use the dataset compiled by Pretzsch and Dieler (2012) which includes 126 yield tables of 52 species, 30 of angiosperm and 22 of gymnosperm taxonomy. Species included the genera *Abies*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Cunninghamia*, *Eucalyptus*, *Fagus*, *Fraxinus*, *Juglans*, *Larix*, *Nothofagus*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Pseudotsuga*, *Quercus*, *Robinia*, *Shorea*, *Thuja*, and *Tilia*. The dataset includes mainly yield tables with moderate thinning regimes, which by definition (Verein Deutscher Forstlicher Versuchsanstalten, 1873, 1902) keep a stand's canopy permanently in such a kind of structure that the tree crowns just touch but hardly overlap each other. The stand area of the mean tree, $\bar{s}a$, ($\bar{s}a = 10,000 \text{ m}^2/\text{trees per hectare}$ given in the yield tables) and the quadratic mean diameter, d_q , (given in the yield tables) were used for deriving the species specific allometric relationships between $\bar{s}a$ and d_q shown in Fig. 4a. Without access to the original experimental plot data of the 126 yield tables I had to use the d_q values as reported in the yield table instead of the arithmetic mean diameter, \bar{d} . As d_q is systematically higher than \bar{d} , the reported intercepts of the $\bar{s}a-d_q$ -relationships might be positively biased compared with $\bar{s}a-\bar{d}$ -relationships. Nevertheless, these relationships are suitable for showing species specific differences of tree growing area requirement and $\bar{s}a-d_q$ -allometry.

Fig. 4a shows in the double-logarithmic grid the considerable interspecific variation of the allometry between stand area and tree diameter. The intercepts of the allometric straight lines amount to $a = -1.96, -3.57, 2.47$ (mean, min, max) and their slopes $\alpha = 1.47, 0.14, 2.33$ (mean, min, max). On average (Fig. 4a: mean line marked by $a =$ angiosperms and by $g =$ gymnosperms) angiosperms differ significantly ($p < 0.05$) from gymnosperms in the intercept ($a = -1.73$ versus $a = -2.12$, see Online Resource 2-Table 4), but not in the slope of their stand area–tree diameter relationships ($\alpha = 1.44$ versus $\alpha = 1.50$, see Online Resource 2-Table 4). That means angiosperms need on average more growing area than the gymnosperms (Fig. 4b). Angiosperms with a tree diameter of $d = 25 \text{ cm}$, for example, occupy on average $sa = 19.51 \text{ m}^2$ while gymnosperms occupy just $sa = 16.90 \text{ m}^2$, i.e., significantly ($p < 0.05$) less tree stand area. The fact that species can differ in the intercept of their allometric crown relationship is represented, e.g., in yield tables by species specific tree numbers per ha at a given stand age (Assmann and Franz, 1965) and by species specific levels of the self-thinning lines (Pretzsch, 2006).

2.2.2. Intraspecific variation and plasticity of crown size in pure stand environment

Crown size and shape of a tree are strongly determined by its local environment in the stand prevailing in the past and at present. While maximum crown extension is achieved under solitary growing conditions, crown width decreases from open grown to dominant and suppressed trees. Stand density and competition can considerably modify the crown allometry; e.g., the $cpa-d$ relationship. In the following this is shown on the basis of 4542 crown

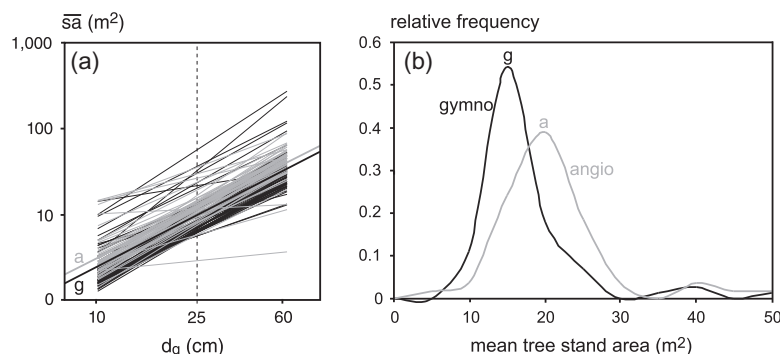


Fig. 4. Overview on relationship between mean tree stand area, $\bar{s}a$, and quadratic mean tree diameter, d_q , in even-aged stands for 52 tree species with 30 of angiosperm (a and grey) and 22 of gymnosperm (g and black) taxonomy according to Pretzsch and Dieler (2012). (a) Allometric relationships between $\bar{s}a$ and d_q for all included species and mean lines for the 30 included angiosperms (a and grey) respectively 22 gymnosperms (g and black). The mean $\bar{s}a$ - d_q -line of angiosperms differs significantly ($p < 0.05$) from the mean line of gymnosperms in its intercept, but not in its slope. (b) Mean tree stand area requirement for trees with $d = 25$ cm calculated on the basis of the species specific $\bar{s}a$ - d_q -allometries shown in (a). For statistical characteristics of the mean regression lines for angiosperms (a and grey) and gymnosperms (g and black) see Online Resource 2-Table 4.

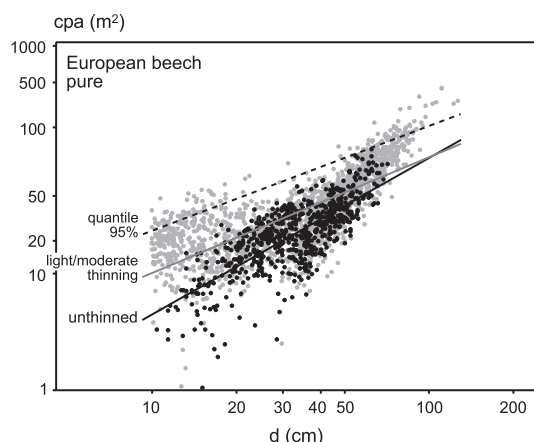


Fig. 5. Allometric relationship between crown projection area, cpa , and stem diameter, d , of European beech derived from crown measurements on long term experimental plots in even-aged stands in Germany. As the data base includes solitary trees as well as trees in thinned and unthinned stands the cpa - d -relationships can be derived for solitary trees (95%-quantile regression), for trees in thinned stands (light/moderate thinning), and for trees growing under self-thinning conditions (unthinned). The thinned and unthinned cpa - d -relationships differ significantly ($p < 0.001$) in both intercept (thinned $>$ unthinned) and slope (thinned $<$ unthinned). The statistical characteristics of the three regression lines are shown in Online Resource 2-Table 4.

projection area measurements of beech crowns in pure stands with spacing and thinning ranging from solitary growing conditions, to moderate thinning, and self-thinning (Fig. 5). The stand age ranges from 57 to 207 years, the surveys come from long-terms plots in Germany measured in the years 1980–2004 and listed in Online Resource 1-Table 3. As young, unthinned beech stands are under-represented in the network of long-term experimental plots, observations for trees with $d < 15$ cm are scarce. The regression lines in Fig. 5 (from top to bottom) for the upper 95% quantile, the group of lightly to moderately thinned stands, and the unthinned plots reveal the broad intraspecific variation of crown allometry. The cpa - d -relationship for light/moderate thinning lies significantly higher ($p < 0.001$) and is significantly shallower ($p < 0.001$) compared with the respective relationship for unthinned stands. According to these cpa - d -allometries a beech with 25 cm stem diameter occupies 58 m^2 when growing without lateral restriction, 27 m^2 under medium stand density, and 16 m^2 when growing close to self-thinning conditions. This morphological plasticity equips beech with high competitive strength. Fig. 6 illustrates that

this crown plasticity can differ considerably between tree species. The data comes from crown measurements on long-term experimental plots in pure and mixed stands in Germany and covers a broad range of tree ages and stand densities (solitary to self-thinning conditions). Based on the 95%- and 5%-quantile of the cpa - d -allometry (Fig. 6, upper and lower lines) the measure of tree crown plasticity, CPL , was derived to quantify interspecific differences. For a reference tree diameter of 25 cm, the 95%- and 5%-quantile lines are used to calculate the expected upper ($cpa_{95\%,25}$) and lower ($cpa_{5\%,25}$) crown projection area, which are used for the measure of crown plasticity $CPL = cpa_{95\%,25}/cpa_{5\%,25}$.

Analyses of the CPL value for various tree species in Europe revealed a maximum value for European beech of $CPL = 5.1$, i.e., its $cpa_{95\%,25}$ value is more than 5-fold compared with $cpa_{5\%,25}$. The species represented in Fig. 6 rank with respect to CPL as follows: European beech ($CPL = 5.1$) $>$ silver fir (4.7) $>$ sessile oak (4.5) $>$ Norway spruce (4.2) $>$ sycamore maple (4.0) $>$ Scots pine (3.7). The highest CPL values out of our set of 14 species (not all are shown) has beech (5.1), while the lowest have red alder (2.8) and silver birch (2.6). The ranking is similar to the species' ranking regarding their shade tolerance (see Section 2.1). Both the potential for lateral crown expansion and shade tolerance are of special importance for competing in mixture.

The scattering of the cpa - d -observations in Fig. 6 underlines that trees rather develop in a broad cpa - d corridor than follow a narrow allometric trajectory with species specific intercept and constant species-overarching slope. The stronger the variation in cpa of trees with a given stem diameter, the higher their structural plasticity when foraging for light. Especially for long-living tree species such as beech, fir and oak the morphological plasticity is highly relevant as it enables continuous acclimation to the local environment in pure stands or to the deep shade in the understory of mixed stands.

2.3. Intraspecific variation of crown morphology

Combined cultivation of selected species may trigger morphological and physiological interactions not known from pure stands. Physiological interactions caused by hydraulic redistribution, combination of isohydric and anisohydric species, or ectomycorrhizal networks were subject of many studies and recently reviewed (Richards et al., 2010). Mechanical interactions by abrasion (Putz et al., 1984) may cause crown shyness (Putz et al., 1984) but can be reduced when combined species fill different canopy layers. Recent studies pointed out that species mixing can modify the

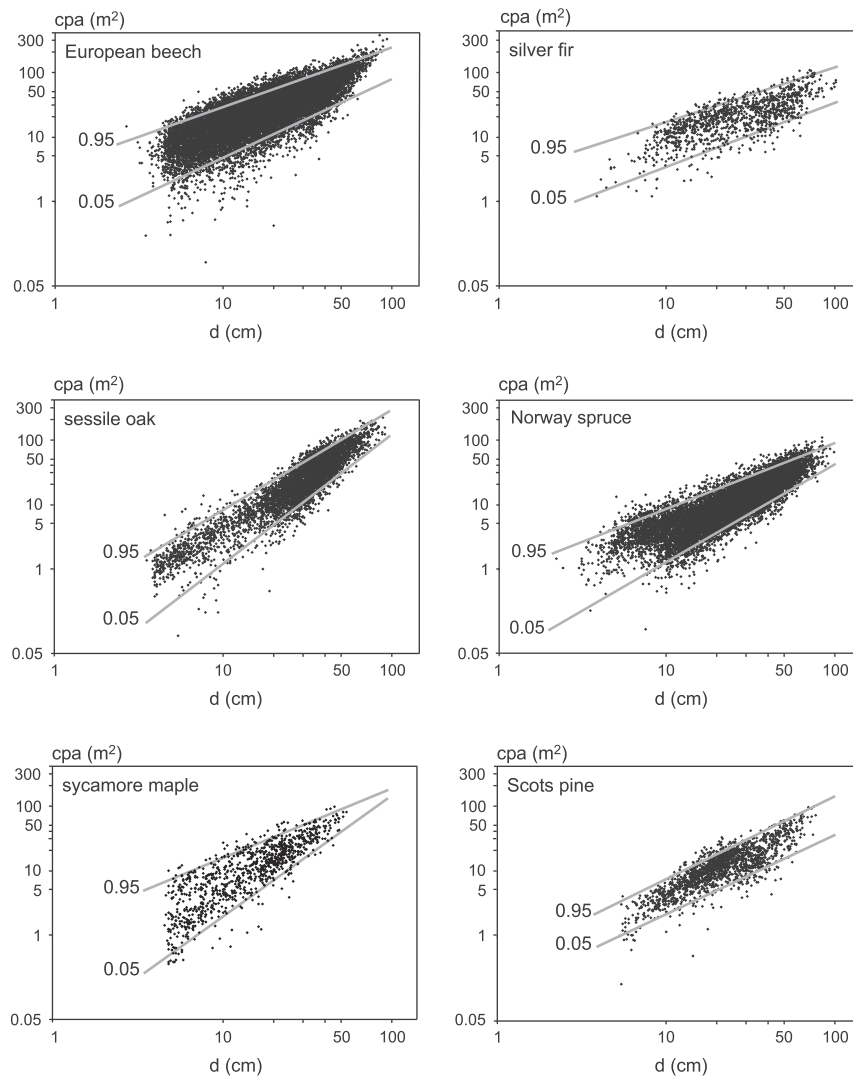


Fig. 6. Allometric relationships between stem diameter, d , and crown projection area, cpa , for European beech (*Fagus sylvatica* L.) ($n = 14,898$), Silver fir (*Abies alba* Mill.) ($n = 1079$), sessile/common oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) ($n = 4,485$), Norway spruce (*Picea abies* [L.] Karst.) ($n = 10,724$), sycamore maple (*Acer pseudoplatanus* L.) ($n = 942$), Scots pine (*Pinus sylvestris* L.) ($n = 1609$) in even-aged and uneven-aged stands. Observed range of crown dimensions on long term experimental plots which cover dense as well as very sparsely spaced stands. The upper and lower lines represent the 95% respectively 5% quantile-regression $\ln(cpa) = a + \alpha \times \ln(d)$. The width of the scattering and the distance between the 95% and 5% quantile regression represents the crown plasticity. The statistical characteristics of the quantile regressions are shown in [Online Resource 2-Table 4](#).

number and length of branches (Bayer et al., 2013; Lintunen and Kaitaniemi, 2010), the crown length and radius (Thorpe et al., 2010), and the crown shape (Schröter et al., 2012). In the following I try to broaden the knowledge about intraspecific morphological variability, by analysing crown measurements from long-term experiments in pure and mixed stands of Norway spruce and European beech in Germany (Pretzsch and Schütze, 2009).

2.3.1. Shift of crown allometry in interspecific compared with intraspecific environment

Crown projection area, crown length, and tree height measured on fully stocked long-term experimental plots in pure and mixed stands of Norway spruce and European beech in Germany (Pretzsch and Schütze, 2009) enable scrutiny of any shifts in tree morphology caused by interspecific versus intraspecific competition. Fig. 7a and b shows that the lateral and vertical crown extension of Norway spruce respectively European beech is higher in mixed versus pure stands. Especially in young and middle aged mixed stands where stand density and competition is at maximum, the crowns become wider and longer than in pure stands. In the

mature stand development phase crowns are less restricted and crown size becomes similar. The h–d allometry, in contrast, is hardly modified by species mixing. As crown measurements in young, densely closed stands are difficult and costly, the data base for trees ($d < 15$ cm) is limited and needs further extension.

In the pure stands scaling between cpa and d is significantly steeper (European beech $\alpha_{cpa,d} = 1.54 \pm 0.02$, Norway spruce $\alpha_{cpa,d} = 1.51 \pm 0.01$) as predicted by West et al. (2009) for the allometric ideal plant ($\alpha_{cpa,d} = 1.33$ in $cpa \propto d^{4/3}$) (see [Online Resource 2-Table 4](#)). In mixed stands, in contrast, the cpa – d -allometry is much shallower (European beech $\alpha_{cpa,d} = 1.08 \pm 0.01$, Norway spruce $\alpha_{cpa,d} = 1.20 \pm 0.01$). According to allometric theory (Enquist et al., 2009; West et al., 2009) scaling between hcb and d should be $hcb \propto d^{2/3}$. However, only beech in the mixed stand ($\alpha_{hcb,d} = 0.67$) behaves like the allometric ideal tree, and the other $\alpha_{hcb,d}$ exponents are mostly lower. The intercept differs considerably; crowns are significantly longer in mixed compared with pure stands.

Assumptions on general species-invariant scaling rules for crown morphology (West et al., 2009) may be useful for rough

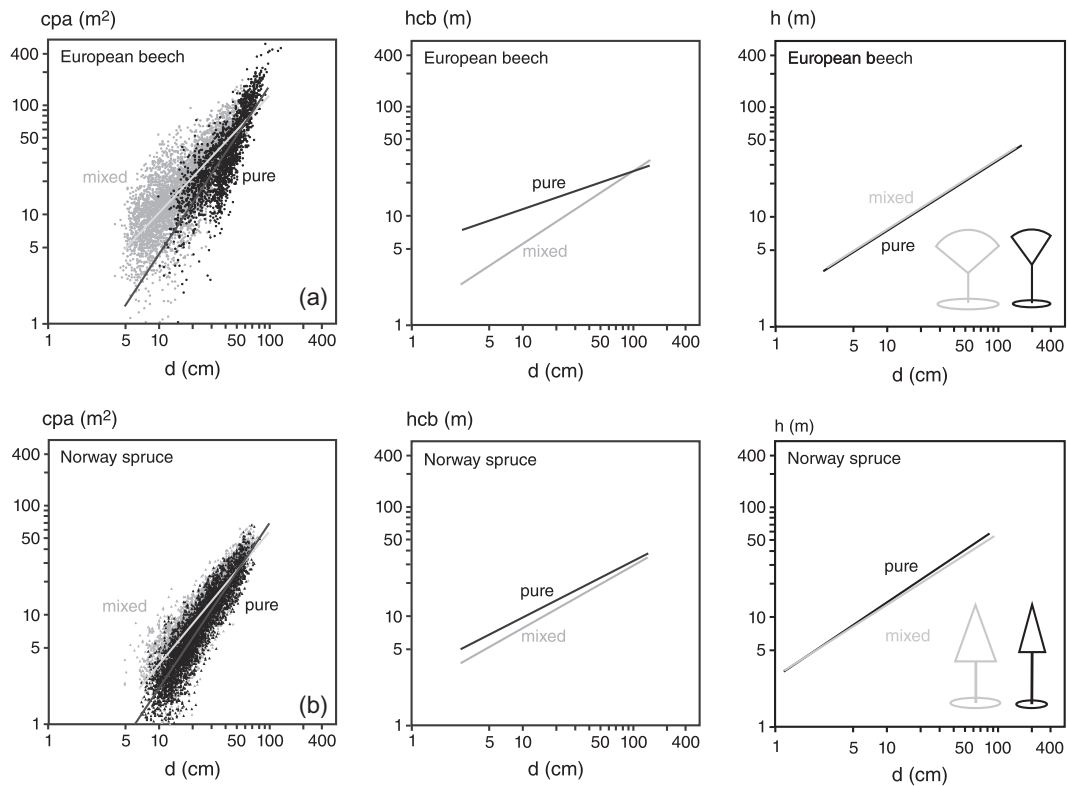


Fig. 7. Crown allometry of (a) European beech and (b) Norway spruce in even-aged mixed stands (grey) compared with even-aged pure stands (black). Mixing significantly increases lateral and vertical crown extension in terms of the relationship between crown projection area, cpa , and tree diameter, d , and height to crown base, hcb , and tree diameter, d . It hardly changes the relationship between tree height, h , and tree diameter, d (from left to right). The statistical characteristics of the regression lines are shown in [Online Resource 2-Table 4](#).

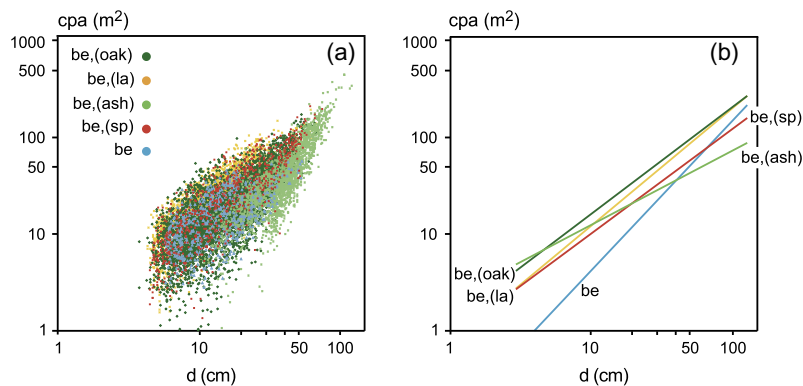


Fig. 8. Allometric relationship between crown projection area, cpa , and the tree diameter, d , for European beech in even-aged pure stands (be, blue) and shift of the allometry when beech is mixed with Norway spruce (be, (sp)), European larch (be, (la)), ash (be, (ash)), and sessile oak (be, (oak)). The data base comprises $n = 10,302$ tree crown measurements in even-aged stands (a) and reveals that crown allometry is significantly modified by the neighbouring species (b). The statistical characteristics of the regression lines are shown in [Online Resource 2-Table 4](#).

scaling of functions and structures of plants from organ to ecosystem level, however, for describing and modelling crown allometry they appear as oversimplification (Niklas, 2004; Pretzsch and Dieler, 2012). Especially in mixed stands variable rather than constant allometric scaling appears as prerequisite for the individual plants competitiveness. Individual tree models, especially when they are coupled with light models as developed by Brunner (1998), Stadt and Lieffers (2000), or Wang and Jarvis (1990) are suitable for considering the shown intraspecific crown variability when simulating 3D light distribution and growth in heterogeneous mixed species stands.

The capacity of coping with crowding, which trees probably developed under interspecific competition in co-evolution, become

triggered and obvious in mixed rather than in pure stands. This is shown by the following analysis, based on densely stocked stands with no or only light thinning. Analysis of $cpa-d$ -allometry of beech in pure stands compared with beech in mixture with Norway spruce, European larch, Common ash, and sessile oak in [Fig. 8](#) shows striking differences. While allometric scaling theory predicts $csa \propto d^{4/3}$ (i.e., $\alpha_{csa,d} = 1.33$) for the allometric ideal plant (West et al., 2009) the allometric exponent is at maximum $\alpha_{csa,d} = 1.54$ in pure beech stands and ranges between $\alpha_{csa,d} = 0.76$ (be, (ash)) and $\alpha_{csa,d} = 1.21$ depending on the species composition of the neighbours. Obviously, a neighbouring beech restricts the crown of a beech more than any other of the analysed species. For a beech with stem diameter 25 cm the allometric

Table 2

Lateral crown expansion of individual trees in even-aged mixed versus pure forest stands of Norway spruce and European beech (above) and sessile oak and European beech (below). The data comes from crown projection measurements on fully stocked experimental plots in Germany (explanation of variables see [Online Resource 3- Fig. 11](#)). Lowercase bold letters (**a** and **c**) behind the standard errors indicate that Welch two sample t-tests revealed significant differences (at level $p < 0.05$ and $p < 0.001$, respectively) between the species behaviour in mixed versus pure stands.

Species combination	N. sp. (E. be.) mixed	N. spruce pure	N.spruce mix/pure	E. be. (N. sp.) mixed	E.beech pure	E. beech mix/pure
n (trees)	4,634	3,623		4,845	3,173	
cpa/sa ($m^2 m^{-2}$)	1.22 (± 0.095) a	0.98 (± 0.042) a	1.24	1.84 (± 0.109) c	1.32 (± 0.073) c	1.39
r_{min}/r_{max} ($m m^{-1}$)	0.51 (± 0.026) c	0.43 (± 0.003) c	0.78	0.36 (± 0.027) c	0.38 (± 0.003) c	1.02
ecc ($cm cm^{-1}$)	1.80 (± 0.020) c	1.90 (± 0.030) c	0.95	5.70 (± 0.060) c	4.40 (± 0.060) c	1.30

Species combination	E. be. (s. oak) mixed	E. beech pure	E. beech mix/pure	s. oak (E. be.) mixed	s. oak pure	s. oak mix/pure
n (trees)	2,326	3,173	0.73	1,959	2,888	
cpa/sa ($m^2 m^{-2}$)	1.48 (± 0.192)	1.32 (± 0.073)	1.12	1.39 (± 0.207) a	0.90 (± 0.074) a	1.54
r_{min}/r_{max} ($m m^{-1}$)	0.35 (± 0.004) c	0.38 (± 0.003) c	0.88	0.38 (± 0.004)	0.38 (± 0.003)	0.88
ecc ($cm cm^{-1}$)	7.4 (± 0.110) c	4.40 (± 0.060) c	1.68	3.30 (± 0.050) c	3.10 (± 0.040) c	1.06

equation shown in [Fig. 8b](#) predicts a crown projection area of $cpa = 17 m^2$. Beeches with the same stem diameter achieve $cpa = 25 m^2$ when mixed with ash, and 27, 37, or even $45 m^2$ when mixed with spruce, larch, or oak, respectively. The ranking of neighbours regarding the effect on crown restriction is beech > ash > spruce > larch > oak. For European beech mixing with each of the other species means reduced competition regarding crown extension in the sense of [Kelty \(1992\)](#) and [Vandermeer \(1989, p 32\)](#). With other words, a neighbouring Norway spruce, sessile oak, or Scots pine means a relief in crown restriction compared with a neighbouring beech. This is in accordance with [Pretzsch and Biber \(2005\)](#) who found that self-thinning is the highest in pure beech stands and much lower in pure stands of the other tree species with the ranking European beech > Norway spruce > Scots pine > sessile oak.

These crown scaling exponents reflect that competition for resources and growing space requirement are species- and neighbourhood-specific and can change with size. Community ecology and population dynamics, silvicultural guidelines (e.g., regulation of mixing proportion), tree growth models for mixed species stands should consider such species specific morphological characteristics.

2.3.2. Variability of crown projection area in inter- versus intraspecific environment

Solitary trees achieve wide and, apart from a slight tendency towards ovality due to one-sided solar irradiation in northern or southern latitudes, rather circular crowns. Suboptimal environmental conditions, in contrast, can cause asymmetric structures ([Møller and Swaddle, 1997](#), pp. 85–100). The symmetry of their crowns indicates unimpeded lateral expansion or at least all-round homogeneous restriction by, for example, water, light or nutrients. When coping with crowding in stands, crowns reduce their lateral extension and more and more lose their symmetry indicating their restriction in growing space and resources. Plastic crowns can at least to some extent overcome their restriction by occupying emerging niches, penetrating neighbouring crowns, or even edging out neighbours. This expansion-driven asymmetry which enables occupation of additional space by directional lateral crown expansion should be distinguished from degeneration-driven asymmetry by die off and mechanical abrasion of branches and crown parts because of overwhelming competition.

In the following I use crown maps from pure and mixed stands of Norway spruce and European beech and sessile oak and European beech on long-term plots in Germany with 8-radii-crown measurements for scrutinizing differences between crown projection in intra- and interspecific environment. The variability of crown projection area can be characterised by three ratios.

The ratio cpa/sa between crown projection area, cpa , and stand area of an individual tree, sa , indicates the degree of crown engagement. The crown projection area, cpa , comes from 8-radii-crown measurements ([Pretzsch, 2009](#), pp. 115–118) and the individual tree stand area by delineation of Thiessen polygons around the individual tree by Dirichlet tessellation ([Pretzsch, 2009](#), pp. 313–314). A value of $cpa/sa = 1$ would indicate identity of cpa and sa . High values ($cpa/sa > 1$) indicate wide crown expansion reaching beyond the trees sa . Small cpa/sa values indicate a trees suppression and crown recession (see [Online Resource 3- Fig. 11](#)).

The ratio r_{min}/r_{max} between the longest and shortest of the 8 crown radii, r_{min} and r_{max} respectively, indicates the crown's rotundity. In [Online Resource 3- Fig. 11](#) the rotundity decreases (from left to right) with stand density due to growing competitive pressure. Crown eccentricity, $exc = \sqrt{(x_s - x_g)^2 + (y_s - y_g)^2}/d_{1.3}$ is based on the Cartesian coordinates of the stem position, x_s and y_s , and on the coordinates of the centre of gravity, x_g and y_g , of the crown, calculated on the basis of the coordinates of the corner points of the crown projection area ($x_g = \sum_{i=1}^8 x_i/8$, $y_g = \sum_{i=1}^8 y_i/8$). The distance between the tree position and the gravity centre of the crown is $\sqrt{(x_s - x_g)^2 + (y_s - y_g)^2}$. Deviation of this distance by the tree diameter eliminates size effects and makes different trees and species comparable. A measure of, e.g., $exc = 0$, 2.0 and 10.2 means that the gravity centre of the crown is perpendicular above the tree position ($exc = 0$), twice ($exc = 2$), or more than ten times ($exc = 10.2$) of the stem diameter deviating from the tree position (see [Online Resource 3- Fig. 11](#), from left to right). Notice, that in [Online Resource 3- Fig. 11](#) the trees' centre of gravity are represented by circles and the trees' stem foot position by the origin of the coordinate system.

By the ratios the crown engagement, rotundity, and eccentricity can be compared between mixed and neighbouring pure stands. The cpa/sa ratios in [Table 2](#) reflect that, except beech when mixed with oak, all three species can significantly expand their crowns laterally far beyond their stand area when growing in mixed compared with pure stands.

The ratio r_{min}/r_{max} reveals that compared with the other species beech crown projection areas are mostly less circular, i.e., more jagged. Mixing significantly increases the rotundity in case of spruce ($p < 0.001$), decreases the rotundity of beech ($p < 0.001$), and leaves the rotundity of the crowns of sessile oak unaffected.

The values of ecc are the highest for beech, especially when growing in mixed stands. Values of $ecc = 5.7$ to 7.4 mean that beeches have plastic crowns for resource capture even distant from their stem position. The measures show that crown morphology can significantly shift from intra- to interspecific competition and trigger the space occupation of the combined species in a species

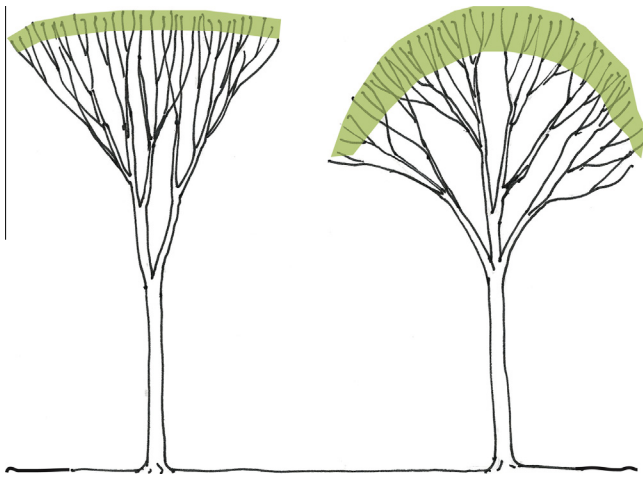


Fig. 9. Schematic representation of (left) broom-like crown structure of adult European beech in even-aged pure stands and (right) bouquet-like crown structures in mixed stands with spruce (according to [Arz, 2013](#)). Beeches when growing in mixture with spruce (right) have significantly less and shorter branches of first order but nearly the twofold number of branches of second and third order. Their angle of the branches is flatter and the crown volume higher in mixed versus pure stands (see [Bayer et al., 2013](#)).

specific way. Mixing increases the crown eccentricity of both beech ($p < 0.001$) and oak ($p < 0.001$) but fosters the centricity in case of Norway spruce ($p < 0.001$).

2.3.3. Species mixing and inner crown properties

Tree crowns as described by [Oldemann \(1990\)](#), [Purves et al. \(2007\)](#), and [Roloff \(2001\)](#) lie somewhere in the continuum between the borderline cases of an umbrella-like crown with most of the leaves allocated close to the convex hull (fractal dimension of the crown surface area $n = 2$) and a bouquet-like crown with leaf surface area distributed all over the crown space (fractal dimension of the crown surface area $n = 3$) ([Zeide, 1998](#)). Terrestrial Laser-scanning (TLidar) and subsequent skeletonization of tree crowns based on the pixel patterns revealed significantly different inner crown structures in mixed versus pure stands of Norway spruce and European beech. [Bayer et al. \(2013\)](#) showed that even when similar in stem diameter and tree height, beeches growing in mixture with spruce had significantly less and shorter branches of first order and because of stronger ramification nearly the twofold number of branches of second and third order compared with pure stands. The added total length of all branches within a crown was higher in mixed compared with pure stands. The angle of the branches was flatter, their bending stronger and the crown volume higher in mixed versus pure stands. The schematic representation in [Fig. 9](#) accentuates the umbrella-like crown shape of beeches when growing in intraspecific interaction (left) with most of the leaf area allocated close to the top of its convex hull. In interspecific environment it is rather bouquet-like (right) with the leaves reaching deeper into the crown volume ([Arz, 2013](#); [Bayer et al., 2013](#)). In case of beech species mixing can obviously modify the fractal dimension of the crown surface area and leaf area from a lower space filling (Euclidian scaling) towards higher space filling of the crown volume (fractal scaling) ([Pretzsch and Dieler, 2012](#)).

3. Conclusions and perspectives for further research

The overwhelming crown plasticity, inner crown variability, and competition superiority of European beech compared to other native trees species applies in particular to its physiological

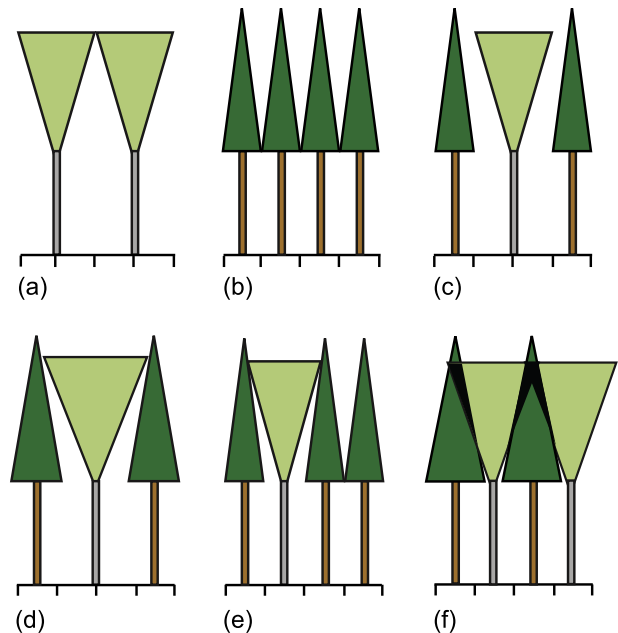


Fig. 10. Potential effects of species mixing on the canopy space filling in even-aged stands when tree crowns have complementary shapes. When two species with complementary crown shapes (a and b) are mixed and keep their shape and space occupation the mixing effect in terms of space filling is simply additive (c). In many cases species mixing enables a wider crown expansion (d), higher stand density (e), or a combination of both (f). The cases (d)–(f) indicate a multiplicative mixing effect by denser canopy space filling.

optimum under mild climatic conditions and on fertile soils which are well supplied with water. On such sites European beech would probably cover more than 2/3 of the Central European forest area ([Bohn et al., 2003](#)). However, since human influence on European forests beech has been severely decimated by clearings for agricultural land or, during the last centuries, by replacing them in the forest by faster and straighter growing conifers such as spruce, fir, or pine species ([Mantel, 1961](#)).

On sites were combinations either of drought and warmth or moistness and low temperatures restrict the growth of beech ([Leuschner, 1998](#)) it cannot bring to bear its high plasticity and efficient space occupation. That applies to the mixed mountain forests in the montane and subalpine zone in Europe (600–1400 m a.s.l.) where beech is often associated with Norway spruce and silver fir. As they are more difficult to access and to harvest, mixed mountain forests were often managed much more extensively and left in a more natural species composition.

Lowland forests at the northeast or southwest border of its natural range, where beech would naturally occur in mixed stands, were exploited much more intensively and mostly converted to age-class-systems on the expense of European beech.

Presently beech is strongly on the advance and becoming the pillar of close-to-nature forestry in the central European lowland, where it once dominated ([Pretzsch et al., 2010, 2013b](#)). There its cultivation in mixed-species stands elucidates and recalls its high competitiveness. In the long term added species such as oak, pine, or spruce could hardly persist without being supported by tending or thinning.

3.1. Conclusions

Mixing of species with varying physiological and morphological traits causes a species selection effect but beyond this may lead to

denser canopy space filling, completer light interception and productivity gains (Forrester et al., 2006; Pretzsch and Schütze, 2005). Suppose the species' behaviour in terms of crown structure and growth remains like in the pure stand (Fig. 10a–c) this would indicate a mere species selection effect without interaction. Any changes of tree crown morphology and canopy structure in interspecific versus intraspecific environment underline that the mixing effect goes beyond a merely selection effect.

The presented tree properties emerging in interspecific in contrast to intraspecific competition indicate that crown expansion may be wider (Fig. 10d), the tree packing density higher (Fig. 10e), or both reactions may be combined (Fig. 10f) causing higher stand density and denser canopy space filling by crowns (Pretzsch et al., 2013a). On top of that, mixing can change inner crowns properties such as branch length, branch angle, number of branches, and their straightness. This morphological plasticity may result in crown and canopy structures in mixed stands which differ considerably from those observed or predicted by theory in pure stands.

The revealed morphological plasticity of tree crowns contradicts allometric theory which predicts species overarching allometric exponents, e.g., $\alpha_{cpa,d} = 4/3$ for the relationship $cpa = a \times d^{2\alpha_{cpa,d}}$ for the allometric ideal plant (Enquist et al., 2009; West et al., 2009). Our analysis showed – in accordance with theory – a broad intra- and interspecific variation of the allometric factor a which represents plant shape and form. But it further showed – in contrast to theory – that the allometric exponent α is species specific in pure stands and on top of it dependent on the neighbouring species in mixed stands. Factor a represents a multiplicative effect of species on the crown expansion. Species specific differences of exponent α mean an exponential difference in the dynamic of the crown expansion with increasing size. Community ecology and population dynamics, silvicultural guidelines (regulation of mixing proportion) and tree growth models for mixed species stands should consider those species specific characteristics of crown shape and scaling.

From research in pure stands it is well known that crown and stem morphology determine wood quality (Rais et al., 2014). So far knowledge of the effect of species mixing on wood quality is very rare although mixed species forests are on the advance (Olsthoorn et al., 1999; Puettmann et al. 2009). In pure stands outer crown and stem characteristics (e.g., crown length, crown width, h/d-value) and inner wood structure and quality (e.g., size and frequency of branches, specific gravity) proved to be so closely correlated, that variables such as h/d-ratio or crown length can be used as proxy variables for wood properties (Øvrum, 2013). Our findings of wider, longer, and often more asymmetric and eccentric crown shapes suggest negative effects of mixing in wood quality. Less and shorter first order branches, more horizontal branch angles and unmodified h/d-ratios might reflect positive or at least neutral effects of mixing on wood quality. Combined analysis of inner and outer properties of crowns and stems are required for further clarification.

Crown properties emerging in interspecific environment are extremely relevant for further development of individual-based growth models. That applies especially for modelling tree growth in temperate climate where trees remedy light limitation by morphological acclimation. In individual-based models, crown size affects both the growth of the particular tree and the light supply and growth of its neighbours. Thus weakness of crown models, e.g., underestimation of crown expansion and plasticity, may result in underestimation of the competitive strength, persistence, and growth of this species by growth and yield models. Furthermore the 3D structure of the stand, the vertical light profile and according mode of competition, as well as the predicted stand productivity might be flawed.

The reviewed literature (Bauhus et al., 2004; Bayer et al., 2013; Dieler and Pretzsch, 2013) and presented own data in this study showed that trees with a given diameter or height can have contrasting crown architectures in mixed stands compared with monocultures. How exactly these architectural differences (e.g., larger crown width or longer live-crown length) as well as differences in canopy structure (e.g., canopy stratification) may change APAR and finally growth in mixed compared with pure stands require further analysis. Statistical analysis of the relationships between crown characteristics and tree growth or canopy characteristics and stand growth in mixed and pure stands may reveal the relevance of the shown contrasting crown and canopy structures in terms of productivity gains or losses. Application of eco-physiological models such as MAESTRO (Wang and Jarvis, 1990) may provide better understanding and evidence of the underlying mechanism (le Maire et al., 2013).

Differences of crown morphology and canopy structure between mixed and pure stands and prognosis errors by ignoring such differences are probably most significant in young to middle aged stands (Figs. 7 and 8) where stand density and the trees coping for crowding is at maximum. Emergent crown properties may be the main reasons why predictions with individual tree models – as long as parameterized for pure stands – mostly differ from observations in mixed stands. This can be remedied by integrating crowns models which are sensitive to intra- and interspecific environment regarding both crown shape and crown scaling.

3.2. Perspectives for further research

So far tree crowns were mostly measured and abstracted regarding their convex hull. Refined and successively repeated measurement of their amorphous surface, their interlocking, and inner structure by TLidar (Dassot et al., 2011; Côté et al., 2012) promise further insight into species specific behaviour of space occupation, resource capture, and growth in pure and especially in mixed stands. By integrating crown models which depend on the local environment within the stand (e.g., on the neighbouring species and stand density), individual tree based models might be essentially improved. Structures are mostly easier to record than processes, however, their contribution to better understanding how individual trees grow, how they interact with their local environment, and how the stand dynamics results from the feedback between tree and stand level is far from being exhausted.

As most processes, functions, and services in ecosystems (e.g., water interception, light interception, animal habitats, wood quality, or landscape aesthetic) base on, result in, or are indicated by structure, a refined analysis of canopy space filling and tree crown structure is of interdisciplinary relevance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.04.027>.

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