
Size-Structure Dynamics in Mixed Versus Monospecific Stands

5

Hans Pretzsch

Abstract

The community of mixed tree species is conceptualised in this chapter by the dynamics of its size distribution. We use experiments of mixed and neighbouring monocultures to show how mixture changes the size-structure dynamics and thereby the productivity of mixed versus monospecific stands. As the main cause of this modification, we identify the predominantly more size-asymmetric partitioning of the growth in favour of dominant trees in mixed stands. Furthermore, mixing can modify the growth allocation at the tree level in favour of the crown size. These differences in the inter- and intra-individual growth distribution may just slightly favour the size of tall trees at the expense of small ones and may slightly increase the canopy density in mixed compared to monospecific stands in a single growth period. However, via the feedback functioning→structure→environmental conditions→functioning, small initial and continuous advantages may result in a significantly different canopy structure, denser stocking, and higher productivity of mixed versus monospecific stands, especially in the advanced and mature phase. We characterise the size and growth distribution pattern emerging in mixed stands using various measures, indices, and relationships. The denser canopy space filling by trees with complementary light ecology may contribute to the general pattern of overyielding of mixed versus monospecific stands.

The community of mixed tree species is conceptualised in this chapter by the dynamics of its size distribution. Analysing the evolution of tree size distributions will provide essential insight into mixed-species population dynamics and provide a link between the stand level addressed in Chap. 4 and the tree level presented in Chap. 6. Mixing effects at the stand level are relevant

H. Pretzsch (✉)

Chair for Forest Growth and Yield Science, Faculty of Forest Science and Resource Management, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
e-mail: Hans.Pretzsch@lrz.tum.de

for decision making and forest planning and indicate that advantageous species interactions are worth further exploration but are insufficient for revealing the underlying causes. Analyses at the tree level may reveal basic growth response patterns for better understanding competition and facilitation. They may also reveal how competition and facilitation result from a modification in the supply, capture, and use efficiency of resources. But the findings at individual tree level are barely sufficient for scaling up to stand-level behaviour because of system properties emerging through interindividual interactions. The size distribution dynamics provide a link between the stand and tree level and a transition between both levels of organisation.

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The familiar size distribution of monocultures can be modified with regard to location, shape, and scaling when tree species are mixed. In this chapter we use experiments of mixed and neighbouring monocultures to show how mixture changes the size-structure dynamics and thereby the productivity of mixed versus monospecific stands. As the main cause of this modification, we identify the predominantly more size-asymmetric partitioning of the growth in favour of dominant trees in mixed stands. Furthermore, mixing can modify the growth allocation at the tree level in favour of the crown size. These differences in the inter- and intra-individual growth distribution may just slightly favour the size of tall trees at the expense of small ones and may slightly increase the canopy density in mixed compared to monospecific stands in a single growth period. However, via the feedback functioning→structure→environmental conditions→functioning (see Chap. 6, Fig. 6.5), small initial and continuous advantages may result in a significantly different canopy structure, denser stocking, and higher productivity of mixed versus monospecific stands, especially in the advanced and mature phase. We characterise the size and growth distribution pattern emerging in mixed stands using various measures, indices, and relationships. The denser canopy space filling by trees with complementary light ecology may increase the light interception and light-use efficiency and contribute to the general pattern of overyielding of mixed versus monospecific stands that was shown in Chap. 4.

5.1 The Tree Size Distribution as Essential Stand Characteristic

The distribution of tree sizes for remaining and removal trees and the underlying growth partitioning between the trees goes far beyond a simple inventory and statistical overview of the state of a population. Rather, it reflects how successfully the involved social classes of one species or different associated species cope with crowding during stand development and their role in the population. As the relative size of trees in a population is strongly coupled with their access to resources, growth, and probability of survival, the size distribution also reflects the present social state and the potential further development of the represented trees of different sizes.

Figure 5.1a–c shows a schematic representation of three common stand structures (left) and how these translate into tree diameter distribution (middle). It

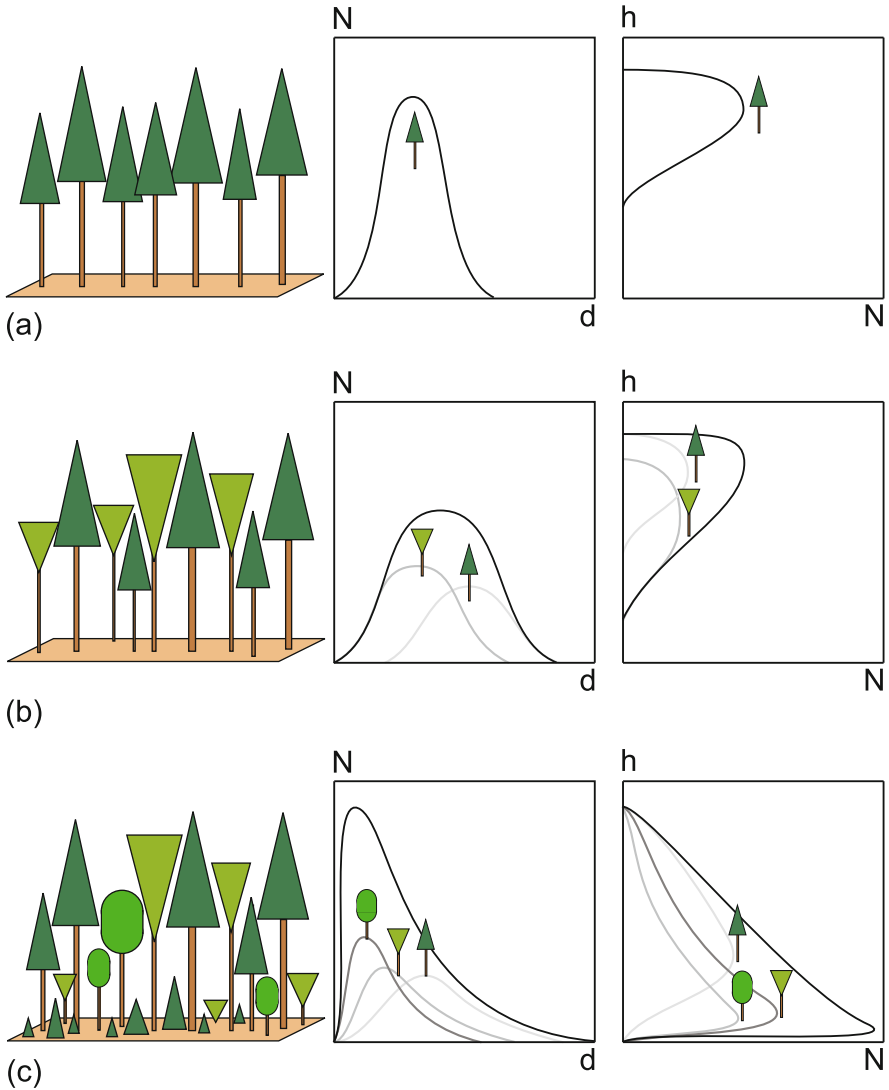


Fig. 5.1 (a–c) The structure of forest stands (*left*) can be described by their specific tree diameter distributions (*centre*) and reflect the vertical layering of the canopy (*right*). From monolayered monospecific stands (a) to monolayered mixed-species stands (b) to multilayered mixed-species stands (c), the vertical heterogeneity increases, and the standing stock, light, and growth are partitioned among an increasingly wider range of tree sizes

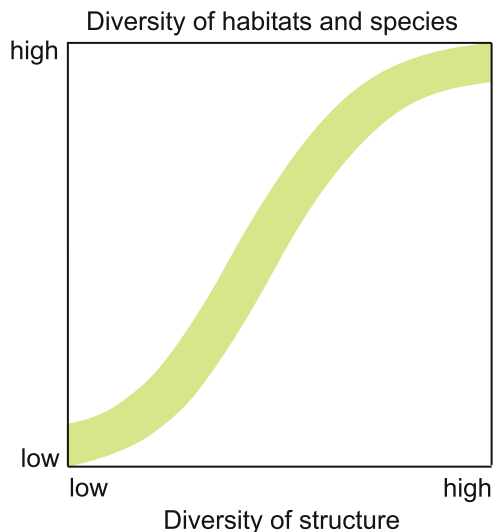
also indicates the vertical height distribution and canopy space filling (right). Monocultures (Fig. 5.1a), especially when even-aged, tend towards a monolayered structure, Gaussian normal distribution of tree number over tree diameter, and a concentration of trees in mainly one height layer. In even-aged (Fig. 5.1b) or

uneven-aged mixed-species stands (Fig. 5.1c), the size distribution may widen and indicate the species' interaction with regard to competition and their spatial niche occupation on the basis of complementarity in ecological traits. Thus, comparing the size-structure dynamics in mixed stands with those in monospecific stands of the same species may considerably contribute to understanding the mechanisms behind the mixing effects which were revealed at the stand level in the previous chapters. The widening of the tree diameter and height distribution of the stands shown in Fig. 5.1a–c indicates an increasing niche separation, inequality of size, and growth partitioning between small and tall trees.

Figure 5.1 illustrates that a variation in tree diameter distribution is coupled with a variation in tree height distribution which again indicates a richer structuring, indentation, and roughness of the crown surface area. Forests and trees provide structures on which, in which, or through which physical, biochemical, ecological, and socio-economic processes take place. Thus, size distribution characteristics can be useful indicators of the state and development of forest ecosystems and for applied management practice (MCPFE 1993). In comparison with direct quantitative measurements of biodiversity, stability, or sustainability (counting plant and animal species, assessment of matter balance, etc.), the use of structural parameters is advantageous as the data can be readily collected or is already included in forest inventory data.

According to Noss (1990), the structural aspects may positively affect compositional and functional aspects of biodiversity (Chap. 10, Fig. 10.8). They can positively influence the diversity of habitats as well as plant and animal species (Fig. 5.2). Stand structures determine the occurrence and population dynamics of owls and woodpeckers to such an extent that habitat suitability and the development of a population can be inferred directly on the basis of given structures (Letcher

Fig. 5.2 Diversity of structure analysed in this chapter has an impact on biodiversity and many other ecosystem functions and services. Schematic representation of the relationship between structure and diversity of habitats and species (adapted from Begon et al. (1998))



et al. 1998; McKelvey et al. 1993). Ammer and Schubert (1999) and Müller et al. (2007, 2012), among others, point to the close relationship between tree and stand structure and the presence of birds, beetles, spiders, lacewings, and soldier beetles. Consequently, size distributions may serve as indicators of the ecological diversity and stability of forest ecosystems and the type of management.

In heavily managed forests, size distributions may represent the silvicultural interference more than the species-specific ability to appropriate resources or adapt to competition. Particularly the lowering of stand density through wide spacing at stand establishment and thinning during further stand development may keep lower social classes or inferior species in subdominant and understorey positions, although these would be outcompeted in fully stocked stands (Fig. 5.1b and c). As the behaviour of trees of different social classes and species becomes most obvious under maximum density, we use mainly fully stocked stands to reveal basic size-growth dynamics in mixed versus monospecific stands in the following.

5.2 Abstracting Stand Dynamics as Evolving Tree Size Distribution

Given that evidence in the literature of mixing effects on the size-structure dynamics is sparse, this chapter is mainly based on our own evaluations of the following datasets: The thinning experiment in European beech Hain 27/1 (survey from 1871, stand age 38 years till present >180 years) was used to illustrate the characteristic size-structure dynamics of a monoculture (Kennel 1973). The species mixing experiment Waldbrunn 105 in sessile oak and European beech (survey from 1935 till present) was used to demonstrate the long-term effect of intra- versus interspecific competition on the size distribution, crown, and stem allometry (Freist-Dorr (1992), Sect. 4.2.2). A set of 42 triplets comprising 126 even-aged (mostly aged between 40 and 60 years), two-species mixed and monospecific stands of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] Karst.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), European beech (*Fagus sylvatica* L.), and sessile oak (*Quercus petraea* (MATT.) LIEBL.) has been pooled and evaluated for this chapter (Pretzsch and Schütze 2014; Pretzsch et al. 2016). To analyse the mode of mortality in mixed versus monospecific stands, we used 11 long-term experiments in Germany in monospecific and mixed stands of European beech and sessile oak and European beech and Norway spruce (Pretzsch and Schütze 2014). To more closely analyse the canopy space filling, we used 253 crown maps in monospecific ($n = 87$), two-species ($n = 111$), and \geq three-species ($n = 55$) mixed stands in Germany (Pretzsch 2014).

The data will be introduced briefly before the passages where it is applied in order to reveal mixing effects on the size-structure dynamics. All the data come from temperate forests where trees compete for nutrients and water and mainly for light through above-ground structural acclimation.

5.2.1 Size-Structure Dynamics in Monocultures: Principle and Example

The development of the trees in a monoculture or a species in a community can be characterised by tree size distribution, the growth distributions between the trees, and the mortality (Hara 1993). In single-cohort monocultures, the diameter distribution is narrow, asymmetric, and right skewed in the early stage and becomes increasingly symmetrical and Gaussian shaped with progressing stand development (Prodan 1965, pp 129–130). Silvicultural treatment cuts mainly the left branch by thinning from below, the right branch by thinning from above, or simply reduces the level of the size distribution through systematic thinning, such as elimination of every n th tree or tree row (Kramer 1988, pp 200–203). Shade-tolerant species tend towards wider size distributions than light-demanding species as a lower light compensation point allows for enhanced persistence of small trees in deep shade (Assmann 1970, pp 92–98).

The size distribution (tree number over tree diameter, basal area, height, or volume) of a forest stand at a given time (Fig. 5.3a) represents the composition and structure of the population. The height of the frequency distribution indicates the population density. The minimum, mean, maximum, coefficient of variation, and Gini coefficient indicate the heterogeneity of the structure, e.g. whether all trees are rather similar or significantly different in size (Peck et al. 2014).

Density and structuring determine the growth distribution between the trees in the stand. In homogeneous monospecific stands, the size growth-size relationship may be linear; in heterogeneous stands it tends to be convex from below as shown

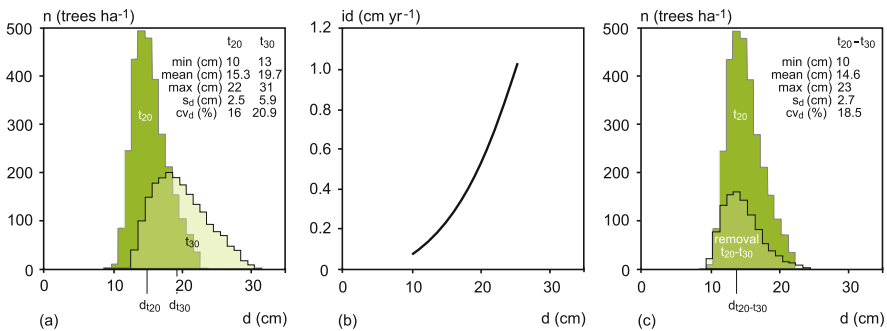


Fig. 5.3 (a–c) Abstracting stand dynamics as evolving tree size distribution. (a) Stem diameter distribution of a stand at age t_{20} and 10 years later t_{30} . (b) The change in size distribution from t_{20} to t_{30} is caused by tree growth (diameter increment in $cm\ yr^{-1}$) depending on size in centimetre. (c) Removal stand in the period $t_{20}-t_{30}$ depending on size. The minimum, mean, maximum, and standard deviation and coefficient of variation of the distributions are 10, 15.3, 22, and 2.5 cm and 16% for t_{20} ; 13, 19.7, 31, and 5.9 cm and 20.9% for t_{30} ; and 10, 14.6, 23, and 2.7 cm and 18.5% for the removal stand between t_{20} and t_{30} . The transformation function (b) is $id = 0.0001 \times d^{2.80}$, with id ($cm\ year^{-1}$) and d (cm)

in Fig. 5.3b. This size growth-size relationship causes a change in the size distribution from t_{20} to t_{30} , as it represents the growth rate of every tree depending on its initial size.

The evolution of the population from t_{20} to t_{30} is also shaped by the removal trees which leave the population due to mortality (e.g. self-thinning, diseases) or harvest. The mode of mortality can again be described by the size distribution of the removal tree number (Fig. 5.3c, frequency distribution for removal trees t_{20} – t_{30}). The drop out of trees can be quantified by number, minimum, mean, maximum size, or by the ratio between the mean tree size of removal and initial stand. For the removal stand shown in Fig. 5.3c applies $d_{\text{out}}/d_{\text{in}} = 14.6/15.3 = 0.95$. If $d_{\text{out}}/d_{\text{in}} = 1.0$, the size of both collectives is equal, whereas small ratios indicate prevailing drop out of small trees, and high ratios mean losses at the right branch of the diameter distribution, i.e. tree losses in the upper canopy.

In this chapter we will apply these three components of size-structure dynamics (initial distribution, transformation function, and distribution of the removal stand) and measures of their position and shape to analyse differences between mixed and monospecific stands at species and whole-stand level. A widening of the initial size distribution (Fig. 5.3a) in mixed versus monospecific stands, for example, would indicate a stronger vertical differentiation and deeper canopy. A shallower $\text{id}-d$ relationship (Fig. 5.3b) would indicate a more even distribution of growth and resources between the trees in a stand. A shift in the removal stand towards the taller diameter classes would indicate that small trees have better conditions for growth and survival in mixed versus monospecific stands.

We use the development of the diameter distribution in the European beech experiment Hain 27/1 from age 51 to 172 in order to illustrate that as the mean diameter increases, the tree number and thereby the kurtosis and peak decrease, the range of the distribution ($d_{\text{max}}-d_{\text{min}}$) widens, and the number of small trees and thereby the skewness decrease because self-thinning eliminates mainly the small trees, i.e. it cuts mainly the left branch of the size distribution (Fig. 5.4).

5.2.2 Size-Structure Dynamics in Mixed-Species Stands: Principle and Example

5.2.2.1 Using Monocultures as a Reference for Distinguishing Between Multiplicative Mixing Effects and Additive Effects

The difference between the characteristic of mixed-species stands and monocultures may be due to a simple additive effect or a multiplicative effect (see introduction to Chap. 4). We use the tree size distributions in Fig. 5.5 to illustrate how to reveal both of these and to distinguish between them. Suppose the tree size distributions D (D stands for frequency distribution) of species 1 and 2 in the monoculture are D_1 and D_2 (Fig. 5.5a and c); then the weighted mean of both distributions in the case of a

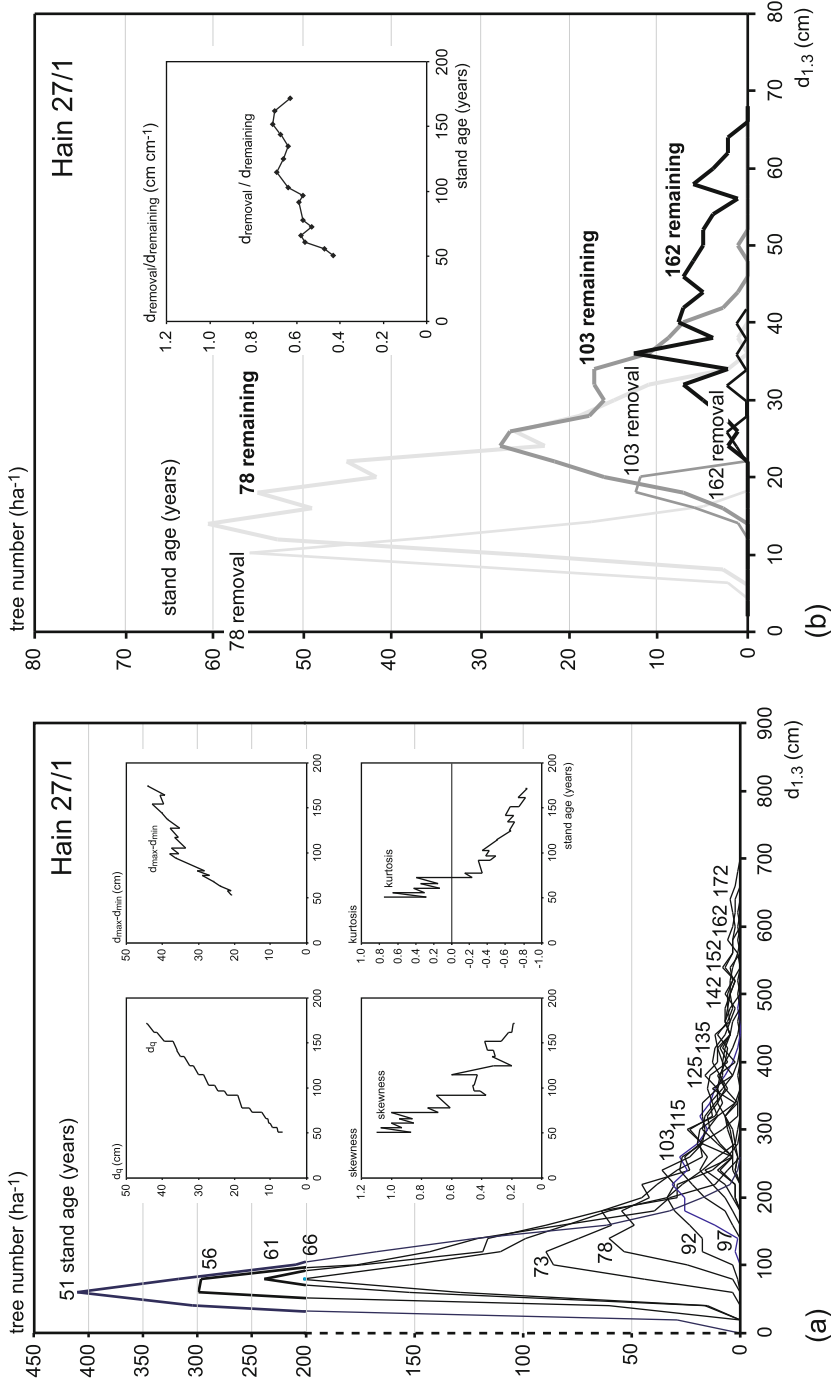


Fig. 5.4 Long-term evolution of the diameter distribution in the European beech experiment Hain 27/1 (slightly thinned A-grade) from age 51 to 172. **(a)** Development of the remaining stand; note that the y-axis is shortened due to space restrictions. For development of mean diameter, d_Q , $d_{max}-d_{min}$, skewness, and kurtosis see insets. **(b)** Remaining and removal stand for selected inventories at age 78, 103, and 162. For development of $d_{removal}/d_{remaining}$, see inset

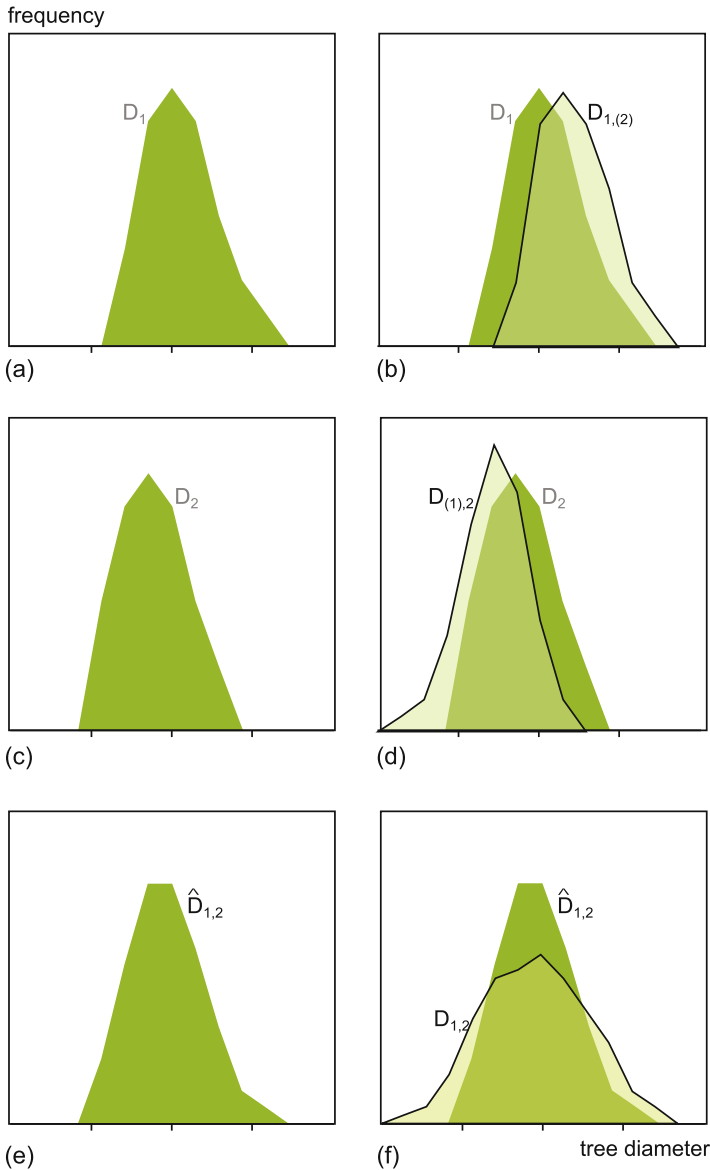


Fig. 5.5 Schematic representation of the comparison between tree diameter distribution in monocultures and in mixed-species stands to quantify multiplicative effects (resulting from species interactions) as opposed to additive effects (resulting only from mixing species with different morphological or physiological traits). At the species level, size distributions D_1 and D_2 in monospecific stands can be compared with the respective distributions $D_{1,(2)}$ and $D_{(1),2}$ in neighbouring mixed stands (a–d). To quantify the mixing effect at the whole-stand level, the weighted mean of both monoculture distributions $\hat{D}_{1,2}$ can be compared with the observed whole-stand distribution $D_{1,2}$ (e and f). Differences between the reference distributions (a, c, e) and the observed size distribution (b, d, f) can indicate interspecific interactions and multiplicative mixing effects

mixture with m_1 as the proportion of species 1 and thus $1-m_1$ for the proportion for species 2, $\hat{D}_{1,2}$, represents the mean of D_1 and D_2 , weighted by the proportions m_1 and $1-m_1$, respectively. $\hat{D}_{1,2}$ is the weighted mean of both monocultures (Fig. 5.5e). It represents the expected distribution under the assumption that mixing simply causes an additive effect, i.e. retains the structural traits of the species as they are in the monoculture. In our example, $\hat{D}_{1,2}$ ($\hat{D}_{1,2} = D_1 \times m_1 + D_2 \times m_2$), where m_1 and m_2 are species proportions $m_1 = m_2 = 0.5$, differs clearly from the two monocultures D_1 and D_2 (compare the distributions shown in (e) with both (a) and (c)). The differences between $\hat{D}_{1,2}$ and D_1 and D_2 are referred to as an additive effect because they are simply the effect of species identity. However $\hat{D}_{1,2}$ also differs from the observed size distribution in the mixed-species stand, $D_{1,2}$ (f). The latter difference between $\hat{D}_{1,2}$ and $D_{1,2}$ indicates a multiplicative mixing effect, i.e. the size distribution of the mixed stand differs from the weighted mean of the neighbouring monospecific stands.

The comparisons between mixed stand and monoculture at the species level ($D_{1,(2)}$ versus D_1 and $D_{(1),2}$ versus D_2) shown in Fig. 5.5 (b and d) reveal how any differences at the stand level (f) emerge from the species level.

The approach for comparing mixed with monospecific stands (as introduced and applied above with reference to their tree diameter distribution) will also be applied for various tree attributes, e.g. for crown projection area, crown length, and individual tree growing area. One reason for using monocultures for this comparison is that mixed stands are often considered as alternatives to monocultures, and the frequency of tree attributes yielded by mixture compared with monocultures may be a basis for decision. Beyond this practical reason, using monocultures as a reference may be the best possible means of revealing the effect of inter- versus intraspecific competition on tree growth and structure.

5.2.2.2 Mixing Can Modify the Size Distribution

Long-term observations of mixed species and general findings on the effect of mixing on the stand diameter distribution dynamics in mixed versus monospecific stands are still rare. In Fig. 5.6 we illustrate the development of the diameter frequency distribution of mixed (grey) versus monospecific (black) plots in the mixed-species experiment Waldbrunn 105 in sessile oak and European beech from 1935 to 2007 as a model example to point out some basic principles.

The diameter frequency distributions of the beech and oak monocultures (Fig. 5.6a and b) are used as references for analysing the mixed stands. Their development is typical for fully stocked even-aged monocultures, usually starting with a high-peaked, left steep, and right shallow tree diameter distribution, i.e. many rather equal-sized individuals with a majority of small ones and only a few tall ones. The initially greater size of tall trees increases through a compound interest effect, while initially small trees tend to drop out due to competition. Due to

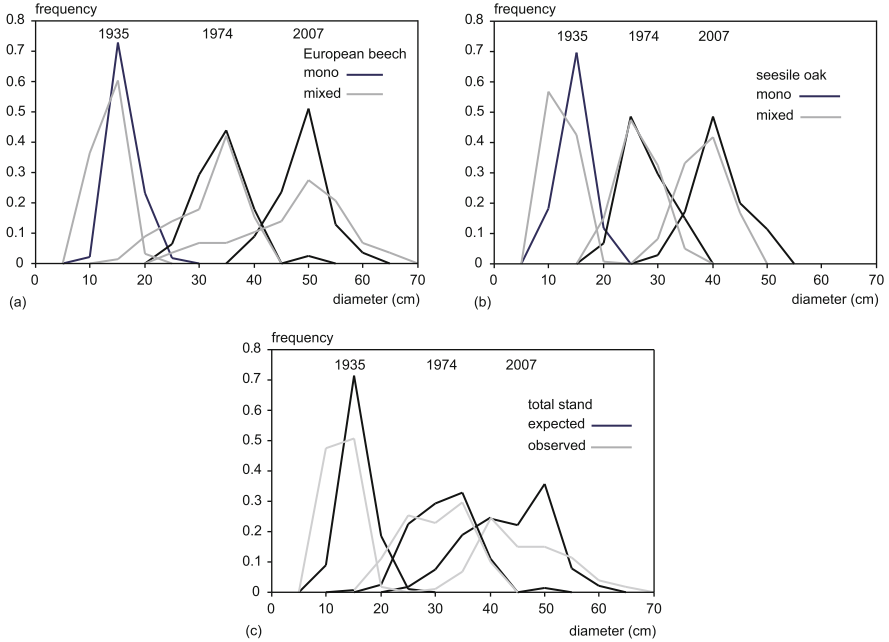


Fig. 5.6 (a–c) Development of the diameter frequency distribution of mixed (*grey*) versus monospecific (*black*) plots in the mixed-species experiment Waldbrunn 105 in sessile oak and European beech from 1935 to 2007. **(a)** The diameter distribution of beech in mixture varies much more widely and shows a greater number of both smaller and taller trees than in the monoculture. **(b)** Diameter distribution of oak in mixture is narrower and behind the development of oak in monoculture. **(c)** Due to the opposite behaviour of beech and oak in the mixed stand, the observed total diameter distribution of both species (*grey*) is not significantly different from the expected (*black*). Notice that in **(a)** and **(b)** the distributions of the species in the mixed stands are scaled up to the unit area of 1 ha in order to make them comparable with the pure stands. In **(c)** the observed diameter distribution of the mixed stand as a whole is compared with the weighted mean distribution of the two pure stands (expected)

the diameter growth which is different for dominant and suppressed trees, the distribution moves rightwards and widens with progressing stand development. The combination of accelerated forward movement at the right side and self-thinning at the left side yields an ever widening, flattening, and symmetric diameter distribution. Thus, the right skewness and kurtosis are at maximum at the beginning and decrease as the stand ages.

The frequency distributions in the mixed stands at species level (Fig. 5.6a and b) and at whole-stand level (Fig. 5.6c) differ from the monocultures as follows: While at the beginning of the survey in 1935 (stand age 45), the diameter distributions of monospecific and mixed stands were rather similar, they increasingly deviated from each other during the following decades of stand development till 2007 (stand age 105). The diameter distribution of beech in mixture varies much more widely and

shows a greater number of both smaller and taller trees than in the monoculture (Fig. 5.6a). The diameter distribution of oak in mixture is narrower and behind the development of oak in monoculture (Fig. 5.6b). Due to the opposite behaviour of beech and oak in the mixed stand, the observed total diameter distribution of both species (Fig. 5.6c, grey) is not significantly different from the expected (Fig. 5.6c, black).

This example underlines that although the whole-stand diameter distribution in the mixed stand does not differ much from the expected distribution, i.e. the weighted mean of the two monocultures' distributions, there might be considerable differences between mixed and monospecific stands at the species level. In our example, this similarity at whole-stand level results from the fact that beech is ahead and oak behind in mixed compared with monospecific stands, so that the first replaces the role of the latter in the mixture.

5.3 Density, Shape, and Location of Size Distributions in Mixed Versus Monospecific Stands

5.3.1 Measures for Characterising Density, Shape, and Location of Size Distributions

To compare the tree diameter distribution of mixed versus monospecific stands, we use measures such as tree number, arithmetic mean diameter, minimum and maximum diameter, diameter range (max-min), and standard deviation of tree diameter.

5.3.1.1 Skewness, Kurtosis, and Other Measures for Characterising Diameter Distributions

To analyse any differences in the shape of the respective distributions, we use the

$$\text{skewness skew} = \frac{\sum_{i=1}^n [(x_i - \bar{x})/s]^3}{n}.$$

In the case of symmetric distribution, skew = 0 (Fig. 5.7a). Where an observed diameter distribution is equipped with many small trees and a low number of tall trees, it is left steep (right shallow) and yields skew > 0. If the distribution is equipped with many tall trees but small trees are rare, it is right steep (left shallow). Skew is useful for characterising the effect of any kind of thinnings (including self-thinning and alien thinning in unmanaged stands) on the shape of the distribution.

Furthermore, we calculated the kurtosis $\text{kurt} = \frac{\sum_{i=1}^n [(x_i - \bar{x})/s]^4}{n} - 3$ which characterises the degree of concentration of tree sizes around the mean. If the concentration resembles the Gaussian normal distribution, kurt = 0. Stronger concentrations around the mean (peaked shapes) are indicated by kurt > 0, whereas lower concentrations

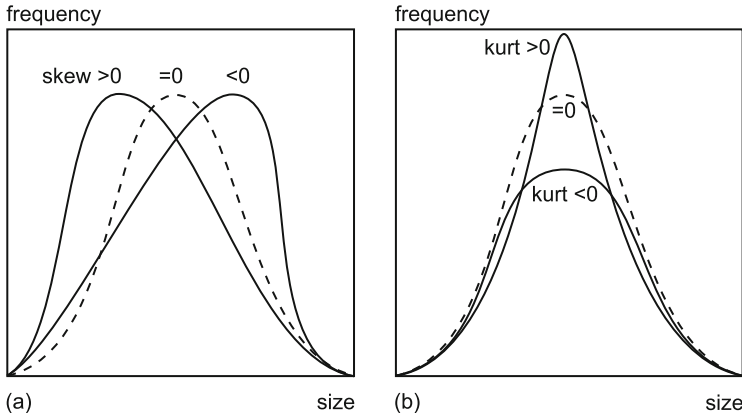


Fig. 5.7 Illustration of skewness (a) and kurtosis (b) of tree diameter distributions

(shallow shapes) yield $kurt < 0$ (Fig. 5.7b). The kurtosis is appropriate for characterising the degree of restriction of a species caused by intra- and interspecific competition.

For the further evaluation, it is important to note that both skewness and kurtosis are invariant to linear transformation, i.e. if the tree diameter distribution of a species occupying a certain portion of the mixed stand is scaled up to 1 ha, the skewness and kurtosis remain unchanged.

5.3.2 Empirical Evidence of Mixing Effects

5.3.2.1 Dataset of 42 Triplets with 126 Plots in Monospecific and Mixed-Species Stands

As a dataset we used 42 triplets in monospecific and mixed stands of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine (Table 5.1). Each triplet consists of three plots with two in monospecific stands and one in a mixed stand of the respective species.

Only those species which play a major role in forestry in both monospecific and mixed-species stands (Brus et al. 2011) were included in the analysis. In order to cover a wide range of growing conditions, the triplets were selected in the lowlands of Poland, the uplands of south Germany, in the low and medium mountain range in south-west Germany, and in the foothills of the Bavarian Forest and Alps (Table 5.1). They lie between 60 and 785 m a.s.l., the mean temperature ranges from 5.5 to 9.5 °C, and the annual precipitation amounts to 556–1350 mm year⁻¹. Brown soils and para-brown soils from loess, loam, or sandy loam are dominant. All included plots represent more or less even-aged and monolayered forest stands.

The plots have not been recently thinned and represent high to maximum stand density. Mixed plots should represent individual tree mixture and a mixing proportion of about 50:50.

5.3.2.2 Density, Shape, and Location of Size Distributions in Mixed-Species Stands Versus Monocultures

The first section of Table 5.1 shows that apart from the mixture of Norway spruce/European beech (mixed/mono = 0.96–1.00), all mixed stands have considerably higher tree numbers than monocultures. On average, there are 9–58% more trees (mixed/mono = 1.09–1.59) in mixed-species stands compared with monocultures (Table 5.1, first section). The minimum tree volumes are mostly lower in mixed compared with pure stands (Table 5.1, second section). The tallest trees, in contrast, can have significantly higher stem volumes in mixed-species stands than in neighbouring monocultures (Table 5.1, third section). However, the mean tree volumes are partly lower and partly significantly higher in mixed compared with pure stands (Table 5.1, fourth section). The differences in the shape of the size distribution were further substantiated by mostly higher right-skewed (skewness $\gg 0$) and higher-peaked (kurt $\gg 0$) size distributions in mixed-species stands compared with neighbouring monocultures (Pretzsch and Schütze 2015).

Table 5.2 shows the range of the frequency distribution for the tree diameter, tree height, and tree volume (from top to bottom). It illustrates that the widening of the tree volume distribution shown in Table 5.1 is coupled with an even stronger widening of the diameter and height distribution. In all cases, the ratios between the range in mixed and pure stands are above 1.0, i.e. the mixed stands are more heterogeneously structured than pure stands. In seven out of eight cases, the range of the diameter distribution is significantly wider in mixed versus pure stands. Regarding the range of the height distribution, mixed stands have a significantly stronger vertical structure in five out of eight cases. This tendency is corroborated by the mostly higher coefficients of variation of tree diameters, tree heights, and tree volumes in mixed compared with pure stands (Pretzsch and Schütze 2015).

In Tables 5.1, 5.2, 5.3, 5.4, 5.5, the columns ‘mean mixed’ and ‘mean mono’ display the arithmetic means of all n observations within the respective groups. The columns ‘mean mixed/mono’, in contrast, report the ratios resulting from the pairwise division of the characteristic of the mixed stand by the respective value of the neighbouring monoculture. The mean of these ratios (mixed/mono) is not necessarily equal to the ratio of the means (mean mixed/mean mono). So, we report both the groupwise arithmetic means (mean mixed and mean mono) as well as the mean ratios of the pairwise comparison (mixed/mono). The mean ratios of the pairwise comparison (mixed/mono) can be used for testing group differences. Our focus was on the relationships between neighbouring mixed-species stands and monocultures (reflected by their pairwise comparison) rather than on their differences in general (reflected by their overall means).

Table 5.1 Tree number per hectare, minimum, maximum, and mean tree volume (mean \pm standard deviation) on the 126 plots of the 42 triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine

Species	n	Tree number (ha ⁻¹)			Tree number mixed/mono 1			Tree number mixed/mono 2				
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
1/2												
N.sp./E.be	11	571 \pm 72	629 \pm 83	681 \pm 112	0.39	1.68	1.00	0.11	0.44	2.33	0.96	0.15
Sc.p./E.be	7	1093 \pm 268	945 \pm 256	1170 \pm 280	0.63	4.01	1.55	0.43	0.51	1.65	1.09	0.16
D.-fir./E.be	18	1051 \pm 218	682 \pm 127	1123 \pm 233	0.58	3.83	1.58	0.19	0.32	2.61	1.19	0.16
N.sp./Sc.p.	6	1075 \pm 78	916 \pm 99	976 \pm 170	0.65	1.84	1.25	0.16	0.67	1.84	1.27	0.21
Species	n	Minimum tree volume			Min tree volume mixed/mono 1			Min tree volume mixed/mono 2				
1/2												
N.sp./E.be	11	0.03 \pm 0.01	0.21 \pm 0.10	0.06 \pm 0.02	0.03	1.21	0.41	0.12	0.17	2.10	0.93	0.20
Sc.p./E.be	7	0.06 \pm 0.02	0.32 \pm 0.11	0.07 \pm 0.02	0.03	1.54	0.51	0.23	0.23	2.02	1.09	0.21
D.-fir./E.be	18	0.04 \pm 0.01	0.60 \pm 0.20	0.20 \pm 0.14	0.00	3.29	0.51	0.22	0.06	2.29	0.99	0.15
N.sp./Sc.p.	6	0.03 \pm 0.01	0.15 \pm 0.09	0.23 \pm 0.08	0.04	4.09	0.95	0.64	0.03	0.45	0.16***	0.06
Species	n	Maximum tree volume			Max tree volume mixed/mono 1			Max tree volume mixed/mono 2				
1/2												
N.sp./E.be	11	3.51 \pm 0.55	2.83 \pm 0.50	2.63 \pm 0.30	0.68	3.02	1.39	0.19	0.78	1.96	1.35**	0.12
Sc.p./E.be	7	1.91 \pm 0.36	1.49 \pm 0.29	1.68 \pm 0.36	0.47	2.80	1.48	0.28	0.52	2.60	1.32	0.25
D.-fir./E.be	18	5.85 \pm 1.15	5.68 \pm 1.15	2.50 \pm 0.51	0.37	2.28	1.01	0.11	0.79	5.77	2.49***	0.26
N.sp./Sc.p.	6	2.25 \pm 0.29	2.10 \pm 0.31	1.65 \pm 0.29	0.66	2.07	1.15	0.20	1.11	1.92	1.43***	0.13
Species	n	Mean tree volume			Mean tree volume mixed/mono 1			Mean tree number mixed/mono 2				
1/2												
N.sp./E.be	11	1.25 \pm 0.23	1.30 \pm 0.30	0.88 \pm 0.15	0.53	2.74	1.15	0.20	0.80	2.55	1.48**	0.15
Sc.p./E.be	7	0.61 \pm 0.12	0.76 \pm 0.18	0.61 \pm 0.17	0.33	1.49	0.92	0.16	0.55	2.50	1.26	0.26
D.-fir./E.be	18	1.34 \pm 0.29	2.61 \pm 0.60	1.34 \pm 0.29	0.21	2.18	0.61	0.10	0.76	2.66	1.60***	0.13
N.sp./Sc.p.	6	0.61 \pm 0.09	0.72 \pm 0.12	0.79 \pm 0.09	0.55	2.32	0.98	0.27	0.50	0.91	0.76	0.06

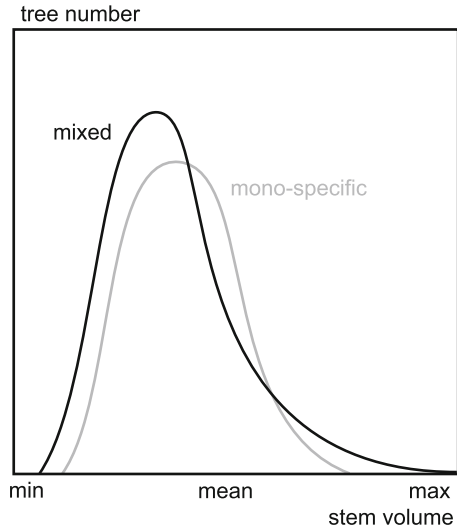
Note that in the columns 'mean mixed', 'mean mono 1', and 'mean mono 2', we report the arithmetic means of all n observations within the respective groups. In the columns 'mean mixed/mono 1' and 'mean mixed/mono 2' in contrast, we report the mean of the ratio resulting from the pairwise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures. *, **, ***, and **** indicate significant differences between mixed-species stands and monocultures at the level $p < 0.05$, 0.01, and 0.001

Table 5.2 Range of stem diameter, d , tree height, h , and stem volume, v , (mean \pm standard deviation) on the 126 plots of the 42 triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine

Species	n	Range d			Range d mixed/mono 1			Range d mixed/mono 2				
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
1/2												
N.sp./E.be	11	45.26 \pm 2.73	33.63 \pm 3.17	36.72 \pm 1.76	0.83	2.09	1.42***	0.12	0.99	1.61	1.24***	0.06
Sc.p./E.be	7	31.31 \pm 3.05	19.41 \pm 2.06	26.79 \pm 2.67	0.98	2.82	1.74**	0.27	0.67	1.70	1.21	0.12
D.-fir./E.be	18	54.38 \pm 6.48	42.67 \pm 4.42	29.06 \pm 3.11	0.50	2.45	1.26*	0.12	0.80	3.29	1.90***	0.15
N.sp./Sc.p.	6	35.77 \pm 1.76	30.63 \pm 1.95	22.73 \pm 2.73	0.90	1.47	1.19*	0.09	1.24	2.12	1.65***	0.15
Species												
1/2												
N.sp./E.be	11	19.56 \pm 1.27	13.53 \pm 1.73	12.98 \pm 1.72	0.90	2.90	1.62**	0.19	1.06	5.85	1.90*	0.41
Sc.p./E.be	7	11.80 \pm 1.65	5.53 \pm 1.25	11.04 \pm 1.06	0.85	6.24	2.85*	0.72	0.72	1.67	1.07	0.11
D.-fir./E.be	18	22.54 \pm 2.15	11.09 \pm 2.12	13.17 \pm 1.49	0.58	15.03	3.91**	0.94	1.15	36.30	3.54	1.93
N.sp./Sc.p.	6	21.55 \pm 1.13	15.52 \pm 2.27	7.61 \pm 2.05	1.01	3.74	1.70	0.44	1.45	9.22	4.13**	1.19
Species												
1/2												
N.sp./E.be	11	3.48 \pm 0.55	2.62 \pm 0.48	2.57 \pm 0.30	0.69	3.14	1.48*	0.20	0.78	1.97	1.36**	0.12
Sc.p./E.be	7	1.85 \pm 0.37	1.17 \pm 0.22	1.62 \pm 0.35	0.52	3.68	1.82*	0.37	0.48	2.63	1.33	0.25
D.-fir./E.be	18	5.81 \pm 1.15	5.09 \pm 1.00	2.30 \pm 0.45	0.35	2.65	1.10	0.13	0.79	5.87	2.64***	0.27
N.sp./Sc.p.	6	2.23 \pm 0.28	1.95 \pm 0.23	1.42 \pm 0.25	0.67	2.04	1.20	0.19	1.23	2.35	1.67	0.18

For further explanation see caption of Table 5.1

Fig. 5.8 Characteristic size distribution of mixed stands compared with monocultures. In this analysis, the minimum tree sizes in mixed stands were lower, and the maximum tree sizes were higher, but the mean size was rather similar compared with monocultures. In mixed stands, the tree numbers were higher, and the size distributions more left steep (skewness $\gg 0$) and more peaked (kurtosis $\gg 0$). In contrast, the size distributions in monocultures were more symmetrical and flatter



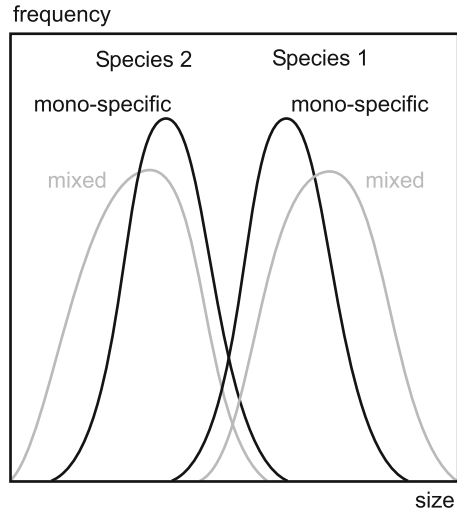
5.3.3 Characteristic Modification of Tree Size Distribution Through Species Mixing

In the temperate forests of our study, the trees compete strongly above ground for light. As a result of this competition for light, tree size distribution, growth partitioning between the trees, and canopy density of mixed-species stands can change fundamentally and may contribute to an overyielding compared with neighbouring monocultures.

Figure 5.8 is a schematic representation of the effect of mixing on the tree size distribution. The total number of trees can be higher in mixed stands compared with monocultures. In addition, the minimum tree size can be smaller and the maximum size larger. The skewness and the kurtosis can also be higher. The higher tree number and lower minimum tree size result mainly from shade-tolerant species like beech which had reduced growth but can survive below more light-demanding and transparent species such as pine. The alien thinning can proceed less rigorously than the self-thinning, especially in the case of beech, which has the lowest self-tolerance of the species investigated (Pretzsch 2006; Zeide 1985). Trees of the species with superior size can accelerate growth and grow ahead. Due to its size superiority, this species can slow down the other species so that the latter lags behind and takes on a more subdominant position. This explains the higher maximum tree size and wide range of sizes in mixed stands compared with monocultures also found by Buongiorno et al. (1994) and Coomes and Allen (2007).

In most cases, one of the two even-aged species is ahead of the other regarding size development. Figure 5.9 is a schematic representation showing that species 1 is ahead of species 2 in the monoculture. The leading species is often more light demanding and grows more quickly, while the slower species is often more shade

Fig. 5.9 In the mixed stand, the accelerated forward shift in the size distribution of species 1 (*right*) can slow down and modify the shape of the size distribution of species 2 (*left*). Schematic representation of how the species' tree size frequency distribution in a two-species mixed stand (*grey lines*) can differ from the size distribution in neighbouring monocultures (*black lines*)



tolerant. Growing in mixture can trigger an additional forward shift in the size distribution of species 1 which is already ahead in the monoculture (e.g. Norway spruce or Douglas-fir in mixture with European beech). Species 2, which is behind the size growth of species 1, may cause a thinning-from-below effect on species 1 by outcompeting smaller population members of species 1. In contrast, species 1 may reduce species 2, similar to a thinning-from-above effect. As a consequence, the total tree size distribution in mixed stands is often broader, with higher skewness and kurtosis than in monospecific stands (Fig. 5.9).

5.4 Relationship Between Size Growth and Size of Trees in Mixed Versus Monospecific Stands

5.4.1 Modes of Competition and Growth Distribution Between the Trees in a Forest Stand

When growing solitarily, it is mainly size that determines a plant's growth-size trajectory (Box 5.1). In temperate forests with light as a limiting factor for individual tree growth, taller trees can pre-empt the light and shade and thus reduce growth of their smaller neighbours. Thus, in a cohort of even-aged trees, growth of smaller trees can fall much further below the potential growth curve and behind that of their fitter neighbours. Diameter growth plotted above diameter (or volume growth versus volume) reveals the interindividual competition and growth partitioning between the trees in a stand (Wichmann 2001, 2002).

Box 5.1 From the Potential Size-Growth Curve of an Individual Tree to the Interindividual Size-Growth Relationship at a Given Point in Time in a Stand

Potential Size Growth as a Function of Tree Size as Reference

In the juvenile phase of tree development, anabolism has the upper hand and drives growth exponentially. However, simultaneously with size growth, maintenance costs increase and affect culmination of the growth rate which then finally tapers off (Zeide 1993). Open-grown trees or trees with constant inhibition follow a unimodal growth-size trajectory which comprises convex (seen from below) curve sections in the juvenile phase (1–3), concave sections in the middle age (4–6), and again convex sections in the mature phase (7–9) (see Avery and Burkhardt (1983, p 266); Schütz (1989, pp 4–5)). The higher the site fertility, the lower the growth limitation and the higher the level of the curve due to the greater resource supply per plant for a given size (Pretzsch and Biber 2010). Box Figure 5.1-1a illustrates this by curves expected for high, medium, and low resource supply. Such growth curves can be derived from long-term survey (real time series) or chronosequences (artificial time series) of trees grown under solitary conditions.

Effect of Interindividual Competition

When growing solitarily it is mainly size that determines the plants' unimodal growth trajectory shown in Box Fig. 5.1-1a. Within a stand, particularly those trees coping with crowding or stress can fall below this trajectory. For trees within a stand, size denotes access to resources, especially to light. In most cases, the taller a tree, the more privileged is its access to resources, space occupation, and repression effect on neighbours (Biging and Dobbertin 1995; Pretzsch 2009). But size is an ambiguous trait; it can also mean higher susceptibility to windthrow (Peltola 1996; Valinger et al. 1993), drought (Condit et al. 1995; Skov et al. 2004), or bark beetle attacks (Coggin et al. 2010). However, in temperate forests with light as a limiting factor for individual tree growth, taller trees shade and thus reduce the growth of their smaller neighbours. In a cohort of even-aged trees, growth of smaller trees falls behind the taller ones. Subsequently, it drops further below the potential than that of fitter neighbours.

This size-dependent growth reduction is behind the phenomenon which forest scientists refer to as diameter increment-diameter line (id-d line) and which is often used to describe and model the growth-size relationship of even-aged stands in a given developmental phase (e.g. Prodan (1965, pp 474–476)). While Box Fig. 5.1-1a shows the potential growth-size trajectories of individual trees with high, medium, and low resource supply, Box Fig. 5.1-1b exemplarily illustrates for trees with high resource supply how competition can transform the unimodal curve of individuals to the linear interindividual growth-size relationships. Diameter growth

(continued)

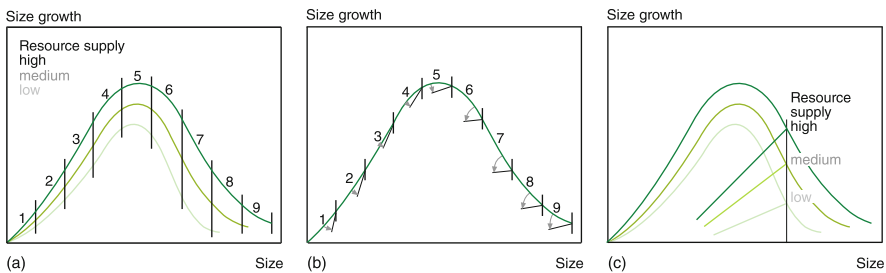
Box 5.1 (continued)

plotted above diameter (or volume growth versus volume) yields a straight line with a steep positive slope in early stand phases and an increasingly flatter slope with progressive stand development (Box Fig. 5.1-1b, segments 1–9).

Site Conditions Can Modify the Size Growth-Size Relationship

Under *ceteris paribus* conditions, trees on fertile sites with a high supply of resources can make more use of their privileged position and exert a more negative effect on the growth of their smaller neighbours (Wichmann 2001, 2002). This should be reflected by steeper slopes of the interindividual size-growth relationships (see straight lines in Box Fig. 5.1-1c), while nutrient limitation should diminish their superiority and the slope of the growth-size relationship (Pretzsch and Dieler 2011).

The absolute growth rate in a defined period, such as 1 year, plotted against plant size at the beginning of the respective period can result in different patterns of growth allocation, representing different modes of competition between trees. Figure 5.10 displays a set of linear (lines 1, 3, 4, and 5) and non-linear (lines 2, 6) growth-size relationships (Weiner 1990). A steeper slope gradient indicates a stronger concentration of growth rates and resources on tall trees in the stand. The



Box Fig. 5.1-1 (a–c) Schematic representation of the relationship between size and growth of individual trees (a) growing without competition, (b) modified by competition, and (c) resulting size-growth relationships for different levels of resource limitation. (a) Potential size-growth relationships of open-growing individual trees on sites with high, medium, and low resource supply. Without competition, the course of growth in dependence on size consists of convex (segments 1–3 and 7–9) and concave (segments 4–6) parts. (b) Unimodal individual growth curves and linear interindividual size-growth relationships caused by competition. Illustration of the relationship between size and growth without competition (unimodal curve) and the growth reduction due to competition (*arrows*) which results in more or less linear interindividual size-growth relationships (*short straight lines*). This growth reduction through competition results in linear size-growth relationships with steep positive slopes in the early stand phase and increasingly flatter slopes with progressive stand development (segments 1–9). (c) On sites with high resource supply, the interindividual growth reduction due to competition causes stronger asymmetry and steeper size-growth relationships than on sites with medium or low resource supply (decreasing slope of the size-growth straight lines with decreasing resource availability)

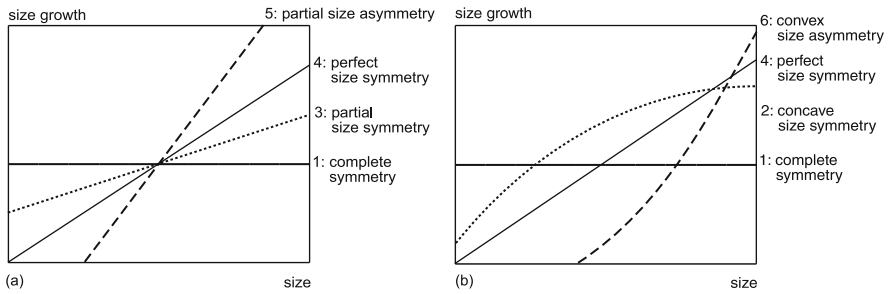


Fig. 5.10 Hypotheses about the relationship between plant size and absolute growth rate. **(a)** Different linear relationships between size and growth and **(b)** non-linear relationships between plant size and growth. Line 1 represents the more theoretical case of a completely symmetrical size-growth relationship where all plants receive the same budget of growth irrespective of size. Line 2 displays non-linear concave size symmetry where growth increases less digressively with size. Line 3 reflects partial size symmetry where growth increases linearly with size. Line 4 represents perfect size symmetry and means that growth increases proportionally with size. Line 5 stands for partial size asymmetry where growth increases linearly with size. Line 6 represents non-linear convex size asymmetry where growth increases progressively with size

case of complete size asymmetry, indicated by a line parallel to the y-axis (slope = ∞ ; a sub-cohort of large plants receives all growth), is rarely observed and not integrated in Fig. 5.10. Note that all relationships in Fig. 5.10a are linear. However, only line 4 represents a linear and proportional increase in the absolute growth rate with increasing size, meaning that only in this case is the relative growth rate equal for all individuals.

Complete symmetry (Fig. 5.10a, line 1) would mean that growth and the resources that competitors receive are independent of their size. Tendency towards complete symmetry (line 1) or partial size symmetry (Fig. 5.10a, line 3; Fig. 5.10b, line 2) is assumed to prevail where below-ground resources (water and mineral nutrients) are a limiting factor, as these are mobile, diffuse quickly and are difficult for larger individuals to pre-empt (van Kuijk et al. 2008). Partial or strong size asymmetry (Fig. 5.10a, line 5; Fig. 5.10b, line 6) means that larger individuals obtain a disproportionately higher share of resources and growth (see, e.g. Fig. 5.3b). This mode of growth-size relationship can be expected on high-quality sites where light is the limiting factor and, as a vectorial resource, can be pre-empted by the larger individuals (Cannell and Grace 1993; Weiner and Thomas 1986).

In order to quantify the mode of competition in mixed versus monospecific stands, tree size growth can be plotted over size (stem volume increment, iv , over stem volume, v). Fitting a straight line ($iv = a + b \times v$) through the iv - v scattergram by OLS regression yields the intercept a and slope b . This procedure can be applied for trees in monocultures and mixed-species stands for comparing them. Based on the resulting intercepts and slopes (Fig. 5.11), it can be analysed whether and how species mixing modifies the mode of competition (Hara 1992; Wichmann 2001, 2002).

The slope b of the relationship $iv = a + b \times v$ indicates and integrates several aspects of the size-growth dynamics of a population. The steeper the slope b , the stronger the pre-emption of light by the highly efficient tall trees, the higher the size

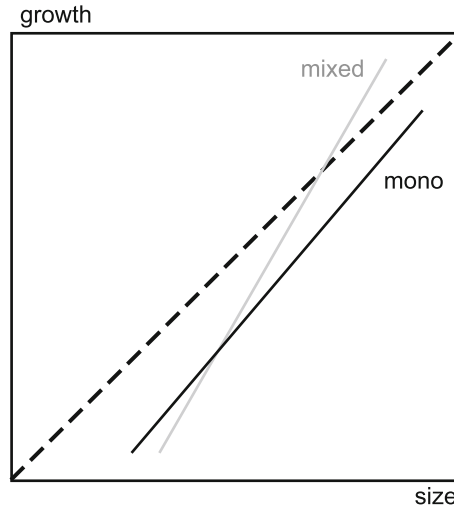


Fig. 5.11 The slope of the $iv-v$ relationships in mixed and monospecific stands indicates how mixing may increase the asymmetry of competition and growth partitioning among the trees in a stand (Schwinning and Weiner 1998). In this schematic graph, mixing favours the growth of tall trees and reduces the growth of small trees

hierarchy within the population, and the stronger the concentration of growth on the tall trees at the expense of their small neighbours. Conversely, this means that steep slopes indicate relatively low growth or even drop out of small trees in favour of tall trees in the stand. The growth-size slope is suitable for indicating and further analysing interindividual growth allocation patterns and their dependency on species mixture. Figure 5.11 represents a reaction pattern where mixing favours the growth of tall trees and reduces the growth of small trees compared with monospecific stands.

5.4.2 Symmetry and Asymmetry of Competition

Comparison of the $iv-v$ relation in mixed-species stands with monocultures may reveal the modification of size asymmetry by species mixing. Of main interest is how the $iv-v$ relationship of the mixed stand as a whole behaves in relation to the monocultures. The overarching analysis of all 84 pairwise comparisons between the mixed-species stands and the monocultures introduced in Tables 5.1 and 5.2 yielded $R_b = 1.14 \pm 0.06$, $n = 84$, $p < 0.05$. This indicates a significant increase in the slope by 14% in mixed-species stands compared with monocultures as schematically shown in Fig. 5.11. An analogous analysis at the species level yielded $R_b = 1.11 \pm 0.05$, $n = 84$, $p < 0.05$. The overall mean slope is $b_m = 0.040$ for mixed stands and $b_p = 0.038$ for monocultures.

Behind these overall mean reaction patterns are species-specific behaviours (Table 5.3). While mixed stands of Norway spruce and European beech have significantly shallower slopes compared with the pure stands of these species, the

Table 5.3 Slope (mean \pm standard deviation) of the iv-v relationship ($iv = a + b \times v$) in mixed-species stands versus monocultures of the 42 triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine

Species	<i>n</i>	Slope <i>b</i> of iv-v relationship				<i>b</i> mixed/ <i>b</i> mono 1				<i>b</i> mixed/ <i>b</i> mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	SE	Min	Max	Mean	SE	Min	Max	Mean	SE
N.sp./E.be	11	0.036 \pm 0.003	0.038 \pm 0.004	0.035 \pm 0.003	0.04	0.48	0.95	0.78***	0.04	0.58	1.14	0.85*	0.06
Sc.p./E.be	7	0.041 \pm 0.005	0.034 \pm 0.007	0.048 \pm 0.005	0.39	0.76	3.64	1.36	0.39	0.37	1.04	0.78*	0.10
D.-fir./E.be	18	0.040 \pm 0.004	0.039 \pm 0.004	0.041 \pm 0.008	0.09	0.69	2.07	1.28**	0.09	0.50	2.50	1.37***	0.11
N.sp./Sc.p.	6	0.032 \pm 0.002	0.034 \pm 0.003	0.030 \pm 0.002	0.13	0.67	1.42	0.95	0.13	0.81	1.28	1.02	0.08

For further explanation see caption of Table 5.1

mixture of Douglas-fir and European beech developed significantly steeper slopes than both the corresponding pure stands. Figure 5.12 illustrates for the mixture of Douglas-fir/European beech the mostly steeper slopes of the iv - v relationship in mixed-species stands (Fig. 5.12b, d, and e) compared with monocultures (Fig. 5.12a

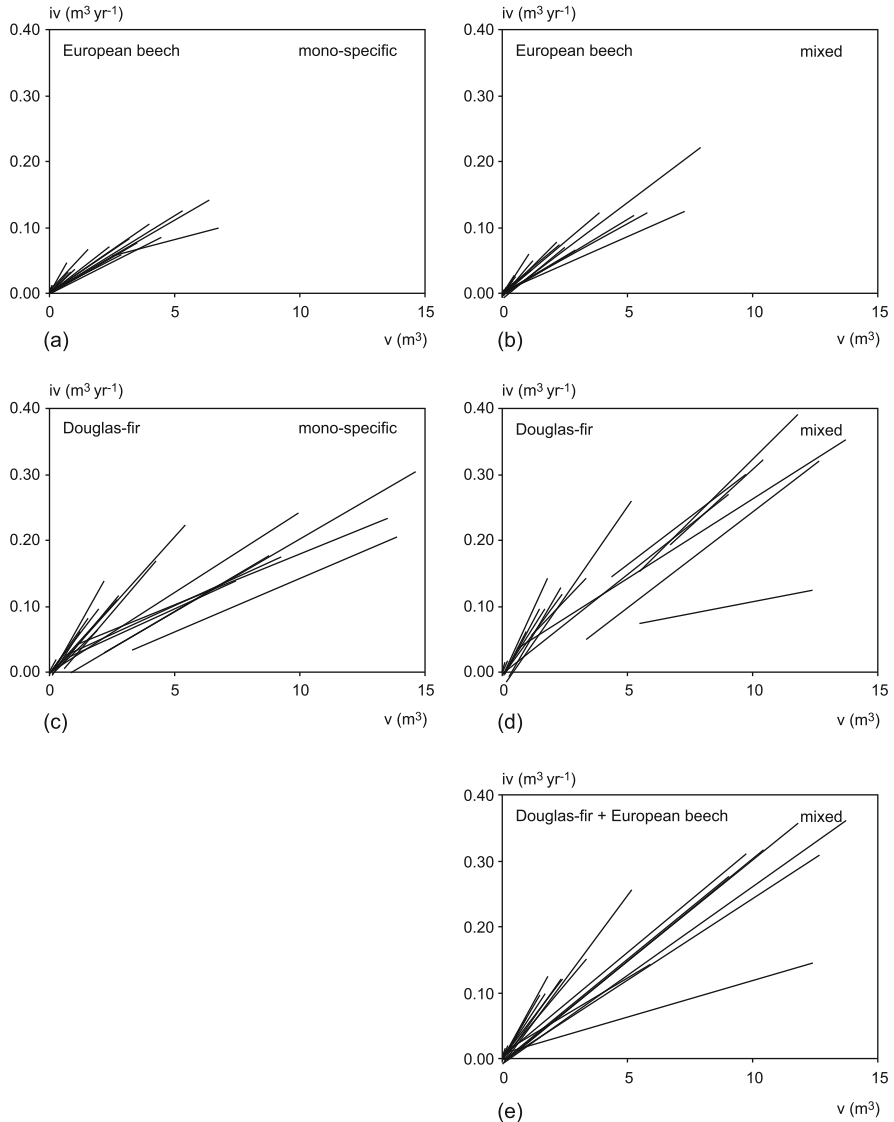


Fig. 5.12 (a–e) Modification of the iv - v relationship by mixing Douglas-fir and European beech compared with the respective monocultures. The asymmetry of growth in the mixed stands (b, d, e) can differ considerably from the corresponding monocultures (a and c). The iv - v relationship is shown for each species in the mixed-species stands separately (b and d) and also for the mixed-species stands as a whole (e). Annual tree volume growth ($\text{m}^3 \text{year}^{-1}$), iv ; tree volume (m^3), v

and b). Table 5.3 shows that the ratios between the slope in the mixed-species stands of Douglas-fir/European beech and the monocultures are significantly higher than 1.0.

The slope b of the $iv-v$ relationship reveals the interindividual competition and growth partitioning between the trees in a stand (Schwinning and Weiner 1998; Wichmann 2001, 2002). The slope can be used to quantify and further analyse the size symmetry and asymmetry of competition, which is also called “mode of competition” by Hara (1993, 1992) and Yokozawa et al. (1998). The mostly steeper slope in mixed compared with monospecific stands indicates a stronger concentration of growth rates and resources on tall trees in the stand. Steep $iv-v$ relationships mean that larger individuals obtain a disproportionately higher share of resources and growth. Schwinning and Weiner (1998) expect this mode of growth-size relationship on high-quality sites where light is the limiting factor and can be pre-empted by the larger individuals. Shallow $iv-v$ relationships are assumed to prevail where below-ground resources (water and mineral nutrients) are a limiting factor, as these are mobile, diffuse quickly, and are difficult for larger individuals to pre-empt. Our finding of mostly steeper slopes in mixed compared with monospecific stands may corroborate the size-asymmetric competition and pre-emption of light by the tall trees at the expense of the growth of their small neighbours.

5.5 Modification of Tree Distribution by Removal Trees

5.5.1 Ratio Between the Diameter of the Removal and Total Stand for Characterising the Mode of Mortality

Based on the mean tree diameter of the removal stand, d_{removal} , and the remaining stand, d_{remain} , the ratio $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remain}}$ characterises the size of the removal in relation to the remaining trees (Fig. 5.13). Note that the latter is a schematic figure with simplified assumptions about the mean diameter of the remaining and removal trees and about the shape of the distributions. The higher the d_{rel} values, the taller the removed trees in relation to the remaining stand. Thinning from below or self-thinning befalls mainly small trees with $d_{\text{removal}} < d_{\text{remain}}$ and yields ratios of $d_{\text{rel}} < 1$. In the case of a schematic thinning, the mean sizes of the removal and remaining trees would be equal, and $d_{\text{rel}} \cong 1$ (range $d_{\text{rel}} = 0.9-1.1$). Thinning from above means tree elimination from the right side of the tree size distribution and can yield $d_{\text{rel}} > 1$. Selective thinning, which eliminates 1–2 of the strongest competitors of each future crop tree, may result in the range $d_{\text{rel}} = 0.8-1.2$. Comparison between a species d_{rel} in the mixed stand and the neighbouring monoculture may reveal how mixing superimposes the self-thinning process in the monoculture which normally reduces the tree number from the left side of the tree size distribution.

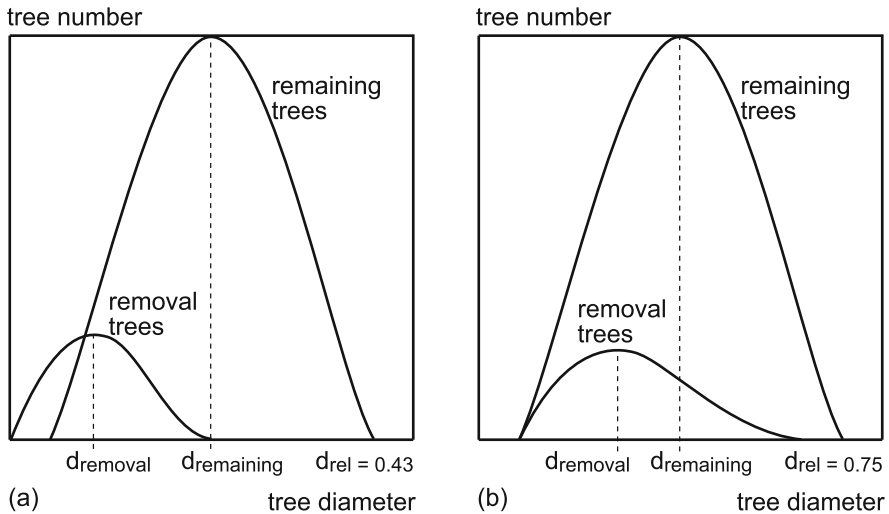


Fig. 5.13 Schematic representation of changes in the removal ratio $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remaining}}$ through mixing. (a) Restriction of the removals to the left side of the diameter distribution in the monospecific stand yields $d_{\text{rel}} = 0.43$, and (b) extension of the removals to the right side of the diameter distribution is reflected by $d_{\text{rel}} = 0.75$

5.5.2 Mode of Tree Mortality in Mixed Versus Monospecific Stands

For analysing the mode of mortality in mixed versus monospecific stands, unthinned or only moderately thinned experimental plots with long-term records of dead and removal trees are the most revealing database. For the following evaluation, a set of 11 fully stocked and at most moderately thinned stands was used, as this best reflects the species-specific mortality in mixed versus monospecific stands. The evaluation was based on more or less even-aged monospecific and mixed stands of European beech and sessile oak and European beech and Norway spruce located in Germany. Altogether we pooled data of 51 triplets of monospecific and mixed stands. The dataset represents the growing conditions of a rather broad time span (1905–2012), a range of stand ages (31–238 years) and mainly experiments from central and southeast Germany. Table 5.4 summarises basic characteristics of the plots; for more detailed information, see Matyssek et al. (2012, pp 243–271), Pretzsch (2009), Pretzsch et al. (2010), and Pretzsch et al. (2013a) who used the same experiments to analyse mixing effects at tree and stand level.

The significantly higher ratio d_{rel} of beech in mixture compared with monocultures (Table 5.4, Fig. 5.14a) indicates that the associated tree species, Norway spruce and sessile oak, exert an alien-thinning effect from above. The mean d_{rel} ratio of the removal beeches in the mixed stand is about 10% higher ($d_{\text{rel}} \cong 0.82$ versus $d_{\text{rel}} \cong 0.73$) than in monoculture, i.e. mortality reaches wider into the right branch of the tree size distribution in mixed stands compared with

Table 5.4 Overview of the differences between mixed and monospecific stands in terms of size distribution, size-growth relationship, and mode of mortality

Variable	European beech			Norway spruce			sessile oak		
	mixed	mono	mixed/mono	mixed	mono	mixed/mono	mixed	mono	mixed/mono
n	68	68	68	41	41	41	32	32	32
d_{mean} (cm)	26.5	29.1	0.92 ± 0.08	37.2	33.2	1.12 ± 0.03	25.0	24.6	1.03 ± 0.05
v_{mean} (m ³)	0.89	1.05	0.82 ± 0.12	1.08	1.41	1.30 ± 0.08	0.62	0.59	1.13 ± 0.15
d_{min} (cm)	14.6	15.2	1.08 ± 0.14	25.8	21.0	1.27 ± 0.11	17.7	17.0	1.07 ± 0.07
d_{max} (cm)	49.0	43.6	0.96 ± 0.07	49.4	46.4	1.07 ± 0.04	35.9	33.7	1.08 ± 0.06
s_d (cm)	74.7	79.3	1.05 ± 0.10	73.6	64.5	1.17 ± 0.09	46.5	41.5	1.13 ± 0.13
d_{rel} (cm cm ⁻¹)	0.82	0.73	1.20 ± 0.09	0.75	0.74	1.03 ± 0.10	0.78	0.79	1.0 ± 0.08

The columns ‘mixed’ and ‘mono’ report the species-specific arithmetic means of all n observations within the respective groups. The column ‘mixed/mono’, in contrast, shows the mean of the ratio resulting from the pairwise division of the characteristic of the mixed stand by the respective value of the neighbouring monoculture. Bold ratios indicate significant ($p < 0.05$) differences between the species behaviour in mixed versus monospecific stands

Number of stands analysed, n ; arithmetic mean diameter, d_{mean} ; arithmetic mean stem volume, v_{mean} ; minimum and maximum tree diameter, d_{min} and d_{max} ; standard deviation of tree diameter, s_d ; $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remaining}}$

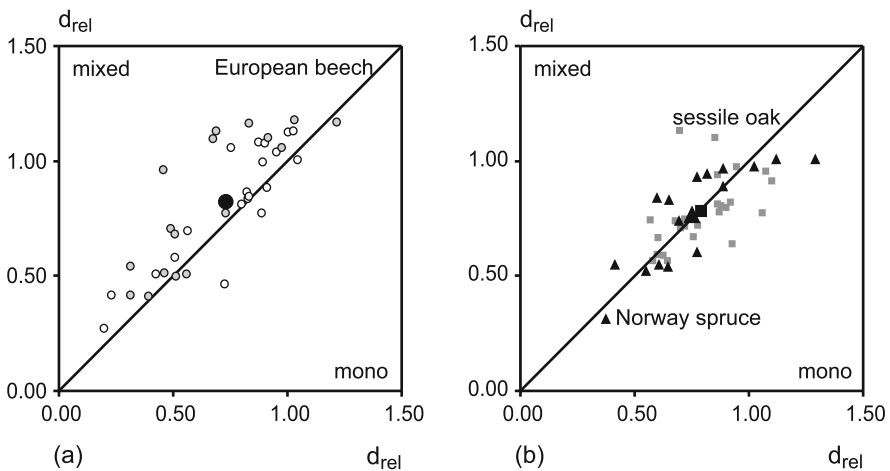


Fig. 5.14 Ratio between the diameter of the removal and remaining stand, d_{rel} , for mixed versus monospecific stands for (a) beech and (b) oak and spruce. Observations close to the bisector line indicate similar behaviour for mixed and monospecific stands, while deviations indicate true mixing effects. (a) Response of beech to admixture of oak is represented by empty circles, its response to spruce by filled circles. The large black circle indicates the mean relationship for beech in mixed versus monospecific stands. (b) Response of oak to the admixture of beech is represented by rectangles and the response of spruce to beech by triangles. The large black rectangle and triangles in the centre, close to the 1:1 line, indicate the mean relationship for oak and spruce in mixed versus monospecific stands

monocultures. In the analysed even-aged mixed stands, Norway spruce and sessile oak are ahead in size growth and obviously able to slow down the growth and reduce the number of beeches during early stand development.

In contrast, the d_{rel} of Norway spruce and sessile oak is not significantly modified by mixing (Fig. 5.14b). The mean tree size growth of Norway spruce and sessile oak can be fostered by mixing. However, their removal ratio is not significantly modified through the presence of beech. Their d_{rel} values indicate a thinning-from-below effect which is rather equal in mixed and monospecific stands ($d_{rel} \cong 0.75$). Table 5.4 underlines that, in the case of European beech, d_{rel} significantly ($p < 0.05$) exceeds 1.0 and indicates the mortality shifts from the smaller diameter classes to the taller trees in mixed stands.

The ratios between mixed and monospecific stand characteristics in Table 5.4 reflect that in the case of beech, size growth tends to be reduced in mixed compared with monospecific stands and in the case of spruce and oak, it is accelerated. The size variation can become wider (spruce and oak), the size inequality greater (beech), and the removal trees larger (beech) in mixed compared with monospecific stands.

5.6 Hierarchy of Tree Size, Tree Growth, and Growth Dominance

5.6.1 Gini Coefficients, GC_v and GC_{iv} , and Growth Dominance Coefficient, GDC

5.6.1.1 Coefficient by Gini and Curve by Lorenz for Characterising the Size and Growth Hierarchy

The coefficient by Gini and curve by Lorenz can be used to quantify the size or growth hierarchy between the trees in forest stands (see de Camino (1976); Kramer (1988, p 82)). We loan from economics the Gini coefficient, GC,

$$GC = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n(n-1) \times \bar{x}}$$

to quantify the relative distribution of stem volume (GC_v) and volume growth (GC_{iv}), respectively, between the trees in mixed versus monospecific stands. Variables x_i and x_j denote size or growth (or other tree characteristics) for the i 'th and the j 'th tree in the stand with $i = 1 \dots n$ trees. $GC = 0.0$ applies for a very homogeneous distribution of the respective tree variable, e.g. maximum equality of size or growth distribution. The stronger the inequality of size or growth between the trees, the higher the GC (Fig. 5.15a and b). The curves of the cumulative distributions together with the sketched stands reflect the inequality of size which can also cause an inequality of growth.

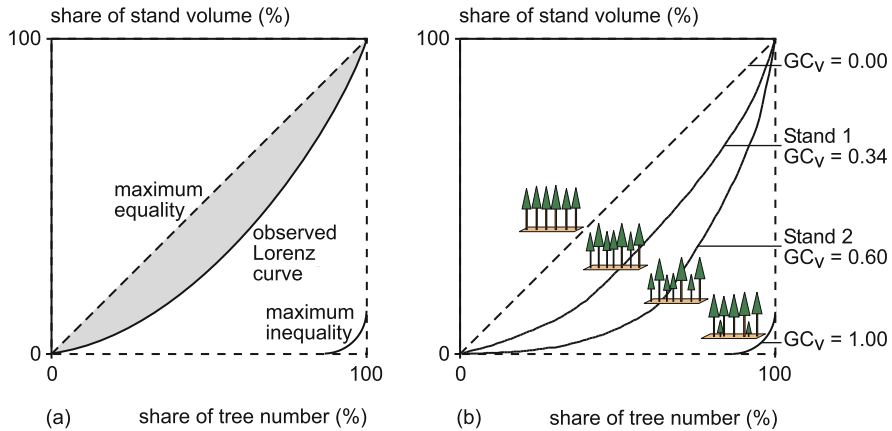


Fig. 5.15 Schematic representation of the stem volume partitioning between the trees in a forest stand. (a) Lorenz curve applied to quantify the degree of equality in stem volume distribution. (b) Equal volume distribution in rather monolayered stands ($GC_V = 0.00$), increasing inequality in heterogeneous stands (Stand 1, $GC_V = 0.34$; Stand 2 $GC_V = 0.60$), and strong inequality (GC_V approaching 1.0)

Application of these measures to mixed and monospecific stands can reveal how mixing modifies the hierarchy between the trees in a population, e.g. whether species mixing can favour the growth distribution towards small understorey trees compared with monocultures. The Lorenz curve (Fig. 5.15a), known for the analysis of income inequality in human populations, can be used to visualise the inequality of growth in forest stands. The larger the area between the bisector line (maximum equality) and the observed Lorenz curve, the greater the inequality, and the higher the GC. The GC is equivalent to the ratio of the grey-coloured area (area between the Lorenz curve and the bisector line is shown in Fig. 5.15a) to the total area of the square, multiplied by two.

5.6.1.2 Curve of the Cumulative Tree Growth as Function of Cumulative Stem Volume: Growth Dominance Coefficient, GDC

The cumulative distribution of tree growth over stem volume combines information about size distribution and the respective growth distribution between the trees in a stand. For this purpose, the trees of the stand are ranked from smallest to largest volume, the cumulative volume of the trees is registered on the abscissa and the cumulative volume growth on the ordinate. The resulting curves illustrate how much smaller trees contribute to the total stand growth compared with taller trees (see Fig. 5.16). In this figure curve 1 indicates a growth dominance of tall trees, curve 3 a growth dominance of small trees, and curve 2, following the bisector line, indicates that all trees contribute to stand volume growth proportionally to their volume (Box 5.2).

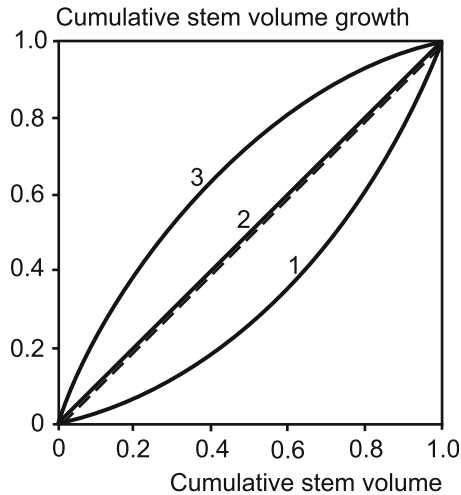
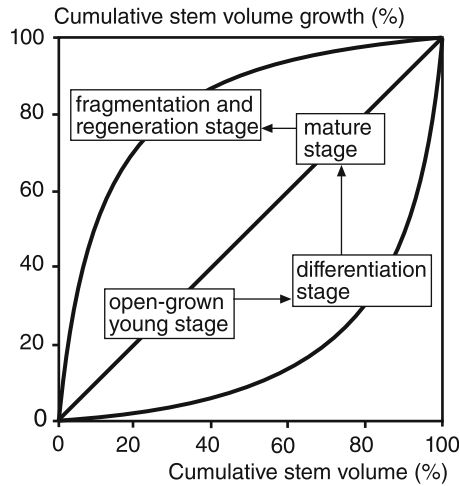


Fig. 5.16 Schematic representation of the cumulative distribution of stem growth (ordinate) over the cumulative distribution of stem volume (abscissa) for forest stands with different competitive status of small compared with tall trees. The curves 1, 2, and 3 represent stands where small trees make a low, medium, and strong contribution to the total stand growth. Curves 1, 2, and 3 result in a growth dominance coefficient of $GDC = 0.17$, 0.0 , and -0.12 , respectively

Box 5.2 Conceptual Model of the Change in Growth Dominance During Stand Development by Binkley et al. (2006)

For a combined view on both the size and growth effect of individuals in a population, Binkley et al. (2006) proposed the analysis of the cumulative distribution of stem volume growth over stem volume (Box Fig. 5.2-1). According to the conceptual model by Binkley et al. (2006), growth dominance—quantified by the coefficient of growth dominance GDC —changes during stand development as follows: In the *open-grown young stage* (phase 1) suppression is low, and therefore individual tree growth is proportional to size (bisector line). Stand closure means the beginning of the *differentiation stage* (phase 2) when large trees grow overproportionally and continuously slow down or outcompete smaller neighbours. Due to this strong competitive pressure, the relative contribution of the stem growth of small trees may stay behind their portion to stem volume causing a convex curve (seen from below). In the *mature stage* (phase 3), growth may again become proportional to size as the growth of tall trees subsides and smaller trees benefit from interruptions of the canopy. In the *fragmentation and regeneration stage* (phase 4), smaller trees come up, benefit from the opened crown, and contribute overproportionally to the stand growth (based on Binkley et al. (2006, p 195, Fig. 2)).



Box Fig. 5.2-1 Different patterns of the cumulative distribution of stem volume growth (y-axis) over cumulative stem volume (x-axis) during mono-cohort forest stand development. In the *open-grown young stage*, suppression is low meaning that individual tree growth is proportional to size (*bisector line*). Stand closure represents the beginning of the *differentiation stage* when large trees grow overproportionally and continuously slow down or outcompete smaller neighbours. In the *mature stage*, growth may again become proportional to size as tall trees subside in growth and smaller ones benefit from interruptions of the canopy. In the *fragmentation and regeneration stage*, smaller trees come up, benefit from the opened crown, and contribute overproportionally to the stand growth (based on Binkley et al. (2006, p 195, Fig. 2))

We use this approach for the subsequent mixed-species stands analysis. When the curve in mixed stands is compared with monospecific stands, it indicates how the contribution of small and tall trees is modified by species mixing. Beyond this graphical representation, the relationship between cumulative tree growth and cumulative stem volume can be characterised by the difference between the Gini coefficients for cumulative growth (GC_{iv}) and the Gini coefficients for cumulative volume (GC_v). This difference ($GC_{iv} - GC_v$) is similar to the growth dominance coefficient GDC used by Binkley et al. (2006) and Pommerening et al. (2016). If the curve follows the bisectoral line, $GDC = 0$ (see line 2 in Fig. 5.16). If it runs above the bisectoral line, $GDC < 0$, and if the curve lies below the bisector line, $GDC > 0$ (see curves 3 and 1, respectively, in Fig. 5.16).

5.6.2 More Unequal Tree Sizes and Tree Growth Partitioning in Mixed Compared with Monospecific Stands but Similar Growth Dominance

The Gini coefficients GC_v in Table 5.5 (upper section) indicate that the inequality is mostly significantly higher in mixed-species stands compared with monocultures ($GC_v \text{ mixed}/GC_v \text{ mono} = 0.95\text{--}2.09$). Figure 5.17a and b illustrates this general

Table 5.5 Gini coefficients for volume, GC_v and Gini coefficients for volume growth, GC_{iv} (mean \pm standard deviation) in mixed-species stands versus monocultures (from top to bottom)

Species	n	GC_v for volume			GC_v mixed/ GC_v mono 1			GC_v mixed/ GC_v mono 2				
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N.sp./E.be	11	0.41 \pm 0.02	0.30 \pm 0.03	0.44 \pm 0.03	0.91	2.24	1.47**	0.14	0.63	1.33	0.95	0.06
Sc.p./E.be	7	0.37 \pm 0.02	0.32 \pm 0.04	0.39 \pm 0.04	0.83	2.64	1.74**	0.27	0.73	1.44	0.98	0.09
D.-fir./E.be	18	0.54 \pm 0.02	0.38 \pm 0.02	0.42 \pm 0.03	0.64	3.37	1.79***	0.18	0.96	3.21	1.38**	0.12
N.sp./Sc.p.	6	0.47 \pm 0.02	0.31 \pm 0.03	0.23 \pm 0.02	0.71	1.84	1.29	0.17	1.50	2.81	2.09***	0.18
Species	n	GC_{iv} for volume growth			GC_{iv} mixed/ GC_{iv} mono 1			GC_{iv} mixed/ GC_{iv} mono 2				
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N.sp./E.be	11	0.42 \pm 0.02	0.35 \pm 0.03	0.47 \pm 0.03	0.78	1.69	1.24**	0.08	0.72	1.28	0.92	0.05
Sc.p./E.be	7	0.40 \pm 0.02	0.29 \pm 0.05	0.45 \pm 0.05	0.78	2.39	1.66*	0.27	0.71	1.33	0.96	0.10
D.-fir./E.be	18	0.59 \pm 0.02	0.39 \pm 0.03	0.45 \pm 0.03	0.72	2.54	1.64***	0.12	0.95	2.90	1.41***	0.10
N.sp./Sc.p.	6	0.49 \pm 0.01	0.41 \pm 0.04	0.28 \pm 0.02	0.80	1.83	1.27	0.15	1.39	2.31	1.83***	0.18

Note that coefficients of GC_v and GC_{iv} close to 0.0 indicate equality of size and growth, respectively. Coefficients close to 1.0 indicate high inequality in size or size growth. For further explanation see caption of Table 5.1

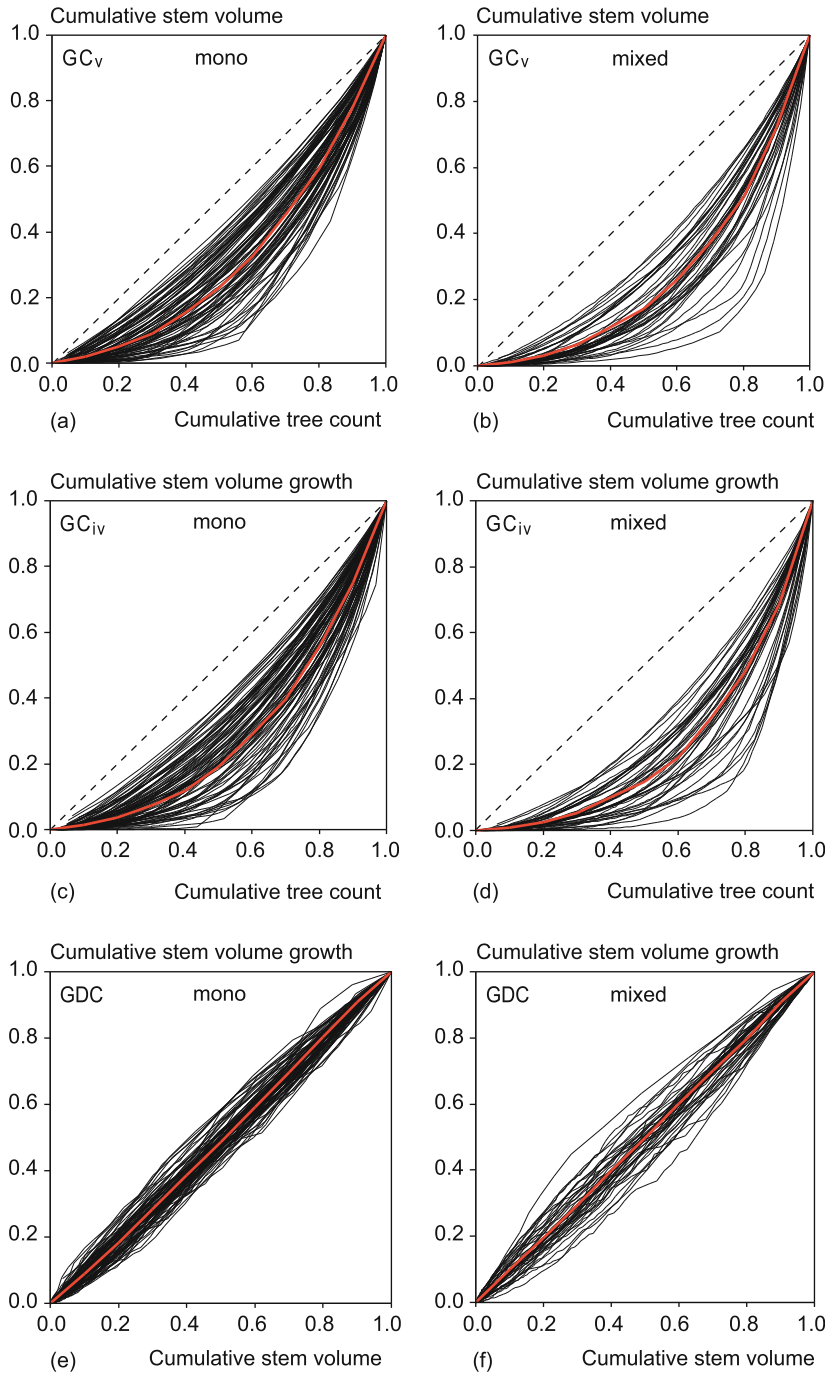


Fig. 5.17 (a–f) Hierarchy of tree volume, stem volume growth, and growth dominance for 84 monocultures (a, c, e) and 42 mixed stands (b, d, f) of the triplet series of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway

tendency. It shows the cumulative stem volume as a function of the cumulative tree count for all monocultures and mixed-species stands of the triplets. The mean curves (bold lines) indicate that the smallest 50% of the trees account for 25% of the total stand volume in monocultures and for just 15% in the mixed-species stands. This inequality in size indicates a high number of small trees and a restricted number of tall trees in mixed stands. In monocultures, in contrast, the trees are more equally sized.

The finding of higher inequality in mixed-species stands versus monocultures also applies for the growth partitioning among the trees within the stands, represented by GC_{iv} (Table 5.5, lower section). This is illustrated by the cumulative stem volume growth as a function of the cumulative tree count in Fig. 5.17c and d. That both GC_v and GC_{iv} are mostly significantly higher in mixed-species stands than in monocultures indicates a more unequal size distribution and growth partitioning in mixed stands.

In contrast, the GDCs show only small and non-significant absolute differences between mixed and monospecific stands (Fig. 5.17e and f). The cumulative stem volume growth as a function of cumulative stem volume always lies close to the 1:1 line ($GDC = 0$). The ratios between GDCs in mixed versus monospecific stands vary strongly but do not differ significantly from $GDC = 1.0$.

5.6.3 Remarkable Growth-Structure Elasticity of Mixed-Species Stands

Both GC_v and GC_{iv} indicate a much more unequal partitioning of stem volume and stem volume growth among the trees in mixed compared with monospecific stands (Fig. 5.17a–d, Table 5.5). Mixed stands have many small trees on the one hand and a strong concentration of volume and growth on a restricted number of tall trees on the other hand. Monocultures have greater equality of size and growth distribution. In monocultures, the largest 20% of the trees account on average for 40% of the stem volume. In mixed stands this figure is 50% (see Fig. 5.17a versus b). In monocultures, the largest 20% of the trees account on average for 44% of the stand growth, whereas in mixed stands this figure is 52% (see Fig. 5.17c versus d).



Fig. 5.17 (continued) spruce/Scots pine (for description of the triplet dataset, see Sect. 5.3.2 and Tables 5.1–5.3). (a and b) Cumulative stem volume, v , as a function of the cumulative tree count, n . On average, the Gini coefficients for monocultures ($GC_v = 0.36 \pm 0.01$) are significantly lower than for neighbouring mixed stands ($GC_v = 0.46 \pm 0.01$) of the same species. (c and d) Cumulative stem volume growth, iv , as a function of the cumulative tree count, n . On average, the Gini coefficients for monocultures ($GC_{iv} = 0.40 \pm 0.01$) are significantly lower than for neighbouring mixed stands ($GC_{iv} = 0.50 \pm 0.02$) of the same species. (e and f) Growth dominance coefficient, GDC, which is the cumulative stem volume growth, iv , as a function of cumulative stem volume, v , and results from $GC_{iv} - GC_v$. On average, GDCs of monocultures ($GDC = 0.02 \pm 0.01$) are not different to those of mixed-species stands ($GDC = 0.01 \pm 0.01$)

Table 5.5 showed that the difference between GC_v and GC_{iv} is rather similar for monospecific (on average $GDC = GC_{iv} - GC_v = 0.40 - 0.36 = 0.04$) and mixed (on average $GDC = GC_{iv} - GC_v = 0.50 - 0.46 = 0.04$) stands. So, the coefficients of growth dominance ($GDC = GC_{iv} - GC_v$) are also similar and near $GDC = 0$ (varying closely around the 1:1 line in Fig. 5.17e and f) for monospecific and mixed stands. As the stem volume growth partitioning is very similar to the stem volume partitioning, the relationship between cumulative growth and cumulative volume is rather proportional.

This reveals a remarkable growth elasticity of mixed-species stands. The reasons for this constant GDC, even under strongly varying stand structure, are probably the complementary ecological traits in mixed stands. A combination of light-demanding species in the upper canopy and shade-tolerant species in the lower canopy ensures that the relative contribution of the stem growth of small trees does not stay behind their portion of stem volume.

According to the conceptual model of growth dominance and the growth dominance coefficient, GDC, by Binkley et al. (2006), most of the 42 triplets are in phase 3, i.e. in the mature stage (Box 5.2). However, both GC_v and GC_{iv} indicate a much more unequal partitioning of stem volume and stem volume growth among the trees in mixed compared with monospecific stands and suggest strong differentiation and competition typical for phase 2. Mixing may release the competitive pressure in mixed stands through niche complementarity and thus result in a proportional relationship between cumulative growth and cumulative volume—although density, inequality, and size asymmetry are much higher than in monocultures. Species mixing seems to equalise the relationship between cumulative growth and cumulative volume and thereby guarantee a continuously low-growth dominance and size-proportional contribution of all trees to the stand growth.

5.7 Modification of the Crown Allometry and thereby the Canopy Space Filling in Mixed versus Monospecific Stands

The addressed changes in the stem size distribution reflect one important effect of mixing on the size-structure dynamics of forest stands. Beyond this, species mixing can also modify the tree height, the crown size, and thereby the canopy space filling (Fig. 5.1a–c).

5.7.1 From Stem Size Distribution to Crown Size Distribution

The mixing experiment Waldbrunn 105 of sessile oak and European beech (see also Fig. 5.6) can be used to illustrate an effect of mixing on the frequency distribution of crown variables that is even stronger than that on tree diameter. Behind this is the crown release effect and crown expansion in mixed or thinned stands which can

result in a wide variability of tree allometry (see Chap. 6) and variation in wood quality parameters (see Chaps. 9 and 11).

Figure 5.18 is based on the tree diameter and crown diameter of the 87-year-old stands in 1989 (first surveyed 1935, 10 successive surveys). Till their present age, the trees on these plots have had sufficient time to adapt their stem and crown shapes to the intra- and interspecific neighbourhood in the monospecific and mixed stands, respectively. Note that the grey lines represent the frequency distributions of the trees in the mixed stands scaled up to the unit area of 1 ha by the mixing proportion of the respective species.

Mixing barely changes the diameter distribution of sessile oak (Fig. 5.18a) and slightly slows the diameter growth of smaller beeches (Fig. 5.18d). The crown diameter distribution of the trees growing in mixture indicates the length and diameters of branches and consequently the branch diameter. In comparison with the neighbouring monocultures, the crown diameter distribution in mixed stands is shifted to the left in the case of oak (Fig. 5.18b) and to the right in the case of beech (Fig. 5.18e).

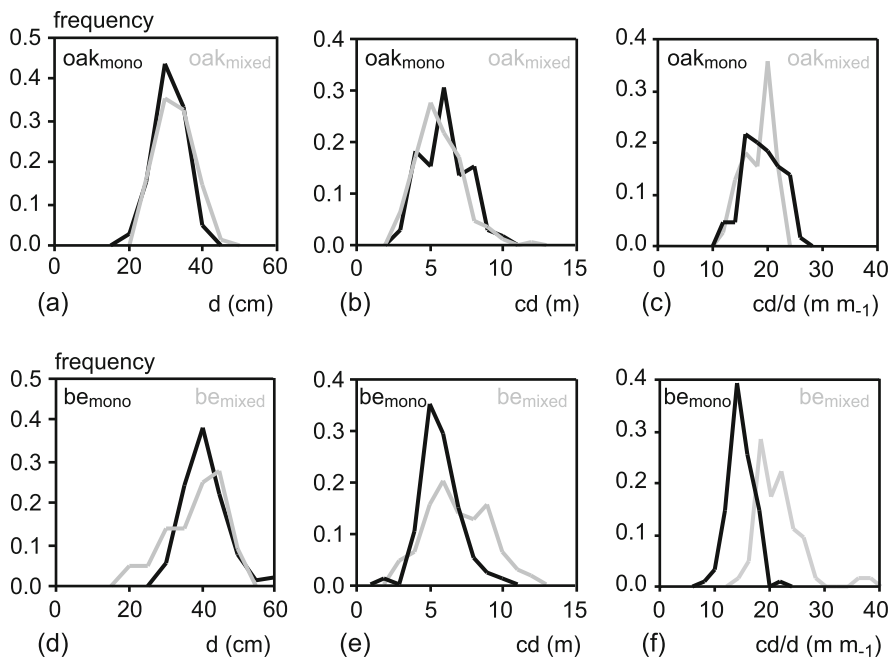


Fig. 5.18 (a–f) Frequency distribution of tree attributes in mixed stands (grey lines) compared with monospecific stands (black lines) of sessile oak (a–c) and European beech (d–f) in the long-term experiment Waldbrunn 105 at age 87. In the case of oak, mixing only slightly modifies frequency distribution of tree diameter, d ; crown diameter, cd ; and the ratio cd/d , compared with monocultures. In the case of beech, mixing shifts and extends the frequency distributions of d , cd , and particularly of the ratio cd/d

The cd/d ratio (Fig. 5.18c and f) indicates how many times larger the crown diameter is in relation to the stem diameter. The cd/d ratio of a tree with $cd = 5\text{ m}$ and $d = 50\text{ cm}$ would be 10 ($cd/d = 500\text{ cm}/50\text{ cm} = 10$), while a tree with the same diameter but a crown width of 10 m would yield $cd/d = 20$ ($cd/d = 1000\text{ cm}/50\text{ cm} = 20$). The higher the cd/d ratio, the broader the crown and the longer and thicker the branches. Note that crown size and branch diameter are closely associated with stem shape, wood strength, and stiffness (see Chap. 9). In the case of oak (Fig. 5.18c), mixing barely shifts the cd/d frequency distribution. However, the cd/d ratio distribution of beech is shifted considerably to the right and is much more extended in mixed compared with monospecific stands (Fig. 5.18f). The evaluation is based on 68 and 30 oaks and on 95 and 65 beeches in monospecific and mixed stands, respectively. The coefficient of variation ranges between 15 and 21% for d , 23 and 28% for cd , and 15 and 20% for cd/d . Especially in the case of beech, the coefficient of variation is high (between 15 and 33%). This example shows the considerable extent to which tree attributes such as crown diameter and cd/d ratio can change in mean and variation, although with regard to the stem diameter, there are only minor differences between mixed stands and monocultures.

In Chap. 6 we will further explore the effect of inter- versus intraspecific neighbourhood on the tree allometry and space occupation. For forest practice, the modification of the frequency distribution by mixing towards taller trees of the leading species (e.g. Norway spruce, sessile oak) and less small-sized and more uniform individuals in the case of beech may cause an improvement in the assortment yield, even if productivity at stand level remains unchanged. Further comparison of the frequency distribution of species in mixed and monospecific stands may be extended to proxies of wood quality such as ratios of h/d or cd/d which may decrease and cl/h , which may increase wood quality (tree height, h ; tree diameter, d , crown diameter, cd ; crown length, cl). Frequency distributions of the latter proxy variables of tree wood quality enable an integrated view of the effect of species mixing on both quality (quality aspects such as distortion, knottiness, wood density, stiffness, and strength) and quantity (number of trees with respective qualities) of the produced wood and potential wood products (Pretzsch and Rais 2016).

5.7.2 Canopy Space Filling in Mixed versus Monospecific Stands

In temperate forests the pre-emption of light by the tallest trees causes size-asymmetric competition (Schwinning and Weiner 1998; Wichmann 2002). Trees can acclimate to size-asymmetric competition through morphological shifts in order to remedy the light limitation (Grams and Andersen 2007). In monospecific stands, especially those that are rather homogeneous in terms of genetics and tree size, all individuals engage in similar behaviour to compete for the growing space and resources that are not sufficient for all. As the resource demands, physiological abilities, and structural variability of competing trees are more similar in monocultures, canopy structure remains mostly homogeneous, competition rather

size asymmetric, and canopy depth low. In mixed stands, in contrast, the trees' elbowroom may 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 (Fish et al. 2006; Putz et al. 1984).

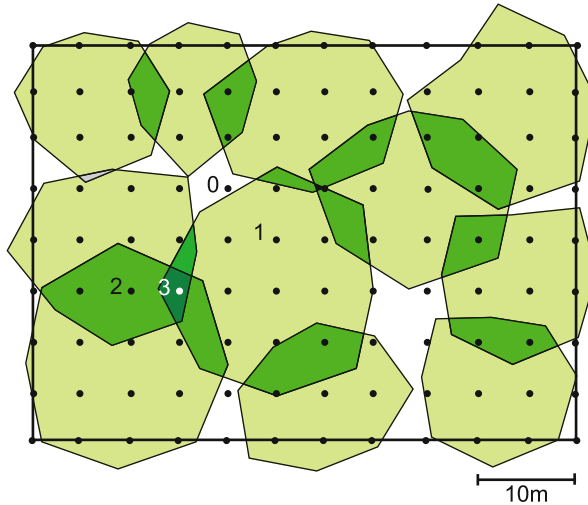
For closer analysis of the canopy space filling, Pretzsch (2014) used 253 crown maps in monocultures ($n=87$) and two-species ($n = 111$) and \geq three-species ($n = 55$) mixed stands in Germany. All three groups comprise even-aged and uneven-aged stands of mainly Norway spruce, European beech, sessile and common oak, Scots pine, silver fir (*Abies alba* Mill.), and sycamore maple (*Acer pseudoplatanus* L.). The following analysis of the canopy space filling in mixed versus monospecific stands is based on combined measurement of tree positions and crown sizes (crown length and crown projection area) on long-term experimental plots. The crown measurements ($n = 35,728$ measured crowns) date back to the 1950s and cover a broad range of tree species growing in monospecific and mixed stands. For a detailed account of eight-radii crown measurements, see Pretzsch (2009, pp 115–118). Among the various measures for assessing forest canopies (Jennings et al. 1999), the ground coverage by crowns, CGC; the sum of the crown projection area, SCPA; and the crown engagement, CE, are of special interest (Box 5.3).

Box 5.3 From Crown Projection Area of Individual Trees to the Canopy Ground Cover, CGC; the Sum of Crown Projection Areas, SCPA; and the Crown Engagement Ratio, CE

The crown projection area of a tree, cpa, results from projection of four or eight crowns. In Box Fig. 5.3-1 the crown projection areas are represented by polygons. The crown projection area can be calculated via the mean crown radius \bar{r}_q , which corresponds to the quadratic mean of four or eight radial measurements r_1, \dots, r_n ($\bar{r}_q = \sqrt{(r_1^2 + r_2^2 + \dots + r_n^2)/n}$). The canopy ground cover, CGC, characterises the cover of the ground by crowns when looking vertically from above. This may be useful for estimating the throughfall of precipitation, deposition, etc. CGC is generally analysed using dot counts of crown maps. For this purpose, a grid is laid over the map. CGC is obtained from the number of dot points covered by the crown, n , divided by the total number of grid dot points, p_{total} ($CGC = p_{\geq 1\text{-fold}}/p_{\text{total}}$). For the stand in Box Fig. 5.3-1 $p_{\geq 1\text{-fold}} = 93$, $p_{\text{total}} = 108$ applies, and $CGC = 93/108 = 0.86$; i.e. 86% of the stand area is covered by crowns.

However, the sun does not shine in a perpendicular direction into forest stands in our latitudes and the sum of crown projection area, SCPA (including the multiple layering), or the crown engagement ratio, CE, may be more relevant for production ecology than CGC. The ratio between the sum of crown projection areas, $SCPA = \sum csa$, and the plot size, A , quantifies the

(continued)



Box Fig. 5.3-1 Crown map with uncovered area portions (white), one-, two-, and \geq threefold crown coverage (light grey, grey, and dark grey). In this example, 14% of the plot area is uncovered, 86% is covered \geq one-fold, and the sum of crown areas is $SCPA = 2310 \text{ m}^2$ which is 105% of the plot area and results in a crown engagement of $CE = 1.05$. The numbers 0–3 in the map represent dots with zero-, one-, two-, and \geq threefold crown coverage

Box 5.3 (continued)

crown engagement, CE , and can be derived in two ways: (1) by summing up the cross-section area of all trees on a plot and dividing by plot size A (then $CE = \sum csa/A$) and (2) based on the results of a dot count evaluation which distinguishes for each grid point between uncovered, onefold covered, two-fold covered ... n -fold covered ($CE = p_{1\text{-fold}} \times 1 + p_{2\text{-fold}} \times 2 + \dots + p_{n\text{-fold}} \times n/p_{\text{total}}$). In our example, the result is $CE = (75 \times 1 + 16 \times 2 + 2 \times 3) / 108 = 1.05$, i. e. the sum of the crown cross-section area is 1.05-fold the stand area.

The stands have a mean plot size of 0.30 ha and stand ages of 16–283 years. Their crown measurements from 1951 to 2013 were used to calculate CGC, SCPA, and CE . All measures vary widely as the plots cover fully but also sparsely stocked stands. From plots with repeated crown surveys, we 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. 5.19a show that the sum of crown area amounts to 150 and 100%, respectively, in monospecific stands and increases with species richness by up to 220% and 180% (95% and 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

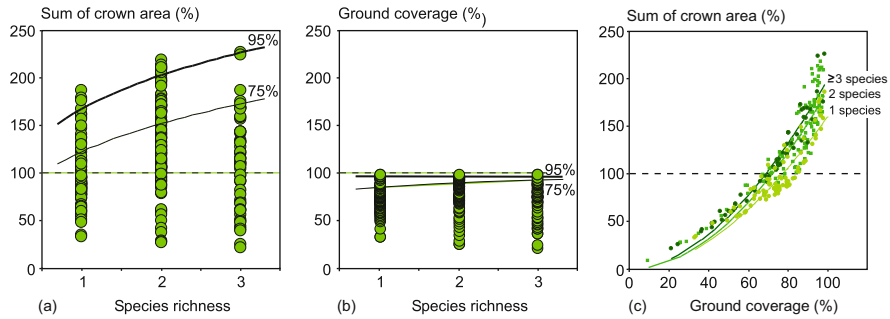


Fig. 5.19 (a–c) Sum of crown projection area per unit area and ground coverage in mixed compared with monospecific stands. (a) Sum of crown projection area per unit area depending on tree species richness, (b) ground coverage depending on tree species richness, and (c) sum of crown projection area per unit area depending on ground coverage and tree species richness. Data 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 from 1951 and 2004, and minimum and maximum stand age of 16 and 283 years, respectively. The 95% and 75% quantile regression lines in Fig. 5.19a and b represent the sum of crown area and ground coverage for fully and loosely stocked stands. The OLS regression lines in Fig. 5.19c represent the mean sum of crown area per unit area depending on ground coverage for \geq three-, two-, and one-species stands (*upper, middle, lower line*, respectively)

the stand area. The relationship between ground coverage by crowns and tree species richness shown in Fig. 5.19b demonstrates that in most fully stocked mono- as well as polycultures, 5–10% of the stand area is uncovered by crowns. The frequently reported mechanical abrasion (Putz et al. 1984) resulting in crown shyness may cause the 5–10% uncovered area in both monospecific and mixed stands. The wide variation in ground coverage below the ceiling line (95% and 75% quantile regression lines) can be attributed to the broad range of thinning grades included in the dataset of 253 crown maps. The above finding that species richness may increase CE even when CGC is similar becomes even clearer in Fig. 5.19c. Especially in denser stands with CGC > 80%, the sum of crown projection area per unit area is about 25% higher in three-species stands compared with monocultures (upper versus lower line in Fig. 5.19c).

Studies in mixed-species stands by Kennel (1965), Pretzsch (2009, pp 267–269), and Preuhlsler (1981) suggest that the sum of crown projection area per unit area is often much higher than the ground coverage due to an up to sevenfold crown overlap especially in polycultures of species with complementary ecology. When studies comparing crown coverage between stands only count once areas which have been covered twice or more often, they neglect that the 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 monospecific and mixed stands of spruce and beech ($n = 110$) as well as oak and beech ($n = 74$), the phenomenon of multiple crown coverage is analysed more closely (see Table 5.6).

Table 5.6 Ground cover by crowns (mean \pm standard error) in even-aged monocultures and mixed stands of Norway spruce, European beech, and sessile oak based on crown maps of unthinned and moderately thinned stands

Species	Stand type	n	Ground cover (%)	Ground	onefold and multiple ground coverage			Rel. sum of crown area (%)
					onefold (%)	twofold (%)	\geq threefold (%)	
Norway spruce	mono	32	77 \pm 2	23 \pm 2	64 \pm 1	12 \pm 2	1 \pm 1	91 \pm 4
European beech	mono	25	83 \pm 3	17 \pm 3	50 \pm 2	26 \pm 3	7 \pm 1	123 \pm 7
N. sp. and E. be	mixed	53	88 \pm 1	12 \pm 1	48 \pm 2	30 \pm 1	10 \pm 1	138 \pm 4
sessile oak	mono	22	64 \pm 4	36 \pm 4	50 \pm 2	12 \pm 3	2 \pm 1	81 \pm 7
European beech	mono	25	83 \pm 3	17 \pm 3	50 \pm 2	26 \pm 3	7 \pm 1	123 \pm 7
s. oak and E. be	mixed	27	85 \pm 3	15 \pm 3	35 \pm 2	30 \pm 2	20 \pm 3	156 \pm 10

The uncovered and covered stand area adds up to 100%. In addition, columns 5–8 give the percentage of onefold, twofold, and \geq threefold crown cover and the relative sum of crown projection areas

The crown measurements cover the period from 1954 till the present and stand ages of between 26 and 207 years. In order to study species-specific behaviour in coping with crowding, only fully stocked and rather even-aged stands were included, in which all species were left unthinned or were only moderately thinned.

Table 5.6 shows that the ground coverage by crowns is on average only 64–83% in monocultures and 85–88% in mixture; i.e. in 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 monocultures is 13–33%. The more multiple coverage in mixed versus monospecific stands is also reflected by a relative sum of crown area of 138–156% in mixed stands compared with 81–123% in monocultures. Even in monocultures, beech achieves 83% crown cover with 33% more than onefold coverage, indicating its outstanding shade tolerance and crown plasticity.

Comparing monocultures and mixed stands reveals the ‘overpacking’ of the canopy space in mixed stands compared with neighbouring monocultures. The term overpacking is used as an analogy with overyielding (see Chap. 4, Box 4.1), which refers to the frequently observed superiority of mixed stands regarding productivity (Vilà et al. 2005; Pretzsch 2005). Particularly species combinations with complementary light ecology such as Norway spruce and European beech as well as 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 monocultures.

Many studies show relatively close relationships between the absorbed photosynthetically active radiation, APAR, and crown size, whether these are 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 they 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 increasing leaf area density. For example, Forrester et al. (2013) found that thinning, pruning, and fertiliser 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 is 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, closer analysis of both may reveal species-specific behaviour in mixed compared with monospecific stands.

A combination of species with different crown shapes and albedos may decrease the reflection and light loss at the upper canopy layer by 5–10%. Particularly 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 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). For example, 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 the upper canopy but, unlike European beech, have difficulty surviving in the deep shade (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 and LCP = 750 and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$). The filling of canopy space by species with complementary light ecology and the closer interlocking of their crowns enables foraging of full as well as weak light as well as a more complete light interception and often results in a lower light intensity at the forest floor of mixed compared with monospecific stands (Mitscherlich 1971, p 82).

5.7.2.1 Temporal Change of Sum of Crown Projection Area in Mixed Versus Monospecific Stands

Figure 5.20a–c shows for monospecific and mixed stands of spruce and beech the change in the sum of crown projection area per unit area with progressing stand development (represented by the quadratic mean tree diameter, d_q , on the x -axis).

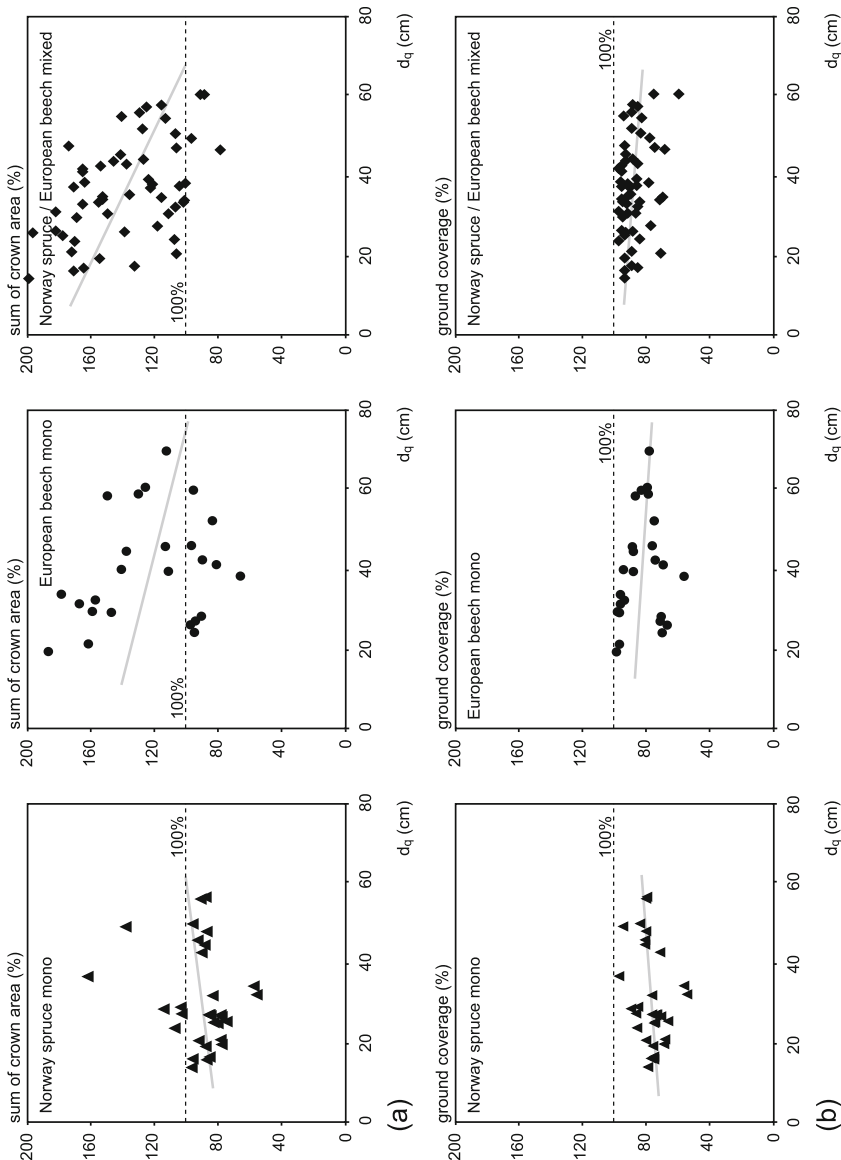


Fig. 5.20 (a–f) Sum of crown projection area, SCPA, per unit area (%) and ground coverage, CGC, (%) in even-aged monospecific and mixed stands of Norway spruce and European beech in dependence on quadratic mean diameter, d_q . Sample size from left to right $n = 32, 25, \text{ and } 54$. (a–c) Sum of crown area in monospecific and mixed stands of Norway spruce and European beech and (d–f) ground coverage by crowns for monospecific and mixed stands of Norway spruce and European beech. For further statistical characteristics, see Pretzsch (2014)

Compared with the respective monocultures (100% line), the mixture of spruce and beech results in values which start and remain much higher even in the advanced phase of stand development (Fig. 5.20c). Choi et al. (2001) found a similar trend in northern hardwood forests. The decrease with stand age 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 monocultures (Fig. 5.20d and e), whereas in mixed stands it remains at about 95% across the stand development (Fig. 5.20f).

5.7.3 Stand Density and Crown Density in Mixed and Monospecific Stands

In the following, we use the triplet data introduced in Sect. 5.3.2 to show the combined effect of both stocking density and canopy density. Furthermore, we analyse how those density and canopy characteristics affect the overyielding of mixed compared with monospecific stands. Stand density will be quantified by the standardised stand density index ($SDI_{1,2} = SDI_{1,(2)} + SDI_{(1),2} \times e_{2 \rightarrow 1}$) introduced in Sect. 4.3.1. The ratio $RD_{1,2} = SDI_{1,2}/SDI_1$ reflects the relationship between the stand density in mixed versus monospecific stands. The quantification of the canopy density was based on the crown cross-section area of all trees on the monospecific and mixed-species plots of the triplets. The crown cross-section areas, cpa , of individual trees were added to get the sum of cpa per plot for the two monocultures of each triplet ($SCPA_1$, $SCPA_2$) and for the mixed stand ($SCPA_{1,2}$). As ratio between the mixed and monospecific stands regarding the sum of crown projection area, we used $RSCPA_{1,2} = SCPA_{1,2}/(SCPA_1 \times m_1 + SCPA_2 \times m_2)$ analogously to the RPA introduced in Chap. 4, Box 4.1.

5.7.3.1 Stand Density and Canopy Density

The stand density index, SDI, in the mixed stands is mostly similar to or significantly higher than the SDI of the neighbouring monocultures (Fig. 5.21a). The pairwise comparison between the SDI in mixed-species stands and that in monocultures yielded a mean ratio of $RD = 1.10 \pm 0.06$. The upper section of Table 5.7 shows that in mixed stands of Douglas-fir/European beech and Norway spruce/Scots pine there can be significantly higher stocking densities compared with monocultures ($SDI_{\text{mixed}}/SDI_{\text{mono}} = 1.53$ and 1.10 , respectively).

The canopy density of mixed-species stands can be significantly higher because of the slightly higher stocking density and a considerably higher sum of crown projection area, caused by wider crown extension. Figure 5.21b illustrates that in most cases the observed sum of crown projection area per hectare in mixed stands,

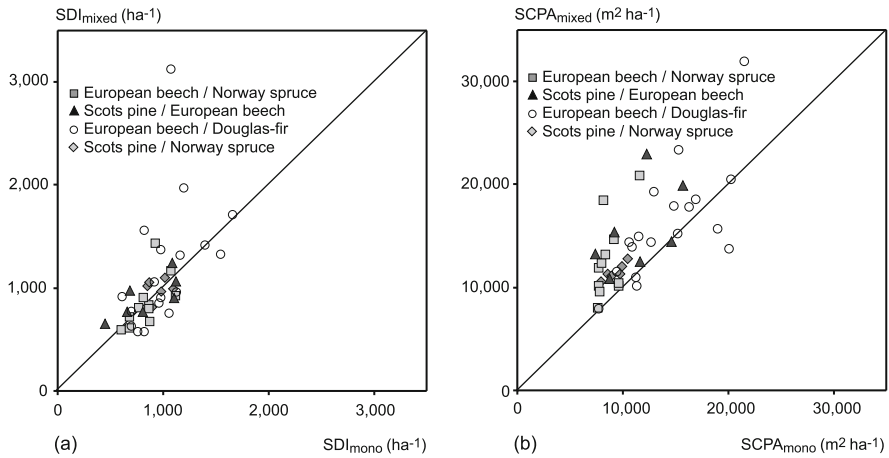


Fig. 5.21 Observed density on 42 mixed stands compared with monospecific stands based on triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine. (a) Observed stand density index in mixed stands compared with the weighted mean of both neighbouring monocultures. (b) Sum of crown projection area per hectare, $SCPA_{mixed}$, in mixed stands plotted over the values for monocultures, $SCPA_{pure}$. Observations above the 1:1 line indicate higher density of stocking or canopy cover in mixed stands compared with monocultures

$SCPA_{mixed}$, is much higher than the weighted mean of the two monocultures, $SCPA_{mono}$. $SCPA$ values of 10,000–30,000 $m^2 ha^{-1}$ in mixed stands mean that a stand area of one hectare is covered between one and three times by tree crowns. The corresponding values for monocultures (7500–20,000 $m^2 ha^{-1}$) are distinctly smaller. On average, the sum of crown projection area amounts to 11,472–16,144 $m^2 ha^{-1}$ in the mixed stands of the triplets and 6933–17,095 $m^2 ha^{-1}$ in the monocultures (Table 5.7, lower section).

For the different species combinations, we found mean RSCPA values of 0.96–1.83, indicating canopies that are 4% lower and 83% denser in mixed-species stands than in monocultures. For all four species combinations separately and also for all triplets together, the RSCPA values mostly exceed the value of 1.0 ($p < 0.001$). The finding that the mean of RSCPA amounts to 1.16–1.83 for Norway spruce/European beech, 1.27–1.60 for Scots pine/European beech, 0.96–1.44 for Douglas-fir/European beech, and 1.06–1.51 for Norway spruce/Scots pine (Table 5.7, lower section) emphasises high canopy densities especially in mixtures with beech. Mixed-species canopies are on average 33% denser than monospecific canopies.

Table 5.7 Stocking density, SDI, and sum of crown projection area, SCPA, in mixed-species stands versus monocultures of the 42 triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine

Species	n	SDI (trees ha ⁻¹)			RD = SDI _{mixed} /SDI _{mono1}			RD = SDI _{mixed} /SDI _{mono2}				
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N.sp./E.be	11	738 ± 59	846 ± 48	661 ± 50	0.50	1.46	0.89	0.08	0.52	2.09	1.17	0.12
Sc.p./E.be	7	863 ± 58	845 ± 100	761 ± 69	0.55	1.60	0.99	0.13	0.68	1.33	1.05	0.09
D.-fir./E.be	18	930 ± 108	1030 ± 69	675 ± 56	0.43	2.11	0.93	0.09	0.55	4.38	1.53*	0.21
N.sp./Sc.p.	6	1046 ± 33	953 ± 39	1248 ± 235	0.99	1.21	1.10***	0.03	0.54	1.34	0.96	0.13
Species		SCPA			RSCPA = SCPA _{mixed} /SCPA _{mono1}			RSCPA = SCPA _{mixed} /SCPA _{mono2}				
	n	Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N.sp./E.be	11	12,625 ± 1183	6933 ± 361	11,097 ± 829	1.15	2.42	1.83***	0.14	0.78	2.13	1.16	0.11
Sc.p./E.be	7	15,566 ± 1636	10,224 ± 1219	12,588 ± 1162	1.03	2.23	1.60***	0.16	0.94	1.81	1.27*	0.13
D.-fir./E.be	18	16,144 ± 1293	17,095 ± 1032	12,227 ± 1170	0.54	1.34	0.96	0.06	0.79	2.75	1.44***	0.11
N.sp./Sc.p.	6	11,472 ± 313	7659 ± 378	10,915 ± 486	1.40	1.72	1.51***	0.05	0.95	1.20	1.06	0.03

The ratio of stand density (RD = SDI_{mixed}/SDI_{mono}) and the ratio of sum of crown projection area (RSCPA = SCPA_{mixed}/SCPA_{mono}) quantify the stand density and crown area in mixed versus pure stands. For further explanation see caption of Table 5.1

5.8 Effect of the Size-Structure Dynamics on Overyielding at the Stand and the Species Level

The data of the 42 triplets with 126 plots in monospecific and mixed-species stands introduced in Sect. 5.3.2 can be applied to analyse relationships between overyielding at the stand level and characteristics at the size distribution level. The analysis of overyielding was based on the relative productivity, RPA, introduced in Chap. 4 (see Box 4.1). It quantifies the mixing effect on the stand productivity.

5.8.1 Overyielding at the Stand and Species Level

On average, the productivity of mixed-species stands on the 42 triplets was 104% of the weighted mean of the neighbouring monocultures. At the species level, the productivity in mixture is 107–118% of the monospecific stands, i.e. the species grow 7–18% more in mixed compared with monospecific stands. On average, European beech benefits the most from growing in mixture, Norway spruce benefits the least, and the other species lie in between. The minimum and maximum values show a broad variation of the mixing effects on both stand and species level.

In the mixture of Scots pine and European beech, both species interact in such a way that the total benefit amounts to 16%. The mixture of Douglas-fir and European beech can be particularly beneficial for beech; however, on average the benefit is 1% and marginal at stand level. The relative productivity at stand level can be different from the mean relative productivity at species level as the former considers the mixing proportions (Sterba et al. 2014) and the coupling between strong positive effects of one species with negative effects of the other.

5.8.2 Relationship Between Size Structure and Over- and Underyielding at the Stand Level

The analysis of how overyielding of the mixed stands of the 42 triplets emerges from the tree distribution level was based on the relative productivity, $RP_{1,2}$, of mixed stands versus monocultures (see Chap. 4, Box 4.1). To explain the mixing effect at the tree distribution level, the relative stand density, RD; the relative sum of crown projection area, RSCPA; the relative slope b of the $iv-v$ relationship, Rb; the relative Gini coefficient of v , iv , RGC_v resp. RGC_{iv} ; and the relative growth dominance coefficient, RGDC, were used. Similar to the relative productivity, RP, the latter six ratios represent the quotients between the distribution characteristics in mixed versus pure stands.

While all other ratios had only weak or non-significant effects on RP, the ratios RD, RGC_v , RSCPA, and Rb had a clearly positive effect. Two of the revealed

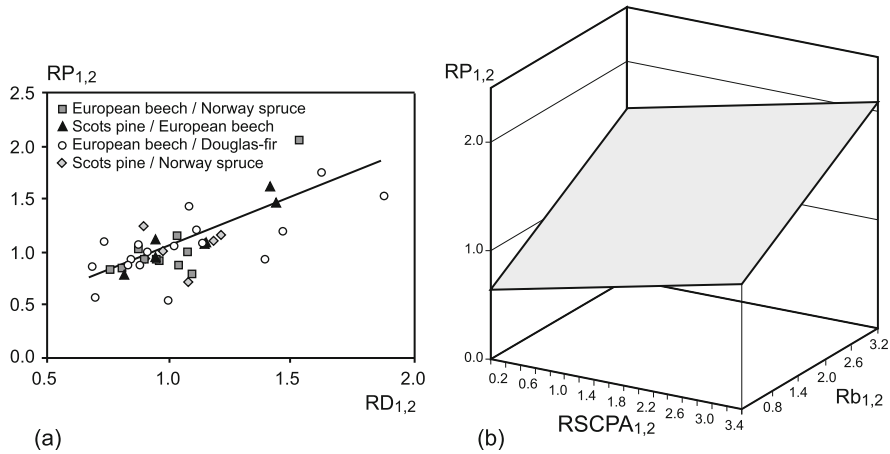


Fig. 5.22 Dependency of overyielding at the stand level $RP_{1,2}$ from (a) the relative stand density, $RD_{1,2}$ ($RP = 0.20 + 0.81 \times RD$, $n = 42$, $R^2 = 0.52$, $p < 0.001$), and (b) the ratio between the sum of crown projection area in mixed and monospecific stands, $RSCPA_{1,2}$, and the ratio between the slope of the $iv-v$ relationship, $Rb_{1,2}$, in mixed and monospecific stands ($RP = -0.16 + 0.62 \times RSCPA + 0.36 \times Rb$, $n = 42$, $R^2 = 0.47$, $p < 0.001$)

relationships between the size structure and over- and underyielding at the stand are visualised in Fig. 5.22a and b.

5.8.3 Increase in Canopy Space Filling and Light Interception

The significantly positive effect of the relative sum of crown projection area, Gini coefficient GC_v , slope of the $iv-v$ relationship, and stocking density on the productivity of the mixed stands suggests that higher light interception and light-use efficiency can be essential causes of their overyielding. Kelty (1992) assumed that the intercepted light may also be used more efficiently when crowns or branches of shade-tolerant species replace more light-demanding species. He speculated that due to the replacement of less efficient organs, crown parts, or whole trees, particularly smaller trees growing in the shade of the lower crown may contribute to the overyielding of mixed versus monospecific stands. Following this assumption, the effect of beech on pine may be compared with thinning pine from below. By eliminating the slow and inefficiently growing understorey trees in monospecific stands, stand growth can be accelerated (Assmann (1970, pp 248–261); Pretzsch (2005)). However, in contrast to thinning, this does not only entail an elimination but also a replacement by even more efficiently growing individuals of a better adapted species.

5.9 Modification of Stand Structure in Monospecific and Mixed-Species Stands by Site Conditions

The triplet data for Scots pine and European beech introduced in Sect. 5.2 reveal how stand structure in monospecific and mixed-species stands can be modified by water availability. Based on the set of 32 triplets of mature and fully stocked monocultures and mixed stands of Scots pine and European beech located along a productivity and water availability gradient (annual mean temperature 6.0–10.5 °C and annual precipitation 520–1175 mm) through Europe, Pretzsch et al. (2016) examined how mixing modifies the stand structure in terms of stand density, horizontal tree distribution pattern, vertical stand structure, size distribution pattern, and variation in tree morphology. In particular, they analysed how site conditions modify these aspects of stand structure. For this typical mixture of a light-demanding and shade-tolerant species, they found that mixing significantly increases the above-mentioned aspects of structural heterogeneity compared with monocultures. Mixing effects such as an increase in stand density and diversification of vertical structure and tree morphology were caused by species identity (additive effects) but also by species interactions (multiplicative effects). The superior heterogeneity of mixed stands over monocultures increases from dry to moist sites (Fig. 5.23).



Fig. 5.23 Stands of Scots pine and European beech (*centre*) have significantly higher structural heterogeneity than monocultures of Scots pine (*left*) and European beech (*right*). The superior heterogeneity of mixed stands over monocultures increases from dry to moist sites (from top to bottom). Canopies can be denser in mixed stands (*centre*) compared with monospecific stands (*left* and *right*) due to wider tree crown extension, multilayering, and higher stocking density. The complete canopy space filling may increase the light interception in mixed stands (after Pretzsch et al. 2016)

Mixed stands of Scots pine and European beech are more heterogeneous in structure and can carry more trees of a given size, and this effect increases with site productivity. The complementary light ecology of these species (pine being light demanding, beech being shade tolerant) increases the light interception or light-use efficiency to such an extent that not only stand productivity (Pretzsch et al. 2016) but also the stand density can be higher than in monocultures (Pretzsch and Biber 2016). For a more detailed analysis of the effect of species mixing on stand density, see Chap. 4, Sect. 4.3.2.

The finding by Pretzsch et al. (2016) that this tendency and vertical structuring increases with site productivity substantiates the assumption that greater light interception explains the increase in density and growth. On rich sites where water and nutrient supply are higher, the light complementarity might become more effective than on poor sites where other environmental conditions are limiting (Forrester and Albrecht 2014).

5.10 Scientific Evidence and Practical Relevance

5.10.1 Size Structure as Link Between Tree-Level and Stand-Level Research on Mixed Stands

The particular pattern of canopy space filling by crowns of different sizes can increase the productivity of mixed over monospecific stands. The combination of species with complementary ecological traits enables a coexistence of trees of variable sizes in different canopy layers. The vertical stratification can be coupled with a denser crown space filling, flooding of light also into deeper canopy layers, higher rates of survival of small trees, more complete light exploitation by crowns, and higher stand density. Even trees in deeper canopy layers contribute to stand growth proportionally to their stem volume. This reveals an amazing elasticity of tree growth over the different sizes and layers which is probably caused by adaptation via allometric plasticity, by optimised species-specific niche occupation (shade tolerant below light demanding), and a combination of small and tall trees (high-growth beside low-growth per tree stand area).

Even stands with similar mean tree dimensions (mean diameter, mean volume) or cumulative hectare-related characteristics (standing stock, biomass) can differ considerably in their size structure and the size-growth partitioning between the trees. These differences can strongly affect stand productivity via differences in resource acquisition, resource-use efficiency, and respiratory losses.

Analysis of mixing effects at the organ or tree level may provide insight into particular patterns and processes. However, their relevance for any overyielding at stand level requires that such analyses are available for trees of different sizes and social positions and that the size-specific patterns can be upscaled to the stand level taking into account the location, shape, and density of the frequency distribution.

As overyielding is strongly determined by a change in the location, shape, and density of the size and size-growth distribution, analyses based on a small number of dominant trees in mixed compared with monospecific stands are barely sufficient for explaining overyielding or underyielding effects at the stand level (Strigul et al. 2008; Webster and Lorimer 2003).

5.10.2 Consequences for Forest Management

The periodic annual growth and total yield of monocultures can be increased through removal of inefficient subdominant and suppressed trees, i.e. by thinning from below. Subdominant and suppressed trees in even-aged stands can have an unfavourable ratio between resource use and growth (Assmann 1970, pp 34–38). Their elimination through thinning leaves more water and nutrients to the remaining trees which use those resources more efficiently and can overcompensate for the growth loss of the removed trees and even increase the total stand growth by about 20–30% above the level of unthinned stands (Pretzsch 2005). Replacing inefficiently slow-growing and excessively respiring trees of one species with a more efficient and shade-tolerant second species in mixed-species stands may have a similar effect to thinning from below in monocultures. A precondition for this increase in efficiency is a combination of species with complementary light ecology, e.g. early-successional light-demanding above late-successional shade-tolerant species. Besides other reasons for leaving small trees (insurance against total stand loss by windthrow, resilience, regeneration), their contribution to stand growth may be used to maintain sustainable and continuous growth in monocultures (Sterba 1999) and particularly in mixed or uneven-aged stands where their share of stand productivity can be considerable.

The close relationship between stand density, canopy space filling, and overyielding (Fig. 5.22) indicates that part of the mixing effect may be a density effect. Higher stand densities might mean a greater light capture and additional increase in productivity. The latter effect would be rather density dependent and could be lost through thinning. The increase in stand density and light capture may be higher the more complementary the ecological niches and the resulting efficiency effects are; i.e. there might be a positive feedback between an increase in light-use efficiency and stand density. An increase in light-use efficiency brought about by combining complementary tree species in different layers would be rather density independent and could scarcely be eliminated by silviculture in the course of density reductions.

The SDI analyses showed that species mixing can increase the maximum stand density, probably because mixed stands capture more light and use the intercepted light more efficiently than neighbouring monocultures (see Sect. 4.3.2). Greater light interception by more extensive crowns, denser canopy space filling, and multilayering may only result in overyielding when the necessary below-ground

resources are not growth limiting. However, increased light-use efficiency by a combination of species with complementary light ecology is likely to always result in higher growth as the available water and nutrients are simply used more efficiently compared with monocultures. European beeches in the shade of Scots pines, for instance, may use the intercepted light more efficiently for growth—i.e. consume less water and nutrients—due to a lower compensation point than would be needed by Scots pines growing under the same competitive constellation. So, the higher interception and use efficiency of light enable a higher stand density and more trees to survive and grow per unit area. Other silvicultural measures such as spacing, thinning, and fertilisation let stands grow faster but pass through the same allometric density trajectories (Long et al. 2004). Mixing, in contrast, can cause a long-lasting increase in the stock of resources in the system and may thereby increase the maximum stand density which means a growth and survival of more and/or taller trees compared with neighbouring monocultures in the same stand development phase.

If silvicultural guidelines for monocultures, e.g. regarding stand density or number of future crop trees, are applied to mixed-species stands without adaptation to their special structure, density, and productivity potential, this can cause a considerable loss of resources and productivity.

5.11 Synthesis

In temperate forests where the nutrient and water supply in the soil is sufficient for all trees so that they are mainly competing above ground for light, overyielding can emerge from tree and size-structure dynamics. On long-term experiments and temporally established triplets in Central Europe, the canopy space filling can be much denser in mixed compared with monospecific stands (Fig. 5.24a). The size distribution can be more right skewed and the kurtosis as well as the number of trees higher as in monocultures. In most of the mixed stands, there was a greater inequality in size and size growth than in monocultures (Fig. 5.24b) but similar growth dominance coefficients. The $iv-v$ relationships indicate a stronger size asymmetry of competition in most of the mixed stands compared with neighbouring monocultures (Fig. 5.24c). Species mixing can cause a higher stocking density and significantly higher sum of crown projection area. Overyielding of mixed compared with monospecific stands increases with the density of stocking and canopy, inequality of size and size growth, and steepness of the size-growth relationship. These differences suggest that deeper entrance into the canopy, more complete interception, and higher use efficiency of light can be main causes of the overyielding of mixed stands (Fig. 5.24d).

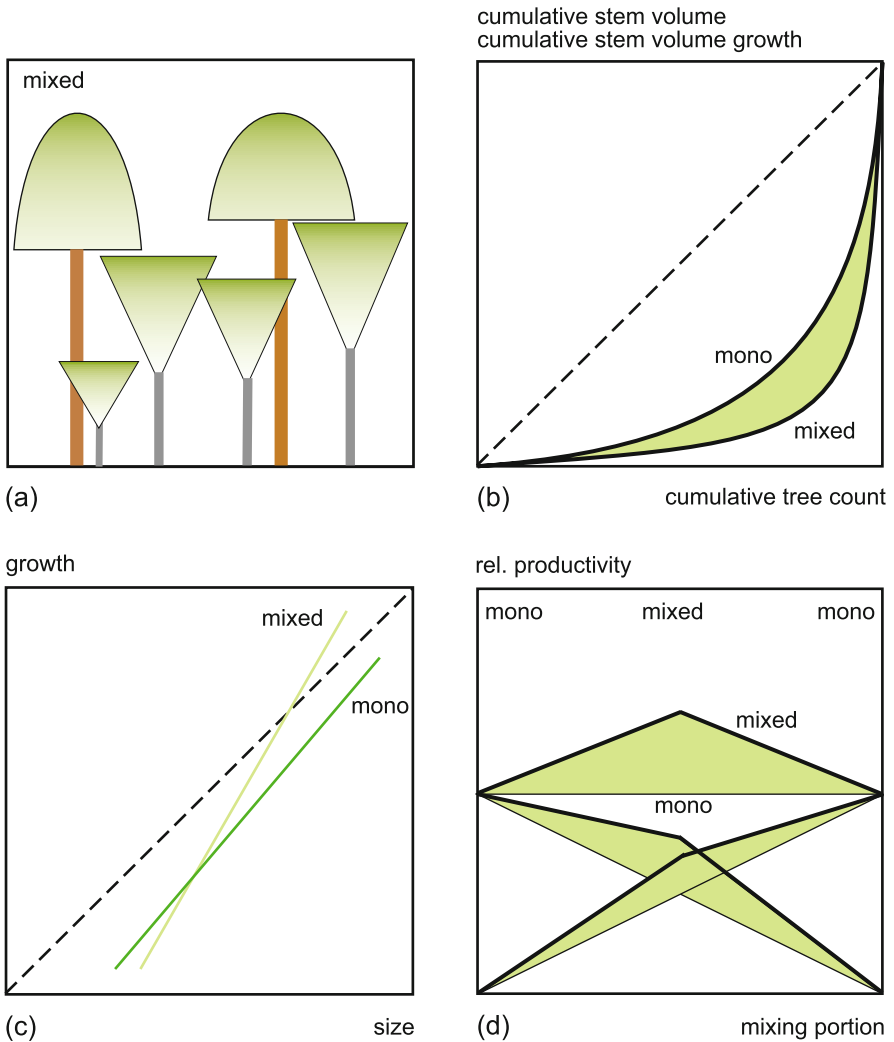


Fig. 5.24 (a–d) Effect of species mixing on the stand structure dynamics and overyielding at the stand level. (a) Canopies can be denser in mixed than in monospecific stands due to wider tree crown extension, multilayering, and higher stocking density. (b) Mixed stands can have higher size inequality and also higher numbers of small compared with tall trees. This is indicated by a steeper increase in cumulative stem volume and cumulative stem growth over cumulative tree count and higher Gini coefficients. (c) In most cases, the $iv-v$ relationships are higher in mixed compared with monospecific stands and indicate more size-asymmetric competition. (d) In most cases, mixed stands overyield neighbouring monocultures. The structural traits suggest that overyielding is partly based on deeper entrance of light into the canopy, more complete interception, and higher use efficiency of light

Take-Home Messages

1. The evolution of the size structure during stand development determines growth and yield as well as a broad spectrum of forest functions including biodiversity, protection, and recreation.
2. The slow but continuous feedback between the within-stand environment→tree growth→stand structure→within-stand environment results in the species' adaptation to the interspecific environment. Due to this continuous adaptation, the size distribution of mixed stands can increasingly deviate from those in neighbouring monocultures with proceeding stand development.
3. The total number of trees can be higher in mixed than in monospecific stands. In addition, the minimum tree size can be lower and the maximum size higher. The skewness and the kurtosis can also be higher.
4. In most cases, the $iv-v$ relationships are higher in mixed than in monospecific stands and indicate more size-asymmetric competition.
5. Mixing of ecologically complementary species can increase the inequality of size and growth distribution between small and tall trees. This is indicated by a steeper increase in cumulative stem volume and cumulative stem growth over cumulative tree count and higher Gini coefficients.
6. The size heterogeneity brought about by mixing can increase the canopy space filling. The diversified canopy space ensures a growth elasticity of small and tall trees.
7. Canopies can be denser in mixed compared with monospecific stands due to wider tree crown extension, multilayering, and higher stocking density.
8. In many cases, mixed stands overyield neighbouring monocultures. The structural traits suggest that overyielding is based on deeper entrance of light into the canopy, more complete interception, and higher use efficiency of light.
9. The effect of the size-structure dynamics on the overyielding at the stand level suggests that common analyses at individual tree level should cover not just dominant trees but the whole size distribution. Upscaling the behaviour of dominant trees from tree to stand level remains questionable if it neglects size-specific reaction patterns and their frequency given that these strongly affect the stand-level productivity.
10. The part of the overyielding in complementary species mixture which is based on denser space filling and higher stocking density can be lost through silvicultural density reductions. In contrast, the increase in light-use efficiency should depend on the degree of complementarity in light ecology rather than on stand density.

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