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Wood quality in complex forests versus even-aged monocultures: review and perspectives

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Abstract As they fulfil many ecological and social functions and services better than even-aged monocultures, heterogeneous pure and mixed-species stands are on the advance in Central Europe. Even so, knowledge of how different stands compare in terms of the quantity and quality of the produced wood remains limited, as forest research has been focused on pure stands in the past. Therefore, the still limited comparative studies on timber quality in mixed versus pure stands were reviewed. Further, approximately 100 studies on the morphology of mixed versus pure stands have been reviewed. As is known, the close connection between morphology and timber quality from many studies in pure stands as well as the morphological and structural properties of trees in mixed stands is used as proxies for their timber quality. The number of studies reporting a decrease or increase in timber strength and stiffness in complex stands compared with homogeneous stands was balanced. Knottiness is mostly higher in complex stands. Wood density behaves indifferently. Distortion, as indicated by eccentricity of crown, bending of stems, or irregularity of the tree-ring width, is generally higher in complex forests. This rather ambiguous pattern becomes clearer by typifying the findings depending on the species-specific morphological plasticity of the trees and the spatial conditions they are exposed to. When growing in strong lateral restriction in even-aged pure or mixed-species stands (type 1), trees follow a "keep abreast" strategy which results in high-quality

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timber especially in case of species with low plasticity. Trees in uneven-aged forests with vertically restricted growing space (type 2) often use a “sit-and-wait” strategy that may result in tapering stem shapes, wide and long crowns with low branch diameters, and high wood density. Distortion may be low in case of species with low morphological plasticity but increase with increasing shade tolerance and plasticity. Growth in widely spaced and heavily thinned pure and mixed stands (type 3) may let trees follow the “stabilisation” strategy. Because of their strong dominance, these trees develop tapering stem shapes, knots of big size and wide appearance along the stem axis, as well as lower wood density, especially in the case of conifers. In arrangements of types 1–3, the “transition” strategy may also emerge, which leads from the “sit-and-wait” stadium to the “keep abreast” strategy. It starts when trees strongly increase their height growth at the expense of the stem diameter growth. It results in slender stems, low knottiness, high wood density, and low distortion, with the result that the tree gets access to the upper canopy at the expense of lateral expansion of stem and crown. In fact, it is not primarily the species mixing that modifies the morphology, structure, and wood quality of the trees but the species-specific morphological plasticity and the structural heterogeneity of the stand. The latter is often higher in mixed than in pure stands and in uneven-aged than in even-aged stands. The more variable the stand structure, the wider the range of wood attributes. The discussion is focused on the relevance of the results for stand management and interdisciplinary research at the intersection of forest growth and yield science and wood science.

Introduction

Because heterogeneous pure and mixed-species forest stands fulfil many ecological and social functions and services, better than even-aged monocultures (Gamfeldt et al. 2013; Hector and Bagchi 2007), they are being increasingly used in Europe (Agestam et al. 2006; Johansson 2003; Rametsteiner and Mayer 2004). Even so, knowledge of how pure and mixed-species stands compare in terms of the quantity and quality of the produced wood remains limited. Past research has mainly focused on pure stands (Puettmann et al. 2009). Forest owners and wood-processing companies require more information on how the ongoing transition from even-aged monocultures to more complex forests modifies tree structure and timber quality.

Components of wood quality result from the tree’s phenotype, which is determined by both the genotype and the environmental conditions, i.e. the species-specific morphological plasticity and spatial arrangement within the stand (Assmann 1970). The genotype depends on the provenance of the chosen plants in the case of artificial stand establishment and the available seed trees in the case of natural regeneration (White et al. 2007). The individual trees’ growing conditions (resource supply, environmental factors) strongly depend on the surrounding stand structure (Pretzsch 2014; Río et al. 2016). Wide spacing and crown release by heavy thinning can increase light supply and foster crown width and length (Curtis and Reukema 1970; Maguire et al. 1999). Suppressed trees in the understorey, in contrast, may react to the light limitation by lateral rather than vertical crown extension.

Intermediate trees may suffer mechanical abrasion of their crowns by taller neighbours (Putz et al. 1984). Morphologically plastic- and shade-tolerant species such as European beech may forage for light more expansively than a straight-growing light-demanding species such as Scots pine (Purves et al. 2007). Branches will extend as far as light and physical space will allow them (resource supply), given the species shade tolerance (depending on, e.g. light compensation point), branching tendencies (genetic plan), and allometry (morphological and physical boundaries). The same applies to root development with respect to water and mineral nutrients, drought tolerance, and rooting depth (Körner 2005).

The effect of the growing space and structural arrangement of the neighbourhood of trees on tree development in homogeneous pure stands has long been the subject of analysis. Spacing and thinning experiments in pure stands highlight the strong effect of the surrounding spatial stand structure on tree growth and morphology and, ultimately, wood structure and timber quality. Many spacing experiments (Reukema and Smith 1987), most clearly those based on Nelder's design (Spellmann and Nagel 1992), and numerous thinning experiments (Baldwin et al. 2000; Kantola and Mäkelä 2004) show a strong decrease in slenderness (*h/d* ratio) when stand density is reduced. Studies where density reduction did not affect slenderness (Pretzsch 2014; Bayer et al. 2013) or even caused it to increase (Saha et al. 2012) are exceptions. The crown ratio ($cl/h =$ crown length/tree height) and crown projection ratio ($cd/d =$ crown diameter/stem diameter) in all reviewed studies increased when stand density was reduced (see, e.g. Hynynen 1995; Longuetaud et al. 2008 for *cl/h*; Metzger 1998; Pretzsch 2014 for *cd/d*). According to all reviewed works, the stem form factor—that is normally used in forest practise for calculating stem volume in addition to the height and to the diameter at breast height—is distinctly reduced by spacing and thinning (e.g. Van Miegroet 1956; Pinkard and Neilsen 2001; Wiedemann 1951). Especially for morphologically plastic species such as beech and oak, competition release can improve the roundness of the crown cross section and reduce its eccentricity (Bleile 2006; Longuetaud et al. 2008). With a few exceptions (e.g. Medhurst and Beadle 2001), wider spacing and stronger thinning always significantly increased the number of living primary branches per tree (e.g. Maguire et al. 1991; Schumacher et al. 1997; Pinkard and Neilsen 2001), which is in line with the higher crown ratio. Mean and maximum branch length and diameter increase significantly with competition release by spacing or thinning (see Deleuze et al. 1996; Kantola and Mäkelä 2004 for branch length; Spellmann and Nagel 1992; Seeling 2001 for branch diameter). Spacing and thinning frequently reduce the wood density of conifers (Bues 1985; Grammel 1990; Hapla 1985) but leave deciduous trees mostly unaffected (e.g. Metzger 1998). The heterogeneity of wood caused by compression wood (Seeling 2001), variability of tree-ring width (von Pechmann 1954; von Pechmann and Courtois 1970), and resin pockets (Bücking et al. 2007; Schumacher et al. 1997) often increases with the degree of both thinning and spacing.

In principle, this dependency of tree shape on the spatial structure of tree surroundings applies to pure as well as mixed stands. The main difference is that many even-aged pure stands provide more homogeneous structures, while uneven-aged mixed stands contain a broader spatial variety and more diverse and irregular structures. Uneven-aged pure stands may lie somewhere in between regarding structural heterogeneity. Thus, in principle, there is no difference in the growth reaction of individual trees in pure and mixed stands; however, the frequency of homogeneous or rather heterogeneous spatial structures surrounding individual trees and thus the variation in resource supply and the variation in morphological shapes may be broader. In particular, in mixed (complex) stands, gaps in the canopy occur more often and can advance regeneration or improve insufficient light access for understorey trees.

In North America and Europe, approximately 15 % of the harvested timber is used for energy production. According to the Food and Agriculture Organization of the United Nations (FAO), the majority of harvested wood, however, goes to the construction industry to produce sawn timber and veneers (approximately 60 % in North America and Europe). Different end products will demand specific raw material wood, and buyer preferences vary according to the product that is made from wood. For instance, there are few requirements if timber is used as fuel wood. A high wood density improves the gross calorific value but is the only characteristic of importance. In contrast, for the production of paper, whether pulp manufacturing or wood-based panel production, the requirements for the material increase. However, the macrostructure is destroyed by these applications during processing. The requirements for the raw material therefore have more impact on the smooth production flow, not on the final product. Consequently, quality requirements vary, going so far that if the wood properties for a particular end-use are suitable, they may exclude any other use.

In this review, focus is put on the use of wood in the field of construction. For structural use, timber quality is crucial and usually clearly defined using indicators such as strength grades which mainly depend on knottiness, density, and the dynamic modulus of elasticity, which are predictors for strength and stiffness (Bacher and Krzosek 2014). It is not focussed on wood properties which influence the surface and appearance of wood and which are relevant for the consumer, especially when timber is used as furniture. People want to have a perfect product without irregularities or defects. For example, a uniform annual ring structure is much more relevant for veneer wood applications. The requirements for appearance-graded timber are less strict and cannot be defined as accurately and objectively as for strength grading. With this chosen definition of wood quality, most other quality requirements are automatically covered.

Although complex mixed stands are increasing, our knowledge of them is rather scarce, for example, what timber quality they will yield compared with pure stands and how techniques of stand establishment, spacing, and thinning can modify their timber quality in the future. The approach of this review was to summarise existing knowledge based on the authors own works and extant literature about tree structure, stem morphology, and timber quality. For that purpose, the authors (1) selected the most relevant variables for timber quality and traits of tree structure and stem morphology which indicate timber quality, (2) reviewed the effect of tree species mixing on those timber quality variables, (3) revealed the heterogeneity of growing space in pure and mixed stands as a main cause of timber properties, and (4) concluded how forest management and forest science should incorporate timber quality in view of the ongoing tendency towards more natural, complex, and heterogeneous forests.

Concept and variables of the review describing the impact of tree species mixing on timber quality

The most important requirements for structural timber can be separated into two groups. First, there are wood properties that directly determine the grade, such as strength, stiffness, and density (structural requirements). These parameters are common worldwide (density is less important for countries other than Europe) to define grades and are further used for the design process. On the basis of board parameters such as knots and annual ring width (visual grading) or grain deviation, eigenfrequency, deflection, and wood density (machine grading), these grade-determining properties are estimated by known relationships. Second, there are wood properties (utility requirements) which primarily affect the usability of sawn timber such as moisture content, distortion, and heterogeneity of wood structure. Therefore, when examining previous investigations, the relevant wood characteristics were strength, stiffness, knottiness, density, distortion, and wood heterogeneity.

Strength such as bending, tensile, and shear strength can only be quantified destructively; therefore, it is estimated by timber characteristics such as wood density and knots (Hanhijärvi and Ranta-Maunus 2008). Stiffness can be described by the static and dynamic modulus of elasticity (Rais and Van de Kuilen 2015). Knots are the most important strength-reducing characteristic, especially for softwood, and can be quantified visually or by optical and X-ray scanning (Hanhijärvi and Ranta-Maunus 2008). Wood density correlates well with both hardness and abrasiveness and is usually measured by weight and volume or X-ray scanning (Beall 2007). Timber distortion increases with the heterogeneity of the ring width pattern, for example, due to spacing, thinning, fertilising, stress events, or alternating climate conditions. It can be characterised by different types of warps, such as twist, cup, bow, and spring (DIN 4074-1 2012).

To build a sound basis for this review, Google Scholar and Web of Knowledge were searched (keywords: wood quality, timber property, tree morphology, tree structure, tree allometry, mixed-species stands, close-to nature forestry, and complex forest stands), corresponding inquiries were sent to a total of 12 colleagues (see acknowledgement), and the authors' own research works were also used.

Using direct wood quality and proxy variables

To compile as much knowledge as possible of the influence of the complexity of forest stands on sawn timber quality, the approach illustrated in Fig. 1 was developed. First, it was searched for a direct link between complex mixed forests and sawn timber properties such as strength, stiffness, or knottiness. It was asked whether publications were available that investigated direct wood quality variables (*D*) in view of complex forest structures? All selected direct wood quality variables

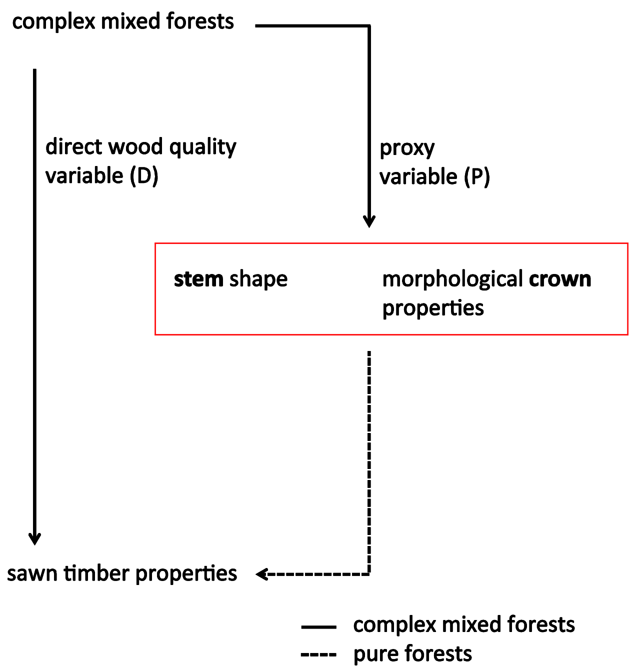

Fig. 1 Impact of mixed forests on wood quality can be described by direct wood quality variables (*D*) and by proxy variables (*P*)

are inherent parts of strength-grading standards around the world. For all *D*s, it was sought to sketch, variable by variable, how a variable differs in complex mixed forests versus monocultures. Unfortunately, present studies comparing, for example, mixed and neighbouring pure stands regarding direct wood quality variables were rare (see Supplementary Material S1).

In order to bridge those knowledge gaps, auxiliary allometric relationships between tree or stand structure and sawn timber properties were derived. As wood quality had to be approached from this perspective, several sections of this review deal with tree morphology, tree structure, stand structure, growth, and yield. In this way, knowledge gaps, which must be remedied by future research, were temporarily bridged.

There are relationships of these sawn timber properties with log, stem, trees, and stand characteristics that enable the use of inventory data for indirectly estimating sawn timber properties. Such characteristics are called proxies (P), as they provide information about sawn timber indirectly. Two categories of proxies can be identified: stem attributes and crown attributes. In such studies, wood properties did not describe the end-product quality for sawn timber, but wood attributes were defined at this stage for log or stem. Typical stem shape attributes are stem eccentricity, stem taper, and slenderness. Morphological crown attributes are crown diameter, crown length, and crown eccentricity. Such proxy variables were frequently measured in investigations of mixed stands but were reported mostly for other purposes. On the other hand, there were analyses of these proxies—mostly from pure monocultures—which indicated a correlation with one or more of the direct wood quality variables.

Use of proxies as measure of timber quality

What characteristics must a proxy (P) have? First, a connection between the proxy and the timber quality should exist. Second, a connection between the proxy and complex stand characteristics should exist. Third, the proxy should be measurable. Finally, it is also advantageous if this proxy is often used for research areas with different objectives (inventory, climate research).

Stem shape is generally used as an indicator for the predisposition to wind and snow damage (Wilson and Oliver 2000; Harrington et al. 2009). Stem shape can be affected by silvicultural treatments (Brazier 1977) and is also influenced by the tree class, namely whether the tree is dominant or suppressed (Brüchert et al. 2000). The stem or log shape can be described well in different ways which can be transformed into each other: the height-to-diameter (*h/d*) ratio (slenderness) and the taper (Fig. 2b). By means of the latter, it is possible to switch between the tree- and log-level. Figure 2 illustrates the suitability of slenderness as a proxy variable. The results are from a previously unpublished study about a sample of approximately 160 Douglas-fir trees [*Pseudotsuga menziesii* (Mirb.) Franco]; the data came from two experimental spacing and thinning trials in Germany as part of the Bavarian network of long-term forestry research plots. The Douglas-fir trees are 40 years old. The mean slenderness throughout a tree's life is influenced by the initial plant density (Fig. 2a): high establishment spacing leads to less slender trees. Furthermore, slenderness and sawn timber quality are strongly correlated ($r^2 = 0.52$, Fig. 2c). The mean strength of a tree describes the non-destructive strength, determined by the grading machine GoldenEye-706 and calculated as the mean value of all boards cut from the tree.

Many studies identify the stem shape as a good indicator of the quality of wood. For different conifers, slenderness and taper predicted timber stiffness at the level of forest stands (Øvrum 2013) and even at the level of individual trees (Roth et al. 2007; Lasserre et al. 2009; Lindström et al. 2009; Lenz et al. 2012; Searles 2012;

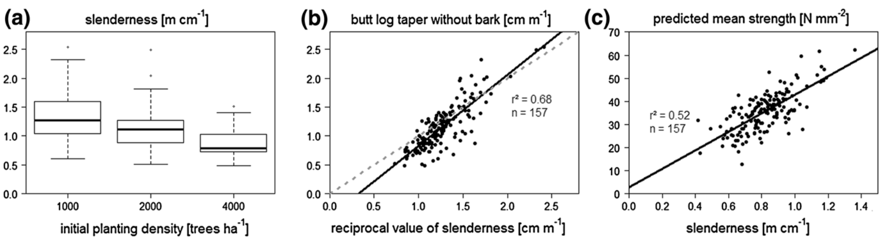

Fig. 2 Slenderness as a proxy is affected by initial planting density (**a**) and affects sawn timber strength (**c**). The slenderness of a tree is transformable to the taper of logs (**b**). Tree slenderness is higher among low establishment spacing. Trees of high slenderness are characterised by high sawn timber strength (Rais 2015)

Sattler et al. 2014). An analysis of Douglas-firs showed a strong dependency between the mean tree slenderness and the mean sawn timber strength of an individual tree (Rais 2015).

Other investigations have also demonstrated that timber strength can be effectively predicted by tree slenderness (Reukema and Smith 1987; Kijidani et al. 2009; Lindström et al. 2009). As noted above, the social situation of a group of trees must be considered for a detailed analysis. Understorey trees that grow up with shelter are characterised by increased slenderness (Bergqvist 1999). Admixing species of the same age results in the more dominant tree species reacting with a lower *h/d* ratio (Erickson et al. 2009). Similarly, Scots pine stems tapered more in the mixture than in the monoculture (Lindén and Agestam 2003), where Scots pine was the dominant tree species in a pine-spruce mixed stand.

Because this approach was crucial for the current study, the authors want to provide another example: knottiness is an important quality variable for sawn timber (Glos and Tratzmiller 1997; Seeling 2001; Stapel and Van de Kuilen 2013). Studies about the effect of mixing on knottiness were missing, so it was additionally looked for investigations about branchiness because the diameter of a branch is closely related to the knot size. Finally, if studies on the effect of mixing on the crown diameter or crown projection were available, an auxiliary allometric relationship between crown diameter, branch length, and branch diameter was derived, and the crown diameter was used as a proxy for knottiness/branchiness (Moore et al. 2009).

Growth and yield simulators with the capacity to evaluate wood quality use the empirically discovered relationships between stand, tree, and wood characteristics. Simulations allow for scenario analyses how silvicultural measures such as stand density management affect wood quantity and quality (Weiskittel et al. 2011).

As a key element of all of these models, crown dimensions have been included in individual-tree growth models because the crown links tree growth and sawn timber quality (Briggs and Fight 1992; Houllier et al. 1995; Mäkelä et al. 2010). Due to its role in carbon acquisition and shading, the crown is the main location of tree interaction (e.g. photosynthesis) and largely determines the growth of other tree components. In a growth quality model approach, the crown shape is a likely candidate to predict wood quality through the relationships among crown dimension, branch length, branch diameter, and knottiness, as indicated by studies that demonstrated the impact of thinning on both crown diameter and branch length (Curtis and Reukema 1970; Maguire et al. 1999; Weiskittel et al. 2007).

Pioneering work which focused on individual-tree models was performed by Newnham (1964), who developed a mathematical model to describe the growth of trees in stands of Douglas-fir. A more complex approach was taken some years later by Mitchell (1975), who incorporated many relationships into a dynamic model (TASS, “tree and stand simulator”). TASS was developed in Canada and upgraded by adding various modules up to the present. For example, SYLVER (“silvicultural treatments on yield, lumber value, and economic return”) integrates silviculture and end-product value (Mitchell and Cameron 1985; Mitchell 1988; DiLucca 1999). Another important growth and yield model which can predict wood quality attributes under various management strategies is ORGANON, which was developed in Oregon, USA (Hann et al. 1997). The output of ORGANON provides, among other variables, crown profiles, taper, height-to-diameter ratio, or diameter increment, which can be applied as inputs to run the timber property models (Maguire et al. 1991) and a subsequent economic evaluation (Briggs and Fight 1992). In Europe, model systems that integrate both growth and wood quality information were developed for softwood by Mäkelä (1997, 2002), Mäkelä and Mäkinen (2003), Colin and Houllier (1991), Houllier et al. (1995), Leban et al. (1996), Hein et al. (2009), Ikonen et al. (2009), Auty et al. (2014). Goulding (1994) and Grace and Pont (1999) modelled the growth and timber quality of *Pinus radiata* in New Zealand.

Evidence of the effect of tree species mixing on timber quality

Overview of the results of the literature review

Table 1 summarises the outcome of the mini-review of approximately 100 publications about wood quality in complex forests versus even-aged monocultures (see Supplementary Material S1). It provides an overview of how mixing and heterogeneity of structure modify the crown and stem structure and can be assigned to four main aspects of timber quality: strength and stiffness, knottiness, wood density, and distortion (first column of Table 1). Some subitems correspond to more than one of the main aspects, i.e. the compression wood of conifers, as the type of reaction wood affects strength and stiffness as well as distortion. The subitems are assigned to what is felt as the most relevant aspect.

Direct analyses of the effect of heterogeneous versus homogeneous stand structures on the strength and stiffness of sawn timber are very rare. A sample size of $n = 2$ allows no general statement (Table 1, line 1). By contrast, many studies ($n = 80$) on the effect of stand structure on slenderness were found. In more than 41 % of the analysed complex forests, the *h/d* ratio was lower than in the homogeneous reference stands, which is probably the result of a competition release by mixing a complementary species. Hence, in approximately the same percentage (44 %) of the analysed complex forests, the *h/d* ratio was higher; according to Table 1, species mixing leaves slenderness and form factors were unaffected in only 15 % and 17 % of species, respectively. The 44 % of cases when *h/d* ratios are higher refer mostly to deciduous trees such as beech, oak, and ash when competing with fast-growing conifers with strong vertical orientation (Table 1, see section strength and stiffness).

Structural heterogeneity mostly increases variables, indicating knottiness, such as crown ratio, crown projection area, and branch diameter (Table 1). A more heterogeneous vertical structure enables deeper light penetration so that leaves and branches grow deeper down in the canopy, and the position of the lowest leaf is much lower in mixed compared with pure stands. An increase in variables was observed describing crown size and branch size in approximately two-thirds of all studies (Table 1, see section on knottiness). Wood density remains largely unaffected by species mixing (78 %) (Table 1, see section on wood density).

Table 1 Results of the review of more than 100 publications on the effects of stand heterogeneity based on direct "*D*" variables or proxy "*P*" variables of wood quality. The table reflects how often the decrease, equality, and increase in tree attributes such as slenderness, crown projection ratios, were found in complex mixed stands versus homogeneous pure stands

Variable name	Direct variable or proxy	Abbreviation	Unit	Sample size	Frequency (%) of reported impact of complex stands on wood properties compared to homogeneous stands		
	D or *P*				Decrease	Neutral	Increase
Strength and stiffness							
Strength and stiffness	*D*	f_m, E_m	N mm^{-2}	2	50	50	0
Slenderness	*P*	h/d	m cm^{-1}	80	41	15	44
Form factor	*P*	v_s/v_c	m^3 m^{-3}	12	33	17	50
Knottiness							
Crown ratio	*D*	cl/*h*	m m^{-1}	44	14	16	70
Crown projection ratio	*D*	cd/*d*	m cm^{-1}	31	23	3	74
Branch diameter	*D*	db	cm	15	27	13	60
Branch length	*D*	lb	m	7	14	15	71
Number of branches	*D*	nb	per tree	7	43	0	57
Wood density							
Wood density	*D*	*R*	g cm^{-3}	9	11	78	11
Distortion							
Crown eccentricity	*P*	dist/*d*	m cm^{-1}	14	21	7	72
Roundness of crown	*P*	r_{min}/r_{max}	m m^{-1}	9	45	22	33
Stem bending	*P*	*b*	cm	15	27	0	73
Reaction wood	*P*	*c*	% $\%^{-1}$	6	17	0	83
Ring width variability	*P*	cv_{ir}	%	15	33	0	67

Bending strength f_m, static bending modulus of elasticity E_m, tree height *h*, tree diameter *d*, volume stem v_s, volume reference cylinder v_c, crown length *cl*, crown diameter *cd*, crown length *cl*, branch diameter *db*, branch length *lb*, number of branches *nb*, wood density *R*, distance between stand point of tree and centre of gravity of the crown *dist*, minimum and maximum radius of the eight crown radii r_{min}, r_{max}, stem bending *b*, compression wood *c*, coefficient of variation in the tree-ring width cv_{ir}

Increased crown eccentricity, stem bending, occurrence of reaction wood, and higher variability of ring width indicate higher timber distortion in complex versus homogeneous stands. The roundness of the crown is less affected by structural heterogeneity (Table 1, see section on distortion).

Reaction patterns depending on species characteristics and competitive situation within the stand

Typology of tree shape evolution depending on the species-specific morphological plasticity and the tree's spatial constellation within the stand

As both the species-specific morphological plasticity and the tree's spatial location within the stand have a specific effect on the tree's morphology and timber quality, the basic combinations of both factors, shown in Fig. 3, are distinguished.

Figure 4 illustrates that crown plasticity differs considerably among tree species. The data come from crown measurements on long-term experimental plots in pure and mixed stands in Germany and cover a broad range of tree ages and stand densities (solitary to self-thinning conditions). Based on the 95 and 5 % quantiles of the cpa–*d*-allometry (Fig. 4, upper and lower lines) and a reference tree diameter of 25 cm, the measure of tree crown plasticity, $CPL = cpa_{95\%,25}/cpa_{5\%,25}$, was derived to quantify interspecies differences. The species represented in Fig. 4 rank as follows with respect to CPL: 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 in this set of 14 species (not all are shown) belong to beech (5.1), while the lowest belong to red alder (2.8) and silver birch (2.6).

A tree's behaviour in different types of stands is primarily determined by its species-specific morphological plasticity. Trees with low morphological plasticity (e.g. Norway spruce, Douglas-fir, sycamore maple, red alder), apical dominance, and rather orthotropic crown extension are labelled with the letter "a" after the type

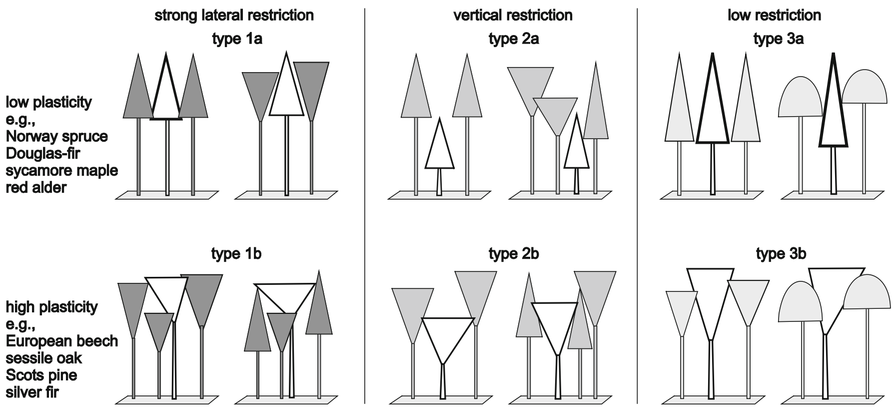

Fig. 3 Spatial constellation of a tree with the stand (type 1 = strong lateral restriction, type 2 = vertical restriction, type 3 = low restriction) and the species-specific morphological plasticity (a = low and b = high) as the main drivers of the morphology and timber quality. The resulting six combinations of spatial constellation (from *left* to *right*) and morphological plasticity (*upper* and *lower line*, respectively) result in types 1a–3b, which have specific effects on the tree structure and wood quality. The reacting individual tree in question (*white*) and its neighbours (*grey*) are shown in a *schematic representation*. Neighbours drawn in *light grey* indicate transparent crowns and low competition, whereas neighbours in *dark grey* indicate low transparency and higher competition

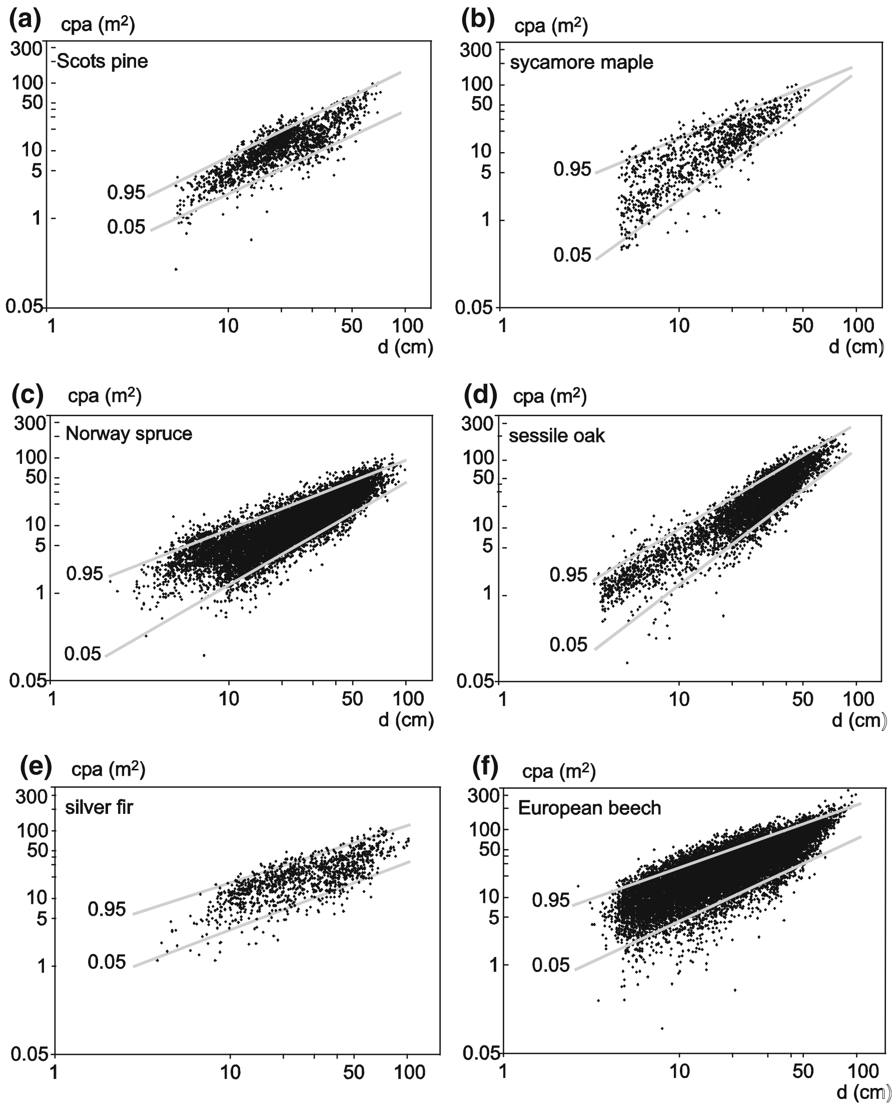

Fig. 4 Morphological plasticity increases from **a** Scots pine (*Pinus sylvestris* L.) ($n = 1609$) to **b** sycamore maple (*Acer pseudoplatanus* L.) ($n = 942$), **c** Norway spruce (*Picea abies* [L.] Karst.) ($n = 10{,}724$), **d** sessile/common oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) ($n = 4485$), **e** silver fir (*Abies alba* Mill.) ($n = 1079$), and **f** European beech (*Fagus sylvatica* L.) ($n = 14{,}898$). The plasticity is indicated by the width of the corridor of the allometric relationships between stem diameter, *d*, and crown projection area, cpa, in even-aged and uneven-aged stands. The observed range of crown dimensions on long-term experimental plots covers both dense and sparsely populated stands. The *upper* and *lower lines* represent the 95 and 5 % quantile regressions, respectively. The width of the scatter and the distance between the 95 and 5 % quantile regression represent the crown plasticity (Pretzsch 2014)

(types 1a–3a, upper line in Fig. 3). Types 1b–3b indicate species with high plasticity (e.g. European beech, sessile and common oak, Scots pine, silver fir), lower apical dominance, and stronger plagiotropic crown extension (type 1b–3b, lower line in Fig. 3) and are labelled with "b" after the type.

The spatial configuration to which a tree is exposed within the stand also has a strong effect on its structural development. The three base types 1–3 are distinguished, characterised by strong lateral restrictions (in fully stocked, mono-layered pure stands and an admixture of species with low crown transparency), vertical restrictions (multi-layered pure and mixed-species stands), and low restrictions (widely spaced and heavily thinned monocultures, admixture of species with high crown transparency) (Fig. 3, from left to right). The configurations on the left (types 1a and 1b) represent rather conservative silvicultural concepts and those in the middle uneven-aged close-to-nature concepts which are the result of forest transformation from plantations to more natural and structured stands (types 2a and 2b). The configurations on the right (types 3a and 3b) represent the intensively spaced and thinned contemporary silvicultural concepts for pure and mixed stands.

The typology allows to assign species not considered in Fig. 3 to one of these six combinations of plasticity and restriction and to predict their reaction in terms of tree structure and wood quality. For example, the behaviour of European larch (high plasticity), when mono-layered and growing densely in association with European beech, may be assigned to type 1b. Similarly, the behaviour of Norway spruce (low plasticity) in the understorey of a selection forest of Norway spruce, silver fir, and European beech, may follow type 2a.

Trees growing with strong lateral restriction (see type 1a and b in Fig. 3)

Closed and rather fully stocked monocultures and mixed-species stands such as type 1 (a and b) were the most common forest structures in the past. They represent a fairly homogeneous stand structure and usually serve as a reference for quantifying the timber quality of more heterogeneous stands, as they are common at present or in planning for the future. Type 1a represents the very common set-up of plantations of vertically fast-growing but laterally low plasticity tree species when densely planted and moderately thinned. Many conifer forest stands were established and treated in this conservative way. Type 1b represents the very common set-up of plantations of laterally plastic tree species that were densely planted and only slightly or moderately thinned in order to keep their shape slim and straight. Many broad-leaved forest stands of or admixed with European beech, common ash, sycamore maple were established and treated in this conservative way.

Common traits of type 1a and b The tree in question (Fig. 3, Type 1 and 1b, white centre tree) must invest mainly in height growth at the expense of stem diameter growth and lateral crown growth to guarantee access to the ample light supply in the upper canopy. The lateral crown extension may be limited by close neighbours due to mechanical abrasion and shading. The crown base continuously shifts upwards due to the lack of light. This applies to pure stands and especially to mixed-species stands when the admixed species is plastic and has low light transparency. High competition usually results in high stiffness, low knottiness, superior wood density, and low distortion. In fact, their superiority in most important timber characteristics was an essential reason for replacing what were heterogeneous forests by rather homogeneous stands with type 1a and 1b configurations (Mantel 1961). Even when growing in fully stocked pure and mixed stands, however, there may be differences in the timber quality depending on the morphological plasticity of the respective tree species.

Special characteristics of type 1a (low morphological plasticity) Examples of this configuration include Norway spruce, Douglas-fir, sycamore maple, or red alder, growing in dense mono-layered stands (Fig. 3, type 1a, left) or mono-layered mixtures with species with low light transparency such as European beech or silver fir (Fig. 3, type 1a, right). Many studies show high slenderness (Baldwin et al. 2000; Pretzsch 2014; Seeling 2001; Reukema and Smith 1987) and form factors (Van Miegroet 1956; Pinkard and Neilsen 2001; Wiedemann 1951) of the stems for type 1a trees. Norway spruce growing in mixture with European beech may result in minor relief from competition and a decrease in slenderness; however, as long as the stands are fully stocked and the neighbours have little light transparency and high competitiveness, the effect on the stem shape remains minor (Fig. 5).

Furthermore, type 1 stands result in low crown ratios (Bücking et al. 2007; Kantola and Mäkelä 2004; Pretzsch 2014), low crown projection ratios (Bayer et al. 2013; Reukema and Smith 1987), and low branch diameter and length (Bayer et al. 2013; Kantola and Mäkelä 2004; Medhurst and Beadle 2001; Pretzsch and Spellmann 1994), all of which indicate low knottiness. Due to their continuous competition with neighbours and accordingly reduced growth rates, the wood density is high for conifers (Wessels 2014). Low morphological plasticity combined with continuous restrictions of growing space results in well-centred and round crowns (Petri 1966; Pretzsch 2014; Seifert 2003; Watson and Cameron 1995), high straightness (Brown 1992; Dippel 1988; Seeling 2001; Seifert 2003, 2004), little

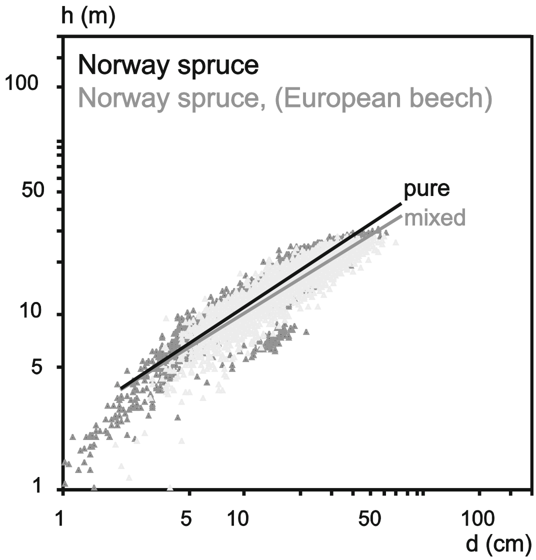

Fig. 5 Species mixing and structural heterogeneity can modify the stem shape and slenderness: the allometric relationship between tree height and tree diameter shows that stems of Norway spruce are more slender in pure stands [$\ln(h) = 1.02 + 0.68 \ln(d)$] than in mixture with European beech [$\ln(h) = 1.09 + 0.64 \ln(d)$]. According to these relationships, spruces of $d_{1.3} = 50$ cm have h/d ratio of 0.80 in pure stands versus 0.73 in mixed stands (according to Pretzsch 2014)

reaction wood (Bücking 2007, Seeling 2001), and rather homogeneous tree-ring width (Preuhsler 1979; Schütz 1997; Strobel 1995), which indicates low timber distortion. In fact, the superiority of type 1 stands in most timber characteristics was an essential reason for replacing originally much more heterogeneous forests with rather homogeneous type 1a and type 1b stands at the beginning of systematic sustainable forestry (Mantel 1961).

Special characteristics of type 1b (high morphological plasticity) This arrangement emerges when plastic species such as European beech, sessile oak, silver fir or Scots pine cope with crowding in monoculture (type 1b, left) or mixed-species stands (type 1b, right). They can make use of their plasticity and forage for light even further away from their centre. This may result in irregular, asymmetrical crowns and stems.

Type 1b represents the common set-up of plantations of laterally plastic tree species that were densely planted and only slightly or moderately thinned in order to keep their shape slim and straight. Many broad-leaved forest stands were established and treated in this way. Tree species with high morphological plasticity require denser crown closure to produce timber of a similarly high quality as low plastic species (type 1a). If the canopy is kept closed, however, monocultures of European beech, sessile and common oak or Scots pine may generate high slenderness (Bleile 2006; Dippel 1982; Utschig 2000) and high form factors (Baldwin et al. 2000; Metzger 1998). Crown extension and the diameter and length of branches remain restricted (Bayer et al. 2013; Lutz 1979; Saha et al. 2012). Wood density remains mostly higher (Bues 1985; Hapla 1985; Sachsse and Grünebaum 1990) than in less densely stocked stands. Kennel (1965) found that in fully stocked mixed stands of Norway spruce and European beech, mixing did not modify the wood density of European beech (Fig. 6, above) but significantly increased the wood density of

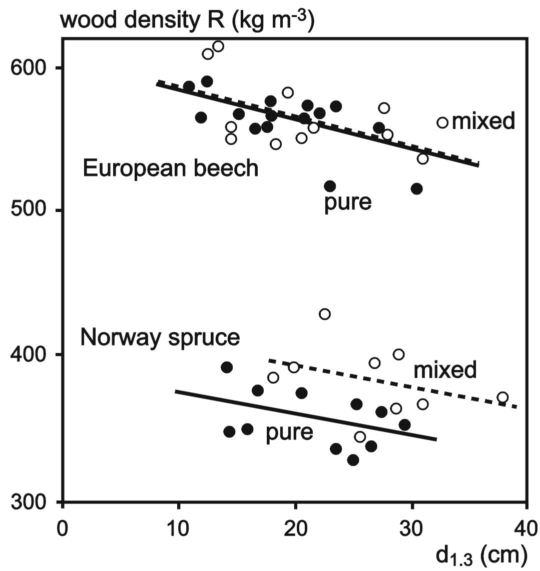

Fig. 6 Comparison of Norway spruce and European beech in mixed stands (*open symbols*) versus pure stands (*filled symbols*) by Kennel (1965) revealed that species mixing did not modify the wood density of European beech (*above*) but significantly increased the wood density of Norway spruce in mixed (*below*, *broken line*) versus pure stands (*below*, *solid line*)

Norway spruce in mixed stands (Fig. 6, below, broken line) compared with neighbouring pure stands (below, solid line). The influence of mixing on wood density is dependent on whether the tree is a conifer, a ring-porous hardwood, or a diffuse-porous hardwood. In ring-porous hardwood species such as oak or ash, in contrast to softwood, wood density increases with an increasing growth rate (Genet et al. 2012; Guilley et al. 1999). In diffuse-porous hardwoods such as beech or maple, wood density is hardly affected by changes in varying ring width (Hakkila 1989). Furthermore, the dependency between ring width and wood density can be influenced by site conditions (Bernhart 1964; Krempl 1977). A dense canopy can contribute to low crown eccentricity (Pretzsch 2014), stem bending (Bäucker et al. 2010; Burger 1941), low reaction wood (von Pechmann et al. 1963), and low ring width variability (Magin 1959; Tham 1988).

When growing in mixed-species stands (Fig. 3, type 1b, left), the timber quality of plastic tree species may decrease even in dense stands as they can develop lower slenderness (Burger 1941; Jonsson 2001; Kennel 1965; Mason and Baldwin 1995), taller branches (Bayer et al. 2013; Seifert 2003, 2004), and more irregular crowns (Pretzsch 2014), all of which may decrease the timber quality.

Trees growing with vertical restrictions (see type 2a and b in Fig. 3)

Living in subdominant positions in multi-layered stands (type 2a and 2b) may relieve the lateral restriction but increase the vertical restriction of crown and stem growth. The resulting type 2 is an arrangement widely spread across uneven-aged forests, for example, selection forest, mixed mountain forests, and even-aged stands when transformed to close-to-nature forest types by underplanting and natural regeneration below the overstorey. These types will become more and more important in uneven-aged close-to-nature stands in the future.

Common traits of type 2a and b A more heterogeneous vertical structure enables deeper light penetration so that leaves and branches can reach into lower layers of the canopy, and the position of the lowest leaf is much lower in mixed stands compared with pure stands. An increase in variables was observed describing crown size and branch size in approximately two-thirds of all studies found. The following general sequence of allocation patterns helps in understanding the timber quality from such stands. When suppressed and waiting in the understorey, the slenderness and form factor of trees may decrease as height growth is strongly reduced and diameter growth continues, so that their stem shape becomes rather conical (sit-and-wait pattern). In Fig. 7, this characteristic decrease in slenderness (*h/d* ratio decreasing to 50–60) of trees with a stem diameter of 5–10 cm is shown for Norway spruce in a selection forest. Trees with the same stem diameter in neighbouring even-aged monocultures maintain *h/d* ratios of 100–120. When receiving sufficient light and the chance to make it into the upper canopy, for example, by the removal of competitors, they enhance their height growth at the expense of diameter growth. Figure 7 shows this increase in the *h/d* ratio for trees in a selection forest with stem diameters of 10–20 cm. This modifies their stems to a more cylindrical shape and results in higher *h/d* ratios and form factors (advancement pattern). As soon as trees have arrived and are growing unhindered in the upper canopy, height growth

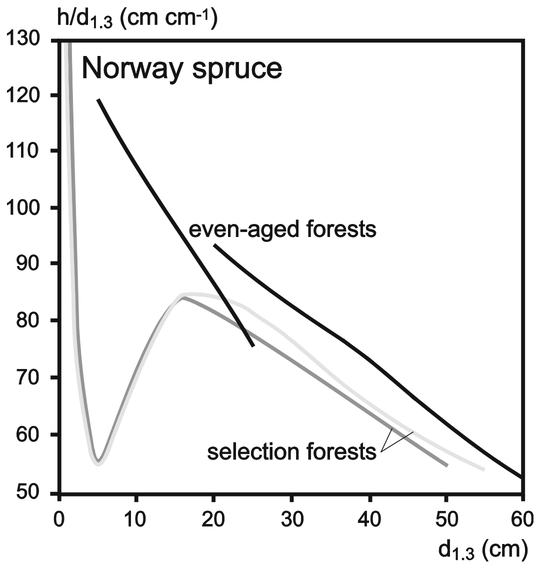

Fig. 7 In even-aged stands, stem slenderness (*h/*d ratio) decreases continuously with advancing size, whereas in uneven-aged, mixed selection forests, slenderness is generally more variable and lower due to reduced height growth in the understorey (according to Kern 1966)

becomes less important for "staying in play" and diameter growth increases in relation to height growth, improving the mechanical stem stability. This may once again decrease both the *h/d* ratio and form factor (stabilisation pattern). In contrast to this up and down trajectory in selections forest, trees in neighbouring pure stands show a continuous decrease in slenderness from the young to the advanced age phase (see Fig. 7, grey vs. black curves).

On top of this up and down relationship between height and diameter growth caused by the characteristic suppression phase in multi-layered forests, silvicultural interference and the loss of old trees may cause further irregularities. Any removal of neighbours by thinning or mortality can cause considerable changes in later restriction by neighbours and therefore a strong variability in the tree-ring width reported by Magin (1959), Preuhsler (1979), and Strobel (1995) and shown in Fig. 8.

When keeping a more or less constant competitive status, a tree's diameter growth at breast height culminates and subsequently tapers off (Fig. 8a, b). Note that radial growth can culminate early and even before the tree reaches 1.30 m in height (Kramer 1988), so that the radial increment at breast height constantly decreases monotonically (Fig. 8a). Alternately, the radial growth culminates later and follows a unimodal trajectory (Fig. 8b). These two approximately 150-year-old trees grew under unchanging competitive status in uneven-aged mixed mountain forests in the Bavarian Alps near Garmisch-Partenkirchen (Pretzsch 2009). Figure 8c, d, in contrast, shows trees of the same stand and age. By coping with crowding in these multi-storeyed forests, they repeatedly changed their competitive status during ontogeny, following a multi-modal growth curve and developing a heterogeneous ring width pattern and wood quality. Figure 8e illustrates the extent to which the removal of neighbours can abruptly change the competitive status, ring

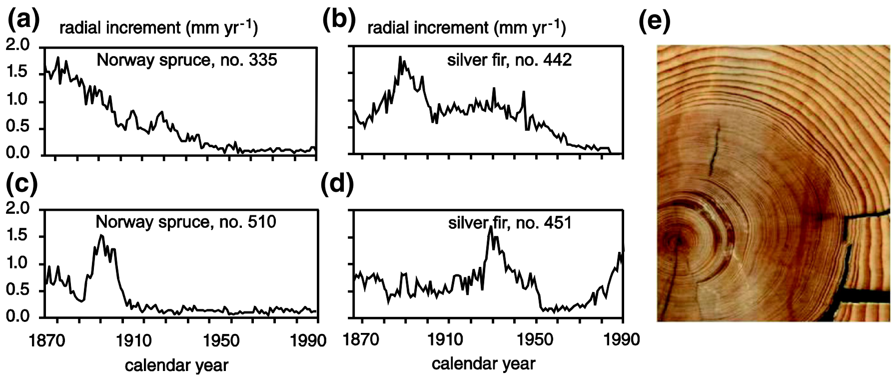

Fig. 8 Annual radial growth at breast height of Norway spruce and silver fir in uneven-aged mixed mountain forests in the Bavarian Alps near Garmisch-Partenkirchen (Pretzsch 2009); ontogeny under unchanging (**a**), (**b**) and repeatedly changing competitive status (**c**), (**d**). Heterogeneous tree-ring pattern at breast height of Norway spruce in uneven-aged mixed mountain forests in the Bavarian Alps near Kreuth (**e**). After a low-growth phase in the understorey lasting more than 100 years, the removal of neighbours abruptly changed the competitive status and the ring width of this tree (Preuhsler 1979)

width, and wood quality of trees after long-lasting low-growth phases in the understorey typical for such mixed-species stands (according to Preuhsler 1979).

For the strength and stiffness of structural timber, the variability of tree-ring width plays a subordinate role but may affect wood properties such as dimensional stability. The heterogeneity of the tree-ring pattern is often higher (67 %) in mixed versus pure stands. While growth is fairly continuous and generally varies due to thinning and weather events in pure stands, species mixing, especially in different layers, may cause the alternation of low-growth and high-growth phases depending on the competitive status of a tree in the understorey, medium, and upper layers (Preuhsler 1979; Piispanen et al. 2014). On the other hand, weather factors and insect predation which cause strong tree-ring width variability in pure stands can be mitigated better in mixed stands, so that the tree-ring pattern can become more regular (Pretzsch et al. 2013; Río et al. 2014).

As a result of this higher variation in the growth rates of the stem and expansion of the crown, the wood strength and stiffness may be lower in complex forests compared with more homogeneous monocultures where tree size and shape development proceed more continuously (Fig. 9). Torquato et al. (2014) investigated differently structured black spruce stands in Canada and detected lower strength and stiffness properties for the complex stands. However, it was difficult to draw a general statement based on an analysis from only two stands.

Special characteristics of type 2a (low morphological plasticity) Living in subdominant positions in multi-layered stands (type 2) may relieve the lateral restriction but increase the vertical restriction of crown and stem growth. Norway spruce that grows in the understorey of even-aged Norway spruce stands (Fig. 3, type 2, left) or in selection forests of Norway spruce, silver fir, and European beech are common examples of such arrangements. The higher the species' shade tolerance, the longer it can "sit and wait" in the understorey with very low height

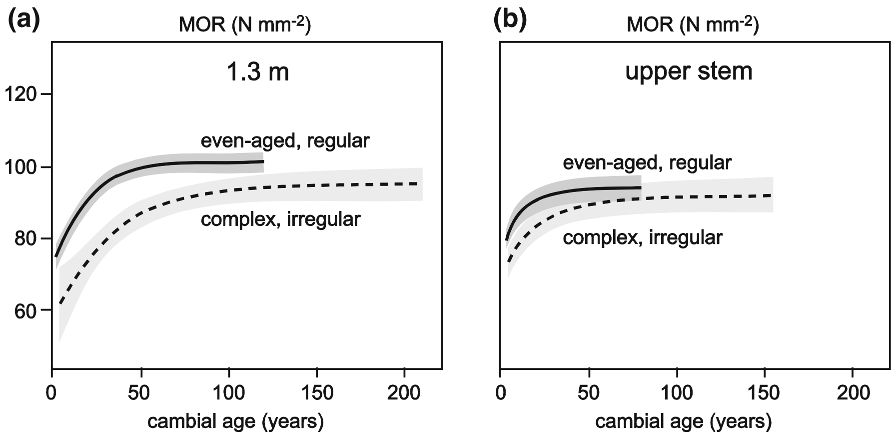

Fig. 9 Relationship between strength (MOR) and cambial age in even-aged pure stands and uneven-aged pure stands of black spruce (Picea mariana (Mill.) B.S.P.) according to Torquato et al. (2014). The strength of timber from complex stands is lower at breast height (**a**) as well as in the top of the stem (**b**)

growth but gradually increasing stem and crown diameter. For subdominant Norway spruces in selection forests, Kern (1966) and Pretzsch (1985) showed that slenderness and form factors may decrease due to the reduced height growth while stem diameter gradually increases. The crowns of such trees are often deeper and wider than trees in even-aged stands (Kern 1966; Schütz 1997), but their branches, when foraging for light in the understory, remain smaller in diameter (Man and Lieffers 1999).

Special characteristics of type 2b (high morphological plasticity) When species with high plasticity are growing in the understory, where they are vertically but not laterally restricted, they can develop very wide and long crowns in both pure and mixed-species stands (type 2b, left and right, respectively). Model examples of this behaviour are trees of European beech or silver fir, which are able to wait and survive a long phase in the understorey until they reach the upper canopy. Due to their plasticity, crowns can become rather eccentric when searching for light in the understorey. Type 2b will become more and more important in uneven-aged close-to-nature stands in the future. Analogously to type 2a trees, they may pass through a suppression phase in which they may develop wide crowns, eccentric crowns, and bent stems to retain access to light. The suppression may increase the stem slenderness and form factors (Dittmar 1990; Man and Lieffers 1999). It may also foster length growth of the branches instead of diameter growth, resulting in relatively slender branches (Klang and Ekö 1999). Asymmetric growing space may increase the stem distortion (Guericke 2001), while concentric growing space results in centric and round crowns (Pretzsch 1985; Preuhsler 1979) with low stem distortion.

Trees growing with low lateral restriction (see type 3a and b in Fig. 3)

Type 3 represents perhaps the most widespread arrangement in contemporary forestry that tends towards the selective thinning and mixing of highly competitive

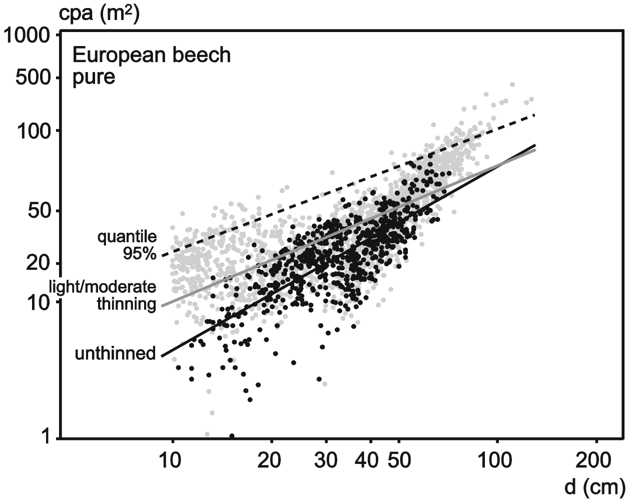

Fig. 10 Allometric relationship between crown projection area, cpa, and stem diameter, *d*, of European beech derived from $n = 4542$ crown measurements on long-term experimental plots in even-aged stands in Germany. The database includes beeches growing in unthinned stands under self-thinning conditions (unthinned), trees in lightly or moderately thinned stands, and solitary trees (95 %-quantile regression) and reveals the high dependence on the spatial arrangement with the stand. The thinned and unthinned cpa–*d* relationships differ significantly ($p < 0.001$) in both intercept (thinned > unthinned) and slope (thinned < unthinned) (Pretzsch 2014)

and fast-growing conifers with less competitive tree species. The competition relief may result from spacing, thinning, or admixture of less competitive species. Silvicultural guidelines for selective thinning or future crop tree thinning generate trees with these types of spatial arrangements (Fig. 3a, b).

Common traits of type 3a and b The release of lateral competition triggers lateral growth, namely the expansion of the crown and stem diameter growth at the expense of height (Dippel 1982; Spellmann and Nagel 1992; Uhl et al. 2015). As a consequence, stem growth rates may increase considerably. As a trade-off, slenderness may decrease, knottiness increase, and wood density grow lower and distortion higher, as the tree's space for searching for light is less restricted. The effect of lateral release is shown for European beech (Fig. 10), as many former conifer stands have been replaced by pure or mixed-species stands of beech. The allometric relationship between the crown projection area cpa and stem diameter *d* (Fig. 10) reveals the broad morphological plasticity of this species in an intra-specific neighbourhood. The cpa–*d* relationship for light/moderate thinning is significantly higher and significantly shallower ($p < 0.001$) compared with the respective relationship for unthinned stands. According to these cpa–*d* allometries, 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 beeches with high competitive strength as well as a strong tendency towards extending crowns and producing long, tall branches when released from competition.

Special characteristics of type 3a (low morphological plasticity) This common arrangement emerges in moderately or heavily thinned monocultures of Norway spruce, Douglas-fir, or sycamore maple (Fig. 3, type 3, left). In this case, the light reaches deeper into the canopy and individual trees have more space for the lateral and vertical extension of their crowns. This arrangement can also emerge when the same species are growing in admixtures with less competitive, highly light-transparent species such as Scots pine or European larch (Fig. 3, type 3, right). In this case, the neighbouring trees may stand rather close together, but because their crowns are more light transparent, there is less restriction on the tree under consideration. For the growth and structure of centre trees, the admixture of light-transparent neighbours may have the same effect as moderate or strong thinning.

The less restricted the growing space is, the lower the slenderness and form factor (Wiedemann 1942), as the stem growth switches from a survival strategy (increase in height growth at the expense of diameter growth) to a stabilisation strategy (increase in stem growth and slowing down of diameter growth) (Pretzsch 2009, pp. 389–391). Lower slenderness and form factors indicate a decrease in timber strength and stiffness (Burger 1941; Jonsson 2001; Wiedemann 1942). Compared with denser stands (type 1), the knottiness, as indicated by the crown ratio (von Lüpke and Spellmann 1999), crown projection ratio (Petri 1966; Thorpe et al. 2010), branch diameter, and length (Bäucker et al. 2010), increases. The wood density of conifers may decrease (Hapla 1982), react indifferently (Cameron and Watson 1999), or even increase (Kennel 1965), while broad-leaved species mostly react indifferently (Kennel 1965; Maurer 1963).

Special characteristics of type 3b (high morphological plasticity) When trees of a morphologically plastic species are growing widely spaced or thinned in pure and mixed stands (type 3b, left and right, respectively), their crowns may become wide and deep with tapering stems and eccentric stem cross sections, and crowns with uneven lateral growth (e.g. extremely one-sided). Examples of this arrangement are heavily thinned pure European beech stands or mixed-species stands of European beech and admixed species with high light transparency and thus low competitive strength (Fig. 11).

The fact that mixing can significantly increase crown size and branchiness and knottiness can be shown by the allometry between crown projection area, cpa, and stem diameter, *d* (cpa–*d*-allometry), of beech in pure stands compared with beech in mixed stands of Norway spruce, European larch, common ash, and sessile oak. While allometric scaling theory predicts cpa $\propto d^{4/3}$ (i.e. $\alpha_{\mathrm{cpa},d} = 1.33$) for the allometrically ideal plant (West et al. 2009), the allometric exponent is at maximum $\alpha_{\mathrm{cpa},d} = 1.54$ in pure beech stands (be = European beech in even-aged pure stands) and ranges between $\alpha_{\mathrm{cpa},d} = 0.76$ [be, (ash)] and $\alpha_{\mathrm{cpa},d} = 1.21$ [be, (oak)] depending on the species composition of the neighbours. Obviously, a neighbouring beech restricts the crown of beech more than any other of the analysed species. For beech with a stem diameter of 25 cm, the allometric equation relationship shown in Fig. 11b predicts a crown projection area (cpa) of 17 m^2. Beech with the same stem diameter achieves a cpa of 25 m^2 when mixed with ash, and 27, 37, or even 45 m^2 when mixed with spruce, larch, or oak, respectively. For European beech, mixing with each of the other species means reduced competition and wider crown

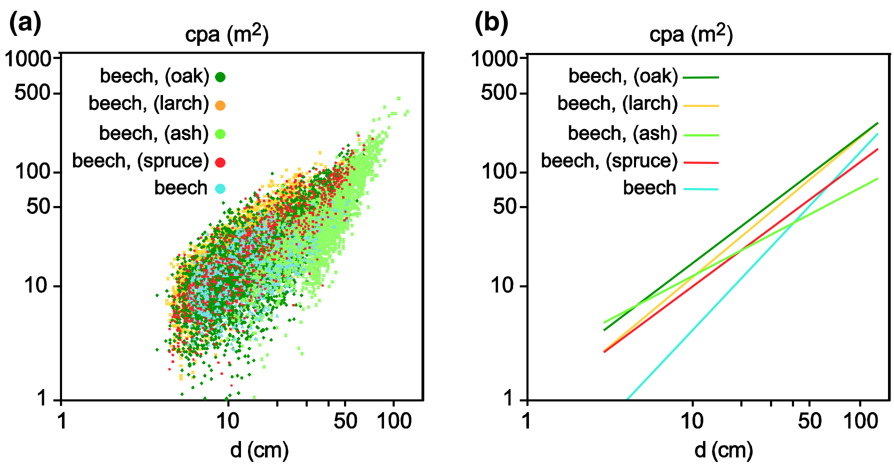

Fig. 11 Relationship between **a** crown projection area, cpa, and the tree diameter, *d*, for European beech in even-aged pure stands (be, *blue*), and **b** shift in the allometry when beech is mixed with Norway spruce [be, (sp)], European larch [be, (la)], ash (be, ash), and sessile oak [be, (oak)]. The database contains $n = 10{,}302$ tree crown measurements in even-aged stands and reveals that crown size significantly increases when modified by the neighbouring species. For statistical characteristics of the regression lines, see Pretzsch (2014)

extension (Fig. 11) with the above-mentioned negative effect on branch size, number, and knottiness.

On top of the increase in crown size, the combination of high plasticity and wide but non-concentric growing space may result in asymmetric stem cross sections and reaction wood. Watson and Cameron (1995) showed that the crown imbalance of Sitka spruce was significantly higher in mixtures with other conifers than in pure stands. They also observed an increase in compression wood in mixed stands. Similar results in terms of crown imbalance (crown rotundity) were revealed by Pretzsch (2014) for European beech. Additionally, crown eccentricity, ecc, was determined by means of the distance between the stem (tree) position and the crown's gravity centre (Fig. 12).

The analysis of several thousand trees by Pretzsch (2014) revealed that compared with other species, beech crown projection areas are mostly less circular, i.e. more jagged [ratio between the largest r_{max} to shortest crown radius $r_{\min} \neq 1$]. Mixing significantly increases rotundity in the case of spruce, decreases the rotundity of beech, and does not affect the rotundity of the crowns of sessile oak. The values of ecc are the highest for beech, especially when growing in mixed stands. Values of ecc = 5.7–7.4 indicate that beeches have plastic crowns for resource capture. 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-specific way. Mixing increases the crown eccentricity of both beech and oak but fosters centricity in the case of Norway spruce. The crown imbalance also influences branchiness and knottiness to some extent because a large crown

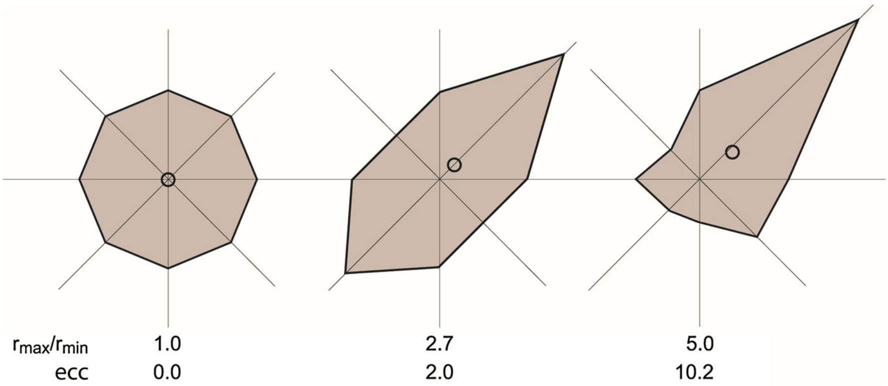

Fig. 12 Schematic representation of the crown projection area (*grey area*) of trees with decreasing crown roundness and centricity (*from left to right*). The ratio between the largest to shortest crown radius (r_{max}/r_{min}) indicates crown roundness (crown imbalance), and the standardised distance between the centre of gravity of the crown projection area and the tree position (ecc) indicates crown eccentricity. The tree's centre of gravity is represented by circles and the tree's stem base position by the origin of the coordinate system (Pretzsch 2014)

expansion in one direction is only possible by forming long branches, which, in turn, results in large branch diameters.

Stand type 3b results from many modern silvicultural concepts of wide spacing, heavy thinning, and diverse species composition and may cause a considerable decrease in *h/d* ratios (Burger 1941; Erviti and Erviti 1994; Kennel 1965; Pretzsch 2014) but can also leave *h/d* ratios unaffected (Lindén and Agestam 2003; Erickson et al. 2009). It often strongly increases knottiness (Bayer et al. 2013; Seifert 2003, 2004) and distortion (Knoke and Seifert 2008; von Pechmann et al. 1963), especially in the case of a non-concentric growing space.

Morphological plasticity and spatial constellation in the stand as the main driving variables for the structure and timber quality of trees in forest stands

Tree morphology as an indicator of timber quality

Crown dimension is a key indicator of the timber quality of trees in both pure and mixed-species stands (Larson 1962; Seifert 2003). The crown size and structure result from species-specific plasticity and space availability and can be used for predicting timber quality. On the one hand, crown size and shape are influenced by the surrounding space availability and are considered to derive from interactions between trees. For instance, crown diameter and branch length are influenced by stand density and reacted positively throughout thinning (Curtis and Reukema 1970; Maguire et al. 1999). On the other hand, crown dimensions can be used to predict wood quality with the development of equations describing the relationships among crown dimension, branch length, branch diameter, and knottiness (Houllier et al. 1995; Poschenrieder et al. 2016). This means that knowledge of the crown dimensions makes it possible to gain direct information about branchiness, one of the most suitable predictors of wood quality at the tree, log, and board level. Furthermore, there are some indirect dependencies between crown dimensions and wood quality. For instance, the live crown ratio negatively influenced the wood quality of small clear wood specimens of white spruce (Kuprevicius et al. 2013). Further, crown ratio was negatively correlated with sawn timber stiffness (Moore et al. 2013).

The presented link between silvicultural management, tree morphology, and timber quality attributes such as strength, stiffness, knottiness, wood density, and distortion is a makeshift one and may be flawed. The effect of site conditions on the structure and timber quality of trees is not yet fully understood. The choice of the provenance, pruning, fertilisation, climate trends, and effects may dominate the presented links. Many relationships between external driving variables and timber quality are not yet sufficiently clarified; for example, further research is required into how the spatial heterogeneity of stands (horizontal and vertical structuring) and the temporal variability of silvicultural thinning (sequence of strong and light thinning) affect wood distortion and heterogeneity in properties.

The generic reaction patterns

Despite these imponderables, this review here has revealed the following general principles regarding the emergence of structure and timber quality of trees in forest stands. Depending on the species-specific morphological plasticity of a tree and its spatial configuration within the stand, four basic emergent allocation patterns of stem and crown growth were found:

(i) “Keep abreast” strategy: when a tree is densely surrounded by competitors of similar size, the strong lateral restriction causes slender stems, low knottiness, high wood density (for conifers), and low distortion of the timber. This reaction pattern is widespread for trees in traditionally and conservatively managed even-aged pure and mixed stands. As this was the standard silvicultural paradigm in the past, high portions of presently harvested timber show this allocation pattern and quality attributes. The “keep abreast” strategy reaction pattern particularly applies to species with low morphological plasticity; the higher the tree’s plasticity and shade tolerance and the crown transparency of its neighbours, the better the tree can maintain its position and this reaction pattern, even when overtopped by neighbours.

(ii) “Stabilisation” strategy: strong dominance, achieved either by vertically overtopping neighbours of the same species or by laterally interfering with less competitive neighbours, results in the “stabilisation” strategy. Because they are already present in the upper canopy with full access to light, these trees do not need to increase in height but instead allocate resources to lateral crown extension to improve their interception of light and stem growth for mechanical stabilisation. This results in tapered stem shapes, large-sized knots along the stem axis, as well as lower wood density, especially in the case of conifers (Reukema and Smith 1987; Weiskittel et al. 2006; Rais et al. 2014); however, if lateral competition is rather symmetric, distortion is low. Additionally, morphologically more plastic tree species follow this stabilisation pattern but may stay less symmetric in their crowns because they tend to bend and form reaction wood under one-sided exposure to wind, snow, and other loading. This response is most obvious in even-aged, heavily thinned pure and mixed stands, but is also widespread in selection forests or mountain forests where individual trees can come to dominance and continuously overtop their neighbours.

(iii) "Sit-and-wait" strategy: when vertically suppressed and waiting in the understorey, trees tend to reduce their height growth but continue their lateral extension of crown and tree diameter. This "sit-and-wait" strategy may result in tapered stem shapes, wide and long crowns with low branch diameters, and high wood density. Distortion may be low in the case of species with low morphological plasticity but can increase with increasing shade tolerance and plasticity.

(iv) "Transition" strategy: the "transition" strategy is the change between the "sit-and-wait" strategy and the "keep abreast" strategy. In terms of mechanical stability under wind or snow damage, this transition phase may be critical. It begins when trees rapidly increase their height growth at the expense of stem diameter growth. This results in slender stems, low knottiness, high wood density, and low distortion, as the tree gains access to the upper canopy; this can be achieved only at the expense of the lateral expansion of the stem and crown.

All four reaction patterns may be most easily observed in special types of stands and management systems; however, they can occur with low frequency in nearly all types of forests. It is the individual tree's combination of morphological plasticity and spatial arrangement that generates tree growth, structure, and subsequent timber quality, not the type of stand per se, although the type of stand certainly determines which of the above allocation strategies occur most frequently.

The relevance of morphological plasticity and spatial constellation

The phenotypic appearance, morphology, and timber quality of a tree result from its inherited genotype and its modification by environmental conditions (Assmann 1970). When environmental conditions (e.g. resource supply, obstruction by neighbours, calamities) in mixed stands differ from pure stands, a given genotype may develop somewhat differently in crown shape (Dieler and Pretzsch 2013). However, there is no basic difference between crown dynamics in pure and mixed stands. In both types, it is determined by stem and branch development, which depend mainly on the species-specific plasticity and the availability of open space for extension (Le Maire et al. 2013; Pretzsch 2014). Compared with mono-layered and even-aged pure stands, all other stand types, such as uneven-aged pure stands, even-aged mixed stands, or uneven-aged mixed stands, are much more heterogeneous in vertical and horizontal structure. The greater the heterogeneity in structure, the more variable is the distribution of light and crown space occupied by neighbouring crowns. As stem and branch growth and the resulting crown shape are mainly driven by the availability of light and growing space, any heterogeneity of these drivers results in more heterogeneous crowns (Wang and Jarvis 1990). In even-aged pure stands, the one-storied structure causes a homogeneous vertical light profile and lateral crown restriction, i.e. rather uniform light and space availability for all trees. Uneven-aged mixed stands with a multi-storied structure represent the extreme opposite; here, nearly open-grown dominant trees with ample light and space, oppressed trees in the medium crown layer with low supplies of light and space, and trees in the understorey with low light supplies but no lateral restrictions may be found (Pretzsch 2010). Erickson et al. (2009) concluded that the size of neighbouring trees influences growth more than species identity. The fact that spatial structure rather than species composition matters with respect to tree crown variability becomes obvious in uneven-aged pure stands, where stand structure can become so heterogeneous that crown variability becomes greater than in mixed stands.

Compared with the restriction in pure stands, interspecific neighbouring trees may trigger the ability for crown expansion and interlocking that species acquired through their mutual co-evolution in the past, but which are irrelevant and undesired in forestry, or even unknown as long as the species grow in pure stands. When crowns and roots are growing in mixed stands, however, they may develop behaviours not known in pure stands but that are highly relevant for understanding, modelling, and predicting mixed stand dynamics (Pretzsch et al. 2015). A synonymous term for the true mixing effect is “multiplicative effect” (Forrester 2014; Kelty 1992; Rothe 1997).

Note that the current findings refer mainly to light-limited temperate forests, where branch growth and crown dynamics depend on light interception and availability of open space for branch extension. In drier climates, water limitations may restrict branch and crown growth, although neither light nor growing space are restricted. In windy environments, growth and tree form are also influenced by wind. A review of how a tree perceives the mechanical load of wind is presented by Telewski (2006). In the authors’ opinion, the impact of wind on tree growth has to be considered, but its impact is similar for all the stands covered in this review.

Impact of species mixing on the frequency distribution of various dendrometric tree attributes

Whether the wood structure and quality shows an additive or multiplicative effect cannot be revealed by sampling only one or two individual trees in a stand. In fact, the frequency of different quality properties needs to be considered in order to obtain reliable results for the entire stand. In natural forests, one can expect a larger variation for wood and morphology traits than in an even-aged plantation as a larger diversity is observed (e.g. in terms of social status: dominant and subordinate trees, understorey and overstorey trees).

Frequency distributions of proxy variables (*P*) such as slenderness, crown projection ratio or crown ratio indicate the quantity and range in wood properties. These distributions are often neglected, although they are important components for wood quality comparison and assessment between different stand structures. From the authors' perspective, there is a large benefit when considering both wood quality and quantity distributions. This allows better planning and control and increases the benefit throughout the entire processing chain, from trees to the end product.

The sessile oak–European beech mixing experiment Waldbrunn 105 was used to illustrate the effect of mixing on the frequency distribution of tree attributes which are relevant for wood quality. Figure 13 is based on the tree diameter and crown diameter of the 87-year-old stands in 1989 (first surveyed in 1935, 10 successive surveys). Until reaching this age, the trees in those plots had sufficient time to adapt their stem and crown shapes to the intra- and interspecific neighbourhood in the pure and mixed stands, respectively. Note in Fig. 13 that the grey lines represent the frequency distributions of the trees in the mixed stands scaled up to the unit area of one hectare by the proportion of the respective species.

Mixing hardly changes the diameter distribution of sessile oak (top, left) and slightly slows the diameter growth of beech (bottom, left). The crown diameter

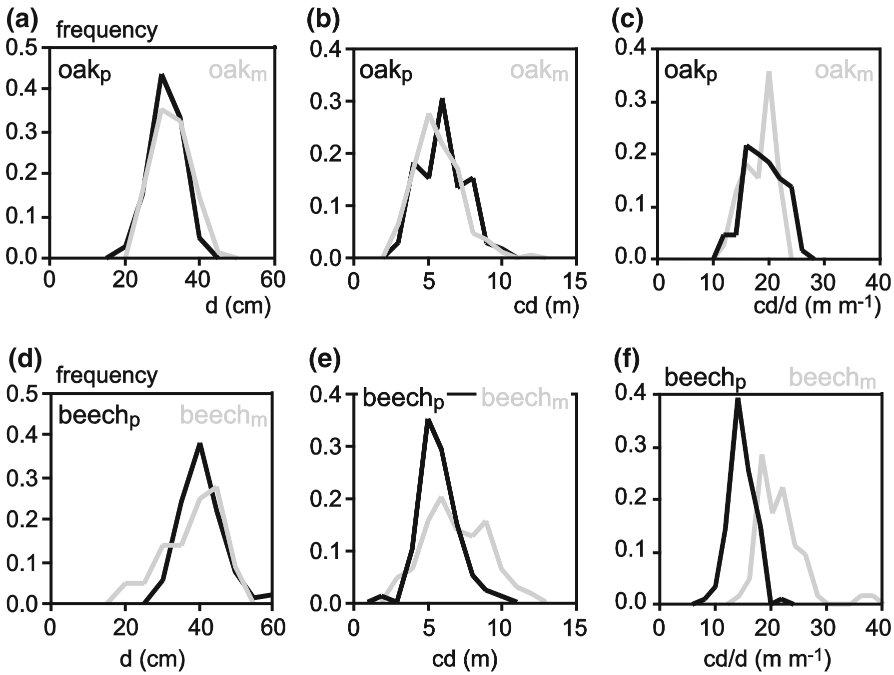

Fig. 13 Frequency distribution of tree attributes in mixed stands (*grey lines*) compared with pure stands (*black lines*) of sessile oak (*top*) and European beech (*bottom*) in the long-term experiment Waldbrunn 105 at age 87. Oak mixing slightly modifies the frequency distribution of tree diameter, *d*, crown diameter, *cd*, and the ratio *cd*/*d*, compared with pure stands. Beech mixing shifts and widens the frequency distributions of *d*, *cd*, and especially the *cd*/*d* ratio

distribution, which indicates the length and diameters of branches and consequently the branch diameter, is shifted considerably to the left in the case of oak (top, middle) and to the right in the case of beech in mixed compared to pure stands (bottom, middle). The *cd/d* ratio (right) indicates the size of the crown diameter in relation to the stem diameter. The *cd/d* ratio of a tree with $cd = 5$ m and $d = 50$ cm would be 10 ($cd/d = 500$ cm/50 cm $= 10$), while a tree with the same diameter but a crown width of 10 m would yield $cd/d = 20$ ($cd/d = 1000$ cm/50 cm $= 20$). The higher the *cd/d* ratio is, the broader the crown and the longer and thicker the branches are.

As illustrated in Table 1, crown size and branch diameter are closely associated with stem shape, wood strength, and stiffness. In the case of oak (top, right), mixing hardly shifts the *cd/d* ratio frequency distribution. However, the *cd/d* ratio distribution of beech is shifted considerably to the right and is much wider in mixed compared to pure stands (bottom, right).

This example shows the extent to which wood-quality-relevant tree attributes such as crown diameter and *cd/d* ratio can change in their mean and variation, although the stem diameter shows only minor differences between mixed and pure stands. Thus, when sampling mean diameter trees to analyse wood quality in mixed versus pure stands, neither the dimensional shift nor the extension of the frequency distribution and variability of wood quality are revealed. Concerning tree and stand modelling and simulation, this example stresses that tree diameter-based model approaches may be sufficient for homogeneous pure stands but are not adequate for reflecting tree structure, crown variability, and wood quality in mixed stands.

With an increase in the scatter of proxy variables, the scatter of strength properties of sawn timber is expected to increase. The material properties of heterogeneous materials such as wood are mostly defined in rules for use in buildings as the fifth percentile value. If the same wood properties are to be guaranteed in timber strength classes in the future, when the variance of the wood properties is increasing, the design of timber structures must be adapted.

Perspectives

Studies have often compared the quality of homogeneous and more complex stands by sampling small numbers of dominant trees in both groups, i.e. in mixed versus pure stands or heterogeneous versus homogeneous stands, assuming that the structure, morphology, and wood quality of the sampled trees are representative of the entire stand. There can be significant differences, however, in the frequency of occurrence of quality-related characteristics in pure and mixed stands. For instance, large beech crowns with large branches appear more frequently in mixed stands but may also be found in smaller numbers in pure stands. Similar developments may be observed for stem and log shape. Future studies should also consider the frequency of trees with defined qualities in both groups. In the future, more effort should be spent on the systematic selection of representatives of various partial groups of the population.

Future research should substitute direct measurement for indirect dendrometric assessment. Better integration of information about wood quality is required for the entire wood supply chain, from the integration of wood quality in forest inventories to silvicultural guidelines, forest models, decision support tools, and wood grading, to rules for log sawing. The silvicultural treatment of the complex stands discussed in this study here has been neglected in the past, yielding below-average wood quality of trees that developed in such stands. Intensified tending and thinning of mixed-species stands may result in better scores with respect to knottiness, distortion, and wood heterogeneity.

Because of their size, fixed position, and longevity, trees are the founder species in ecosystems (Whitham et al. 2006). Their morphology and structures determine the living conditions of many ecosystem components, as well as ecosystem functioning and services beyond wood and timber quality (Hector and Bagchi 2007). The shading effects of their crowns and water uptake of their roots influence the light and water supply and thus, the habitats of flora and fauna in their surroundings. All animals that need tree structures to live, such as birds, bats, and insects, are strongly affected by tree morphology and stand structure. Fungi, insects, and woodpeckers, for example, are significantly dependent on inner tree characteristics such as wood density, knottiness, and stem rot. While the relevance of morphology and structure of mixed stands for their superior biodiversity, protection, recreational and aesthetical value is undisputed, the effect of structural heterogeneity on wood and timber quality requires greater consideration in the future.

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