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Growth–density relationship in mixed stands – Results from long-term experimental plots

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ABSTRACT

Forest management mainly controls wood growth through the regulation of stand density. Knowledge of the growth–density relationship is based on numerous studies in pure stands. Currently, in times of more climate plasticity and more nature-oriented forests, silviculture with mixed stands is demanded of forest policy. It is well known that the competition mechanisms in mixed stands are different to those of pure stands. Hence, the question arises for forest managers whether the regulation of density must be different, too.

In an attempt to answer this question, we investigated 481 stand surveys from 124 long-term experimental plots of European beech stands, mixed with conifers and also broadleaf trees. With generalized additive models, we estimated the influence of the density on stand volume growth and how it changed with stand development and shade tolerance of the admixed species. The density of the mixed stands was given on a relative scale. 100% density took into account the maximum species-specific density plus a mixed stand specific addition.

We found that mixed stands have a constant growth level in the medium- to high-density phase (70–100%). Although we have tried to take into account the higher density in mixed stands, 10% of the stands outperformed the 100% benchmark and exhibited a growth gain in this over-dense phase (>100%). Finally, the growth-density response resembles a cubic function with a saddle or optimum between medium- to high-density phase and an increase of growth in the low-density and the over-density phase. The inclusion of stand development led to the oblation of the growth–density response in younger ages. The admixture of shade-intolerant species with beech caused a more intensified cubic course of the relationship.

Finally, we could show that a short-term decrease of the density also has an effect on growth. In terms of growth, weak thinnings are better than severe thinnings. Thinnings from above have a significant positive effect on growth, especially for longer observation periods of up to 10 years.

We concluded that mixed stands need an adapted thinning compared to pure stands. Regular, weak thinnings from above with a very high stand density enables maximum volume growth gains in European beech mixed stands. We could show that the growth-density relationship is conceptually different to pure stands, because mixing effect causes density section above 100%. However, the study emphasizes the need for a systematic experimental setup for a better understanding of intraspecific interactions at different densities.

1. Introduction

Stand density steering is among the most important silvicultural measures, of similar significance as species selection, stand regeneration, or initial spacing (Nyland, 2016). In contrast to these measures, density steering occurs continuously throughout the whole stand development. It thus affects a whole range of ecological, economic, and socioeconomic ecosystem factors and functions (Cao et al., 2008; del Río et al., 2017). Numerous studies have therefore analyzed measures for stand density quantification (Reineke, 1933; Zeide, 2005), techniques of density reductions by thinning (Nyland, 2016, p. 406), stand growth reactions to thinning (Mäkinen and Isomäki, 2004a, 2004b), and basic principles of growth–density relationships (Assmann, 1950; Curtis et al., 1997; Langsæter, 1941; Zeide, 2001). One of the most important

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findings was the uniform growth–density relationship and its dependence on tree species, site conditions, and stand development phase (Pretzsch, 2009, p. 410). Most of the studies were related to monospecific and even-aged stands. Analogous research into mixed stands and their response to density reduction is rare (Puettmann et al., 1992) but urgently needed in view of the increasing importance and occurrence of mixed-species stands (Forest Europe, 2015). Research into monospecific stands provides suitable measures for density and growth density quantification that may be useful and adaptable to mixed stands.

However, essential differences are found in mixed stands which directly influence the above-mentioned principles and reveal the need for additional investigation of thinning in mixed stands. The over-density of mixed vs. monospecific stands (Pretzsch and Biber, 2016) appears to be one of the most influential differences of the growth–density relationship. At the very least, the higher density in mixed stands as independent variable results in a displacement or a dilation of growth curve in comparison to growth-density relationship of pure stands. If a tree species is mixed with different species, the different mixing types have different maximum densities (Shaw, 2006; Woodall et al., 2005). This is a result of the different ecological traits and space requirement of the species (Andrews et al., 2018; Assmann, 1954). Therefore, we decided against using basal area or relative proportion to unthinned stands as a benchmark, but apply a relative density measure, which based on maximum densities of the mixed species in pure stands plus a mixing type specific addition which is derived by pure and mixed experimental plots of a former study (Pretzsch, 2019).

Stand growth as the independent variable is influenced by the mixing type. Larocque et al. (2013) described how competition, facilitation, and complementarity mechanisms form the mixing effect. The ecological traits of species and the site define which mechanism occurs in order to achieve the limiting resource (Forrester, 2014). Facilitation and complementarity can result in overyielding in those stands, and stem distance is inevitably a parameter which triggers this interaction (Forrester et al., 2013).

Overyielding also changes over the development of the stand (Binkley, 2003; Thurm and Pretzsch, 2016). The growth of an individual tree is related to its diameter (Badoux, 1949; Kahn and Pretzsch, 1997) and so the diameter distribution of a stand influences stand growth. Pure stands initially show a narrow and right-skewed distribution. As the stand develops, the distribution becomes more and more symmetrical and Gaussian-shaped (Prodan, 1965). Mixed stands form a greater inequality in diameter distribution (del Río et al., 2016; Liu et al., 2002) and the inequality increases with the development of the stand. Therefore it is important to take age into account, too.

In addition, it must be considered how the size distribution will be regulated. Thinning experiments are the traditional experimental setups to investigate the growth–density relationship. They include different thinning regimes and usually manage the size distribution from above (crown thinning) or from below (low thinning). The changed size distribution in mixed stands will thus react differently to management regulations.

To investigate the growth–density relationship, the thinning experiments were established as long-term experimental plots. This is necessary to avoid over- or underestimation, which might occur in short-term setups (Pretzsch, 2020a). The rapidly increasing number of mixed stand studies of recent years have applied different methods to investigate the mixing effect (del Río et al., 2016; Vanclay, 2006). Long-term experimental setups including mixed and the respective pure stands are limited (Binkley, 2003) and only a few contain different density grades (Puettmann et al., 1992).

This paper analyzes some of the above-mentioned topics, based on the data of 124 long-term experimental plots in mixed-species stands across Germany. With knowledge gained from pure stand experiments, we will discuss the differences to mixed stands and derive recommendations for their regulation.

Our null hypothesis is that growth in mixed stands responds as growth in pure beech stands. We hypothesize that: 1) Low-density (<70%), high-density (95–100%), and over-dense (>100%) stands achieve lower annual stand volume growth than medium-density stands (70–95%). 2) The development of this growth–density relationship is reduced as the stand develops, visible by increasing stand age and mean diameter at breast height. 3) The mixture of beech with tree species with different light requirements does not lead to a changed growth–density relationship. 4) Despite the changed structure and density of mixed stands, thinnings from above do not lead to a change in growth.

2. Material and methods

2.1. Data

To test our hypotheses, we analyzed 124 long-term experimental plots in northern and southern Germany. The plots are at about 20 to 1,240 m above sea level, with mean annual temperatures between 5.5 and 8.0 °C and annual precipitation of 597 to 1,347 mm (Table 1). The plots represent the growing behavior of European beech (*Fagus sylvatica* L.) in the distribution center of its realized niche (see Fig. 1).

The stands were even-aged high forest systems as well as all-aged selection systems. Almost 50 percent of the stands were based on natural regeneration. European beech was admixed in all stands with an average proportion of 36.9% (Table 2). We included six mixing types in our analysis, where European beech is mixed with a) Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), b) Scots pine (*Pinus sylvestris* L.), c) sessile or pedunculated oak (*Quercus petraea* (Mattuschka) Liebl.; *Quercus robur* L.), d) European larch (*Larix decidua* Mill.), e) Norway spruce (*Picea abies* (L.) H.Karst.), and f) spruce and silver fir (*Abies alba* Mill.). The stands were established in two- or in the case of spruce/fir/beech in three-species stands. Additional species were however to be found in the plots in very small proportions (Prop = 15%, see Table 2). Growth data of these minor species were added to the main tree species that was ecologically closest.

To calculate the growth parameters of the stand after DESER-Norm (Johann, 1993) diameter at breast height of all tree and tree height at a representative collective of tree were measured with an average interval of 7 years (e.g. Pretzsch, 2009). The oldest measurement comes from 1934. However, 90% of the measurements were collected since 1982. In the end we had 481 stand surveys to work with.

2.2. Calculation of density and mixing proportion

The calculation of the mixing proportion and consequently the stand density is not simple in forest stands with multiple tree species (Dirnberger and Sterba, 2014). At first, you have to consider the intraspecific growing-space requirements of the different admixed species (Vospernik and Sterba, 2015). In a second step, you have to take into account that the mixture of species can increased the maximum stand density in comparison of the respective pure stands (Pretzsch and Biber, 2016). To consider both effects, we used an approach in which density based on the species-specific maximum stand density in pure stands plus a mixed stand specific addition (see also Pretzsch and del Río, 2020).

The first step of density calculation is the standardization of the species-specific densities. Therefore, we calculate the relative density of each admixed species to what would be expected in respective, fully stocked pure stand. The maximum stand density for one species (species1) in pure stand is based on the relation between its quadratic mean diameter at breast height (Dg) and its stem number per hectare (N), $\ln(N_{species1.max}) = a + b \ln(Dg_{species1})$ (Reineke, 1933). For the analysis, we used the species-specific coefficient a and b derived by a study by Pretzsch (2019, see Supplementary material S1). The ratio between current stem number ($N_{species1}$) and the maximum stem number of a species ($N_{species1.max}$) results in its species-specific, relative density $Dens_{species1} = N_{species1} / N_{species1.max} * 100$.

The second step would be to consider that the achievable density in

Table 1
Climatic summary of the 124 experimental plots. Climate data based on Wordlclim2.0 (Fick and Hijmans, 2017).

Mixing type	Temperature (°C)			Precipitation (mm)			Experimental Plots	
	Mean	Min	Max	Mean	Min	Max	Plot Number	Survey Number
Douglas-fir/ E.beech	7.9	7.7	8.0	973	921	1040	6	26
E.larch/ E.beech	8.2	8.2	8.2	597	597	597	1	2
N.spruce/ E.beech	7.0	5.6	8.1	1107	796	1347	35	139
N.spruce/ S.fir/ E.beech	6.5	5.0	8.2	1234	792	1339	33	151
Oak/ E.beech	7.9	6.3	8.8	874	688	1333	36	129
S.pine/ E.beech	8.1	7.5	8.4	808	766	879	13	34
Summary	**7.3**	**5.0**	**8.8**	**1031**	**597**	**1347**	**124**	**481**

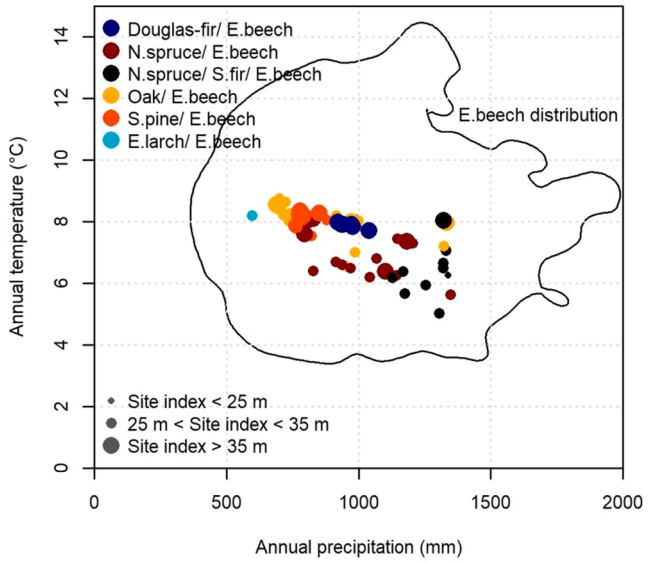


Fig. 1. Overview of the climatic range of our trials (colored dots) based on climate data from Wordlclim2.0 (Fick and Hijmans, 2017). The size of the dots represents the site index of European beech per plot. The bioclimatic envelope (black line) represents the distribution of E. beech in Europe based on a collection of European national inventory data from Thurm et al., 2018.

mixed stands is often higher than the maximum stand density in pure stands of the same species (Pretzsch and Biber, 2016). The density differences were included in our study by the density modification coefficient *DMC*. This enables a standardization of the different mixtures onto a common scale (Pretzsch and del Río, 2020). The density modification coefficient describes the ratio between the density that would be expected in a mixed stand, based on pure stand measurements, to the actually measured density in the mixed stand. The applied factors for our six mixing types adapted from a study by Pretzsch (2019). The single factors are listed in the Supplementary material S2.

The density sum of a given stand is related to the density modification coefficient for a species combination *DMC*. Dens represents the relative density of the whole mixed stand

$$Dens = \frac{\sum(Dens_{species1} + \cdots Dens_{speciesn})}{DMC^{*}100}{*}100. \quad (1)$$

This means that 100% density in a Douglas-fir / European beech mixed stand in our analysis has a 20% greater density compared to what would be expected in a combination of both pure stands without species interaction, i.e. according to the weighted mean density of both monospecific stands.

To calculate the mixing proportion $Prop_{species1}$, we related the species-specific density to the sum of all species density in the stand.

$$Prop_{species1} = \frac{Dens_{species1}}{\sum(Dens_{species1} + \cdots Dens_{speciesn})}. \quad (2)$$

2.3. Growth–density relationship

Assmann (1961) described the relationship of stand density and stand volume growth as an optimum curve. Based on thinning trials, he reasoned that maximum periodical growth occurs at sub-maximum stand densities. We used generalized additive models (GAM) for our analysis to enable such a flexible relationship. Fitting models to such data requires an approach that takes into account the nested structure of the data. Usually, a mixed regression model with a random effect on the experimental plot level is applied. In this specific case, however, we decided against that, because this yielded more plausible results from a

Table 2
Overview of the most important growth parameters of the six mixing types. The data were separated into the amount of E. beech and the admixed species (Mix). The density based on eq. (1) and is summarized for the whole stand (Overall). Mixing proportion (Prop) is also separated for E. beech and admixed species and the additional species with minor share (see eq. (2)). For the mixing type N.spruce/ S.fir/ E.beech, we aggregated the growth parameters of spruce and fir into Mix because of the minor differences. Dg – Mean quadratic diameter at breast height, IV - Periodic annual volume growth of the mixed stand, Density – based on eq. (1). Standard deviation is in italic and brackets.

Mixing Type	Dg (cm)		Height (m)		Age (yr)		IV (m^3/ha/yr)		Basal area (m^2/ha)		Density (%)	Prop (%)		
	Beech	Mix	Beech	Mix	Beech	Mix	Beech	Mix	Beech	Mix	Overall	Beech	Mix	Other
Douglas-fir/ E.beech	26.3	50	26.8	34.1	70.5	70.5	3.5	13.6	20.4	49.8	64.0	30	53.6	16.4
	(10.5)	*(21)*	*(7.9)*	*(10.5)*	*(32.7)*	*(32.7*	*(1.7)*	*(6.7)*	*(7.6)*	*(16.6)*	*(10.8)*	*(15.7)*	*(13.7)*	*(17.8)*
E.larch/E.beech	48.9	72.7	37.4	43	127	127	6.7	1	17.6	50.2	75.6	38.1	25.8	36.1
	(0.7)	*(1.3)*	*(0.3)*	*(1.4)*	*(2.8)*	*(2.8*	*(0.5)*	*(1)*	*(4)*	*(6.3)*	*(13.7)*	*(6.6)*	*(1.5)*	*(5)*
Oak/E.beech	36.7	37.5	28	27.6	115	116	6.2	4.7	11.1	27.1	70.0	46.7	36.7	16.6
	(13)	*(14)*	*(5.6)*	*(5.2)*	*(45.2)*	*(47.7*	*(3.5)*	*(3.4)*	*(4.3)*	*(8.2)*	*(23.8)*	*(23.7)*	*(28.8)*	*(19.7)*
N.spruce/ E.beech	27.5	41.9	26.1	32	98.2	90.7	6.5	8.1	15.2	40.7	69.7	53.4	40.2	6.4
	(7.9)	*(10.5)*	*(4.8)*	*(5.2)*	*(28.6)*	*(29.7*	*(3.6)*	*(5.5)*	*(5.5)*	*(12.3)*	*(16.4)*	*(21.4)*	*(19)*	*(9.7)*
N.spruce/S.fir/E.beech	28.8	39.4	22.2	27.5	195	204	2	4	10.6	40	77.0	24	70.9	5.1
	(9.1)	*(12.2)*	*(5)*	*(5.8)*	*(65.5)*	*(64.9*	*(1.9)*	*(2.8)*	*(5.4)*	*(13.4)*	*(25.4)*	*(17.3)*	*(18.2)*	*(8.4)*
S.pine/E.beech	20.3	29.2	21.6	24.3	68.9	83.8	5.3	7.5	17.7	43.4	85.2	29.5	57.7	12.8
	(7.6)	*(14)*	*(4.8)*	*(5.7)*	*(32.8)*	*(54.9)*	*(2.6)*	*(4.3)*	*(5.9)*	*(11.3)*	*(22.6)*	*(15.8)*	*(16.8)*	*(8.1)*
Mean	**31.4**	**45.1**	**27.0**	**31.4**	**112.5**	**115.3**	**5.0**	**6.5**	**15.4**	**41.9**	**73.6**	**37.0**	**47.5**	**15.6**

biological point of view, i.e. a non-linear growth–density relationship. Due to the deliberate omission of random effects, the significances obtained with this model must be considered progressive to some degree.

The model parameters are derived from the first hypothesis. The relation between periodic annual volume growth of the whole mixed stand (IV) and stand density (Dens) is as follows:

$$IV_{i,j,t} = f_1 Dens_{i,j,t} + MixType_{i,j} + \varepsilon_{i,j,t}. \quad (3)$$

MixType are the six species combinations. This categorical parameter should consider the various growth levels of the different mixing types. By considering the mixing type in the model as intercept, we have here a first step towards a mixing type specific curve fitting. This would require a data where each mixture captures the full density range. The indices i and j represent the trial and the plot level. t is the respective period. Standard smoothing terms are used with five degrees of freedom (5 knots) to restrict growth–density response function. The smoothing function f_n is fitted by thin plate splines, while n is a consecutive numbering of the different splines per model. ε always represents the residual error of the respective model.

2.4. Influence of stand development

To test the second hypothesis, we add the stand development parameters tree age (Age) or quadratic mean diameter (Dg) of European beech to Eq. (3). The use of the diameters of the entire stand would lead to an indirect consideration of the mixing type (E. beech Douglas-fir stand reached high dg, than E. beech oak stand at the same age). Since the mixing type is considered a separate variable MixType, we will only use the diameter of E. beech here. Both parameters were included as interaction.

$$IV_{i,j,t} = f_1 Dens_{i,j,t} * f_2 Age_{i,j,t} + MixType_{i,j} + \varepsilon_{i,j,t}. \quad (4)$$

$$IV_{i,j,t} = f_1 Dens_{i,j,t} * f_2 Dg_{i,j,t} + MixType_{i,j} + \varepsilon_{i,j,t} \quad (5)$$

2.5. Influence of ecological traits

The different ecological traits of the admixed species were added as categorical variable EcoTrait. We divided the mixed stands into two groups (light and shade) based on the shade tolerance index of Niinemets and Valladares (2006). The "light" group includes the shade-intolerant *Quercus species, Larix decidua*, and *Pinus sylvestris*; the other mixed types we assigned to the "shade" group with the more shade-tolerant *Abies alba, Pseudotsuga menziesii*, and *Picea abies*.

$$IV_{i,j,t} = f_1 Dens_{i,j,t} * f_2 EcoTrait_{i,j} + f_3 Age_{i,j,t} + \varepsilon_{i,j,t}. \quad (6)$$

With the inclusion of the ecological groups, the variable MixType of the previous models becomes obsolete. In order to avoid that the variable EcoTrait explains correlations of the stand development, age as the best fitting variable (based on model quality) was added to Eq. (6).

2.6. Thinning effects

We also used generalized additive models to analyze the influence of density changes on the volume growth. The relative growth change (IVC) from one period to the next period (five years later, Eq. (7)) or the second next (ten years later, Eq. (8)) serves as dependent variable.

$$IVC_{t1} = \frac{IV_{t+1}}{IV_t} \quad (7)$$

$$IVC_{t2} = \frac{IV_{t+2}}{IV_t} \quad (8)$$

The relative growth change was put into relation to the basal area of removal stand (BAR) and the thinning method (THM). The thinning method is a numerical variable, based on the ratio of the quadratic mean diameter (Dg) of the removal stand of all species to the Dg of the whole remaining stand. Thus, values below one are equivalent to a thinning from below.

$$THM_t = \frac{Dg_{t,removal}}{Dg_{t,remain}} \quad (9)$$

The applied model for the five and ten years relative growth change looks as follows:

$$IVC_{i,j,t} = f_1 THM_{i,j,t} * f_2 BAR_{i,j,t} + f_3 Dens_{i,j,t} + MixType_{i,j} + \varepsilon_{i,j,t}. \quad (10)$$

All analyses were done in the software environment of R 3.6.1 (R Core Team, 2018). The generalized additive models were performed with R-package *mgcv* (Wood, 2011).

3. Results

3.1. Growth–density relationship

With an average stand age of 114 years, our investigated mixed stands had a mean basal area of 41.9 m^2/ha. This basal area is high in comparison to monospecific beech stands of the same age (see Table 2, Yield table European beech = 32.0 m^2/ha, 115 years, site index 1.0 Schober, 1972). The calculated density of 73.5% (*Dens*) is comparatively low and results from the mean beech proportion of 39.6% and the respective density modification coefficient (*DMC*) which are applied to density(see also the comparison of basal area and density in Fig. 2). On average, E.beech was 13.7 cm thinner and 4.1 m smaller (Dg = 31.4 cm, height = 27.0 m) than the admixed species (Dg = 45.1 cm, height = 31.4 m). Periodic annual volume growth was higher in medium-density to over-dense stands (16.7 m^3/ha/yr) than in low-density stands (12.2 m^3/ha/yr, see Table 3).

The relation between volume growth and stand density is depicted in Fig. 3 and Table 4. The response is significant with a R^2 of 0.45. The curve shows a constant level from 70% to 100%, the area of medium-density to high-density. When mixed stands become over-dense, a further increase in volume growth can be seen.

3.2. Influence of stand development

The second research question (Eq. (4) and (5)) intended to highlight

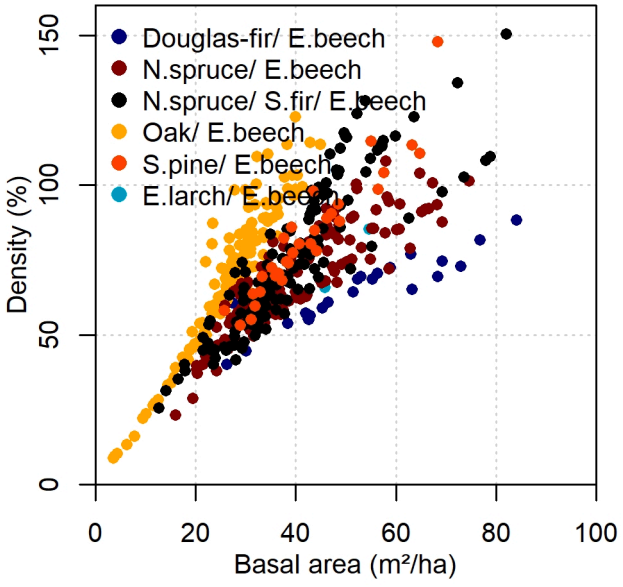


Fig. 2. Relation between basal area per hectare and density of the stand for the six mixing types. Each point represents a single stand survey.

Table 3
Stand characteristics of the plot data separated by density classes low-density, medium-density stand and over-dense stands. IV = Periodic annual volume growth. Standard deviation is in italic and brackets.

	Low-density stands (<=70%)				Medium-density to high-dense stands (>70% & <=100%)				Over-dense stands (>100%)			
	Density (%)	Basal area (m^2/ha)	IV (m^3/ha/yr)	N	Density (%)	Basal area (m^2/ha)	IV (m^3/ha/yr)	N	Density (%)	Basal area (m^2/ha)	IV (m^3/ha/yr)	N
Douglas-fir/ E.beech	59.3	42.8	17.9	19	76.8	68.8	27.1	7	–	–	–	–
	(7.9)	*(12.5)*	*(6.0)*	*(19.0)*	*(6.2)*	*(10.0)*	*(7.8)*	*(7.0)*	–	–	–	–
E. larch/ E.beech	65.9	45.8	20.4	1	85.3	54.7	14.8	1	–	–	–	–
	–	–	–	*(1.0)*	–	–	–	*(1.0)*	–	–	–	–
Oak/E.beech	51	21.3	8.8	61	83.3	31.3	13.1	58	109.4	38.2	14.1	10
	(18.0)	*(7.2)*	*(4.6)*	*(61.0)*	*(9.4)*	*(4.3)*	*(2.6)*	*(58.0)*	*(7.0)*	*(4.3)*	*(1.5)*	*(10.0)*
N.spruce/ E.beech	57.8	32.4	13.3	77	83	49.8	17.3	57	102.9	63.4	20	5
	(9.9)	*(7.0)*	*(4.4)*	*(77.0)*	*(7.7)*	*(8.9)*	*(5.9)*	*(57.0)*	*(3.3)*	*(8.7)*	*(5.0)*	*(5.0)*
N.spruce/S.fir/E.beech	56.1	30.6	8.9	74	82.5	42.7	11.4	48	116.6	59.3	13.2	29
	(10.3)	*(6.5)*	*(5.0)*	*(74.0)*	*(9.3)*	*(7.3)*	*(4.3)*	*(48.0)*	*(12.7)*	*(11.3)*	*(6.2)*	*(29.0)*
S. pine/E.beech	62.3	32.1	13.7	9	84.1	42.5	17.8	19	123	62.9	23.6	6
	(6.1)	*(3.5)*	*(2.3)*	*(9.0)*	*(8.8)*	*(5.3)*	*(4.9)*	*(19.0)*	*(19.5)*	*(5.5)*	*(8.1)*	*(6.0)*
Mean	**58.7**	**34.2**	**13.8**	**40.2**	**82.5**	**48.3**	**16.9**	**31.7**	**113.0**	**56.0**	**17.7**	**12.5**

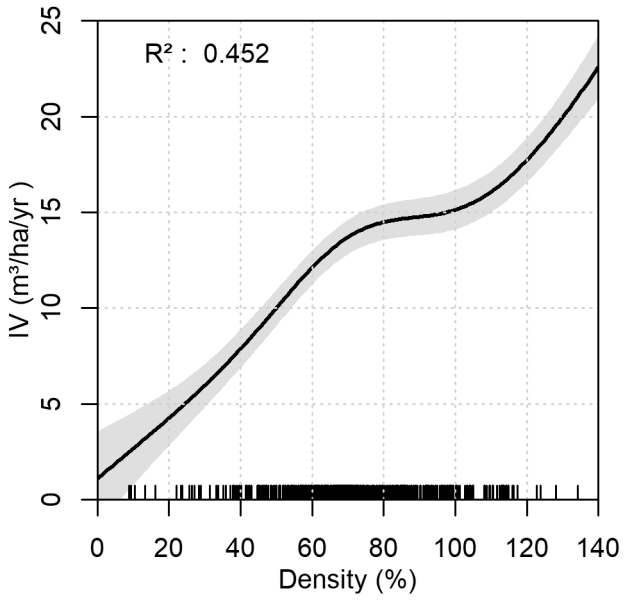


Fig. 3. Relationship between stand density and annual volume growth (IV) of all investigated mixed stands. Upward ticks on the x-axis represent the density of the single measuring surveys to show their distribution. Model overview in Table 4.

the mentioned relationship between density and stand growth with stand development (see Fig. 4). The inclusion of age as predictor variable as an interaction to density slightly increased the performance of the first model (R^2 = 0.49, Fig. 4 a, Table 4, Eq. (4)). The interaction with Dg did not increase the R^2 (R^2 = 0.44, Fig. 4 b, Table 4, Eq. (5)). Nevertheless, R^2 is only a limited sign of model quality for GAM and therefore it is still useful to look at the response. Both variables led to a flat growth response in younger stand development and an increase in older stand development.

3.3. Influence of ecological trait

The consideration of the ecological groups light and shade also led to an altered growth–density relationship (Eq. (6) in table 5, Fig. 5). The more shade-tolerant mixed stands exhibited a higher growth in medium- to high-density stands (70–100%). The shade-intolerant mixed stands, however, saw a drastic increase in the over-dense areas (>100%). The lower coefficient of determination is caused by the exclusion of the categorical variable mixing type to the benefit of the shade-tolerant group.

3.4. Thinning effects

How growth five and ten years after thinning was influenced by density increase can be seen in Fig. 6. The proportion of explained variance of the models are low (R^2 0.03 and 0.05). However, the direction of effects was significant in the 10-year model and at least

Table 4
Statistical characteristics of the GAM depicted in Fig. 3 and Fig. 4. Edf - Effective degrees of freedom.

	Eq. (3)			Eq. (4)			Eq. (5)		
	edf	p-value		edf	p-value		edf	p-value	
f(Dens)	3.75	0.00	***						
f(Dens*Age)				3.64	0.00	***			
f(Dens*Dg)							4.88	0.00	***
MixType	Estimate	p-value		Estimate	p-value		Estimate	p-value	
Intercept	21.02	0.00	***	23.14	0.00	***	22.22	0.00	***
E.larch/E.beech	−4.19	0.21		−1.19	0.71		−2.44	0.47	
Oak/E.beech	−9.36	0.00	***	−7.02	0.00	***	−7.88	0.00	***
N.spruce/E.beech	−5.62	0.00	***	−4.10	0.00	***	−5.08	0.00	***
N.spruce/S.fir/E.beech	−10.86	0.00	***	−6.04	0.00	***	−10.28	0.00	***
S.pine/E.beech	−4.96	0.00	***	−3.49	0.00	**	−4.10	0.00	***
R^2		0.45			0.49			0.44	
N		481			481			481	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '(*)' 0.1 ' ' 1
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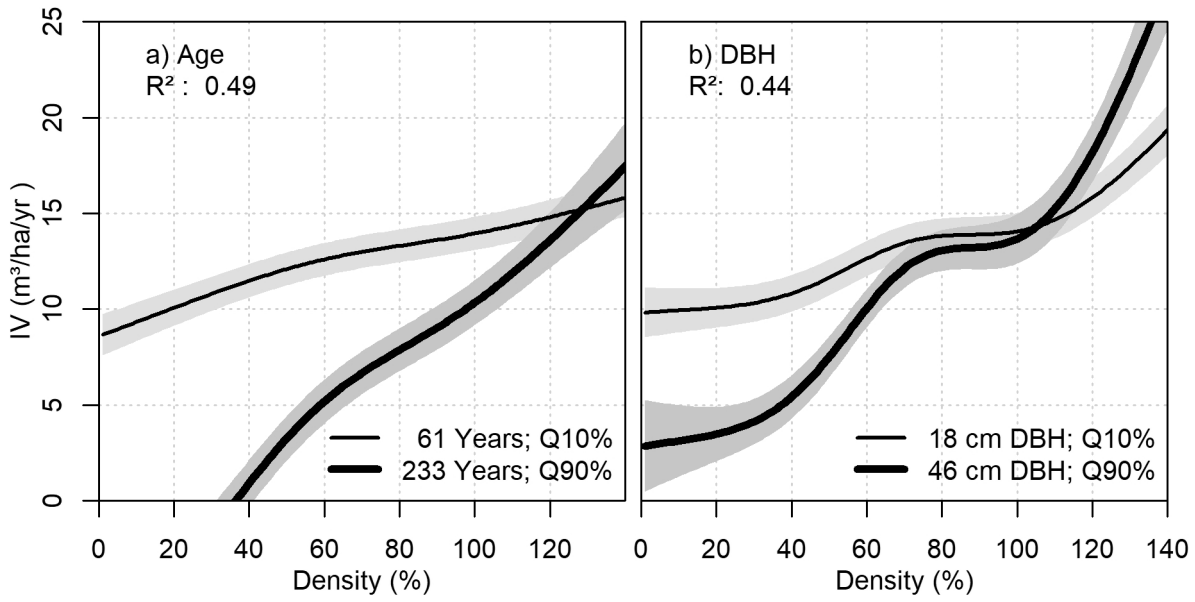


Fig. 4. Relationship between stand density and annual volume growth (IV) and its interaction to a) age and b) diameter at breast height. Q10% and Q90% gives the respective quantiles of the whole data set. Model overview in Table 4.

Table 5
Statistical characteristics of the GAM depicted in Fig. 5 and Fig. 6.

	Eq. (6)			Eq. (10) (5 years)			Eq. (10) (10 years)		
	edf	p-value		edf	p-value		edf	p-value	
f(Dens*Light)	2.75	0.00	***						
f(Dens*Shade)	2.24	0.00	***						
f(Age)	3.12	0.00	***						
f(THM*BAR)				2.287	0.06	(*)	2.000	0.01	*
f(Dens)				2.797	0.05	(*)	2.464	0.08	(*)
	Estimate	p-value		Estimate	p-value		Estimate	p-value	
Intercept	13.06	0.00	***	1.01	0.00	***	1.10318	0.00	***
E.larch/E.beech				0.33	0.272		–		
Oak/E.beech				−0.03	0.637		−0.09		
N.spruce/E.beech				0.04	0.571		−0.05		
N.spruce/S.fir/E.beech				0.01	0.882		−0.07		
S.pine/E.beech				0.11	0.23		−0.15		
R^2		0.48			0.03			0.05	
N		479			320			218	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '(*)' 0.1 ' ' 1.

slightly significant in the five-year model. The results shows that, weak thinnings can improve growth after five years (see Fig. 6a). However, growth gain turn into loss when the amount of harvested trees (removal stand) reached 10 m^2/ha. Thinning from above further enhances this effect. Mixed stands benefit particularly from thinning after a longer period of time (see Fig. 6b), but only if thinning is carried out as thinning from above and if the amount of harvested trees in thinning is lower than 8 m^2/ha.

4. Discussion

4.1. Growth–density relationship

On the basis of our results, we can ask how mixture influences the density–growth relationship compared to pure stands. Rejecting our first hypothesis, we did not find a growth optimum in the medium-density phase of density, but there was a phase of constant growth. The optimum response in this phase is described very well in pure beech stands (e.g. Nagel and Spellmann, 2008; Nord-Larsen and Johannsen, 2007; Schober, 1972) and also for our other admixed species (e.g. Assmann, 1961). Different authors have described the strength of the optimum quite differently, which is driven by the site quality and also by stand development. Bryndum (1987) and Nord-Larsen and Johannsen (2007) investigated the growth–density relationship in Danish trials. Both derived curves where the growth of the optimal basal area does not differ significantly from the growth at the maximum basal area, whereas Nagel and Spellmann (2008) and Pretzsch (2004) found clear growth differences between optimum and maximum density.

Nevertheless, all authors agree that European beech tolerates a great density increase before it reaches the critical stand density or rather a significant increase of growth loss (e.g. Nagel and Spellmann, 2008; Nord-Larsen and Johannsen, 2007; Schober, 1972). This is in line with our growth–density response, although our investigated stands had a proportion of E. beech of only 39%. The other investigated species reached their critical density just earlier and have a smaller optimum range (Curtis et al., 1997; Mäkinen and Isomäki, 2004a, 2004b; Pretzsch, 2009). We assumed that European beech is able to stabilize the use efficiency of the stand due to its high crown plasticity (Schröter et al., 2012). When the density increases, European beech in mixed stands can occupy free spaces, something not possible in pure conifer stands in particular (Jucker et al., 2014). The establishment of this positive effect naturally presupposes a homogeneous distribution of

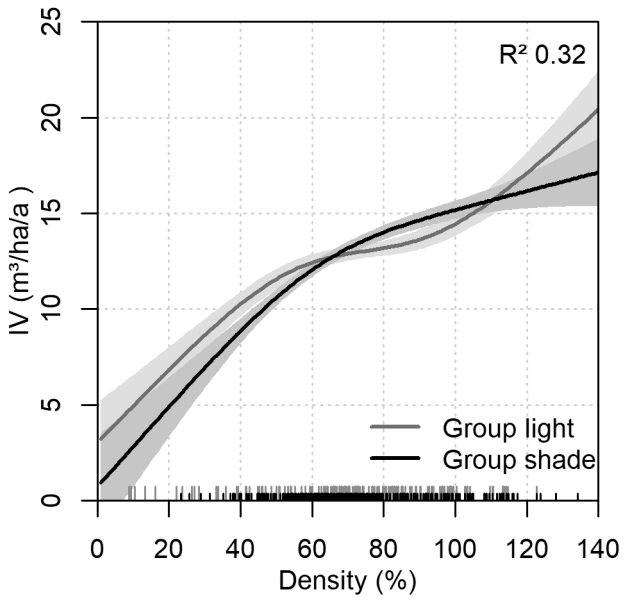


Fig. 5. Relationship between stand density and annual volume growth (IV) for *F. sylvatica* admixed with shade-intolerant ("light" group – *Quercus species, L. decidua*, and *P. sylvestris)* or shade-tolerant species ("shade" group – *A. alba, P. menziesii*, *and P. abies*) based on an index of Niinemets and Valladares (2006). The short and the long upward ticks on the x-axis show the density distribution of the light (lomg) and the shade group (short). Model overview in Table 5.

beech over the stand area.

In our study, it could not be confirmed that growth depression occurs after the medium-density phase. We assumed that the mixing effect prevents this depression, which is known from pure stands. Several authors could show that higher density and greater intra-specific interaction support an overyielding in mixed stands (Amoroso and Turnblom, 2006; Condés et al., 2013; Forrester et al., 2013). We assumed that the high-density phase in pure stands leads to increased competition with inefficient individuals in terms of water and nutrient use (Pretzsch, 2009). In mixed stands, complementarity and facilitation become dominant interactions instead of competition.

Another assumption in our first hypothesis was that in the over-dense phase in mixed stands there should be a further decrease in growth. Instead, our response curve shows an additional increase in this phase, which cannot be explained by a pure growth–density relationship. Therefore, we will discuss over-density before looking at the growth response. Over-density, in this sense, cannot occur in pure stands. The maximum density in even-aged, monospecific stands is clearly restricted through the self-thinning line of the respective species (Pretzsch, 2006a; Reineke, 1933; Vospernik and Sterba, 2015). That's why estimations of density–growth response in pure stands can use unthinned stands as a starting point or null expectations (Nagel and Spellmann, 2008; Pretzsch, 2020a). In mixed stands, this null expectation is difficult to find. The mixing proportion and the ecological trait of the combined species determine the maximum density (Shaw, 2006). The prerequisite for a null expectation is therefore the same proportion of mixture between thinned and unthinned stands. However, this can usually only be achieved through regulation of the species, to establish for example a 50:50 mixture.

The lack of this null expectation thus causes a methodological disruption (Binkley, 2018). We have tried to replace the missing null expectation in field with a calculated benchmark. It was derived from the maximum density of the tree species and the influence of the mixing effect (see chapter 2.2). Nevertheless, despite the addition being specific to mixing type, it is not able to take into account either mixing proportions. For additional tree species there are no density modification coefficients yet and so far they can only be added to one of the major species. In addition, site conditions are an important factor, which determines the resulting mixing effects and thus the degree of possible overdensity. So it is not surprising that 10% of our stands exceeded the mixing type-specific benchmarks.

Now we want to look into the additional growth gain in this over-dense phase. Nearly all of our investigated species combinations are involved in this phase, so we did not suppose a mixing effect with a specific species combination.

We assumed that it might be an accumulation of additional species which triggers the extra growth gain. Liang et al. (2016) could exhibit in a worldwide study that stand growth shows a logarithmic growth with an increasing number of species per stand. Our experimental plots in the over-dense phase have a greater number of species as well. Nearly all of these stands have three to seven tree species, although only in small

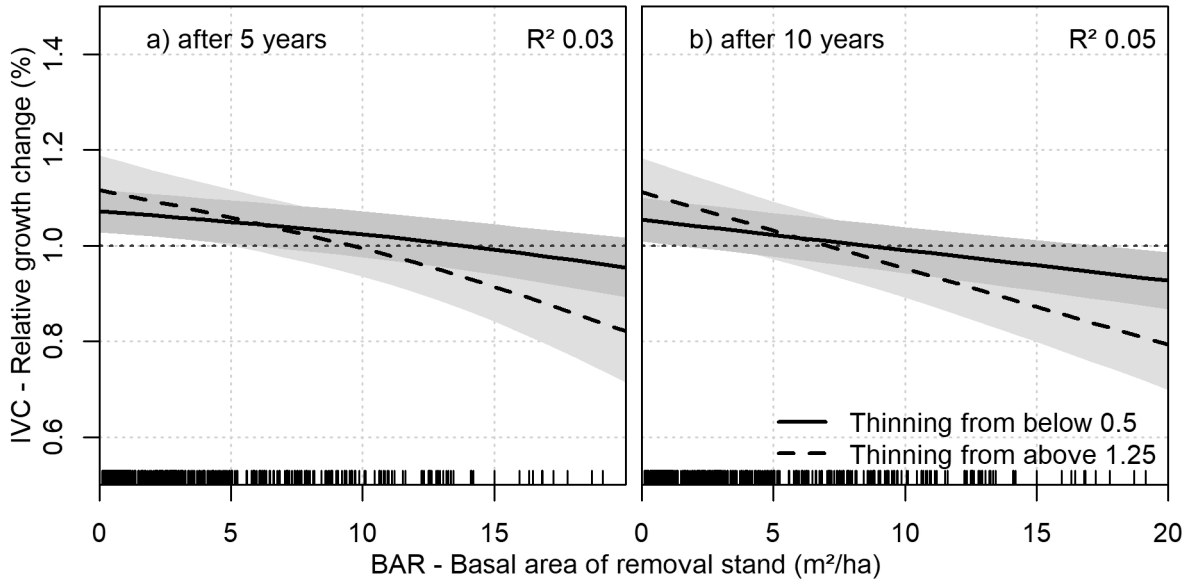


Fig. 6. Relationship between basal area of the harvested trees (removal stand - BAR) and the relative annual volume growth change (IVC), which is the ratio between the growth a) 5 years or b) 10 years after thinning to the growth before thinning (see Eqs. (7) and (8)). The upward ticks on the x-axes show the distribution of the basal area of the removal stand. Model overview in Table 5.

proportions. So the over-dense phase is thought to be a consequence of the larger number of species. The species occupy small empty niches which cannot be filled by the main species. Regrettably, we were unable to confirm our theory. A consideration of the number of species per plot or even better the proportion of the different species in our model led to an overfitting because of the comparably low number of experimental plots.

It is essential to mention that we are aware that our nearly cubic function includes unknown parameters. An omitting of the over-dense plots or a smoothing of the curve would have led to a more understandable curve. However, we decided to publish this growth response to promote scientific discussion.

4.2. Influence of stand development

Our second hypothesis deals with the influence of stand age and diameter at breast height on the growth–density relationship. We found that the curve progression intensified with age of the stand. Although there is only a small influence of age effect on model quality, this response is comparable to what we know from pure stands. Regardless of the species, several authors have described that young stands are likely to be better able to compensate for density decreases than older stands (e.g. Nagel and Spellmann, 2008; Nord-Larsen and Johannsen, 2007; Pretzsch, 2004).

Different studies of mixed stands found that the mixing effect occurs mainly in older stands (Binkley, 2003; Thurm and Pretzsch, 2016; Zhang et al., 2012). Zhang et al. (2012) assumed that two life stages lead to this response. The young stage includes aggrading and an increasingly closed canopy, while in mature stages competition steps into the background and complementarity effects appear.

A study by Thurm and Pretzsch (2016) in European beech Douglas-fir stands showed that overyielding of mixed stands is related to increasing age. This effect results from a higher differentiation of the Douglas-fir crown layer and the underlying European beech layer. The light-related mixing effect of this species combination leads to a niche complementarity in the crown area. A study of European beech and Scots pine by Forrester et al. (2018) also highlighted how the crown structure in mixed stands is adapted to generate a minimal crown overlap. Consequently, a decrease in stand density would suppress the complementarity effects in mixed stands (Amoroso and Turnblom, 2006; Forrester et al., 2018).

In our study we also included plenter forest to a small degree. We assigned this stand type a very high age based on the oldest beech trees in the stands. This is slightly biased because obviously plenter forests have trees in different stages of life. A reason for the strong sensitivity of density loss in these stands might be the large diameter distribution. The different life stages of adjacent trees means a very high artificial inequality. This size inequality might reduce stand growth (Bourdier et al., 2016). Schütz (2003, p.123) mentioned that plenter forests seem to achieve comparable growth rates as high forests, but he also noted that they require very high growing stocks. It has to be mentioned that the effect of age on the growth–density relationship can be found for mean Dg as well. This means that the discussed effect is not only a result of the plenter forests but also of the mature high forests.

4.3. Influence of ecological trait

The influence of the admixed species and its ecological traits is one of the main factors which regulate the growth–density relationship. On the one hand the admixed species forces the general growth level; on the other hand it influences the course of the relationship. We try to consider this species-specific effect by the inclusion of mixing type as categorical fixed effect. This enables at least a consideration of the different growth levels of tree species. It would be better to allow each species combination an individual course, but this wasn't possible due to the comparably low number of experimental plots.

Nevertheless, we grouped mixing types to see if there are general mechanisms like shade tolerance which manipulate the course of the growth–density relationship. Our results showed that European beech mixed with more shade-tolerant species produces significantly higher growth in the medium- to high-density phase. This finding is not surprising because of the overall higher growth level of this species (Schober, 1975) and also of these mixing types (Pretzsch and Schütze, 2016).

In addition to this effect, we observed that the course of the shade-tolerant mixtures resembles a logarithmic curve, while shade-intolerant species showed the growth gain in the over-dense phase. As mentioned before, we assumed that this growth gain comes from additional minor species. The establishing of these species is only possible if the mixed stand reduces competition for the limiting resource, light (Forrester and Albrecht, 2014). The more shade-tolerant conifers and also European beech are known for their lower canopy light transmission (Ellenberg and Dierschke, 2010; Valladares and Niinemets, 2008). The mixture of European beech with shade-intolerant species might have the consequence that the light was not yet fully captured and is available for a productive understory or secondary stand. Pretzsch et al. (2018) could show that especially in drought conditions, small trees are able to compensate for declines in growth. Forrester (2019) came to the conclusion that inequality in tree size can have positive as well as negative effects on tree growth. In the study at hand, we did not test this effect of inequality in relationship to growth. Nevertheless, a growth gain might be possible due to high stand density.

4.4. Thinning effects

Alongside the general growth–density relationship, we wanted to investigate how changes in density influenced growth in mixed stands. We found that weak thinning has a positive effect on stand growth, while severe thinnings (>8 m^2/ha) led to a growth decline. Although the explanatory power of our model was quite weak, the orientation of the growth change-thinning amount curves was significant and an interpretation of the effect is meaningful. The weak explanatory power partly results from the absence of other major influencing factor, like climate, soil moisture and distrubances (e.g. Anderegg and HilleRisLambers, 2019; Mohren and Rabbinge, 1990).

Our analyzed plots aren't explicit thinning experiments with defined thinning concept like A, B and C Grade knowing from monocultures and with several repetitions (Hummel, 1953; Verein Deutscher Forstlicher Versuchsanstalten, 1902). Such concepts would enable to investigate the thinning effects much more clearly. However, the knowledge about the relationship between thinning and volume growth is very important, especially in times of increased amount of mixed stand for climate change adaption. In the absence of existing long-term thinning trials with mixed stands, our results can therefore provide first insight.

One of the few studies that have realized different thinning intensity for mixed stands was Primicia et al. (2016). They investigated mixed and also pure stands of Scots pine and European beech with three different thinning intensities. They were able to show that moderate thinning of 20% of the remaining stand (around 8 m^2/ha in this study) leads to the highest benefit for the stand volume growth. Furthermore, they found that there is no negative influence of beech on pine growth in mixed stands. This is in line with our findings.

Our study also divided thinning type into thinning from above and from below. Especially in mixed stands this is an important consideration. Size inequality there is much more pronounced than in pure stands (Riofrío et al., 2017), and thinning affects this inequality. We could see this effect in the second period after thinning, where weak thinning from above led to a significant gain of growth.

Several studies exhibited that thinning from above did not increase volume growth in pure stand (Bradford and Palik, 2009). We assumed that a reason for the positive effect of thinning from above in our mixed stand might be the removal of the inefficient trees (see Pretzsch, 2006b;

Sterba, 2019, 1999; Vuokila, 1980). The removal of a dominant tree leads to growing space for intermediate and suppressed trees. In successful mixtures, these suppressed trees have usually a higher shade-tolerance than the predominant trees (Toïgo et al., 2018). For example, the removal of one E. larch leads to the promotion of two overtopped E. beeches. Now, smaller trees can increase their growth disproportionately because they are physiologically younger than the dominant collective. The effect is especially known from permanently suppressed Silver firs, which are still able to react like young trees (Schütz, 1969). To a certain degree, E. beech is also capable to this trait.

Finally, the dominate species growth faster because of more light availability (Thurm and Pretzsch, 2016) and reached its individual culmination point of growth early than in pure stands, because of higher availability of resources (Pretzsch, 2020b). At a certain stand development the dominant trees become inefficient regarding their area use compared to the suppressed trees (Assmann, 1961; Sterba, 1999). Now, this released tree species shift this point to older age and thus keep the stand growth at a greater level.

5. Conclusions

Our study gives some initial insights into the growth–density relationship of the most important broadleaf tree in Central Europe mixed with the other main tree species. The results show that the growth–density relationship of these stands is different to what we know from beech pure stands. We are aware that our presented relationship, with its growth gain in the over-dense phase, includes unknown variables. This can only be resolved by a broader set of plots.

However, our results enable initial data-based recommendations. One silvicultural conclusion would be to always maintain density at a high level to increase production. This enables the mixing effects of facilitation and complementarity. Further species are welcome to further increase the density and occupy empty niches.

High density can be achieved by weak to moderate thinnings, which should be repeated regularly. This leads to the highest growth gains if they are carried out as thinnings from above. A prerequisite, however, is homogeneous distribution of admixed species over the stand area.

In this study we have a strong focus on the influence of stem volume growth, which represents quantitative productivity of mixed stands. However, current silvicultural systems are also triggered by quality productivity and the quality and the value of the stems. First analyses forecast that the stiffness of European beech boards in mixed stands is worse than in pure stands (Rais et al., 2020). More attention must be paid to such aspects.

We could show that the shade tolerance of the admixed species has an influence. However, to transfer these findings into practice, it is necessary to get more insights into species-specific responses. Also, site quality is a factor which influences the mixing effect as well as the overyielding (e.g. Forrester et al., 2013; Pretzsch et al., 2010; Thurm and Pretzsch, 2016).

Thinning experiments of one tree species, consisting of an unthinned plot (A grade) and clearly defined thinning grades (e.g. B, C grade, see Hummel, 1953; Verein Deutscher Forstlicher Versuchsanstalten, 1902), have been a fundamental pillar of growth research for a long time. This experimental setup was able to exhibit principles of density and growth. The mixture of species causes several additional factors. To investigate the individual factors influencing the growth–density relationship, new experimental concepts are required. Therefore, we need long-term trials which vary a) relative densities of species, b) mixing proportion, and c) across gradients in site fertility for a clear assessment of the benefits to be derived from species mixtures (Binkley, 1984).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118909.

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