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Tree ring wood density of Scots pine and European beech lower in mixed-species stands compared with monocultures

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ABSTRACT

Mixed species stands are on the advance in Central Europe and many recently published studies have reported that they can overyield monocultures in terms of volume growth. However, as forest research has in the past been focused on monocultures, knowledge of how mixed-species stands and monocultures compare in terms of wood quality remains limited. Based on five triplets of fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.), we analysed whether tree species mixing modifies wood quality and, more precisely, tree ring wood density.

From a total of 322 trees we sampled increment cores for the analyses of tree ring width and tree ring wood density using a LIGNOSTATION™. We found that tree ring width of Scots pine was, on average, 14% wider in mixed compared with pure stands. Tree ring width of European beech did not differ between pure and mixed stands. Tree ring wood density was lower in mixed stands compared to pure stands for both Scots pine (−12%) and European beech (−8%). Tree ring wood density and tree ring width were negatively correlated in the case of Scots pine and positively correlated for European beech.

When considering tree size and Stand density index, it was found that only tree ring width and mean tree ring wood density of European beech were influenced by stand density. Tree size had a significant effect only on tree ring wood density of European beech. The overall result of larger tree rings of Scots pine in mixed stands and a lower tree ring wood density of both species in mixed stands compared to pure stands was not influenced by stand density or tree size.

Based on the measured values of tree ring wood density we conducted estimates of how mixed stands performed in terms of biomass. We found stem biomass to be 8% lower in mixed stands compared to pure stands. Reasons for the revealed differences in tree ring wood density and consequences for, among others, overyielding, carbon storage, and wood quality are discussed.

1. Introduction

Many recent studies provide evidence that mixed-species stands can overyield monocultures by up to 30% (Bielak et al., 2014; Zhang et al., 2012). Such comparisons can be based on basal area growth (Hein and Dhôte, 2006), stem volume growth (Pretzsch et al., 2015), stem biomass growth (Thurm et al., 2016), or total above-ground biomass (Pretzsch et al., 2010). On a series of 32 triplets in pure and mixed-species stands of Scots pine and European beech along a gradient through Europe, Pretzsch et al. (2015) and Pretzsch et al. (2016) found an average overyielding of 12% in basal area and 8% in volume growth on mixed stands. Concerning the five triplets examined in this study (Pretzsch et al., 2015), volume growth and basal area growth were found to be about equal in pure and mixed stands. Scots pine was more productive in mixed stands in terms of basal area growth (+18%) and volume growth (+18%) while European beech was negatively influenced by the mixing (basal area growth −21%, volume growth −12%) when compared to the neighbouring pure stands (Table A5).

The mean overyielding in volume growth of mixed stands found on the 32 triplets and possibly the higher productivity of Scots pine

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in mixed stands found on the selection of five triplets may result from a more complex structure in mixed stands – both above and below ground (Pretzsch, 2014) – leading to a complementary resource use by the associated species (Richards et al., 2010) and a resulting reduction in competition (Vandermeer, 1989). Positive effects of a more complex structure on productivity can additionally result from e.g., hydraulic lift, atmospheric nitrogen fixation or frost protection, potentially leading to a facilitation (Callaway and Walker, 1997) of one or more species in mixture and can result in an overyielding (Forrester et al., 2006; Vandermeer, 1989). Such an overyielding is often achieved through morphological acclimation to inter-specific environments (Metz et al., 2013; Pretzsch and Dieler, 2012) where mixing can modify e.g. crown morphology (Bayer et al., 2013; Pretzsch, 2014) and root-shoot relationship (Bolte et al., 2004; Robinson et al., 2010). However, not much is known about how wood properties may be influenced by interspecific neighbourhoods.

When exploring structural differences between pure and mixed stands and the performance of species in a mixture, tree ring width and tree ring wood density can reveal more information on the processes behind mixing effects. In the case of drought, Metz et al. (2016) found wider tree rings for European beech in mixed stands compared to pure stands; this is explained by an enhanced water supply for Beech in mixed stands, which is consistent with their analysis of stable isotopes. Wider tree rings in coniferous trees are known to result in a lower tree ring wood density (DeBell et al., 1994; Franceschini et al., 2013). For European beech, tree ring wood density is not particularly influenced by tree ring width (Diaconu et al., 2016). The actual effect of tree ring width on tree ring wood density might furthermore depend on the timing of climatic events influencing growth throughout the growing season (Bouriaud et al., 2004; Franceschini et al., 2013) and the general fertility of sites (Diaconu et al., 2016). Dutilleul et al. (1998) found that the negatively correlated tree ring width and tree ring wood density in Spruce was no longer valid for very high growth rates induced by site fertility or climatically favourable conditions.

A reduction in tree ring wood density might be an appropriate indicator for reduced stress from drought events. Schuldt et al. (2016) recently showed that the vessel diameter of European beech increased and the vessel number decreased on sites with high precipitation, while the contrary was found on dry sites. As vessel density was negatively related to tree ring wood density (Schuldt et al., 2016) and Beech was found to be less water stressed in the neighbourhood of Pine (Metz et al., 2016), one may expect lower tree ring wood density in mixtures of Pine and Beech.

However, other than by Kennel (1965), the effect of mixing on tree ring wood density has hardly been explored. This is a significant lack of knowledge, as tree ring wood density has a strong effect on stem stability, wood quality, carbon content and storage, as well as on decomposition rates. If tree ring wood density differs between monocultures and mixed-species stands, it can also change how mixed stands perform in terms of dry mass productivity and C-fixation compared with monocultures.

In order to address this topic, we sampled tree ring wood density on five triplets of fully stocked monocultures and mixed stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) at different locations in Europe in order to analyse whether tree species mixing modifies wood quality. As it has the advantage of being non-destructive and time-saving, we applied high-frequency densitometry to measure tree ring width and tree ring wood density.

By further exploring the previously found overyielding in volume of mixed stands of Scots pine and European beech, we tried to find out: if tree ring width and tree ring wood density are, on average, different in pure and mixed stands (QI); if tree ring wood density is independent of tree ring width (QII); and if tree ring width and tree ring wood density in pure and mixed stands are different for equal tree size and at equal stand density (QIII). Based on QI–QIII we developed the following hypotheses:

HI: Mean tree ring width and mean tree ring wood density in pure and mixed stands are equal.
HII: Tree ring width and tree ring wood density are independent.
HIII: For trees of equal size and at equal stand density, mean tree ring width and mean tree ring wood density in pure and mixed stands are equal.

2. Material and methods

2.1. Material

2.1.1. Study area

Each of the five locations examined in this study consists of a triplet containing one mixed stand of Scots pine and European beech and one pure stand of each species. Three of the triplets are located in the south of Germany (Alzenau, Bamberg and Steigerwald), one in eastern Germany (Teupitzer Forst) and one in northern Spain (Huerta de abajo) (Fig. 1). Their similarity in terms of stand characteristics (Pretzsch et al., 2015) provides the basis for comparisons between pure and mixed stands. Geographical data of the five triplets is presented in Table 1.

2.1.2. Data

In this study we measured the tree ring width and tree ring wood density of 163 tree cores of Scots pine and 159 tree cores of European beech, sampled in 2015. Only dominant trees were sampled. Among those, random sampling was applied. The stands are between 40 and 80 years old (Pretzsch et al., 2015), when relating to total tree age. All tree cores (one per tree) were taken either from the northern or the eastern side of the trees at breast height. The latest fully built tree ring valid for our analysis is from 2014. Due to a decreasing sample size when going back further in time, we included only tree rings from 1950 and later. Since only a few samples contained juvenile wood and did not change model outcomes significantly in test runs, all tree ring data from 1950 until 2014 was included. There has been no thinning on the plots in recent years, which is why stand density index (SDI) is close to maximum (Pretzsch et al., 2015).

SDI values of the mixed stands were calculated by adding up individual SDI values per species in the mixture in order to obtain one SDI value per mixed stand and triplet.

Table A1 shows the most important characteristics of the five locations and their pure and mixed stands of Scots pine and European beech examined in this study. For a more detailed overview of the trees examined in this study see Table A2.

2.2. Methods

2.2.1. High-frequency densitometry

For the measurements of ring width and tree ring wood density of Scots pine and European beech, we used a LIGNOSTATION™. The use of high-frequency densitometry allows for non-destructive and quick measurements (Schinker et al., 2003) compared to the commonly used X-ray densitometry (Wassenberg et al., 2014).

For the measurements using a LIGNOSTATION™, a probe moves along the wood surface with a pressure of 1 N, which is needed to prevent the measurement of air between the probe and wood sample material (Schinker et al., 2003). The tip of the probe contains a transmitting electrode as well as a receiving electrode; the two being separated from each other by a metal shield to avoid direct

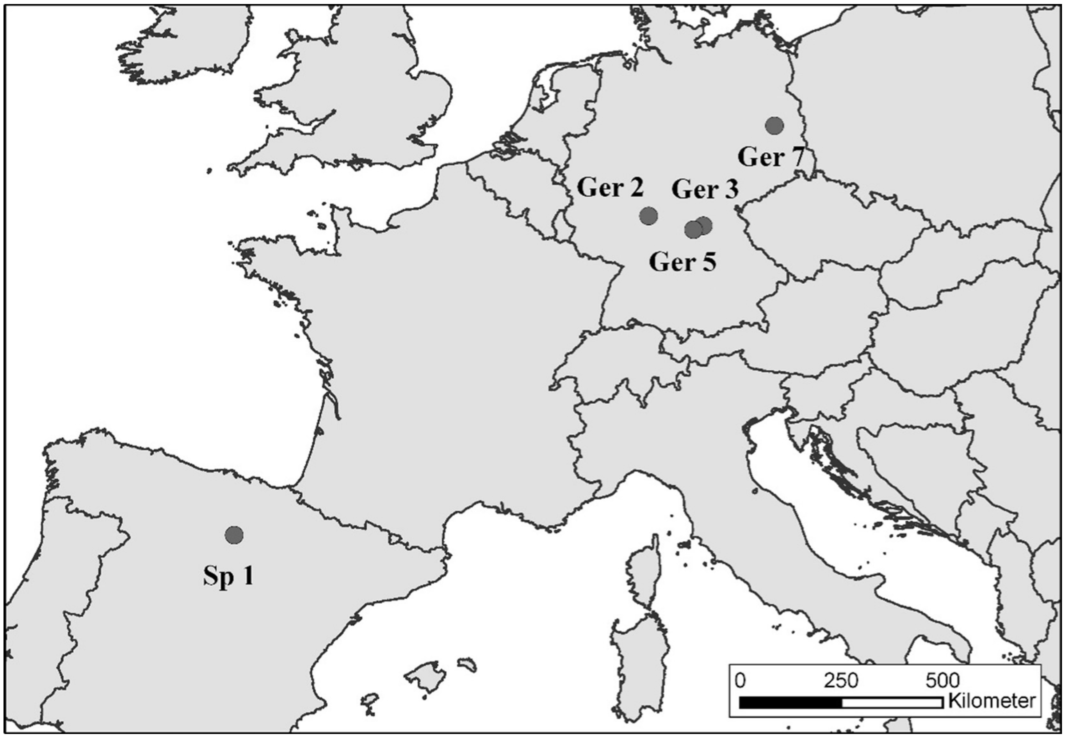

Fig. 1. The analysed triplets Alzenau (Ger 2), Bamberg (Ger 3), Steigerwald (Ger 5), Teupitzer Forst (Ger 7), Huerta de abajo (Sp 1).

Table 1
Geographical information about the triplets.

Name	Code	Latitude N	Longitude E	Altitude a.s.l. (m)	Precipitation (mm year^{-1})	Temperature (°C)	Geological substrate
Alzenau	Ger 2	50°06′48.74″	09°03′54.36″	250	720	9.0	Slightly loamy sand
Bamberg	Ger 3	49°53′11.64″	10°58′13.12″	250	650	8.0	Loamy sand
Steigerwald	Ger 5	10°38′10.10′′	49°47′55.91′′	125	713	9.5	Slightly loamy sand
Teupitzer Forst	Ger 7	52°04′45.55″	13°37′06.05″	60	520	8.6	Sandy
Huerta de abajo	Sp 1	42°05′57.00″	−03°−10′−19.00″	1290	860	8.9	Sandy loam

Reference period for climate data: 1994–2013.

'flow' of the electromagnetic field. The dielectric properties of wood are determined by the ratio of cell wall material and air. By measuring the amount of the transmitted signal received on the other side of the shield, the tree ring wood density of the sample material is calculated automatically (Schinker et al., 2003).

All tree cores were stored in the same room prior to the scanning process to avoid big differences in humidity and temperature. If no diamond fly cutter is available, Wassenberg et al. (2015) suggest sanding for sample preparation as the best solution. We sanded the sampled tree cores with 180-, 400- and 800-grid sanding paper using a belt sander and 1200-grid sanding paper in manually applied sanding in order to achieve an adequately smooth surface to ensure an accurate and uninterrupted scan (Wassenberg et al., 2015, p. 11). Even though the absolute values of tree ring wood density obtained in this way may differ from other measuring methods, relative comparisons are still possible because all samples were measured under the same conditions and adjustments. The only alteration we applied was to reduce the adjustments for height by 1 mm for European beach leading to a higher pressure of the probe on the wood surface for the samples of this species. We did so because using the same height adjustments for European beech as for Scots pine did not yield any reasonable measurement results. We assumed that the higher tree ring wood density of European beech created the need to apply a higher pressure on the sample surface.

When comparing values for tree ring wood density measured in this study to mean values per species generated by water displacement measurements in other studies, the differences between values produced by the two methods, especially for European beech, become visible. Further calibration of the LIGNOSTATION™ would be needed to generate absolute values in tree ring wood density. We assumed that our samples had a humidity of about 12% after they had been stored at room temperature. When comparing high-frequency densitometry and water displacement measurements from different untreated stands, Kemmerer (2016) and Räbel (2016) found values from high-frequency densitometry to be 4% higher for Scots pine and 20% lower for European beech compared to water displacement measurements. Correction factors of 0.92 for Scots pine and 1.19 for European beech (Table A6) deduced from this comparison were used in our study to convert measured values of the LIGNOSTATION™ into absolute tree ring wood density values. These were then used for biomass calculations (Table A5).

Since the focus of our study was to compare pure and mixed stands, measuring relative differences in tree ring wood density was the main objective. In order to estimate the difference between our results measured and real values of tree ring wood density (Table A6), we compared our results to 30 samples of Scots pine and 30 samples of European beech analysed in water in displacement measurements (Saranpää, 2003b). The samples come from different sites and are aggregated into a mean value which serves as a reference.

2.2.2. Linear mixed effects model

Dealing with hierarchical or nested data means taking into consideration that samples are not independent from each other. Samples belonging to one group or repeated measures of a certain location or individual might have the same random effects (Crawley, 2009, p. 627). The sampling data does therefore not meet the assumption of independence which would be necessary in linear regression models (Zuur et al., 2009, p. 102). By including not only fixed effects but also random effects, linear mixed effects models are applied in order to avoid the so-called 'pseudoreplication' (Crawley, 2009, p. 629). The random effect included in our models addresses intercorrelation of the samples caused by being part of the same triplet as well as tree rings belonging to one tree.

In order to address hypotheses HI–HIII, we set up model functions to describe the effect of mixing, diameter at breast height (DBH) and stand density index (SDI) on ring width and tree ring wood density using linear mixed effects models. Non-significant factors in the initial model functions were then eliminated in stepwise reduction resulting in final model functions ([*1*.a], [1.*b*], [2], [3.*a*], [3.*b*]). Stepwise reduction is used in order to acquire a model function with correct p-values describing the effect of different factors on a variable (Crawley, 2009, p. 635). For HI, only the mixing effect and the nested design of the data are considered ([1.a], [1.b]) and predictions for operational decisions concerning mean ring width and mean tree ring wood density per tree over all examined triplets are made. For HII, using single tree ring data was necessary for analysing the influence of ring width on tree ring wood density ([2]). The model functions for HIII are supposed to analyse the effects of mixing on mean ring width and mean tree ring wood density in pure and mixed stands for equal tree size and stand density ([3.a], [3.b]). Here, as for HI, we used mean values per tree to enable values of stand density to be included in the model function.

For the application of linear mixed-effects models we used the lme function of the nlme package in R (Pinheiro et al., 2016).

We set up the following model functions in order to address questions QI–QIII:

QI: Are mean tree ring width and mean tree ring wood density equal in monocultures and mixed-species stands?

The following model functions describe the mixing effect on mean ring width and mean tree ring wood density, respectively, in order to examine if there are significant differences between pure and mixed stands.

$$RW_{ij} = a_0 + a_1 * Mix_{ij} + b_i + \varepsilon_{ij} \tag{1.a}$$

$$MD_{ij} = a_0 + a_1 * Mix_{ij} + b_i + \varepsilon_{ij} \tag{1.b}$$

RW_{ij} is the mean ring width per tree j on triplet i. MD_{ij} is the mean tree ring wood density per tree j on triplet i. Mix_{ij} is the effect of mixing on tree ring width or tree ring wood density for tree j on triplet i. Parameter a_0 is the intercept, thus tree ring width or tree ring wood density in pure stands, i.e. the mixing factor equals 0. Potential differences in site characteristics on the different triplets are addressed by a random effect b_i for triplet i. The error term ε_{ij} contains the remaining unexplained variation for tree j on triplet i.

QII: Is tree ring wood density independent from tree ring width?

The influence of tree ring width on tree ring wood density is defined by the following model function.

$$D_{ijk} = a_0 + a_1 * Mix_{ij} + a_3 * RW_{ijk} + b_{ij} + \varepsilon_{ijk} \tag{2}$$

D_{ijk} is the tree ring wood density of a tree ring k (according to the calendar year) of tree j on triplet i. RW_{ijk} is the width of a tree ring k of tree j on triplet i and is examined as the main effect. Differences between the triplets due to site characteristics and the nested design of tree rings belonging to one tree are addressed by random effect b_{ij}. All remaining variation that is not explained by the model is contained in ε_{ijk}.

QIII: Are tree ring width and tree ring wood density equal in pure and mixed stands for equal tree size and stand density?

In order to analyse if the effect of mixing on tree ring width depends on stand characteristics, we included stand density index in the model. As tree ring width and DBH in even-aged stands represent the same information, DBH was not included in this model function.

$$RW_{ij} = a_0 + a_1 * Mix_{ij} + a_4 * SDI_{ij} + a_6 * Mix_{ij} * SDI_{ij} + b_i + \varepsilon_{ij} \tag{3.a}$$

For analysing the mixing effect on tree ring wood density for equal tree size and at equal stand density we chose to include diameter at breast height (DBH) and stand density index (SDI). Even though values of individual tree rings were used for the analysis under HII, we used mean values per tree for tree ring width and tree ring wood density in this case in order to enable the expansion of the model by the static SDI values. Non-significant factors, such as three-way and most of the potential two-way interactions were eliminated in stepwise reduction. The interaction term of a main effect with the mixing factor Mix_{ij} addresses the influence of a main effect in the mixed stand. Model functions were only applied if a visual precheck of the data was considered meaningful.

$$MD_{ij} = a_0 + a_1 * Mix_{ij} + a_2 * DBH_{ij} + a_4 * SDI_{ij} + a_5 * Mix_{ij} * DBH_{ij} + a_6 * Mix_{ij} * SDI_{ij} * b_i + \varepsilon_{ij} \tag{3.b}$$

We then applied a correction factor to the tree ring wood density values measured in this study (Table A6) and used volume measurements from previous studies on the same triplets (Pretzsch et al., 2015) for a rough calculation of biomass of both species in order to compare their performance in pure and mixed stands (Table A5).

3. Results

Tree ring width in Scots pine and European beech declined over time (Fig. 2). Tree ring wood density was more constant over time and was lower in mixture than in pure stands for both species.

3.1. QI: Are mean tree ring width and mean tree ring wood density equal in pure and mixed stands?

First, when only examining the effect of mixing, Scots pine appeared to have a 14% higher tree ring width in mixed stands compared to pure stands. Tree ring width of European beech showed an opposite trend in mixed stands (−5%) compared to pure stands but the difference was non-significant. Tree ring wood density of Scots pine was 12% lower in mixed stands compared to pure stands. For European beech, tree ring wood density was 8% lower in mixed stands compared to pure stands (Fig. 3 and Table 2).

3.2. QII: Is tree ring wood density independent from tree ring width?

When looking at all tree rings, tree ring wood density of Scots pine was negatively correlated with tree ring width and thus significantly decreased with increasing tree ring width (Fig. 4 and Table 2). Tree ring wood density in European beech was positively correlated with tree ring width and therefore significantly

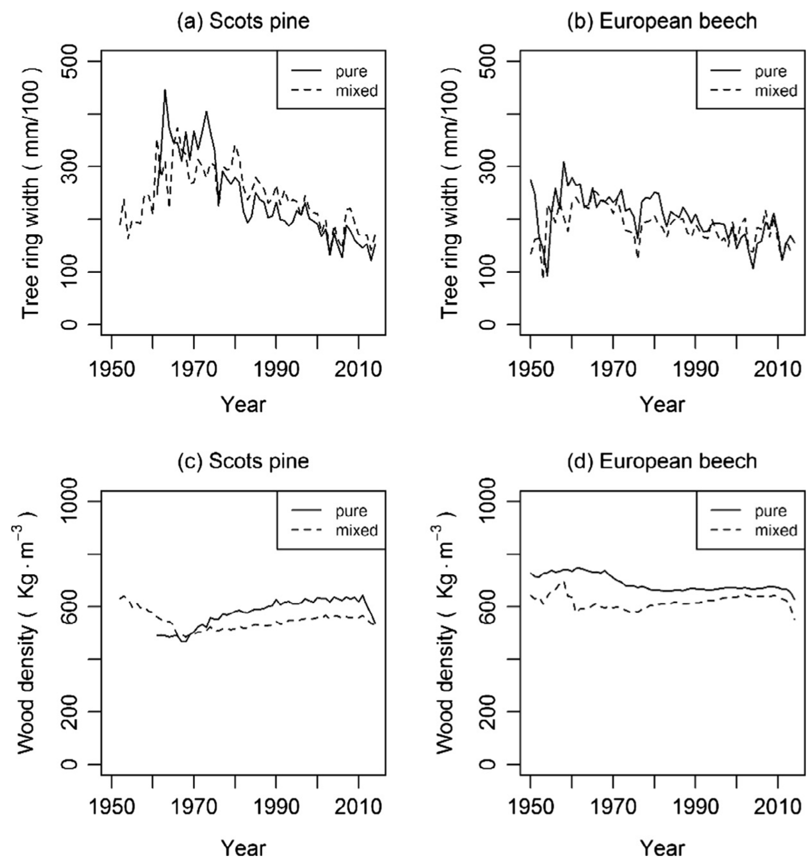

Fig. 2. Tree ring width of Scots pine (a) and European beech (b) and tree ring wood density of Scots pine (c) and European beech (d) in pure and mixed stands from 1950 to 2014.

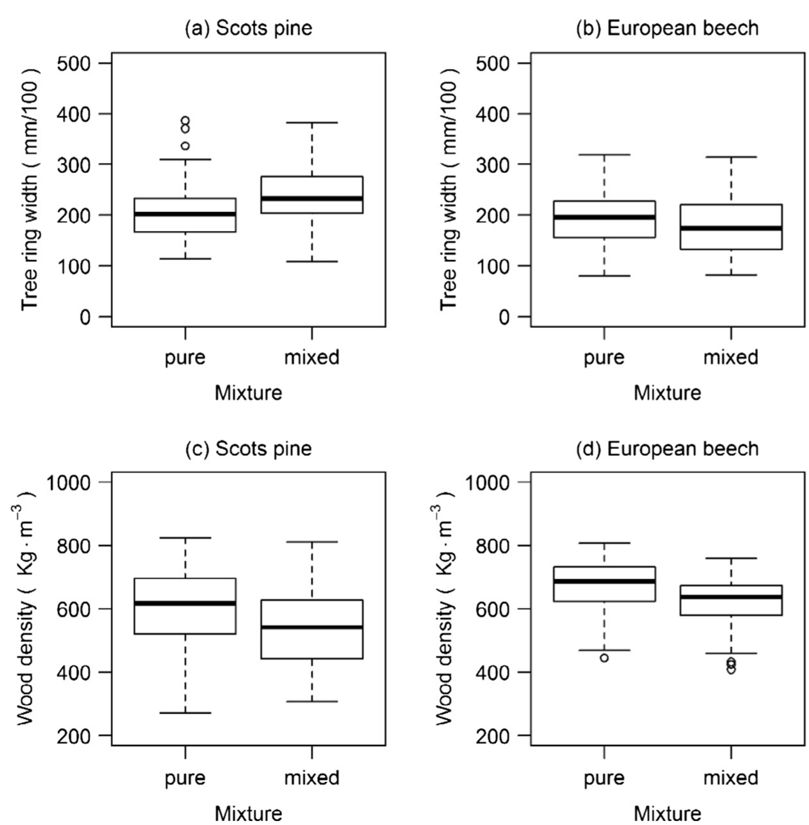

Fig. 3. Differences between pure and mixed stands in mean tree ring width of Scots pine (a) $p < 0.05$, $R^2 = 0.07$ and European beech (b) n.s. and differences in mean tree ring wood density of Scots pine (c) $p < 0.001$, $R^2 = 0.39$ and European beech (d) $p < 0.001$, $R^2 = 0.09$.

Table 2
Results of linear mixed-effects model functions QI–QIII.

Model function	Depend. var.	Species	Value	Intercept	Mix	DBH	RW	SDI	Mix * DBH	Mix * SDI	Mixing effect (%)	R^2 (conditional)
				a_0	a_1	a_2	a_3	a_4	a_5	a_6		
		Sc.p.	Mean			239.3	219.90	986.50				
		E.be.	Mean			227.00	186.96	815.70				
QI	Mean ring width	Sc. p.	Value	206.80	**29.03**						**14.04**	0.07
			SE	6.25	8.92							
			p-value	.000	.001							
	Mean ring width	E. be.	Value	191.38	−10.21						−5.33	0.07
			SE	10.33	8.81							
			p-value	.000	.248							
	Mean wood density	Sc. p.	Value	595.63	−**72.87**						−**12.23**	0.39
			SE	28.16	15.79							
			p-value	.000	.000							
	Mean wood density	E. be.	Value	665.43	−**50.1**						−**7.53**	0.09
			SE	11.09	13.35							
			p-value	.000	.000							
QII	Wood density	Sc. p.	Value	629.27	−**95.85**		−**0.10**					0.79
			SE	38.98	3.13		0.01					
			p-value	.000	.000		.000					
	Wood density	E. be.	Value	637.93	−**12.00**		**0.048**					0.66
			SE	8.05	2.95		0.008					
			p-value	.000	.000		.000					
QIII	Mean ring width	Sc. p.	Value	190.8	**30.44**			n.s.		n.s.	**15.95**	0.07
			SE	22.88	9.11							
			p-value	.000	.001							
	Mean ring width	E. be.	Value	254.99	n.s.			−**0.08**		n.s.	0.00	0.12
			SE	28.57				0.03				
			p-value	.000				.017				
	Mean wood density	Sc. p.	Value	not analysed[a]								
			SE									
			p-value									
	Mean wood density	E. be.	Value	490.17	−**48.14**	**0.27**		**0.14**	n.s.	n.s.	−**7.23**	0.18
			SE	46.61	12.98	0.09		0.04				
			p-value	.000	.000	.003		.001				

Scots pine, Sc. P.; European beech, E. be.; grey parts, not included in model; non-significant effects eliminated in stepwise reduction, n.s.
Values in bold significant at $p < 0.05$.
Calculation of mixing effect (%) by inserting mean values in linear mixed-effects model function.
[a] Visual pre-check showed no meaningful dependency of data.

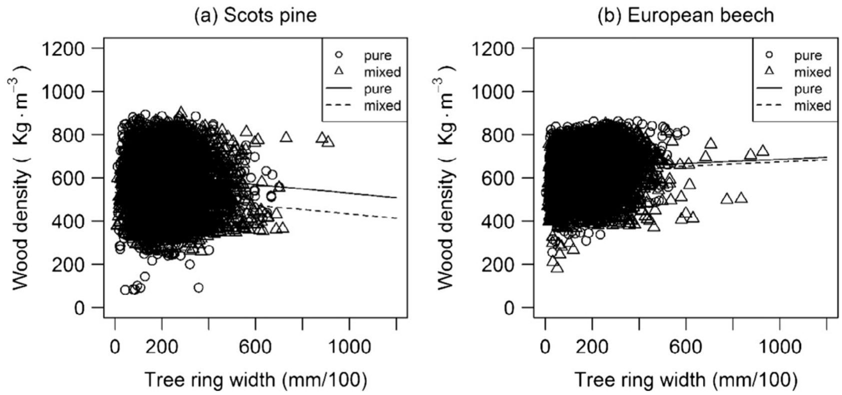

Fig. 4. Correlation of tree ring width and tree ring wood density in pure and mixed stands of Scots pine (a) $p < 0.001$, $R^2 = 0.79$ and European beech (b) $p < 0.001$, $R^2 = 0.66$. Total number of observations/tree rings: 13301.

increased with increasing tree ring width. Interaction effects with mixture were eliminated due to non-significance.

3.3. QIII: Are mean tree ring width and mean tree ring wood density equal in monocultures and mixed-species stands of equal tree size and equal stand density?

When examining not only mixing, but also stand density index (SDI) as potential effects on tree ring width, it was found that SDI did not have any effect on tree ring width of Scots pine. For European beech, tree ring width and stand density index were negatively correlated. After considering the effect of stand density index, it was shown that mixing still did not have any effect on tree ring width in European beech (Fig. 5 and Table 2).

When calculating tree ring width using the expanded model function (Tables 2 and A3), it was found that tree ring width of Scots pine in mixed stands was 16% higher than in pure stands. For European beech no difference in tree ring width between pure and mixed stands was found. These values differ slightly from HI due to different model functions used for their calculation. Nevertheless, the results show that when considering tree size and stand density, the mixing effect found under HI for Scots pine remains valid.

The effects of mixture, DBH and SDI on tree ring wood density of Scots pine and European beech are presented in Fig. 7 and Table 2.

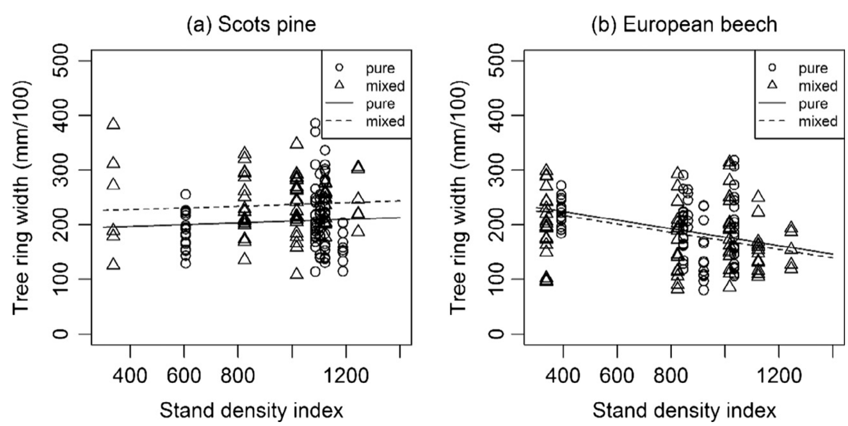

Fig. 5. Effect of stand density index on tree ring width of Scots pine and European beech. For Scots pine ($R^2 = 0.07$): SDI (a) n.s. For European beech ($R^2 = 0.12$): SDI (b) $p < 0.05$.

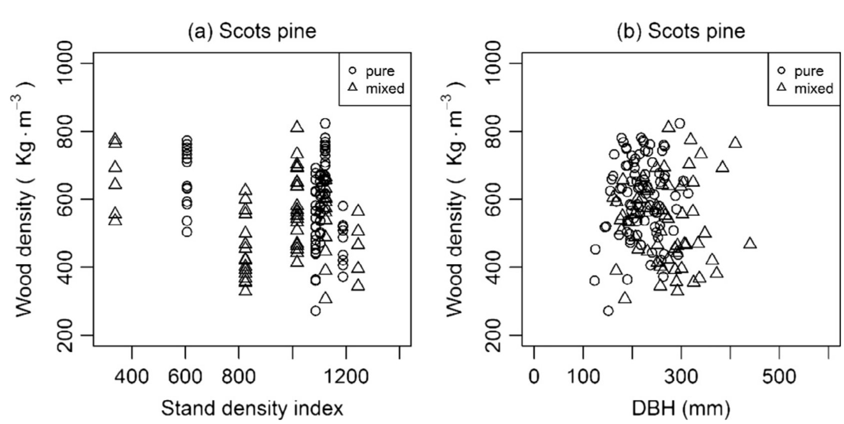

Fig. 6. Tree ring wood density, SDI and DBH in pure and mixed stands of Scots pine. No model was fitted to the data.

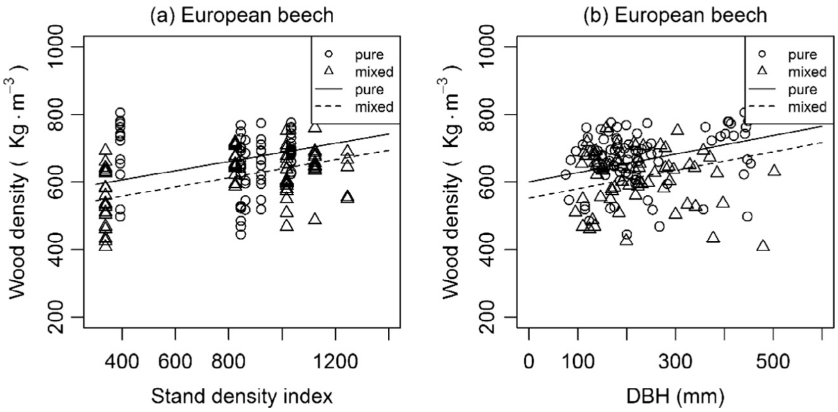

Fig. 7. Tree ring wood density, SDI and DBH in pure and mixed stands of European beech. (a) and (b) Mixing effect, SDI and DBH significant p < 0.005, R^2 = 0.18.

For Scots pine, testing of possible relationships between DBH, SDI and tree ring wood density were not considered after a visual pretest showed that in the given data no relationships can be found (Fig. 6). The 12% lower tree ring wood density of Scots pine in mixed stands found under HI therefore remains valuable and demonstrates that the mixing effect is reliable and does not change with stand density or tree size. The negative relationship between tree ring wood density and tree ring width is not visible in DBH since mean DBH values per tree are used.

For European beech, SDI and DBH significantly influenced tree ring wood density, but the size of the effect was equal in pure and mixed stands. In the mixture, tree ring wood density of European beech was found to be 7% lower than in pure stands. This shows that the mixing effect found under HI (−8%) is still present and significant after excluding the effects of tree size and stand density index (Tables 2 and A4).

After measuring mean tree ring wood density of pure and mixed stands, we used the generated values from HI to calculate how mixed stands were performing compared to pure stands in terms of biomass production (Table A5). Scots pine was producing 11% more biomass in mixed stands than in pure stands. European beech in mixed stands produced 10% less biomass. In total, biomass was 8% lower in mixed stands compared to pure stands. To calculate biomass we applied correction factors of 0.92 for Scots pine and 1.19 for European beech in order to enable comparisons of tree ring wood density values between the two species. Correction factors were derived from an internal study comparing high-frequency densitometry and water displacement measurements (Table A6) and help to overcome the issue of high-frequency measurements not providing absolute tree ring wood density values (see Methods).

4. Discussion

4.1. Interpretation of results

Tree ring width of Scots pine was found to be significantly higher in mixed stands versus pure stands, whereas tree ring width of European beech was not significantly influenced by the mixing with Scots pine. Tree ring wood density was lower in mixed stands for both species.

The results can contribute to understanding the differences between pure and mixed stands in terms of basal area growth and volume growth. When trying to explain mixing effects on volume growth, significant variations in allometric variables between species can play an important role and should therefore be considered (Monserud and Marshall, 1999).

Studies about tree ring wood density are still rare but Kennel (1965) found that tree ring wood density of European beech was not affected by the mixing with Norway spruce when examining fully stocked mixed stands of Norway spruce and European beech. Norway spruce, however, had a significantly higher tree ring wood density in the mixed stands. Pretzsch and Rais (2016) found that in seven of the nine reported comparative studies concerning complex and homogeneous stands, tree ring wood density was not influenced by the mixing of species even though tree ring width variability seems to increase in complex stands.

We hypothesise that the differences in tree ring wood density between the pure and mixed stands of our study are a result of acclimatisation to an inter-specific neighbourhood. For that purpose, tree species may change their growth partitioning in mixed-species stands. The internal tree resource allocation may prioritise growth and expansion at the expense of stability and defence when coping with inter-specific competition. The size growth of a tree enhances its access to light and, consequently, both species will follow the strategy of growth rather than defence (Matyssek et al., 2005, 2012).

Most of the comparisons of productivity in mixed and pure stands are based on stem volume production (Liang et al., 2016; Pretzsch et al., 2015). Comparisons based on total biomass production may produce different results, as tree species mixing can change stem-crown allometry (Bayer et al., 2013), root-shoot relationship (Thurm et al., 2017) and also tree ring width and tree ring wood density (Pretzsch and Rais, 2016). An increase in crown size in relation to stem size in mixed-species stands as reported by Dieler and Pretzsch (2013) and Pretzsch (2014) would mean that the overyielding is even higher when calculated for the total above-ground volume of mixed versus pure stands. However, the decrease in root in relation to shoot growth as reported by Thurm et al. (2017) and the lower tree ring wood density in mixed stands revealed in our study can consequently modify the overyielding of mixed stands as soon as total biomass is taken into account. In our study, biomass in mixed stands calculated from stem volume and tree ring wood density is lower than in pure stands despite the measured overyielding in volume on mixed stands.

When examining the relation between tree ring width and tree ring wood density, we found tree ring wood density of both Scots pine and European beech to be clearly dependent on tree ring width, negatively related in the case Scots pine and positively related in the case of European beech. Supporting our findings, Genet et al. (2012) state that the way in which tree ring width and tree ring wood density are related depends on whether the tree is a conifer, ring-porous hardwood or diffuse-porous hardwood. In ring-porous trees like oak or ash, growth rate and tree ring wood density were found to be positively correlated, whereas softwood species like Pine show a decreasing tree ring wood density with increasing growth rate. Tree ring wood density in diffuse-porous hardwood species, like beech, acer or birch is usually not influenced by tree ring width (Diaconu et al., 2016; Hakkila, 1989).

Finally, when also considering tree size and stand density for HIII in order to test if the differences between pure and mixed stands found for HI represent real mixing effects, the mixing effect on tree ring width were shown to still be significant for Scots pine.

Tree ring width of European beech remained unaffected by mixing for equal tree size and stand density as found under HI.

When looking at tree ring wood density, the non-existing influence of stand density and tree size on tree ring wood density of Scots pine show that the mixing effects found under HI are valid.

For European beech, we found a 7% lower tree ring wood density in mixed compared to pure stands. Differing values in the results found under HI come from an only approximate means of calculating tree ring wood density involving the insertion of mean values in the final model function. Nevertheless, the significantly lower tree ring wood density of European beech in mixed stands compared to pure stands is visible even though stand density is considered in HIII.

The fact that stand structure can influence tree ring wood density is also stated by Bues (1985), Grammel (1990), Hapla (1985), Todaro and Macchioni (2011), Brazier and Mobbs (1993), Larocque and Marshall (1995), Moore et al. (2015) and Zhang et al. (2006) who found a reduction in tree ring wood density of coniferous trees with increasing spacing and thinning which could not be shown in our study. Tree ring wood density of deciduous trees is rather known to remain unaffected in most cases (Metzger, 1998; Pérez and Kanninen, 2005). This differs from the results of our study which showed a significant effect of SDI on tree ring wood density for European beech. These findings still suggest that stand density should be taken into account when examining mixing effects in order to exclude potential dependencies of tree ring wood density on stand density. Apart from stand structure and species-specific traits, climatic conditions and site characteristics can have an impact on the correlation of tree ring width and tree ring wood density (Bernhart, 1964; Krempl, 1977).

4.2. Relevance for forest management

The consequences of a reduction in tree ring wood density could include e.g. a loss of mechanical stability (Anten and Schieving, 2010) against e.g. breakage by wind or snow since tree ring wood density is strongly correlated with timber strength (Saranpää, 2003b), hardness and abrasiveness (Bacher and Krosek, 2014; Pretzsch and Rais, 2016). It still remains to be proven whether or not the reduction in tree ring wood density in mixed stands found in this study negatively influences stability.

When it comes to carbon storage, a lower tree ring wood density results in lower carbon content in a given stock of standing volume. Our finding that tree ring wood density of both species in mixed stands is lower than in pure stands indicates a lower amount of carbon storage under ceteris paribus conditions; i.e. if other characteristics such as stem shape, root-shoot and stem-crown allometry are similar in pure and mixed stands. As the proportion of crown, branches and twigs in relation to stem is higher in mixed than in pure stands (Dieler and Pretzsch, 2013) part of the lower biomass associated with tree ring wood density reduction may be cancelled out or overcompensated by a higher branch fraction. Allometric functions made for pure stands will have to be adapted to mixed stands and include differences in allometric traits of individual trees in mixture and interaction effects (Pretzsch, 2014) in order to estimate and compare productivity of pure and mixed stands.

When the resource-use efficiency of a forest (Binkley, 2012), e.g. biomass per ha of forest, is calculated, an overyielding in volume of mixed forests can lead to the conclusion that resource-use efficiency is higher. When focussing on the production of quality timber only, an overyielding in stem volume found on mixed stands can be an advantage disregarding a lower tree ring wood density, given that stability is still sufficient despite reductions in tree ring wood density. Ongoing studies on within-tree growth partitioning in mixed versus pure stands will clarify how mixed stands perform compared to pure stands. Here, results depend on whether stand productivity is defined by stem volume productivity, which is of primary interest for forestry, or by total biomass production, which is relevant for ecosystem understanding and carbon balance.

4.3. Methodological considerations

The analysis of tree ring wood density in this study is especially interesting as it is usually measured by weight and volume or X-ray scanning (Beall, 2007; Saranpää, 2003a). The new method used in our analysis, high-frequency densitometry, offers an alternative to these time-consuming and destructive methods. When comparing high-frequency densitometry and X-ray densitometry, Schinker et al. (2003, p. 235) found similar results for tree ring wood density of Norway spruce. Until now, high-frequency densitometry has mostly been used to calculate relative values and variations in tree ring wood density. To achieve absolute mass density values, a more accurate calibration for each tree species would be necessary (Wassenberg et al., 2014).

Concerning sample preparation, an extra device – when using a belt sander instead of a diamond fly cutter – can be useful for a more precise alignment of the sample on the belt sander. Manually induced contact of the sample on the belt sander can lead to a lower geometrical accuracy of the surface. Reducing the grain size of the sanding paper in order to reduce problems caused by sanding dust on the wood surface could also be considered to improve scanning results (Wassenberg et al., 2015, p. 14). More studies on the precision of high-frequency densitometry are currently being conducted.

Concerning the statistical method in our study, a larger sample size and stands with more homogenous stand densities could help to clarify the effect of SDI on tree ring width and tree ring wood density. Biomass calculated in this study also varied between locations. This suggests the need to verify correction factors through an expansion of this study to the whole set of 32 triplets and also to measure tree ring wood density of all examined triplets also in water displacement measurements. Since some of the tree rings included in this analysis were juvenile wood and thus not as representative as a normal tree ring, we also ran parts of the analysis for the last 30 years only and compared results. As results were not significantly different from the dataset containing all 65 years from 1950, the data was still included in the analysis thereby providing a larger sample pool.

4.4. Perspectives

This study is based on a limited dataset. In further studies, more triplets could be included in order to find out if the outcome of this study applies to other triplets, different site characteristics and climatic conditions. Also, inter-annual climatic conditions, which can influence tree ring width and tree ring wood density tested on pure and mixed stands (Bouriaud et al., 2004; Miina, 2000; Olivar et al., 2015; Ponton et al., 2001), might have to be considered. Additionally, different species compositions could be tested for inter-species reactions, potential competition or niche separation and resulting differences in tree ring width or tree ring wood density. In ongoing research, mixing effects on tree ring wood density are also being analysed in greater detail by taking tree cores not only from breast height, but also from different heights across the tree stem.

Another relevant topic is the effect of inter-annual climatic conditions on tree ring wood density. Since the triplets examined in this study have not undergone any silvicultural treatments in recent years, similar studies on more intensively managed and productively used sites could provide further results. In particular, the combination of initial stand structure and short-term and long-term silvicultural treatments that imply changes in stand structure seems to be an interesting topic in the investigation of mixing effects and should be analysed more intensively in this context. In any case, tree ring wood density should be examined further in order to improve estimates of biomass production, carbon storage, stem stability and decomposition rates in mixed-species forests. These factors may be especially important when trying to gather a more complete estimate of forest resources and the question of how to manage them sustainably in the long term.

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Appendix A.

See Tables A1–A6.

Table A1
Stand characteristics of pure and mixed stands of Scots pine and European beech.

Triplet	Species	n	Stand age (years)	N (trees ha^{-1})	d_q (cm)	h_q (m)	SDI (ha^{-1})	V ($m^3\ ha^{-1}$)	IV ($m^3\ ha^{-1}\ year^{-1}$)
Ger 2	Sc p. mono	22	55	1461	21.21	25.28	1122	581	21.90
	Sc p. mixed	22	55	471	26.83	27.39	528	329	10.50
	E. be. mono	21	55	2022	16.46	22.39	1034	474	21.50
	E. be. mixed	20	55	604	21.94	25.98	490	300	13.73
Ger 3	Sc p. mono	21	47	2054	16.81	20.69	1086	407	19.99
	Sc p. mixed	13	47	1529	15.56	20.59	714	255	12.97
	E. be. mono	19	47	2090	14.22	20.95	845	334	16.87
	E. be. mixed	13	47	1099	13.49	19.29	408	144	7.19
Ger 5	Sc p. mono	19	57	1324	22.31	22.43	1103	517	17.69
	Sc p. mixed	19	57	346	29.55	26.15	452	256	7.27
	E. be. mono	14	57	1635	17.48	23.88	921	482	22.50
	E. be. mixed	16	57	489	21.07	24.99	372	219	8.76
Sp 1	Sc p. mono	9	40	1667	20.24	16.20	1188	399	12.40
	Sc p. mixed	6	40	1082	21.32	17.33	838	310	11.65
	E. be. mono	6	40	2542	12.75	16.38	862	248	15.34
	E. be. mixed	5	40	1477	11.20	15.22	407	99	5.23
Ger 7	Sc p. mono	16	80	1579	13.75	15.49	605	162	7.77
	Sc p. mixed	6	80	82	25.94	21.79	87	44	1.94
	E. be. mono	18	80	300	29.54	24.40	392	266	9.36
	E. be. mixed	20	80	327	21.17	17.31	250	105	5.04

Five triplets were included consisting of one mixed-species stand and two mono-specific stands each.
Scots pine, Sc. P.; European beech, E. be.; monocultures, mono; mixed-species stands, mixed.
Tree number (trees ha^{-1}), N; quadratic mean diameter (cm), dq; height of the tree with quadratic mean diameter (m), hq; stand density index (trees ha^{-1}), SDI; standing volume ($m^3\ ha^{-1}$), V; periodic annual volume increment ($m^3\ ha^{-1}\ year^{-1}$), IV.

Table A2
Sample trees of Scots pine and European beech in pure and mixed stands.

Species		Unit	Mean	SD (±)
Sc. p. mono (n = 87)				
	Diameter at breast height	mm	218.06	40.69
	Crown radius[a]	m	1.49	0.54
	Crown ratio	m m^{-1}	0.29	0.06
	Tree ring width	mm/100	207.24	55.40
Sc. p. mixed (n = 66)				
	Diameter at breast height	mm	267.27	61.02
	Crown radius[a]	m	1.44	0.53
	Crown ratio	m m^{-1}	0.28	0.08
	Tree ring width	mm/100	236.51	53.69
E. be. mono (n = 78)				
	Diameter at breast height	mm	237.16	110.35
	Crown radius[a]	m	1.79	0.6
	Crown ratio	m m^{-1}	0.52	0.17
	Tree ring width	mm/100	191.67	53.14
E. be. mixed (n = 74)				
	Diameter at breast height	mm	216.39	89.71
	Crown radius[a]	m	2.22	0.94
	Crown ratio	m m^{-1}	0.61	0.17
	Tree ring width	mm/100	182.01	60.04

Five triplets were included consisting of one mixed-species stand and two mono-specific stands each.
Scots pine, Sc. P.; European beech, E. be.; monocultures, mono; mixed-species stands, mixed
[a] No data available for triplet Ger 7.

Table A3
Calculations of overall tree ring width resulting from linear mixed effects model QIII.

	Intercept	Mix	DBH	SDI	Mix * DBH	Mix * SDI	Result	Diff. absolut	Diff. in%
	a_0	a_1	a_2	a_4	a_5	a_6			
Results lme Sc. P.	190.8	30.44							
Mean value									
Ring width Sc. p. pure							190.80		
Ring width Sc. p. mixed							221.24	30.44	15.95
Results lme E. be.	254.99			−0.08					
Mean value				815.70					
Ring width E. be. pure							189.73		
Ring width E. be. mixed							189.73	0.00	0.00

Scots pine, Sc. p.; European beech, E. be.; linear mixed-effects model, lme.

Table A4
Calculations of overall tree ring wood density resulting from linear mixed effects model QIII.

	Intercept	Mix	DBH	SDI	Mix * DBH	Mix * SDI	Result	Diff. absolut	Diff. in%
	a_0	a_1	a_3	a_4	a_5	a_6			
Results lme Sc. P.	Not analysed[a]								
Mean value									
Wood density Sc. p. pure									
Wood density Sc. p. mixed									
Results lme E. be.	490.17	−48.14	0.27	0.14					
Mean value			227	815.7					
Wood density E. be. pure							665.66		
Wood density E. be. mixed							617.52	−48.14	−7.23

Scots pine, Sc. p.; European beech, E. be.; linear mixed-effects model, lme.
[a] Visual pre-check showed no meaningful dependency of data.

Table A5
Calculation of basal area, volume and biomass on the five triplets examined in this study and the difference between pure and mixed stands.

Stand variable	$Mixed_{obs}/Mixed_{exp}$		$Sc.p._m/Sc.p._p$		$E.be._m/E.be._p$	
	Mean	SE	Mean	SE	Mean	SE
BA	1.03	0.10	1.13	0.20	0.92	0.05
V	1.07	0.10	1.22	0.18	0.91	0.08
PAIBA ($m^2\ ha^{-1}\ year^{-1}$)	0.98	0.08	1.18	0.35	0.79	0.19
PAIV ($m^3\ ha^{-1}\ year^{-1}$)	1.02	0.09	1.18	0.25	0.88	0.10
Biomass (kg)	0.92	0.12	1.11	0.13	0.90	0.13

Variables listed include basal area (BA), volume (V), periodic annual basal area increment (PAIBA) and periodic annual volume increment (PAIV).

Table A6
Correction factors deduced from study on the comparison of water displacement measurements and high-frequency densitometry.

Species	Wood density ($kg\ m^{-3}$)		Correction factor
	Water displacement	High frequency	
Sc. p.	554.25	609.74	0.92
E. be.	701.85	592.70	1.19

Scots pine, Sc. P.; European beech, E. be., mean values from internal study on comparison of water displacement method and high-frequency densitometry.

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