

Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level

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Abstract The temperate, humid climate and nutrient-rich soils in the pre-alpine areas of southern Bavaria represent conditions where European beech and Norway spruce come out with rather equal above ground biomass production when cultivated in pure stands. In order to reveal the effect of mixture we established 37 experimental plots in even-aged pure and mixed stands of Norway spruce and European beech covering an age span of 37–155 years. The site conditions ranged from warm, dry and base-rich to cool, wet and acidic sites. The ratio of above ground biomass growth of Norway spruce in relation to European beech decreases from 1.14:1 in the monocultures to 1.04:1 in the mixed stands. The mixing of spruce and beech results in a mutual stimulation of biomass production and acceleration of size growth. Together both species produce up to 59% more above ground biomass than the neighboring pure stands. On average the overyielding amounts to 21% in the case of Norway spruce and 37% in the case of European beech. A total of 67% out of the plots indicate overyielding and 57% transgressive overyielding. In mixed stands both species' tree sizes are significantly ahead of the corresponding pure stands. Facilitation of spruce and competitive reduction of beech yields mutualism with respect to growth on tree and

stand level. Consequences for analyzing and modeling interspecific competition and for silvicultural prescriptions are discussed. Ecological implications of the mixing effect on the occurrence and stability of natural and man-made mixed stands of spruce and beech are considered.

Keywords Facilitation · Competitive reduction · Antagonism · Mutualism · Niche differentiation · Species interaction · Crown efficiency · Resource exploitation · Resilience

Introduction

Species mixing in forest stands is described to affect ecology, productivity and socio-economy (Cannell et al. 1992; Knoke et al. 2005; Knoke and Seifert 2007; Olsthoorn et al. 1999; Scherer-Lorenzen et al. 2005). Whether or not mixing increases productivity always was a central question (Cotta 1828; Gayer 1886; Hartig 1791, 1804; Möller 1922; Wiedemann 1942, 1943) and is debated to this day (Frivold and Frank 2002; Mielikäinen 1985; Piotto 2007; Pretzsch and Schütze 2005). However, even for the mixture of Norway spruce and European beech, which is the best investigated mixture in central Europe, this question is not nearly answered yet. Early investigations by Schwappach (1909), Wimmenauer (1914), Dietrich (1927, 1928), Hofmann (1923), Flury (1926, 1931), and Zimmerle (1949) provided basic growth and yield data, emphasized the alteration of growth curves on tree and stand level by mixing, and revealed a stabilizing effect concerning productivity and stand structure in view of disturbances. However, their elaborated comparisons with pure stands were questionable as based on yield tables instead of neighboring pure stands with equivalent site conditions.

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More sophisticated comparisons were based on one or more mixed stands, differing in proportion or spatial pattern of species mixing, with the two pure stands of Norway spruce and European beech right next to it. Such studies compare pure and neighboring mixed stands regarding volume production (Wiedemann 1942; Spellmann 1996), basal area growth (Rothe 1997), or dry mass production of stem–wood exclusively (Burger 1941; Kennel 1965). By covering site conditions from warm, dry and base-rich to cool, wet and acid sites, these investigations reflected that the relation between the above ground biomass production of both species strongly depends on the particular site conditions. The relation of above ground biomass production between pure spruce and pure beech stands can be 1:1, i.e., balanced, on temperate, humid and calcareous sites. However, it changes towards 2:1 on cool, wet and acid sites, as they are more favorable for Norway spruce (Assmann 1961, pp 351–355). Evaluation of the very few available long-term experiments considering above ground stem biomass production showed, that mixture can result in a productivity of -20 to $+10\%$ compared to pure stands, depending on given site conditions (Pretzsch 2005). An integrated evaluation of the available comparisons of pure versus mixed stands is difficult for a number of shortcomings, which highly influence the outcome. Just a few studies are based on dry matter production (Kennel 1965), most of them use rather small plots (Metlin 1985), comparability of the neighboring pure stand concerning site conditions and stand developmental phase remains often questionable (Kennel 1965), and the determination of the mixing proportion is often unclear or flawed (Assmann 1961). Furthermore, nearly all known studies refer to productivity under more or less undisturbed “normal” conditions and neglect, that mixture can achieve a superior productivity via higher stability and risk distribution, when examined over long periods of time (Spellmann 1996). Evaluation of long-term experiments with occasional interruptions of canopy by thinning, wind-throw, or bark beetle attacks indicate that resilience of growth can be higher in mixed stands, even when they are inferior in productivity under normal conditions (Pretzsch 2003).

Overyielding or just neutral replacement effect of mixing on productivity?

Supposing the unlikely case that the species 1 and 2 grow absolutely identical, then the productivity $p_{1,2}$ of the mixed stand of both is the same as the productivity of species 1 or 2 in a monoculture, i.e., $p_{1,2} = p_1 = p_2$. Productivity of pure and mixed stands would be identical, and as none of the species changes absolute level or course of growth, the initial ratios between the species concerning productivity and mixing proportion also remain unchanged during the

stand development. In this and all subsequent examples p refers to above ground biomass growth of a stand in a given time period ($t \text{ ha}^{-1} \text{ a}^{-1}$).

Supposing the case that the mixed species 1 and 2 differ in productivity ($p_1 \neq p_2$) but strictly keep to their development in the pure stand. Then the productivity $p_{1,2}$ of the mixed stand results from the productivity that both species would achieve in pure stands (p_1, p_2), weighted with their mixture proportions (m_1, m_2): $p_{1,2} \cong p_1 m_1 + p_2 m_2$. In this case, the mixed stand’s productivity can considerably exceed one of the neighboring pure stands. But as long as $p_{1,2}$ equals the proportion-weighted sum of comparable neighboring pure stands’ productivity, we consider a simple replacement with a neutral effect on the stand’s overall productivity. Such a replacement means a *redistribution of available resources* from one species to another but not an exploitation of more or new resources.

A direct positive mixing effect is supposed when the mixed stand’s productivity $p_{1,2}$ is superior to the combination of two pure stands with corresponding size ($p_{1,2} > p_1 m_1 + p_2 m_2$) or when the mixed stand’s productivity even exceeds both, pure stand of species 1 and 2 ($p_{1,2} > p_1$ and $p_{1,2} > p_2$). These cases are referred to as ordinary overyielding and transgressive overyielding, respectively. By analogy underyielding means $p_{1,2} < p_1 m_1 + p_2 m_2$ or $p_{1,2} < p_1$ and $p_{1,2} < p_2$. An overyielding can be caused either by an *occupation of more space*, e.g., by means of a denser horizontal packing of trees, a multi-layered exploitation of light, an avoidance of empty spaces resulting from crown shyness. Or it is affected by a *more efficient exploitation of a given space* in the mixed stand compare to the same space in the monoculture, e.g., by increase of leaf area density and crown efficiency.

Usually the growth of the neighboring pure stands (p_1, p_2) serves as reference for the detection of any (positive or negative) mixing effects. Especially, if the comparison is based on the periodical annual volume or biomass increment in only one survey period, this approach can be rather misleading. Except for simple replacement with a just neutral effect on productivity, even minor initial mixing effects can result in considerable compound interest effects for stand dynamics seen in the long term. Especially in phases of stand development when one species grows quicker and overtops its interspecific competitors it can increase in mixing proportion by edging out and replacing the other species. A quicker or slower growth of one of the species complicates the analysis of mixing effects, because the growth on the mixed plot becomes less and less comparable with that on the pure stand plot (Bristow et al. 2006; Wiedemann 1942, 1943).

Supposing a species is superior in a given mixed stand compared to its growth in the neighboring pure stand. Then the superior size growth can cause an earlier and higher

culmination of the growth curve (Fig. 1, left). However, the other side of advanced plant size growth are increased expenses for maintenance and accelerated aging. Consequently the species' growth curve may culminate earlier but afterwards decline quicker and enter earlier into a phase of lower increment than in the neighboring pure stand. A comparison of growth at age t_1 would indicate a superiority of the species in the mixed stand, by contrast a comparison at age t_2 would indicate an inferiority. In order to get a comprehensive idea of the species' growth in pure versus mixed stand the comparison should cover several stand ages. This way the comparison reveals whether the considered species has just a temporal (Fig. 1, left) or a continuous (Fig. 1, right) benefit from the mixture.

A mixed stand's superiority in productivity also can be caused by a higher growth *resilience under disturbance*. The mixture of several species can cause a diversification of the exploited niches and a distribution of risks. As a rule, mixed stands are more elastic in their growth response to changing site conditions and show greater resilience towards calamities. The relationship between the above ground biomass production of pure and mixed stands under "normal" conditions may shift considerably once risks are included. The decisive factor, in essence, is the probability of the occurrence of disturbances and damage. For example, the frequently observed production and financial superiority of artificial pure Norway spruce stands under more or less undisturbed conditions is often reversed and turns into inferiority if disturbances are included in the calculation (Knoke et al. 2005).

Questions and hypotheses in this study

This paper will not continue the long series of comparisons between growth of pure and mixed stands with varying and

sometimes inconsistent results (Kennel 1965; Rothe 1997) by just applying conventional methods to another new data set. By tracing presumed mixing effects from stand to tree level we rather try to reveal different causes for mixing effects, reconcile apparently inconsistent and confusing results, and revive the somehow stuck mixed stand research by introducing new methods. We analyze even-aged pure and mixed stands of Norway spruce and European beech on temperate, humid and nutrient-rich sites in pre-alpine South Bavaria. On these sites the above ground biomass production of both species in monocultures is high and rather balanced. Such conditions appear most suitable for scrutiny of the following questions:

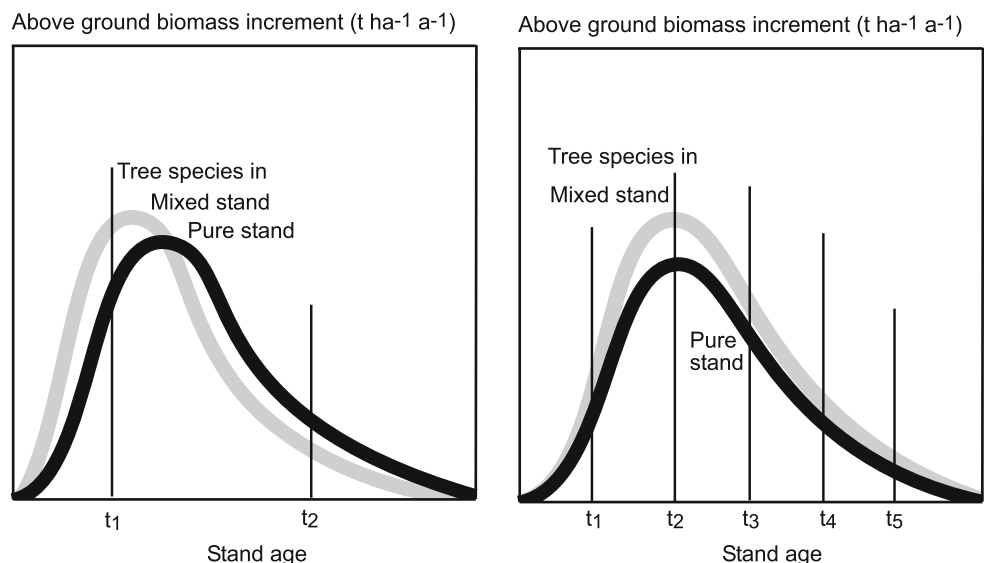
1. Does species mixing result just in a neural replacement effect or in an over- or underyielding of above ground biomass?
2. Is stand density or crown coverage affected by mixing?
3. Are mean tree sizes in the mixed stands different from those in the neighboring pure stands?
4. Is the crown efficiency of individual trees in mixed stands different from the efficiency in the adjacent monocultures?
5. What are the causes that lead to over- or underyielding? In order to answer this question, we trace the effects of species interaction from stand to individual tree level.

Data and methods

Age series FRE 813/1-6 and SON 814/1-9 of pure and mixed stands of Norway spruce and European beech

Out of the continuous range from warm, dry and base-rich sites to cool, wet, and acidic sites which are suitable for

Fig. 1 Unimodal biomass increment curves of a species in a pure stand (black) and in a neighboring mixed stand (gray) in schematic representation. *Left* If mixing alters a species' increment curve, comparison of increment at time t_1 and t_2 yield inconsistent results. In this case, comparison reflects accumulated differences due to altered aging, rather than differences in productivity between mixed and pure stand under ceteris paribus conditions. *Right* If mixing just increases the level of biomass production without altering the rhythm of the increment curve, comparison at time $t_1 \dots t_5$ deliver consistent results



mixed stands of Norway spruce and European beech, we analyze two age series on temperate, humid, and nutrient-rich sites in pre-alpine South Bavaria. The age series FRE 813/1-6 represents the warmer site which is supplied with less precipitation but provided with a higher water-retention capacity. SON 814/1-9 represents the colder, ample precipitation provided site with lower water-retention capacity. Nutrients are more scarcer on age series FRE 813 compared with SON 814, where moraine material constitutes the middle and lower soil layers. On both age series the above ground biomass production of the two species in monocultures is high and rather balanced. All plots are on more or less flat terrain and comparable in slope and exposition. The following description of the two age series' particular site conditions is based on one representative soil profile in each case.

The six mixed spruce-beech stands of age series FRE 813 are located between 11°23'24"E to 11°31'36"E, and 48°14'24"N to 48°30'00"N in the ecological region 12.8 "Tertiäres Hügelland. Oberbayerisches Tertiärhügelland" in South Bavaria near Freising, 35 km northeast of Munich. The stands are located 480–515 m above sea level. Mean annual temperature is 7.7°C and precipitation 814 mm, and 15.0°C and 476 mm during vegetation period. Length of the vegetation period (days $\geq 10^\circ\text{C}$) is 155 days on average. The stands FRE 813/1-6 are stocking on eutric cambisols (FAO) which is equivalent to "Braunerde-Parabraunerde aus tertiärer oberer Süßwassermolasse mit quartärer Lößüberdeckung" according to the German Soil Classification System. Soil texture in 0–100 cm depth is based on 60% silt, 20% clay, 20% sand; below 100 cm the quantity of sand increases to 80% mainly at silt's expense. The base saturation in humus is about 90%. In the upper mineral soil (10 cm depth) it is 10%, and it increases again to 90% in the depth from 50 to 140 cm. The effective cation exchange capacity is 450 $\mu\text{mol}_\text{C} \text{ g}^{-1}$ in the humus layer. In the mineral soil it is rather stable between 50 and 100 from the top to the depth of 140 cm. The pH(H₂O)-value amounts to 6 in the humus layer and 4–5 in the mineral soil. The C/N-ratio is 25 in the humus layer and decreases from 18 in the upper mineral soil to 3 in the depth of 140 cm. Natural vegetation would be a *Galio-odorati-Fagetum association* dominated by European beech.

The nine mixed spruce-beech stands of age series SON 814 (west–east spread: 10°28'45"E–10°31'39"E, north–south spread: 47°31'05"N–47°32'31"N) are located in the ecological region 14.4 "Schwäbisch-Bayerische Jungmoräne und Molassevorberge. Westliche kalkalpine Jungmoräne" in South Bavaria near Schongau, some 60 km southwest of Munich. The stands are situated 785–800 m above sea level. Mean annual temperature is 6.8°C and precipitation 1,114 mm, and 13.9°C and 648 mm during the vegetation period. Length of the vegetation period

(days $\geq 10^\circ\text{C}$) is 140 days on average. The stands SON 814/1-9 are stocking on haplic alfisols (FAO) which is equivalent to "Parabraunerde aus Pleistozän über Altmoräne". Soil texture from 0 to 80 cm depth is based on silt, clay, and sand with a third each; below 80 cm the quantity of silt and sand increases to 80% at clay's expense. The base saturation in humus is about 70%. In 10–20 cm depth it decreases to 5%, and from 20 to 120 cm depth it increases again to 95%. The effective cation exchange capacity is 460 $\mu\text{mol}_\text{C} \text{ g}^{-1}$ in the humus layer. In the mineral soil it increases steadily from 100 in the upper part to 250 in the depth of 120 cm. The pH(H₂O)-value amounts to 5.5 in the humus layer. In the mineral soil it increases from 4.5 in the upper to 8.5 in the lower layer. The C/N-ratio is 30 in the humus layer and increases from 17 in the upper mineral soil to 20 in the lower layer. Natural vegetation would be a *Luzulo-Fagetum association*.

Most of the six plots near Freising FRE 813/1-6 and the nine plots near Schongau SON 814/1-9 comprise parts where the considered species occur in pure and mixed structure (Fig. 2). In total 37 partial plots with pure Norway spruce, pure European beech, and mixture of spruce and beech are available for this study; the total plot area amounts to 6.74 ha. The partial plot size ranges between 0.1 and 0.3 ha and amounts to 0.18 ha in average. The partial plots represent monocultures of spruce and beech right next to a partial plot with both species in mixture. The plots were not thinned since at least 10–20 years before the establishment; i.e., stand growth in the considered survey periods approach maximum density and self-thinning conditions. Annual mortality rates of 5–8% of the trees substantiate this assessment. For further information about the plots cf. Pretzsch et al. (1998), Pretzsch and Schütze (2005), and Prinz (2007).

Table 1 characterizes both age series by growth and yield data. We evaluated stand level data with standard procedures reported in Pretzsch (2002) and present them in advance in order to set out the productivity of the chosen stands. The plots cover an age range of more than 100 years and a mean and top height range from up to 25 m. Site index expressed by top height at age 100 ranges from 37 to 44 m in FRE 813 and 33–41 m in SON 814 in the case of Norway spruce. The corresponding site index for European beech amounts to 30–36 and 25–34 m in FRE 813 and SON 814, respectively. The data in Table 1 on stand basal area and standing volume refer to the year 1994 and reflect the sites' very good to outstanding growing conditions. Volume increment is reported for the period 1994–1999. Volume is given as merchantable wood > 7 cm minimum diameter at the smaller end.

Compared with the yield tables of Assmann and Franz (1965) for Norway spruce and Schober (1967) for European beech both species represent excellent growing

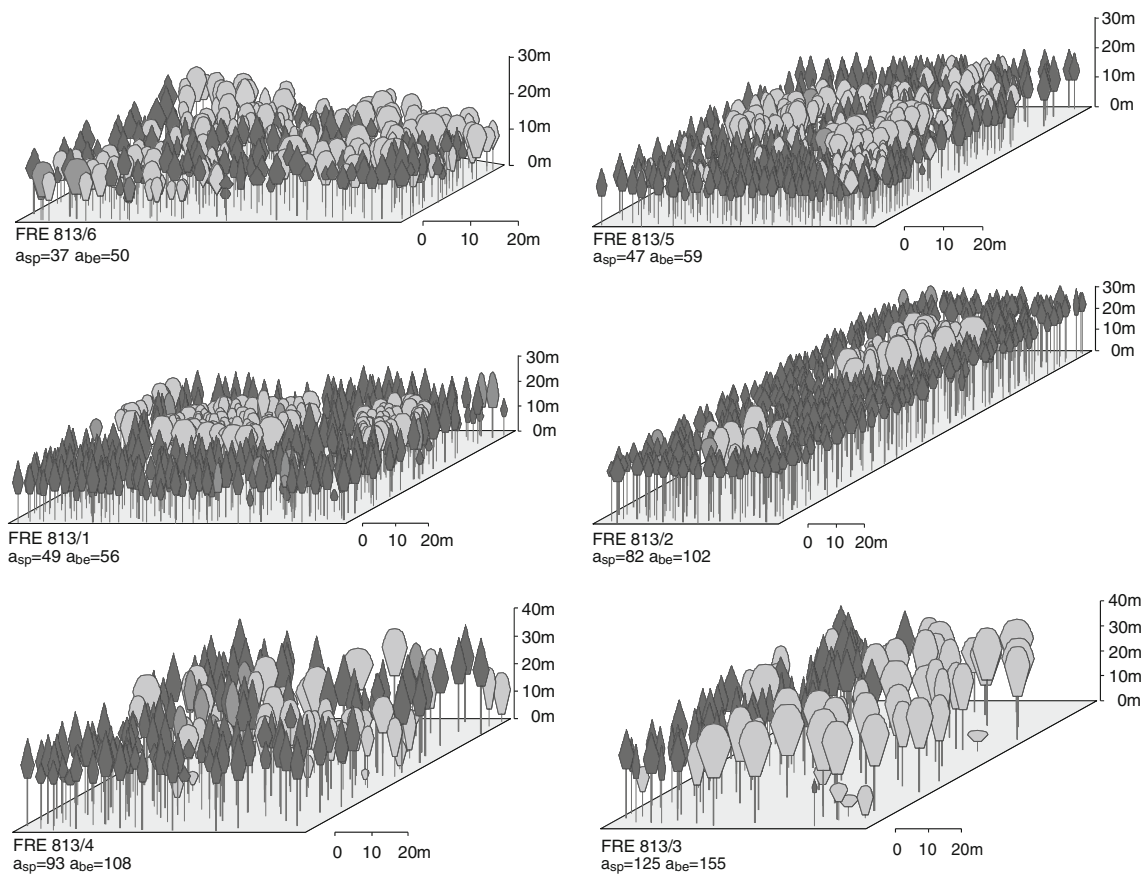


Fig. 2 Age series FRE 813 in the year 1994; artificial time series from young (*top left*) to mature mixed stands (*bottom right*). Age of spruce a_{sp} and age of beech a_{be} refer to the year 1994. All plots were

inventoried 1994 and 1999 by measurement of stem positions, crown dimensions, tree diameter, and tree height

conditions, with only slight differences: on average FRE 813 represents better growing conditions for European beech, while SON 814 is more favorable for Norway spruce. The stand level data in Table 1 applies to each experimental plot as a whole; later we split up each plot to parts which represent Norway spruce and European beech in pure and mixed stands (Table 3).

Methods

Measurements on tree and stand level

The plots were inventoried for the first time in Autumn 1994. Tree age was detected by ring analyses on increment cores. Stem co-ordinates were measured with the theodolite LEICA TC500. Diameter at breast height was measured with girth tape, tree height and height of the crown base (base of the crown’s lowest primary branch) with the clinometer VERTEX. The 8 crown radii per tree (N, NE, . . . , NW) were measured with the optical perpendicular instrument type biritz + hatzlTM. The whole

standard measurement procedure was repeated in Autumn 1999 and is described in detail by Pretzsch (2002). In total, the following evaluation is based on a plot area of 6.74 ha, 6,156 individual trees in 1994 (4,139 Norway spruces and 2,017 European beeches), and 5,002 trees in 1999 (3,301 Norway spruces and 1,701 European beeches) (Table 2). Crown projection area (cpa) $cpa = \bar{r}^2 \pi$ was based on the quadratic mean radius $\bar{r} = \sqrt{(r_1^2 + r_2^2 + \dots + r_8^2)/8}$. Compared with planimetry by linear or spline-based smoothing of the crown periphery, the quadratic mean approach results in medium cpa (Pretzsch 1992, pp 123–129). For estimation of the trees’ entire above ground biomass w (in kg) in dependence on diameter at breast height d (in cm) we applied allometric functions for Norway spruce $w = 0.044 d^{2.659}$ and for European beech $w = 0.114 d^{2.503}$ developed by Pretzsch and Schütze (2005). Biomass increment Δw results as the difference between the two successive surveys divided by time period of 5 years ($\Delta w = (w_{1999} - w_{1994})/5$). The survey period ranges over 5 years from 1994 to 1999 in FRE 813 and over 10 years from 1994 to 2004 in SON 814.

Table 1 Growth and yield characteristics on the age series FRE 813/1-6 and SON 814/1-9, shown for the total stand and Norway spruce and European beech, separately

Age series	Age (years)	Top height (m)	Site index h_o age 100 ^a	Stem number (trees ha ⁻¹)	Stem diameter (cm)	Basal area (m ² ha ⁻¹)	Standing volume (m ³ ha ⁻¹)	Mixing proportion ^b	Periodic annual increment (m ³ ha ⁻¹ a ⁻¹)	
FRE 8131-6	Total	–	–	201–1,558	–	23.9–59.1	386–887	–	15.4–24.8	
	N. spruce	37–120	19.0–40.0	36.7–44.3	101–1,107	17.1–43.8	13.4–50.6	105–747	39–78	3.7–17.9
	E. beech	45–161	16.8–40.7	30.1–36.1	39–792	12.1–52.4	8.5–21.5	55–445	22–61	3.3–10.0
SON 8141-9	Total	–	–	294–2,658	–	41.3–69.9	515–1,041	–	11.7–28.9	
	N. spruce	45–120	20.1–40.2	32.8–40.6	154–2,110	15.2–54.0	20.8–62.0	216–996	44–86	6.1–31.5
	E. beech	75–135	19.5–35.8	25.4–34.4	79–852	15.3–40.4	6.7–24.9	83–439	14–56	2.1–15.6

Stand variables refer to Autumn 1994, periodical annual increment refers to the 5-year period 1994–1999 in FRE 813 and to the 10-year period 1994–2004 in SON 814

^a According to the yield tables from Assmann and Franz (1965) and Schober (1967) for Norway spruce and European beech, respectively, the sites represent top growing conditions for both species

^b We report the mixing proportion Norway spruce: European beech on the basis of the adjusted basal area (cf. “Methods”)

Table 2 Plot and sample sizes summarized for Norway spruce, European beech and in total on the age series FRE 813/1-6 and SON 814/1-9

Age series	Plot area (ha)	Sample size first and (second) survey					
		<i>d</i>	<i>h</i>	<i>hcb</i>	<i>stco</i>	<i>cpa</i>	
FRE 8131-6	Total	2.87	2,491 (2,083)	491 (556)	490 (535)	2,490	984 (131)
	N. spruce	1.74	1,796 (1,482)	238 (323)	238 (323)	1,796	571 (82)
	E. beech	1.13	695 (601)	253 (233)	252 (212)	694	413 (49)
SON 8141-9	Total	3.87	3,665 (2,919)	1,437 (1,697)	1,437 (1,697)	3,541	1,963 (1,569)
	N. spruce	2.14	2,343 (1,819)	843 (1,057)	843 (1,056)	2,250	1,300 (984)
	E. beech	1.73	1,322 (1,100)	594 (640)	594 (640)	1,291	663 (585)
Total	Total	6.74	6,156 (5,002)	1,928 (2,253)	1,927 (2,232)	6,031	2,947 (1,700)
	N. spruce	3.88	4,139 (3,301)	1,081 (1,380)	1,081 (1,379)	4,046	1,871 (1,066)
	E. beech	2.85	2,017 (1,701)	847 (873)	846 (852)	1,985	1,076 (631)

d Diameter at breast height, *h* tree height, *hcb* height to crown base, *stco* stem co-ordinate, *cpa* crown projection

First numbers represent the measurements in 1994. Numbers in brackets indicate the number of repeated measurements in Autumn 1999 and 2004, respectively

Nomenclature, relations and variables for analyzing the mixing effect

We developed a framework for the analysis of mixing effects with respect to stand and tree parameters. In the following introduction the key variable above ground biomass productivity p (t ha⁻¹ a⁻¹) serves as example. We consider an experimental setup where one plot represents pure Norway spruce, one plot pure European beech and a third plot both species in mixture. We denote the biomass productivity p of the pure Norway spruce stand as p_{sp} , that of the European beech stand as p_{be} and that of the mixed stand as $p_{sp,be}$. We refer to the biomass production per hectare of Norway spruce in the mixed stand as $p_{sp,(be)}$, and to that of European beech as $p_{(sp),be}$. In order to get these variables we need the share of production $pp_{sp,(be)}$ and

$pp_{(sp),be}$ of both species and their mixing proportions m_{sp} and m_{be} . That enables us to calculate $p_{sp,(be)} = pp_{sp,(be)}/m_{sp}$ and $p_{(sp),be} = pp_{(sp),be}/m_{be}$. The share $pp_{sp,(be)}$ represents Norway spruce's contribution to the biomass production in the mixed stand, and $p_{sp,be} = pp_{sp,(be)} + pp_{(sp),be}$. In contrast $p_{sp,(be)}$ reflects the contribution $pp_{sp,(be)}$ scaled up to 1 ha by the mixing proportion of this species, i.e., $p_{sp,(be)} = pp_{sp,(be)}/m_{sp}$.

Now we are equipped for the calculation of

$$\hat{p}_{sp,be} = p_{sp}m_{sp} + p_{be}m_{be}, \quad (1)$$

which represents the expected biomass a mixed stand would produce if both species produce the same as in neighboring pure stands of the same size of area. If the observed productivity in the mixed stand is higher than the expected productivity $\hat{p}_{sp,be}$, i.e.,

$$p_{sp,be} > p_{sp}m_{sp} + p_{be}m_{be} \tag{2}$$

we notice overyielding. And when even

$$p_{sp,be} > p_{sp} \quad \text{and} \quad p_{sp,be} > p_{be} \tag{3}$$

we notice transgressive overyielding of the mixed stand compared with both species in pure stands.

The following quotients apply the previous variables for the comparison between pure and mixed stands: the ratio $p_{sp} : p_{be}$ compares the productivity of the considered species in monoculture. The ratio $p_{sp,(be)} : p_{(sp),be}$ addresses the same relation in the mixed stand. It reveals how mixing changes the relative strength of both species. Over- or underyielding can be quantified by ratio $p_{sp,be} : \hat{p}_{sp,be}$ which amounts to 1.0 when the mixed stand grows like neighboring pure stands of the same size. However, values above or below 1 indicate and quantify over- and underyielding, respectively. For example, $p_{sp,be} : \hat{p}_{sp,be} = 1.5$ means overyielding by 50%. Transgressive overyielding is indicated by $p_{sp,be} > p_{sp}$ and $p_{sp,be} > p_{be}$. The ratios $p_{sp,(be)} : p_{sp}$ and $p_{(sp),be} : p_{be}$ reflect from which species over- or underyielding comes from. They set each species' production per hectare in mixed stands into relation with its production per hectare in the neighboring monoculture. Other variables, e.g., diameter d , crown length cl , and cpa are named and applied analogously.

Species specific wood densities, calculation of mixing proportions and standardization of tree diameters

In the course of inventories, standing volume is measured in $m^3 ha^{-1}$ and stand productivity in $m^3 ha^{-1} a^{-1}$. Volume is mostly given as merchantable wood > 7 cm minimum diameter at the smaller end. In order to make the productivity of species with different specific wood densities comparable and to come to plausible mixing proportions, the standing volume is multiplied by the species specific wood density (Trendelenburg and Mayer-Wegelin 1955). Kennel (1965) assumed a wood density of $390 kg m^{-3}$ for Norway spruce and $560 kg m^{-3}$ for European beech. He showed that the mixture as such did not change the wood density significantly, and calculated the stock and growth of standing above ground stem biomass for comparing pure and mixed stands. In contrast to this approach we apply species-specific biomass functions on tree level, which allow up-scaling to standing above ground biomass ($t ha^{-1}$) and biomass production ($t ha^{-1} a^{-1}$) of the stands including branch and leaf biomass.

In this study we calculate the mixing proportion on the basis of the standing above ground biomass of spruce and beech in the mixed stand $W_{sp,(be)}$, $W_{(sp),be}$ and the mixed stand in total $W_{sp,be}$. So the mixing proportion of spruce is $m_{sp} = W_{sp,(be)}/W_{sp,be}$ and that of beech $m_{be} =$

$W_{(sp),be}/W_{sp,be}$. We assume that the share of above ground biomass of both species expresses best their access to and exploitation of above and below ground resources and thus their proportion in the mixture. As production and standing biomass always refers to 1 ha, a mixing proportion of $m_{sp} = 0.8$ means that 0.8 ha or 80% of the stand is occupied by Norway spruces.

In order to apply the stand density index (SDI) by Reineke (1933) for comparing stand density of pure and mixed stands we adjusted the stem diameter according to Keller (1995). Supposing a stem is a stereometric body with the volume v and the diameter d , then simple geometrical scaling yields $v \propto d^3$ and by rearrangement $d \propto v^{1/3}$. With other words, a relationship between two volumes corresponds with a relationship between their diameters, raised to the power of 1/3. Applying the relation between the wood densities of Norway spruce and European beech, 0.39:0.56, the relation between the diameter becomes $0.39^{1/3}:0.56^{1/3} = 0.731:0.824 = 1:1.28$. Following this relationship, the diameter of European beech was weighted by 1.128 to raise it to the level of Norway spruce (cf. "Crown coverage and stand density in pure and mixed stands").

Quantification of inter-tree competition

A tree's access to growing space is quantified by the competition index (CI), frequently used by individual-tree models to quantify inter-tree competition (Pretzsch and Schütze 2005). The competitors of a particular tree are identified from the application of a virtual reverse cone. The axis of this cone is equal to the tree axis and its vertex is placed within the crown of the tree. The relative height within the crown and the angle of the vertex are species specific. Any tree, whose top is inside this virtual cone, is regarded as a competitor. For any competitor the angle between the insertion point of the cone and the top of the competitor tree is determined. This angle is weighted by the relation between the crown cross-sectional areas (CCA) of the competitor and the respective tree. These areas are calculated according to crown models either in the height of the cone vertex, if the cone vertex is above the maximum crown width, or in the height of maximum crown width, if the vertex is below. In addition, the angle β is also multiplied by a species-specific light transmission coefficient according to Ellenberg (1963). The CI is then defined as the sum of all competitor contributions

$$CI_i = \sum_{j=1}^n \beta_j \cdot \frac{CCA_j}{CCA_i} \cdot TM(j) \tag{4}$$

with CI_i = competition index for tree i , β_j = angle between cone vertex and top of competitor j , CCA_j , CCA_i = crown

cross-sectional area of trees j and i , respectively, $TM_j =$ species specific light transmission coefficient for tree j , $n =$ number of competitors of tree i . $TM = 1.0$ for Norway spruce and 0.8 for European beech. Competition index reflects to which extend an individual tree occupies the limited growing space within a stand [for further explanation cf. Pretzsch (2001), pp 218–222].

Detection of mixing effects on individual tree level

For scrutiny whether mixing changes crown efficiency we use the following parameters, calculated for 2,630 trees (889 spruces in pure stand 797 spruces in mixture, 455 beeches in pure stand 489 beeches in mixture): efficiency of cpa

$$EEX = \Delta w / cpa (\text{kg m}^{-2} \text{a}^{-1}) \quad (5)$$

reflects the mean annual biomass growth per unit of cpa. Crown projection area (m^2) represents the cpa at the beginning of the respective period.

The crown efficiency EEX was then related to cpa, CI and a factor pm in a regression of the following form:

$$\ln(EEX) = a_0 + a_1 \ln(cpa) + a_2 \ln(CI + 1) + a_3 pm. \quad (6)$$

The CI reflects to what extend a tree' access to resources (growing space) is restricted by competitors. The binary dummy variable pm indicates whether the tree belongs to a pure stand $pm = 0$ or mixed stand $pm = 1$.

The regression was calculated for each plot of the series FRE 813/1-6 and SON 814/1-9 and both species (15 plots \times 2 species = 30 strata). The aim of the regression is to quantify how mixing (pm) influences crown efficiency (EEX) when size and competition effects are eliminated. Adding 1.0 prevents the term $\ln(CI + 1)$ from becoming undefined when $CI = 0$. The term $a_3 pm$ reflects the mixing effect. This becomes apparent when we rearrange Eq. (6) to

$$EEX = e^{a_0} cpa^{a_1} (CI + 1)^{a_2} e^{a_3 pm}. \quad (7)$$

In the case of pure stand $pm = 0$ and $e^{a_3 pm} = 1$, so that the term leaves the crown efficiency EEX in Eq. (7) unchanged. If $pm = 1$, crown efficiency is multiplied by $\text{mult} = e^{a_3}$, which reflects directly the synergy effect of mixing on crown efficiency.

As cpa is one of the determinants of EEX [cf. Eq. (5)] it is included on both sides of Eqs. (6) and (7). This increases the reported significance level and the R^2 of the overall model. However, for our biological considerations it is important to use no other dependent variable in order to obtain optimal parameter estimates for explaining EEX. Leaving out cpa as an explanatory variable would make no sense from a biological point of view, as this would indicate that Δw is directly proportional to cpa. The biologically plausible formulation of Eq. (7) guarantees

meaningful parameter estimates. Parameter a_1 , the exponent of cpa, is of twofold interest: If it is not different from 0, cpa is not meaningful for explaining EEX, but it would be directly proportional to Δw . If it is not different from -1 , cpa would not contribute to estimation of biomass production Δw .

For further explanation and examples see "Results". All evaluations were carried out in SPSS, Version 14.0.

Results

Standing biomass and biomass growth in pure and mixed stands

Table 3 displays the key information for the subsequent refined analysis of mixing effects on stand level. The periodical annual above ground biomass production in the pure stands (left) ranges from $p_{sp} = 5.0\text{--}13.4$ ($\text{t ha}^{-1} \text{a}^{-1}$) in the case of Norway spruce and $p_{be} = 3.8\text{--}18.1$ ($\text{t ha}^{-1} \text{a}^{-1}$) in European beech stands. Standing biomass in the pure spruce stand $W_{sp} = 137\text{--}683$ (t ha^{-1}) is rather similar to that of pure beech $W_{be} = 73\text{--}807$ (t ha^{-1}). However, there is a tendency that in FRE 813 European beech is superior while in SON 814 Norway spruce is. Total biomass production of the mixed stands $p_{sp,be}$ (right) ranges from $p_{sp,be} = 7.4\text{--}13.6$ ($\text{t ha}^{-1} \text{a}^{-1}$) and remains more stable with progressing stand development than in the pure stands. In mixture standing biomass ranges from $W_{sp,(be)} = 92\text{--}399$ (t ha^{-1}) in case of Norway spruce and $W_{(sp),be} = 84\text{--}340$ (t ha^{-1}) in case of European beech. Ranging from $W_{sp,be} = 177\text{--}649$ (t ha^{-1}) total biomass is more stable during stand development but not considerably different from the standing biomass of the pure stands. Standing biomass of the mixed stand is used to evaluate the mixing proportions according to $m_{sp} = W_{sp,(be)} / W_{sp,be}$ for spruce and analogously m_{be} for beech. Mixing proportion (above ground biomass Norway spruce:European beech) is $0.53:0.47$ on average and ranges from $0.35:0.65$ to $0.64:0.36$. The biomass production p_{sp} and p_{be} of the pure stands and the species' proportions m_{sp} and m_{be} of standing biomass in the mixed stand (left part of the table) are applied for calculating the expected annual biomass production $\hat{p}_{sp,be}$ following Eq. (1). In six out of nine cases, i.e., in 67% of the observations, we find that total production in the mixed stand exceeds the expected production ($p_{sp,be} > \hat{p}_{sp,be}$). In other words, the mixed stand is superior to the productivity expected from pure stands of the same size. In five out of nine cases (plots FRE 813/6, 4, 3 and SON 814/8, 5), i.e., in 56% of the observations, the productivity of the mixed stand even exceeds the productivity of both pure stands ($p_{sp,be} > p_{sp}$ and $p_{sp,be} > p_{be}$). This indicates a transgressive overyielding, which was hardly

Table 3 Above ground standing biomass and periodic annual biomass production on the plots FRE 813/1-6 and SON 814/1-9

Age series	Plot	Age ^a	Pure stands						Mixed stands					
			N. spruce		E. beech		Total $\hat{p}_{sp,be}$	N. spruce		E. beech		Total $p_{sp,be}$		
			Standing biomass (t ha ⁻¹)	Biomass production (t ha ⁻¹ a ⁻¹)	Standing biomass (t ha ⁻¹)	Biomass production (t ha ⁻¹ a ⁻¹)		Biomass production ^b (t ha ⁻¹ a ⁻¹)	Standing biomass (t ha ⁻¹)	Biomass production (t ha ⁻¹ a ⁻¹)	Standing biomass (t ha ⁻¹)	Biomass production (t ha ⁻¹ a ⁻¹)	Standing biomass (t ha ⁻¹)	Biomass production (t ha ⁻¹ a ⁻¹)
FRE 813	6	42	137	11.6	73	6.8	9.3	92	6.5	84	5.7	177	12.2	
	5	47	166	12.8	362	18.1	–	–	–	–	–	–	–	
	1	49	255	11.3	424	11.6	11.5	142	5.8	263	5.5	406	11.3	
	2	82	358	8.2	807	9.9	–	–	–	–	–	–	–	
	4	93	209	5.0	409	8.5	6.3	285	6.2	161	3.8	446	10.0	
	3	120	337	5.1	358	7.2	5.9	303	4.3	193	3.3	496	7.6	
SON 814	7	55	308	12.3	343	11.5	–	–	–	–	–	–	–	
	4	60	480	13.4	371	11.4	–	–	–	–	–	–	–	
	9	65	517	9.8	330	8.9	9.3	145	3.7	185	5.1	330	8.8	
	8	70	321	9.6	253	8.9	9.3	213	7.1	142	5.0	355	12.1	
	5	90	363	8.7	422	9.6	9.2	242	4.9	340	8.7	582	13.6	
	1	110	683	10.4	392	3.8	7.9	255	4.5	154	2.9	409	7.4	
	2	115	684	6.8	406	7.3	–	–	–	–	–	–	–	
3	120	683	10.4	493	6.9	9.1	399	5.9	250	3.7	649	9.6		

Missing values in the mixed stand section of the table are due to missing mixed plots or unrepresentative small plots (<0.05 ha)

^a Stand age refers to Norway spruce

^b The biomass production of the pure stands p_{sp} and p_{be} (left part of the table) and the species' mixing proportions m_{sp} and m_{be} of standing biomass in the mixed stand (left part of the table) are applied for calculating the expected annual biomass production $\hat{p}_{sp,be} = p_{sp}m_{sp} + p_{be}m_{be}$ which serves as reference for the comparison with mixed stands

ever found in mixed stands of Norway spruce and European beech.

Scrutiny of mixing effects on stand level

In order to assess the relative productivity of Norway spruce compared with European beech we apply the quotient $p_{sp}:p_{be}$, which sets the periodical annual biomass growth of spruce in pure stand p_{sp} in relation to that of beech in pure stand p_{be} . Table 4 displays the results on plot level, age series level, and in total. On the plots FRE 813 productivity of spruce is slightly lower than beech (0.92:1), while SON 814 represents noticeable (but not statistically significant) superiority of Norway spruce (1.31:1). For this and all subsequent quotients we scrutinize via *t* test whether the quotient deviates from 1.0 for plot and age series level; quotients significantly ($P < 0.05$) above and below 1.0 are set in bold numbers.

The quotient $p_{sp,(be)}:p_{(sp),be}$ reflects the productivity of Norway spruce compared with European beech in the mixed stand, where $p_{sp,(be)} = pp_{sp,(be)}/m_{sp}$ and $p_{(sp),be} = pp_{(sp),be}/m_{be}$ are the species specific and area related productivities in mixture. Mixing extends the relation between Norway spruce and European beech to 1.19:1 in the case of FRE 813 and reduce it to **0.91:1** in the case of SON 814.

In other words, the mixture fosters spruce in FRE 813 but beech in SON 814. In total, the relation between spruce and beech amounts to 1.14:1 in monoculture and 1.04:1 in mixture, i.e., it becomes closer, though not significant on level $P < 0.05$.

The quotient $p_{sp,be} : \hat{p}_{sp,be}$ reveals any overyielding by mixing. It sets the observed total biomass production $p_{sp,be}$ of the mixed plots in relation to the productivity of a combination of pure stands of the same size $\hat{p}_{sp,be}$ [cf. Eq. (1)]. We notice an average overyielding by mixing of **1.29** on the plots FRE 813 and 1.14 on the plots SON 814. In other words, the mean productivity increases in the mixture by 29 and 14%, respectively. In total $p_{sp,be}:\hat{p}_{sp,be}$ amounts to **1.21** (Table 4, bottom).

By setting the respective species' area related productivity in mixed stands $p_{sp,(be)}$ and $p_{(sp),be}$ in relation to the productivity in the neighboring pure stand p_{sp} and p_{be} , respectively, we find out which species is responsible for the overyielding in the mixture. The quotient $p_{sp,(be)}:p_{sp}$ ranges from 1.07 to 1.94 on FRE 813 and 0.69 to 1.34 on age series SON 814. In the case of FRE 813 Norway spruce increases the growth in mixture significantly by factor **1.47**. In contrast, the relation $p_{(sp),be}:p_{be}$ amounts to 0.72 to 1.76 and 1.02 to 2.07. In the case of age series SON 814 beech increases the growth in mixture significantly by factor **1.49** on average.

Table 4 Ratios for the comparison of stand level production of pure stands versus mixed stand of Norway spruce and European beech

Meaning of the ratios: $p_{sp};p_{be}$ production of pure spruce versus pure beech; $p_{sp,(be)};P_{(sp),be}$ production of spruce in mixture versus beech in mixture; $p_{sp,be} : \hat{p}_{sp,be}$ observed production in mixed stand versus production expected according to pure stands of the same size; $p_{sp,(be)};P_{sp}$ production of spruce in mixture versus spruce in pure stand; $P_{(sp),be};P_{be}$ production of beech in mixture versus beech in pure stand. All quotients are based on periodic annual biomass production ($t\ ha^{-1}\ a^{-1}$). For further explanation cf. “Methods”

Age series	Plot	$p_{sp};p_{be}$	$p_{sp,(be)};P_{(sp),be}$	$p_{sp,be} : \hat{p}_{sp,be}$	$p_{sp,(be)};P_{sp}$	$P_{(sp),be};P_{be}$
FRE 813	6	1.71	1.04	1.31	1.07	1.76
	5	0.71	–	–	–	–
	1	0.97	1.96	0.98	1.46	0.72
	2	0.82	–	–	–	–
	4	0.59	0.93	1.59	1.94	1.22
	3	0.71	0.83	1.29	1.40	1.20
FRE 813/1-6		0.92	1.19	1.29	1.47	1.23
SON 814	7	1.06	–	–	–	–
	4	1.18	–	–	–	–
	9	1.11	0.93	0.94	0.86	1.02
	8	1.07	0.95	1.30	1.23	1.39
	5	0.90	0.78	1.47	1.34	1.55
	1	2.76	0.93	0.93	0.69	2.07
	2	0.93	–	–	–	–
	3	1.51	0.99	1.06	0.92	1.40
SON 814/1-9		1.31	0.91	1.14	1.01	1.49
Total		1.14	1.04	1.21	1.21	1.37

Size differences between pure and mixed stand trees

In the sequel we apply the arithmetic mean diameter d , crown length cl , cpa , and the above ground tree biomass w for analyzing whether the trees in pure and neighboring mixed stands are equal in size (Fig. 3, Table 5). Any difference in size indicates that trees in pure and mixed stands are in different ontogenetic phases. This would mean, that our comparison on stand level in the last section is flawed, as the neighboring stands are rather at the same physical age, but they represent a diverging development state, as a result of the mixing.

In order to reveal any differences between tree size in mixed and pure stands, we apply ratios which set the tree sizes in mixed stands in relation to corresponding sizes in pure stands. They are of the same type like the quotients we applied in the previous section on stand level (cf. “Nomenclature, relations and variables for analyzing the mixing effect”). Figure 3 reflects, whether the trees in mixed stands are ahead in size compared to members of the same species in the neighboring pure stands. The quadrants in the graphs are divided in sectors with equal size relationship between mixed stand (ordinate) and pure stand (abscissa). Observations on the bisector line reflect equality of mixed and pure stand (quotient = 1.0). Observations above that line, in the sector 1.0–1.1, 1.1–1.2, etc., show superiority of the mixture by 0–10, 10–20%, etc. Observations below the bisector line, e.g., in the sector 0.9–1.0, 0.8–0.9, etc., reflect inferiority of trees in mixed stands. In Fig. 3 and all subsequent graphs Norway spruce is represented by triangles and European beech by circles. Filled

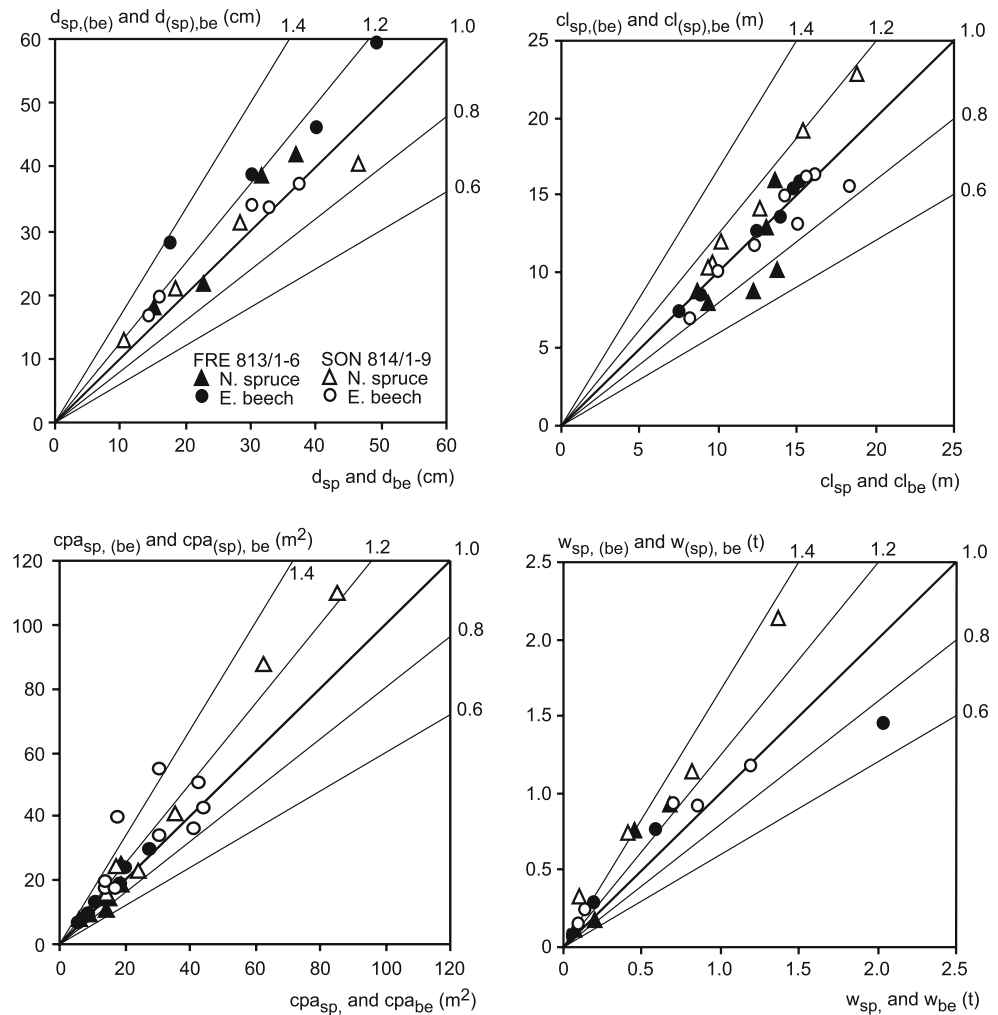
symbols represent age series FRE 813/1-6 and unfilled SON 814/1-9.

Altogether more observations lie above the bisector line than below. In the case of Norway spruce the quotients for d , cl , cpa , and w range between 0.96–1.56, 0.72–1.18, 0.77–1.29, and 0.90–2.97, respectively. Diameter and tree biomass are considerably ahead in the mixed stands, while crown length and cpa of Norway spruce are hardly affected by mixing. In the case of beech the quotients for d , cl , cpa , and w have the ranges 0.87–1.23, 0.84–1.25, 0.94–2.23, and 0.71–1.66, respectively. In addition, Fig. 3 shows that the superiority of mixed versus pure stands increases with size, i.e., the mixed stand trees can even improve their lead with progressing stand development. Table 5, reflects that the size superiorities in mixed stands are not just tendencies but statistically significant ($P < 0.05$) in the majority of the analyzed tree attributes. While in total Norway spruce is especially superior concerning tree diameter and tree biomass (+21 and +64%, respectively), European beech is superior in diameter and biomass (+9 and +27%, respectively) but also in length and projection area of tree crowns (+4 and +29%, respectively).

Crown coverage and stand density in pure and mixed stands

The cpa (m^2) of all $i = 1, \dots, n$ individual trees are applied for calculating the Crown projection Area Index $CAI = \sum_{i=1}^n cpa_i/A$. CAI ($m^2\ m^{-2}$) represents, analogously to the leaf area index LAI , the sum of cpa in relation to area A of

Fig. 3 Comparison between mean tree size in pure stands (*abscissa*) and mixed stands (*ordinate*) of Norway spruce (*triangles*) and European beech (*circles*) with respect to arithmetic mean diameter, *d*; crown length, *cl*; crown projection area, *cpa*; and above ground tree biomass, *w*. *Filled* and *unfilled symbols* represent plots in FRE 813 and SON 814, respectively. *Symbols on or close to the bisector line* reflect an equality of pure and mixed stand mean size; the mean values exceeding the line (>1.0) indicate that mixed stand trees are superior in size, and vice versa



the stand. If CAI amounts to 2.0 the sum of the *cpa* is twice as large as the plot area and each part of the plot would be covered twice by crowns, on average. In pure spruce stands CAI reaches values from 0.5 to 1.5 and in pure beech stands CAI = 1.0–3.0 (Fig. 4). In contrast, CAI values between 1.25 and 2.25 are prevailing in mixed stands. Mixing raises the canopy density compared with pure spruce stands, and reduces it compared with pure beech stands. CAI of mixed stands lies in between the two species in monoculture and remains remarkably stable over a broad range of different ages, mixing proportions and sites. A *t* test of the quotient $CAI_{mixed} \cdot CAI_{pure}$ against 1.0 shows a significant positive effect in the case of spruce ($CAI_{sp,be} : CAI_{sp} = 1.61, P < 0.05$), and a non significant negative effect in the case of beech ($CAI_{sp,be} : CAI_{be} = 0.93$) (cf. Table 6).

For comparison of stand density we apply the SDI by Reineke (1933) $SDI = N_{obs}(25/d_{obs})^r$ and adapted it to the considered species using $r = -1.664$ for Norway spruce and $r = -1.789$ for European beech (Pretzsch and Biber 2005). N_{obs} stands for the observed tree number per hectare

and d_{obs} for the observed quadratic mean diameter. SDI is an age independent density measure and thus appropriate for density studies with respect to age series. In order to make the observed tree diameters and resulting SDI measures of Norway spruce and European beech stands comparable we first standardize them, following the method presented in the “Data and methods”. As explained there, the diameter of beeches was weighted by 1.128 to raise it on the level of Norway spruce.

Figure 5 shows the resulting relation between $\ln(d)$ and $\ln(N)$, which serve as the basis for the comparison of packing densities: Integrating over all plots of FRE 813 and SON 814 the SDI yields (mean \pm SE) $SDI_{sp} = 1123 \pm 83$ for Norway spruce, $SDI_{be} = 971 \pm 72$ for European beech, and $SDI_{sp,be} = 1071 \pm 73$ for the mixed stands. On average the mixed stands’ density is 5% lower compared to the pure Norway spruce stands, and it is by 10% higher than the pure European beech stands. However, variance analysis yields significant differences neither between the pure stands, nor between the pure and the mixed stands.

Table 5 Results for Norway spruce and European beech on FRE 813/1-6 and SON 814/1-9

Age series	Plot	$d_{sp,(be)}:d_{sp}$	$cl_{sp,(be)}:cl_{sp}$	$cpa_{sp,(be)}:cpa_{sp}$	$w_{sp,(be)}:w_{sp}$	$CI_{sp,(be)}:CI_{sp}$	$EEX_{sp,(be)}:EEX_{sp}$
Norway spruce							
FRE 813	1	0.96	0.73	0.77	0.90	1.18	1.22
	2	–	0.72	0.95	–	2.07	1.14
	3	1.14	1.18	1.29	1.37	1.51	0.80
	4	1.22	0.98	0.97	1.63	1.39	1.22
	5	–	0.86	1.24	–	0.76	1.29
	6	1.19	1.00	0.99	1.52	1.24	1.86
FRE 813/1-6		1.13	0.91	1.03	1.36	1.36	1.25
SON 814	1	1.14	1.00	1.15	1.39	0.72	2.11
	2	–	0.96	1.07	–	0.79	1.51
	3	1.20	1.04	–	1.56	–	–
	4	–	0.94	1.14	–	0.81	1.36
	5	1.27	1.04	0.99	1.80	0.90	1.18
	7	–	0.98	1.06	–	1.37	0.82
	8	1.56	–	1.06	2.97	1.25	1.39
	9	–	–	–	–	–	–
	SON 814/1-9		1.29	0.99	1.08	1.93	0.97
Total		1.21	0.95	1.06	1.64	1.17	1.32
Age series	Plot	$d_{(sp),be}:d_{be}$	$cl_{(sp),be}:cl_{be}$	$cpa_{(sp),be}:cpa_{be}$	$w_{(sp),be}:w_{be}$	$CI_{(sp),be}:CI_{be}$	$EEX_{(sp),be}:EEX_{be}$
European beech							
FRE 813	1	1.15	1.18	0.94	1.41	1.29	1.13
	2	–	1.25	1.41	–	0.15	1.36
	3	0.87	1.22	1.29	0.71	0.09	0.98
	4	1.10	1.12	1.16	1.28	0.34	1.54
	5	–	1.11	1.42	–	0.65	0.80
	6	1.23	1.10	1.12	1.66	0.53	1.14
FRE 813/1-6		1.09	1.16	1.22	1.26	0.51	1.16
SON 814	1	1.02	1.00	0.95	1.06	0.79	1.60
	2	–	0.86	1.75	–	0.86	1.14
	3	0.99	1.03	1.15	0.97	0.77	0.97
	4	–	1.04	1.08	–	0.40	1.18
	5	1.11	0.84	2.23	1.31	0.74	2.22
	7	–	0.85	1.22	–	0.76	0.88
	8	1.13	0.99	1.35	1.36	0.62	1.06
	9	1.22	0.95	1.01	1.64	1.03	0.95
	SON 814/1-9		1.10	0.95	1.34	1.27	0.75
Total		1.09	1.04	1.29	1.27	0.64	1.21

Trees size of Norway spruce and European beech in mixed stands in proportion to tree size in the corresponding pure stand. The quotient $d_{sp,(be)}:d_{sp}$, e.g., represents mean diameter of spruce in mixed stand in proportion to mean diameter of spruce in the neighboring pure stand. Such quotients are listed for mean tree diameter d , crown length cl , crown projection area cpa , and above ground tree biomass w

Quotients which deviate significantly from 1.0 are set in bold letters (significance on $P < 0.05$)

Crown efficiency on individual tree level in pure and mixed stands

This evaluation is based on 2,630 Norway spruce and European beech trees which were measured twice: on age

series FRE 813 in the years 1994 and 1999, and SON 814 in the years 1994 and 2004. The 1,686 spruces (797 and 889 trees in pure and mixed stands, respectively) cover a tree age from 37 to 125 years, annual biomass growth $\Delta w = 0.05\text{--}95.9 \text{ kg a}^{-1}$, $cpa = 1.0\text{--}93 \text{ m}^2$, $CI = 0\text{--}52$. Efficiency of

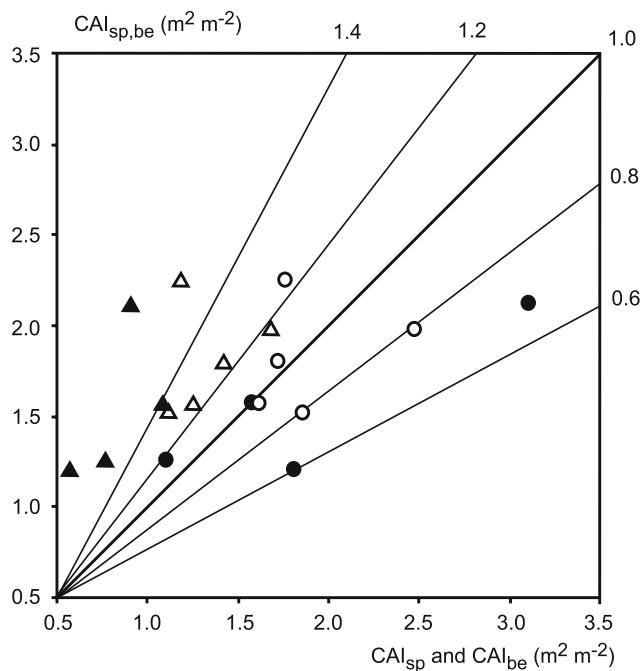


Fig. 4 Crown projection area index of the pure stands (CAI_{sp} , CAI_{be}) of Norway spruce (triangles) and European beech (circles), respectively in comparison to the corresponding mixed stands ($CAI_{sp,be}$). Filled and unfilled symbols represent plots in FRE 813 and SON 814, respectively. Symbols on the bisector line indicate equality of CAI in pure and mixed stands, symbols exceeding the bisector line (>1.0) indicate denser canopies for mixed stands, symbols below reflect denser canopies in pure stands

Table 6 Comparison of the canopy density of mixed stands versus pure stands by means of the Crown area index (CAI)

Age series	Plot	$CAI_{sp,be}:CAI_{sp}$	$CAI_{sp,be}:CAI_{be}$
FRE 813	1	2.31	0.68
	3	1.64	1.13
	4	2.09	0.66
	6	1.44	0.99
FRE 813/1-6		1.87	0.87
SON 814	1	1.26	0.97
	3	1.36	0.82
	5	1.90	1.28
	8	1.26	1.05
	9	1.18	0.80
SON 814/1-9		1.39	0.98
Total		1.61	0.93

Crown area indices of the mixed stands $CAI_{sp,be}$ are set in relation to the CAI values of the corresponding pure stands, separately for Norway spruce CAI_{sp} and European beech CAI_{be}

Quotients which deviate significantly from 1.0 are set in bold letters (significance on $P < 0.05$)

$cpa\ EEX = \Delta w/cpa$ ranges from 0.01 to $4.30\ kg\ m^{-2}\ a^{-1}$. The 944 beeches (455 and 489 trees in pure and mixed stands, respectively) cover a tree age from 45 to 155 years,

annual biomass growth $\Delta w = 0.08\text{--}89.8\ kg\ a^{-1}$, $cpa = 1.8\text{--}151.3\ m^2$, $CI = 0\text{--}23$, and $EEX = 0.01\text{--}1.87\ kg\ m^{-2}\ a^{-1}$.

For both species we find an increase of mean crown efficiency EEX in the mixed stand (Fig. 6, left). In the case of Norway spruce the increase in EEX is coupled with an increase of the CI (right). In contrast, European beech simply benefits from lower CI values in mixture which cause higher crown efficiency EEX. Table 5 shows that in total mean CI of Norway spruce tends to be higher in mixed stands compared with the pure stand ($CI_{sp,(be)}:CI_{sp} = 1.17$), in other words Norway spruce seems to get under higher competitive pressure in the mixed stand. However, the average crown efficiency is by 32% higher compared with the pure stand ($EEX_{sp,(be)}:EEX_{sp} = 1.32$). In contrast, European beech, occupies more favorable positions in the mixed stand compared with the pure stand of beech ($CI_{sp,(be)}:CI_{sp} = 0.64$). Therefore, beech crowns are on average more efficient in the mixed stand than in the pure stand.

For scrutiny of any mixing effects on tree level we fitted Eq. (6) to the individual tree data of Norway spruce and European beech on each plot by linear regression. The model shall reveal whether mixing changes tree crown efficiency under ceteris paribus conditions; i.e., when other decisive factors like size and competition are eliminated. On a trial basis we included other individual tree variables (tree diameter, tree height, crown length) in Eq. (6), however, they did not improve the result significantly.

The results of the regression analysis are presented in Table 7. In case of SON 814/6 and 9 the rows are not complete as in several cases the two pure stand variants are realized but a sufficient number of Norway spruces in mixture are missing. The sample size ranges from $n = 22$ to 347 in the case of spruce and $n = 13\text{--}129$ in the case of beech. In summary in 27 out of 30 cases, that means in 90% of the calculated regressions, the overall model is significant ($P < 0.05$). The overall coefficient of determination is higher for Norway spruce ($R^2 = 0.22\text{--}0.78$) than for European beech ($R^2 = 0.11\text{--}0.71$).

A detailed summary of the statistical results for the parameters a_0 , a_1 , a_2 , and a_3 , respectively, yields a significance ($P < 0.05$) in 50, 53, 87, and 54% of the regression functions. In addition to the plot-wise analyses we pooled the data of all spruces and beeches separately for the age series FRE 813 and SON 814 (not shown in Table 7) and found all parameters individually and also the model as a whole highly significant ($P < 0.001$). However, in the following we apply especially parameter a_3 from the plot-wise analyses for the quantification of mixture effects and use it for further statistical analysis for the complete age series.

Deriving the antilogarithm as in Eq. 7) $EEX = e^{a_0} cpa^{a_1} (CI + 1)^{a_2} e^{a_3 pm}$ facilitates the interpretation of the four included regression parameters. Parameter a_0

Fig. 5 $\ln(N) - \ln(d_g)$ —relationships for pure Norway spruce (*left*), pure European beech (*right*), and mixed stands of Norway spruce and European beech (*below*). As reference line we added the upper boundary line $\ln(N) = 12.5 - 1.664 \ln(d_g)$ for Norway spruce in South Germany according to Pretzsch and Biber (2005)

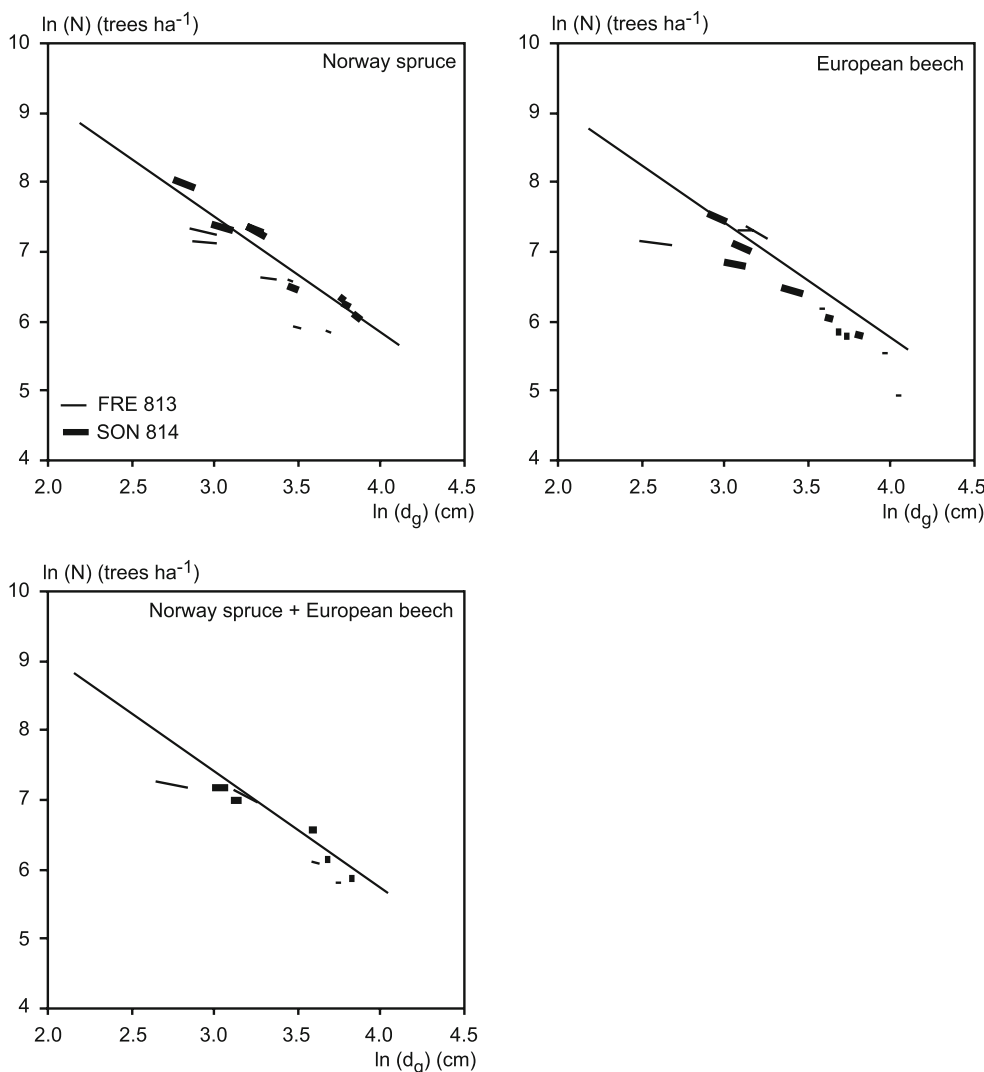
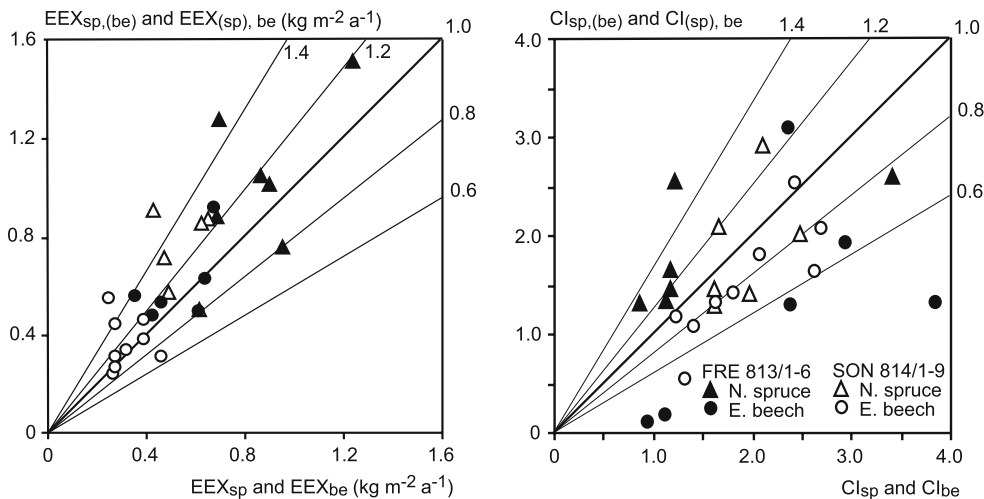


Fig. 6 Comparison of crown efficiency EEX (*left*) and CI (*right*) in pure stands (*abscissa*) with mixed stands (*ordinate*). Triangles represent Norway spruce and circles European beech. Filled and unfilled symbols represent plots in FRE 813 and SON 814, respectively. Symbols on or close to the bisector line reflect an equality of mean tree attributes in pure and mixed stands; the values exceeding the line (>1.0) indicate that mixed stand trees come out higher regarding the analyzed attribute, and vice versa



represents the intercept in the logarithmic model and e^{a_0} describes the crown efficiency in pure stand when $cpa = 1$ and $CI = 0$. Parameter a_1 reflects the effect of crown size on crown efficiency. A value of $a_1 = -0.64$ in the case of FRE

813/1, for instance, means that crown efficiency decreases by 0.64% when crown size increases by 1%. Thereby, a_1 reflects the size dependent ontogenetic drift of a crowns' productivity. A closer analysis of a_1 reveals that it is

Table 7 Results for Norway spruce and European beech on FRE 813/1-6 and SON 814/1-9

Age series	Plot	<i>n</i>	<i>a</i> ₀	<i>a</i> ₁	<i>a</i> ₂	<i>a</i> ₃	mult _{sp}	<i>R</i> ²	p-tail
Norway spruce									
FRE 813	1	105	2.80	−0.64	−2.21	0.41	1.51	0.78	0.00
	2	127	2.79	−0.65	−1.99	0.85	2.33	0.42	0.00
	3	28	4.11	−1.06	−1.96	0.12	1.13	0.72	0.00
	4	35	0.58	−0.03	−1.48	0.52	1.69	0.68	0.00
	5	88	0.86	−0.16	−1.44	0.35	1.43	0.76	0.00
	6	61	0.33	−0.10	−1.95	1.02	2.78	0.66	0.00
FRE 813/1-6							1.81		
SON 814	1	84	1.39	−0.41	−1.30	0.52	1.68	0.33	0.00
	2	154	2.35	−0.58	−1.68	0.19	1.21	0.35	0.00
	3	32	1.68	−0.50	−1.19	0.37	1.45	0.22	0.07
	4	144	1.48	−0.32	−1.56	0.05	1.05	0.34	0.00
	5	70	5.10	−1.44	−2.22	−0.01	0.99	0.32	0.00
	6	22	1.19	−0.51	−0.56	−	−	0.02	0.84
	7	347	1.09	−0.38	−1.68	0.27	1.31	0.33	0.00
	8	98	−0.20	0.15	−0.98	0.35	1.42	0.38	0.00
	9	28	3.03	−0.79	−2.12	−	−	0.64	0.00
SON 814/1-9							1.30		
Total							1.53		
Age series	Plot	<i>n</i>	<i>a</i> ₀	<i>a</i> ₁	<i>a</i> ₂	<i>a</i> ₃	mult _{be}	<i>R</i> ²	p-tail
European beech									
FRE 813	1	82	3.53	−0.88	−2.21	0.06	1.07	0.56	0.00
	2	15	−1.06	0.18	−0.16	0.00	1.00	0.18	0.52
	3	13	3.36	−0.78	−1.30	−0.06	0.94	0.71	0.01
	4	27	0.73	−0.33	−1.36	0.52	1.69	0.49	0.00
	5	57	3.52	−0.71	−2.14	−0.72	0.49	0.45	0.00
	6	129	0.71	−0.19	−1.68	−0.26	0.77	0.50	0.00
FRE 813/1-6							0.99		
SON 814	1	35	1.96	−0.60	−1.70	0.23	1.26	0.28	0.01
	2	41	3.75	−1.02	−1.75	0.11	1.12	0.41	0.00
	3	73	−2.12	0.31	−0.15	−0.35	0.71	0.11	0.04
	4	19	4.75	−1.20	−3.36	−0.39	0.68	0.51	0.01
	5	46	−1.73	0.24	−0.51	0.27	1.31	0.35	0.00
	6	58	0.60	−0.29	−0.62	−0.51	0.60	0.23	0.00
	7	68	−0.84	−0.03	−0.88	−0.01	0.99	0.13	0.03
	8	66	2.78	−0.71	−2.24	−0.61	0.55	0.59	0.00
	9	100	3.01	−1.00	−2.05	0.09	1.09	0.55	0.00
SON 814/1-9							0.92		
Total							0.95		

Species-specific regressions for crown efficiency EEX (kg m^{−2} a^{−1}) in dependence of crown projection area cpa (m²), competition index (CI), and pm where pm = 0 for pure and pm = 1 for mixed stand ($\ln(\text{EEX}) = a_0 + a_1 \ln(\text{cpa}) + a_2 \ln(\text{CI} + 1) + a_3 \text{pm}$)

Most regressions and regression coefficients are significant ($P < 0.05$). Variable mult = e^{a_3} is of specific interest as it reflects whether crown efficient is modified by mixing: mult = 1 means no mixing effect, mult > 1 positive, and mult < 1 negative mixing effect on crown efficiency

positive in the early stage of a tree but becomes negative in subsequent phases. Analogously to a_1 , parameter a_2 reflects the decrease of crown efficiency with increasing competition. Norway spruces on FRE 813/1, for instance, suffer a

2.22% loss of crown efficiency, when CI increases by 1% ($a_2 = -2.22$).

Parameter a_3 is of particular interest for us as it quantifies the effect of mixing on crown efficiency. We use

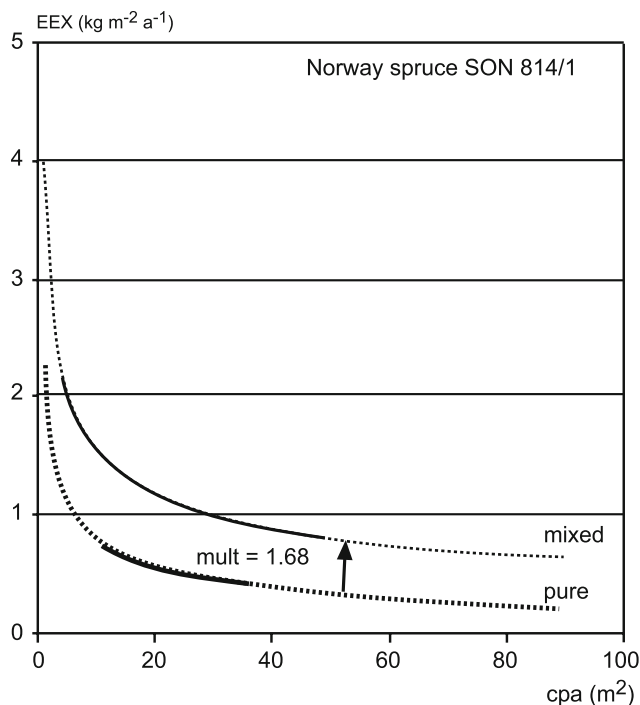


Fig. 7 Principle for the detection of mixing effects on individual tree level by the multiplier $\text{mult} = e^{a_3 \text{pm}}$ [cf. Eq. (6)]. Efficiency of crown projection area EEX for spruce on plot SON 814/1 in dependence on crown projection area according to equation $\text{EEX} = e^{1.39 \text{cpa} - 0.41 (\text{CI} + 1)^{-1.30}} e^{0.52 \text{pm}}$. EEX in pure stand ($\text{pm} = 0$, lower curve) is shifted upwards by $\text{mult} = e^{0.52} = 1.68$ in the neighboring mixed stand where $\text{pm} = 1$ (upper curve). For demonstration CI is set constant to 0.5

Norway spruce on plot SON 814/1 as example for interpreting a_3 (Fig. 7). Linear regression yields $\ln(\text{EEX}) = 1.39 - 0.41 \ln(\text{cpa}) - 1.30 \ln(\text{CI} + 1) + 0.52 \text{pm}$ with $a_3 = 0.52$, thus $\text{mult} = e^{0.52} = 1.68$. The lower curve in Fig. 7 represents EEX depending on cpa in pure stand. For this explanation CI is set constant to $\text{CI} = 0.5$ and represents a dominating tree. The upper curve shows the same

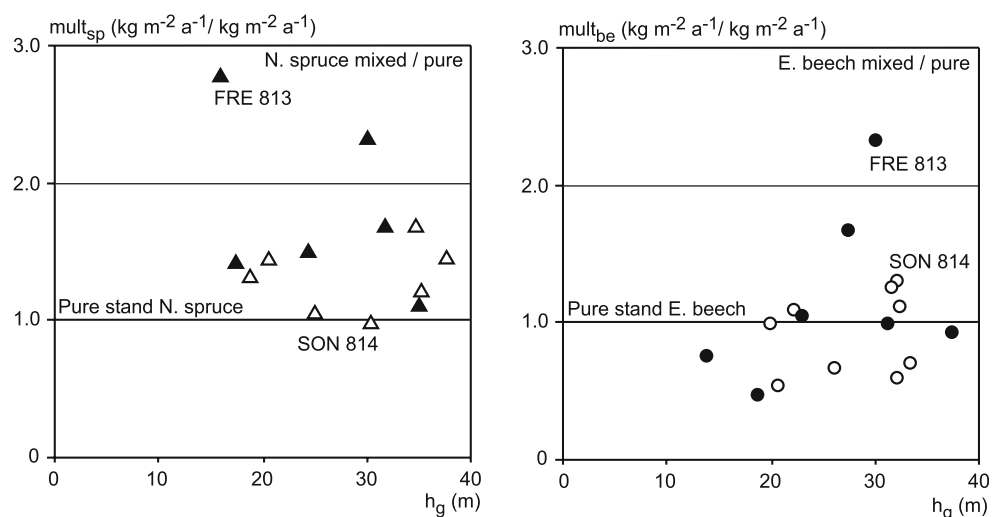
relationship in the neighboring mixed stand. Multiplier $\text{mult} = e^{0.52}$ raises the curve by a factor of 1.68 and indicates that crown efficiency of spruce is increased by 68% via admixture of beech, under ceteris paribus conditions. In Table 7 we display in the column with heading “mult” the multiplier $\text{mult} = e^{a_3}$ which reveals for each plot and species whether positive ($\text{mult} > 1.0$), neutral ($\text{mult} = 1.0$), or negative effects ($\text{mult} < 1.0$) of mixing are detected.

Figure 8 summarizes the mixing effect on crown efficiency ($\text{mult} = e^{a_3}$) for all plots of the age series FRE 813 and SON 814. The plot specific values of mult are depicted in dependence of mean stand height, separately for Norway spruce (left) and European beech (right). When $\text{mult} = 1.0$, crown efficiency in mixed stand equals that in pure stand. In contrast, $\text{mult} > 1.0$ or $\text{mult} < 1.0$ indicates that mixing stimulates or reduces crown efficiency. In the case of Norway spruce (left) mult_{sp} ranges from 1.0 to 3.0 and indicates that positive mixing effects are prevailing. This finding applies for all stand development phases from mean height 15 to 40 m. The positive effect is continuous and independent from the stage of stand development. In the case of European beech $\text{mult}_{\text{be}} = 0.5\text{--}1.5$ (right).

An integrated evaluation yields $\text{mult}_{\text{sp}} = 1.53 \pm 0.14$ (mean and SE) for Norway spruce and $\text{mult}_{\text{be}} = 0.95 \pm 0.09$ for European beech. A *t* test for significant deviation from $\text{mult} = 1.0$ (pure stand conditions) reveals significant positive mixing effects for spruce ($P < 0.001$, $n = 13$). The same test for beech ($P < 0.05$, $n = 15$) results in no significant mixing effects. In accordance to the findings on stand level Norway spruce shows a benefit from mixture on individual tree level, too. Unlike on stand level, crown efficiency of beech shows no positive mixing effect but reacts rather neutral.

We tested the hypothesis, whether the factors mult of Norway spruce and European beech on the plots are

Fig. 8 Multipliers for Norway spruce and European beech (mult_{sp} , mult_{be}) from Table 7 displayed over stand mean height of the corresponding plots for Norway spruce (left) and European beech (right). Symbols above the 1.0-line indicate a positive effect of thinning on crown efficiency, symbols below the 1.0-line reflect a reduction of crown efficiency in the mixed stand compared with the corresponding pure stand. Filled and unfilled symbols represent plots in FRE 813 and SON 814, respectively



correlated with each other. A negative correlation would indicate that an accelerated growth of one of the species reduces the productivity of the other. That might be the effect of their competition for limited common resources. However, correlation coefficient c between mult_{sp} and mult_{be} proved to be not significant ($n = 13$, $c = -0.02$, $P < 0.951$).

Discussion

The following discussion applies to even-aged pure and mixed stands of Norway spruce and European beech on temperate, humid and nutrient-rich sites in pre-alpine South Bavaria, where either of the two champions of European forest ecosystems are at their best. Here, the productive strength of both species is high and rather balanced, so that forest practice cultivates them successfully in mixture. In contrast, most previous studies dealt with site conditions where Norway spruce is superior (Kennel 1965; Spellmann 1996; Wiedemann 1942). However, the 1:1 relation of biomass production of Norway spruce and European beech on our sites is suited best for analyzing both species' behavior under interspecific competition and for revealing of any positive or negative interactions with respect to productivity. As the competition between both species is rather symmetric, the stands represent a key position on the continuous range from warm, dry and base-rich beech-sites to cool, wet and acid spruce-sites and provide key information about this mixture.

The mixing proportion (above ground biomass Norway spruce:European beech) is 53:47 on average and ranges from 35:65 to 64:36. The presented comparison of mixed with pure stands is based on age series of experiments (artificial time series) which grow under "normal" and rather undisturbed conditions. Occurrence of disturbances like wind-throw, ice-breakage, or bark beetle calamities can additionally change the performance of the pure and mixed stand due to a differing resilience after disturbances (Dhôte 2004; Knoke et al. 2005; Pretzsch 2003). We also emphasize, that the analysis includes only the above ground net biomass growth (NG). However, NG is just a part of gross biomass production GPP, and neglects that respiration, transpiration, fructification and turn-over consume plenty of resources and can modify the environmental factors in forests to a considerable extend. (Seifert and Müller-Starck 2008; Rötzer et al. 2008)

Comparability of pure versus mixed on stand level: methodological consideration

On the long run mixing can alter the ontogenetic aging of the trees, the progress of stand development and the shape of the increment curves (Kennel 1965; Mitscherlich 1970,

p. 122; Wiedemann 1942). Supposed a growth curve in the mixed stand is considerably ahead of the adjacent pure stand, so that due to advanced size growth and aging its growth curve increases earlier and higher, but also declines earlier (Fig. 1, left). Then a comparison of the (already) decreasing growth in the mixed stand with the (still) higher growth of the pure stand, e.g., at time t_2 , reflects accumulated differences due to altered aging, rather than differences in productivity between mixed and pure stand under ceteris paribus conditions. The accumulated aging effect can superimpose on a mixing effect or even mask a positive mixing effect, when periodical increment of neighboring stands are compared. The ultimate method to avoid such entanglement is to keep pure and neighboring mixed stands under long-term survey over decades or even centuries. This enables a comparison of the accumulated total biomass production for each of the successive surveys and a differentiated statement of the overall performance of mixed stands compared to pure stands. However, we already stressed, that complete long-term trials in mixed stands are rare and hardly representative in terms of site conditions (Pretzsch 2005; Spellmann 1996). This study was not based on a real long-term time series of successive observations, but on an age series of pure and mixed stands. The age series revealed that the superiority of the mixed stand is not limited on occasional periods, like shown in Fig. 1 (left), but continuous like in Fig. 1 (right). The crown efficiency allowed us to eliminate the size effects and reveal, whether a species is more efficient or not because of mixing under ceteris paribus conditions.

Evidence of overyielding for mixed stands of Norway spruce and European beech compared with pure stands

While monocultures are mostly man-made, mixed stands would frequently be the normal case without influencing forest management. Maybe by keeping species separated in monocultures special traits, potential mutualism, abilities of common and successful resource exploitation remain unused and the potential environmental capacity incompletely exploited. Indeed, our results show that when Norway spruce and European beech are unleashed on each other by mixing, they produce together 1.14–1.29 times the biomass of the corresponding pure stands with the same area (cf. Table 8, $p_{\text{sp,be}} : \hat{p}_{\text{sp,be}}$). Table 8 compiles the revealed mixing effects on stand level, mean tree level and individual tree level in a consistent way. Performance of, e.g., above ground biomass growth, mean diameter, and crown efficiency in mixed stands is divided by the corresponding performance of the species in pure stands. So, quotients greater than 1.0 reflect superiority of the mixed stand, values close to 1.0 reflect equality of mixed and pure stand, and values less than 1.0 indicate inferiority of the

Table 8 Synopsis of the effect of mixing Norway spruce and European beech

	FRE 813	SON 814	Total
Stand scale			
$p_{sp}:p_{be}$	0.92	1.31	1.14
$p_{sp,(be)}:p_{(sp),be}$	1.19	0.91	1.04
$p_{sp,be} : \hat{p}_{sp,be}$	1.29	1.14	1.21
$p_{sp,(be)}:p_{sp}$	1.47	1.01	1.21
$p_{(sp),be}:p_{be}$	1.23	1.49	1.37
$CAI_{sp,be}:CAI_{sp}$	1.87	1.39	1.61
$CAI_{sp,be}:CAI_{be}$	0.87	0.98	0.93
$SDI_{sp,be}:SDI_{sp}$	1.13	0.87	0.95
$SDI_{sp,be}:SDI_{be}$	0.95	1.23	1.10
Mean tree scale			
$d_{sp,(be)}:d_{sp}$	1.13	1.29	1.21
$d_{(sp),be}:d_{be}$	1.09	1.10	1.09
$cl_{sp,(be)}:cl_{sp}$	0.91	0.99	0.95
$cl_{(sp),be}:cl_{be}$	1.16	0.95	1.04
$cpa_{sp,(be)}:cpa_{be}$	1.03	1.08	1.06
$cpa_{(sp),be}:cpa_{be}$	1.22	1.34	1.29
$w_{sp,(be)}:w_{sp}$	1.36	1.93	1.64
$w_{(sp),be}:w_{be}$	1.26	1.27	1.27
Individual tree scale			
$CI_{sp,(be)}:CI_{sp}$	1.36	0.97	1.17
$CI_{(sp),be}:CI_{be}$	0.51	0.75	0.64
$EEX_{sp,(be)}:EEX_{sp}$	1.25	1.40	1.32
$EEX_{(sp),be}:EEX_{be}$	1.16	1.25	1.21
$mult_{sp}$	1.81	1.30	1.53
$mult_{be}$	0.99	0.92	0.95

For key variables on stand level, mean tree and individual tree level the performance of mixture is set in relation to the corresponding pure stand. Values greater than 1.0 reflect superiority of the mixed stand, values close to 1.0 reflect equality of mixed and pure stand, and values less than 1.0 indicate inferiority of the mixed stand. p_{sp} , p_{be} production in pure stands of spruce and beech, respectively; $p_{sp,(be)}$, $p_{(sp),be}$ production of spruce and beech in the mixed stand, respectively; $p_{sp,be}$, $\hat{p}_{sp,be}$ observed and expected production in the mixed stand, respectively

CAI crown area index, SDI stand density index, d stem diameter in 1.30 m, cl crown length, cpa crown projection area, w above ground biomass, CI competition index, EEX crown efficiency, $mult$ mixing effect on crown efficiency

For further explanation of variables cf. “Methods” and “Results”

mixed stand. Concerning biomass production on stand level ($p_{sp,be} : \hat{p}_{sp,be}$) we consider a surplus of 29, 14, and 21% for FRE 813, SON 814, and in total, respectively.

Because the evaluation of mixing effects on productivity is based on the expected production $\hat{p}_{sp,be}$ it always remains questionable to some extent, as it depends on the approach for calculating the mixing proportion [Eq. (1)]. Mixing portions can be based on the species share in standing basal

area, standing volume, basal area or volume adjusted to the species specific wood density, cpa , or above ground biomass (Assmann 1961, pp 351–355). However, our evidence of transgressive overyielding ($p_{sp,be} > p_{sp}$ and $p_{sp,be} > p_{be}$) is rather unambiguous as completely based on measured variables and not on questionable mixing proportions (Table 3). In five out of nine cases the mixed stand produces even more than both corresponding pure stands. We observe a transgressive overyielding which has been reported for other species (Frivold and Frank 2002; Kelty 1992; Mielikäinen 1985) but not for the mixture of Norway spruce and European beech.

While the relationship between biomass production of pure Norway spruce in relation to pure European beech stands is 0.92:1 on age series FRE 813, 1.31:1 on SON 814 and 1:1.14 in total, it reverses to 1.19:1 and 0.91:1, and 1:1.04 in the mixed stand (Table 8). In each case the inferior species, Norway spruce in the case of FRE 813 and European beech in SON 814, benefits considerably from the mixture. The surplus of biomass production in mixture stems from both species, but mainly from the species which is less productive in the pure stand. According to Helms’ (1998, p. 120) definition of mutualism as “...an interaction between the individuals of two or more species in which the growth, growth rate, or population size of both are increased in a reciprocally beneficial association ...”. This definition applies to the interaction of Norway spruce and European beech on the age series FRE 813 and SON 814. So, we can reject any antagonism or just neutral overall effect of mixing. Table 4 rather shows that the benefit from mixing is a significant observation and not only a slight trend. Evidence for transgressive overyielding and mutualism between Norway spruce and European beech was never reported before; however, the presented results seem well-founded as they go beyond previous investigations in the following points.

In contrast to previous investigations on sites more favorable for Norway spruce, we investigated Norway spruce and European beech on sites where their productivity is very good and their productivity is rather balanced, so that positive interactions are very likely. The comparison is based on above ground dry biomass. Previous analysis was restricted on basal area growth (Rothe 1997), volume production (Kramer 1988; Spellmann 1996; Wiedemann 1942), or dry mass production of the stems exclusively (Kennel 1965). The latter comparisons were restricted just to parts of the net stem growth of both species and neglected branches, twigs, and leaves. However, these organs represent a considerable portion of the productivity which differs from species to species (Pretzsch 2006, Pretzsch and Mette 2008). Total above ground biomass production represents as good as possible the contribution of both species to resource exploitation,

carbon allocation and retention and thereby the key for quantification of the mixing effect on productivity. An evaluation with respect to total tree biomass compartments for pure and mixed stand trees and a subsequent comparison of pure and mixed stand with respect to total biomass production (above + below ground) is desirable but the necessary data base not nearly available. We chose two age series for the comparison in order to trace the mixing effect from juvenile to mature stand development phase. As long as a comparison is merely based on one more or less narrow phase of the stand development (Kennel 1965; Mettin 1985; Rothe 1997) it remains hard to judge, whether an observed (positive or negative) mixing effect is continuous or just a temporary phenomenon as a result of a diverging growth rhythm of the considered species in pure and mixed stands (cf. Fig. 1, left). In this study we reveal a permanent overyielding and increase of crown efficiency which substantiate the positive mixing effect (cf. Fig. 1, right).

The few existing complete long-term plots represent mainly typical wet and acid soils favorable for growth of Norway spruce (Pretzsch 2005). In contrast, here we analyze two types of sites where productivity of spruce and beech is more balanced and which represent site conditions where forest planning frequently decides to establish a mixture of spruce and beech newly or to transform pure Norway spruce stands into mixed stands.

Causal explanation

Explanation means tracing a phenomenon observed on one scale to the scale of next higher resolution. In our case findings on stand level can be substantiated by tree level analysis. Individual tree analysis revealed that crown efficiency of Norway spruce is raised by 81 and 30% in FRE 813 and SON 814, respectively (cf. mult_{sp} , Table 8). Under ceteris paribus conditions (i.e., equal size, equal CI) Norway spruce produces more biomass with a given supply of radiation, due to the mixing. According to Rothe (1997), Wiedemann (1942, 1943), and Mettin (1985) we speculate that beech fosters crown efficiency of Norway spruce. Unlike the shallow roots of Norway spruce searching closely below the surface, the root system of European beech reaches further down to better supplied soil layers (Bolte and Villanueva 2006; Rötzer et al. 2008; Schmid 2002; Schmid and Kazda 2002). A part of the scarce nutrients (nitrogen, phosphate, calcium, potassium) are transferred to the stand parts stocked with European beech by means of leaf shedding in autumn. This transfer is the more beneficial for Norway spruce, the more intensive it is spatially intermingled with European beech. The finding, that the positive effect on growth of Norway spruce on the site in FRE 813 (suboptimal for growth of Norway spruce) is higher than in SON 814 (optimal for Norway spruce) appears plausible.

The more the photo-production is limited on a given site by shortage of nutrients, the clearer is the increase of efficiency after better supply of the limited resource (Körner 2002, p. 928; Schulze et al. 2002; p. 359). In addition, nutrient supply might be improved in the mixed stand, as soil temperature and mineralization are superior to pure stands (Rothe 1997; Wiedemann 1942). Especially in fall and spring, when European beeches are leafless, radiation reaches deep into the stand and stimulates decomposition processes. On the one hand existing crowns assimilate more carbon, due to the increased crown efficiency. On the other hand the compensation point of photoproduction probably shifts to the left, as mineral nutrients either are incorporated in enzymes and pigments, or activate directly the process of photosynthesis (Larcher 2003; pp 134–136). So, a lower radiation supply can yield already a positive net production. Consequently the crown density and leave area index might be increased. As result, Norway spruce grows quicker so that in total mean diameter and mean tree biomass are 21 and 64% ahead of their fellows of the same age in the neighboring pure stand (cf. $d_{\text{sp,(be)}}:d_{\text{sp}}$ and $w_{\text{sp,(be)}}:w_{\text{sp}}$, in Table 8). Crown length *cl* and *cpa* hardly differ between pure and mixed stands. So, in the case of Norway spruce, the increased production on stand level goes along with an accelerated size growth on tree level.

European beech behaves completely different. Its productivity on stand level is much higher in mixture compared with pure stands (cf. $p_{(\text{sp}),\text{be}}:p_{\text{be}}$ in Table 8). But beech's crown efficiency is hardly affected by the mixture (cf. mult_{be} in Table 8). It even decreases slightly to 0.99, 0.92, and 0.95 in FRE 813, SON 814, and in total, respectively. Thorough analysis of the CAI, crown length, *cpa* and *CI* reveals that European beech occupies the available space in an omnipresent way (Table 8). Crowns are not more efficient, but they are larger, more scattered and in better positions compared with the pure European beech stand. Under interspecific competition they use their ability to penetrate and occupy crown space with relative low biomass investment (Pretzsch 1992; Pretzsch and Schütze 2005) and they can fill niches due to their sit-and-wait strategy, which are heavily contested under intraspecific competition in the pure beech stand (Pretzsch 2005). In summary, the overyielding of European beech is an effect of multi-layering, adaptation, gap dynamic and high efficiency of space occupation.

Ecological implications

The study objects are artificially established stands on sites, where European beech would dominate without human influence. Also on the pre-alpine sites of SON 814 Norway spruce would play just a minor role. The artificial combination of both species ranges from individual-tree mixture

over groups to larger clusters (Fig. 2). It results in a mutual stimulation and acceleration of growth. Norway spruce increases its crown efficiency and growth maybe as a result of an improved nutrient supply via European beech. European beech also increases growth in the mixed stand. In order to keep up with Norway spruce it brings to bear its outstanding capacity of space occupation. Both, Norway spruce and European beech, benefit from the mixture and produce mostly more above ground biomass than the neighboring pure stands. Regarding growth and yield, the mutual benefit of both species in symbiosis gives evidence for mutualism (Begon et al. 1998, pp 329–355). Kelty (1992) distinguishes between “competitive reduction” (i.e., two or more species have reduced competition in mixture compared to pure stands) and “facilitation” (i.e., in mixture one species affects positively the growth of another species). On our mixed plots European beech benefits from “competitive reduction” as interspecific competition is less severe than the intraspecific contest in the pure European beech stand. Norway spruce on the other hand benefits from a continuous “facilitation” by European beech as this species probably improves the mixed stands nutrient supply by deeper soil exploitation, higher turnover, and activation of the humus layer (Rothe and Binkley 2001).

For forest management the revealed mutual promotion of the species and resulting overyielding is highly relevant. It shows how to increase or even maximize the level of growth and yield during a given rotation period. However, the considered mutualism concerning growth and yield must be temporary. Because seen in the long term and including alternation in generations, European beech would dominate and rather outcompete Norway spruce on the considered sites. While increase of above ground production, acceleration of size growth and ontogeny are helpful traits for maximization of growth and appreciated by forest management, they are not at all sufficient for a superior fitness of individuals, long-term selection success and dominance of a species in a community. For long-term success the adaptability to wait in the understory, efficient gap dynamic, ability to survive under disturbances, and tricks to poison or even impede awkward neighbors are indispensable. In this view, the mutualism concerning yield is practically relevant but limited in its long-term effect. Beech promotes spruce and keeps it as a “softer” competitor than members of the same species, but only to prove that European beech is finally stronger due to superiority in space occupation. Maybe under natural conditions European beech enables Norway spruce to reach from the alpine and mountainous zone down to the pre-alpine, sub-mountainous and plain regions occasionally and isolated. Improvement of nutrient supply via beech, increase of water use efficiency enable growth and reproduction, where it hardly would be possible without the support of beech. However, pure Norway spruce

stands could not develop here naturally due to the overwhelming competition of beech.

Previous investigations addressed mostly sites, where the relative productivity of both species is rather unbalanced. Assmann (1961) and Kennel (1965) considered a relation between biomass production of Norway spruce and European beech up to 2:1. On our plots the ratio is much closer to 1, so that both species have the chance to make use of all their traits and growth-based competitive strategies acquired by co-evolution. The vertical and fast growing Norway spruce profits from the asymmetric above ground competition. But among all other indigenous species European beech shows the best adaptation to asymmetric competition for light (Roloff 2001). In addition European beech is well adapted for successful contest below ground, where competition is rather symmetric. Beech has access to deeper soil layers. So Norway spruce appears as a less rigorous competitor to European beech than trees of the same species. Exactly that seems to be the benefit of beech: release from intraspecific competition and interspecific competition instead. According to Lyr et al. (1967) European beech uses water more efficiently for biomass production. Especially in view of increasing water limitation caused by climate change, topsoil rooting by Norway spruce is more risky than subsoil rooting by European beech and means higher susceptibility to drought (cf. Schmid 2002; Bolte and Villanueva 2006).

Conclusions

By tracing the mixing effect from stand to individual tree level we found out, that the species benefit from the mixture has different causes and therefore also lead to different silvicultural implications. In mixture Norway spruce shows a continuous growth acceleration of the individuals. So the same amount of crown space enables more growth as crown efficiency is raised. This is equivalent with a rise of the site index or at least the yield level. As the underlying cause is a physiological increase of efficiency, this benefit is independent from stand density and may be even accelerated by thinning. The benefit of European beech is a reaction to crowding and an adaptation to the spatial characteristics of the mixed stand. Promotion of selected spruces by thinning will on the one hand direct its benefit from mixing on a restricted number of trees. On the other hand it will stimulate beech’s omnipresent space filling strategy furthermore and keep or even increase its surplus due to mixing. Mean tree sizes are further ahead in mixed stands and stem numbers per hectare are lower, so that the production losses due to a multitude of inefficient subdominant and suppressed trees and the necessity of tending and thinning are lower, too.

Individual tree models should consider that mixture changes the crown efficiency of Norway spruce due to a change of site conditions on small patches. European beech develops traits and strategies hardly observed in pure stands, where intraspecific competition and self-thinning is more rigorous compared with other species (Pretzsch 2006). So, in mixture new interactions emerge: increase of physiological efficiency here, stimulation of structural adaptation there. When individual tree models are parameterized for pure stands and extrapolate to mixed stands without integration of interaction effects, they neglect these effects. The view should be just the other way around. The mixed stand is the field where species developed and show their strategies and traits; in pure stands these characteristics might be hidden. Long-term experiments and age series covering different site conditions can help to quantify and subsequently integrate mixing effects in models. Appropriate approaches are site-specific modifiers affecting crown efficiency, growth rates, and tree allometry.

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