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Aboveground productivity of pure and mixed Norway spruce and European beech stands

Susanne Sprauer[1] · Jürgen Nagel[1]

Abstract The aim of this study was to compare increment in mixed stands to the respective pure stands adopting, as an example, mixed stands comprising Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.). Using data from two mixed stand age series, in the Solling and in Harz Mountains, first we investigated whether the growth reduction effect arising from competing trees is dependent on the species of the competitors. We than explored whether increment predictions from the forest growth simulation package TreeGrOSS revealed differences between pure and mixed stands and, if so, what factors play a role and what may cause these increment differences. The analysis was based on a simulated trial series in which the parameters such as percentage mixture, age, site quality class, and stocking level were varied. The results indicate that neighboring Norway spruce restrict the basal area increment of both European beech and Norway spruce more than European beech competitors with the same crown cross-sectional area. In the majority of cases, the simulation produced an increment gain in mixed stands compared with pure stands. The amount of increment gain in a mixed stand depended on the percentage mixture, age, site quality class, and stocking level and could be related to changes in stand structure and their effects on aboveground competition.

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Introduction

Based on numerous mixed stand trials in Central Europe, in which Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) are grown, both in pure stands and in various mixtures, Pretzsch et al. (2010) were able to show that the increment of dry wood in mixed stands compared with pure stands ranged from −46 to 138 %. Their results show that site is a major determining factor of whether mixed stands are more productive than the corresponding pure stands. Many studies of growth in Norway spruce–European beech mixed stands have investigated the question broadly at the stand level (Kennel 1965; Pretzsch and Schütze 2009; Pretzsch et al. 2010) or compared single trees in pure and mixed stands (Sterba et al. 2002). However, effects related to the growth constellation of individual trees, e.g., the species of a tree's neighbors, may also be a cause of gain in or loss of production. Therefore, to understand growth in mixed stands, more detailed analyses than those afforded at the stand level are required (Dieler and Pretzsch 2012).

At tree level, competition may influence the productivity in pure and mixed stands. Biber (1996) showed that the crown of a neighboring Norway spruce restricted the growth of Norway spruce and European beech more than a same-sized crown of a neighboring European beech. In competitive interactions belowground, fine rooting of European beech may be facilitated when growing next to Norway spruce due to reduced competitive pressure compared with a European beech neighbor (Bolte et al. 2013).

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It has been suggested that Norway spruce in mixture with European beech benefits from improved nutrient availability, especially on poor sites due to nutrient uptake of European beech in deeper soil layers and improved litter characteristics (Rothe 1997; Pretzsch et al. 2010). Another mixture effect at stand level may arise from a more shallow rooting system of Norway spruce found in some mixed stands with European beech compared with pure stands (Schmid and Kazda 2000; Schume et al. 2004) and a higher transpiration rate of European beech trees compared with Norway spruce (Hietz 2000; Schume et al. 2004). This may result in lower water availability in dry periods (Rothe 1997) and reduced nutrient uptake of Norway spruce in mixture with European beech compared with pure stands. However, such effects at stand level were excluded in this study to reveal effects at tree level.

In this study, based on the data from Norway spruce–European beech mixed stands, we investigated firstly whether the species of neighboring trees, apart from other differences arising as a result of species-specific crown size, affects the basal area growth of single trees. Thus, we analyzed whether species-specific competition is revealed, which tree species benefits from or is inhibited by which neighboring species in their growth, and how large the differences in the competition effects of each are.

Then, with the forest growth simulation package Tree-GrOSS (Nagel 1999; Hansen and Nagel 2014), we tested whether a gain in or loss of increment occurred in mixed stands compared with the sum of the corresponding pure stands at the stand level, that is whether total increment is larger in mixed stands than in spatially separated stands of both species with the same total area. Here, we also investigated whether the consideration of species-specific effects of competition leads to essential differences in the simulation package predictions at the stand level. As both species have different growing space requirements and as the growing conditions are essentially dependent on the arrangement of crowns in the three-dimensional crown space, it is difficult to determine whether an increment gain or loss can be expected in mixed stands when using growth functions at the single-tree level. Therefore, this question was investigated with the assistance of simulated trial series of pure and mixed stands. These simulated trials should help determine, at the single-tree level, what factors in the immediate neighborhood of individual trees might cause a higher relative productivity in mixed stands. The advantage of simulated trials over experimental sites is that essential factors, such as diameter distribution and tree size, can be set constant in pure and mixed stands, whereas, in trial plots, these factors often diverge over the course of experiment or are difficult to control. Furthermore, in simulations it is possible to vary several potential influence factors, which would be virtually impossible in a real trial

due to the large area and extensive resources required. The literature reports a wide range of increment gains and losses in mixed stands of Norway spruce and European beech compared with corresponding pure stands (Pretzsch et al. 2010). We investigate whether stand age, site quality, and stocking level influence the productivity of mixed as compared to pure stands and thus can help to explain the differences found in relative productivity of mixed stands.

Methods

The first step was to investigate whether the effect of competing trees on the increment of European beech and Norway spruce was dependent on the species of a competing tree (species-specific competition effect). Then, the increment in mixed stands was investigated using the forest growth simulation package TreeGrOSS, and subsequently, the potential causes of an increment gain or loss compared with the sum of the corresponding pure stands were elaborated with the assistance of the simulated experiments.

Species-specific competition effects

Data from two mixed stand age series from the Northwest German Forest Research Station were used to investigate the effects of species-specific competition. They comprised six sites in the Solling and five sites in the Harz Mountains which were measured three times at 5-year intervals and which permitted the calculation of basal area increment (BAI) for single trees. The sites consisted of different age classes (Table 1). The species mixture (by basal area) varied from a European beech percentage of 24–73 %. Norway spruce trees were dominant in height, sometimes to a considerable extent. The sites are described in more detail in Biber (1996).

In the forest growth simulation package TreeGrOSS, the BAI is represented as a function of the crown surface area (CSA), age (age), competition index ($C66$), and a thinning release index ($C66c$):

$$BAI = e^{(p_0 + p_1 \ln(CSA) + p_2 \ln(age) + p_3 C66 + p_4 C66c)} \qquad (1)$$

where p_0–p_4 are the model parameters to be estimated. The competition index of a tree (reference tree) is calculated as sum of crown cross-sectional area (CCA) of all trees in the zone of influence (circle around the tree with a diameter twice the crown width) at a height ($h66$) corresponding to 66 % of the crown length of the reference tree from the tree top. Thus, each competing tree is weighted by the CCA at height $h66$ lying within the zone of influence. Shares in CCA outside the zone of influence are not taken into account. Trees lower in height than the $h66$ of the reference tree were not included, whereas the entire crown projection

Table 1 Summary of the mixed stand data used at the time of the first survey (white—values from the Solling age series, gray—values from the Harz Mountains age series)

Plot number	European beech					Norway spruce			
	BA[a] [%]	Age [years]	BA [m²/ha]	QMD[b] [cm]	H$_m$[c] [m]	Age [years]	BA[a] [m²/ha]	QMD[b] [cm]	H$_m$[c] [m]
95650200	24	41	6.9	10.9	12.4	31	21.0	16.4	14.2
95750200	56	46	15.7	11.7	14.1	37	11.8	22.1	16.5
95850200	35	73	11.2	24.1	23.6	68	20.6	35.5	27.0
95950200	43	85	14.1	25.1	23.1	85	18.2	40.2	27.6
96050200	38	122	15.0	32.3	28.3	117	24.3	47.0	32.5
96150200	73	127	24.2	46.5	32.7	124	8.8	56.8	34.9
96250200	41	33	7.0	8.5	9.4	33	9.8	16.9	12.6
96350200	46	58	17.5	18.2	17.5	52	18.2	26.3	20.2
96450200	29	69	12.8	15.1	16.7	58	30.9	29.4	22.4
96650200	59	130	17.6	41.1	29.0	130	11.8	51.7	32.1
96750200	37	165	14.9	40.4	27.7	142	24.8	51.5	33.6

[a] Basal area

[b] Quadratic mean diameter at breast height

[c] Height of the mean basal area tree

area inside the zone of influence was considered for trees whose crown base was above *h66* of the reference tree. For trees at the edge of the stand, the value was corrected by considering that part of the influence zone falling within the stand (*F*) (Hansen and Nagel 2014). By considering species-specific crown sizes, the size-related differences in the competition effects between the species were described. To investigate any further differences, the competition index was calculated separately for European beech (number: n_{be}) and Norway spruce (number: n_{sp}):

$$C66_{\text{be}} = \frac{1}{F} \sum_{i=1}^{n_{\text{be}}} \text{CCA}_i \quad \text{and} \quad C66_{\text{sp}} = \frac{1}{F} \sum_{j=1}^{n_{\text{sp}}} \text{CCA}_j \qquad (2)$$

Thus $C66_{\text{be}}$ describes the competition arising from neighboring European beech and $C66_{\text{sp}}$ that from neighboring Norway spruce. By using these species-specific competition indices, the following relationships for the estimation of the BAI of European beech (BAI$_{\text{be}}$) and Norway spruce (BAI$_{\text{sp}}$) were derived, respectively:

$$\text{BAI}_{\text{be}} = e^{\left(p_0 + p_1 \ln(\text{CSA}) + p_2 \ln(\text{age}) + p_{3\text{be}} C66_{\text{be}} + p_{3\text{sp}} C66_{\text{sp}} + p_4 C66c\right)}$$
$$(3)$$

$$\text{BAI}_{\text{sp}} = e^{\left(p_0 + p_1 \ln(\text{CSA}) + p_2 \ln(\text{age}) + p_{3\text{be}} C66_{\text{be}} + p_{3\text{sp}} C66_{\text{sp}} + p_4 C66c\right)}$$
$$(4)$$

Then, we checked whether the model coefficients of the species-specific competition indices were significantly different from zero and thus the indices significantly

affected BAI, and whether differences in the competition effect of the two species as implied by their model coefficients occurred. As an alternative to logarithmic age, the logarithmic tree height (*h*) was tested as a predictor, and the model (including age on the one hand or height on the other) explaining the larger proportion of the total variance was chosen.

As the data set included a number of plots, a mixed model was adapted, which, in addition to the explanation variables, also considered random effects at the trial plot level. The model fit was conducted with the statistics package R (R Development Core Team 2009) and the library mgcv (Wood 2006).

Increment in mixed stands

In the second step, the relative increment gain or loss in mixed stands with different percentage mixtures compared with the combination of pure stands was estimated with the growth model in the simulation package TreeGrOSS. Two variants were tested: the standard variant with the unchanged growth model from TreeGrOSS and an alternative variant with a modified version of the growth model which took into account the different competition effects of Norway spruce and European beech (see above).

In this investigation, increment in the volume of merchantable timber (>7 cm dbh) in pure and mixed stands was used as a measure of the productivity of the stands.

The relative productivity of the mixed stands compared with pure stands was derived from the ratio of the total productivity in the mixed stand to the sum of the productivities of the pure stands on the same total area, weighted by the respective percentage mixture.

Generation of stands

To investigate possible competition effects, 13 trial series were generated, i.e., defined (Table 2) to simulate their growth in a next step. The trials differed in relation to age, site quality class, and stocking levels, where site quality class is indicated by Schober's yield classes I–III and stocking level describes the actual basal area of a stand divided by its basal area from the yield table with moderate

thinning (Schober 1987). For each of these 13 trial series, 21 stands were generated with the simulation package: both a European beech and a Norway spruce pure stand as well as mixed stands with percentage mixtures in 5 % classes (each 5–95 %). For a mixed stand with a percentage mixture of 50 % of both species, each species was assumed to have half the basal area of its respective pure stand. In addition to the parameters varied for the purpose of the investigation (age, site quality class—indicated by yield class—and stocking level), for every stand—separated by species if relevant—the basal area, quadratic mean diameter, height of the mean basal area tree, and the maximum diameter were necessary to generate a diameter distribution. These parameters were extracted from the yield tables (Schober 1987) or estimated by the authors in

Table 2 Starting values of the trial series for the simulation of mixed European beech–Norway spruce stands

Trial series	Species	Yield class	Age (years)	H_m^a (m)	BA^b (m²/ha)	QMD^c (cm)	D_{max}^d (cm)	Stocking level
1	beech	I	50	17.6	21.6	12.9	16.8	1.0
	spruce	I	50	21.2	38.7	19.3	25.1	1.0
2	beech	I	75	25.6	27.8	23.0	30.0	1.0
	spruce	I	75	28.6	45.8	28.8	37.4	1.0
3	beech	I	100	31.4	31.0	33.6	43.4	1.0
	spruce	I	100	33.3	48.3	37.6	48.9	1.0
4	beech	II	75	22.0	26.8	20.2	26.3	1.0
	spruce	I	75	28.6	45.8	28.8	37.4	1.0
5	beech	III	75	18.4	25.9	16.8	21.8	1.0
	spruce	I	75	28.6	45.8	28.8	37.4	1.0
6	beech	III	75	18.4	25.9	16.8	21.8	1.0
	spruce	II	75	24.5	42.2	24.6	32.0	1.0
7	beech	III	75	18.4	25.9	16.8	21.8	1.0
	spruce	III	75	20.1	38.1	19.4	25.2	1.0
8	beech	I	75	25.6	27.8	23.0	30.0	1.0
	spruce	II	75	24.5	42.2	24.6	32.0	1.0
9	beech	I	75	25.6	27.8	23.0	30.0	1.0
	spruce	III	75	20.1	38.1	19.4	25.2	1.0
10	beech	I	75	25.6	22.2	23.0	30.0	0.8
	spruce	I	75	28.6	36.6	28.8	37.4	0.8
11	beech	I	75	25.6	16.7	23.0	30.0	0.6
	spruce	I	75	28.6	27.5	28.8	37.4	0.6
12	beech	II	75	22.0	26.8	20.2	26.3	1.0
	spruce	II	75	24.5	42.2	24.6	32.0	1.0
13	beech	II	75	22.0	26.8	20.2	26.3	1.0
	spruce	III	75	20.1	38.1	19.4	25.2	1.0

[a] Height of the mean basal area tree

[b] Basal area

[c] Quadratic mean diameter at breast height

[d] Maximum diameter at breast height

case of the maximum diameter. Within a given trial series, the same starting values were used.

Simulation of pure and mixed stands

The standard version of TreeGrOSS package includes a statistical, semi-distance-dependent single-tree growth model for Northwest Germany. The model's height and diameter growth functions for European beech and Norway spruce were parametrized using a large database of experimental plots of the Northwest German Forest Research Station. Height increment is modeled by potential height growth (a function of age and site index) and a modifier function which reflects tree height in comparison with stand top height. Diameter increment is estimated directly by a function of CSA, age, crown competition, and thinning release (Eq. 1). Diameter increment is also indirectly influenced by site index, because CSA is larger on better sites at the same age. For further details, see Hansen and Nagel (2014).

The TreeGrOSS package was extended to include an additional method that generates model stands sequentially for the trial series (Fig. 1) and simulates, i.e., forecasts, these for the duration of a simulation step (5 years). The forecast was carried out for every stand using the standard method in the simulation package and with the assistance of a new Java class which considered species-specific competition effects (using the BAI models according to

Eqs. 3 and 4). Forest operations were not simulated; therefore, the thinning release was set to zero. From the beginning and end stands, volume increment was calculated for the tree species and the total stand. Each simulation was repeated ten times because of the stochastic elements in the simulator. The results indicate the mean values of each of the simulation scenarios conducted.

Results

Species-specific competition

The results of the model fit showed that, with the exception of the thinning release index, all model parameters were significantly different from zero ($p < 0.001$). For Norway spruce, the model including age described the BAI better than the model including tree height instead. A larger part of the variance in the European beech model, in contrast, was explained by height. Both models were reparameterized without the thinning release index so that all the remaining variables had a highly significant influence on the BAI of European beech and Norway spruce (Table 3). The proportion of variance explained by the model amounts to 0.59 for Norway spruce and 0.63 for European beech.

For both tree species, CSA affected BAI positively, whereas age and height were found to have a negative effect. The effect of the separate competition indices for
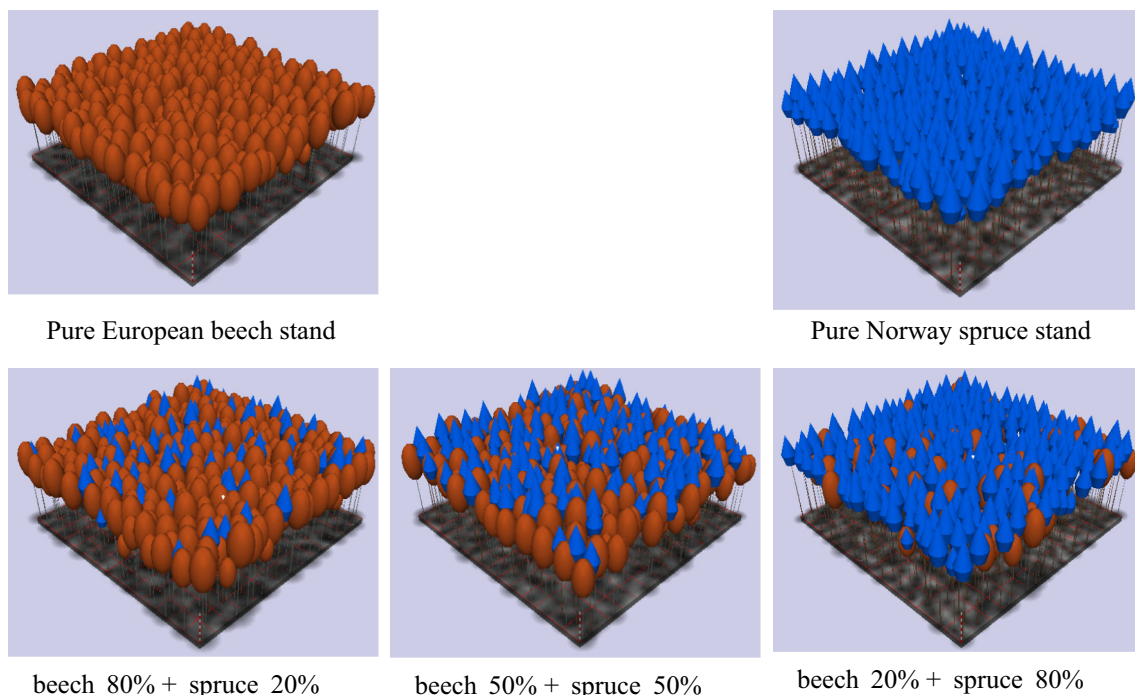

Pure European beech stand

Pure Norway spruce stand

beech 80% + spruce 20%

beech 50% + spruce 50%

beech 20% + spruce 80%

Fig. 1 Pure and mixed stands in the growth simulation package TreeGrOSS

Table 3 Results of the model fit (parameter estimates ± standard error) for data from the Norway spruce–European beech mixed stand age series

	Norway spruce model	European beech model
p_0: intercept	4.75417 (±0.25)	1.54416 (±0.12)
p_1: ln(CSA)	0.99934 (±0.03)	0.97163 (±0.02)
p_2: ln(age)	−0.91135 (±0.06)	
p_2: ln(height)		−0.46741 (±0.06)
p_{3be}: competition European beech	−0.70106 (±0.06)	−0.39999 (±0.02)
p_{3sp}: competition Norway spruce	−1.09982 (±0.07)	−0.67592 (±0.04)

All parameters were significantly different from zero ($p < 0.001$)

European beech and Norway spruce was negative. The coefficients indicate that BAI of European beech and Norway spruce was more affected by neighboring Norway spruce than by neighboring European beech.

From the estimated model parameters, competition-weighting factors were derived. This showed that the CCA of neighboring European beech, with a factor of $p_{3be}/p_{3sp} = 0.64$, had less influence on the BAI of Norway spruce and, with a factor of $p_{3be}/p_{3sp} = 0.59$, less influence on the increment of European beech than a neighboring Norway spruce with the same CCA. Thus, in the analysis of growth in mixed stands, this means that a Norway spruce profited from interspecific rather than intraspecific competition. In contrast, the growth of a European beech was inhibited more by interspecific competition than by competition from trees of the same species. The CCA of a Norway spruce affected European beech growth by a weighted factor of $p_{3sp}/p_{3be} = 1.69$.

Increment in mixed stands

The results of the simulations for each trial are presented in Figs. 2, 3 and 4. The increasing percentage of European beech from 0 % in pure Norway spruce stands to 100 % in pure European beech stands is shown on the abscissa, and the relative productivity of the entire stand (black), the Norway spruce (light gray) and European beech (dark gray) is plotted on the ordinate. Here, the productivity of each of the pure stands was scaled to 1. When the productivity of a tree species in the mixed stand is identical to that in a pure stand, we expect the relative productivity of the species in the mixed stands to lie on a line between 0 (pure stand of the other species) and 1 (productivity in pure stand) (dotted line). If the values lie above this line, then a positive effect of the species mixture occurs, that is the productivity in the mixed stand is higher. Conversely, values lying below the line indicate a negative effect of species mixture, hence a lower productivity than in pure stands. For the total stand, the relative productivity is one if the productivity of both species in the mixed stand corresponds to that in the pure stands or if the positive effect of the mixture on one

species compensates for the negative effect on the other (dotted line). If the productivity of the total stand lies above or below one, this shows relative productivity of the mixed stand is higher or lower than the combination of the pure stands, respectively. The values of the solid lines were obtained from the simulation with the standard model and those with the dashed lines from the simulation including species-specific competition effects.

The results of trial series 1–3 show the influence of age on relative productivity (Fig. 2). For the underlying stands, the starting values for both tree species were based on yield class I, and a stand age of 50, 75, and 100 years were selected. For Norway spruce, a clear positive effect of the stand mixture was evident at age 50 years. In stands aged 75 years, this effect was lower, and for the simulation of a 100-year-old stand, it was merely marginal. For European beech, no clear trend was evident. Using the standard model, an increment gain resulted in all three stand ages due to species mixture. However, in the simulation with a species-specific competition calculation, either no gain in increment or even an increment loss was observed.

Overall, the results showed that an increment gain was obtained in the mixed stands in the simulated trial series, due initially to the marked increment gain of Norway spruce and later, in older stands, relied increasingly on the increment gain of European beech in the standard variant. The increment gain declined with age. With increasing percentage of European beech, the increment gain increased initially, reaching a maximum when similar proportions of European beech and Norway spruce were reached, and then declined as the percentage of European beech continued to increase.

The results of the simulation variant with the additional consideration of species-specific competition effects differed from those from the standard model: For the relative productivity of Norway spruce, the differences between the two competition calculations increased with age. Yet, the growth curves showing the species-specific competition effects lay above the standard variant curves as expected, meaning the standard model tends to underestimate the gain in productivity due to the mixture. For European beech, the differences between the results of both
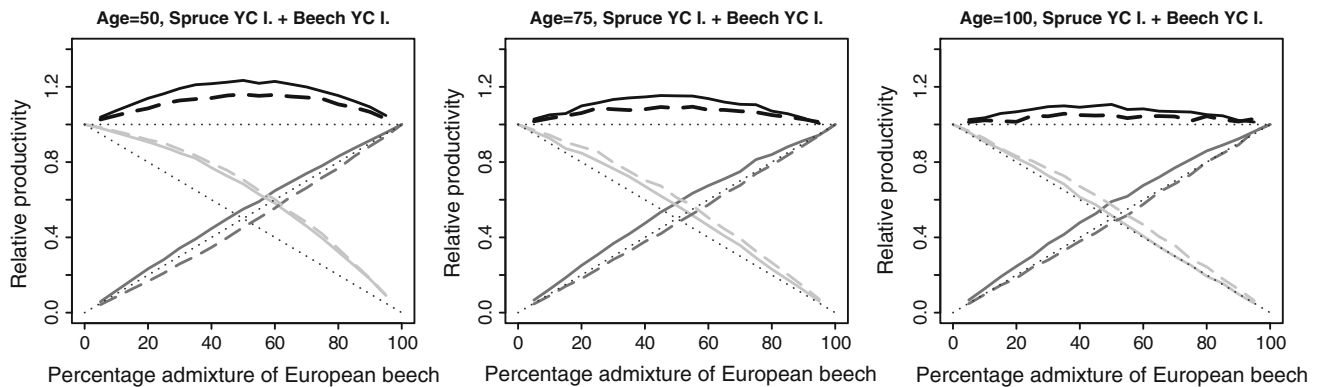
Fig. 2 Relative productivity by increasing percentage mixture of European beech at different ages in the simulated trial series 1–3. Legend: *black* = relative productivity of the total stand, *dark gray* = relative productivity of European beech, *light gray* = relative productivity of Norway spruce calculated with the standard model (*solid line*) and the weighted competition (*dashed line*). *Dotted lines* = reference line, equal productivity in pure and mixed stands

competition calculations were considerably larger than that in the case of Norway spruce. The consideration of species-specific effect of competition led to a marked reduction in relative productivity compared with the standard model.

On the basis of the 75-year-old trials series in which site quality class differed, an investigation of the influence of site quality class of both species on the relative productivity was conducted. The results showed that, depending on the percentage mixture, European beech in mixed stands achieved a steady increment gain in the standard variant on most sites regardless of site quality class, whereas the variants including species-specific competition effects produced virtually no increment gain or loss compared with the pure stand (Fig. 3). The relative productivity of European beech increased on favorable sites (yield class I) only when the growing conditions of the site were clearly poorer for Norway spruce (yield class III) as shown in the left subfigure of the bottom row in Fig. 3.

Norway spruce reacted more sensitively to different site conditions than European beech. Essentially the relative productivity of Norway spruce increased in mixed stands with increasing site quality class for Norway spruce and decreasing site quality class for European beech. In cases in which the site quality class for European beech was greater than for Norway spruce, a negative effect of the species mixture on Norway spruce productivity was found. Compared to the standard variant, consideration of the species-specific competition effects resulted in a higher relative productivity for Norway spruce.

The total relative productivity was positive for most trial series. The exceptions were Norway spruce yield class II together with European beech yield class I, as well as Norway spruce yield class III together with European beech yield class II. In these cases, the increment gain in European beech did not compensate for the

increment loss in Norway spruce, so that, for total productivity, a negative effect of species mixture was revealed. If the conditions for Norway spruce worsened further still (European beech yield class I, Norway spruce yield class III), this led to an enhanced positive effect of species mixture on European beech, which then overrode the increment loss of Norway spruce so that an increment gain resulted for the total stand in both simulation variants.

The relative productivity of the trial series was also influenced by stand density (stocking level) (Fig. 4). The positive effect of the species mixture in the trial series with yield class I for both European beech and Norway spruce declined as the stocking level decreased. In this case, the positive effect of species mixture of both species was affected. At a stocking level of 0.6, only a minimal positive species mixture effect could be detected.

Discussion

Species-specific competition effects

In this study, we used the competition index *C66* to describe competitive effects on BAI of Norway spruce and European beech. It reflects species-specific differences in lateral crown size in terms of CCA and possible differences between intraspecific and interspecific competitor spacing. Thus the model coefficients for Norway spruce and European beech competition in the BAI models (Eq. 3 and 4) can be interpreted as follows: A Norway spruce competitor exerts a greater competitive pressure than a European beech competitor at the same distance with equal CCA, meaning that Norway spruce competitors limit growth of both Norway spruce and European beech more than European beech

competitors. We suppose that this is due to Norway spruce crowns usually extending to greater heights than European beech crowns and thus reducing light availability of neighboring trees more than lower European beech trees. Other studies in mixed and pure stands of Norway spruce and European beech confirmed a superior growth of Norway spruce in mixed as compared to pure stands (Kennel 1965; Rothe 1997). The increment gain in mixed stands was attributed to superior height of Norway spruce compared with

European beech and thus better social status of Norway spruce in mixed stands (Kennel 1965). Similarly, Rothe (1997) concluded that the increment gain of Norway spruce due to mixture results from differences in competition for light between Norway spruce in mixed and pure stands and that other growth factors (water, nutrients and temperature) play a minor role.

The differences in species-specific competition effect found in this investigation are in concordance with Biber's
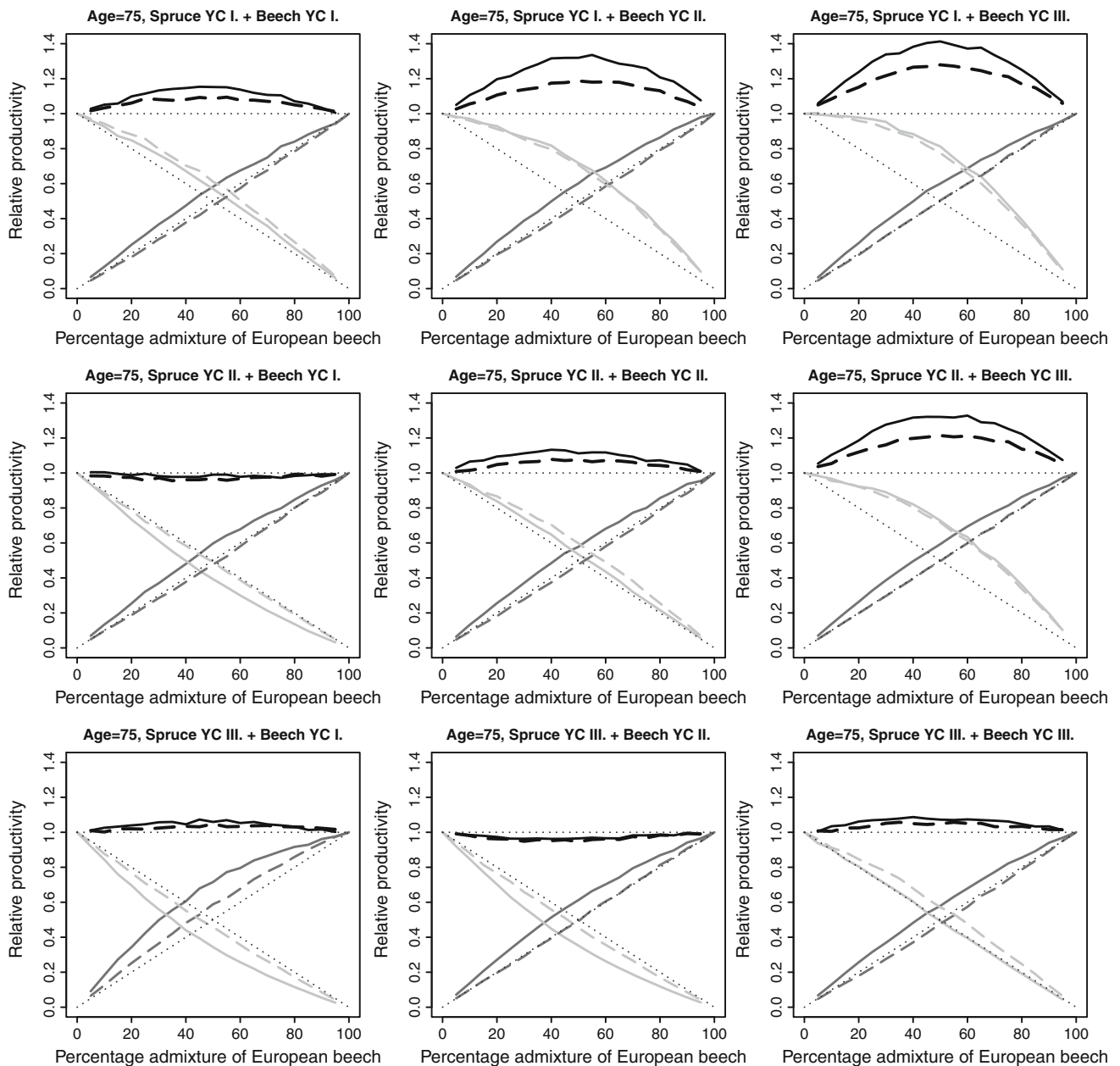

Fig. 3 Relative productivity of the simulated trials series by increasing percentage mixture of European beech in relation to yield class for European beech (increasing from *left* to *right*) and yield class for Norway spruce (increasing from *top* to *bottom*). Legend: *black* = relative productivity of the total stand, *dark gray* = relative

productivity of European beech, *light gray* = relative productivity of Norway spruce calculated with the standard model (*solid line*) and the weighted competition (*dashed line*). *Dotted lines* = reference line, equal productivity in pure and mixed stands
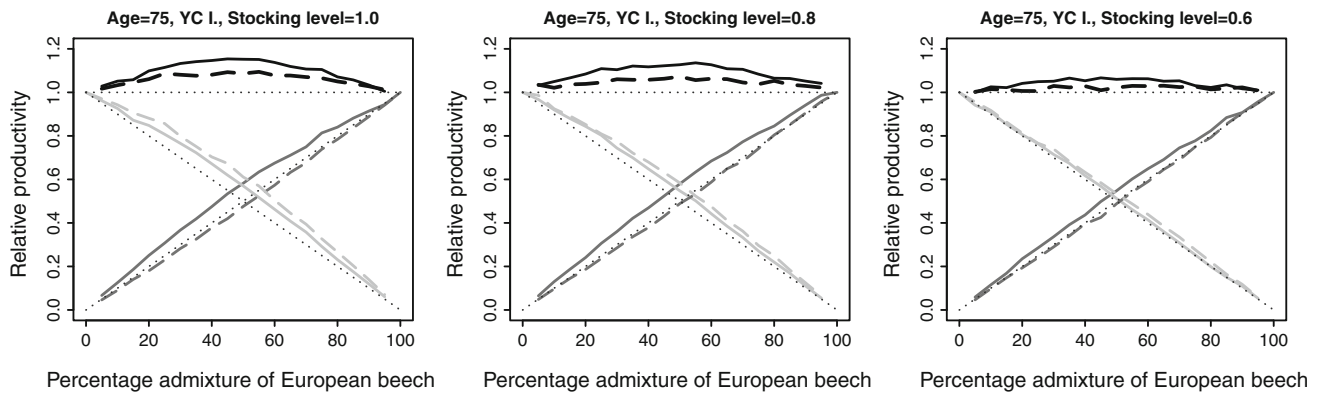
Fig. 4 Relative productivity by increasing percentage mixture of European beech for decreasing stocking in the simulated trial series 2, 10, and 11. Legend: *black* = relative productivity of the total stand, *dark gray* = relative productivity of European beech, *light gray* = relative productivity of Norway spruce calculated with the standard model (*solid line*) and the weighted competition (*dashed line*). *Dotted lines* = reference line, equal productivity in pure and mixed stands

(1996) results as he also discovered that Norway spruce neighbors restricted the BAI of European beech and Norway spruce more than European beech neighbors. At sites with similar productivity for both species, European beech was disadvantaged by the direct competition from Norway spruce, whereas depending on its social class, Norway spruce could benefit from a European beech neighbor (Grundmann 2009).

However, these findings seem to be limited to situations where the height of Norway spruce exceeds the height of European beech, and therefore, the increment gain of Norway spruce due to mixture depends on site characteristics and age of the two species. Examples for seemingly contrary results were found on fertile sites (Pretzsch et al. 2010) and for younger stands (Sterba et al. 2002) where growth of Norway spruce was reduced in mixture with European beech as compared to pure stands. But as these results originate from comparison of pure and mixed stands, it is well possible that effects at tree level like differences in competition for light are overlain by effects at stand level such as reduced water supply in mixed stands with European beech (e.g., Rothe 1997).
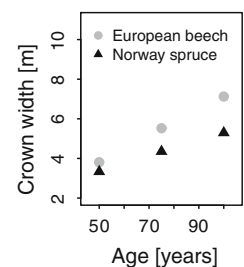
Increment in mixed stands

On the basis of predictions with the growth simulation package TreeGrOSS, results prove that a higher relative productivity can be obtained in mixed as compared to pure stands as Pretzsch et al. (2010) claimed. The effect of the species mixture was evident in the standard variant as well as in some of the trial series in which species-specific competition effects were considered.

Given similar starting values for age and tree size, the relative productivity of a mixed stand declines with age on sites affording both tree species favorable conditions. This

decline is due primarily to the reduction in the relative productivity of the Norway spruce component, while the relative productivity of European beech remains relatively constant with age. The European beech increment gain arising from the species mixture in the standard variant can be explained in relation to the CCA of both species, which was determined in the simulation using the crown width function from Hansen and Nagel (2014). For the simulated trial series presented (yield class I for Norway spruce and European beech), the crown width, and therefore the CCA of European beech, lies above that for Norway spruce at all ages (Fig. 5). According to the competition calculation from the simulation, at a given age and for the same crown height, a Norway spruce contributes less to the total competition value $C66$ of a reference tree than a European beech. If, however, the species-specific competition effect is considered in the simulation, then the increase in productivity due to the smaller CCA of neighboring Norway spruce trees compared with European beech neighbors is overcompensated by their higher species-specific competition effect, so that sometimes even a small negative mixture effect on European beech results.

The increment gain in Norway spruce at all the ages considered arises from the reduction in competition occurring because the European beech competitors are

Fig. 5 Crown width of European beech and Norway spruce at 50, 75, and 100 years, each based on the diameter and height of the mean basal area tree for yield class I (Schober 1987)

smaller in height than the Norway spruce competitors. Sterba et al. (2002) assume a similar effect in older mixed stands and explain the increment gain in Norway spruce with European beech neighbors over those with Norway spruce neighbors by the lower European beech trees and the consequent improved light conditions for Norway spruce. With increasing age, the height difference diminishes due to differences in the height growth dynamic of the two species with Norway spruce reaching its maximum growth earlier than European beech (cf. Table 2). With decreasing height difference, the advantage to Norway spruce from European beech neighbors over Norway spruce neighbors declines. This explains the decrease in Norway spruce increment gain arising from the species mixture with age.

In addition to age, yield class—as an indicator of the site conditions—also influences relative productivity in mixed stands. The combination of assumed site quality classes may, in part, be theoretical (Norway spruce yield class I. with European beech yield class III. etc.), but they assist the investigation of principle relationships. The simulation results show that, largely irrespective of site conditions, the European beech component in the simulated mixed stand produces a slight increment gain in the standard variant and, when species-specific competition effects are considered, shows virtually no mixture effects. The effect of mixture increases slightly on good European beech and simultaneously poor Norway spruce site in both variants. Here, too, European beech benefits presumably from lesser lateral crown expansion of Norway spruce compared with European beech. An additional positive effect occurs when European beech is superior in height to Norway spruce. In the combination European beech yield class I- Norway spruce yield class III, the mean height of European beech is 25.6 m, whereas that of Norway spruce is only 20.1 m. In this case European beech benefits more still from the lower height of Norway spruce neighbors compared with European beech neighbors. In the variant that considers species-specific competition, there is nearly no mixture effect on productivity of European beech over a wide range of site conditions, whereas productivity of Norway spruce is clearly influenced by the combination of site quality classes. This relative constancy of production under different conditions might be attributed to the high morphological plasticity of European beech and its ability to adapt to conspecific and heterospecific neighborhoods. European beech is well known for highly plastic crowns (Schröter et al. 2012) and studies in mixed and pure stands showed that crown morphology varies depending on species mixture (Dieler and Pretzsch 2013). European beech was also shown to alter morphology and distribution of fine roots in heterospecific as compared to conspecific neighborhoods (Bolte and Villanueva 2006; Bolte et al. 2013).

In contrast, Norway spruce responds more sensitively to site differences than European beech. In particular, height difference between the two species appears to play a role. For example, if, as a result of the site conditions or the site quality class of both species, Norway spruce is superior in height (cf. Table 2), then an increment gain results from the species mixture: the greater the height advantage of Norway spruce, the larger the increment gain. However, if Norway spruce is overshadowed by European beech, then a negative mixture effect on Norway spruce results. This effect is explained by the reduced competition from lower neighbors and increase in competition from neighbors that are dominant in height, respectively.

For the whole stand, the simulated results reveal a positive relative productivity for most trial series. Generally, as the relative productivity of European beech is largely independent of site conditions, the greater the height advantage of Norway spruce over European beech, the higher the relative productivity.

The simulated trial series, which differ in relation to stocking levels, show that the effect of species mixtures decreases for both species with decreasing stocking. This appears feasible because mixture and species of the neighbors influence the competition index in this simulation study. If competition is lower, then the differences between the situation in pure and mixed stands, and hence the productivity differences, are smaller.

Our results show that productivity of European beech and Norway spruce is influenced by species-specific traits of competitors. Local stand structure changes depending on the species composition due to variation in height, inter-tree spacing, and lateral crown size. The standard model reflects species-specific differences in spacing and lateral crown size by applying a sensitive competition index. However, the results show that there are other species-specific traits of competitors that influence growth of European beech and Norway spruce. It is important to identify the underlying factors to come to a more comprehensive understanding of mixed stands. Furthermore, neglecting these differences causes the simulation of mixed stands to underestimate Norway spruce productivity and to overestimate European beech productivity to an even greater extend.

Through the investigation of simulated stands whose essential characteristics are kept constant, it is possible to elaborate the influence of the individual neighboring species on the growth of a reference tree in isolation and to understand better how its growth is affected by age, site quality class, and stocking. However, in the process, other parameters are ignored, which in reality can enhance, dominate, or interact with the effects mentioned. Thus, belowground processes such as the competition for water and nutrients play a role as well as differences between pure and mixed stands at the stand level. The latter

includes, for example, possible changes in nutrient and water availability through the species mixture (Pretzsch et al. 2010). Furthermore, the history of the stand is also ignored and, hence, the fact that pure and mixed stands can develop differently from the outset. In this study, a single-tree mixture was adopted for the generation of the mixed stands. Thus, for other types of mixtures (i.e., group-wise), smaller mixture effects can be expected because, possibly, larger stand areas may occur in which trees are mainly surrounded by neighbors of the same species.

When comparing the productivity of actual mixed stands to the combination of corresponding pure stands across a broad spectrum of site conditions, in the majority of cases Pretzsch et al. (2010) found, in concordance with the results of this simulation study, an increment gain in mixed stands compared with pure stands. The extent of increment gain or increment loss they found, on average $+0.51$ (-7.23 to $+11.06$) m^3/ha/year, was well above the values obtained in this study, which ranged from -0.7 to $+5.2$ m^3/ha/year in the standard variant and from -0.1 to $+4.7$ m^3/ha/year in the simulation including species-specific competition effects. However, in relation to the influence of site on the mixture, the results deviate. Whereas the results of this simulation study suggest that an increase in the effect of species mixture with site quality class for Norway spruce can be expected, their results indicate declining mixture effects as the site quality class for Norway spruce improves. Conversely, in the simulation, the mixture effects tended to decrease with increasing site quality class for European beech, whereas Pretzsch et al. (2010) report increment gains particularly for good site quality class for European beech. These differences in relation to the effect of site show just how complex the analysis of the effect of species mixtures on productivity is and suggest that many factors play a role which overlie one another and possibly even interact.

In summary, the following points need to be emphasized:

(1) Assuming the same CCAs, Norway spruce benefits, as shown by its BAI, when subjected to competition from surrounding European beech trees rather than its own species. In contrast, European beech growth is restricted more by the CCA of neighboring Norway spruce than by neighboring European beech trees.

(2) Simulations with the forest growth package Tree-GrOSS show that the predicted growth in mixed stands differed from that in the pure stands both with and without the tree species-specific competition effects.

(3) Results show that a considerable relative increment gain can be explained by changed stand structures in

mixed stands and their effect on aboveground competition.

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