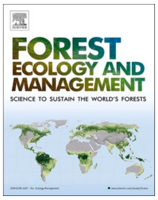
Forest Ecology and Management 539 (2023) 121008

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Mortality reduces overyielding in mixed Scots pine and European beech stands along a precipitation gradient in Europe

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ARTICLE INFO

Keywords:
Mixed species stands
Gross and net overyielding
Tree mortality
Self- and alien-thinning
Dropout stem volume
Stand density
Demixing

ABSTRACT

Many studies show that mixed species stands can have higher gross growth, or so-called overyielding, compared with monocultures. However, much less is known about mortality in mixed stands. Knowledge is lacking, for example, of how much of the gross growth is retained in the standing stock and how much is lost due to mortality. Here, we addressed this knowledge gap of mixed stand dynamics by evaluating 23 middle-aged, unthinned triplets of monospecific and mixed plots of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) repeatedly surveyed over 6–8 years throughout Europe. For explanation of technical terms in this abstract see Box 1.

First, mixed stands produced more gross growth (+10%) but less net growth (−28%) compared with the weighted mean growth of monospecific stands. In monospecific stands, 73% of the gross growth was accumulated in the standing stock, whereas only 48% was accumulated in mixed stands. The gross overyielding of pine (2%) was lower than that of beech (18%). However, the net overyielding of beech was still 10%, whereas low growth and dropout of pine caused a substantial reduction from gross to net growth.

Second, the mortality rates, the self- and alien-thinning strength, and the stem volume dropout were higher in mixed stands than monospecific stands. The main reason was the lower survival of pine, whereas beech persisted more similarly in mixed compared with monospecific stands.

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https://doi.org/10.1016/j.foreco.2023.121008
Received 13 January 2023; Received in revised form 3 April 2023; Accepted 8 April 2023

Third, we found a 10% higher stand density in mixed stands compared with monospecific stands at the first survey. This superiority decreased to 5% in the second survey.

Fourth, the mixing proportion of Scots pine decreased from 46% to 44% between the first and second survey. The more than doubling of the segregation index (S) calculated by Pielou index (S increased from 0.2 to 0.5), indicated a strong tendency towards demixing due to pine.

Fifth, we showed that with increasing water supply the dropout fraction of the gross growth in the mixture slightly decreased for pine, strongly increased for beech, and also increased for the stand as a whole.

We discuss how the reduction of inter-specific competition by thinning may enable a continuous benefit of diversity and overyielding of mixed compared with monospecific stands of Scots pine and European beech.

1. Introduction

Many studies report an overyielding of mixed stands (del Río et al., 2022, Jactel et al. 2018, Liang et al. 2016, Binkley et al. 2003). For a definition of overyielding and other technical terms see Box 1. The total stem volume or biomass growth of mixed stands can be up to 30% higher than the weighted mean of neighbouring monospecific stands (del Río et al., 2022, Jactel et al., 2018). In a mixture with nitrogen-fixing trees, the overyielding can even be higher (Binkley et al., 2003, Forrester et al., 2006). Due to structural and functional niche complementarity, mixed species stands' canopy packing can be denser than monospecific stands (Jucker et al., 2015, Pretzsch 2014). Thus ceteris paribus, the maximum stand density of mixed stands can be higher (Ammer 2019, Pretzsch and Biber 2016). The overyielding can be caused by species complementarity and inter-specific facilitation (Forrester and Bauhus 2016, Kelty 1992, Ammer 2019), and can continue from young to mature forest stands (Pretzsch and Schütze 2021). Although analyzed frequently and preferentially, total annual or periodical stand growth and over- or underyielding in terms of total stand growth are only one component for understanding mixed stands and when comparing them with monocultures. Mortality is another important but much less considered component. The few available studies, e.g., Binkley et al. (2003) or Searle et al. (2022) highlighted that mixing can significantly change mortality compared with monospecific stands and modify how much of the total stand growth is accumulated in the standing stock and how much drops out.

Box 1

Explanation of technical terms as used in this study.

Technical term	Explanation
alien-thinning	natural elimination of trees caused by inter-specific competition
competition	Ecological interaction in which one organism or species consumes a resource that would have been available to and could have potentially been consumed by the other, and hence the fitness of one is lowered by the presence of another
demixing	competition-based reduction of a species' mixing proportion with progressing stand development
dropout volume	stem volume dropout caused by competition-related mortality and natural disturbances
gross stand growth	annual stand growth in terms of basal area, stem mass or stem volume growth per year in a defined survey period
intra- and interspecific competition	competition within one species or between two or more species
mortality rate	ratio between the number of trees per unit area that died within a defined survey period and the initial tree number at the beginning of the period
natural thinning	natural elimination of trees caused by intra- or inter-specific competition
net stand growth	gross stand growth minus natural dropout of basal area, stem mass, or stem volume per year in a defined survey period
over- and underyielding	growth of a mixed species stand in relation to the weighted mean of neighboring monospecific stands of the same age, treatment, and site conditions; it can be calculated based on gross or net stand growth
relative stand density, SDI	A widely used measure developed by Reineke (1933) that expresses the relative stand density in terms of the relationship of a number of trees to their quadratic mean diameter. In order to eliminate the effect of stand development phase, the ratio is allometrically adjusted to an index stem diameter of 25 cm
self-thinning	natural elimination of trees caused by intra-specific competition
spatial segregation	horizontal mixing pattern of trees where different species occur rather in clusters or groups than in individual tree mixture
standing stock	accumulated basal area, stem volume, or stem mass per unit area of a forest stand at a given point in time or at a given stand age

For a deeper understanding of mixed species stand dynamics, the growth, mortality, and ingrowth at both the stand and species levels are essential for accurately comparing the performance of mixed-species stands to monocultures and for informing management strategies. Here, we focus on even-aged mixed-species stands within one rotation without ingrowth of young trees. In the early phase of such stands, as long as there is sufficient space for all trees, most of the annual growth is accumulated in the standing stock and the dropout by self- or alien-thinning is still low. With progressing stand development, stand density increases, space becomes scarce, and the annual size growth becomes concomitant with the dropout of trees.

According to Zeide (2001), the elimination of trees by competition in unmanaged stands is called natural thinning. Following Harper (1977, p. 171), self-thinning is the natural thinning that occurs mainly in monocultures caused by conspecifics. On the other hand, alien-thinning is the natural thinning of mixed populations when one species is reduced or outcompeted by another species. In this study of unthinned stands, "gross growth" refers to the total growth of the stand whereas 'dropout' refers to the portion of growth that is eliminated by competition-based mortality (self- or alien-thinning). The'net growth' is defined as the difference between gross growth and dropout volume. Fig. 1 visualizes the difference between gross and net growth based on the saw-tooth curve of stand basal area, volume, or mass development within a given survey period.

All three components - gross growth, dropout, and net growth - are relevant for stand dynamics and production ecology. The gross growth indicates the site-specific productivity level. The dropout shows the ephemeral part that results in turnover that finally causes deadwood (Pach et al., 2022) and carbon emissions, and provides nutrients for the survivers (Anderegg et al., 2013). The net growth is the part of the gross growth that is retained in the standing stock, i. e. the permanently visible result (Binkley et al., 2003, Franklin et al., 2009). Over a rotation length, the dropout in unthinned stands can add up to about 30% of the gross growth, i. e., only about 70% of the gross growth is accumulated in the standing stock (Assmann 1970, pp. 227-228). For instance, in stands of Scots pine or European beech, which are in the focus of this study, on sites with good quality in Central Europe, the gross volume yield until age 120 may be 1000 $m^3\ ha^{-1}$, whereas the standing stock is only 700 $m^3\ ha^{-1}$ (Pretzsch and Grote, 2023 accepted, Pretzsch et al., 2016).

Most mixed stand studies deal with gross growth, showing that mixed stands can have higher gross growth than monocultures (e.g., Ruiz-Peinado et al., 2021, Steckel et al., 2020, Thurm et al., 2016). However, even if their gross growth is higher and they overyield

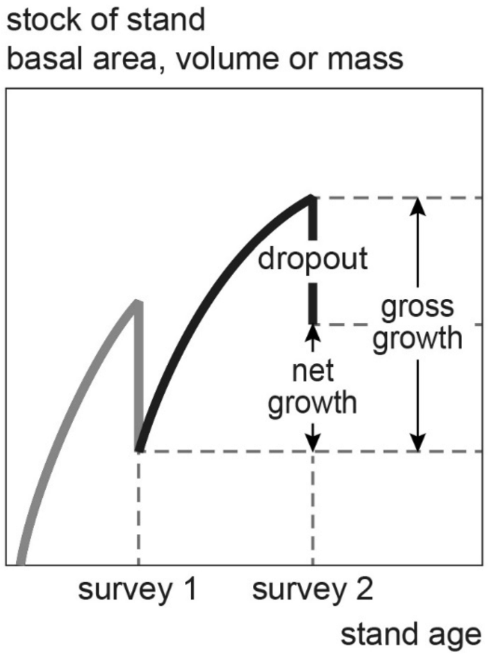

Fig. 1. Schematic visualization of gross stand growth, net stand growth and dropout, based on the saw-tooth curve of stand basal area, volume, or mass development within a given survey period. In this study of unthinned stands the dropout represented the competition-based elimination of trees (i.e., self-thinning + alien-thinning; see Box 1).

monospecific stands, the net growth of mixed stands may be lower due to a higher dropout. An inferior net growth at the species level may reduce one species' mixing proportion or even contribute to continuous demixing, although the stand level indicates an overyielding. Thus, an indication of gross growth over- or underyielding is part of the story but not sufficient for system understanding and management of mixed stands.

In mixture the productivity of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) can be significantly higher than the weighted mean productivity of monospecific stands of the same species (Pretzsch et al., 2015, del Río et al., 2022) and the overyielding can even increase with water supply (Pretzsch 2022a). Jactel et al. (2018) found the increase of overyielding with humidity as a general trend and hypothesized that under moist conditions, tree species mixtures can better benefit from the complementarity of light use; this may be especially true for mixtures of light-demanding and shade-tolerant species such as Scots pine and European beech (Barbeito et al., 2017). Mixing can also increase stand density throughout a broad range of site conditions (Pretzsch and Biber 2016). Based on inventory data along a wide ecological gradient Condés and del Río (2015) showed that the site conditions modified the interactions between Scots pine and European beech in mixed stands versus monospecific stands in terms of growth and mortality and could result in a stand density increase by mixture (Condés et al., 2017). The latter studies addressed the role of mortality in overyielding which can be studied better on long-term plots with repeated measurements as they provide more complete details on gross growth, volume dropout by mortality, and net growth (Fig. 1). Condés and del Río (2015) found stronger competition reduction with increasing humidity. These results and other studies suggest a stronger competition for light at humid sites (Weiner and Thomas 1986, Pretzsch and Biber 2010) that might be partially released by mixing species (Forrester 2014) but may also trigger higher above-ground growth and mortality for staying in the game. All three components are essential for understanding the effects of mixing on stand dynamics (Binkley et al., 2003, Searle et al., 2022).

To provide a more conclusive overview of the mixing effects on the stand and species level, we here exemplarily analyzed the gross growth, dropout, and net growth as well as the resulting stand density and mixing proportions, based on the repeated measurements of 23 triplets of unthinned monospecific and mixed middle-aged stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.). More specifically, we studied the gross and net overyielding at the stand and species level (Q1), the mortality, natural thinning, and dropout of stem volume (Q2), the stand density (Q3), the development of the proportions and patterns of species mixing (Q4), and the dependency of growth and mortality on site conditions (Q5).

2. Material and methods

2.1. Material

We based this study on a set of triplets of Scots pine and European beech (Fig. 2) that were established and surveyed first in 2013/2014 along a stand productivity gradient through Europe mainly determined by water supply (Heym et al., 2017). Out of the original 32 triplets established for analyzing the growth and overyielding of mixed versus monospecific stands (Pretzsch et al., 2015), we used 23 that were still intact for repeated measurement in 2020/2021.

The 23 triplets are spread over 11 countries (Fig. 3). The triplets represent the overlap of the natural ranges of Scots pine and European beech very well (see Supplementary Figures 1 and 2), with triplets at the northern border in Lithuania and the southern range in Bulgaria and Spain. The study covers the far southwest region in Spain and reaches to the eastern border of Ukraine. Most triplets are in the central European area in Germany, the Czech Republic, and Poland, where mixed stands of Scots pine and European beech have a share of up to 30% of the forest area (Brus et al., 2012). For the triplets in the entire study region, the mean annual temperature ranges from 8.2 to 11.8 °C, the annual precipitation from 723 to 1,178 mm, and the elevation from 20 to 1,289 m a. s. l. (Table 1) The meteorological data refer to the period 2013–2021 and were based on Harris et al. (2020, updated annually). For more plot details see Supplementary Table 1.

All triplets are sets of three rectangular plots, including one pure stand of Scots pine, one pure stand of European beech, and one mixed stand of these species. The plot size varies between 0.014 and 0.473 ha. All triplets represent even-aged, fully stocked and mono-layered forest stands. The plots were not thinned in the last 2–3 decades before their establishment and represent approximately maximum stand density. Mixed plots represent individual tree- and group-mixtures, and the mixing proportion (based on the SDI values, see section 2.3) of Scots pine varied between 18 and 72% according to the first survey (Pretzsch et al., 2015) and between 8 and 63%, according to the second survey. The plots within a triplet have similar site conditions. The pure stands are used as the reference for the mixed stands and for quantification of mixing effects in terms of overyielding or underyielding of mixed compared with pure stands. We inventoried the plots to derive the dendrometric state variables for the tree and the stand level.

2.2. Tree and stand measurement and variables

From each tree that was>7 cm of diameter at 1.30 m height, we recorded the species identity, measured the x- and y-coordinates at the first survey, and all stem diameters at breast height and survival status (alive/dead) in both surveys. Tree height (h) and height to crown base (hcb) of a subset of trees were measured in both surveys. For this purpose, we sampled about 30 trees per species uniformly over the whole diameter range. In the successive survey, we preferably used the same sample trees to measure the tree height and height to the crown base. However, we replaced them with neighbours of similar stem diameter in case they had died. Crown radii in the eight cardinal directions were measured only at the first survey but of all trees. The stand age was derived from tree ring counting on the increment cores and in some

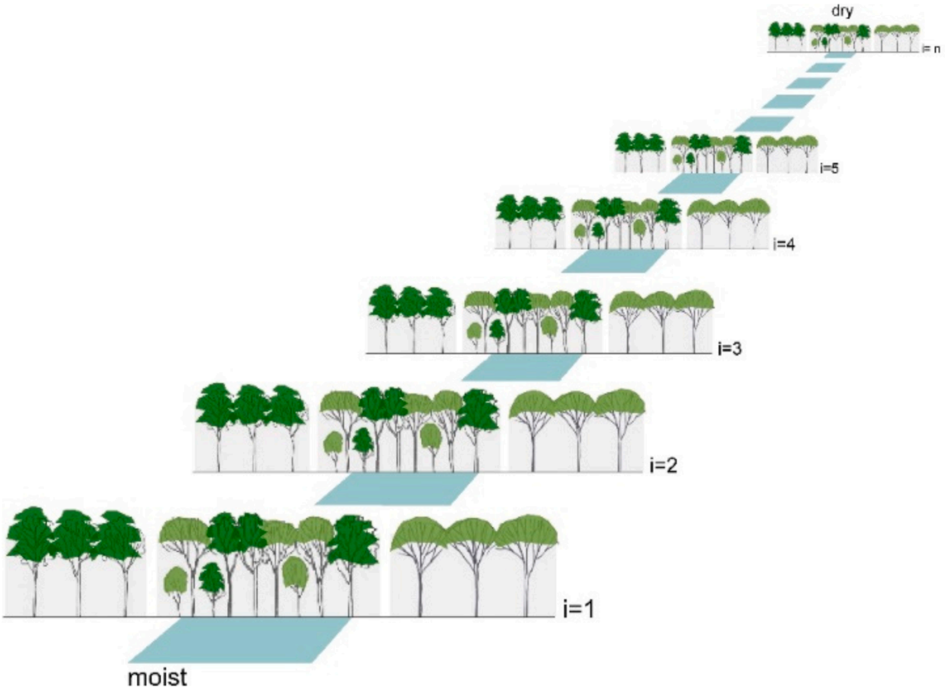

Fig. 2. Principle of the transect study: an ecological gradient from moist to dry sites included 23 triplets, consisting of pure Scots pine stands, pure European beech stands, and mixed stands of Scots pine and European beech, which were established in autumn 2013/2014 and re-measured in 2020/ 2021.

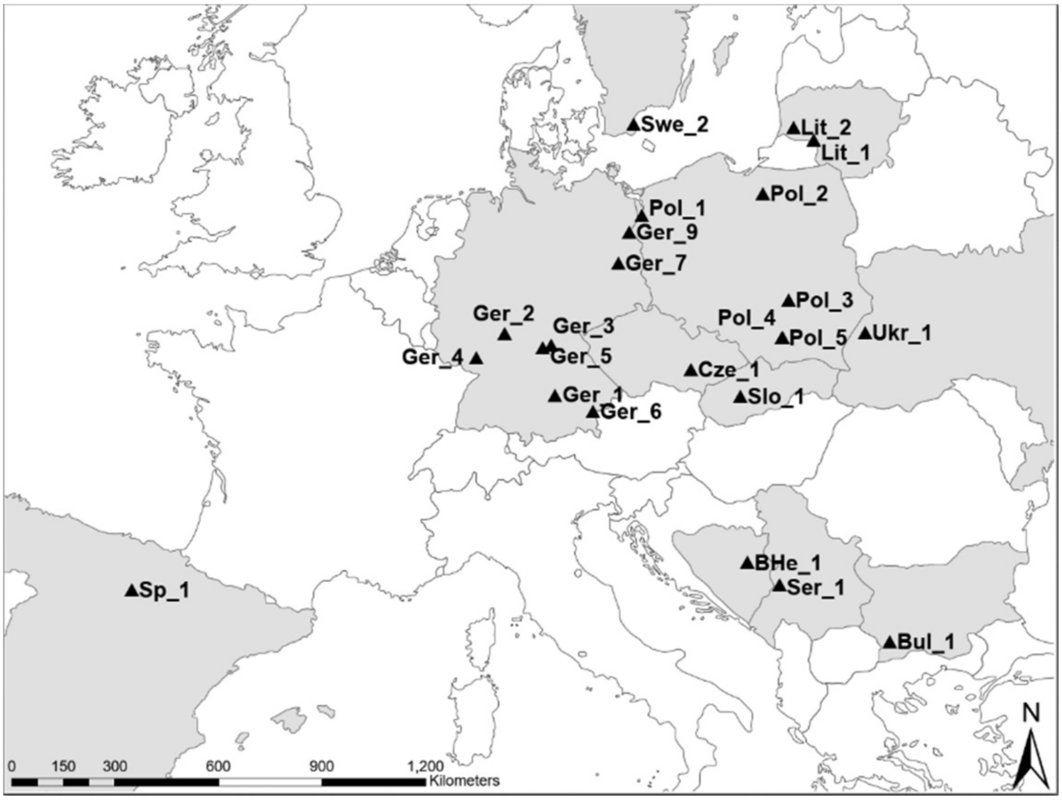

Fig. 3. Location of the 23 triplets of pure and mixed stands of Scots pine and European beech, which were remeasured in the autumn of 2020 and 2021. The triplets are spread over 11 countries: Bosnia-Herzegovina (BHe 1), Bulgaria (Bul 1), the Czech Republic (Cze 1), Germany (Ger 1–7, 9), Lithuania (Lit 1–2), Poland (Pol 1–5), Serbia (Ser 1), Slovakia (Slo 1), Spain (Sp 1), Sweden (Swe 2), and Ukraine (Ukr 1). The triplet numbers refer to the first (2013–2014) survey. For further information see Supplementary Table 1 and Supplementary Figures 1 and 2.

Table 1
Overview of the 23 triplets of Scots pine (S. pi.) and European beech (E. be.) used for this study. The sample tree numbers refer to the first (2013/2014) and second (2020/2021) survey, and the mean annual temperature (T), annual precipitation (P) and aridity index (Ma) (de Martonne, 1926) refer to the period 2013–2021.

Species combination		plot size (ha^{-1})	Number trees 1st survey (trees $plot^{-1}$)	Number trees 2nd survey (trees $plot^{-1}$)	Longitude (°)	Latitude (°)	Elevation (m a. s. l.)	T (°C)	P (mm yr^{-1})	Ma (mm °C^{-1})
S.pi. & E.be. mixed	mean	0.142	96	95	15.785	49.650	371	9.8	723	36.8
	min	*0.037*	*40*	*40*	*−3.172*	*41.900*	*20*	*8.2*	*532*	*26.0*
	max	*0.462*	*190*	*188*	*23.662*	*55.710*	*1289*	*11.8*	*1178*	*60.9*
S.pi. mono	mean	0.063	52	51	15.797	49.650	370	9.8	723	36.8
	min	*0.014*	*20*	*20*	*−3.167*	*41.900*	*20*	*8.2*	*532*	*26.0*
	max	*0.148*	*234*	*217*	*23.660*	*55.710*	*1339*	*11.8*	*1178*	*60.9*
E.be. mono	mean	0.078	52	51	15.790	49.630	368	9.8	723	36.8
	min	*0.018*	*20*	*20*	*−3.176*	*41.900*	*20*	*8.2*	*532*	*26.0*
	max	*0.473*	*141*	*142*	*23.670*	*55.710*	*1252*	*11.8*	*1178*	*60.9*

cases corrected by historical documentation of the stand establishment. For this purpose we read off the tree age by tree ring counting on increment cores (which reach the pith at a height of 1.30 m), sampled during the first survey. This average tree age was then increased by the estimated time it likely took the tree to grow to reach 1.3 m (3 years in case of Scots pine and 5 years in case of European beech). Stand ages were assumed to be identical to mean tree age in the case of naturally regenerated stands. In planted stands, stand age was assumed to be the mean tree age minus three years to account for the usual age of plants coming from the nursery.

The stand level characteristics were derived from the successive inventories of the tree diameters, tree heights, and records of the dropout trees. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (Biber 2013, Johann 1993). For estimating the stem volume in dependence on tree diameter, tree height and form factor, we used the approach by Franz et al. (1973) with the stem form equations and coefficients published by Pretzsch (2002, p. 170). The results encompassed the quadratic mean tree diameter, stand basal area, and stand volume. By applying the generalized stem biomass functions (see Supplementary Table 2) by Forrester et al. (2017) for Scots pine and European beech, we also calculated the stem mass for the total stand, dropout, and remaining stand for both surveys (more information about the measurements and evaluation is given by Pretzsch et al. (2015), and data is provided by Heym et al. (2017).

The remaining stem volume at the first survey (V1remain), the total stem volume at the second survey (V2total), the remaining stem volume at the second survey (V2remain), and the length n of the survey period in years were used to calculate the annual stem volume gross growth, net growth, and dropout (Fig. 1) as follows: mean annual gross growth= (V2total-V1remain)/n, mean annual net growth=(V2remain-V1remain)/n, and mean annual stem volume dropout=(V2total-V2remain)/n. The gross growth, net growth, and dropout of the stand basal area and stem mass were calculated analogously.

2.3. Specific metrics used in this study

We repeatedly combined tree and stand variables with the annotation $x_{\text{S.pi.}}$ or $x_{\text{E.be.}}$ if we refer to the characteristic in the monospecific stands of Scots pine or European beech, respectively. The expression $x_{\text{S. pi., E.be.}}$ refers to the mixed stand in total and $x_{\text{S.pi., (E.be.)}}$ or $x_{\text{(S.pi.), E.be.}}$ to the characteristics of Scots pine or European beech in the mixed stand respectively.

For characterizing the site conditions, stand structure, natural thinning process, and mortality we used the following variables and metrics.

T, P: mean annual temperature and annual precipitation based on gridded data provided by national meteorological services or on the Climatic Research Unit (CRU) Time-Series (TS) Version 3.10 database (Harris et al., 2020) were used.

de Martonne index: For characterizing the climatic conditions, we used the de Martonne aridity index ($M = P/(T + 10)$) (de Martonne, 1926). We selected these annual climate variables as they describe in a simple way the large variability of climates covered by study sites, from the Mediterranean to boreal climates, and are related to productivity variation at large scales (Huang and Xia 2019).

Site index: For site indexing, we used the height *hq* of the tree with the quadratic mean stem diameter at age 100 and applied the yield tables by Wiedemann (1943) for Scots pine and Schober (1975, 1967)) for European beech. As input variables for the site indexing we used *hq* of each stand read off the diameter-height curves and the stand age.

SDI: Stand density index according to Reineke (1933), calculated with exponents $\alpha_{N,d} = -1.593$ for Scots pine and $\alpha_{N,d} = -1.789$ for European beech, according to Pretzsch and Biber (2005).

Mixing proportion, m: The mixing proportions were based on the SDI values. The mixing proportions m_1 and m_2 reflect the area proportions of the two species in the observed mixed stands (Dirnberger and Sterba, 2014). To standardize the density and calculate the unbiased area-related mixing proportions, we applied the equivalence factors introduced by Pretzsch and Biber (2016) and calculated based on the unthinned monospecific stand plots of each triplet. The equivalence factors adjust for the species-specific differences in the growing space requirement when calculating area related mixing proportion.

The coefficient of variation of stem diameter, CVd: was used as a simple but meaningful measure for the tree size variation (del Río et al., 2016, Schall et al., 2018). CVd is related to the vertical stand heterogeneity. As the stem diameter is allometrically linked with tree height, a high CVd value indicates a rich vertical structuring within the stand.

dNddq as a measure for self- and alien-thinning: The ratio dNddq = dN/N/ddq/dq quantifies the proportion of trees eliminated by a certain increase in average diameter. The tree elimination is represented by dN/N and the increase in stem diameter by ddq/dq. The smaller the ratio, the more trees drop out with the same increase in diameter. A slope of dNddq = −1.605 is well known as a self-thinning slope in monospecific stands (Reineke 1933); lower ratios, e.g. dNddq = −2.00 of a species in mixed stands would indicate a detrimental alien-thinning effect of inter-specific compared with intra-specific competition (Harper, 1977, p. 171). A higher slope would mean a competition release and improved species persistence in mixed stans compared to monospecific stands.

Mortality rate, Mort: Mortality rate calculations were based on the tree numbers N_b at the beginning and N_e at the end of the n-years-long observation periods (Pretzsch et al., 2020). Using the compound interest formula $N_e = N_b \times 1.0r^n$ (r = decimale interest rate, n = number of years), the mean annual mortality rates, MR, and mortality percentages, MP = MR × 100, were calculated to compare the mortality of various tree groups of interest (e.g., monospecific vs. mixed). For this purpose, the basic equation $N_e = N_b \times 1.0r^n$ was transformed to $1.0r = \sqrt[n]{N_e/N_b}$ and $r = \sqrt[n]{N_e/N_b}$, with r representing the annual rate of tree number change, e.g. 0.95. The mortality rate MR is 1-r, i.e., $MR = 1 - \sqrt[n]{N_e/N_b}$ and the percentage of mortality is $MP = MR \times 100$. Note that the term 1.0r is the convention of writing ‘1.0 + r’ in financial mathematics, with r being the decimal interest rate.

Dropout basal area, stem volume, stem mass: The dropout of basal area, stem mass or volume was calculated as the difference between the standing stock at the second survey with and without the dropout by self- and alien thinning.

Aggregation Index R by Clark and Evans (1954) ***for quantifying the horizontal distribution:*** The x- and y-coordinates of the stems were used for quantifying their horizontal spatial distribution by the aggregation index C&E by Clark and Evans (1954). R is based on the nearest neighbor principle; for plot edge correction we applied the method by Donnelly (1978). R uses the distance to the nearest neighbor from all trees on the plot to calculate the mean observed distance $\bar{r}_{obs}$. The observed mean distance is devided by the mean distance $\bar{r}_{exp}$ expected under random distribution (Poisson distribution) of the points (Pretzsch 1997). The index by Clark and Evans is the ratio $R = \bar{r}_{obs}/\bar{r}_{exp}$ and can theoretically range from 0 at maximum tree clustering to 2.1491 at the regular hexagonal distribution of trees. It indicates random distribution if $R = 1.0$. $R > 1.0$ indicates regular and $R < 1.0$ clumped tree distribution. We calculated the R-values for both surveys to analyze the development of the horizontal distribution pattern.

Segregation index S by Pielou (1961)***:*** The intermingling of Scots pine and European beech was quantified by the segregation index, S, proposed by Pielou (1961), which is based on the nearest neighbor principle. From each tree on a given plot, this index uses the species identity and 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 the case of a random independent distribution $S = 1 - \text{observed number of mixed pairs} / \text{expected number of mixed pairs}$. Values close to −1.0 indicate a strong association between species, intermingling $S = 0$ indicates an independent distribution and S close to 1.0 indicates a separated occurrence in clusters.

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 of the two monospecific stands, $m_1 \times p_1 + m_2 \times p_2$, according to $O_{1,2} = (p_{1,2})/(m_1 \times p_1 + m_2 \times p_2)$. The productivity of the monospecific stands, p_1 and p_2, was derived from the monospecific experimental plots. If $O_{1,2} > 1.0$, it indicates an overyielding of the mixed stand compared with the weighted mean of the monospecific stands. The overyielding was calculated for both gross growth (total growth in a given period) and net growth (total growth minus dropout in a given period). 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). The required mixing proportions were derived as introduced above.

2.4. *Characteristics of stand growth and structure*

In Table 2, we summarize the main dendrometric stand characteristics. We quantified the growth and yield in terms of stand basal area (m^2 ha^{-1} yr^{-1}), stem volume (m^3 ha^{-1} yr^{-1}), and stem mass (t ha^{-1} yr^{-1}). However, gross and net overyielding analyses were based on the stem volume; for analogous analyses based on basal area and stem mass, see Supplementary Figures 3 and 4.

The mean C&E aggregation indices of 0.89–0.94 indicate for all stand types a closeness to the random distribution pattern of the trees on average (Table 3). However, the minimum and maximum values reveal that Scots pine represents a broader range of distribution patterns, from clumped to regular, compared to the mixed stand and the monospecific beech stands. The segregation index S shows that both species were randomly mixed on average but that the triplets also cover stands with strong association and segregation between the two species. The average mixing proportion was close to parity. CVd indicates that the average structural diversity was highest in the mixed stands and the lowest in the Scots pine monocultures, but the ranges were similar. The average SDI values were the highest in the Scots pine stands, the lowest in the beech monocultures, and in between in the mixed stands, although the greatest SDI was found in a mixed stand.

2.5. *Statistical evaluation*

For testing differences of overyielding values from zero and for testing group differences regarding net and gross growth, mortality and density (Q1-Q4), we used the one and two-sample t-tests.

For analyzing the dependencies of growth and mortality on site conditions (Q5), we used OLS regression. For all calculations, we used the statistical software R 3.6.3 (R Core Team 2022).

3. Results

3.1. *Gross versus net overyielding at the stand and species level (Q1)*

Fig. 4a shows for the mixed stands a total overyielding (ratio of mixed to monospecific stand growth > 1) of gross stem volume growth (OG) and a total underyielding (ratio < 1) of net stem volume growth (ON). The gross overyielding amounted to $OG_{S.pi,E.be} = 1.12 \pm 0.08$ (mean ± SE) and the net overyielding to $ON_{S.pi,E.be} = 0.39 \pm 0.25$; the

Table 2

Stand characteristics of the triplets of pure and mixed species stands of Scots pine and European beech. (S.pi., E.be.) characteristics for the mixed stand of Scots pine and European beech as a whole; S.pi., (E.be.) and (S.pi.), E.be. for Scots pine and European beech in the mixed stand; S.pi. and E.be. characteristics for the monocultures of Scots pine and European beech, respectively. N, tree number per ha; dq quadratic mean stem diameter; hq height of the tree with the quadratic mean stem diameter; BA stand basal area; V standing stem volume (merchantable wood with diameter > 7 cm at the smaller end); W standing stem mass per hectare; IBA, IV, and IW, mean periodic gross growth of basal area, stem volume, and stem mass per hectare.

species		N (ha^{-1})	dq (cm)	hq (m)	BA (m^2ha^{-1})	V (m^3ha^{-1})	W (t ha^{-1})	IBA ($m^2ha^{-1}yr^{-1}$)	IV ($m^3ha^{-1}yr^{-1}$)	IW (t $ha^{-1}yr^{-1}$)
S.pi., E.be.	mean	833	25	24	44.4	560	195	0.78	13.08	3.93
	min	*234*	*15*	*12*	*13.4*	*165*	*64*	*0.12*	*4.56*	*1.27*
	max	*2103*	*45*	*39*	*79.8*	*1111*	*350*	*1.42*	*27.3*	*6.99*
S.pi., (E.be.)	mean	293	31	25	23.4	288	88	0.32	4.88	1.39
	min	*32*	*17*	*13*	*4*	*44*	*15*	*0.08*	*0.02*	*0.34*
	max	*914*	*53*	*36*	*44.6*	*660*	*181*	*0.81*	*12.92*	*3.23*
(S.pi.), E.be.	mean	540	22	22	21	272	107	0.46	8.19	2.54
	min	*114*	*11*	*9.8*	*9.5*	*96*	*50*	*0.17*	*2.18*	*0.88*
	max	*1533*	*44*	*38*	*40.4*	*538*	*200*	*0.75*	*19.14*	*4.29*
S.pi.	mean	859	26	23	45.1	522	163	0.79	12.55	3.33
	min	*225*	*14*	*12*	*24.8*	*202*	*75*	*0.28*	*0.02*	*0.33*
	max	*1764*	*42*	*33*	*68.8*	*1036*	*278*	*1.47*	*21.66*	*5.72*
E.be.	mean	898	24	23	38.3	517	201	0.75	14.1	4.24
	min	*178*	*13*	*11*	*19.9*	*208*	*100*	*0.13*	*0.65*	*1.02*
	max	*2385*	*47*	*42*	*56.7*	*907*	*317*	*1.27*	*29.12*	*7.37*

Table 3

Structural characteristics (mean, minimum, and maximum values) of the monospecific and mixed species plots of Scots pine and European beech based on the last survey in 2020/2021. C&E, Clark and Evans index (1954); S Pielou segregation index (1961), m, mixing proportions of Scots pine and European beech; CVd, coefficient of variation of stem diameter; SDI, stand density index according to Reineke (1933).

species	group		C & E (./.)	S (./.)	m S.pi. (./.)	m E.be. (./.)	CVd (./.)	SDI (ha^{-1})
S.pi., E.be.	mixed	mean	0.94	0.05	0.44	0.56	0.39	694
		min	*0.42*	*−0.39*	*0.08*	*0.37*	*0.17*	*218*
		max	*1.22*	*0.62*	*0.63*	*0.92*	*0.53*	*1275*
S.pi.	mono	mean	0.89	–	–	–	0.27	730
		min	*0.17*	–	–	–	*0.10*	*426*
		max	*1.44*	–	–	–	*0.51*	*1046*
E.be.	mono	mean	0.94	–	–	–	0.36	624
		min	*0.43*	–	–	–	*0.24*	*335*
		max	*1.34*	–	–	–	*0.50*	*962*

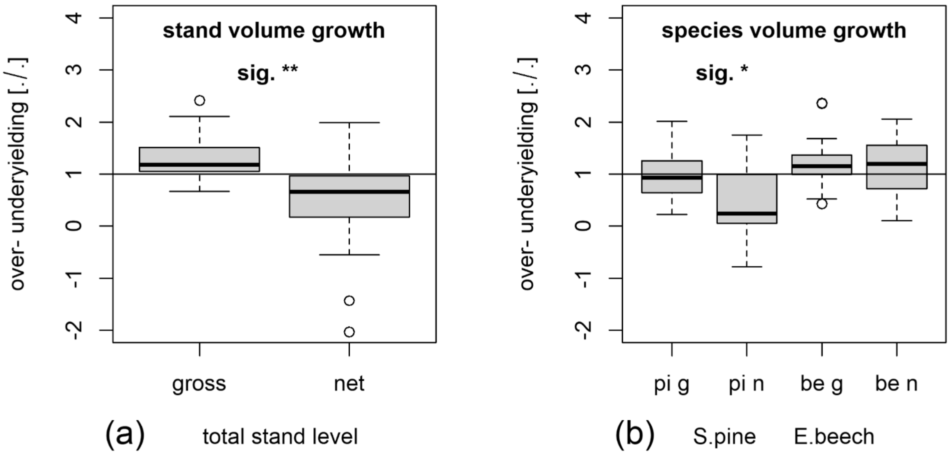

Fig. 4. Relative over- and underyielding of both gross and net growth of stem volume growth (m^3 ha^{-1} yr^{-1}) visualized for (a) the total stand and (b) the species level. The y-axis represents the ratio of the growth in mixed stand compared with monospecific stands. The ratio is shown for gross and net overyielding. Abbreviations pi and be, Scots pine and European beech; g and n, gross and net overyielding. The symbols ** and * indicate significant differences between the boxes below at level $p \leq 0.01$ and $p \leq 0.05$, respectively.

$OG_{S.pi,E.be}$ value was slightly ($p = 0.078$) >1.0 (1.0 = parity of mixed and monospecific stand growth) and the $ON_{S.pi,E.be}$ value was significantly ($p = 0.013$) lower than 1.0 The gross overyielding was significantly ($p = 0.004$) different from the net overyielding (see Supplementary Table 3 for statistical evaluation).

The analyses at the species' level (Fig. 4b) revealed that Scots pine (first and second box from the left) showed no significant overyielding ($p = 0.220$) regarding gross growth ($OG_{S.pi,(E.be)} = 1.11 \pm 0.15$) and a slight ($p = 0.054$) underyielding of net growth ($ON_{S.pi,(E.be)} = 0.62 \pm 0.22$). European beech in contrast (Fig. 4b, third and fourth box from the left) showed a significant ($p = 0.021$) gross growth overyielding ($OG_{(S.pi),E.be} = 1.22 \pm 0.10$) but no significant ($p = 0.35$) net growth underyielding ($ON_{(S.pi),E.be} = 0.99 \pm 0.16$). The results of the test of OG and ON against 1.0 and of the group comparison between gross and net mean values are shown in Supplementary Table 3. An analysis of the gross and net overyielding based on the stand and species basal area and stem mass growth yielded similar results (Supplementary Figures 3 and 4).

The upper part of Table 4 reveals that the mixing effects at the stand level are only partially reflected when quantified by the gross growth. The mean observed gross stem volume growth was 13.35 m^3 ha^{-1} yr^{-1} in mixed stands whereas the weighted mean of the monospecific stands was 12.15 m^3 ha^{-1} yr^{-1}, i. e. by 10% ($p = 0.207$) higher. The mean observed net growth was 28% lower ($p = 0.061$) than the weighted mean of the monospecific stands. The reason for this discrepancy is the 113% higher ($p < 0.001$) dropout in the mixed stands. From the gross yield in monospecific stands, 73% is allocated in the standing stock,

Table 4

Partitioning of the mean gross stand volume growth (m^3 ha^{-1} yr^{-1}) into dropout and net growth (from left to right) and comparison of mono with mixed stand growth (from top to bottom). All fractions are given in m^3 ha^{-1} yr^{-1} as well as in percentage of values of gross growth and monospecific stands set to 100%. See Supplementary Tables 4 and 5 for results on stand basal area and stand stem mass growth.

Group		gross (m^3 ha^{-1} yr^{-1})			dropout (m^3 ha^{-1} yr^{-1})			net (m^3 ha^{-1} yr^{-1})		
		abs	SE	rel	abs	SE	rel	abs	SE	rel
S.pi., E.be., exp.	abs	12.15	0.72	*100*	3.26	0.60	*27*	8.89	0.98	*73*
	rel	*100*			*100*			*100*		
S.pi., E.be., obs.	abs	13.35	1.26	*100*	6.96	1.17	*52*	6.40	1.68	*48*
	rel	*110*			*213*			*72*		
S.pi. mono	abs	11.76	0.92	*100*	3.42	0.94	*29*	8.34	1.24	*71*
	rel	*100*			*100*			*100*		
S.pi., (E.be.)	abs	12.02	1.57	*100*	11.53	3.45	*96*	0.48	3.64	*4*
	rel	*102*			*337*			*6*		
E.be. mono	abs	13.13	1.16	*100*	2.89	0.91	*22*	10.23	1.64	*78*
	rel	*100*			*100*			*100*		
(S.pi.), E.be.	abs	15.44	1.69	*100*	4.19	1.03	*27*	11.25	2.26	*73*
	rel	*118*			*145*			*110*		

whereas it is only 48% in the mixed stands. In mixed stands, we observed that 52% of the gross growth dropped out, whereas the dropout based on the weighted mean of the monocultures was only 27%.

The lower part of Table 4 shows that the mixing reactions of Scots pine and European beech differed in gross yield but even more in net yield, in agreement with Fig. 1. The mean gross yield of Scots pine in mixed stands is 2% greater than the mean expected (relation between S. pi., (E.be.) and S.pi. mono, 102%), whereas the mean gross yield of European beech increases to 18%. The picture changed when we looked at the net mixing reactions. The high dropout of Scots pine of 11.53 m^3 ha^{-1} yr^{-1} caused an only very low net growth of 0.48 m^3 ha^{-1} yr^{-1}. In the case of European beech, the dropout of 4.19 m^3 ha^{-1} yr^{-1} was lower, however, high enough to reduce the 18% greater mean gross growth to a 10% greater mean net growth.

In the mixed stands the strong reduction of the gross growth to 48%, from 13.35 to 6.40 m^3 ha^{-1} yr^{-1} at the whole stand level, occurred mainly at the expense of Scots pine. From the gross growth of Scots pine in mixture 96% ended as dropout whereas it was only 27% in case of European beech.

This means that the classically reported gross overyielding was positive at the stand level, but due to the dropout of Scots pine, the net overyielding becomes negative (net underyielding). The gross growth of Scots pine in mixed stands was similar to that in monospecific stands (Table 4). However, the alien-thinning in the mixture caused a strong dropout, resulting in negative net overyielding (Fig. 1). In contrast, beech benefits from growing in a mixture; the surplus in terms of gross growth can also be accumulated as net growth; so overyielding of gross and net growth is more similar. In the mixed stands Scots pine lost most of the gross growth by dropout (dropout by alien-thinning), and European beech could keep most of the gross growth in the standing stock (accumulation).

The mean volume gross growth, net growth, and dropout values calculated over all triplets in Table 4 revealed the absolute level and relevance of mixing effects in terms of stem volume. These mean values are based on the means of the gross and net growth as well as on the dropout over all plots. Due to the different productivity levels along the gradient, both calculation approaches don't necessarily yield the same results in over- and underyielding.

3.2. Mortality, natural thinning, and stem volume dropout (Q2)

Table 5 (column Mort) shows that, at the stand level, the tree number-related mortality was 33% higher ($p < 0.10$) in mixed stands (0.024) compared to the weighted mean of monospecific stands (0.018). The higher mortality rate of the stand as a whole was mainly due to a 95% higher ($p < 0.001$) mortality of Scots pine in mixed stands (0.037) compared with monospecific stands (0.019). The mortality of beech was 13% higher ($p < 0.10$) in mixed (0.017) compared with monospecific stands (0.015).

Table 5 (column dNddq) shows that the mean alien-thinning line in the mixed stands (-1.554) was 12% steeper than the mean self-thinning line (-1.388) in the monospecific stands. The steeper slope in mixed compared to monospecific stands is mainly caused by Scots pine, which had a slope of −1.113 in monocultures and −2.459 in mixed stands.

Table 5 (column dropout volume) and Fig. 5 show that in the mixed stands the mean stem volume dropout (6.96 m^3 ha^{-1} yr^{-1}) was 103% higher than the weighted mean of monospecific stands (3.26 m^3 ha^{-1} yr^{-1}). It was especially the higher dropout of Scots pine in the mixed stands compared to the monospecific stands that caused this higher turnover in the mixed stands (Fig. 5b). Analyses of the dropout based on the stand and species basal area and stem mass, yielded similar results (Supplementary Figures 6 and 7).

3.3. Stand density (Q3)

For both surveys, we calculated the SDI of the remaining trees for monospecific and mixed species stands and found a higher stand density in the mixed stands (Fig. 6a). At the first survey, the weighted mean SDI of the monospecific stands was SDI = 640 ± 40 ha^{-1}, and the density of the mixed stands was 10% higher (699 ± 46 ha^{-1}). The superiority decreased from the first to the second survey (Fig. 6b); at the second survey, the mixed stand was still 5% denser (694 ± 47 ha^{-1} in the mixed versus 664 ± 40 ha^{-1} in the monospecific stands). The majority of the observations and the overall means (empty and filled rectangles) of both surveys lie above the bisectional line.

3.4. Change of mixing proportion and pattern (Q4)

On average, the mixing proportion of Scots pine was 0.46 ± 0.03 at the first survey and 0.44 ± 0.03 at the second survey (Fig. 7a). This decrease of the mixing proportion of Scots pine in favour of European beech by 2% was caused by the higher dropout of pine compared to beech, but not significant.

The segregation index by Pielou (1961) was S = 0.02 ± 0.06 at the first survey and S = 0.05 ± 0.06 at the second survey (Fig. 7b). This reveals a trend towards demixing and segregation of both species caused by the dropout of Scots pine. Small S-values indicate an aggregation of both species, i. e. close inter-specific neighbourhood. High S-values indicate a segregation of Scots pine and European beech, i.e. dominance of the intraspecific neighbourhood. The more than doubling of the S-value from 0.02 to 0.05 indicate a tendency from independent to separated occurrence of both species; the change was marginally significant ($p < 0.065$).

3.5. Dependencies on site conditions (Q5)

We tested using the site index, Martonne Index, mean annual temperature and mean annual precipitation within the survey period as independent variables for explaining gross-overyielding, mortality and net-overyielding. Only mean annual precipitation and the Martonne index showed some significant effects on gross and net overyielding; the effects of mean annual precipitation were stronger and more consistent and are shown in the following.

At the stand level, gross overyielding significantly increases and the net overyielding significantly decreases with increasing annual precipitation (Fig. 8a) (see Table 6 for statistical characteristics of the

Table 5

Mortality rates (Mort), natural thinning slopes (dNddq), and absolute dropout stem volume (dropout) in the 6–8-years survey period for mixed versus monospecific conditions at the stand and species level.

Group	Mort mean (./.)	± SE (./.)	dNddq mean (./.)	± SE (./.)	dropout volume mean m^{3}ha^{-1}yr^{-1}	± SE m^{3}ha^{-1}yr^{-1}
S.pi., E.be., exp.	0.018	± 0.004	−1.388	± 0.323	3.26	± 0.60
S.pi., E.be., obs	0.024	± 0.004	−1.554	± 0.468	6.96	± 1.17
S.pi. mono	0.019	± 0.005	−1.113	± 0.522	3.42	± 0.94
S.pi., (E.be.)	0.037	± 0.009	−2.459	± 0.445	11.53	± 3.45
E.be. mono	0.015	± 0.003	−0.966	± 0.209	2.89	± 0.91
(S.pi.), E.be.	0.017	± 0.004	−1.243	± 0.316	4.19	± 1.03

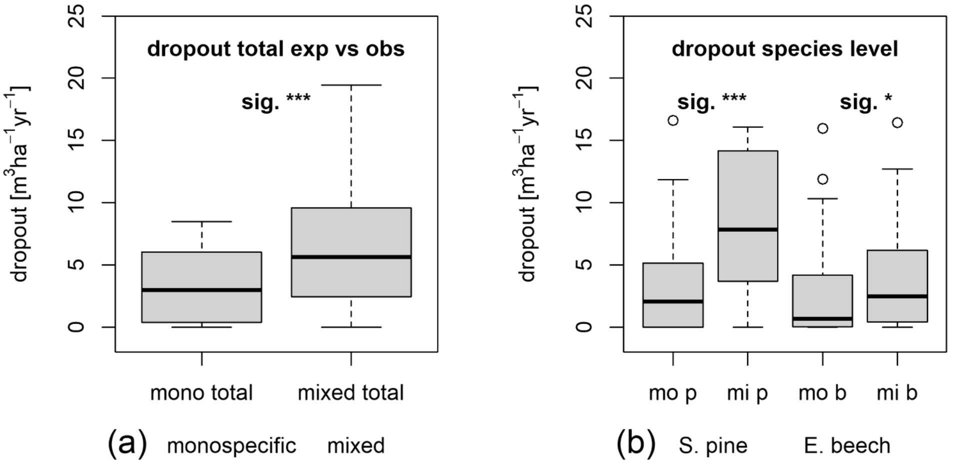

Fig. 5. Dropout in mixed versus monospecific stands at stand level (a) and species level (b). The box plots display the mean dropout (± SE) by natural thinning during the survey period in m^3 $ha^{-1}yr^{-1}$. The symbols *** and * indicate significant differences between the boxes below at level $p \leq 0.001$ and $p \leq 0.05$, respectively.

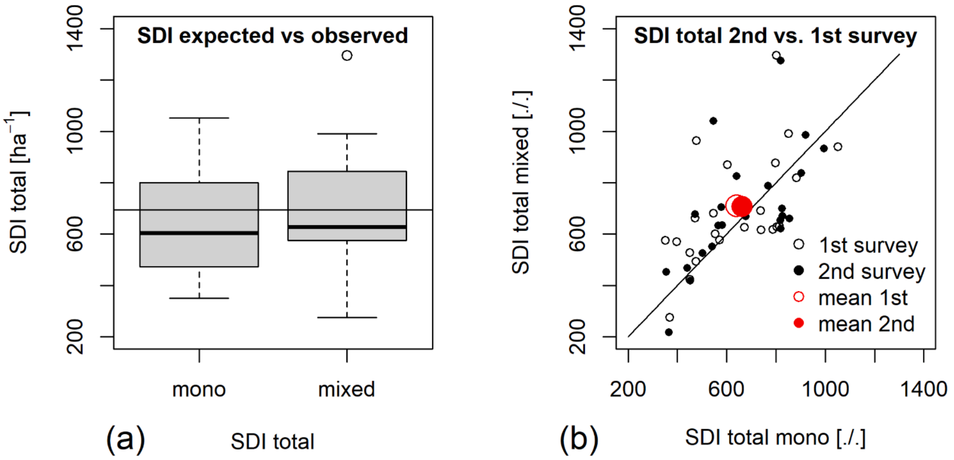

Fig. 6. Visualization of the stand density differences between monospecific and mixed stands at the first survey (a). The horizontal line reflects the mean SDI of 696 ha^{-1} for the mixed stands. Change of the stand density relationships between mixed and monospecific stands from the first to the second survey (b). Points above the bisectional line indicate triplets where the stand density on the mixed plots was higher than the weighted mean of the neighbouring monospecific stands.

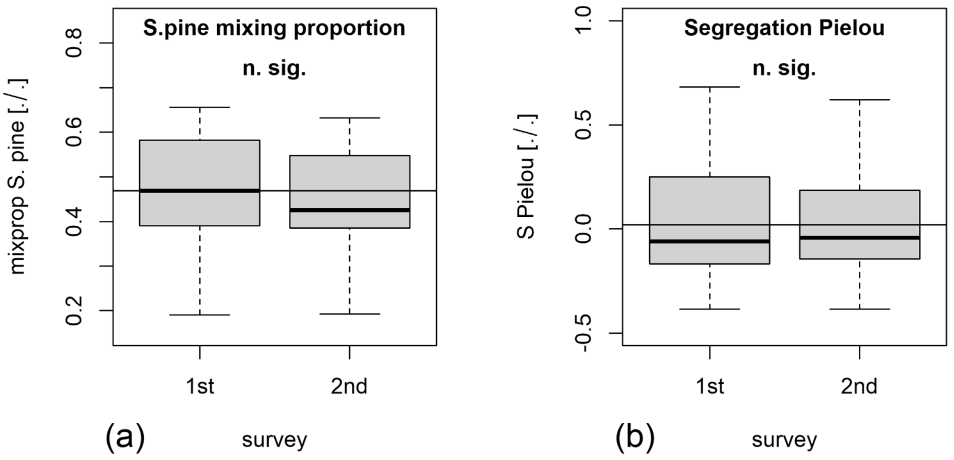

Fig. 7. Change of (a) the mixing proportion of Scots pine and (b) the segregation index by Pielou (1961) from the first survey (2013/2014) to the second survey (2020/2021) on the mixed plots of the 23 triplets.

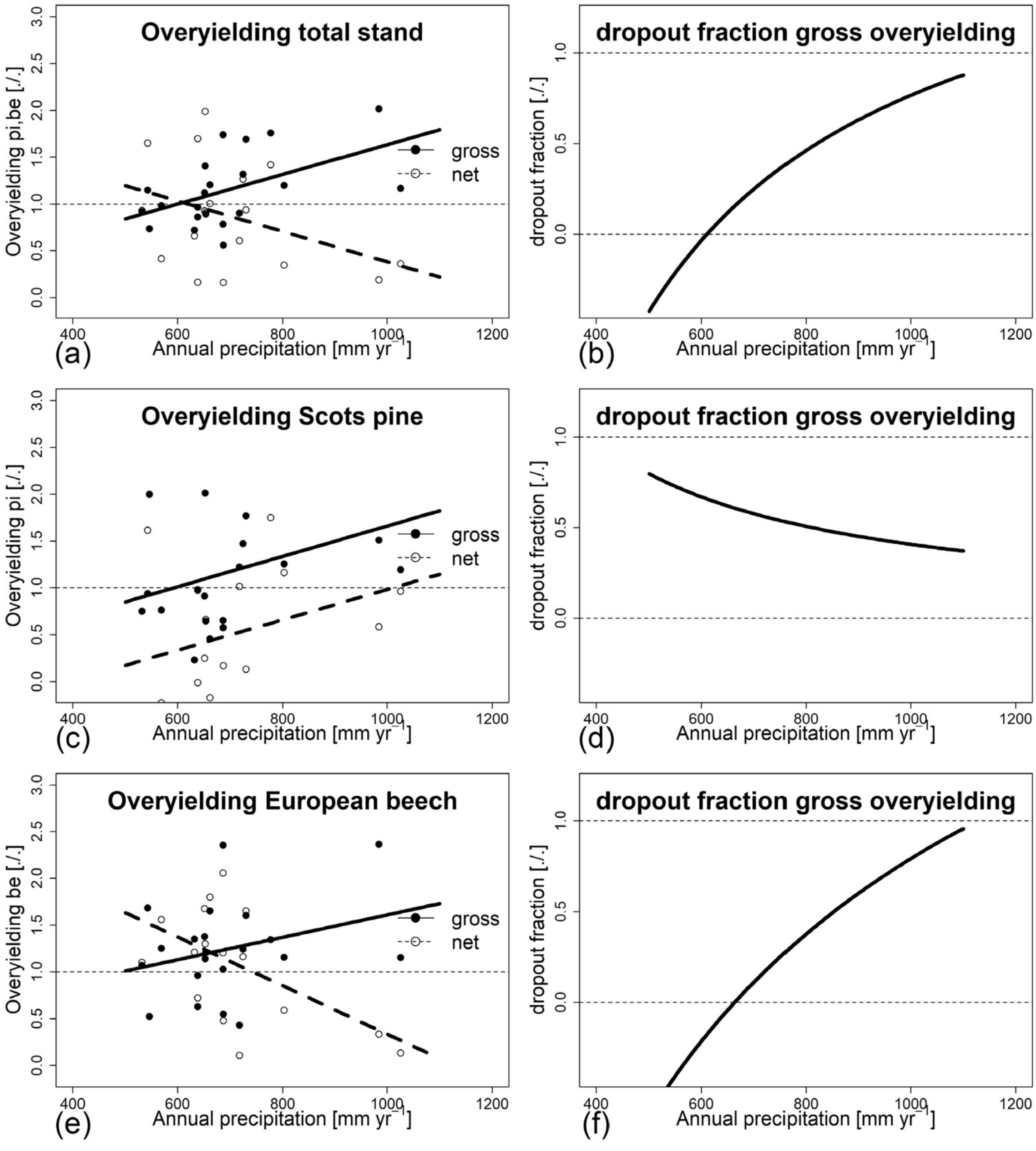

Fig. 8. Net and gross over-yielding significantly ($p < 0.05$) depend on annual precipitation in case of the mixed stands in total and also in case of Scots pine and European beech in the mixed stands, separately (a, c, and e). Dropout fraction of the gross overyielding depending on annual precipitation for the mixed stands in total and of Scots pine and European beech in the mixed stands separately (b, d, and f). Gross overyielding is represented by filled circles and solid lines; net overyielding is indicated by empty circles and broken lines. See Table 6 for statistical characteristics.

regression). Based on the two diverging curves, we calculated the dropout fraction of the gross growth as the difference between gross and net overyielding divided by gross overyielding (Fig. 8b). This dropout fraction is low on dry sites and increases degressively with water supply, i.e., the better the water supply, the higher the fraction of the gross growth that dropped out during the survey period.

Scots pine contributed to the mixture with a low gross overyielding and an even lower net overyielding which both significantly increased with water supply (Fig. 8c). The resulting dropout from the gross overyielding slightly decreases with water supply (Fig. 8d). The dropout fraction is about 0.6 on dry sites and 0.4 on moist sites; on sites with medium water supplies about 60% of gross overyielding end as dropout (Fig. 8d).

In the case of European beech, the relationships between gross and net overyielding and water supply were significant, however, strongly diverge (Fig. 8e) (see Table 6 for statistical characteristics of the regression). Similar to the pattern at the stand level, the dropout fraction is low on dry sites and high on wet sites (Fig. 8f).

For the natural thinning slopes and the mortality, we found a clear effect of species mixing but no significant dependency on the site conditions. For Scots pine, the alien-thinning in the natural thinning quotient dN/N/ddq/dq was consistently lower in the mixture than in monocultures and independent of the water supply (Supplement Figure 7). Note that more negative slopes mean a stronger elimination of trees with an increasing mean stem diameter. In the case of European beech, alien-thinning was not significantly different from self-thinning, and there was a slight tendency toward higher natural thinning slopes on wet sites. The results of the mortality study corroborated these findings. Compared with monospecific stands, the mortality rates were significantly higher in mixed stands in the case of Scots pine and similar in the

Table 6

Statistical relationship between gross and net overyielding and mean annual precipitation in the survey period. The underlying model equation was $y = a_0 + a_1 \times P + a_2 \times group + a_3 \times P \times group$ for the total stand and European beech and $y = a_0 + a_1 \times P + a_2 \times group$ for Scots pine. Y was the over-/underyielding in terms of stem volume growth, P was the mean annual precipitation and group was a categorical variable for an indication of gross or net overyielding (group = 0 or group = 1, respectively). Significant regression coefficients are indicated by bold letters.

Characteristics	Total stand	Scots pine	European beech
a_0	0.046	0.039	0.410
std(a_0)	± 0.548	± 0.644	± 0.608
p-tail	0.933	0.952	0.504
a_1	**0.002**	**0.002**	0.001
std(a_1)	± 0.001	± 0.001	± 0.001
p-tail	0.049	0.080	0.174
a_2	**1.962**	**−0.677**	**2.518**
std(a_2)	± 0.795	± 0.230	± 0.881
p-tail	0.019	0.006	0.007
a_3	**−0.003**	–	**−0.003**
std(a_3)	± 0.001	–	± 0.001
p-tail	0.007	–	0.004
R^2	0.20	0.20	0.17

case of European beech (Supplementary Figure 7, c and d). For both species, the relationship to the water supply was not significant.

4. Discussion

4.1. Net overyielding as a result of gross overyielding and mortality

Clarification of the relationships between gross growth, mortality and net growth is relevant for understanding and managing mixed stands. The overyielding regarding the gross growth is just one aspect to consider when comparing between mixed and monospecific stands; the other aspect is the net effect on stand yield, which is calculated by subtracting dropout due to mortality from gross growth (net growth = gross growth minus dropout by mortality). If the overyielding is accumulated in the standing stock, it can be used for carbon storage and further exploited for wood production even without thinning, if it accelerates the dropout, thinnings may be necessary for the exploitation of the dropout as wood products. Suppose it is a zero-sum game with overyielding by one species and underyielding of the other species. In that case, it may change the mixing proportion, cause demixing and thus reduce any mixing effects in terms of overyielding unless silvicultural interventions would counteract the natural demixing. These are only a few possible effects and consequences.

Many studies showed that mixed species stands can have higher gross growth, or overyielding, compared with monocultures (del Río et al., 2022, Jactel et al., 2018, Liang et al., 2016). Although the tree dropout is of similar importance for understanding stand dynamics, much less is known about the mortality in mixed stands (Binkley et al., 2003, Searle et al., 2022) and hardly anything about how much of the gross growth is accumulated in the standing stock and how much drops out by mortality. Contradictory reports in the literature regarding the magnitude of mixing effects at stand level may, among others, result from whether mortality was considered or not. For example, the report by Jactel et al. (2018), which was based on permanent surveys, arrived at contradictory results regarding the relationship between overyielding and site quality compared to the study by Toïgo et al. (2015), which was based on inventory data. Similarly, mortality may explain part of different species admixture effects on growth report at tree and stand levels for a given mixture, which often do not completely match (e.g. Pretzsch et al 2020; del Río et al 2022; Vospernik et al 2023), and highlight the relevance of simultaneous analyses of different processes at different levels (Forrester and Pretzsch 2015). Information from temporal plots and stand growth reconstruction based on increment cores can provide valuable insights into stand dynamics (Gadow and Hui 1999). However, permanent plots with repeated measurements as used in this study provide more complete details on gross growth, mortality and net growth.

Most of the above-mentioned studies retrospectively derive stand growth based on the increment cores of the surviving trees in mono- and mixed species stands, sometimes including a rough estimation of past mortality. The derived stand growth and overyielding are only accurate if all trees survived the addressed period. Only in this case, i.e. when there is not tree mortality, gross growth is equal to net growth. Any stem volume dropout due to mortality within the addressed period means that the survivor-based stand growth underestimates the gross growth, and that the net growth remains vague if the number of dropout trees and their growth until their death within the period are unknown. Repeated full surveys as applied in this study record both the survival status (dead or alive) and the size (stem diameter) of all trees at the beginning and end of a survey period. In this way they enable the calculation of gross and net stand growth and the respective overyielding (Pretzsch et al., 2019). As the considered period was only rather short, the revealed differences between net and gross overyielding should not be generalized. However, the results corroborate that mortality deserves more consideration when comparing mixed with monospecific forest stands (Pretzsch and Grote, 2023, accepted, Searle et al., 2022).

The first survey and analyses of 32 triplets in 2013/2014 were based on increment cores and included the 23 triplets, which we now measured a second time 6–8 years later in 2020/2021. The first survey showed an overyielding of volume growth by 8%, mainly caused by improved growth of beech in the mixture. The density was 20% higher, and pine was growing at a faster rate in mixed stands compared to monospecific stands. The superiority was independent of the site conditions (Heym et al., 2017, Pretzsch et al., 2015). This first analysis was based on a one-time measurement and the growth reconstruction by increment cores could hardly consider the dropout in the 5-years reconstruction period from 2009 to 2013. The second survey of the triplets in 2020/2021 corroborated that compared with monospecific stands, the mixed stands produced significantly more gross growth than expected (Pretzsch et al., 2015; Condés et al., 2018). This suggests that pine-beech mixed stands can be superior in productivity and carbon fixation (Osei et al., 2022). However, this gross surplus is only about half as large as the net growth (48%), reducing the difference to monospecific stands, where 73% of the gross growth was accumulated in the standing stock (Table 4).

Behind these stand-level findings, we observed very different species-specific behaviours. In the mixed stands, Scots pine enables the overyielding of European beech but its net growth is reduced by the intense competition with beech. For Scots pine, without management, the dropout of stem volume was, on average, 3.42 m^3 ha^{-1} yr^{-1} in the monospecific stand but more than threefold (11.53 m^3 ha^{-1} yr^{-1}) in the mixture (Table 4). The exposure of Scots pine to beech competition in the mixture is also corroborated by a 95% higher mortality rate under inter-specific competition in the mixed stands, in agreement with other studies on tree mortality (Condés & del Río 2015; Archembeau et al., 2020). For European beech, the differences between mixed and monospecific stands are much lower, although the dropout is also higher in mixed stands. The more light-demanding Scots pine contributed less to the gross overyielding and also suffered a higher dropout by self- and alien-thinning than the more shade-tolerant European beech. However, the net overyielding of beech was still 10%, whereas we found a strong net underyielding at the stand level. In essence, the natural dropout of stem volume due to self-thinning was significantly higher in mixed than in monospecific stands. Interestingly, considerable parts of the gross overyielding end up as higher dropout (accelerated turnover), and another part as an accumulation of standing volume (increased stand density).

In the 23 triplets analysed here, we found a 10% significantly higher stand density in mixed compared with monospecific stands at the first survey. This superiority decreased to 5% at the second survey. The mixing proportion of Scots pine decreased from 46% at the first to 44% in the second survey. The more than doubling of the index by Pielou from 0.02 to 0.05 indicated a strong tendency to demixing caused by the dropout of pine. Thus, within the observation period, the stand density was continuously higher in mixed versus monospecific stands (Pretzsch & Biber 2016). The mixing proportion changes in favour of the more shade-tolerant European beech, but it does not outcompeted Scots pine, so the mixing effects will probably continue. However, Scots pine can be expected to be out-competed by European beech on the long term in fully stocked stands because it cannot regenerate under high beech shade.

4.2. Causal explanations with special emphasis on the water supply

Accompanying measurements on the 32 triplets at the first survey suggested that the superior gross stem volume growth on the mixed plots may result from a higher canopy packing density (Pretzsch et al., 2016), complementary light and nutrient use (de Streel et al., 2020, Forrester et al., 2018), changes in stem and crown allometry (Barbeito et al., 2017, Pretzsch 2019), improved drought resilience or resistance and temporal stability related to between species growth asynchrony (del Río et al., 2017, 2022, de Streel et al., 2022) and a decrease of wood density (Zeller et al., 2017). In the long term, the soil fertility of the mixed stands can improve compared with the monospecific stands (Błońska et al., 2018).

At the stand level, the SDI was higher in the mixed stands than in the monocultures (see section 3.4), which indicates a higher packing density and leaf area index in the mixed stands. This is in line with Harper (1977, p. 183-194) who found that higher density and, therefore, lower light supply reduce the slope $\alpha_{N,dq}$ of the self-thinning line (see dNddq in Table 5), i.e. accelerate the elimination of trees with increasing mean stem diameter dq of the stand, ceteris paribus. This means that in the mixed stands, the trees do not simply develop faster along the same thinning line as in monocultures, but a given increase in dq eliminates even more trees. Compared with the monocultures, we found a slight steepening of $\alpha_{N,dq}$ in mixed stands for European beech and a strong one for Scots pine. However, these results present some uncertainties as i) the slopes found for a short period (6–8 years) may not necessary represent the long term pattern, as mortality can occur at discret steps triggering oscillations in natural thinning line (Pretzsch & Biber 2005), and ii) the natural thinning lines may vary with site conditions (Condes et al., 2017), variation not considered in our analyses.

We hypothesize that the higher dropout in mixed stands, which increases with water supply, is caused by a higher density, structural heterogeneity, and competition for light. The trees, especially Scots pine, must reach out for light for continued growth and survival. Under moist conditions (high precipitation and de Martonne values), the sufficient water supply enables a higher stand density (Pretzsch et al 2022b) and shifts the competition mainly to above ground for light, usually size-asymmetric competition, increasing tree mortality (Condés & del Río 2015; Pretzsch et al 2022a). Thus the trees in mixed stands strongly compete by overtopping and edging out each other to improve their light supply and survival probability (Barbeito et al., 2017, Dieler and Pretzsch 2013, Pretzsch et al., 2016). This requires high growth rates of the survivors but also causes high dropout of the losers of the inter-specific competition. Under dry conditions, the same may emerge below ground (Göransson et al., 2016, Lei et al., 2012). Thus the competition driven growth allocation may increase above ground on moist sites and below ground under dry conditions. This may explain why there is a higher dropout on moist sites above ground than on dry sites (Fig. 8).

The mortality pattern aong the water supply gradient, explains the differences between gross and net overyieldingon moist and dry sites. Although in the results based on the first inventory we did not find any pattern of overyielding with site conditions (Pretzsch et al 2015), the more precise data used in this study corroborates that gross overyielding increases with water supply (Jactel et al 2018). However, the greater mortality and dropout at humid sites reverses the pattern of net overyielding.

4.3. Consequences for forest science and management

The triplets used in this study were measured only twice. This means that our results represent the stand growth and mixing effects only over a relatively short 6–8-year period out of a total 100–150-year stand development period (Gadow et al., 1999). Analogous analyses in other age phases or periods with other climate conditions or with silvicultural interventions may modify the magnitude of the mixing effects on growth and mortality. However, the differentiation between gross and net overyielding caused by mortality is a phenomenon of general relevance. Note, that in unthinned monospecific stands within one rotation, about 30% of the total stem volume growth ends as turnover (Assmann 1970, p. 227-228, Pretzsch 2009, p. 59–61) due to natural thinning. Our results suggest that this fraction seems higher in mixed stands and needs more attention when analyzing, modelling, or managing mixed stands.

Retrospective analyses of mixed stand growth based on increment cores extracted from the survivors lack information about the dropout at the stand and species level in the past. It requires long-term experiments or temporary plots with repeated inventories to quantify both remaining and dropout trees. The recurrence interval of inventories should be less than five years in young forest stand and ten years in mature forest stands to approximate the size and time of the dropout trees. Unthinned monospecific and mixed plots, as used in this study, are particularly relevant as they reflect the effect of mixing on the maximum stand density, growth, and dropout under natural conditions. They enable quantification and modelling of gross growth overyielding, mortality and net growth overyielding.

How can tree and stand modelling consider the relationships between gross growth, mortality and overyielding and their dependency on site conditions? This is possible with process-based ecophysiological models for mixed stands that depend on environmental conditions and with explicit consideration of individual trees or at least differently sized social classes (e.g. Grote and Pretzsch 2002, Deckmyn et al., 2008, Grote et al., 2020, Jonard et al., 2020). In such models, carbon assimilation, growth and mortality at tree or stand level can be dynamically represented based on water supply. The range between low growth and dropout on dry sites and high growth and dropout on moist sites is then inherently integrated.

Statistical tree and stand models frequently use the natural thinning line for predicting mortality (Monserud et al., 2004). They need to consider the revealed differences between self-thinning and alien-thinning in order to accurately predict growth and manage stand density. Logistic models often used for predicting individual tree mortality (Palahí et al., 2003) should certainly be species-specific but also consider the species composition of the local neighbourhood of trees. The position, stem and crown size, and species identification, are necessary for accurate analyses and prediction of the dropout and net growth at the stand and species level.

Knowledge of gross growth, mortality, and net growth is essential for sustainable management and the derivation of the annual cut. Mortality rates at the stand and species level provide information about dropout and demixing in terms of individuals. Dropout in terms of basal area, volume, or mass provides cumulative information about turnover and the neglect of timber in untreated stands under suspended active management. The state and any shifts in the mixing proportion are important for diversity management as one species may need to be promoted in order to maintain it as long as it is silviculturally desired. Appropriate silvicultural prescriptions require knowledge of the maximum stand density in mixed stands and the density-growth relationship.

If not harvested, about 96% of the gross overyielding of Scots pine would drop out by self-thinning and especially by alien-thinning (Table 4). Accelerated turnover due to self-thinning and alien thinning may improve the soil humus content, nutrition status, and water storage capacity, among other things. But it may also contribute to demixing if one species loses more than the other in the mixture. Silvicultural interventions in favour of Scots pine may exploit the overyielding of European beech and maintain the facilitation by Scots pine by counteracting its suffering due to alien-thinning and decrease. Otherwise, Scots pine would lose, and its role as benefactor would decline. The interventions should consider that the density of mixed stands can be 5–10% higher than in monospecific stands (Pretzsch and del Río 2020, Pretzsch and Biber 2016). Elimination of beeches, especially in the vicinity of pines, would contribute to both the harvest of the overyielding (and avoid its dropout) and reduce the competitive pressure on pine (and its dropout).

This may allow a continuous benefit of diversity, overyielding and maintenance of the advantages of mixed stands compared with monospecific stands of Scots pine and European beech (Tiebel et al., 2016). Establishing and maintaining both tree species in troops and groups would reduce the inter-specific competition and need for silvicultural interventions. Temporaly separating the two speceis by giving Scots pine a 10 or 20 years earlier start and lead in the development may also reduce inter-specific competition and the need for silvicultural interventions. However, both measures would reduce the mixing intensity and thereby many other beneficial ecosystem services of species mixtures such as stability (Schwaiger et al., 2018), biodiversity (Dieler et al., 2017), recreational value (Felton et al., 2016).

5. Conclusions and perspectives

For understanding and managing mixed species stands, not only their growth, but also mortality behaviour is essential at both the stand and species level. Our study showed higher gross growth, mortality, and turnover of Scots pine and an increased accumulation of net growth of European beech in mixed compared to monospecific stands. This underpins that the frequent studies of the gross growth of mixed stands need to be complemented by analyses of the mortality. A better insight into gross growth, mortality and net growth at the stand and species level shows where any overyielding remains and points the way on how to exploit the overyielding, maintain the species diversity, and avoid demixing. The revealed site-dependencies of the mixing effects emphasize the need for site-specific silvicultural guidelines and suggest further empirical studies of the growth and mortality of mixed versus monospecific stands depending on site conditions, stand density, and species combinations.

CRediT authorship contribution statement

Hans Pretzsch: Conceptualization, Funding acquisition, Investigation, Methodology, Formal analyses, Writing – original draft, Writing – review & editing, Visualization. **Michael Heym:** Formal analyses, Writing – original draft, Writing – review & editing, Visualization, Data curation. **Torben Hilmers:** Formal analyses, Writing – original draft, Writing – review & editing, Visualization. **Andrés Bravo-Oviedo:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing. **Shamim Ahmed:** Writing – review & editing. **Christian Ammer:** Provision of measurements and data, Writing – review & editing. **Admir Avdagić:** Provision of measurements and data, Writing – review & editing. **Kamil Bielak:** Provision of measurements and data, Writing – review & editing. **Felipe Bravo:** Provision of measurements and data, Writing – review & editing. **Gediminas Brazaitis:** Provision of measurements and data, Writing – review & editing. **Marek Fabrika:** Provision of measurements and data, Writing – review & editing. **Vaclav Hurt:** Provision of measurements and data, Writing – review & editing. **Viktor Kurylyak:** Provision of measurements and data, Writing – review & editing. **Magnus Löf:** Provision of measurements and data, Writing – review & editing. **Maciej Pach:** Provision of measurements and data, Writing – review & editing. **Quentin Ponette:** Provision of measurements and data, Writing – review & editing. **Ricardo Ruiz-Peinado:** Provision of measurements and data, Writing – review & editing. **Dejan Stojanovic:** Provision of measurements and data, Writing – review & editing. **Miroslav Svoboda:** Provision of measurements and data, Writing – review & editing. **Barbara Wolff:** Provision of measurements and data, Writing – review & editing. **Tzvetan Zlatanov:** Provision of measurements and data, Writing – review & editing. **Miren del Río:** Conceptualization, Funding acquisition, Investigation, Formal analyses, Writing – original draft, Writing – review & editing.

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.

Acknowledgements

The networking in this study has been supported by COST Action FP1206 EuMIXFOR. The study received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No952314 and under the Marie Skłodowska-Curie grant agreement No 778322. The first author also wishes to thank the German ScienceFoundation (Deutsche Forschungsgemeinschaft) for funding the project "Structure and dynamics of mixed-species stands of Scots pine and European beech compared with monospecific stands; analysis along an ecological gradient through Europe" (# DFG PR 292/15-1). Felipe Bravo is grateful for Funds by the Junta de Castilla y León through the projects "CLU-2019-01 and CL-EI-2021-05 - iuFOR Institute Unit of Excellence" of the University of Valladolid and the co-financing by the European Regional Development Fund (ERDF "Europe drives our growth"). Miren del Río thanks for the support by the Spanish Ministerio de Ciencia e Innovación (# PID2021-126275OB-C21/C22). Dejan Stojanović thanks the Ministry of Education, Science and Technological Development of the Republic of Serbia for funding. Tzvetan Zlatanov thanks the Ministry of Education and Science of the Republic of Bulgaria (# DO1-405/18.12.2020 LTER-BG). All contributors thank their national funding institutions to establish, measure and analyze data from the triplets. Thanks are also due to Monika Bradatsch for the graphical artwork, and to two anonymous reviewers for their constructive criticism.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121008.

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