



Mixing degree, stand density, and water supply can increase the overyielding of mixed versus monospecific stands in Central Europe

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ABSTRACT

Tree species mixtures can overyield monospecific stands and provide many other advantageous regulating and provisioning ecosystem services. So far, the effect of mixing on growth were mostly described at the individual tree level or cumulatively at the stand level. How overyielding emerges from the mixing pattern, how it is modulated by the current environmental conditions, and how overyielding develops with progressing stand age is largely unexplored. However, such knowledge might promote the silvicultural design of mixed stands.

Here, we use 50 long-term experimental plots in Germany with repeated spatially explicit stand inventories. They cover monospecific and mixed species stands of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* [Matt.] Liebl.) and European beech, and Scots pine (*Pinus sylvestris* L.) and European beech. The stands represent medium to very good site conditions, fully to moderately thinned 15–238 years-old stands with mixing patterns ranging from single-tree and group-mixture to monospecific stands.

The main hypothesis is that mixing pattern, environmental conditions, and stand age modulate the stand growth and overyielding of mixed versus monospecific stands. Based on metrics of mixing the mixing pattern and indices of environmental conditions we show that mixed stands of European beech were on averaged by 12–36% more productive than respective monocultures. Overyielding can increase with stand density, mixing degree, regularity of horizontal tree distribution, tree size variation, site index, and water supply. Overyielding continued throughout the whole rotation time.

The found overyielding suggests general facilitative effects of mixing in terms of bioclimate or soil conditions, independent of the mixing pattern. In addition to this general effect, overyielding was increased by stand density and mixing degree. This suggests a strong competition reduction due to structural complementarity. That the overyielding increases in moist years, points to the competition reduction as dominant cause. We hypothesize that in moist years competition for light and nutrient becomes stronger, so that species complementarity is more important and competition reduction may operate stronger and more beneficial for growth than in years with growth limitation by water.

The findings stress the relevance of spatially explicit approaches of analyzing and modelling facilitation and competition at the stand and tree level. Silvicultural prescriptions may incorporate the findings that the analyzed mixtures with European beech in general overyield monospecific stands and that the benefit can be further increased by stand density, mixing degree, and tree size variation. Beneficial effects of mixtures can be expected on medium to high quality sites, in dry years, and even more in moist periods.

1. Introduction

Mixed species forests (Liang et al. 2016, Mason et al., 2018, Gamfeldt et al. 2013) can overyield monospecific stands and provide many other advantageous regulating and provisioning ecosystem services (Dieler et al. 2017, Biber et al. 2015, Potschin-Young et al. 2018). The meta-analysis of 126 case studies by Jactel et al. (2018) found a mean

overyielding of mixed stands of 15%. Mixed-species forest stands in Europe can overyielding monospecific stands by 2–59% in terms of stand volume growth or mass growth (Pretzsch et al. 2020, 2015, 2010, Thurm et al., 2016, Steckel et al. 2019, Ruiz-Peinado et al. 2021). Although mono- and mixed species stands can strongly vary in terms of mixing proportion (ranging from 0 to 100% share of the respective component species), horizontal tree distribution (ranging from

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aggregated to random and regular pattern), and intermingling (ranging from clustered to grouped and single tree mixture), most studies are based on a simple comparison of mixed with monospecific stands. For comparing both kind of stands they make a discrete distinction between mono- and mixed species stands based on threshold of mixing proportion or other characteristics (Jactel et al. 2018, Piotta, 2008). A deeper understanding of the effects of mixing proportions, horizontal tree distribution, or mixing degree on stand growth and overyielding is still missing and the methodological and empirical basis for respective analyses is still poor (Pretzsch and Schütze 2021). Notice, that the key technical terms used in this study are summarized in Box 1.

Facilitation and competition reduction are the main concepts for explaining the overyielding of mixed versus monospecific stands (Williams et al. 2017, Forrester, 2014, Kelty, 1992). Facilitation may be caused among others by hydraulic lift (Zapater et al., 2013, Steckel et al., 2019), provision of nutrients by deep rooting species to shallow rooting neighbors (Rothe and Binkley 2001, Augusto et al., 2002, Jonard et al., 2008), or by atmospheric nitrogen fixing tree species (Forrester et al. 2006). Facilitation is assumed to be especially relevant under harsh growing conditions (Holmgren et al., 2010; Maestre et al. 2009), e.g., on nutrient-poor sites or in dry years. Competition reduction, in contrast, may be more relevant on rich sites and in moist years when competition for light and nutrient is strong (Belluau et al. 2021, Jactel et al. 2018). Complementarity of crown and root allometry may allow a competition reduction and enable a higher packing density of crowns (Jucker et al. 2015). In addition, the mixing of complementary tree species may reduce crown shyness and mechanical abrasion (Fish et al. 2006, Hajek et al. 2015). In summary, competition reduction may increase the stand density in terms of stand basal area and SDI (Williams et al. 2017, Thurm and Pretzsch 2021), crown projection area, or leaf area index (Peng et al., 2017). In this way, competition reduction may finally also increase the stand growth (Zeller and Pretzsch 2019, Fichtner et al. 2018, Jactel et al. 2018) of mixed compared to monospecific stands (Barbeito et al. 2017, Juchheim et al. 2017, Zeller et al. 2021).

Facilitation and competition reduction may be modulated by stand structure and environmental conditions and they also may change with progressing stand age (Jucker et al. 2020). Due to a lack of appropriate experimental plots the effects of different mixing patterns on overyielding were so far mainly analysed by model simulations (Rötzer, 2013, Rötzer et al. 2012, Pretzsch et al. 2012, Pukkala et al. 1994). The results of these studies suggest that the mixing degree may increase inter-specific interactions, stabilize growth, and cause overyielding. The stress gradient hypothesis (Holmgren et al., 2010; Maestre et al. 2009) posits that under water stress and harsh conditions facilitation between species may increase (Vallet et al., 2015), but some studies found an opposite trend (Belluau et al. 2021, Jactel et al. 2018, del Río et al. 2014). Due to missing long-term experiments most studies are based on young or middle-aged stands (Toigo et al., 2015; Piotta, 2008; Pretzsch et al., 2010, 2013, 2015) and leave it open how the mixing effects develop with progressing stand age (Zeller and Pretzsch 2019). Analyses of overyielding with indication of mixing effects or overyielding at different ages are mostly based on chronosequences as real time series are missing (Pretzsch and Schütze 2021, Torresan et al. 2020).

Facilitation and competition reduction may operate at different spatial scales and depend on the prevailing environmental conditions. For instance, competition reduction based on complementary tree allometry operates most efficiently in close distance at the tree-tree level. In contrast, the effects of facilitative improvement of soil (Prescott and Grayston 2013, Prescott, 2002) or bioclimate (Leuchner et al. 2012) by mixing reach further due to leaf dispersion by wind and water transport by roots or microbial networks (Steidinger et al. 2019, Nickel et al. 2018). Competition reduction as underlying principle may be indicated by increased overyielding especially in wet growth periods. This applies as ample water supply increases the competition for light and nutrient in a way that complementary space and resource use and competition reduction can operate more effective than in dry years

when water but not light is the growth limiting factor. A continuation or even increase of the overyielding with progressing stand age may suggest cumulative facilitation due to enriched soil fertility of mixed compared to monospecific stands.

Further insights how overyielding depends on the mixing pattern can contribute to both a better understanding overyielding and an improved silvicultural design of mixed species stands. Suppose a mixing proportion of 50:50 in single-tree and group-mixture pattern would cause the same overyielding this would suggest a broad stand level effect of mixing by, e.g., improvement of the soil or bioclimate. An increase of overyielding with mixing degree, in contrast, would suggest a close-distant mixing effect, e.g., a reduction of competition or crown shyness by crown or root complementarity. How the mixing pattern affects stand growth and overyielding, is essential to know for improving the silvicultural design of mixed-species stands. If a high mixing degree is the precondition of harnessing overyielding, individual tree mixtures might be preferred, whereas group mixtures would hardly exploit the potential of overyielding. In addition, knowledge of the effect of mixing pattern on growth is essential for stand modelling and silvicultural treatment (Bauhus et al., 2017, Pretzsch and Zenner 2017).

The main objective of this study was to improve the knowledge about the effect of mixing pattern and environmental conditions on stand growth. Therefore, we posit as the main hypothesis that the mixing pattern and environmental conditions modulate the stand growth and overyielding of mixed versus monospecific throughout the whole rotation turnus. Certainly, the stand growth is only one of many ecosystem services (Potschin-Young et al. 2018). However, a better understanding of the relationships between the mixing pattern and growth is relevant for assessment and knowledge-based steering of most other ecosystem services (Dieler et al. 2017).

This study based on in total 50 large long-term experimental plots in Germany which were repeatedly measures since the early 1990's (Pretzsch and Schütze 2021). The plots were established in monospecific and mixed species stands of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* [Matt.] Liebl.) and European beech, and Scots pine (*Pinus sylvestris* L.) and European beech. Thus they covered the main tree species mixtures in Central Europe (Brus et al. 2012). In order to reveal how stand growth and overyielding of mixed vs. monospecific stands are modulated by mixing pattern we sampled circular sections from the 50 large long-term experimental plots, quantified the stand structure and growth on them. The resulting data on stand structure and growth was used for testing the following hypotheses about mixed stands compared with monospecific stands:

H I: Overyielding increases with the mixing degree.

H II: Overyielding increases with improving environmental conditions.

H III: Overyielding continues from young to old stand ages.

The findings were discussed regarding their implications for analyzing and modelling facilitation and competition at the tree and stand level. We derived consequences for silvicultural prescriptions and management.

2. Material and methods

2.1. The study plots

2.1.1. The concept of age series

The study was based on eight age series (see example in Fig. 1) with 50 long-term plots in Germany with repeated spatially explicit stand inventories. They were established in 15–238 year-old stands and covered the main mixtures with European beech in Central Europe. The plots represent European beech growing in intra- and inter-specific neighbourhood with Norway spruce, sessile oak, or Scots pine throughout the whole rotation. The plots represented medium- to high-quality site conditions (Table 1), were fully stocked and the mixing

Box 1

Explanation of the main technical terms.

Term or concept	Explanation	Source
Aggregation	The horizontal tree distribution ranging from clumped (strong aggregation) to random (medium) and regular (low aggregation) distribution	Clark and Evans (1954)
Association, segregation	Intermingling patterns where species occur mainly in inter-specific (association) and intra-specific (segregation) neighborhood	Pielou (1961)
Competition reduction	Occurs when the interspecific competition for a limiting resource in mixtures is less than the intraspecific competition for this resource in the monocultures.	Kelty (1992), Vandermeer (1992)
Mixing degree	Intensity of intermingling of species in terms of inter-specific (association) and intra-specific (segregation) neighborhood	Pommerening et al. (2002), Pielou (1961)
Facilitation	Facilitation is a form of ecological interaction between different species that benefits at least one of the participants and causes no harm to the other	Stachowicz (2001)
Intermingling of species	horizontal distribution pattern in mixed-species stands	Gadow (1993)
Mixing pattern	Umbrella term that addresses the horizontal and vertical tree distribution in mixed-species stands	
Overyielding	When the production of biomass in species mixtures exceeds the stand growth expected on the basis of the growth of the contributing species in a monoculture	Forrester and Pretzsch (2015)
Rotation length, rotation time	Period between regeneration establishment and final cutting of even-aged forests	Helms (1998)
Single-tree-, row-, group-, and cluster-mixture	Intermingling patterns with increasing contiguous intra-specific growing space per species	Bauhus et al. (2017)
Stand structure	Horizontal and vertical tree distribution with the main aspects horizontal tree distribution, stand density, size differentiation, mixing proportion, and species intermingling	Pretzsch (2009, 1997)
Vertical stand structure	Vertical tree distribution pattern in terms of tree height variation.	del Río et al. (2017)

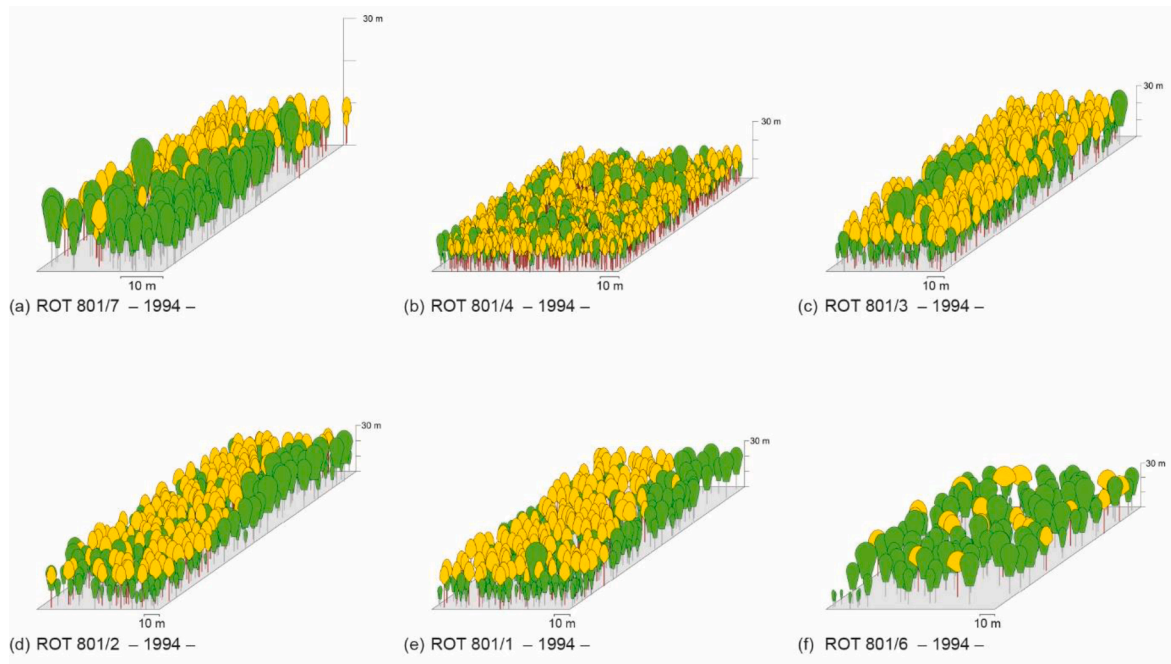


Fig. 1. Age series ROT 801 in sessile oak (yellow) and European beech (green) with six plots as an example for the setup of the eight age series used for this study. (a)–(f) show the six plots ranked by age increasing from 32 to 223 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Location, climate characteristics, and site conditions of the eight age series included in this study.

Age series	Name	Species combination	Longitude	Latitude	Elevation a.s.l	Annual precipitation	Mean temperature	Soil type	Substrate	Geology	Ecoregion
			°	°	m	mm yr ⁻¹	°C				see caption
FRE 813	Freising	N. sp., E. be.	11.66	48.42	515	814	7.7	parabrown soil	loam	tertiary sand	12.8
SON 814	Schongau	N. sp., E. be.	10.77	47.87	790	1114	6.8	brown soil	loam	Günz-Mindel lower moraine	14.4.1
NOR 811	Nordhalben	N. sp., E. be.	11.59	50.31	590	850	5.5	brown soil	stony loam	clay shale	8.1
KEH 804	Kelheim	s. oak, E. be.	11.76	48.93	455	721	7.5	brown soil	silt loam	tertiary sediments	6.2
ROT 801	Rothbuch	s. oak, E. be.	9.44	49.95	375	960	7.0	brown soil	silt loam	lower sandstone	2.2.1
SWE 803	Schweinfurt	s. oak, E. be.	10.30	50.13	340	660	8.0	brown soil	silt loam	lower trias	4.1
GEI 832	Geisenfeld	S. pi., E. be.	11.22	48.57	430	725	7.6	brown soil	loamy sand	tertiary sand	12.8
AMB 833	Amberg	S. pi., E. be.	11.83	49.35	480	650	7.5	brown soil	sandy loam	chalkstone	6.5

The ecoregion numbers indicate the following units (translation to English in brackets): 12.8 Oberbayerisches Tertiärhügelland (Upper Bavarian tertiary hills), 14.4.1 Westliche kalkalpine Jungmoräne (Western limestone young moraine region), 8.1 Franconwald (Franconian Forest), 6.2 Südlicher Oberpfälzer Jura (Southern Upper Palatinate jurassic region), 2.2.1 Hochspessart (Upper Spessart region), 4.1 Nördliche Fränkische Platte (Northern Franconian plateau region), 6.5 Oberpfälzer Jurarand (Upper Palatinate jurassic borderline region) (according to Arbeitskreis Standortkartierung (1985) Forstliche Wuchsgebiete und Wuchsbezirke in der Bundesrepublik Deutschland, 170p.).

N.sp., Norway spruce, and E. be. European beech; s. oak, sessile oak; S. pi., Scots pine.

patterns ranged from single-trees to cluster-mixture. Most of the stands were planted and even-aged. On some of the plots moderate thinning from above was applied in the second half of the 20–30-year survey period.

The eight age series were established in the 1990's for ad hoc data acquisition for parameterisation of an individual tree simulator for monospecific and mixed species stands in South Germany (Pretzsch et al. 2002). The plots belonging to one age series were established on similar sites and in close distance to each other. Since their establishment and initial survey the age series were remeasured up to five times. In this way the original chronosequences became real time series of long-term surveys. For instance, if the survey of a 30-year-old stand (e.g., first survey carried out 25 years ago) was repeated four times, the originally 30 year-old stand may be 55 years old at present and thus overlap with the survey data of the originally 50 year-old stand. For all considered mixtures we covered an age span of at least a whole rotation turnus.

The three-dimensional visualisation of the age series ROT 801 in Fig. 1, was based on the first inventory and tree coordinate measurements in 1994. The repeated measurements (last survey 2009) of the stem diameters, tree heights, and crown sizes are explained in detail in the next section. Supplementary Fig. 1 shows, for example, the crown maps of ROT 801. It reflects that the plots of this age series covers single-tree- as well as group-mixture of sessile oak and European beech. It also includes monospecific parts of both species. The crown sizes were visualized by concentric circles calculated as the quadratic mean of the eight crown radius measurements. The plot size increased from the young to the old stands (see 10 m scale at the bottom of each of the crown maps) in order to cover representative sections of the representative stand development phases. For instance, on ROT 801 the plot sizes varied according to stand ages between 0.09 and 0.81 ha.

2.1.2. Site characteristics

Information about location, climate characteristics, and site conditions of the eight age series is given in Fig. 2 and Table 1. The site has experienced environmental changes during the last 30 years; the mean air temperature increased by approx. 1 °C, whereas mean precipitation slightly decreased from 1990 to 2020. Both trends result in a negative progression of soil water availability as indicated by the soil moisture index, SMI, in Fig. 3. Applied mainly in climate research (Samaniego et al., 2010, 2013), the SMI has been successfully related to tree-ring

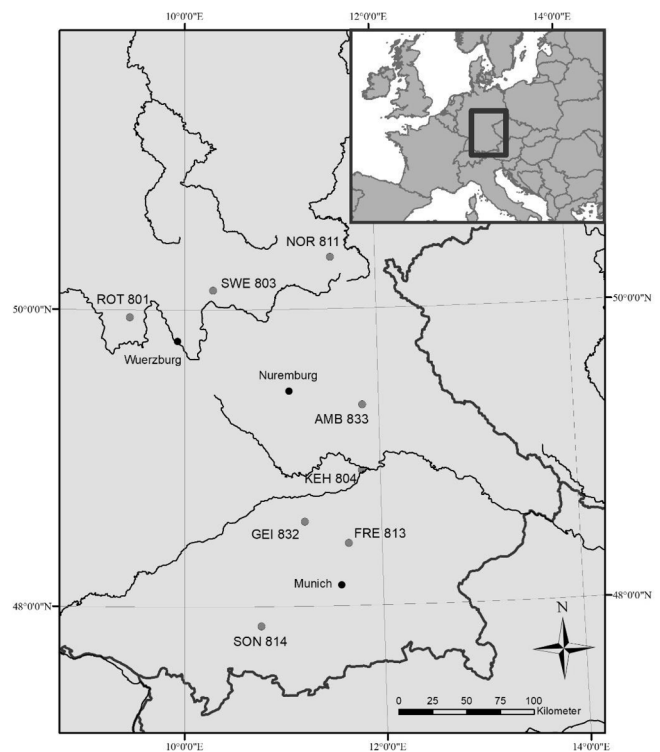


Fig. 2. Location of the eight age series NOR 811, SWE 803, ROT 801, AMB 833, KEH 804, GEI 832, FRE 813, and SON 814 (from north to south) in Germany (for further information see Table 1).

series in dendroecological studies to identify and analyse drought events (Schwarz et al. 2020).

We used the annual soil moisture index, SMI, for calculating the mean values for survey periods and for analysing how mixing effects are modulated by water supply (see H II). In this way we included any temporal changes of the water supply in the evaluation (see Section 2.3.1).

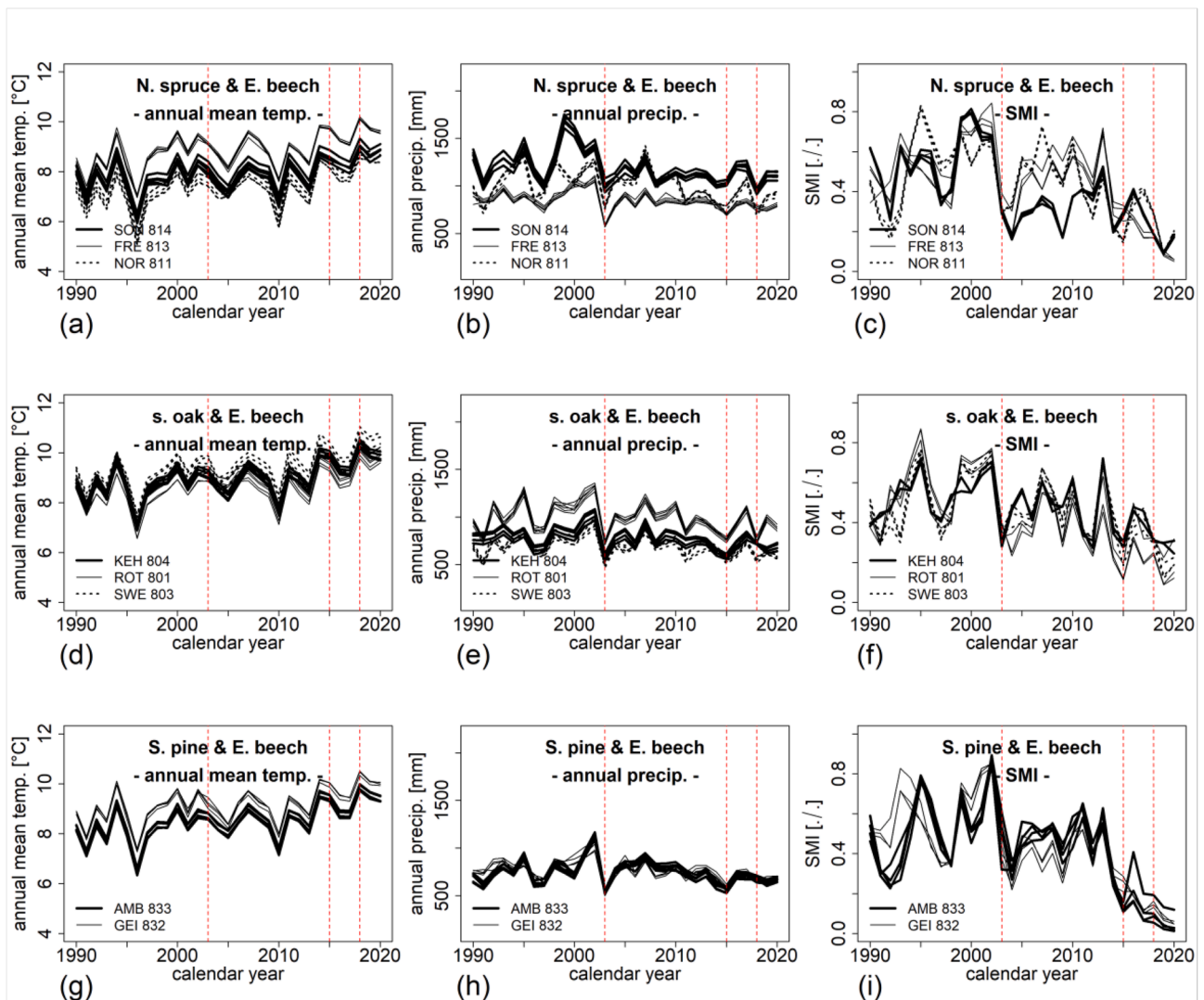


Fig. 3. Mean annual air temperature, annual precipitation and soil moisture index, SMI, on the plots of (a-c) Norway spruce and European beech, (d-f) sessile oak and European beech, and (g-i) Scots pine and European beech (Source: [DWD Climate Data Center \(2021\)](https://www.dwd.de/EN/Service/ClimateDataCenter/ClimateDataCenter.html) and <https://www.ufz.de/index.php?en=37937>, access July 15th, 2021).

2.1.3. Overview of measurements and metrics

Table 2 summarises the abbreviations and explanations of the main measurement variables, structural metrics, and the target variables used in this study. From all trees higher than 1.30 m, we recorded the species identity, measured the x- and y-coordinates of the tree positions at the first survey, and all stem diameters at 1.30 m stem height in the courses of each of the up to five surveys. Tree height (h) and height to crown base (hcb) of a subset of 30 trees selected uniformly over the whole diameter range were measured at each survey. Crown radii in the eight cardinal directions were measured only at one or two surveys. All these variables were also measured for the ingrowth since the first survey. The stand age was read off from the historical documentation of the stand establishment. If such documents were not available we derived the tree age by tree-ring counting on increment cores sampled at the foot of the trunks of three trees of each species per plot. Stand ages were assumed to be identical with mean tree age in case of natural regenerated stands. In planted stands, stand age were assumed to be mean tree age minus three years to take into account the usual age of plants coming from the nursery.

2.2. Descriptive data evaluation

2.2.1. Derivation of stand level characteristics

The main stand level characteristics were derived from the successive inventories of the tree diameters, tree heights, and records of the removal trees. The evaluation was based on the standard methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (in German “Deutscher Verband Forstlicher Forschungsanstalten”) (Biber, 2013, Johann, 1993). In the course of the repeated surveys the stem diameters were measured completely, the tree heights only randomly. For estimation of the individual tree height, h , depending on the stem diameter and tree age we parameterized the model

$$\ln(h) = a_0 + a_1 \times \ln(d) + a_2 \times \ln(\text{age}) + a_3 \times \ln(d) \times \ln(\text{age}) \quad (1)$$

for each species on each of the eight age series separately. For model parameters see Supplement Table 1. The tree heights were used for stem volume estimation in dependence on tree diameter, tree height, and form factor. For considering the stem form we used the approach by Franz et al (1973) with the stem form equations and coefficients published by Pretzsch (2002, p. 170).

Table 2

Overview of the metrics used in this study to characterise mixing pattern, stand growth, and overyielding on the sample circles.

Variables' and metrics' names	Abbreviation	Unit	Explanation and Indication
height of the tree with quadratic mean diameter	hq	m	indication of stand development phase, site index
stand volume growth	IV	$\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$	$IV = V_2 - V_1 + V_{\text{removal}}$
mixing proportion	m_1, m_2	./.	SDI based shares of the mixed species
segregation index by Pielou (1961)	S	./.	1-mixed pairs/equal pairs
aggregation index Clark & Evans (1954)	C & E	./.	observed/expected distance to nearest neighbor
coefficient of variation of d	CVd	cm	variation of tree size and height structure
site index of species 1 and 2	SI_1, SI_2	cm^{-1}	mean height at age 100
stand density index by Reineke (1933)	SDI	ha^{-1}	Reineke's SDI standardized for E. beech; a proxy for canopy density and light supply
overyielding of mixed vs. monospecific stands	O	./.	ratio between growth of mixed stands and the weighted mean growth of the monospecific component stands

The tree heights were also used for fixing the sample circle size for analyzing the relationship between stand structure and stand growth and overyielding (see Sections 2.3 and 2.4). The chosen circle radius of $sr = 0.25 \times hq$ (hq = height of the tree with the quadratic mean diameter) was large enough for estimating local growth and small enough for assessing different mixing proportions and intensities. For site indexing we used hq at age 100 and applied the yield tables (moderate thinning) by Norway spruce by Wiedemann (1936/42), for Scots pine by Wiedemann (1943), for European beech by Schober (1967, 1975), and for sessile oak by Jüttner (1955).

2.2.2. Rationale of analyzing the effect of stand structure and environmental conditions on overyielding

To analyse how stand growth (overyielding of mixed vs. monospecific stands) is modulated by the mixing pattern we sampled circular sections from the large plots, quantified the mixing pattern and growth on them, and analysed the relationships between mixing pattern and growth. The procedure comprised the random sampling of x-, and y-coordinates on the large plot and the construction of a sample circle with radius sr . All trees within this circle were used to derive characteristics of the mixing pattern and growth on the sample circles. This study and a preliminary study by Pretzsch and Schütze (2021) showed that this circle size resulted in the highest correlations between the characteristics of stand structure and growth. Each circle yielded a set of structural metrics, such as the segregation index by Pielou (1961), the aggregation index by Clark and Evans (1954), the stand density index by Reineke (1933), and the mixing proportion of the component tree species as introduced in Section 2.4. For each of the circles we also calculated the stand growth and for plots with mixing proportions $\geq 20\%$ the overyielding as introduced also in Section 2.4. The plots with mixing proportions $< 20\%$ provided the stand growth of the monospecific component species stands.

For positioning the sample circle centres we selected x- and y-coordinates randomly in a range that ensured that the sample circles and their surrounding buffer strip did not exceed the plot-edges (see Supplement Fig. 2). Choosing the sample circle radius depending on the mean height hq of the trees on the plot at the beginning of the respective survey period resulted in smaller circle areas in young stands and larger

areas in old stands. On average there were 18 trees on the sample circles and the circle size was 20 m^2 in young and 300 m^2 in old stands. By choosing the sample circle depending on the tree size we considered that the required stand area for capturing the mixing pattern and growth on the plots increases with age and average tree size.

The stand structure on the circles covered with species mixtures at a given survey was finally statistically related to the growth in the subsequent survey period. For example, the mixing structure of the survey in 2000, was related to the growth in the period 2000–2005. Per plot ($n_1 = 50$) we sampled on average 10 circles ($n_2 = 10$) for each of the on average four survey periods ($n_3 = 4$). Thus we obtained altogether data from about $n = 2000$ circles ($n_1 \times n_2 \times n_3 = 50 \times 10 \times 4 = 2000$). We used the circles with mixing proportions of $< 20\%$ of the component tree species as reference for monospecific stand structure and growth and for calculation of the overyielding as introduced in the next section. As about half of the 2000 circle represented monospecific stand conditions we finally arrived at 952, 1299, and 1177 mixed circles in stands of Norway spruce/European beech, sessile oak/European beech, and Scots pine/European beech, respectively. This data was used for analyzing how periodic overyielding of stem volume growth in mixed stands is modulated by mixing pattern and water supply.

2.2.3. Metrics for quantifying stand structure and growth in the sample circles

Mixing proportion: The trees in each circle were used to calculate the mixing proportions based on the SDI values according to Reineke (1933). The mixing proportions m_1, m_2 should reflect the area proportions of two or more species in the observed mixed stands (Dirnberger et al. 2017). To standardise the density and to calculate the unbiased area-related mixing proportions we applied the equivalence factors by Pretzsch and Biber (2016). The equivalence factors adjust these species-specific differences (see Supplementary Table 2 for the equivalence factors applied in this study).

Segregation index S by Pielou (1961): The intermingling of the two species was quantified by the segregation index, S, proposed by Pielou (1961). S is based on the nearest neighbor principle. From each tree in a given area this index uses the species identity as well as the species identity of the nearest neighbor. The index sets the observed number of mixed species pairs in relation to the expected number of mixed species pairs in case of a random distribution (Eqs. (2) and (3)).

$$S = 1 - \frac{\text{observed number of mixed pairs}}{\text{expected number of mixed pairs}} \quad (2)$$

S can be calculated according to Eq. (3) using the total number of trees, N, and the number of the following observed and expected subsets.

$$S = 1 - \frac{b + c}{N} \quad (3)$$

b = base tree species 1 and the nearest neighbor belonging to species 2
c = base tree species 2 and the nearest neighbor belonging to species 1

The sum $b + c$ represents the observed number of mixed pairs.
m = total number of base trees belonging to species 1
n = total number of base trees belonging to species 2
v = total number of the nearest neighbors belonging to species 1
w = total number of the nearest neighbors belonging to species 2

$$S = 1 - \frac{N \times (b + c)}{(v \times n + w \times m)} \quad (3)$$

The resulting index S lies between minus 1.0 and + 1.0. S values around zero indicate an independent distribution of both species. $S < 0$ indicates an intermingling and association of both species. $S > 0$ indicates a segregation, i.e. a tendency towards a separated occurrence of both species (Pretzsch 2009).

Using the species mixture of Norway spruce (red triangles) and European beech (green circles) Fig. 4a–c visualizes the principles of the segregation index S by Pielou (1961). The Fig. 4 shows the two species occurring strongly intermingled, independently, or separated (from a to

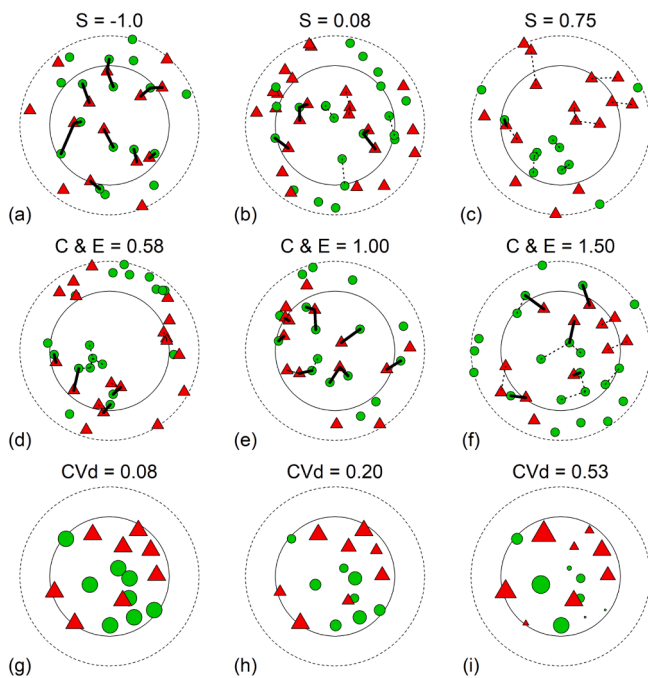


Fig. 4. Visualization of the segregation index S by Pielou (1961), aggregation index C&E by Clark and Evans (1954), and variation coefficient CVd of the stem diameter distribution for a mixture of Norway spruce (red triangles) and European beech (green circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

c) resulting in Pielou indices of $S = \text{minus } 1.0$ to $S = 0.75$. Values close to minus 1.0 indicate strong association and intermingling, $S = 0$ indicates independent distribution, and S close to 1.0 a separated occurrence in groups or clusters. In Fig. 4 the nearest neighbors are indicated by connecting lines. Mixed species pairs are indicated by bold connecting lines. Equal species pairs are indicated by broken connecting lines.

Aggregation index by Clark and Evans (1954): The C&E aggregation index was used for characterizing the horizontal tree distribution pattern. It indicates whether the trees are clumped, randomly distributed or regularly distributed. C&E lies between 0 (maximal clumping, the smallest mean distance to nearest neighbors) and 2.1491 (strictly regularly distributed in hexagonal pattern with maximum mean distance to the nearest neighbors) and can be calculated according to Eqs. (4) and (5).

$$C\&E = \text{observed mean distance to nearest neighbor} / \text{expected mean distance to nearest neighbor} \quad (4)$$

$$C\&E = \overline{dist}_{obs} / 2 \times \sqrt{n/A} \quad (5)$$

The index uses the observed mean distance \overline{dist}_{obs} to the nearest neighbor, i.e., the arithmetic mean of all distances between all trees and their nearest neighbor. This is divided by the expected mean distance, $\overline{dist}_{exp} = 1/2 \times \sqrt{n/A}$, to the nearest neighbor in case of a Poisson distribution pattern. Variable \overline{dist}_{exp} is calculated based on the respective total tree number, n , and underlying area A . A clustered tree distribution on the plot is indicated by low C&E values, C&E = 1 indicates random distribution, and the more the C&E values exceed 1.0, the more regular

is the respective horizontal tree distribution (Fig. 4, d-f). Whereas Clark and Evans (1954) named the aggregation index R , we call it C&E in the following in order to distinguish it from the coefficient of determination R .

Coefficient of variation of stem diameter: The coefficient of variation, CVd, of the stem diameter was used as a simple but meaningful measure of the tree size variation. Fig. 4, g-i shows rather similar trees sizes, medium and strong stem diameter variation indicated by the symbol sizes of both species. The CVd value increases with the site variation from CVd = 0.08–0.53. As the stem diameter is allometrically linked with tree height, a high CVd value also indicates a rich vertically structuring of the stand. In addition to S and C&E which characterize the horizontal distribution pattern, CVd indicates the vertical structure of the stand.

(a-c) The segregation index is $S = -1.0$ if both species are closely intermingled and it increases when they grow separately from each other. Mixed species pairs are indicated by bold connecting lines, equal species pairs are indicated by broken connecting lines.

(d-f) Increase of C&E from clustered to random and regular horizontal distribution pattern.

(g-i) The coefficient of variation of the stem diameter distribution increases from uniform to variable stem diameters, indicated by CVd = 0.08–0.53. Stem diameters are indicated by symbol sizes.

The analysis was based on the trees in the inner circle with radius sr . For nearest neighbor analyses of the trees at the edge of the inner circle we included a buffer zone with radius $sr + \text{mean tree-tree distance}$. Nearest neighbors are indicated by connecting lines; in several cases the nearest neighbors of edge trees were in the buffer zone.

Stand density by Reineke (1933): To characterize the stand density on the circles and analyse the density effect on stand growth on the circle we used the Stand Density Index, SDI, by Reineke (1933). The SDI is a measure of relative density. It provides the stand density in terms of trees per hectare for a stand with an index mean tree diameter of 25 cm. The SDI represents a proxy for the canopy density on the circles and the light supply of the respective trees. For calculating SDI all trees within the circle except the central tree were used to calculate the local density n on circle area a . $N = 10.000/a \times n$ was the respective tree number upscaled to one hectare. For the n trees, we calculated the quadratic mean stem diameter d_q ; based on N and d_q we then calculated the local density $SDI = N \times (25/d_q)^\alpha$ around each individual tree. The local SDI was calculated using the species-specific allometric exponents of $\alpha = -1.664$ for Norway spruce, -1.593 for Scots pine, -1.789 for European beech, and -1.424 for sessile oak, derived by Pretzsch and Biber (2005). Note that these exponents α were derived on unthinned and A-grade plots of long-term experiments in South Germany that are located in the same area as the ages series of this study. The used exponents

deviated from the species-overarching exponent of -1.605 , as proposed by Reineke (1933).

To standardise the density and to calculate the unbiased area-related mixing proportions and leaf area indices, we applied the equivalence factors by Pretzsch and Biber (2016). They take into consideration that the analyzed species vary per se in the growing area requirement and maximum stand density in fully stocked stands. For example, a European beech with a stem diameter of 25 cm may require approximately double the growing space as a Norway spruce of the same diameter, that is, the density in terms of trees per hectare is only half of that of Norway spruce. The equivalence factors adjust these species-specific differences (Pretzsch and del Río 2020).

Quantification of over- and underyielding: For quantifying any tree

species mixing effects on stand growth we calculated the ratio between the observed stand stem volume growth of the mixed stand, $p_{1,2}$, and the weighted mean growth of the two monospecific stands, $m_1 \times p_1 + m_2 \times p_2$ according to

$$O_{1,2} = (p_{1,2}) / (m_1 \times p_1 + m_2 \times p_2) \quad (6)$$

In this equation $p_{1,2}$ represents the growth of the mixed stand, m_1 and m_2 represent the mixing proportions of species 1 and 2 (see beginning of Section 2.2.2), and p_1 and p_2 are the productivities of the monospecific stands. If $O_{1,2} > 1.0$, this indicates an overyielding of the mixed stand compared with the weighted mean of the monospecific stands. For further explanation of the ratio of relative stand growth $O_{1,2}$ of mixed vs. monospecific stands see Pretzsch et al. (2017), Kennel (1965), Vandermeer (1992) and Jactel et al. (2018). In this study the growth of the monospecific stands, p_1 and p_2 , was derived from the monospecific parts of the experimental plots (circles with mixing proportion $m_1 < 0.20$ and $m_2 < 0.20$, respectively). $O_{1,2}$ was used for analyzing any dependencies of the mixing effects on stand structure regarding S, C&E, CVD etc.

2.3. Statistical models

2.3.1. Analyzing the dependency of overyielding on stand structure, stand age, and environmental conditions

For testing H I-III we applied the linear mixed effect models 1, a-c for

the mixtures of Norway spruce/European beech, sessile oak/European beech, and Scots pine/European beech, respectively. In the following equations the lower letters i and k represent the k^{th} observation on the i^{th} sample circle.

$$O_{ik} = a_0 + a_1 \times SDI_{ik} + a_2 \times S_{ik} + a_3 \times m_2 + a_4 \times C\&E_{ik} + a_5 \times age_{ik} + a_6 \times SMI_{ik} + a_7 \times S \times m_{2ik} + a_8 \times S \times SMI_{ik} + b_i + \epsilon_{ik} \text{ (Model 1a)}$$

$$O_{ik} = a_0 + a_1 \times SDI_{ik} + a_2 \times S_{ik} + a_3 \times m_2 + a_4 \times CVD_{ik} + a_5 \times age_{ik} + a_6 \times SI_{2ik} + a_7 \times SMI_{ik} + a_8 \times S \times SMI_{ik} + b_i + \epsilon_{ik} \text{ (Model 1b)}$$

$$O_{ik} = a_0 + a_1 \times SDI_{ik} + a_2 \times S_{ik} + a_3 \times m_2 + a_4 \times C\&E_{ik} + a_5 \times CVD_{ik} + a_6 \times age_{ik} + a_7 \times SMI_{ik} + a_8 \times S \times SMI_{ik} + b_i + \epsilon_{ik} \text{ (Model 1c)}$$

By these models we analyzed the dependency of the overyielding of mixed versus monospecific stands depending on the spatial mixing pattern (H I), the site conditions and periodic soil moisture index (H II), and depending on the stand age (H III).

2.3.2. Analyzing the relationships between stand structure and stand age

We further applied the models 2–6 to analyze the bivariate relationships between stand structure and stand age.

$$SDI_{ik} = a_0 + a_1 \times age_{ik} + b_i + \epsilon_{ik} \text{ (Model 2)}$$

$$S_{ik} = a_0 + a_1 \times age_{ik} + b_i + \epsilon_{ik} \text{ (Model 3)}$$

$$C\&E_{ik} = a_0 + a_1 \times age_{ik} + b_i + \epsilon_{ik} \text{ (Model 4)}$$

$$CVD_{ik} = a_0 + a_1 \times age_{ik} + b_i + \epsilon_{ik} \text{ (Model 5)}$$

$$m_{2ik} = a_0 + a_1 \times age_{ik} + b_i + \epsilon_{ik} \text{ (Model 6)}$$

In all models a random effect $b_i \sim N(0, \tau^2)$ was implemented at the circle level to consider that we sampled circles at the plot level in sub-

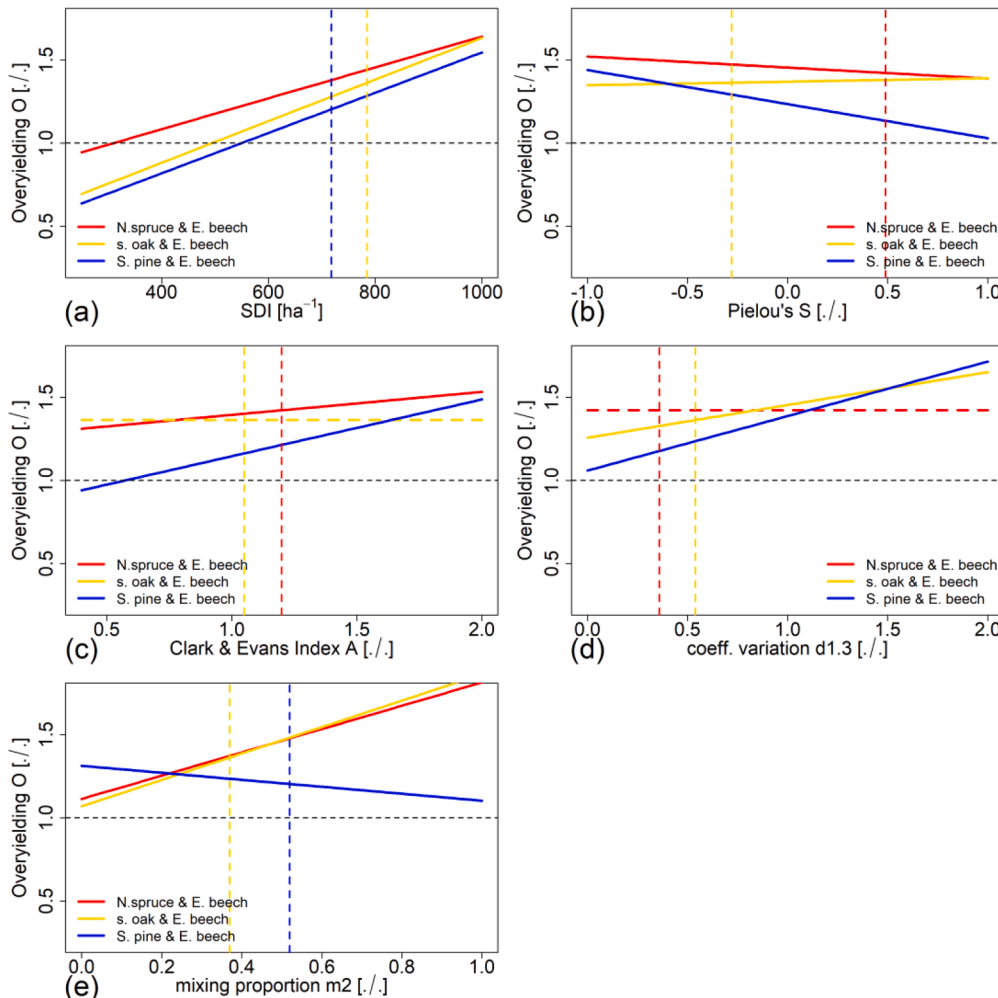


Fig. 5. Overyielding as modulated by (a) stand density index, (b) Pielou's segregation Index S, (c) Clark and Evans' index, C&E, (d) coefficient of variation of the stem diameter, CVD, and (e) mixing proportion m_2 of European beech. The overyielding is shown for mixed versus monospecific stands of Norway spruce/European beech (red), sessile oak/European beech (gold), and Scots pine//European beech (blue). Solid lines indicate significant relationships at the level ($p < 0.10$), broken lines indicate non-significant relationships. The horizontal lines (1.0-line) represents $O = 1.0$, i.e., parity of growth of mixed and monospecific stands. For this visualization all other variables except those in question were set to their overall mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sequent survey periods. In this way we covered the temporal correlation between the successive surveys. With $\epsilon_{ik} \sim N(0, \sigma^2)$, we denoted independently and identically distributed errors. In all equations a_0, \dots, a_n are the parameters of the fixed effects (see Supplementary Figs. 3-5 for visual residual diagnostics of models 1, a-c). The different age series of one species combination (e.g. FRE 8, SON, NOR) represent different site index levels, thus they correlated strongly with the site index. The different survey periods (e.g., including the drought years 2003, 2015, 2018) represented distinct differences in water supply, thus the calendar year correlated strongly with mean annual temperature, annual precipitation, and SMI. To not eliminate the effects of site index and periodical water supply we did not implement random effects at the age series and year level. Random effects at the age series and year level would have eliminated the effects on stand growth and overyielding which we wanted to analyse.

For all calculations, we used the statistical software R 4.1.0 (R Core Team, 2021), and we used the libraries nlme (Pinheiro et al., 2021) and lme4 (Bates et al., 2015).

Table 3

Overview of some stand structure and growth characteristics on the sample circles shown separately for the three tree species mixtures. The table reflects the mean, standard deviation, minimum, and maximum of the stand age, site index of species 1 and 2, SI, soil moisture index, SMI, quadratic mean stem diameter, dq, mixing proportions of both component species 1 and 2, m_1, m_2 , stand density index, SDI, Pielou's index, S, Clark and Evans' index, C&E, coefficient of variation of stem diameter, CVd, current growth of standing stem volume, IV, and overyielding, O, of mixed versus monospecific stand growth on the sample circles.

Variable	Unit	Mean (sd. dev)	Min-max
<i>Norway spruce & European beech</i>			
age	years	82.10 (26.17)	36.00-131.00
SI species 1	m	31.89 (2.02)	25.81-36.29
SI species 2	m	30.46 (2.74)	27.61-39.13
SMI	./.	0.48 (0.09)	0.30-0.61
dq ₁	cm	30.68 (10.45)	12.44-48.59
dq ₂	cm	24.87 (8.15)	10.56-46.64
m ₁	./.	0.66 (0.23)	0.01-0.99
m ₂	./.	0.34 (0.23)	0.01-0.99
SDI _{total}	ha ⁻¹	778.92 (173.98)	239.17-1584.43
S	./.	0.39 (0.53)	-1.00-1.00
C&E	./.	1.21 (0.19)	0.49-1.73
CVd	./.	0.34 (0.11)	0.08-0.78
IV	m ³ ha ⁻¹ yr ⁻¹	16.30 (7.01)	1.55-56.96
O	./.	1.36 (0.36)	0.14-1.98
<i>sessile oak & European beech</i>			
age	years	98.38 (42.21)	21.00-223.00
SI species 1	m	27.15 (2.28)	22.82-30.63
SI species 2	m	20.56 (5.61)	13.91-45.35
SMI	./.	0.52 (0.05)	0.45-0.64
dq ₁	cm	27.99 (11.60)	5.57-59.73
dq ₂	cm	14.96 (3.90)	6.51-34.37
m ₁	./.	0.70 (0.15)	0.10-0.98
m ₂	./.	0.30 (0.15)	0.02-0.90
SDI _{total}	ha ⁻¹	829.91 (217.15)	218.15-1690.58
S	./.	-0.48 (0.85)	-1.00-1.00
C&E	./.	1.06 (0.19)	0.38-1.67
CVd	./.	0.53 (0.14)	0.16-1.34
IV	m ³ ha ⁻¹ yr ⁻¹	11.37 (4.58)	0.17-35.15
O	./.	1.26 (0.38)	0.06-2.00
<i>Scots pine & European beech</i>			
age	years	86.58 (49.17)	18.00-124.00
SI species 1	m	32.28 (4.44)	29.01-40.91
SI species 2	m	32.74 (9.94)	25.43-51.66
SMI	./.	0.46 (0.05)	0.41-0.61
dq ₁	cm	23.91 (10.18)	8.93-31.60
dq ₂	cm	19.01 (7.45)	8.50-24.68
m ₁	./.	0.40 (0.26)	0.09-0.93
m ₂	./.	0.60 (0.26)	0.07-0.91
SDI _{total}	ha ⁻¹	908.75 (208.56)	334.72-1427.95
S	./.	0.16 (0.26)	-0.50-1.00
C&E	./.	1.11 (0.11)	0.90-1.52
CVd	./.	0.39 (0.06)	0.23-0.52
IV	m ³ ha ⁻¹ yr ⁻¹	13.71 (4.95)	5.62-25.38
O	./.	1.12 (0.43)	0.42-1.96

Table 4

Results of fitting the linear mixed effect models 1, a-c to the age series data of Norway spruce/European beech, sessile oak/ European beech, and Scots pine// European beech. AIC comparisons suggested using the circle as random variable. For visualization of the results see Figs. 5-7.

Fixed eff.	N. spruce & E. beech		s. oak & E. beech		S. pine & E. beech	
	est	se(est)	est	se(est)	est	se(est)
n	952		1299		1177	
intercept	-0.2778	0.1378	-0.7105	0.2028	-0.4972	0.1311
SDI	0.0009	0.0001	0.0013	0.0001	0.0012	0.0001
S Pielou	0.2763	0.1346	0.4004	0.2551	-0.5293	0.1256
m ₂	0.8534	0.0925	0.7940	0.0792	-0.2099	0.0506
C&E	0.1381	0.0601			0.3413	0.0494
CVd			0.1972	0.0790	0.3277	0.0757
age	0.0035	0.0006	0.0008	0.0005	0.0050	0.0008
SI sp. 2			0.0116	0.0043		
SMI	0.4117	0.1702	0.6201	0.2179	0.1210	0.1038
S × m ₂	-0.3125	0.1251				
S × SMI	-0.4181	0.2375	-0.7296	0.4838	0.6485	0.2452
rand. Eff.	Std. dev		Std. dev		Std. dev	
circle b _i	0.0853		0.1576		0.2111	
residuals	Std. dev		Std. dev		Std. dev	
ε _{ij}	0.3096		0.3139		0.2643	
AIC	556.28		775.24		302.62	
corr R ²	0.23		0.28		0.44	

3. Results

3.1. Overview of stand structure and growth at the stand and sample circle level

The stand volume was the highest (1774 m³ ha⁻¹) in the mature stands of Norway spruce/European beech. The annual stem volume growth was the highest in Scots pine/European beech (36.2 m³ ha⁻¹ yr⁻¹) and the lowest in mixed stands of sessile oak/European beech (18.8 m³ ha⁻¹ yr⁻¹). Supplementary Table 3 shows the stand characteristics over all surveys and reflects that all three considered species mixtures are represented by young to old stands. The range of the site indices of both component species is rather wide although the stands represent medium to excellent site conditions. The wide range of site indices within each age series is codetermined by the strong improvement of site index values in young stands due to environmental changes in the last decades (Spiecker et al. 2012).

The characteristics derived from the sample circles (Table 3) over all surveys for which the periodical stand growth in the subsequent survey period was available, were similar to the findings at the stand level. The characteristics summarized in Table 4 were the basis for analyzing the relationship between mixing pattern and overyielding. All latest surveys could not be included as the growth characteristics for the subsequent periods were not yet available. Therefore, the range of stand ages at the sample circle level was slightly lower than at the stand level. The site index values, SI, were similar to the findings at the stand level. The values of the soil moisture index, SMI, strongly varied, as the surveys covered some extremely dry years (Fig. 3). The quadratic mean diameters ranged between 6 cm and nearly 60 cm and reflect the wide range of stand development phases covered by the sample circles. The mean mixing proportion of European beech was m₂ = 0.34 in Norway spruce/European beech, similar in sessile oak/European beech (m₂ = 0.30), and much higher in Scots pine/European beech (m₂ = 0.60). The variation of the SDI values was low between the three mixtures but high within each group. Interestingly, the Pielou index indicates on average a tendency towards segregation in Norway spruce/European beech and sessile oak/European beech stands and a more independent distribution for Scots pine/European beech. However, the range of S values shows that the sample circles represent the whole range from close association to strong segregation of the two species. The values C&E and CVd also strongly varied between the circles. The overyielding was on average O

= 1.36 for Norway spruce/European beech, $O = 1.26$ for sessile oak/European beech, and $O = 1.12$ for Scots pine/European beech. The wide range of structural characteristics and IV values was promising for the following statistical analysis of the relationships between stand structure and stand growth.

3.2. Overyielding increases with the mixing degree (H I)

The scrutiny of H I for the mixtures of Norway spruce/European beech, sessile oak/European beech, and Scots pine/European beech was based on models 1, a-c, respectively. The effects of the variables SDI, Pielou's S, mixing proportion m_2 , Clark and Evans' Index C&E, coefficient of variation of the stem diameter CVd, and the mixing proportion m_2 are provided in Table 4 in terms of the model parameters. Table 4 represents the regression coefficients and their standard errors, the standard deviation of the random effects at the circle level, the residuals, the AIC, Akaike information criterion according to Akaike (1981), and the corrected R^2 (conditional R^2 including random effects). Variables with significant effects (level $p < 0.10$) are highlighted by bold types in Table 4, and they are visualized by solid lines in Fig. 5. Non-significant relationships are represented by horizontal broken lines.

Overyielding increased with stand density in all three mixtures (Fig. 5a). The standardized mean SDI values range between 718 and 785 (vertical broken lines). Stands with this density showed an overyielding of $O = 1.2-1.4$. Higher densities can even increase the overyielding.

The effect of Pielou's S was significantly negative for the mixture of Norway spruce/European beech and Scots pine/European beech (Fig. 5b). Notice, that low S values mean species association and strong intermingling, whereas high S values indicate species segregation. This means that the overyielding increased with the degree of intermingling, for both species combinations. In mixed stands of sessile oak and European beech the overyielding slightly increased when the species are growing segregated; i. e., European beeches growing close to sessile oaks may cause growth reduction.

Overyielding increased with increasing C&E values, i. e., with a regularity of tree distribution in case of Norway spruce/European beech and Scots pine/European beech (Fig. 5c). However, O was not affected by the horizontal tree distribution in case of sessile oak/European beech.

Tree size variation indicated by the variation coefficient of the stem diameter, CVd, was beneficial for overyielding in sessile oak/European beech and Scots pine/European beech mixtures. We found no significant

effect of CVd on overyielding in Norway spruce/European beech stands (Fig. 5d).

Mixing proportion of European beech increased the overyielding in the species combinations with Norway spruce and sessile oak, but reduced the overyielding in mixtures with Scots pine (Fig. 5e).

Very obvious is that most lines in Fig. 5 lie above the 1.0-line. The 1.0-line represents the equality of mixed and monospecific stand growth ($O = 1.0$). Relationships following this 1.0-line would indicate no differences between the growth of mixed and monospecific stands. Any decrease below this level occurred only beyond the range of mean structural values (vertical broken lines). In essence there was a strongly positive effect of increasing stand density (Fig. 5a), species association and intermingling S (Fig. 5b), regularity of horizontal tree distribution, C&E (Fig. 5c), and variation coefficient of stem diameter distribution CVd (Fig. 5d) on overyielding of all species combinations. The effect of mixing proportion m_2 of European beech on overyielding was less unitary (Fig. 5e).

The three models (models 1, a-c) were subject to the usual visual residual diagnostics. For this purpose, the residuals of all three were plotted against the fitted values (see Supplementary Figs. 3-5). In no case the plots suggested a violation of variance homogeneity. Likewise, normality of errors was verified by making normal q-q plots of the residuals. Supplementary Table 4 shows the prevailing low correlations between the independent variables in models 1, a-c.

3.3. Overyielding increases with improving environmental conditions (H II)

The site index of European beech varied between 20 and 35 m mean height at a stand age of 100 years. Independent on the site index, the overyielding was always positive ($O > 1.0$). In case of sessile oak/European beech there was even an additional positive effect of site index on overyielding (see Table 4, estimate 0.0116 ± 0.0043 , row SI sp. 2, column sessile oak/European beech).

Except in extremely dry stands of sessile oak and European beech ($SMI < 0.2$) the mixed stands were always more productive than monospecific stands along the whole range of SMI values. Under average SMI conditions of 0.49–0.52 the advantage was 20–35%. Fig. 6b reflects this by values of $O = 1.2-1.35$ in the mean SMI range of 0.49–0.52 (indicated by the broken vertical lines). Interestingly, the benefit of growing in mixture increased significantly with the periodical water

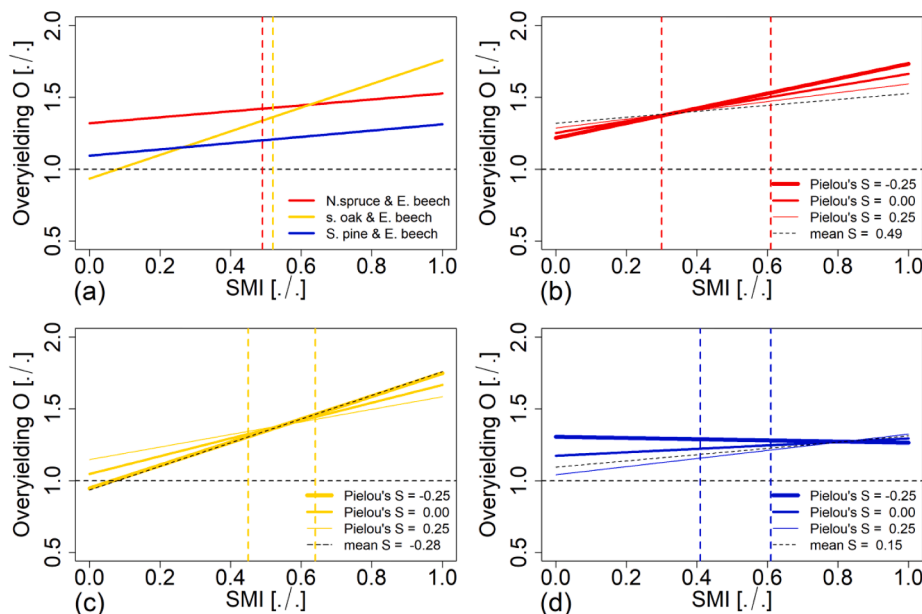


Fig. 6. The effect of the soil moisture index, SMI, on the overyielding, O, of mixed versus monospecific stands.

supply in terms of SMI in all three mixtures (Fig. 6a).

Fig. 6, b-d show the relationship between SMI and overyielding for different assumed levels of strong, medium and low species intermingling ($S = -0.25, 0$, and 0.25 , indicated by bold medium and thin lines). In addition, the black dotted lines in Fig. 6, b-d show the SMI-O relationship also for the mean intermingling ($S = 0.49, -0.28$, and 0.15) in the respective mixed stands. In case of Norway spruce/European beech and sessile oak/European beech we found that strong intermingling improved the positive effect of SMI on O, i. e., a positive interaction. In mixed stands of Scots pine/European beech, the interaction was negative, i.e., the beneficial effect of SMI on O was reduced in stands with strong intermingling (Fig. 6d). In the range of average SMI values (range between the vertical broken lines) overyielding increased with increasing intermingling. This means that both intermingling and SMI can increase the overyielding and can have a positive interaction effects.

(a) mean effect of SMI on O shown for Norway spruce/European beech (red), sessile oak/European beech (gold), and Scots pine//European beech (blue).

(b-d) effect of SMI on O as modulated by the species' intermingling quantified by Pielou's segregation index S. The relationships are shown for (b) Norway spruce/European beech, (c) sessile oak/European beech, and Scots pine//European beech (d).

The horizontal lines (1.0-line) represent $O = 1.0$, i.e., parity of the growth of mixed and monospecific stands. Solid lines indicate significant

relationships at the level $p < 0.10$. For the visualization all other variables except those in question (O, SMI, S) were set to their overall mean values. The dotted lines in (b-d) indicate the relationship between O and SMI for mean S values of $S = 0.49, -0.28$, and 0.15 .

3.4. Overyielding continues from young to old stand ages (H III)

Overyielding in mixed stands of Norway spruce/European beech and Scots pine/European beech was the lowest in young stands and increased continuously with stand age (Fig. 7a). The change of mixing pattern with progressing age showed a slight decrease of stand density (Fig. 7b), a strong trend to inter-specific association (Fig. 7c), and a continuous change from random to regular distribution pattern (Fig. 7d). The coefficient of variation of stem diameter (Fig. 7e) showed a mixture-specific behaviour and the mixing proportion m_2 (Fig. 7f) remained rather constant over stand age (see also model characteristics in Table 5).

The relationships are shown for mixed species stands of Norway spruce/European beech (red), sessile oak/ European beech (gold), and Scots pine/European beech (blue). Solid lines indicate significant relationships at the level ($p < 0.10$), broken lines indicate non-significant relationships. The horizontal line in (a) represents $O = 1.0$, i.e., parity of growth of mixed and monospecific stands. For the visualization all variables except those in question were set to their overall mean values.

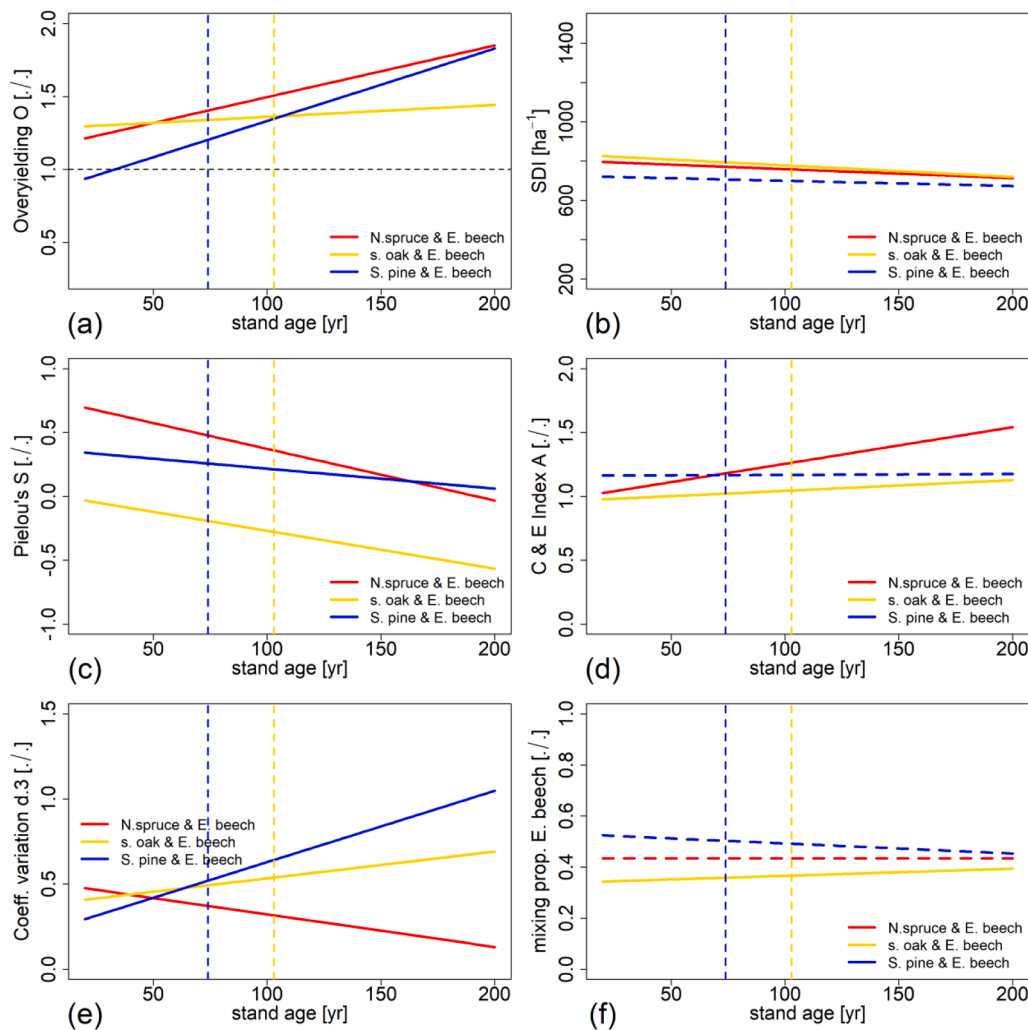


Fig. 7. Relationship between stand age and (a) overyielding, (b) stand density index SDI, (c) Pielou's S, (d) Clark and Evans' Index C&E, coefficient of variation of stem diameter, CVd, and (f) mixing proportion of European beech m_2 . Relationships are based on Model 1, a-c, in case of (a) and based on Models 2-6 in case of (b)-(f).

Table 5

Results of fitting the linear mixed effect models $2-6 y_{ik} = a_0 + a_1 \times age_{ik} + b_i + \varepsilon_{ik}$. As variable y we inserted and analysed SDI, Pielou's segregation index S , Clark and Evan's Index C&E, coefficient of variation CVd of stem diameter, and mixing proportion m_2 of European beech (models 2–6). AIC comparisons suggested using the sample circle as random variable.

Fixed eff. Variable	N. spruce & E. beech		N. spruce & E. beech		N. spruce & E. beech	
	est	se(est)	est	se(est)	est	se(est)
n	952		1299		1177	
SDI ~ age						
intercept	804.7426	26.2971	837.0818	26.3222	725.8914	38.1067
age	-0.4582	0.2793	-0.5878	0.1528	-0.2636	0.4588
rand. eff.						
circle b_i	45.1368		53.3191		63.6340	
residuals						
ε_{ij}	161.3019		197.8423		189.7292	
$S \sim age$					1177	
intercept	0.7769	0.1233	0.0271	0.0291	0.3737	0.0948
age	-0.0040	0.0008	-0.0030	0.0002	-0.0016	0.0009
rand. eff.						
circle b_i	0.3157		0.0314		0.1939	
residuals						
ε_{ij}	0.4621		0.3247		0.3284	
C&E ~ age						
intercept	0.9688	0.0272	0.9598	0.0262	1.1620	0.0474
age	0.0029	0.0003	0.0008	0.0001	0.0001	0.0004
rand. eff.						
circle b_i	0.0426		0.0554		0.0985	
residuals						
ε_{ij}	0.1756		0.1853		0.1575	
CVd ~ age						
intercept	0.5143	0.0203	0.3766	0.0171	0.2105	0.0667
age	-0.0019	0.0002	0.0016	0.0001	0.0042	0.0003
rand. eff.						
circle b_i	0.04529		0.0369		0.1580	
residuals						
ε_{ij}	0.0987		0.1154		0.1021	
$m_2 \sim age$			1299			
intercept	0.4352	0.0242	0.3378	0.0126	0.5322	0.0270
age	-0.0001	0.0003	0.0003	0.0001	-0.0004	0.0003
rand. eff.						
circle b_i	0.0377		0.0195		0.0399	
residuals						
ε_{ij}	0.1568		0.1211		0.1568	

4. Discussion

4.1. Explanation of the overyielding

In essence, the overyielding may be higher by increasing stand density and mixing degree, and it may be increased in wet compared to dry growth periods. The mean overyielding of mixed stands of 12–36% that we found over all kind of mixing patterns suggests that there are far-distantly (at the stand level) operating beneficial mechanisms in mixed compared with monospecific stands. This general overyielding may be attributed to a stand-wide facilitative effect caused by improvement of the soil conditions (e.g., accelerated decomposition and turnover), deeper light penetration of the canopy space (e.g., light flecks), or favourable bioclimatic conditions with the stand (e.g., improved air temperature and moisture, wind speed, CO₂-concentration). Literature provides evidence of nutrient and humus improvement (Augusto et al. 2002, Rothe and Binkley 2001), intensified rooting (Schmid and Kazda 2001), or increased microbial diversity and mycorrhizal networks (Steidinger et al. 2019, Nickel et al. 2018).

The additional increase of the overyielding, O , with increasing mixing intensity (decreasing S value) in stands of Norway spruce/European beech and Scots pine/European beech suggests close-distant (at the tree-level) operating mechanism such as competition reduction by crown complementarity. The increase of overyielding with intermingling intensity at parity of all other variables in case of Norway spruce/European beech and Scots pine/European beech (Fig. 5b) indicates an additional benefit from growing in close interspecific neighborhood. This positive effect of intense intermingling may be based on

competition reduction caused by morphological complementarity and spatial niche separation (Pretzsch, 2014; von Felten and Schmid 2008). Another cause may be temporal asynchrony of resource uptake and growth (del Rio et al., 2017; Jucker et al. 2015), resulting in a reduction of the inter-specific compared to intra-specific competition (Metz et al. 2020, Forrester, 2017, Pretzsch 2017). A well-described example of the crown shape complementarity is the combination of \blacktriangle -shaped Norway spruce or Scots pine (bottom heavy) and ∇ -shaped European beech (top heavy) crowns. It enables a higher canopy packing density and light use (Barbeito et al., 2017, Jucker et al., 2015; Pretzsch, 2014). In addition, it may reduce the mechanical abrasion and crown shyness (Hajek et al., 2015; Fish et al., 2006, Meng et al. 2006). This can result in a higher stand density (Thurm and Pretzsch, 2021) and leaf area (Pretzsch and Schütze 2021, Peng et al., 2017) in mixed compared with monospecific stands. In this study the higher crown packing density may have increased the stand density as described by Williams et al. (2017) and Jucker et al. (2015) and contributed to the increase of overyielding with stand density.

Whereas the stress gradient hypothesis (Holmgren and Scheffer 2010, Maestre et al. 2009) posits that under water stress facilitation may increase facilitative interactions between species, we found an opposite trend. In our study overyielding in all mixtures strongly increased with increasing soil moisture (Fig. 6a). This suggested that overyielding is at least partly based on competition reduction in our stands. If soil moisture, SMI, increases, competition for light or nutrients may increase. So, any inter-specific interactions that improve availability, uptake or use efficiency of light or nutrient will become more relevant for growth. In this way high soil moisture may increase the positive effect of species

complementarity and overyielding. In contrast, the limitation of water may hamper the trees' potential to harness the benefits of complementary structure and traits for resource acquisition (Freschet et al. 2013). The increase of O in moist periods and its decrease in dry periods is in line with Jactel et al. (2018) who found an analogous behaviour on moist versus dry sites.

The positive interaction effect of S and SMI on O in stands of Norway spruce/European beech and sessile oak/European beech (Fig. 6, b and c) indicates that SMI can be better exploited when species are intensively intermingled (low S values). In very dry periods, in contrast, it is more beneficial to grow separately. In mixed stands of Scots pine/European beech it was vice versa; in dry periods it was more beneficial to grow in inter-specific conditions than in wet periods. This may suggest facilitative effects such as hydraulic redistribution in those stands which represent the driest conditions in the set of analysed stands.

The overyielding was low in young stands but increased significantly in all three mixtures with proceeding stand development (Fig. 6a). We hypothesize that the beneficial effects of mixing may be amplified by continuous diversification of the litter and decomposers which accelerate the turnover and result in an improvement of the soil conditions and nutrient supply (Talkner et al. 2009). Another reason may be the continuous allometric acclimation of the crowns and roots to the inter-specific neighborhood and increasing occupation of the canopy and roots space (Jucker et al. 2020). Especially the plasticity of European beech (Bayer et al. 2013, Schröter et al. 2012) may cumulatively improve the complementary space occupation above (Juchheim et al., 2017; Pretzsch, 2014; Seidel et al., 2013) and below ground (Juchheim et al. 2017, Bolte et al. 2013).

4.2. Review of the applied material and methods

In this study we calculated the overyielding based on the merchantable stem volume growth (stem parts ≥ 7 cm at the smaller end) and based on form factors by Franz et al. (1973) mainly derived from stems in monospecific stands. Form factor equations or allometric relationships for trees in mixed stands were not yet available (Forrester, 2014, 2017). Aboveground stem volume, biomass, or carbon sequestration would probably be slightly higher for trees in mixed compared to monospecific stands due to the more plastic and extensive crown space occupation (Pretzsch, 2019, Bayer et al. 2013, Dieler and Pretzsch 2013). The wood density of trees in mixed stands might be lower compared with monospecific stands as found by Zeller et al. (2017). The overyielding calculated on the basis of the above ground biomass would be similar in magnitude to the overyielding that we calculated based on stem volume. The plus of volume growth by the more extended crown may be partly counterbalanced by the minus due to lower wood density.

In other studies the introduced characteristics of stand structure and mixing pattern were mainly used for describing mixed species stands (del Río et al. 2016, Pommerening et al. 2000). Here, we used them for analysing the effect of the mixing pattern on the overyielding of mixed stands. The aspect of intermingling, for example, could be quantified very well by the index of segregation by Pielou (1961), as this index indicates the number of mixed pairs and in this way the degree of intermingling. Our study suggests, that in addition to competition indices (Olivier et al. 2016, del Río et al. 2014, Pukkala et al. 2014) structural metrics such as the segregation index by Pielou (1961) or the aggregation index by Clark and Evans (1954) are useful for quantifying and modelling the neighborhood of trees and its effect on tree growth. This study suggests the use of structural metrics for describing, analyzing, and modeling the growth of mixed stands.

The circle-based sampling of structure and growth on mono- and mixed species trials in this study is a makeshift for analysing relationships between structure and growth. It may be used as long as appropriate experiments are not available. Occasional moderate thinnings from above on some of the plots in the second half of the 20–30-year survey period were considered by the current stand density. In further

analyses, how mixing pattern and environmental conditions code-terminate the dynamics of mixed stands, future experiments should cover stand density, thinning, mixing proportion, and mixing patterns as experimental factors. The effect of environmental conditions may be revealed by establishing future multi-factorial experiments on different sites. Such kind of experiments require large plots and will provide substantial knowledge for better understanding, modeling, and silvicultural design of mixed-species stands (Uhl et al. 2014).

4.3. Relevance for silvicultural prescriptions and management

Mixed species stands of Norway spruce/European beech, sessile oak/European beech, and Scots pine/European beech represent more than two thirds of the tree species mixtures in Central Europe (Brus et al. 2012). In view of climate change especially the area of the more drought resistant mixtures with sessile oak and Scots pine will likely further increase in future (Pretzsch et al., 2013, 2015). Certainly stand growth represents only one of many ecosystem services which determine silvicultural strategies and prescriptions (Biber et al. 2015). However, stand growth is crucial for many other services (Dieler et al. 2017, Potschin-Young et al. 2018). Tree and stand growth determine, e.g., forest structure, habitats, and biodiversity, wood supply, financial income, and C-sequestration (Schwaiger et al. 2019, Biber et al. 2015).

Most relevant for silvicultural prescriptions is our finding that growth of mixed stands was generally higher compared with monospecific stands and that the superiority continued throughout the whole rotation. The overyielding can be further increased by, among others, strong intermingling, vertical structuring, and regular horizontal distribution. In contrast to the general superiority, the species-specific reaction patterns are much more difficult to include in extensive silviculture. The selection of a defined number of future crop trees and release by removal of neighbours at the end of the pole stage (stand age about 20 years and mean tree height about 12 m) is a common silvicultural prescription for monospecific stands since long (Abetz 1974, 1988). Recently it has been transferred to mixed species stands (Utschig et al. 2011, BaySF 2009, 2010). However, silvicultural prescriptions based on monospecific stands may be misleading when applied to mixed-species stands (Bastien 1997, Llobet 2004). For instance, they may neglect that mixed stands often have higher stand densities and growth rates. Thus, when silvicultural guidelines for monospecific are applied to mixed stands they may prescribe overly strong stand density reductions, and thereby they may undercut maximum stand growth. Our findings suggest that the number of crop trees may be chosen higher in mixed than in monospecific stands due to the increase of crown packing and maximum stand density in mixtures. A regular distribution of crop trees may be advantageous and by thinning from above the size structure may be kept heterogeneous which again can be beneficial for overyielding (see Fig. 5).

The component tree species may initially grow in monospecific groups or clusters to avoid inter-specific outcompeting in the early stand age. This may be achieved by group mixtures at the beginning. In middle-aged and mature stands the initial group mixtures may be transformed to single tree mixtures by removal of neighbors of the same species and disintegration of the inter-specific groups and clusters. In this way the initial grouping is later transformed to a single-tree mixture with full potential of facilitative and competition reduction effects as revealed in this study.

The results of this study suggest a superior growth of mixed species stands under climate change in terms of drought years. Even in dry years we found an overyielding, though it significantly increased in wet years. Overyielding improved when water supply was ample, however, it was still significant in dry years. That mixed stands did not show any underyielding compared with monospecific stands is in line with Jactel et al. (2018) who found higher overyielding on wet sites but still no underyielding on dry sites. This indicates that growing in inter-specific neighborhood is beneficial in dry years and it can be even more

beneficial in wet years. It suggests, that mixing is beneficial under current conditions and also under future drier site conditions. Maybe the benefits of mixtures are based on facilitation in dry years and on competitive reduction in wet years. The mixing effects were positive in term of stand growth along the whole environmental gradient represented in this study.

5. Conclusions and next steps

This study showed a generally higher growth of mixed stands with European beech compared with monospecific stands. The overyielding continued throughout the whole rotation turnus, and it increased with water availability. Such general statements are essential for further development of silvicultural prescriptions for mixed species stands (Pretzsch et al. 2021, Bauhus et al., 2017). The effect of mixing proportion of beech, mixing pattern and size variation on overyielding were less general but species dependent.

Here, we used existing age series with large plots for extracting information about mixing pattern and growth by a circle sampling approach. This was a makeshift. It bridges the knowledge gap as long as multi-factorial experiments are not yet available for deriving urgently needed know-how for advanced silvicultural prescriptions for mixed stands. Poorly substantiated silvicultural prescriptions may cause high silvicultural efforts and costs to avoid demixing and bestow the potential of overyielding. New mixed-species experiments should consider especially stand density, mixing proportion, mixing degree as experimental factors and cover a broad range of site conditions and tree species combinations. Such experiments may contribute to further quantification and understanding of the mixing effects and their dependence on the mixing pattern. This may result in an overview and typing of species combinations and their main mixing reactions and create the basis for more general silvicultural prescriptions for mixed species stands.

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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Author contributions statement

HP initiated and conceptualised the study, HP evaluated the data, wrote, and revised the manuscript.

Appendix A. Supplementary material

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