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ASSMANN REVIEW

Effect of tree species mixing on the size structure, density, and yield of forest stands

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Abstract An increasing number of studies provide evidence that mixed-species stands can overyield monocultures. But it is still hardly understood, how the overyielding at the stand level emerges from the tree, canopy, and size structure. Analyses of 42 triplets with 126 mixed and mono-specific plots in middle-aged, two-species stands of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] Karst.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and European beech (*Fagus sylvativa* L.) in Central Europe revealed that mixed-species compared with mono-specific stands can have (1) higher tree numbers, higher right skewness and kurtosis of the size distribution, higher inequality of tree sizes, and thereby higher stocking densities and sum of crown projection areas, (2) growth–size relationships with stronger size asymmetry of growth and higher inequality of size growth, and (3) higher stand productivity coupled with higher maximum stand density, canopy space filling, and size asymmetry. These differences depend on the species assemblage. They suggest a deeper entrance of light into the canopy as well as a higher light interception and light-use efficiency as main causes of the overyielding and overdensity. We discuss implications for research and silviculture and draw conclusions for designing and managing resource-efficient production systems.

Keywords Size hierarchy · Size asymmetry of competition · Size asymmetry of growth · Space filling · Complementary light use · Growth partitioning · Growth elasticity

Introduction

The focus of classical forest science was on even-aged monocultures, while mixed-species stands were simply approximated as weighted mean of mono-specific stands. However, recent empirical works on specific species mixtures (Griess and Knoke 2011; Pretzsch et al. 2010, 2013a), simulation model studies (Morin et al. 2011), as well as meta-analyses (Paquette and Messier 2011; Piotto 2008; Zhang et al. 2012) showed that the productivity of mixed stands can exceed the weighted mean productivity of monocultures by 50 % in mixture with nitrogen-fixing species (Forrester et al. 2006) and by 20–30 % in other mixtures (Pretzsch et al. 2013b; Toïgo et al. 2015a). The above studies revealed that the overyielding can be in an order of magnitude which is practically relevant and therefore worthwhile further exploration, but except for mixtures involving nitrogen-fixing species they hardly tell anything about the underlying causes. However, a better understanding of the emerging properties in mixed stands and the causes of overyielding is required for systematically designing and managing more resource-efficient mixed-species production systems (Forrester 2014).

Behind any over- or underyielding of mixed-species stands in relation to neighbouring monocultures is always a modified supply, capture or use-efficiency of resources

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(Binkley et al. 2004; Richards et al. 2010; Toïgo et al. 2015b). Assuming that the nutrient and water supply in the soil are sufficient for all trees, analysis can be focused on the light environment (Hara 1993), but even when water and mineral nutrient supply is sub-optimal, light can strongly determine the mixing effects (Forrester 2014; Forrester and Albrecht 2014). However, quantifying the light conditions in mixed-species stands and comparing them with monocultures is very challenging and costly and at best feasible for selected individual trees, e.g. for dominant trees. Furthermore, it is rather difficult to scale up from individual tree growth to stand-level reaction patterns as the light supply, capture, and use-efficiency vary among others with tree species, age, tree size, and hierarchical position (Binkley et al. 2013; Webster and Lorimer 2003).

In temperate forests which are in the focus of this study, tree and crown size, as well as size growth, reflect the state and effect of the light regime. So, as long as individual tree-based information about light interception is not available, tree size and its growth may be used—like in this study—as a proxy for light interception and for tracing mixing effects from the individual tree to the size distribution and stand level. Many studies show relatively close relationships between APAR and crown size, whether it is quantified in terms of leaf area, crown surface area, crown projection area, crown length, or crown width (Binkley et al. 2013; Forrester et al. 2012). These relationships will probably vary between species and growing conditions but as long as these are known, tree and especially crown size characteristics should be a reasonable proxy for light interception. In contrast to light measurements, records of tree size and tree growth have the advantage of being easier to measure and often available from past inventories of long-term plots (Forrester et al. 2013; Pretzsch 2014). So, this study analyses how size and canopy structure are modified by tree species mixing and may determine the light interception and productivity of mixed compared with pure stands.

Forest stands can considerably differ in their size structure and size growth partitioning between the trees, even when they have similar mean tree dimensions (mean diameter, mean volume) or cumulative hectare-related characteristics (standing stock, biomass). Especially in mixed-species stands, any differences in size structure can strongly determine stand productivity via differences in resource acquisition, resource-use efficiency, and respiratory losses. So, the analysis or modelling of mixed-species stands by their mean tree characteristics or by stand sum values is rather questionable. Analysing their development in general and overyielding in particular requires information about the size structure and growth partitioning between the differently sized individuals. Measures for characterizing the density, location, and shape of the size distribution, such as skewness, kurtosis, and the Gini coefficient for tree size (Katholnig 2012; Pretzsch and Schütze 2014; Wichmann 2001, 2002), may reveal differences between the size structure of pure and mixed stands. The Gini coefficient for volume growth quantifies the inequality of the growth distribution between the trees of a stand (Binkley et al. 2006; Pretzsch and Schütze 2014). The size symmetry and asymmetry of growth, which expresses the kind of resource limitation a stand is suffering, may be characterized by the slope of the relationship between tree growth and tree size (Hara 1992, 1993; Schwinning and Weiner 1998).

When these measures are calculated for mixed-species stands and neighbouring monocultures, the ratio between mixed-species stands and monocultures reflects the mixing effect at size distribution level. The analogous ratio between the productivity of mixed-species stands and monocultures reflects the mixing effect on the stand productivity. Latter characteristics of the size distribution and stand productivity were used for analysing the relationship between the canopy and size structure and the overyielding of mixed-species stands versus monocultures. The study was based on 42 triplets comprising 126 even-aged two-species mixed stands and monocultures of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] Karst.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and European beech (*Fagus sylvatica* L.) in Central Europe. By covering a rather wide range of site conditions, we wanted to achieve generalizable results. In detail, we scrutinized

1. how species mixing modifies the location, shape, and density of the tree size distribution and thereby the stocking density and canopy space filling compare with monocultures,
2. whether the relationship between tree size and growth is modified by species mixing, and
3. whether changes in the canopy and size structure are responsible for the overyielding and density of mixed-species stands compared with monocultures.

The paper in hand is part of the review series in memory of Ernst Assmann (*1903, †1979) who was a German pioneer in forest production ecology and silviculture of pure and mixed-species stands (Pretzsch et al. 2015a).

Materials and methods

Material

As a basis for this study, we used 42 triplets in monocultures and mixed-species stands of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine in Germany and

Poland (Fig. 1, Supplement Tables 1 and 2). Each triplet consists of three plots with two in monocultures and one in a mixed stand of the respective species. We included just such species which play a major role in both monocultures and mixed-species stands in Central Europe (Brus et al. 2011). As we were interested in general relationships between the size structure and stand productivity, we tried to cover a wide range of growing conditions. So, the triplets were selected in the lowland of Poland, the uplands of Southern Germany, in the low and medium mountain range in South-West Germany, and in the foothills of the Bavarian Forest and Alps (Fig. 1). They lie between 60 and 785 m a.s.l., the mean temperature ranges from 5.5 to 9.5 °C, the annual precipitation amounts to 556–1350 mm year^{-1}, and the Martonne index ranges between 33.2 and 75.0 (Supplement Table 1). The Martonne index (1926) ($M =$ annual precipitation (mm)/(mean annual temperature (°C) $+ 10$)) characterizes the water supply. The higher the Martonne index, the better the water supply for plant growth; the lower this index, the stronger the likelihood of drought. Most frequently, the plots are on brown soils and para-brown soils consisting of loess, loam, or sandy loam. The mean stand height at age 50 depends on the species-specific course of height growth and the prevailing site conditions; it ranges between 12.4 m on poor sites and 33.3 m on the most fertile sites. The total yield at age 50, derived from the commonly used yield table by Wiedemann (1936/1942) for Norway spruce, Wiedemann (1943) for Scots pine, Bergel (1985) for Douglas-fir, and Schober (1967) for European beech, also varies with species and site conditions and ranges from 109 $\text{m}^3\ \text{ha}^{-1}$ on poor to 1088 $\text{m}^3\ \text{ha}^{-1}$ on fertile sites (Supplement Table 1). For plot-specific stand ages and SDI values, see Supplement Table 2.

All included plots represent more or less even-aged and mono-layered forest stands. Stand ages were available from the stand chronicle of the forest administration, and were verified by the tree ring analyses of the increment cores. In this way, we guaranteed the equality of stand ages within each triplet. In order to avoid density effects due to different thinnings in the past, we included only fully stocked stands without any thinnings, at least in the last 10–20 years. So, the plots are fully stocked and should represent maximum stand density. Mixed plots represent individual tree mixture and a mixing proportion of about 50:50. Plot sizes range between 0.05 and 0.5 ha. In order to sample representative stand sections with similar accuracy, we chose larger plots for old than for young stands and also larger plot for mixed than for the neighbouring pure stands. All three plots within a triplet are equal in site conditions. For this purpose, all three plots of a triplet were chosen in close vicinity. Based on available local soil maps and own additional soil sampling, we guaranteed a maximum similarity of the soil conditions for the three plots of each triplet. This site equality at the triplet level was an important criterion for

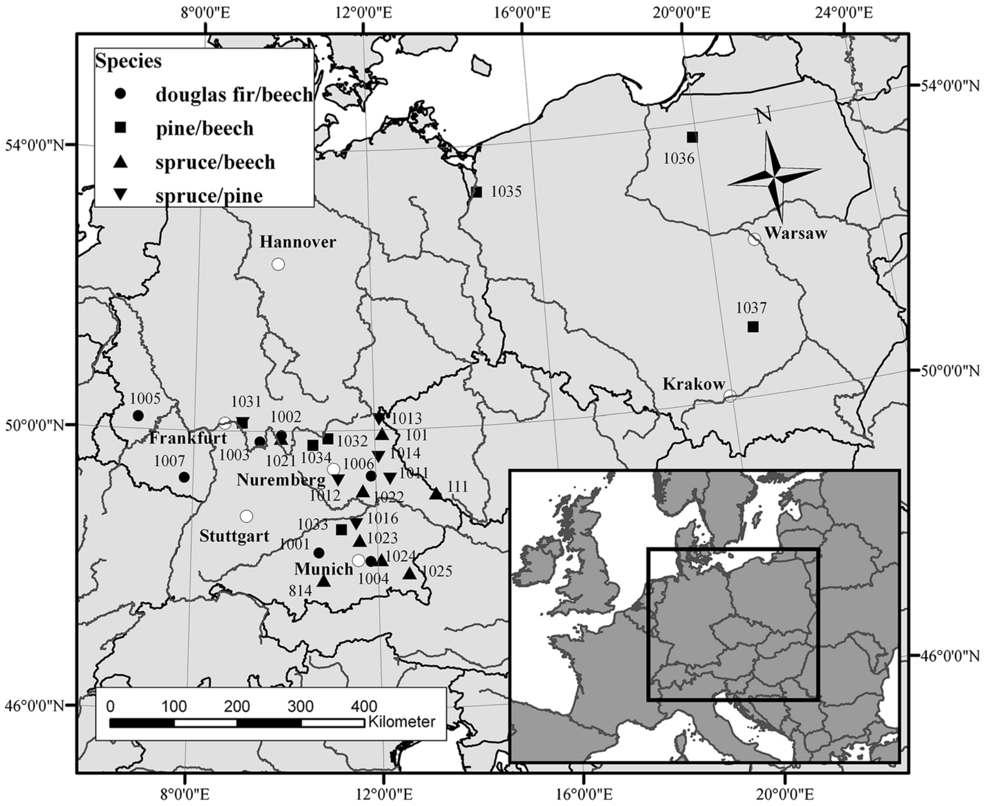

Fig. 1 Location of the 42 triplets in monocultures and mixed-species stands of Douglas-fir/European beech (*circle symbol*), Scots pine/European beech (*square symbol*), Norway spruce/European beech (*triangle symbol*), and Norway spruce/Scots pine (*inverted triangle symbol*) in Germany and Poland included in this study

plot selection, as otherwise differing site conditions would flaw the search for mixing effects by comparing monocultures with mixed stands within each triplet.

Table 1 shows the stand characteristics of the 42 triplets comprising 126 plots altogether. Most triplets represent middle stand ages (60–80 years). In case of Douglas-fir/European beech, we also selected young and old stands. For this species assemblage, we found triplets of different ages (young, middle, and advanced development stand phase) in close vicinity and with equal site conditions (see Table 1, third section).

Field measurement, tree ring analysis

The plots were inventoried in order to derive the required dendrometric state variables at the tree and the stand level, such as diameter, basal area, height, and volume. Diameter at breast height was measured with a girth tape. Tree height and height of the crown base (height of the crown's lowest primary branch at the stem) were measured with VERTEX height measurement devices. Stem co-ordinates were measured by the theodolite LEICA TC500. Measurements of crown radius were carried out with the biritz + hatzl$^{\mathrm{TM}}$ optical perpendicular instrument in the eight cardinal and subcardinal compass directions (N, NE,… NW).

In order to retrospectively determine the tree and stand growth, we took increment cores from a subsample of the trees. We used them for a tree ring analysis that allowed us to calculate the individual tree diameters from 5 years ago. In addition, we felled sample trees in order to reconstruct the heights they had 5 years earlier, based on the visible shoot lengths. For this purpose, we mainly chose dominant sample trees, aged similar to the stand age. Based on these retrospectively measured tree heights and tree diameters, we could establish statistical height–diameter relationships for the time of measurement and also for 5 years before. These relationships were developed separately for the both species and also separately for the two pure and the mixed stands of each triplet. We used them for estimating the present and past individual heights of all trees without height measurements. Using common species-specific form factors (Franz et al. 1973), we were able to calculate the present stem volumes. The present volumes (in the year 2013) and the periodic annual volume increment in the last 5 years (from 2009 to 2013) at the tree and the stand level were the main input variables for the subsequent evaluations.

Data evaluation

Evaluation of basic stand characteristics and overyielding

Stand characteristics Stand characteristics such as mean tree dimensions, standing stock, and periodic annual volume increment per hectare were evaluated following the DESER-Norm 1993 (Johann 1993; Pretzsch 2009, pp 181–222). This norm suggests how to calculate and document in a standardized way the state, growth, and yield variables for long-term plots based on tree diameter and height measurements. It includes standards for plausibility checks of the underlying diameter and height measurements, for regression sampling of heights by applying tree diameter–height curves, and for volume estimation based on form factors. The DESER-Norm further provides a standard for calculating and reporting characteristics of the mean tree (e.g. d_q, h_q, d_{100}, h_{100}), of cumulative stand values (e.g. BA, V) separately for the total, remaining, and removal stand, and also of growth and yield characteristics (e.g. $\mathrm{PAI_{BA}}$, $\mathrm{PAI_V}$, $\mathrm{MAI_{BA}}$, $\mathrm{MAI_V}$) for the total stand. Throughout this paper, we used the terms d_q for the quadratic mean diameter of the stand and h_q for the height of the tree with the quadratic mean diameter in order to indicate that both stand variables were based on the quadratic mean diameter but not on the arithmetic mean diameter. As mixture-specific form factors are not yet available for the considered species, we had to use the form factor functions for pure stands (see Franz et al. 1973).

Overyielding and underyielding, relative productivity RP The standard set-up for comparing the performance of mixed-species stands with monocultures comprises mixed- and mono-specific plots. Our triplets are a special case of this concept. In this design, the periodic annual volume increment in the monocultures of species 1 and 2 is named p_1 and p_2, respectively. The productivity of the mixed-species stand in total is $p_{1,2}$, the share of species 1 and 2 is $pp_{1,(2)}$ and $pp_{(1),2}$ ($p_{1,2} = pp_{1,(2)} + pp_{(1),2}$), and their mixing portions (shares of the stand area) are m_1 and m_2 ($m_1 + m_2 = 1$). Based on these variables, we firstly calculated the relative productivity $\mathrm{RP}_{1,2} = p_{1,2}/\widehat{p}_{1,2}$ for the stand as a whole. It resulted from the observed productivity of the mixed stand $p_{1,2}$ divided by the productivity $\widehat{p}_{1,2}$, expected without any mixing effects. The expected productivity $\widehat{p}_{1,2}$ was derived from the productivity of both species in the neighbouring monocultures, p_1 and p_2, and their mixing portions m_1 and m_2 ($\widehat{p}_{1,2} = m_1 \times p_1 + m_2 \times p_2$). Our approach to calculating the mixing portions m_1 and m_2 will be introduced in the subsequent sections. Secondly, the species-specific relative productivity RP of species 1 and 2 in mixed-species stands versus monocultures was of interest. For species 1, the relative productivity in mixed-species stand versus monoculture was $\mathrm{RP}_{1,(2)} =$ -$pp_{1,(2)}/p_1 \times m_1$, with $pp_{1,(2)}$ being the share of productivity of species 1 in the mixed stand, p_1 the productivity of species 1 in monoculture, and m_1 the mixing portion. For species 2 in the mixed-species, the concept was applied analogously ($\mathrm{RP}_{(1),2} = pp_{(1),2}/p_2 \times m_2$).

Table 1 Stand characteristics of the triplets of monocultures and mixed-species stands included in this study

Species	n	Stand age (years)	N (trees ha^{-1})	d_q (cm)	h_q (m)	SDI (ha^{-1})	V (m^3 ha^{-1})	IV (m^3 ha^{-1} year^{-1})
N. sp. + E. be.	11	82	571			738	564	17.5
		60–123	*210–887*			*539–1126*	*351–847*	*12.0–21.9*
N. sp. mixed	11	77	209	37.5	30.5	363	299	8.4
		57–113	*64–383*	*27.7–58.4*	*24.9–40.9*	*219–639*	*160–472*	*3.8–14.2*
E. be. mixed	11	86	361	28.0	26.4	375	265	9.0
		60–132	*143–635*	*17.6–38.3*	*20.6–35.3*	*234–658*	*172–483*	*5.6–12.5*
N. sp. mono	11	69	629	32.7	28.4	846	615	20.8
		50–113	*210–1095*	*21.7–52.3*	*20.8–40.7*	*607–1127*	*418–814*	*9.3–33.2*
E. be. mono	11	84	681	26.9	26.0	661	454	15.7
		54–132	*296–1325*	*15.6–37.4*	*19.3–35.1*	*512–1029*	*275–709*	*9.4–25.3*
Sc. p. + E. be.	7	60	1093			863	488	19.0
		45–84	*532–2628*			*719–1123*	*355–629*	*14.4–24.2*
Sc. p. mixed	7	60	519	26.9	25.7	468	262	8.4
		45–84	*219–1529*	*15.6–34.5*	*20.6–29.8*	*332–714*	*176–329*	*3.1–13.0*
E. be. mixed	7	60	574	21.6	24.9	396	224	10.7
		45–84	*267–1099*	*13.5–29.1*	*19.3–28.9*	*237–490*	*137–329*	*7.2–13.7*
Sc. p. mono	7	60	945	27.3	25.7	845	463	15.0
		45–80	*286–2054*	*16.8–37.2*	*20.7–31.9*	*450–1122*	*296–581*	*5.3–21.9*
E. be. mono	7	60	1170	22.5	25.5	761	449	19.1
		50–84	*431–2090*	*14.2–32.0*	*21.0–29.1*	*554–1034*	*304–564*	*13.0–27.6*
E. be. + D.-fir	18	61	1051			930	679	22.4
		25–120	*216–3258*			*546–2275*	*52–1279*	*10.1–39.9*
E. be. mixed	18	61	655	21.5	22.8	389	228	6.7
		25–120	*141–1755*	*7.8–36.4*	*7.5–33.9*	*155–900*	*18–485*	*2.6–13.3*
D.-fir mixed	18	61	395	49.2	32.5	541	451	15.8
		25–120	*35–1894*	*9.1–83.2*	*8.4–48.6*	*220–1496*	*34–1016*	*5.7–32.1*
E. be. mono	18	63	1123	25.7	24.1	675	416	14.0
		25–120	*172–3333*	*8.7–53.6*	*10.9–39.2*	*244–1143*	*35–811*	*5.1–21.4*
D.-fir mono	18	63	682	41.2	33.1	1030	934	26.7
		25–120	*182–2157*	*11.5–74.0*	*11.8–50.5*	*617–1665*	*110–2071*	*12.6–45.0*
N. sp. + Sc. p.	6	77	1075			1046	621	19.2
		60–89	*853–1354*			*989–1207*	*472–875*	*12.2–28.4*
N. sp. mixed	6	78	751	22.2	22.3	604	333	11.2
		60–93	*608–941*	*17.6–26.9*	*18.4–26.7*	*523–765*	*216–521*	*5.4–18.1*
Sc. p. mixed	6	76	324	30.8	27.1	442	282	7.9
		60–85	*239–413*	*27.3–36.2*	*23.3–31.0*	*335–501*	*231–354*	*6.7–10.3*
N. sp. mono	6	74	916	26.4	25.6	953	616	20.2
		60–93	*635–1304*	*19.4–33.1*	*22.3–29.7*	*853–1099*	*475–856*	*16.8–22.5*
Sc. p. mono	6	71	976	29.3	26.2	1248	539	17.1
		60–85	*472–1558*	*25.6–33.7*	*23.8–29.2*	*736–2233*	*434–721*	*13.1–24.7*

Included were 42 triplets consisting of 42 mixed-species stands and 84 neighbouring mono-specific stands of the respective tree species. Growth and yield characteristics are given for the monocultures, for the species in the mixed stands, and for the mixed stand as a whole. Means are given in upright letters, minimum and maximum values in italics

Norway spruce, N. sp.; European beech, E. be.; Scots pine, Sc. p.; Douglas-fir, D.-fir.; monocultures, mono; mixed-species stands, mixed

Tree number (ha^{-1}), N, quadratic mean diameter (cm), d_q, height of the tree with quadratic mean diameter (m), h_q, stand density index (trees ha^{-1}), SDI, standing volume (m^3 ha^{-1}), V, periodic annual volume increment (m^3 ha^{-1} year^{-1}), IV

This concept formed the basis for quantifying over- and underyielding according to Bielak et al. (2014), Loreau (1998), and Pretzsch et al. (2010, 2013a). In many earlier works, it proved to be useful for estimating the effect of mixing on the growth and yield of stands of herbaceous (Harper 1977; Vandermeer 1989) and woody (Kennel 1965; Zöhrer 1969) plants. Comparisons between mixed-species stands and monocultures with respect to other tree and stand variables (e.g. tree size, stand volume, stand density, and yield) followed the same nomenclature and algorithm.

Maximum stand density and carrying capacity in mixed-species stands versus monocultures, RD For quantifying the stand density and species mixing portions, the tree number per unit area (N, ha^{-1}) is rather ambiguous as the species of interest may differ in current mean tree size and growing area requirement. Stand basal area (BA, $\mathrm{m}^2\ \mathrm{ha}^{-1}$) is more appropriate; however, most informative is the stand density index (SDI, ha^{-1}) as it considers—like BA—both tree number and size, but is in addition based on the allometric theory in addition (Pretzsch 2006; Reineke 1933). Reineke (1933), who designed the $\mathrm{SDI} = N \times (25/d_q)^{-1.605}$, based it on the allometric relationship between tree number, N, and the quadratic mean diameter of a stand, d_q. Any comparisons of the SDI values of different species as well as calculations that strive for a combined SDI in mixed-species stands have to consider species-specific growing area requirements (Assmann 1954; Sterba et al. 2014).

A first step for comparing the maximum stand density and thereby the carrying capacity of pure and mixed stand was the quantification of the growing area requirement of the involved species. The species-specific growing area requirement of associated species 1 and 2 was quantified by means of the species-specific maximum stand densities (SDIMAX_1, SDIMAX_2) of the unmanaged, fully stocked monocultures of the triplets ($\mathrm{SDIMAX}_1 = N_1 \times (25/dq_1)^{-1.605}$ and $\mathrm{SDIMAX}_2 = N_2 \times (25/dq_2)^{-1.605}$, respectively). These maximum densities were used for deriving the equivalence coefficients $e_{2\Rightarrow1} = \mathrm{SDIMAX}_1/\mathrm{SDIMAX}_2$ and $e_{1\Rightarrow2} = \mathrm{SDIMAX}_2/\mathrm{SDIMAX}_1$ which can be used for converting the SDI from one species to the other. For calculating mean equivalence coefficients, we used the unmanaged, fully stocked pure stands of the triplets, i.e. pairs of pure stands of Norway spruce and European beech ($n = 11$), Scots pine and European beech ($n = 7$), Douglas-fir and European beech ($n = 18$), and Norway spruce and Scots pine ($n = 6$). On average, we found the following mean equivalence coefficients (mean ± SE) for conversion between European beech (be), Norway spruce (sp), Scots pine (pi), and Douglas-fir (D-f): $e_{\mathrm{be}\Rightarrow\mathrm{sp}} = 1.32 \pm 0.09$, $e_{\mathrm{be}\Rightarrow\mathrm{pi}} = 1.10 \pm 0.06$, $e_{\mathrm{be}\Rightarrow\mathrm{D\text{-}f}} = 1.61 \pm 0.15$, and $e_{\mathrm{pi}\Rightarrow\mathrm{sp}} = 0.87 \pm 0.12$, respectively. These mean values are reported just to show the average relationship between the growing area requirement of the considered species.

For comparing the maximum stand density and thereby the carrying capacity in a second step, we used the triplet-specific equivalence coefficients, i.e. the ratio derived from the two pure stands of each triplet. These individual, triplet-specific equivalence coefficients for each triplet were used to calculate a species-overarching SDI for the mixed stand ($\mathrm{SDI}_{\underline{1},2} = \mathrm{SDI}_{1,(2)} + \mathrm{SDI}_{(1),2} \times e_{2\Rightarrow1}$). We used the underscore of the 1 in $\mathrm{SDI}_{\underline{1},2}$ to indicate that the combined SDI has been converted to the level of species 1. By this conversion, the stand densities of different species can be combined.

In a third step, we used the resulting $\mathrm{SDI}_{\underline{1},2}$ values for calculating the ratio $\mathrm{RD}_{1,2} = \mathrm{SDI}_{\underline{1},2}/\mathrm{SDI}_1$ between the maximum stand density in the mixed stand versus the monoculture. RD reveals whether the mixed-species stands have the same maximum stand density as the pure stands ($\mathrm{RD} = 1$), whether the mixed-species stand has a higher ($\mathrm{RD} > 1.0$) or lower maximum stand density ($\mathrm{RD} < 1.0$) compared with the monoculture.

Mixing portions, m_1 and m_2 Based on the total stand density, e.g. standardized to species 1 ($\mathrm{SDI}_{\underline{1},2} = \mathrm{SDI}_{1,(2)} + \mathrm{SDI}_{(1),2} \times e_{2\Rightarrow1}$), and the shares of species 1 ($\mathrm{SDI}_{1,(2)}/\mathrm{SDI}_{\underline{1},2}$) and 2 ($\mathrm{SDI}_{(1),2} \times e_{2\Rightarrow1})/\mathrm{SDI}_{\underline{1},2}$), the mixing proportions m_1 and m_2 of species 1 and 2 were calculated as follows

$$m_1 = \mathrm{SDI}_{1,(2)}/(\mathrm{SDI}_{1,(2)} + \mathrm{SDI}_{(1),2} \times \mathrm{SDIMAX}_1/\mathrm{SDIMAX}_2)$$

$$m_2 = (\mathrm{SDI}_{(1),2} \times \mathrm{SDIMAX}_1/\mathrm{SDIMAX}_2)/(\mathrm{SDI}_{1,(2)} + \mathrm{SDI}_{(1),2} \times \mathrm{SDIMAX}_1/\mathrm{SDIMAX}_2).$$

By quantifying the mixing proportions in this way, we considered any species-specific differences in the growing area requirements, as recommended by Sterba et al. (2014).

Sum of crown projection area in mixed-species stands versus monocultures, RSCPA Crown cross-section area $\mathrm{cpa} = \bar{r}^2\pi$ was calculated using the quadratic mean radius $\bar{r} = \sqrt{(r_1^2 + r_2^2 + \cdots + r_8^2)/8}$ of the 8 crown radii measured per tree. The crown projection areas, cpa, of all n trees of a stand were summed up in order to obtain the cumulative crown projection area $\mathrm{SCPA} = \sum_{i=1\ldots n} \mathrm{cpa}_i$ for the monocultures of each triplet (SCPA_1, SCPA_2) and for the mixed stand ($\mathrm{SCPA}_{1,2}$). The ratio between mixed-species stands and monocultures regarding the sum of their crown projection area is $\mathrm{RSCPA}_{1,2} = \mathrm{SCPA}_{1,2}/(\mathrm{SCPA}_1 \times m_1 + \mathrm{SCPA}_2 \times m_2)$. Latter formula indicates that we compare the sum of crown projection area observed in the mixed stands ($\mathrm{SCPA}_{1,2}$) with the weighted mean of the sum of crown projection areas in neighbouring monocultures

($\mathrm{SCPA}_1 \times m_1 + \mathrm{SCPA}_2 \times m_2$). RSCPA reveals whether the mixed-species stands have the same sum of crown projection area as the pure stands (RSCPA = 1), whether the mixed-species stand has a higher (RSCPA > 1.0) or lower (RSCPA < 1.0) sum of crown projection area than the monoculture.

Characterizing the canopy and size structure

Skewness and kurtosis The comparison of the tree size distributions of mixed-species stands versus monocultures was based on the individual tree volumes, v. We used measures such as the arithmetic mean volume, the minimum and maximum volume, the volume range (max–min), and the standard deviation of the tree volume. For analysing any differences in the shape of the respective distributions, we used the skewness as third potency moment (Bortz 1993, pp 45–46). In case of a symmetric distribution, skew = 0. Suppose an observed size distribution is equipped with many small trees and a low number of tall ones, it is right-skewed and yields skew >0. If the distribution is equipped with many tall trees, but small are rare, it is left-skewed and yields skew <0. Furthermore, we calculated the kurtosis as fourth potency moment (Bortz 1993, pp 45–46) which characterizes the degree of concentration of tree sizes around the mean. A concentration in accordance with the Gaussian normal distribution is indicated by kurt = 0. Stronger concentrations around the mean (peaked shapes) are indicated by kurt >0, while lower concentrations (shallow shapes) yield kurt <0.

Gini coefficient, GC The curve by Lorenz (Fig. 2) and coefficient by Gini can be used for quantifying the size or growth hierarchy between the trees in forest stands (see de Camino 1976; Kramer 1988, p 82). By applying the curve by Lorenz and coefficient by Gini to mixed and pure stands, we revealed how mixing can modify the hierarchy between the trees in a population, e.g. whether species mixing can favour the stem volume or stem volume growth towards small understorey trees compared with pure stands.

The Lorenz curve (Fig. 2a), known for analysing the inequality of income in human populations, can be used for visualizing the inequality of growth in forest stands. The larger the grey area (see Fig. 2a) between the bisector line (maximum equality) and the observed Lorenz curve, the stronger is the inequality. Beyond this graphical representation, we used the Gini coefficient, GC,

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

for quantifying the relative distribution of tree volume (GC_v) and volume growth (GC_{iv}) in mixed-species stands and monocultures of all 42 triplets. Variables x_i and x_j denote size or growth (or other tree characteristics) for the ith, respectively, the jth tree in a stand with $i = 1 \ldots n$ trees. GC = 0.0 means that all trees are equal in size or growth, respectively. The higher the GC, the stronger the inequality of size or growth between the trees (Wichmann 2001, 2002). Notice, that the GC is equivalent to the grey area between the Lorenz curve and the bisector line (see Fig. 2a) divided by the total area of the square, multiplied by 2.

The ratios $\mathrm{RGC}_v = \mathrm{GC}_{v,\ \mathrm{mixed}}/\mathrm{GC}_{v,\ \mathrm{mono}}$ and $\mathrm{RGC}_{iv} = \mathrm{GC}_{iv,\ \mathrm{mixed}}/\mathrm{GC}_{iv,\ \mathrm{mono}}$ were calculated separately for both species of each triplet and used for indicating the effect of tree species mixing on the Gini coefficient for tree volume and volume growth.

Quantifying the size symmetry and size asymmetry of growth In order to quantify the size–growth relationship and indicate the mode of competition in mixed-species stands versus monocultures, tree size growth was 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 yielded the intercept a and the slope b. The procedure was applied for the trees in the monocultures of the triplets as well as for the mixed stands. The resulting values for a and b indicate, whether and how species mixing modifies the size symmetry and size asymmetry of growth (Hara 1992; Wichmann 2001, 2002). The ratios $\mathrm{Ra} = a_{\mathrm{mixed}}/a_{\mathrm{mono}}$ and $\mathrm{Rb} = b_{\mathrm{mixed}}/b_{\mathrm{mono}}$ were used for indicating the effect of tree species mixing on the size symmetry and size asymmetry of growth.

The analysis of the canopy and size structure was based on stem volume and stem volume growth due to weak alternatives. Stem diameter and diameter growth would have been easier to assess and closer to measurement. However, calculating cumulated diameters, respectively, cumulated diameter growth as a basis for the Gini coefficients (GC) would have been less indicative, as the same diameter growth can mean a high contribution to stand growth in case of a thick tree, but just a low contribution when produced by a thin tree. Above-ground biomass or total tree biomass and biomass growth would have been even more informative than stem volume. Functions for estimating tree volume for this purpose are in work (Pretzsch et al. 2014), but not yet sufficiently validated for the species in this study.

The Excel macros (programmed in Visual Basic 2010 language) for deriving the cumulative size growth curves and Gini coefficients and other measures for growth partitioning, will be gladly provided to interested readers.

Statistical evaluation

For comparing given characteristics x of the tree size distributions (e.g. tree number, tree volume, skewness,

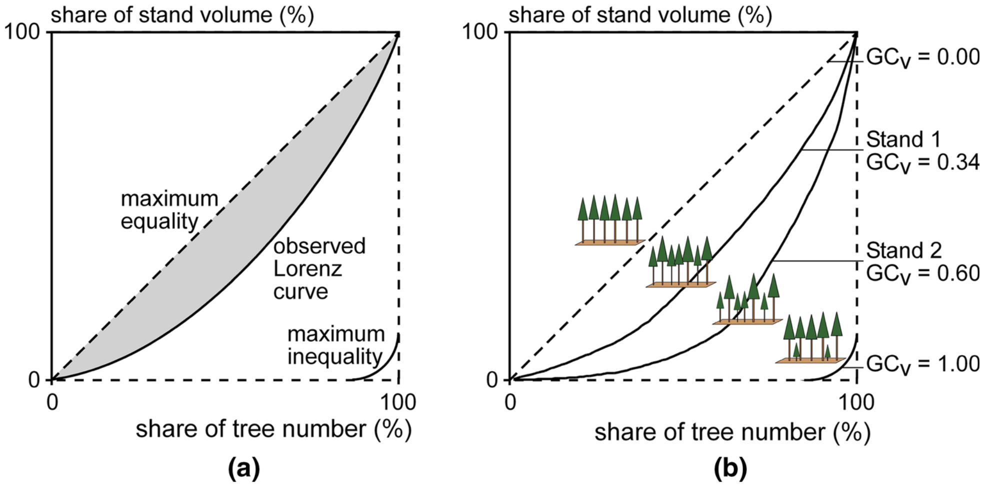

Fig. 2 Schematic representation of the stem volume partitioning between the trees in a forest stand. **a** Lorenz curve applied for quantifying the degree of equality of stem volume distribution. **b** Equal volume distribution in rather mono-layered stands ($GC_v \cong 0$), increasing inequality in heterogeneous stands (Stand 1, $GC_v = 0.34$; Stand 2 $GC_v = 0.60$), and strong inequality (GC_v approaching 1.0)

kurtosis, and Gini coefficients) between mixed-species stands (x_{mixed}) and monocultures (x_{mono}), we used ratios ($\text{Rx} = x_{\text{mixed}}/x_{\text{mono}}$) between these characteristics in mixed stands versus monocultures (Tables 2, 3, 4, 5, 6, Supplement Table 3–4). The mean ratio $\bar{R}x$ and its standard error, SE, provide a simple basis for testing whether the performance of mixed-species stands and monocultures differs. If 1.0 is beyond the confidence intervals $\overline{R}x \pm t_{n-1,\alpha=0.05} \times \text{SE}$, $\overline{R}x \pm t_{n-1,\alpha=0.01} \times \text{SE}$, $\overline{R}x \pm t_{n-1,\alpha=0.001} \times \text{SE}$ (with t being the critical value of the t distribution with $n - 1$ degrees of freedom and a selected two-sided transgression probability α), the differences can be considered as significant at the level $p \leq 0.05$*, $p \leq 0.01$**, or even $p \leq 0.001$*** (Tables 2, 3, 4, 5, 6 and Supplement Tables 3–4, right columns).

Using linear models, we tried to explain the variability of the overyielding (e.g. represented by RP) of mixed versus pure stands by the variability of the canopy and size structure (e.g. represented by RSCPA or Rb). For this purpose, we used OLS linear regression. All calculations were carried out using the software package IBM SPSS Statistics (Version 22).

Results

The mean heights on the triplets of 20–30 m at a stand age of 60–80 years indicate a majority of medium-to-high site indexes and mediocre to fertile sites (Table 1). The shares of standing stock in the mixed stands reflect that mixing proportions are mostly around 50:50 and never below 30:70.

The listed SDI values (Table 1, Supplement Table 2) substantiate that we selected fully stocked stands close to maximum stand density. Sterba (1991) and Pretzsch (2009, p 272) report SDI ranges of 900–1100 for Norway spruce, 600–750 for Scots pine, 700–900 for Douglas-fir, and 500–600 for European beech. The pure as well as mixed-species stands selected for this study mostly exceed these ranges. The high stand density of the plots may be further corroborated by comparing them with SDI values of the yield tables commonly used for the species considered in our study. SDI values for moderately thinned stands on best site classes are 901 trees ha^{-1} for Norway spruce according to the table by Wiedemann (1936/1942), 781 trees ha^{-1} for Scots pine (Wiedemann 1943), 827 trees ha^{-1} for Douglas-fir (Bergel 1985), and 587 trees ha^{-1} for European beech (Schober 1967). Maximum stand density lies about 10–20 % above the stand density of moderate thinning (Assmann 1970, pp 245–346). Most SDI values given in Table 1 for pure stands even significantly exceed the maximum densities extrapolated from the yield table densities for moderate thinning.

Over all the triplets with the different species combinations, the standing stock varies between 488 and 679 m^3 ha^{-1} in the mixed-species stands and 416–934 m^3 ha^{-1} in the monocultures; maximum standing stock is achieved by monocultures and mixed-species stands of Douglas-fir and European beech. Notice that the table presents both the characteristics for the mixed stands in total and the share of both species. The mean standing volume of the Norway spruce/European beech mixed stands, for instance, amounts to 564 m^3 ha^{-1}; the mean shares of Norway spruce and European beech are 299 and 265 m^3 ha^{-1}, respectively. The periodic annual volume increment ranges between 2.6 m^3 ha^{-1} year^{-1} in the young mixed stands of Douglas-fir and European beech, and 45.0 m^3 ha^{-1} year^{-1} in older stands of the same mixture.

Density, shape, and location of size distributions in mixed-species stands versus monocultures

The first section of Table 2 shows that apart from the mixture of Norway spruce/European beech (mixed/mono =

Table 2 Tree number per hectare, minimum, maximum, and mean tree volume (mean ± 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 1/2	*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
N. sp./E. be	11	571 ± 72	629 ± 83	681 ± 112	0.39	1.68	1.00	0.11	0.44	2.33	0.96	0.15
Sc. p./E. be	7	1093 ± 268	945 ± 256	1170 ± 280	0.63	4.01	1.55	0.43	0.51	1.65	1.09	0.16
D.-fir./E. be	18	1051 ± 218	682 ± 127	1123 ± 233	0.58	3.83	1.58	0.19	0.32	2.61	1.19	0.16
N. sp./Sc. p.	6	1075 ± 78	916 ± 99	976 ± 170	0.65	1.84	1.25	0.16	0.67	1.84	1.27	0.21
Species 1/2	*n*	Minimum tree volume			Min tree volume mixed/mono 1				Min tree volume mixed/mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	0.03 ± 0.01	0.21 ± 0.10	0.06 ± 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 ± 0.02	0.32 ± 0.11	0.07 ± 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 ± 0.01	0.60 ± 0.20	0.20 ± 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 ± 0.01	0.15 ± 0.09	0.23 ± 0.08	0.04	4.09	0.95	0.64	0.03	0.45	0.16***	0.06
Species 1/2	*n*	Maximum tree volume			Max tree volume mixed/mono 1				Max tree volume mixed/mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	3.51 ± 0.55	2.83 ± 0.50	2.63 ± 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 ± 0.36	1.49 ± 0.29	1.68 ± 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 ± 1.15	5.68 ± 1.15	2.50 ± 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 ± 0.29	2.10 ± 0.31	1.65 ± 0.29	0.66	2.07	1.15	0.20	1.11	1.92	1.43***	0.13
Species 1/2	*n*	Mean tree volume			Mean tree volume mixed/mono 1				Mean tree number mixed/mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	1.25 ± 0.23	1.30 ± 0.30	0.88 ± 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 ± 0.12	0.76 ± 0.18	0.61 ± 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 ± 0.29	2.61 ± 0.60	1.34 ± 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 ± 0.09	0.72 ± 0.12	0.79 ± 0.09	0.55	2.32	0.98	0.27	0.50	0.91	0.76	0.06

Notice, 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 pair-wise division of the characteristic of the mixed-species stands by the respective value of the neighbouring monocultures

“*”, “**”, and “***” indicate significant differences of mixed-species stand versus monoculture at the level $p < 0.05$, 0.01, and 0.001

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 2, first section). The minimum tree volumes are mostly lower in mixed compared with pure stands (Table 2, second section). The tallest trees, in contrast, can have significantly higher stem volumes in mixed-species stands than in neighbouring monocultures (Table 2, third section). However, the mean tree volumes are partly lower and partly significantly higher in mixed compared with pure stands (Table 2, fourth section). The differences in the shape of the size distribution are 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 (Supplement Table 3).

Table 3 shows the range of the frequency distribution for the tree diameter, tree height, and tree volume (from top to bottom). It underpins that the widening of the tree volume distribution shown in Table 2 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. The range of the diameter distribution is in seven out of eight cases significantly wider in mixed versus pure stands. For the range of the height distribution, mixed stands are in five out of eight cases significantly stronger vertically structured. 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 as shown in Supplement Table 4.

Table 3 Range of stem diameter, *d*, tree height, *h*, and stem volume, *v*, (mean ± 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 1/2	*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
N. sp./E. be	11	45.26 ± 2.73	33.63 ± 3.17	36.72 ± 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 ± 3.05	19.41 ± 2.06	26.79 ± 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 ± 6.48	42.67 ± 4.42	29.06 ± 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 ± 1.76	30.63 ± 1.95	22.73 ± 2.73	0.90	1.47	1.19*	0.09	1.24	2.12	1.65***	0.15

Species 1/2	*n*	Range *h*			Range *h* mixed/mono 1				Range *h* mixed/mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	19.56 ± 1.27	13.53 ± 1.73	12.98 ± 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 ± 1.65	5.53 ± 1.25	11.04 ± 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 ± 2.15	11.09 ± 2.12	13.17 ± 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 ± 1.13	15.52 ± 2.27	7.61 ± 2.05	1.01	3.74	1.70	0.44	1.45	9.22	4.13**	1.19

Species 1/2	*n*	Range *v*			Range *v* mixed/mono 1				Range *v* mixed/mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	3.48 ± 0.55	2.62 ± 0.48	2.57 ± 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 ± 0.37	1.17 ± 0.22	1.62 ± 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 ± 1.15	5.09 ± 1.00	2.30 ± 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 ± 0.28	1.95 ± 0.23	1.42 ± 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 2

Table 4 Gini coefficients for volume, GC_v and Gini coefficients for volume growth, GC_{iv} (mean ± standard deviation) in mixed-species stands versus monocultures (from top to bottom)

Species 1/2	*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 ± 0.02	0.30 ± 0.03	0.44 ± 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 ± 0.02	0.32 ± 0.04	0.39 ± 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 ± 0.02	0.38 ± 0.02	0.42 ± 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 ± 0.02	0.31 ± 0.03	0.23 ± 0.02	0.71	1.84	1.29	0.17	1.50	2.81	2.09***	0.18

Species 1/2	*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 ± 0.02	0.35 ± 0.03	0.47 ± 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 ± 0.02	0.29 ± 0.05	0.45 ± 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 ± 0.02	0.39 ± 0.03	0.45 ± 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 ± 0.01	0.41 ± 0.04	0.28 ± 0.02	0.80	1.83	1.27	0.15	1.39	2.31	1.83***	0.18

Notice 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 2

Notice, that in Tables 2, 3, 4, 5, and 6 and Supplement Tables 3–4, 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 pair-wise 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 group-wise arithmetic means (mean mixed and mean mono) as well as the mean ratios of the pair-wise comparison (mixed/mono). The mean ratios of the pair-

Table 5 Slope (mean ± 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 1/2	*n*	Slope *b* of *iv*–*v* relationship			*b* mixed/*b* mono 1				*b* mixed/*b* mono 2			
		Mean mixed	Mean mono 1	Mean mono 2	Min	Max	Mean	SE	Min	Max	Mean	SE
N. sp./E. be	11	0.036 ± 0.003	0.038 ± 0.004	0.035 ± 0.003	0.48	0.95	0.78***	0.04	0.58	1.14	0.85*	0.06
Sc. p./E. be	7	0.041 ± 0.005	0.034 ± 0.007	0.048 ± 0.005	0.76	3.64	1.36	0.39	0.37	1.04	0.78*	0.10
D.-fir./E. be	18	0.040 ± 0.004	0.039 ± 0.004	0.041 ± 0.008	0.69	2.07	1.28**	0.09	0.50	2.50	1.37***	0.11
N. sp./Sc. p.	6	0.032 ± 0.002	0.034 ± 0.003	0.030 ± 0.002	0.67	1.42	0.95	0.13	0.81	1.28	1.02	0.08

For further explanation, see caption of Table 2

Table 6 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 1/2	*n*	SDI (trees ha^{-1})			RD = SDI$_{\text{mixed}}$/SDI$_{\text{mono 1}}$				RD = SDI$_{\text{mixed}}$/SDI$_{\text{mono 2}}$			
		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 1/2	*n*	SCPA			RSCPA = SCPA$_{\text{mixed}}$/SCPA$_{\text{mono 1}}$				RSCPA = SCPA$_{\text{mixed}}$/SCPA$_{\text{mono 2}}$			
		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$_{\text{mixed}}$/SDI$_{\text{mono}}$) and the ratio of sum of crown projection area (RSCPA = SCPA$_{\text{mixed}}$/SCPA$_{\text{mono}}$) quantify the stand density and crown area in mixed versus pure stands. For further explanation, see caption of Table 2

wise comparison (mixed/mono) were used for testing group differences (see "Statistical evaluation" section Statistical evaluation). Our focus was on the relationships between neighbouring mixed-species stands and monocultures (reflected by their pair-wise comparison) rather than on their differences in general (reflected by their overall means).

Hierarchy of stem size and stem growth

The Gini coefficients GC$_v$ in Table 4 (upper section) indicate that the inequality is mostly significantly higher in mixed-species stands compared with monocultures (GC$_v$ mixed/GC$_v$ mono = 0.95–2.09). Figure 3a, b illustrates this general 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 applies also for the growth partitioning among the trees within the stands, represented by GC$_{iv}$ (Table 4, lower section). This is illustrated by the cumulative stem volume growth as a function of the cumulative tree count in Fig. 3c, 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.

Size symmetry and asymmetry of growth

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 stands as a whole behaves in relation to the monocultures. The overarching analysis of

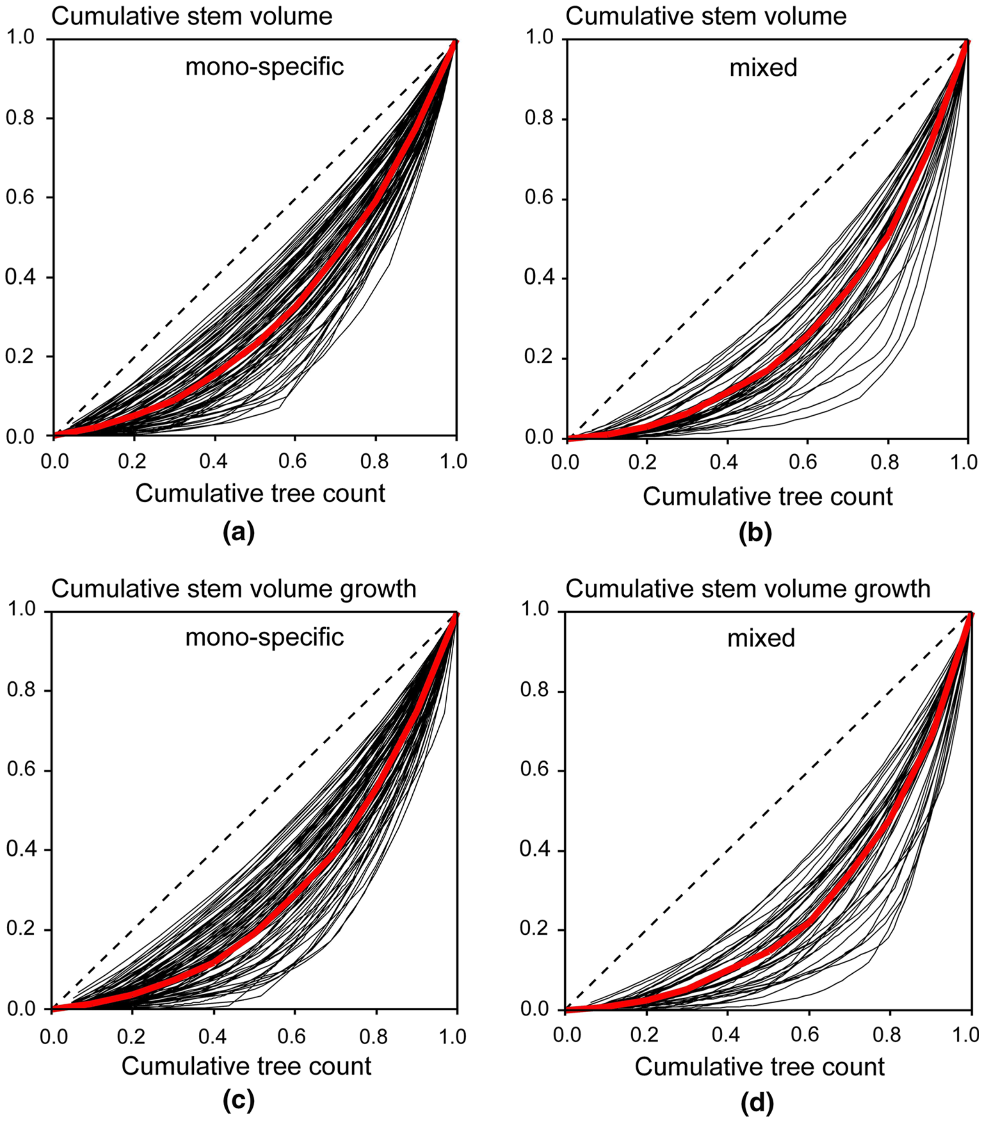

Fig. 3 Hierarchy of stem size and stem growth for 84 monocultures (**a**, **c**) and 42 mixed-species stands (**b**, **d**) of the triplet series of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine. The *bold red curves* represent the overall mean. **a**, **b** Cumulative stem volume, v, as a function of the cumulative tree count, n. On average, the Gini coefficients GC_v for monocultures ($GC_v = 0.36 \pm 0.01$) are significantly lower than for neighbouring mixed-species stands ($GC_v = 0.46 \pm 0.01$). **c**, **d** Cumulative stem volume growth, iv, as a function of the cumulative tree count, n. On average, the Gini coefficients GC_{iv} for monocultures ($GC_{iv} = 0.40 \pm 0.01$) are significantly lower than for neighbouring mixed-species stands ($GC_{iv} = 0.50 \pm 0.02$)

all 84 pair-wise comparison between the mixed-species stands and the monocultures yielded $Rb = 1.14 \pm 0.06$, $n = 84$, $p < 0.05$. This indicates a significant increase in the slope by 14 % in mixed-species stands compared with monocultures. An analogous analysis at the species level yielded $Rb = 1.11 \pm 0.05$, $n = 84$, $p < 0.05$. 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). While mixed stands of Norway spruce and European beech have significantly shallower slopes compared with the pure stands of both species, the mixture of Douglas-fir and European beech developed significantly steeper slopes as both corresponding pure stands.

Figure 4 illustrates for the mixture of Douglas-fir/European beech the mostly steeper slopes of the iv–v relationship in mixed-species stands (Fig. 4b, d, e) compared with monocultures (Fig. 4a, b). Table 5 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.

Stand density and canopy density

The stand density index, SDI, in the mixed stands is mostly similar or significantly higher than the SDI of the neighbouring monocultures (Fig. 5a). The pair-wise comparison between the SDI in mixed-species stands versus monocultures yielded a mean ratio of $RD = 1.10 \pm 0.06$. The upper section of Table 6 shows that mixed stands of Douglas-fir/European beech and Norway spruce/Scots pine there can be significant higher stocking densities compared with monocultures (SDImixed/SDImono = 1.53 and 1.10, respectively).

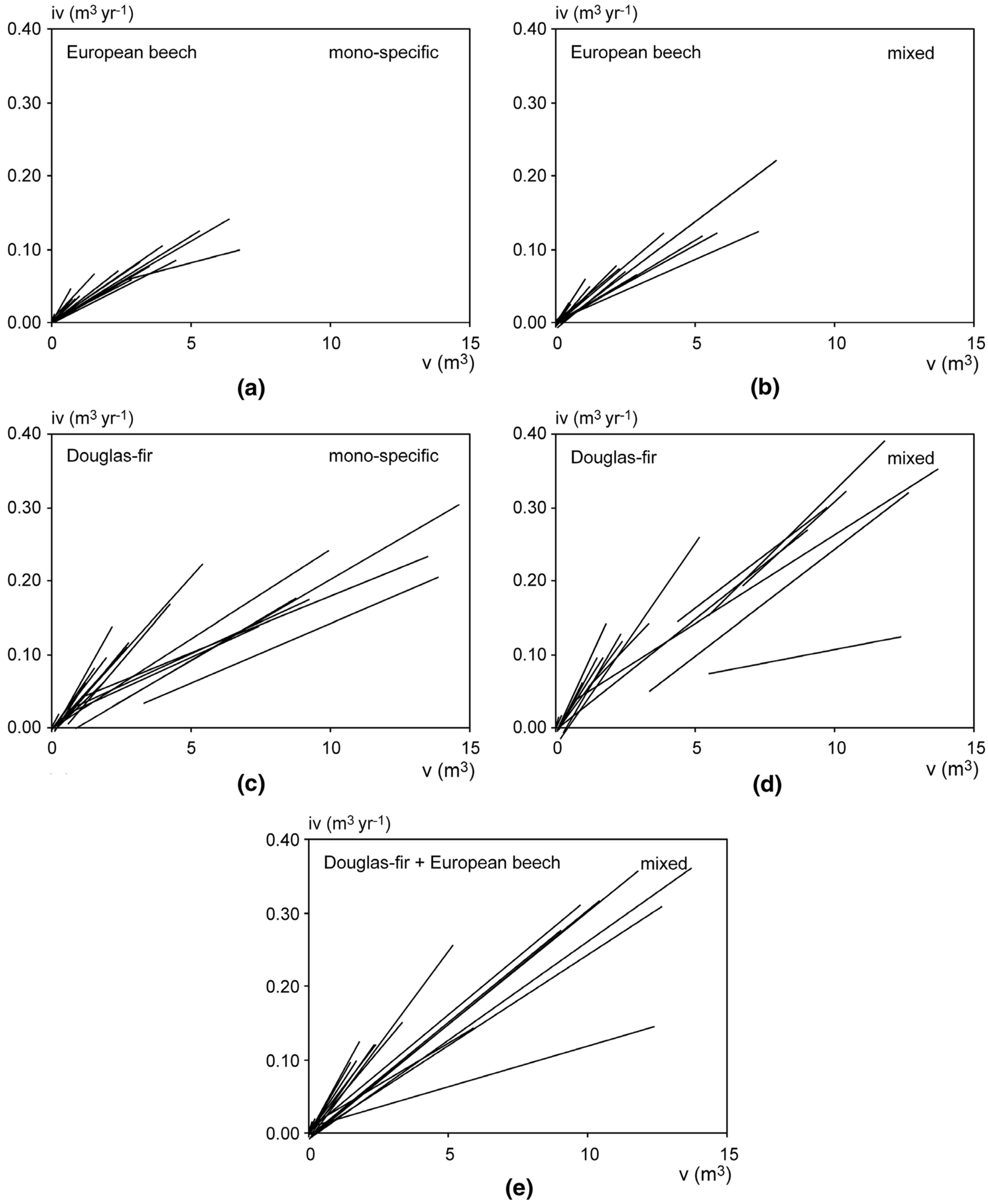

Fig. 4 Modification of the *iv*–*v* relationship by mixing Douglas-fir and European beech compared with the respective monocultures. The asymmetry of growth in the mixed stands (**b**, **d**, **e**) can differ considerably from the corresponding monocultures (**a**, **c**). The *iv*–*v* relationship is shown for each species in the mixed-species stands separately (**b**, **d**) and also for the mixed-species stands as a whole (**e**). Annual tree volume growth (m^3 $year^{-1}$), *iv*; tree volume (m^3), *v*

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 5b illustrates that in most cases the observed sum of crown projection area per hectare in mixed stands, $SCPA_{mixed}$, 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 one up to 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

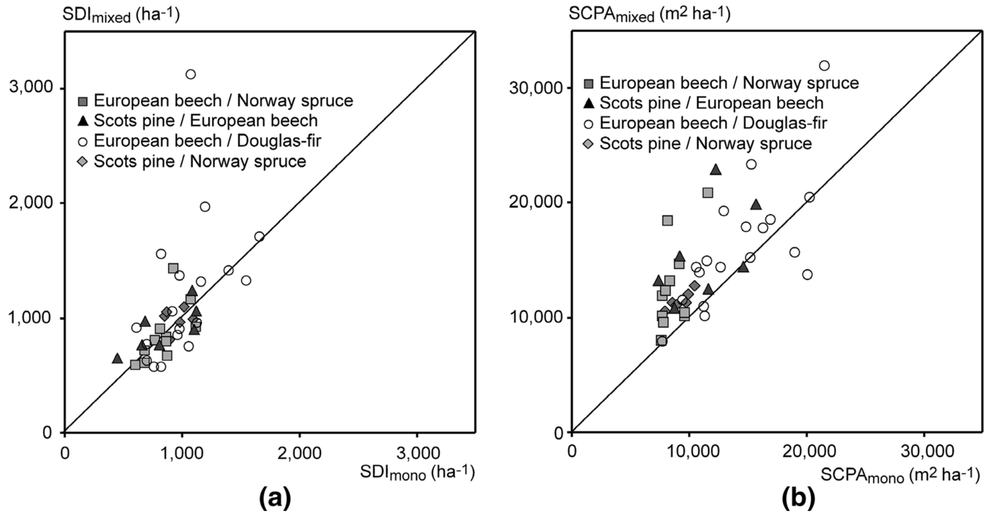

Fig. 5 Observed density on 42 mixed stands compared with monocultures based on triplets of Norway spruce/European beech, Scots pine/European beech, Douglas-fir/European beech, and Norway spruce/Scots pine. **a** Observed stand density index in mixed stands, SDI$_{mixed}$, compared with the weighted mean of both neighbouring monocultures, SDI$_{mono}$. **b** Sum of crown projection area, SCPA$_{mixed}$, per hectare in mixed stands plotted over the values for monocultures SCA$_{mono}$. Observations above the 1:1 line indicate higher density of stocking or canopy cover in mixed-species stands compared with monocultures. Stand density index of pure and mixed-species stands (ha^{-1}), SDI$_{mono}$, SDI$_{mixed}$, respectively; sum of crown projection area of pure and mixed-species stands (m^2 ha^{-1}), SCPA$_{mono}$, SCPA$_{mixed}$, respectively

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 6, lower section).

For the different species combinations, we found mean RSCPA values of 0.96–1.83, indicating by 4 % lower to 83 % denser canopies 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 6, lower section) emphasizes high canopy densities especially in mixtures with beech. Mixed-species canopies are on average by 33 % denser than mono-specific canopies.

Overyielding at the stand and species level

On average, the productivity of the mixed-species stands amounts to 104 % of the weighted mean of the neighbouring monocultures (Table 7). At the species level, the productivity in mixed-species stands amounted to 107–118 % of the monocultures, i.e. the species grow by 7–18 % more in mixed-species stands compared with monocultures. On average, European beech benefited the most when growing in mixture, while Norway spruce benefited the least. The minimum and maximum values showed a broad variation of the mixing effects at both the stand and the species level. In the mixture of Scots pine and European beech, both species interacted in a way that the total benefit amounts to 16 %. The mixture of Douglas-fir and European beech can be particular beneficial for beech (average benefit = 27 %). Only two comparisons revealed significant ($p < 0.01$) overyielding of mixed versus pure stands; European beech benefited significantly when growing in mixture with Douglas-fir, and European beech showed also overall a significant benefit when growing in mixture with the considered conifers.

Relationship between size structure and over- and underyielding at the stand level

We analysed the dependency of the overyielding at the stand level, RP, on the characteristics of the canopy and size structure. The dependent variables were the RP values of all 42 triplets. They quantify the mixing effects at stand level. The independent variables were the ratios between mixed-species stands and monocultures of the following variables: the stand density, RD, the sum of crown projection area, RSCPA, the slope b of the iv–v relationship, Rb, and the Gini coefficients of v, iv, RGC$_v$, and RGC$_{iv}$.

While all other ratios had only weak or nonsignificant effects on RP, the ratios RD, RGC$_v$, RSCPA, and Rb had a clear positive effect as identified with univariate linear models but also in combination (Table 8). Two of the revealed relationships between the size structure and the over- and underyielding at the stand level are visualized in Fig. 6a, b.

Table 7 Over- and underyielding of mixed-species stands versus monocultures

Species	n	$RP_{1,2}$ ± SE (min–max)	$RP_{1,(2)}$ ± SE and $RP_{(1),2}$ ± SE (min–max)			
		Total stand	N. sp.	Sc. p.	D.-fir	E. be
N. sp./E. be	11	1.03 ± 0.11 (0.78–2.04)	1.05 ± 0.16 (0.57–2.57)			1.06 ± 0.08 (0.64–1.53)
Sc. p./E. be	7	1.16 ± 0.11 (0.79–1.62)		1.21 ± 0.14 (0.86–1.88)		1.13 ± 0.11 (0.74–1.61)
D.-fir./E. be	18	1.01 ± 0.09 (0.18–1.74)			1.08 ± 0.09 (0.37–1.73)	1.27 ± 0.10** (0.54–2.02)
N. sp./Sc. p.	6	1.03 ± 0.08 (0.72–1.24)	1.09 ± 0.13 (0.65–1.50)	0.96 ± 0.08 (0.74–1.31)		
Total	42	1.04 ± 0.05 (0.18–2.04)	1.07 ± 0.11 (0.57–2.57)	1.10 ± 0.09 (0.74–1.88)	1.08 ± 0.09 (0.37–1.73)	1.18 ± 0.06** (0.54–2.02)

The mixing effect on productivity at the total stand level, $RP_{1,2}$, and the species' level, $RP_{1,(2)}$ and $RP_{(1),2}$ (±standard error) are given for the various mixture on the triplets and the dataset as a whole (see last line "total")

Norway spruce, N. sp.; European beech, E. be.; Scots pine, Sc. p.; Douglas-fir, D.-fir

** Significant overyielding at the level $p < 0.01$

Table 8 Effect of the size structure on the relative productivity, $RP_{1,2}$, of mixed-species stands versus monocultures at the stand level

Variable	n	Intercept	RD	RSCPA	Rb	R^2	$p <$
$RP_{1,2}$	42	0.20 ± 0.14	0.81 ± 0.13			0.52	0.001
$RP_{1,2}$	42	−0.16 ± 0.21		0.62 ± 0.12	0.36 ± 0.10	0.47	0.001

Model equations are $RP_{1,2} = a + b \times RD$ and $RP_{1,2} = a + b \times RSCPA + c \times Rb$

Relative productivity of mixed-species stands versus monocultures, $RP_{1,2}$, ratio between the density of mixed versus mono-specific stands, RD, ratio the between sum of crown projection area in mixed versus mono-specific stands, RSCPA, and ratio between the slope b (*iv*–*v*-slope) in mixed versus mono-specific stands, Rb

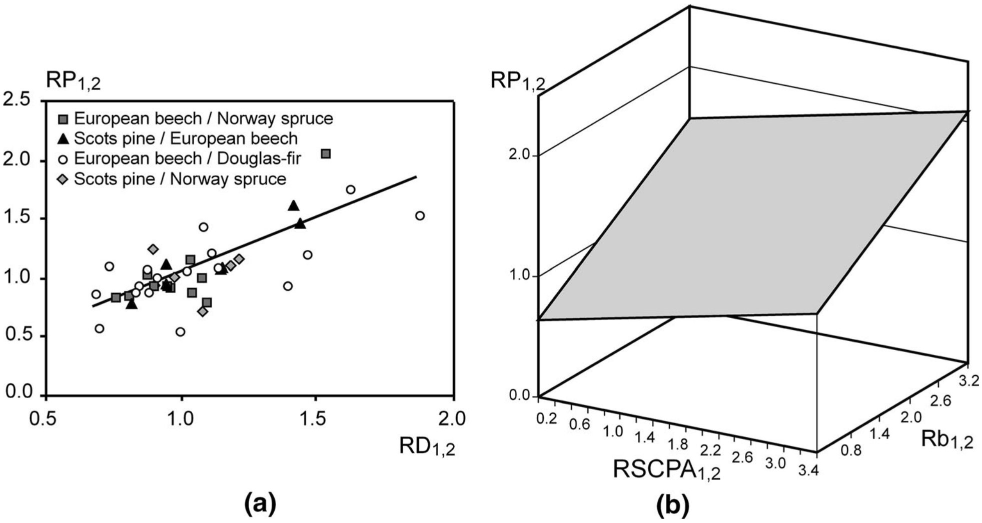

Fig. 6 Dependency of the overyielding at the stand level $RP_{1,2}$ of **a** the relative stand density, $RD_{1,2}$, ($RP = 0.20 + 0.81 \times RD$, $n = 42$, $R^2 = 0.52$, $p < 0.001$), and **b** the ratio between the sum of crown projection area in mixed-species stands and monocultures, $RSCPA_{1,2}$ and the ratio between the slope of the *iv*–*v* relationship, $Rb_{1,2}$ in mixed-species stands and monocultures ($RP = -0.16 + 0.62 \times RSCPA + 0.36 \times Rb$, $n = 42$, $R^2 = 0.47$, $p < 0.001$). Ratio of maximum stand density between mixed and pure stands, $RD_{1,2}$; relative stand productivity of mixed versus pure stands, $RP_{1,2}$; ratio between the sum of crown projection area of pure versus mixed-species stands $RSCPA_{1,2}$, ratio between the slope of the size–growth relationship in mixed versus pure stands, $Rb_{1,2}$

Discussion

In monocultures, especially when they are rather homogeneous in genetics and tree sizes, all individuals compete in a similar way for the growing space and resources. In other words, the resource demands, physiological abilities, and structural variability of the trees are similar to their competitors. However, the crown extension is restricted by intra-specific competition, and the canopy structure remains rather homogeneous (Kelty 1992). Consequently, the sum of crown projection area is often lower than the stand area (Pretzsch 2014), and the canopy is not too deep (Otto 1994, p 214). Inter-specific competition may widen the trees' elbowroom, modify the tree size distribution, and the growth partitioning between the trees. These differences in canopy structure between mixed-species stands and neighbouring monocultures may contribute to the overyielding.

In this study, we used even-aged fully stocked pure stands as reference for revelation of mixing effects on stand structure and productivity. Even-aged mono-specific stands which are artificially regenerated may be a doubtful point of reference when used in comparisons with natural or near-natural forests. Nevertheless, they are useful benchmarks as they often represent the silvicultural business as usual. Mixed stands may be more likely to be implemented when they show some advantages over the mono-specific reference stand.

Modification of tree size distribution by species mixing

Figure 7 summarizes in schematic representation the effect of mixing on the tree size distribution. The total number of trees was higher in mixed-species stands compared with monocultures (Table 2). The corresponding stand density indices and the sum of crown projection areas underpin that stocking density and canopy density can be considerably higher in mixed-species stands compared with monocultures (Table 6). In addition, the minimum tree size was lower, the maximum size higher, and the skewness as well as the kurtosis higher in mixed stands, too. The higher tree number and lower minimum tree size result mainly from shade-tolerant species like beech, which can survive below the comparably transparent conifer crowns of pine, for example. As beech has a low self-tolerance compared with other species (Pretzsch 2006; Zeide 1985), self-thinning in beech monocultures proceeds rather rigorously. Admixture of other species can reduce competition, so that the alien-thinning proceeds less rigorously than the self-thinning (Pretzsch et al. 2012).

In the mixed stands, the species of superior size can accelerate growth and thus increase its lead. Due to its superiority, this species can slow down the other species, causing them lagging behind and accumulating in subdominant positions. This explains the higher maximum tree sizes and wider tree size ranges in mixed-species stands compared with monocultures which was also found by Buongiorno et al. (1994) and Coomes and Allen (2007).

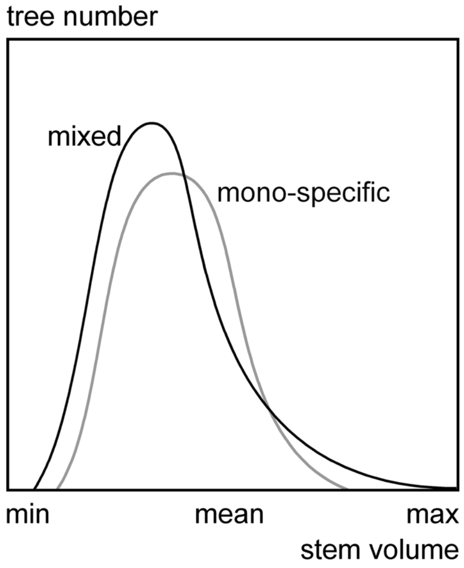

Fig. 7 Characteristic size distribution of mixed-species stands compared with monocultures. In this analysis, the mixed stands minimum tree sizes were lower, the maximum tree sizes were higher, but the mean size was rather similar compared with monocultures. In mixed-species stands, the tree numbers were higher, the size distributions more left steep (skewness $\gg 0$) and more peaked (kurtosis $\gg 0$) while the size distributions in monocultures were more symmetric and flatter

The wider range of tree volumes 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 were above 1.0, i.e. the mixed stands are more heterogeneously structured than pure stands (Table 3). Because of this, light may reach deeper into such a canopy and facilitate survival and growth of subdominant and understorey trees, especially when they belong to a shade-tolerant species. The significantly higher inequality of the tree sizes in mixed-species stands compared with monocultures is substantiated by the much more convex shape of the cumulative tree volume as a function of cumulative tree count (Fig. 3a, b) and the much higher GC_v values (Table 4, upper section).

Stronger size asymmetry of growth in mixed-species stands compared with monocultures

The more unequal tree size distribution in mixed-species stands compared with monocultures results from characteristic differences in the growth partitioning between the trees of mixed versus mono-specific populations. This is reflected by both the slope of the *iv*–*v* relationship and the coefficients GC_{iv}.

The slope of the *iv*–*v* relationship reveals the inter-individual competition and growth partitioning between the trees in a stand (Schwinning and Weiner 1998; Wichmann 2001, 2002). It reveals the size symmetry or asymmetry of growth, for which the term "mode of competition" was coined in several studies by Hara (1992, 1993) and Yokozawa et al. (1998). The steeper the slopes, the stronger resource supply and growth rates are concentrated on the tall trees in the stand on the expense of their smaller neighbours. Steep slopes can be expected on good sites, where light is the limiting factor, which—as a vectorially distributed resource—can be easily pre-empted by the larger individuals (Weiner 1990). Shallow slopes are assumed to prevail on poor sites under limitation by below-ground resources (water and mineral nutrients), as they are mobile, diffuse quickly, and thus are more difficult to pre-empt by larger individuals (Pretzsch 2010). Le Moguedec and Dhote (2012) showed for European beech and Deleuze et al. (2004) showed for Norway spruce and Douglas-fir that the slope can also be increased by decreasing stand density; just for oak Le Moguedec and Dhote (2012) found that the slope of the size growth–size relationship was independent of the stand density.

We found for the mixture of Norway spruce and European beech that the slope of both species significantly decreases compared with the pure stands (Table 5). The same applies for European beech in the mixture with Scots pine. This decrease in inequality and size asymmetry of growth may be caused by the complementary light ecology of the associated species. Del Río et al. (2014) also found a reduction in size asymmetry for European beech in mixture with pine and oak due to lower competition for light. In contrast, mixing of Douglas-fir and European beech resulted in a significantly steeper slope of mixed versus pure stands, which indicates a less complementary light use and stronger inter-specific competition. Mixing of Norway spruce and Scots pine leaves the slopes unmodified (Table 5), although the stand density is higher in mixed versus pure stands. The variation of the reaction patterns reflects that the growth partitioning between the trees in a mixed stand depends on both the species-specific traits and any complementary between the species assemblages. Complementary traits may cause relief of competition and flattening; similar traits may result in an aggravation of the competition for resources and a steepening of the size growth–size relationship.

While the *iv*–*v* relationship quantifies the relationship between the growth rates of small and tall individuals, GC_{iv} indicates in addition their frequency and their contribution to the total stand growth. The GC_{iv} values (Table 4, lower section) and their graphical representation indicate a much more unequal partitioning of stem volume growth among the trees in mixed stands (Fig. 3d) compared with monocultures (Fig. 3c). Mixed stands show a stronger concentration of volume growth on a restricted number of tall trees. That means, e.g. that in monocultures the largest 20 % of the trees account on about 40 % of the stand growth, while it is more than 50 % in the mixed stands (see Fig. 3c, d). These and the subsequent mean percentages were read off the mean curves shown in Fig. 3 (bold red curves).

Amazingly, the partitioning pattern of the stem volume growth (Fig. 3c, d) is very similar to the partitioning of stem volume (Fig. 3a, b). Similar to the partitioning of stem volume growth, the largest 20 % of the trees account on average for 40 % of the stem volume in pure stands, while it is 50 % in mixed stands (see Fig. 3a, b). So, the GC_v and GC_{iv} values are very similar within the group of mono-specific stands. The absolute level of GC_v and GC_{iv} is higher in mixed stands, but within the group of the mixed stands the GC_v are again very similar to the GC_{iv} values (Table 4). That means that the stronger size inequality in mixed stands does not cause a severe growth reduction in smaller trees. Even under strongly varying stand density and structures in mixed stands compared with mono-specific stands, the relative contribution of the stem growth of small trees does not stay behind their portion to stem volume. This is probably caused by the complementary species-specific ecological traits in mixed stands (with, e.g. light-demanding species in the upper and shade-tolerant ones in the lower canopy) and reveals a remarkable growth elasticity of mixed-species stands.

Effect of size structure on overyielding

At both the stand and the species level, there was a wide variation of the relative productivity of mixed stands versus monocultures (Table 7). On average, there was a tendency towards overyielding; however, only for European beech, we found a significant overyielding. A part of this wide variation of the overyielding may be caused by the spatial variation (Forrester 2014; Pretzsch et al. 2010, 2013a; Toïgo et al. 2015a) or temporal variation (Bielak et al. 2014; Forrester et al. 2013; Río et al. 2014) of the environmental conditions between the triplets. Our statistical evaluation showed that part of the variation of the relative productivity of mixed stands versus monocultures can be explained by the canopy and size structure of the mixed stands.

The relative productivity of mixed stands versus monocultures increased especially with the stand density, crown projection area, size asymmetry, and size inequality. It seems to be this particular pattern of canopy space filling by crowns of different sizes, which increases the productivity of mixed-species stands over monocultures (Pretzsch

2014). The combination of species with complementary ecological traits enables a coexistence of trees of variable sizes in different canopy layers. The vertical stratification means a denser crown space filling, light flooding also into deeper canopy layers, higher survival of small trees, complete light exploitation by crowns, and higher stand density. Even trees in deeper canopy layers contribute to stand growth proportionally to their tree volume. That reveals an amazing elasticity of tree growth over the different sizes and layers which is probably caused by adaptation via allometric plasticity (Bayer et al. 2013) and by an optimized species-specific niche occupation, for example by growing shade-tolerant below light-demanding species (Kelty 1992).

The wider extension of the crowns and higher cumulative crown projection area in inter- versus intra-specific environments indicates a higher light interception (Pretzsch and Dieler 2011). Assuming that the nutrient and water supply in the soil are rather sufficient for all trees on the considered sites, light may be the limiting factor for growth, and a better supply, interception, or use-efficiency may considerably increase the stand growth (Hara 1993). The sum of the crown projection area, slope of the *iv*–*v* relationship, and stocking density had a significantly positive effect on the relative productivity of the mixed-species stands versus monocultures (Table 8; Fig. 6). By combining species which are complementary in terms of light ecology, the canopy space filling, canopy deepness, light interception, and light-use efficiency may increase relative to monocultures due to the following reasons: First, combining species with different crown shapes and albedos may decrease the reflection and light loss at the upper canopy layer by 5–10 %. Especially the rather notched canopies of conifers with light wells and low albedos reflect less light compared with deciduous forests (Otto 1994, p 213; Dirmhirn 1964, p 132). Second, mixing of light-demanding with shade-tolerant species may increase the light interception due to complementary, species-specific light compensation points (LCP), and light saturation points (LSP). For example, 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 pine, spruce, or Douglas-fir (Ellenberg and Leuschner 2010, p 103–105). Third, the canopy space filling by species with complementary light ecology and their closer crown interlocking enables foraging full as well as weak light, a more complete light interception, and often results in a lower light intensity at the forest floor of mixed stands compared with monocultures (Mitscherlich 1971, p 82). Fourth, the intercepted light may also be used more efficiently when crowns or branches of shade-tolerant species replace more light-demanding species (Forrester and Albrecht 2014; Kelty 1992).

It is well known that elimination of the slow and inefficiently growing understorey trees in monocultures can accelerate stand growth (Assmann 1968, 1970, pp 248–261; Pretzsch 2005). The replacement of less efficient by better performing trees in the lower canopy layers may have a similar positive effect on stand productivity.

Many studies show that mixing effects and overyielding can vary temporarily (Forrester 2014; Río et al. 2014) and spatially (Pretzsch et al. 2013a; Toïgo et al. 2015a) depending on the prevailing environmental conditions. In this study, we were primarily interested in finding any relationships at all between size structure and overyielding; further evaluations may show whether the revealed relationships are modified by the environmental conditions.

Analysing the effect of canopy and size structure on overyielding. Methodological considerations

For the ongoing transition from monocultures to mixed-species stands forest practitioners concerned with silviculture, forest management and planning need sound knowledge of mixed-stands dynamics. The best possible foundation for this would be long-term experimental plots. In case of a lack of long-term experiments, data from forest inventory plots (del Río and Sterba 2009; Vallet and Perot 2011) or temporal plots (Pretzsch et al. 2015b) may be used as a way out. When using temporal plots as in this study, the following shortcomings need to be considered.

While site conditions are similar for all plots in well-designed long-term experiments, they may differ between mono-specific and mixed plots in forest inventories or triplets of temporary plots as established for this study. The occurrence of mixed stands may even indicate specific site conditions different from nearby monocultures. When establishing our plots, we used the existing soil classification in order to ensure that, in each of the 42 triplets, our mono-specific reference stands have similar site conditions as the mixed-species stands.

Another shortcoming of temporary plots with rather unknown stand history may be uncertainty regarding their stand age (because of underplanting), provenance (especially in case of conifers cultivated in the lowlands beyond their natural range), and the kind of stand establishment (natural regeneration, sowing, planting, spacing). Such uncertainties within triplets may strongly affect the outcome of the mixture–monoculture comparison. In order to avoid such flaws, we determined the stand age of all plots by increment coring; the provenances and kinds of stand establishment were examined using the forest inventories and forest stand records of the respective forest enterprises.

As we did not know the maximum stand density for all included sites, we selected just fully stocked stands which are close to the maximum density and thus represent the site-specific carrying capacity. However, in contrast to unmanaged and fully stocked long-term experiments with known stand history, the triplets in this study may not always represent maximum stand density and carrying capacity due to silvicultural interference longer ago. This, to some extent, might influence the stand density index values reported for the mixed-species plots (Table 6). It also might slightly have influenced the species proportions which we calculated for the mixed-species plots, and as a result of this also the reported over/underyielding (Table 7). Recent studies demonstrated the influence of species proportion definition on the magnitude of identified over-/underyielding (Dirnberger and Sterba 2014; Huber et al. 2014). These works recommend to define species proportion by area, where the reference is the area each species would occupy in a fully stocked pure stand. This corresponds with the approach we used in this study for quantifying mixing proportions (see “Evaluation of basic stand characteristics and overyielding” section).

Our study shows that species mixing can significantly alter the scale (tree number, SDI), location (mean tree dimension), or shape (skewness, kurtosis, Gini coefficients) of the distribution of size and size growth compared with monocultures. This finding is of considerable relevance for analysing and interpreting mixing effects revealed at the individual tree level in many studies (e.g. Pretzsch and Schütze 2009; Río et al. 2014). It underpins, that inference from the performance of individual trees growing in mixed compared with mono-specific stands (e.g. dominant sample trees) to mixing effects at stand level can be misleading (Strigul et al. 2008; Webster and Lorimer 2003). Species interactions identified at the tree level cannot be directly up scaled to the stand level. However, Perot and Picard (2012) suggest point process application to link the growth of individual tree to the structure of the stand, and thus aggregate the individual-based data to obtain reliable estimates for the growth at stand level. As long as the scaling of mixing effects from the tree to the stand level does not consider the shown differences in distribution of size and growth, the results may be biased (Zhao et al. 2006). The same applies for studies which quantify the mixing effects by comparing the mean tree growth in mixed-species stands with monocultures. Even if the mean tree size and growth are similar in mixed-species and mono-specific stands, the upscaling to the stand level might be biased because of the differences in tree size structure as shown in this study. Thus, for better understanding the mixing effects, individual trees of different sizes as well as their size distribution should be analysed in mixed and mono-specific settings.

This would also provide the data and relationships for further improving single-tree-based forest growth models. The main reason why such models such as BWIN (Nagel 1999), MOSES (Hasenauer et al. 2006), PROGNAUS (Sterba and Monserud 1997), or SILVA (Pretzsch et al. 2002) are useful for predicting mixed-species stand dynamics is, that they deduce the stand growth by upscaling from the individual tree level and consider the size structure by competition indices. As they base their predictions on the individual tree size, the local density, and the inter- and intra-specific growth constellation, they consider and prognosticate differences in the size growth dynamics between mixed-species and stands and monocultures.

Consequences for forest management

The periodic annual volume increment and total yield of monocultures can be increased by removing inefficient subdominant and suppressed trees, i.e. by thinning from below. Subdominant and suppressed trees can have an unfavourable ratio between resource use and growth (Assmann 1970, pp 34–38). Eliminating such trees by thinning leaves more water and nutrients to the remaining trees which use these resources more efficiently. Thus, they can overcompensate for the growth loss of the removed trees and even raise the total stand growth about 20–30 % above the level of unthinned stands (Pretzsch 2005). In mixed stands, the effect of shade-tolerant species may be something similar to the thinning from below. While by thinning from below inefficiently slow growing and excessively respiring trees are completely removed, species mixing may replace a less adopted species by another, which is more resource efficient and shade tolerant. A precondition for this increase in efficiency and growth is a combination of species with complementary ecological traits.

Maximum stand density and canopy density can be higher in mixed-species stands compared with monocultures. The close relationship between maximum stand density and overyielding indicates that tree species mixing can increase both productivity and carrying capacity. Latter benefit of species mixing may be “thinned away”, i.e. reduced by stand density reductions. Thus, silvicultural guidelines in terms of stand density management curves, which were developed for monocultures (Assmann 1956, 1968), should not be straightforwardly used for mixed-species stands. Stand density reductions down to the level of the monocultures may reduce the potential gains due to species mixing as the potential light interception and stand carrying capacity will not be fully exploited.

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