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Mixing increases drought exposure through a faster growth in beech, but not in oak

Kristoffel Jacobs[a,*], Damien Bonal[b], Catherine Collet[b], Bart Muys[c], Quentin Ponette[a]

[a] Earth and Life Institute, Environmental Sciences, Université catholique de Louvain, Louvain-la-Neuve, Belgium
[b] Université de Lorraine, AgroParisTech, INRA, UMR Silva, 54000 Nancy, France
[c] Department of Earth and Environmental Sciences, Division of Forest, Nature and Landscape, KU Leuven, Leuven, Belgium

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ABSTRACT

Promoting mixed forests is often seen as a management option to increase the resilience of forests to droughts. However, mixing can also improve tree growth, and if faster-growing trees use more water, they may be exposed to higher risks of drought. Across Belgium, we tested whether increased tree growth in mixed sessile oak/common beech stands results in increased drought exposure of these forests in severe dry summers. We sampled wood cores from 222 trees in mixed and corresponding pure stands at eight different sites and measured ring widths and stable carbon isotope composition ($\delta^{13}C$) in the wood formed during 2001 (wet summer as a reference year) and 2003 (severe dry summer). Pre-drought growth (PG), an index of tree growth in normal climatic conditions, was calculated as the mean ring width in the five years preceding the drought, and drought exposure was assessed as the difference in $\delta^{13}C$ between the dry and the reference year. Growth of individual beech trees was faster in mixtures and both mixing and pre-drought tree growth were positively related to beech drought exposure. These two effects were not independent: the increased drought exposure in mixed stands was an effect of the faster growth. Analysis of $\delta^{13}C$ values suggests that in reference conditions, beech trees in mixtures had a less conservative water use than trees in pure stands, but that they shifted to a functioning similar to that in pure stands under drought. By contrast, growth and drought exposure of oak trees did not differ between pure and mixed stands. Our results emphasize the different strategies of these two species regarding their response to mixing and drought. Beech maximizes its growth as a result of greater resource capture in mixed stands, but this increases the risk of suffering from severe droughts. Oak, on the other hand, exhibits lower variability in growth and in drought exposure across pure and mixed stands. We should stress that if mixing is used as a management strategy to mitigate the negative effects of climate change on temperate forests, forest managers should be aware that the performance benefits of mixed forests in non-drought years could in fact hinder the drought resistance of these forests in severe drought years.

1. Introduction

In temperate Europe, drought is a major stress factor for forest ecosystems. This is evidenced by numerous dendrochronological studies showing that annual growth is often correlated with precipitation (see Penninckx et al., 1999; Lebourgeois et al., 2004, 2005; and Scharnweber et al., 2011 for examples for oak and beech). For a tree, maintaining sap flow is necessary to replace water lost by evapotranspiration at the leaves and this becomes difficult under conditions of soil drought (e.g. Leuzinger et al., 2005). Due to climate change, droughts like those that hit Europe during the summers of 1976 and 2003 are expected to increase in frequency in the 21st century (Dai, 2013), raising concerns over the ability of temperate forests to sustain and recover from these drought events (Allen et al., 2010).

When co-existing species differ in resource usage patterns, interspecific competition may be weaker than intraspecific competition, according to the niche complementarity principle. Available light, for example, may be more efficiently used in a mixture of species showing different degrees of shade tolerance (Forrester, 2014). Differences in rooting patterns (i.e. vertical distribution, maximum depth) may lead to better soil exploration (Schmid, 2002), though it is not clear whether this process often plays an important role (Jacob et al., 2013). Complementarity may also occur on a temporal scale (del Río et al., 2017). When, under drought-limiting conditions, an isohydric species limits its water usage through stomatal regulation, admixed anisohydric species can have a larger share of the remaining soil water (Pretzsch et al.,

* Corresponding author.
E-mail address: kristoffel.jacobs@uclouvain.be (K. Jacobs).

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2014).

Furthermore, in mixed forests, one species may improve the habitat of another through facilitation of resource acquisition and use (Reiss et al., 2009). The interactions that are possible between a set of species and the ecological relevance of these interactions depend on species identity (ecological traits) in combination with abiotic site conditions (Ammer, 2019).

Managing forests toward species mixtures has been promoted with several objectives. Mixed forests often show increased growth compared with monocultures of the constituent species (i.e. overyielding; Ammer, 2019). Higher resistance to drought has also been hypothesized to be the result of mixing. This is important in regions where drought is expected to increase with climate change, yet there are conflicting empirical results. Pretzsch et al. (2013b) observed that the resistance and resilience of European beech (*Fagus sylvatica* L.) growth during the summer droughts of 1976 and 2003 were higher in mixtures with oak than in pure stands. Lebourgeois et al. (2013) found a similar increase in drought resistance for *Abies alba* in mixtures. However, Grossiord et al. (2014a) found higher drought exposure, expressed as the increase in $\delta^{13}C$ from a wet to a dry year, of trees in mixtures for several tree species in the boreal zone, and no positive effects of mixing in hemiboreal, mountainous beech, or Mediterranean forests (Grossiord et al., 2014b). Metz et al. (2016) observed that beech trees that grew in mixtures with different combinations of species, while generally growing faster than beech in pure stands, had higher growth reductions during the drought years of 1976 and 2003.

Although faster growth is considered a potential benefit of mixing, it may be accompanied by higher demand for water (Ammer, 2019), which in turn could increase susceptibility to drought in mixtures compared with pure stands, unless compensated for by higher availability of water through facilitation mechanisms or by an increase in water-use efficiency. Forrester (2015) observed that some but not all trees in mixtures had higher growth than trees in corresponding pure stands. Those trees growing faster in mixtures had higher water-use efficiency than trees in pure stands, while the trees in mixtures that did not show faster growth did not increase their water-use efficiency either. If higher growth is accompanied by higher water consumption, this may negatively impact water availability under drought conditions. In grasslands, species diversity has been observed to be positively related to evapotranspiration in reference conditions, but not under drought, because the higher water consumption of the most diverse grasslands led to faster depletion of the water reserves (Verheyen et al., 2008).

Increased growth, resulting from complementary interactions, could increase tree susceptibility to drought if optimizing for growth trades off against optimizing for stress resistance. Under conditions that are not water-limited, trees can, for example, shift carbon allocation away from belowground fine roots towards aboveground shoots, or optimize their wood anatomy towards efficient water transport that may be less tolerant to water deficits (Schuldt et al., 2016).

Drought is expected to become a major stress factor for forest ecosystems and mixing is increasingly being used by forest managers as a potential strategy to improve drought resistance of forests to future severe droughts. In this context, it is essential to gain a better understanding of the possible trade-offs between mixing effects on growth and mixing effects on drought resistance. While some studies have examined mixing effects on productivity (Pretzsch et al., 2013a) and on drought resilience (Pretzsch et al., 2013b; Lebourgeois et al., 2013) separately, little is known about the relationship between performance enhancement and buffering effects of mixing. In this study, we investigated this relationship in pure and mixed sessile oak (*Quercus petraea* (Matt.) Liebl.) – beech (*Fagus sylvatica* L.) forests across Belgium. These two species, which frequently co-occur in Western and Central Europe, differ in a number of ecological traits, leaving room for complementarity processes (Pretzsch et al., 2013a). One important such trait is shade tolerance (Toïgo et al., 2018), which is higher in beech than in oak. Regarding water, sessile oak is better adapted to drought-limiting situations, partly due to its ability to develop deeper roots than beech (Leuschner et al., 2001a). Sessile oak is also able to maintain high photosynthesis and transpiration under lower leaf water potentials than beech (Leuzinger et al., 2005), potentially allowing temporal complementarity of soil water use among species. Finally, while sessile oak is more stress tolerant, beech appears to be a much stronger competitor in less stressful conditions. As a result, beech often grows faster in mixed than in pure stands (see, for example, del Río et al., 2014).

Our main hypothesis was that beech trees would benefit (in terms of growth) from being admixed with oak in reference years, but that increased growth in mixed forests would result in increased drought exposure of beech in dry years. For oak, we expected the opposite pattern, namely that growth would be lower in mixed forests, resulting in a decreased exposure to the 2003 drought. To test this hypothesis, we sampled oak and beech trees in pure and mixed stands, using a triplet approach (Forrester & Pretzsch, 2015), at eight different sites. The response to summer drought was assessed as the difference in wood carbon isotope composition ($\delta^{13}C$) between a wet (2001) and a dry (2003) year. This was introduced by Grossiord et al. (2014a) as a way to extract the effect of drought exposure from the $\delta^{13}C$ measurements. We used pre-drought growth (ring width averaged over five years) as an indicator of growth under normal conditions. We first tested for a mixing effect on drought exposure. We then analysed whether this mixing effect was related to the impact of mixing on growth by looking successively at the relationship between mixing and growth, and between growth and drought exposure, while accounting for effects at tree level, such as local neighbourhood and tree dimensions, in addition to stand and site effects.

2. Materials and methods

2.1. Study sites

Eight study sites were selected in Belgium, spanning a range of climate and soil conditions. Five sites are located in the Ardennes region (Table 1) on acid loamy soils with a high stone content but contrasting soil depth and drainage. Three other sites have soils ranging from sandy to loamy, and from excessive to insufficient drainage. We divided the study sites into three categories of water availability (see section 2 of the supplementary material for more details).

At each site, a triplet of stands was selected: a mixed stand consisting of sessile oak and common beech and a pure forest stand of each of the two species. The three stands were selected for homogeneity in site and stand conditions. With the exception of the Ave-et-Auffe and Eupen sites, where the maximum distance between stands was 2 and 5 km, respectively (Table 1), all three stands within one triplet were located next to each other.

2.2. Stands and target trees

In each triplet we aimed for seven dominant target trees of each species in both the pure and the mixed stands. The exact number of target trees deviates slightly and is given in Table 1 in the supplementary material.

Dendrometric measurements were performed in the winter of 2015–2016. We measured total height, trunk diameter and location of all trees with a circumference at breast height greater than 50 cm within an 18 m radius of each target tree (Table 2). On each target tree we measured at least four crown radii. For each target tree, we calculated Hegyi's competition index, *ci*, based on the circumference of neighbouring trees within the 18 m radius (Hegyi, 1974; Contreras et al., 2011):

$$ci = \frac{1}{C130_{target}} \sum \frac{C130_{neighbour}}{dist_{target,neighbour}},$$

Table 1
Selected site characteristics of the eight triplets. In addition to long-term (1954–2015) averaged climate indices (total P, P-PET over the vegetation period), P-PET and SPEI values over the summer period (July-September) are given for the two years under study (2001, 2003). The sites are ranked according to elevation.

	Long. and lat.	Ecoregion	Altitude	Soil type	Soil water availability category[a]	Mean yearly precipitation 1954–2015	Mean P-PET Mar-Sept 1954–2015	P-PET Jul-Sept		SPEI Jul-Sept	
			(m)	(WRB 2014)		(mm)		2001	2003	2001	2003
Buggenhout (BU)	4° 13′ 5″E; 50° 59′ 39″N	Mid-Flemish sloping sandy-loamy area	20	Stagnosol fragic	wet	800	−97.81	85.37	−138.07	1.92	−0.83
Ave-et-Auffe (AV)	5° 8′ 56″E; 50° 6′ 9″N 5° 7′ 44″; 50° 7′ 3″	Calestienne	250	Cambisol calcaric	dry	865	–33.54	40.72	−163.73	1.46	−1.49
Baileux (BA)	4° 23′ 59″E; 50° 1′ 23″N	Atlantic Ardenne and Ardenne basins	300	Cambisol dystric	dry	1081	52.09	82.64	−142.38	1.35	−1.44
Arlon (AR)	5° 32′ 54″E; 49° 38′ 45″N	Cotes de Florenville	340	Cambisol dystric	dry	1112	40.78	75.11	−138.94	1.31	−1.28
Grune (GR)	5° 24′ 28″E; 50° 9′ 2″N	Centro-Eastern Ardenne	420	Cambisol dystric	optimal	1001	54.40	61.32	−102.44	1.11	−1.07
Eupen (EU)	6° 6′ 30″E; 50° 36′ 39″N 6° 3′ 47″E; 50° 33′ 53″N	Centro-Eastern Ardenne	440	Cambisol dystric skeletic	optimal	1112	127.13	62.84	−141.22	0.56	−1.76
La Roche (LR)	5° 35′ 32″E; 50° 11′ 45″N	Centro-Eastern Ardenne	450	Cambisol dystric	optimal	967	24.42	34.32	−128.37	0.97	−1.25
Vecmont (VE)	5° 28′ 37″E; 50° 9′ 37″N	Centro-Eastern Ardenne	450	Stagnosol skeletic	wet	989	43.16	50.78	−116.57	1.04	−1.17

[a] See description in section 2 of the supplementary material.

Table 2
Mean and ranges of stand characteristics across the eight selected triplets. Stand age is based on mean age of the cored trees in 2014. Tree number (N) and stand basal area are based on all trees within 18 m of any of the cored trees. Partial tree number and stand basal area are calculated for both species separately in the mixed stand.

Stand	Stand age (years)	N (trees ha^{-1})	Stand basal area (m^2ha^{-1})
Mixed stand		220 (139–286)	32.2 (24.8–46.2)
Oak in mixed stand	154 (113–213)	86 (46–131)	15.0 (8.2–23.9)
Beech in mixed stand	109 (86–172)	125 (79–155)	16.6 (12–22)
Pure oak stand	134 (89–187)	239 (180–313)	29.3 (22–39)
Pure beech stand	113 (54–175)	152 (102–234)	25.2 (16–30)

where $C130_{target}$ (cm) represents the circumference of the target tree at the height of 130 cm, $C130_{neighbour}$ (cm) the circumference of each neighbour at 130 cm, and $dist_{target,neighbour}$ (m) the distance from the neighbour to the target tree. For each target tree, we calculated the basal area BA_{target} (m^2ha^{-1}) of its neighbours as the sum of the basal area of each neighbouring tree (the target tree not included) divided by the area of the circle described by the 18 m radius. While each target tree was selected in either a pure or a mixed stand, the proportion of species in each target tree's neighbourhood is variable within stands. We quantified this variability using a mixing coefficient:

$$mixing = \frac{BA_{target,heterospecific}}{BA_{target}},$$

where $BA_{target,heterospecific}$ (m^2ha^{-1}) is calculated using the same formula as the general basal area but summing over only heterospecific neighbours. We also calculated D/d as the ratio of the arithmetic mean crown diameter (m) to the trunk diameter at 130 cm height (m), a variable that reflects past competition. A summary of the dendrometric measurements is shown in Table 2 of the supplementary material.

2.3. Climatic data

Grid-based daily precipitation and mean daily temperature were obtained from the RMI (Royal Meteorological Institute of Belgium). We calculated the potential evapotranspiration (PET) on a monthly basis using the Thornthwaite method (Thornthwaite, 1948). The standardized precipitation-evapotranspiration index (SPEI) was calculated using the R SPEI package (Vicente-Serrano et al., 2009; Beguería & Vicente-Serrano, 2017). SPEI is a drought index that can be calculated over different time frames and represents a standardized deviation from the usual P-PET of the time frame considered.

In order to test the effect of drought on trees, we selected two different years: a drought year (2003) and a reference year without drought (2001). The main criterion for the choice of drought year was a meteorological drought occurring in summer at all sites (Fig. 1), based on both absolute and relative (SPEI) indices of precipitation deficit on several timescales. The reason we focused on summer is that wood formed at the beginning of the growing season is dependent on carbon that was assimilated in the previous year and temporarily stored in the tree tissues. This confounds the relationship between the climatic conditions and wood $\delta^{13}C$ (Offermann et al., 2011). Hence, we limited the isotopic measurements to latewood.

In order to select a year with summer drought and a reference year, we calculated several indices based on the P-PET from July to September: a site-specific average of P-PET over the years 1954–2015, and the corresponding SPEI values for the years 2001 and 2003. In 2003, the three-month SPEI from July to September was below or near −1 for all sites, which we consider an indicator of drought (Table 1). Monthly values for P-PET were consistently negative from June to September. As reference year we selected 2001 because the complete

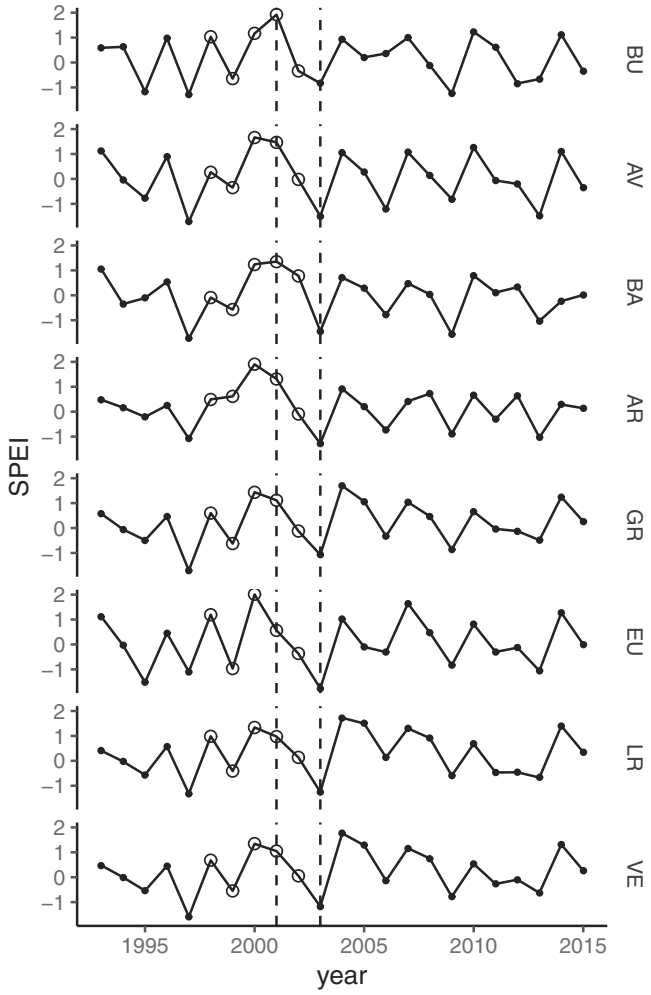

Fig. 1. SPEI values for each site calculated during the period July-September at all sites. Vertical dashed lines represent the reference year (2001) and the drought year (2003). Open circles represent years used for calculating pre-drought growth (1998–2002). See Table 1 for site names.

growing season was average to wet. It is very close in time to 2003, and changes in stand structure and atmospheric isotopic composition can therefore be ignored. The year 2002 was excluded as a reference year because of the occurrence of a minor precipitation deficit.

2.4. Wood sampling, treatment and dendrochronological measurements

Two wood cores were obtained from each target tree at breast height (130 cm) in winter 2014–2015, using an increment borer, from the northern and eastern side of the tree towards the centre. Cores were prepared using a sliding microtome, oven-dried and scanned at high resolution. We then measured ring widths using ImageJ (Schneider et al., 2012) with the ObjectJ plug-in. The measurements were cross-dated with the COFECHA software (Holmes, 1983). We averaged the results of two cores from each tree in order to obtain one ring width per tree and per year. We then calculated for each tree the pre-drought growth (PG, $mm\ yr^{-1}$) as the average radial growth for the years 1998 to 2002. We thus obtained a general indicator of tree growth during the period under study while excluding any potential influence of the 2003 drought. From each tree, one core was chosen for isotopic measurements. This choice was essentially random, except when the selected core was discarded for practical reasons, for example when the rings were too narrow. From the tree rings corresponding to the years 2001 and 2003, the last third was cut out with a scalpel. Wood produced at the beginning of the growing season was not used because it is

dependent on photosynthates of the previous summer, which complicates the relationship with climate. The wood samples obtained were then ground, weighed and analysed by mass spectrometry. Stable carbon isotope compositions ($\delta^{13}C$) were calculated as $(\frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1) * \frac{1}{1000}$. These are studied because they show a clear link with the availability of water that trees were exposed to during tree growth (Saurer et al., 1995). $\delta^{13}C$ is higher (less negative) under drought conditions, and tends to be closely correlated with water-use efficiency (the ratio of carbon assimilation to transpiration), to the extent that differences in $\delta^{13}C$ can be interpreted as differences in water-use efficiency (Farquhar et al., 1989). A summary of these measurements is given in Table 3 of the supplementary material.

2.5. Statistical analysis

2.5.1. Pre-drought growth

We constructed linear mixed models explaining pre-drought growth of trees (1998–2002) for both species separately, using trees from both mixed and pure stands. The effect of mixing was integrated through the mixing coefficient.

$$PG_{i,j} = \alpha + \beta \cdot mixing_{i,j} + a_i + e_{i,j}$$

for tree j at site i, where α represents the intercept, β the fixed parameter corresponding to the mixing effect, a_i the random parameter corresponding to the site effect and $e_{i,j}$ the residual term. We used AIC to test for additional variables: competition index $ci_{i,j}$, crown-to-trunk diameter ratio $(D/d)_{i,j}$ and trunk circumference $C130_{i,j}$ as a substitute for tree age.

2.5.2. Drivers of drought exposure

For each tree we calculated the difference in $\delta^{13}C$ between the two sampled years ($\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$). This enabled us to distinguish between natural variation in $\delta^{13}C$ between trees and the effects of drought. $\Delta\delta^{13}C$ represents the drought exposure of a tree as the increase in $\delta^{13}C$ from the reference to the drought year, and should be positive if the 2003 summer drought is reflected in the tree's physiology and recorded in the stable carbon isotope signature. In order to test whether this is the case, we constructed for each species separately a mixed model including only an intercept in $\Delta\delta^{13}C$ integrating site as a random effect. Firstly, no distinction was made between trees from pure and mixed stands.

$$\Delta\delta^{13}C_{i,j} = \alpha + a_i + e_{i,j}$$

for tree j at site i, using the same parameter names as in the previous equation.

Secondly, we tested the impact of mixing on drought exposure by adding the mixing coefficient as a fixed effect to this model.

$$\Delta\delta^{13}C_{i,j} = \alpha + \beta \cdot mixing_{i,j} + a_i + e_{i,j}$$

where β represents the fixed parameter corresponding to the mixing coefficient. The other parameter names are the same as those used in previous equations. This model was extended by adding additional fixed variables. Site-level water availability was modelled using two dummy variables dry_i and wet_i, which take a value of 1 (for sites in the wet and dry categories, respectively) or 0; sites in the optimal water availability category are modelled by a 0 for both variables. The other variables were $(P - PET)_i$ for long-term average P-PET, $ci_{i,j}$ for the competition index, pre-drought growth $PG_{i,j}$, trunk circumference $C130_{i,j}$ and $(D/d)_{i,j}$ for the crown-to-trunk diameter ratio. We used AIC to test for the inclusion or exclusion of each of these variables and removed any insignificant variable from the model.

2.5.3. δ^{13}C in reference and drought years

In order to better understand the results of the drought exposure ($\Delta\delta^{13}C$) models, we tested whether growth and mixing act on the $\delta^{13}C$ of either 2001 or 2003. Hence, for each species, two models were constructed explaining $\delta^{13}C$ in 2001 and 2003, respectively.

$$\delta^{13}C_{i,j} = \alpha + \beta \cdot mixing_{i,j} + \gamma \cdot PG_{i,j} + a_i + e_{i,j}$$

where γ represents the fixed parameter corresponding to the pre-drought growth effect and the other variables are taken from previous equations. Again, we used AIC to test for the inclusion or exclusion of the fixed variables.

We assessed all mixed models for the inclusion of the fixed effects as random slopes, but likelihood ratio tests indicated that this did not improve the models.

All statistical analyses were performed in R (R Core Team, 2017) using lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2017) and MuMIn (Barton, 2017) packages.

3. Results

3.1. Pre-drought growth

Pre-drought growth varied between 0.49mm yr^{-1} and 4.21mm yr^{-1} for oak, and between 0.66 mm yr^{-1} and 5.45mm yr^{-1} for beech, with considerable differences between sites (see Table 3 in supplementary material). The pre-drought growth model resulted in a positive effect of mixing that was significant in the case of beech, but not in oak (Table 3). For both species, the ratio of crown diameter to stem diameter was positively and significantly related to growth. No other fixed variables were selected for the pre-drought growth model using AIC.

3.2. Drought exposure

For both species, the simple intercept model yielded a significantly positive $\Delta\delta^{13}C$ (Table 4 [i]), which indicates an overall effect of the summer drought of 2003. While $\Delta\delta^{13}C$ values were on average positive

Table 3
Model results for pre-drought growth (PG) of beech and oak. Models test for (i) mixing, (ii) the crown-to-trunk diameter ratio (D/d) and (in the case of beech) mixing. In each case, the site effect was added as a random intercept. For models (ii), variables not shown were removed from the models based on significance or AIC. Marginal R^2 (R^2m) represents the variance explained by fixed factors, while conditional R^2 (R^2c) represents the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013).

	Beech					Oak				
(i)	estimate	SE	Pr(> |t|)			estimate	SE	Pr(> |t|)		
intercept	2.23	0.27	1.71×10^{-5}	R^2m	0.05	1.73	0.19	5.96×10^{-6}	R^2m	0.01
mixing	0.93	0.30	0.0021	R^2c	0.43	−0.29	0.19	0.13	R^2c	0.47
				AIC	299.02				AIC	204.91
(ii)										
intercept	1.72	0.29	8.44×10^{-5}	R^2m	0.16	0.86	0.33	0.012	R^2m	0.05
D/d	0.02	0.0050	1.00×10^{-5}	R^2c	0.54	0.04	0.015	0.010	R^2c	0.44
mixing	0.81	0.27	0.0035	AIC	290.07				AIC	201.53

Table 4
Model results for drought exposure ($\Delta\delta^{13}C$) of beech and oak. The models tested for (i) intercept, (ii) mixing, (iii) pre-drought growth (PG) and (iv) both mixing and pre-drought growth. In each case, the site effect was added as a random intercept. For models (iii) and (iv), variables not shown were removed from the models based on significance or AIC (no significant models for oak). Marginal R^2 (R^2m) represents the variance explained by fixed factors, while conditional R^2 (R^2c) represents the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013).

	Beech					Oak				
(i)	estimate	SE	Pr(> |t|)			estimate	SE	Pr(> |t|)		
intercept	0.73	0.19	3×10^{-4}	R^2m	0	0.49	0.12	2×10^{-4}	R^2m	0
				R^2c	0.28				R^2c	0.22
				AIC	283.35				AIC	214.87
(ii)										
intercept	0.54	0.22	0.035	R^2m	0.03	0.58	0.14	0.0012	R^2m	0.01
mixing	0.59	0.28	0.034	R^2c	0.34	−0.26	0.21	0.21	R^2c	0.23
				AIC	281.62				AIC	216.59
(iii)										
intercept	0.16	0.29	0.57	R^2m	0.06					
PG	0.22	0.08	0.0090	R^2c	0.34					
				AIC	281.56					
(iv)										
intercept	0.12	0.29	0.67	R^2m	0.07					
mixing	0.44	0.28	0.14	R^2c	0.37					
PG	0.19	0.087	0.034	AIC	282.11					

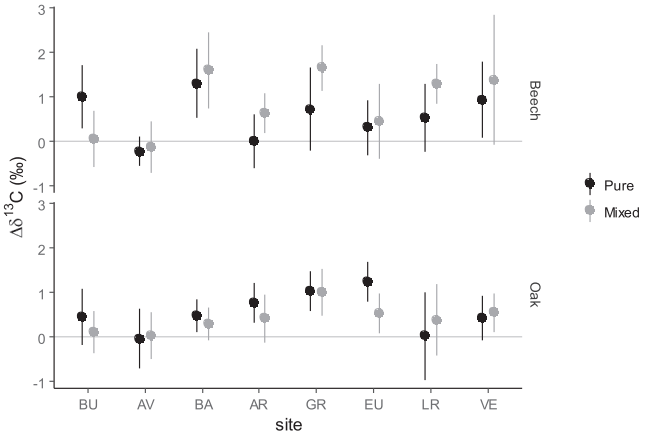

Fig. 2. Mean and standard deviations of tree drought exposure ($\Delta\delta^{13}C = \delta^{13}C_{2003} - \delta^{13}C_{2001}$) values grouped by species, site and stand. See Table 1 for site names.

(Fig. 2), there was a large variability in $\Delta\delta^{13}C$ among trees of both species, with values ranging from −1.24‰ to 1.76‰ for oak, and from −0.98‰ and 3.28‰ for beech (Fig. 2). For the Ave-et-Auffe site, $\Delta\delta^{13}C$ was negative on average (Table 3 in ESM), though not significantly different from 0 ($p = 0.38$ using a *t*-test on pooled $\Delta\delta^{13}C$ values for both species).

For beech, mixing had a significantly positive effect on $\Delta\delta^{13}C$, which means beech trees were more exposed to the 2003 drought when growing in mixtures; for oak, there was no effect of mixing (Table 4 [ii]).

The addition of other explanatory variables in these statistical models resulted for beech in three distinct models that were comparable in AIC. One includes only a mixing effect, the second only pre-drought growth (mean ring width 1998–2002) and the third contains both effects together. While effects of both pre-drought growth and mixing were significantly positive when used separately (Table 4, Fig. 3b, c), mixing lost its significance in the model when these two variables were combined. Pre-drought growth explained $\Delta\delta^{13}C$ better in beech than mixing (in terms of R^2m). The combined model barely explained more variation than pre-drought growth alone. Minimizing the AIC of the drought exposure model for oak resulted in a simple intercept model without any fixed variables (Table 4). Unlike in beech, neither mixing nor pre-drought growth was clearly related to $\Delta\delta^{13}C$ in oak (Table 4, Fig. 4). For neither species, substituting the mixing coefficient with a binary stand variable (pure versus mixed) improved the drought exposure model.

3.3. Carbon isotope composition in reference and drought years

In order to better understand the observations for the beech drought exposure model, we tested whether these effects were related to an effect on $\delta^{13}C$ in either 2001 or 2003. The trends were less clear than they were for $\Delta\delta^{13}C$ and may be site-specific (Fig. 5). Nevertheless, $\delta^{13}C$ was negatively related to both pre-drought growth (significantly) and mixing (not significantly) in 2001, while there was no effect in the drought year (Table 5, Fig. 5).

For oak, neither mixing nor pre-drought growth had a significant effect on $\delta^{13}C$ in either 2001 or 2003 (Table 4 in ESM).

4. Discussion

The increase in wood $\delta^{13}C$ from 2001 to 2003 (values were on average less negative in 2003; Table 4 [i]) indicates that most trees from both species adapted their physiology as expected in response to the meteorological summer drought of 2003, in both pure and mixed stands (Ehleringer & Cooper, 1988; Farquhar et al., 1989). The Ave-et-Auffe site is, however, an exception, as both oak and beech showed lower $\delta^{13}C$ values on average in 2003 than in 2001, though not significantly so (Fig. 2). Several hypotheses can be put forward to explain this local pattern. First, it could indicate either that there was no summer drought in 2003 or that the reference year (2001) may have actually been dry. However, the climatic data does not support either hypothesis (Fig. 1). The 2003 summer drought hit Ave-et-Auffe at least as much as it did the other sites, and was markedly drier than in 2001. Second, site-specific soil characteristics could explain the observed pattern. Ave-et-Auffe is indeed specific among the sites because of its superficial soil and calcareous bedrock. This, in combination with a low yearly precipitation, classifies Ave-et-Auffe as a dry site (Table 1). This is supported by the relatively high (less negative) values of $\delta^{13}C$ in 2001 (Table 3 in supplementary material). Even during a reference summer, trees at this site have to limit their evapotranspiration by stomatal regulation, more than at other sites. Why, then, did the precipitation deficit of 2003 not lead to extreme exposure to drought at this site? The type of calcareous bedrock found on this site is typically highly fissured

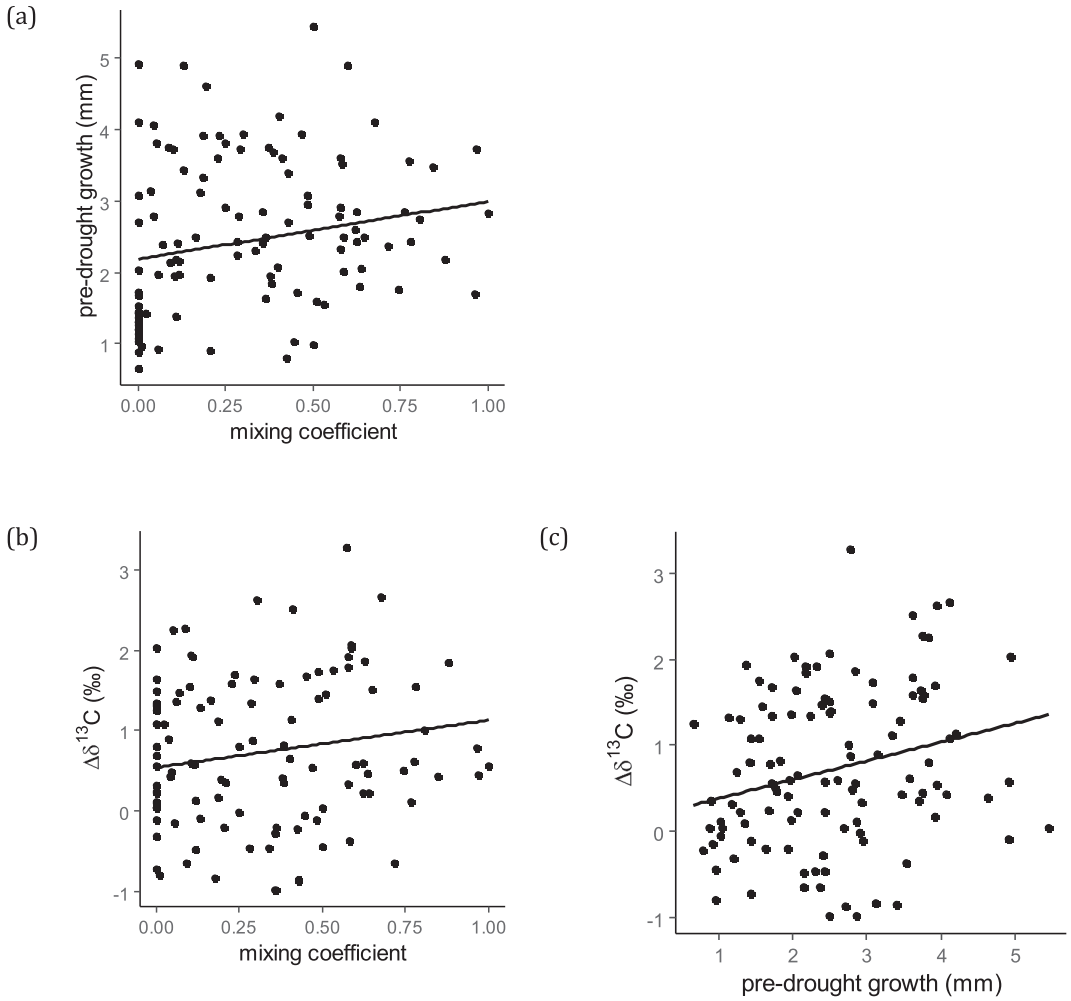

Fig. 3. Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for beech across all sites. Solid lines represent values predicted by the linear models documented in Tables 3 (ii) and 4 (ii and iii). A similar plot, grouped by site, is shown in Fig. 1 of the supplementary material.

and water-permeable, and roots can penetrate very deep down. We suspect that this acted as an additional water source that is only slightly affected by temporary precipitation deficits. The additional water source is not sufficient to avoid a water shortage in typical summers, but it does protect the trees against more extreme precipitation deficits. Furthermore, trees growing in drier sites build a hydraulic architecture that is adapted to deal with water shortage (Schuldt et al., 2016). This may have proven beneficial during the 2003 drought.

4.1. Drivers of drought exposure

Our primary objective was to investigate the effect of mixing on drought exposure ($\Delta\delta^{13}C$) and how tree growth mediates this effect. In beech, mixing enhanced pre-drought growth, while at the same time both mixing and pre-drought growth had a significant positive effect on drought exposure (Fig. 3). The effects of these two variables are not independent because when both were introduced into one model, the mixing effect on drought exposure was replaced by the effect of pre-drought growth. This indicates that the positive effect of mixing on $\Delta\delta^{13}C$ in beech is essentially caused by the increased growth of beech observed in mixtures.

It is interesting to note that at the Buggenhout site, where the relationship for beech between pure and mixed stands for pre-drought growth is reversed (trees in mixtures grow more slowly), the relationship between pure and mixed stands for $\Delta\delta^{13}C$ is also reversed (trees in mixtures were less exposed to the 2003 drought; see Fig. 3 in ESM). Though we don't have any clear explanation for the particular pattern at this site, this provides additional evidence for the hypothesis that mixing influences $\Delta\delta^{13}C$ due to its impact on growth.

Differences in $\delta^{13}C$ can be interpreted as differences in water-use efficiency of the trees during the two summers (Farquhar et al., 1989). For beech, drought exposure ($\Delta\delta^{13}C$), and thus the increase in water-use efficiency under drought conditions, was more pronounced, as trees grew faster (Fig. 3c). This could suggest that fast growth led to higher water-use efficiencies under drought conditions; however, this was not the case. Instead, fast growth was associated with lower water-use efficiencies than low growth in the reference year, but not in the drought year (Fig. 5b). Water-use efficiency is defined as the ratio of carbon assimilation to transpiration. The observed pattern then suggests that beech trees must use more water, as they grow faster. Indeed, in reference years, the faster-growing trees showed a combination of lower water-use efficiency and higher carbon assimilation (necessary for growth) relative to slow growing beeches. Why would faster-growing trees have higher water use and lower water-use efficiency than more slowly growing ones in the reference year? Could water availability be a common driver of water use, water-use efficiency and growth? This is unlikely, as we don't expect water availability to limit growth in reference conditions, irrespective of mixing degree. Hence, this relationship requires a different explanation. At species level, fast growth is associated with a competitive strategy, which trades off against stress tolerance (Grime et al., 1997; Ouédraogo et al., 2013). Fast-growing species often use resources at a high rate, giving them a competitive

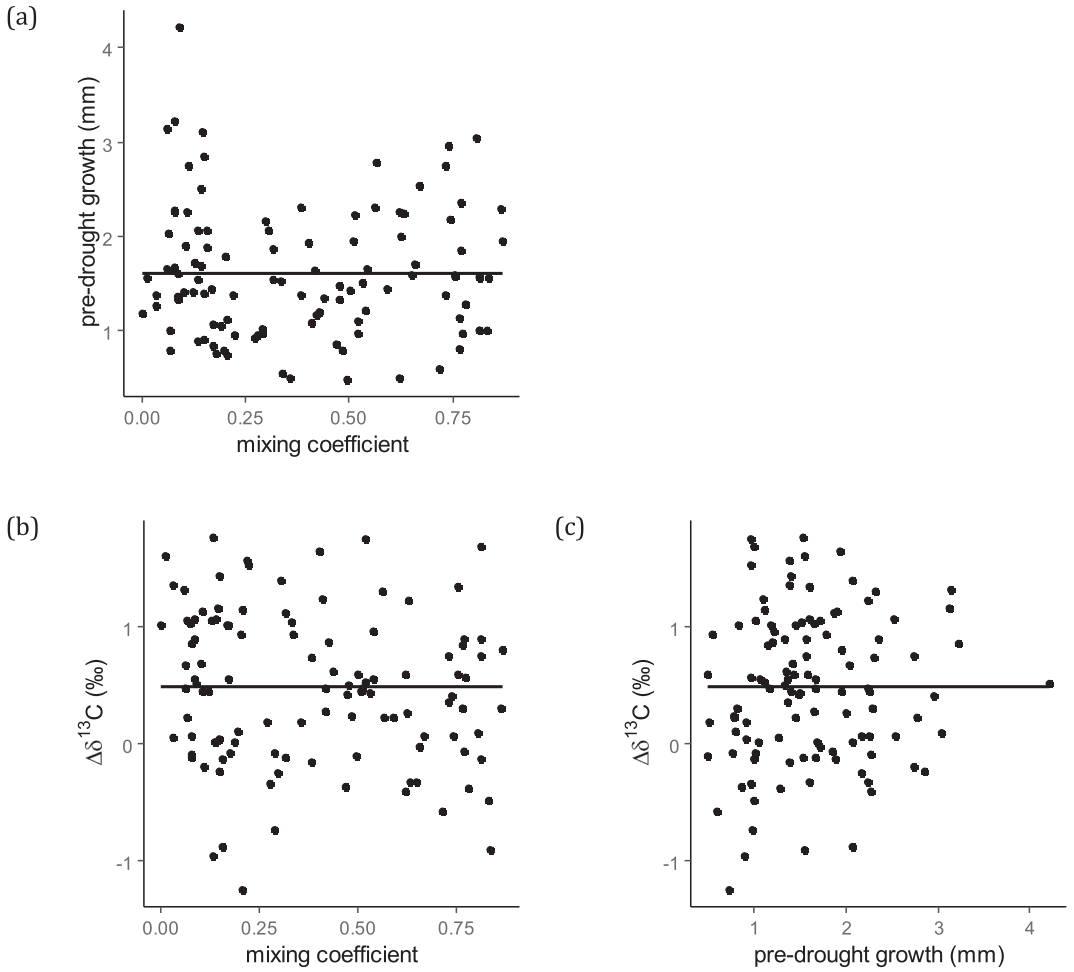

Fig. 4. Relationships between $\Delta\delta^{13}C$, mixing and pre-drought growth for oak across all sites. Solid lines represent values predicted by the linear models documented in Tables 3 (ii) and 4 (i). A similar plot, grouped by site, is shown in Fig. 2 of the supplementary material.

edge in environments where these resources are available. Slow-growing species, on the other hand, are adapted to less productive environments and are better able to cope with resource shortages, such as droughts. Beech is more competitive than oak and grows faster, and therefore needs more resources to maintain this growth. We assume that those beech trees that benefit from higher resource availability adapt their structure and functioning to assimilate resources more quickly. Wood anatomical traits associated with efficient water transport have been found to be more evident in faster-growing beech branches (Schuldt et al., 2016). The faster-growing beech trees in our study may thus have had higher water use in reference conditions, not necessarily because they had more soil water available, but because they developed more efficient systems for accessing it and transporting it up to the leaves. The higher drought exposure then results from these trees not being able to maintain their high water use under conditions of drought during the summer of 2003.

The faster growth observed for beech in mixtures was related to higher water use, but may also indicate higher use or use efficiency of other resources (see section on selection effect versus complementarity). A high resource-using strategy is possible in mixtures, either because resources are more available, or because beech is more efficient than oak in accessing and using them. Mixed with oak, beech

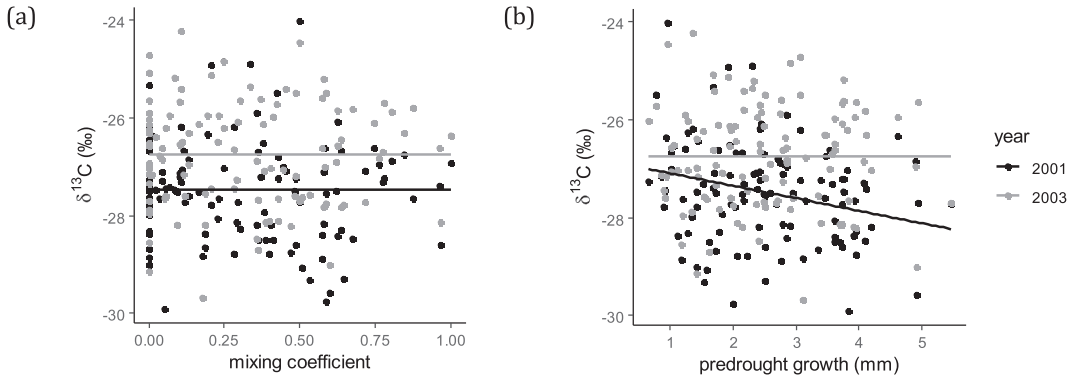

Fig. 5. Beech $\delta^{13}C$ in 2001 and 2003 plotted against mixing (a) or pre-drought growth (b). Statistical tests are given in Table 5. Solid lines represent values predicted by the linear models documented in Table 5 (i and iii) for 2001 and 2003. A similar plot, grouped by site, is shown in Fig. 3 of the supplementary material.

Table 5
Model results for $\delta^{13}C$ in beech in 2001 and 2003. In addition to the intercept (i), the models test for (ii) mixing, (iii) pre-drought growth (PG) and (iv) both mixing and pre-drought growth. In each case, the site effect was added as a random intercept. Marginal R^2 (R^2m) represents the variance explained by fixed factors, while conditional R^2 (R^2c) represents the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013). See Table 4 in supplementary material for results for oak.

	2001					2003				
(i)	estimate	SE	Pr(> |t|)			estimate	SE	Pr(> |t|)		
intercept	−27.48	0.20	0	R^2m	0	−26.75	0.14	0	R^2m	0
				R^2c	0.23				R^2c	0.080
				AIC	317.95				AIC	329.11
(ii)										
intercept	−27.29	0.24	$<2 \times 10^{-16}$	R^2m	0.024	−26.74	0.18	$<2 \times 10^{-16}$	R^2m	5.9×10^{-5}
mixing	−0.61	0.33	0.064	R^2c	0.28	−0.030	0.36	0.93	R^2c	0.080
				AIC	316.93				AIC	331.33
(iii)										
intercept	−26.84	0.3233	$<2 \times 10^{-16}$	R^2m	0.06	−26.7	0.30	$<2 \times 10^{-16}$	R^2m	5.4×10^{-4}
PG	−0.255	0.09825	0.01	R^2c	0.30	−0.023	0.10	0.82	R^2c	0.085
				AIC	316.19				AIC	333.79
(iv)										
intercept	−26.8	0.33	$<2 \times 10^{-16}$	R^2m	0.07	−26.69	0.30	$<2 \times 10^{-16}$	R^2m	5.3×10^{-4}
mixing	−0.41	0.33	0.23	R^2c	0.31	−0.0095	0.37	0.98	R^2c	0.085
PG	−0.22	0.10	0.033	AIC	317.07	−0.022	0.11	0.84	AIC	335.93

can, for example, benefit from lower light interception of oak crowns (Leuschner et al., 2001a; Meier & Leuschner, 2008). Regarding nutrient acquisition, beech could benefit from its tendency to dominate the most superficial soil layer when mixed with oak (Leuschner et al., 2001b; Zapater et al., 2011). Positive mixing effects on growth in reference conditions seem to have the drawback that trees are less adapted to dealing with water deficits and are thus less resistant to drought. Ammer (2019) points out a possible adverse effect of higher productivity in mixtures, i.e. that this can lead to increased transpiration. This relationship was found in young forest plantations in Panama by Kunert et al. (2012), who observed higher growth, more sapwood and higher stand transpiration with increasing species diversity. If, under reference conditions, increased growth in mixed stands is related to increased water usage, then this can be expected to affect water relations during drought as well. Some authors argue that, as a result of higher transpiration, water resources are more quickly depleted when droughts build up (e.g. Verheyen et al., 2008). This was observed in grasslands, for instance, where evapotranspiration was higher in diverse than in monospecific grasslands. Yet this pattern was not observed under drought conditions, because the higher water use of biodiverse grasslands caused faster depletion of the water reserves. Higher drought exposure ($\Delta\delta^{13}C$) of mixed forest stands, linked with faster tree growth, has also been observed by Grossiord et al. (2014a). Contrary to our findings, this resulted from a positive relationship between growth and $\delta^{13}C$ in the drought year, which could indicate that the trees in mixtures had less water available than those in monocultures under drought conditions, because their faster growth prior to the drought was linked with faster depletion of the water reserves. Forrester (2015) also observed higher water use, in combination with higher water-use efficiency for trees in mixtures, but only for the subset of individual trees that grew faster due to mixing. Since, in our case, we did not observe higher $\delta^{13}C$ for fast-growing beech trees, we cannot conclude that under drought conditions, the faster-growing trees had less water available (per unit of carbon assimilated) than the more slowly growing ones. There is thus no evidence for faster depletion of the water reserves (Fig. 5b). However, for beech, fast-growing trees had to reduce their water use during drought more so than did trees that grew more slowly, which means they were not able to maintain their higher water consumption under conditions of drought. We do not have the necessary data to assess whether or not beech trees halted their growth during the peak of the summer drought of 2003, but this may have been the case (Van der Werf et al., 2007). If so, no more carbon allocation has taken place and further drought is undetected by $\delta^{13}C$ measurements in the tree rings. The lack of significant difference in $\delta^{13}C$ between trees that differ in degree of mixing or pre-drought growth could indicate that trees reached a common site-specific threshold above which they were no longer able to allow photosynthesis by regulating water use.

We did not find a similar mechanism in oak. We hypothesized that oak growth would decrease due to mixing which, however, was not the case (Fig. 4a). Hence, we are not able to test the hypothesis that as a consequence of a lower growth, the oaks would be less exposed to the drought in mixture. While not universal, a lack of mixing effects on $\delta^{13}C$ has previously been reported for sessile oak specifically (Bonal et al., 2017) and in mixtures in general (Grossiord et al., 2014b; Forrester et al., 2016). This does not rule out that tree growth mediates the mixing effect on drought exposure, since we found no mixture effect on oak growth (Fig. 4a). Although a tendency towards increasing drought exposure with higher pre-drought growth was observed at some sites (Fig. 2 in ESM), this was not statistically significant on average (Fig. 4c). The lack of significance might be explained by the range in pre-drought growth, which was smaller for oak (Fig. 4c) than for beech (Fig. 3c). Conservative but stable growth can be an adaptation to water stress (Ouédraogo et al., 2013). Compared with beech, sessile oak combines lower growth (see, for example, the growth of pure stands in Figs. 3a and 4a) with higher tolerance to drought stress. Another hypothesis for the absence of mixing effects may be the fact that we sampled dominant oaks in mature forests, which minimizes the effects of beech domination on oak in the dataset. This could explain why oak was not affected by the presence of beech in the vicinity, either in its growth or in its exposure to drought.

4.2. Selection effect versus complementarity

Loreau and Hector (2001) consider two types of mechanisms between species in mixed forests: selection and complementarity. The results of this study are compatible with the selection effect, which implies that the fastest-growing species in pure stands (beech) benefits most from the mixture in terms of growth. This is linked with the competitiveness of beech. Its shade tolerance, together with its ability to grow faster and higher, is responsible for its ability to invade pure oak forests and to become dominant (Hein & Dhôte, 2006). Mixing has also been observed to increase beech growth with different admixed species (for example, del Río et al., 2014). This does not mean, however, that complementary interactions do not play any role. The combination of a shade-tolerant and a heliophilous species can lead to more efficient use of available light (Forrester, 2014), which would especially

benefit the shade-tolerant beech. Such complementarity could explain why the increase in beech growth due to mixing is not compensated for by a decrease in oak growth, as we would have expected. On the other hand, the negative effects of beech on oak may be minimized by the oak selection criteria used in this study, as previously stated (dominant oaks in mature forests). The increased water use of beech due to mixing in reference conditions (as evidenced by increased pre-drought growth in combination with lower water-use efficiency) did not affect oak $\delta^{13}C$, probably because water was sufficiently available and beech did not reduce it below oak demand. Complementarity could improve water relations during droughts, though we did not observe this for either oak or beech. Hydraulic lift (Moreira et al., 2003) probably plays no role at most of our study sites because many have shallow soils and lack a water table, but vertical stratification of the roots in mixtures could still improve the exploitation of the soil and ease competition for water in mixtures during drought. However, complementarity for water appears to have been too weak to significantly affect water relations. Alternatively, high water use by beech trees preceding the precipitation deficit could have contributed to the soil drought, cancelling out any effects of complementarity in water use between oak and beech.

4.3. Conclusions and implications for forest management

Mixing species is often advocated as a strategy to mitigate the negative effects of climate change (Jactel et al., 2009). There may be benefits in terms of performance and drought resistance, although this varies according to species combination and site (Ammer, 2019). In our case, we observed faster growth for beech trees in mixtures, but this resulted in higher drought exposure during a severe drought. The fact that the $\delta^{13}C$ during the 2003 drought was not higher in mixtures than in pure stands suggests that the trees in mixtures shift to a functioning similar to that in pure stands. However, it is not clear whether this would still be the case under more extreme and/or more frequent droughts, as are expected in the future. While managing forests towards greater productivity may reduce risk exposure due to shorter rotation times, faster growth could also increase drought sensitivity, leaving the forest more vulnerable overall when shifting to a climate with recurrent drought events. In the absence of any water limitation, trees may indeed optimize their structure towards faster growth by, for example, increasing their above- to below-ground ratio, which could in turn put them at higher risk under conditions of reduced water availability. Any possible complementarity for water that could have benefited beech in this mixture seems to have played at most only a minor role during the 2003 drought. Our results thus emphasize the need for managers to consider whether for a combination of species, there is a complementarity for water that acts during drought and whether complementary mechanisms in non-drought conditions could hinder the ability of those trees to withstand droughts.

5. Declaration of authorship

QP, CC and DB designed the methodology. KJ conducted field work, performed the tree ring measurements and analysed the data. All authors contributed to the interpretation of the results. KJ and QP led the writing of the manuscript, with substantial contributions from all other authors.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118593.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. New Phytol. 221, 50–66. https://doi.org/10.1111/nph.15263.

Barton, K., 2017. MuMIn: Multi-Model Inference.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beguería, S., Vicente-Serrano, S.M., 2017. SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index.

Bonal, D., Pau, M., Toigo, M., Granier, A., Perot, T., 2017. Mixing oak and pine trees does not improve the functional response to severe drought in central French forests. Ann. For. Sci. 74. https://doi.org/10.1007/s13595-017-0671-9.

Contreras, M.A., Affleck, D., Chung, W., 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. For. Ecol. Manage. 262, 1939–1949. https://doi.org/10.1016/j.foreco.2011.08.031.

Dai, A., 2013. Increasing drought under global warming in observations and models. Nat. Clim. Change 3, 52–58. https://doi.org/10.1038/nclimate1633.

del Río, M., Condés, S., Pretzsch, H., 2014. Analyzing size-symmetric vs. Size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. For. Ecol. Manage. 325, 90–98. https://doi.org/10.1016/j.foreco.2014.03.047.

del Río, M., Pretzsch, H., Ruiz-Peinado, R., et al., 2017. Species interactions increase the temporal stability of community productivity in Pinus sylvestris-Fagus sylvatica mixtures across Europe. J. Ecol. 105, 1032–1043. https://doi.org/10.1111/1365-2745.12727.

Ehleringer, J.R., Cooper, T.A., 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76, 562–566. https://doi.org/10.1007/BF00397870.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Ann. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537. https://doi.org/10.1146/annurev. pp. 40.060189.002443.

Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. For. Ecol. Manage. 312, 282–292. https://doi.org/10.1016/j.foreco.2013.10.003.

Forrester, D.I., 2015. Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. Tree Physiol. 35, 289–304. https://doi.org/10.1093/treephys/tpv011.

Forrester, D.I., Bonal, D., Dawud, S., et al., 2016. Drought responses by individual tree species are not often correlated with tree species diversity in European forests. J. Appl. Ecol. 53, 1725–1734. https://doi.org/10.1111/1365-2664.12745.

Forrester, D.I., Pretzsch, H., 2015. Tamm review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. For. Ecol. Manage. 356, 41–53. https://doi.org/10.1016/j.foreco.2015.08.016.

Grime, J.P., Thompson, K., Hunt, R., et al., 1997. Integrated screening validates primary axes of specialisation in plants. Oikos 79, 259–281. https://doi.org/10.2307/3546011.

Grossiord, C., Granier, A., Gessler, A., et al., 2014a. Does drought influence the relationship between biodiversity and ecosystem functioning in boreal forests?

Ecosystems 17, 394–404. https://doi.org/10.1007/s10021-013-9729-1.
Grossiord, C., Granier, A., Ratcliffe, S., et al., 2014b. Tree diversity does not always improve resistance of forest ecosystems to drought. Proc. Natl. Acad. Sci. 111, 14812–14815. https://doi.org/10.1073/pnas.1411970111.
Hegyi, F., 1974. A simulation model for managing jack-pine stands. Roy. College Forest. 30, 74–90.
Hein, S., Dhôte, J.-F., 2006. Effect of species composition, stand density and site index on the basal area increment of oak trees (Quercus sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. Ann. Forest Sci. 63, 457–467. https://doi.org/10.1051/forest:2006026.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.
Jacob, A., Hertel, D., Leuschner, C., 2013. On the significance of belowground overyielding in temperate mixed forests: separating species identity and species diversity effects. Oikos 122, 463–473. https://doi.org/10.1111/j.1600-0706.2012.20476.x.
Jactel, H., Nicoll, B.C., Branco, M., González-Olabarría, J.R., Grodzki, W., Långström, B., Moreira, F., Netherer, S., Orazio, C., Piou, D., Santos, H., Schelhaas, M.J., Tojic, K., Vodde, F., 2009. The influences of forest stand management on biotic and abiotic risks of damage. Ann. For. Sci. 66, 701. https://doi.org/10.1051/forest/2009054.
Kunert, N., Schwendenmann, L., Potvin, C., Hölscher, D., 2012. Tree diversity enhances tree transpiration in a Panamanian forest plantation. J. Appl. Ecol. 49, 135–144. https://doi.org/10.1111/j.1365-2664.2011.02065.x.
Lebourgeois, F., Bréda, N., Ulrich, E., Granier, A., 2005. Climate-tree-growth relationships of European beech (Fagus sylvatica L.) in the French Permanent Plot Network (RENECOFOR). Trees 19, 385–401. https://doi.org/10.1007/s00468-004-0397-9.
Lebourgeois, F., Cousseau, G., Ducos, Y., 2004. Climate-tree-growth relationships of Quercus petraea Mill. stand in the Forest of Bercé ("Futaie des Clos", Sarthe, France). Ann. For. Sci. 61, 361–372. https://doi.org/10.1051/forest:2004029.
Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For. Ecol. Manage. 303, 61–71. https://doi.org/10.1016/j.foreco.2013.04.003.
Leuschner, C., Backes, K., Hertel, D., et al., 2001a. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For. Ecol. Manage. 149, 33–46. https://doi.org/10.1016/S0378-1127(00)00543-0.
Leuschner, C., Hertel, D., Coners, H., Büttner, V., 2001b. Root competition between beech and oak: a hypothesis. Oecologia 126, 276–284. https://doi.org/10.1007/s004420000507.
Leuzinger, S., Zotz, G., Asshoff, R., Körner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. Tree Physiol. 25, 641–650. https://doi.org/10.1093/treephys/25.6.641.
Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76. https://doi.org/10.1038/35083573.
Meier, I.C., Leuschner, C., 2008. Leaf size and leaf area index in Fagus sylvatica forests: competing effects of precipitation, temperature, and nitrogen availability. Ecosystems 11, 655–669. https://doi.org/10.1007/s10021-008-9135-2.
Metz, J., Annighöfer, P., Schall, P., et al., 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. Glob. Change Biol. 22, 903–920. https://doi.org/10.1111/gcb.13113.
Moreira, M.Z., Scholz, F.G., Bucci, S.J., et al., 2003. Hydraulic lift in a neotropical savanna. Funct. Ecol. 17, 573–581. https://doi.org/10.1046/j.1365-2435.2003.00770.x.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
Offermann, C., Ferrio, J.P., Holst, J., et al., 2011. The long way down-are carbon and oxygen isotope signals in the tree ring uncoupled from canopy physiological processes? Tree Physiol. 31, 1088–1102. https://doi.org/10.1093/treephys/tpr093.
Ouédraogo, D.-Y., Mortier, F., Gourlet-Fleury, S., et al., 2013. Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa. J. Ecol. 101, 1459–1470. https://doi.org/10.1111/1365-2745.12165.
Penninckx, V., Meerts, P., Herbauts, J., Gruber, W., 1999. Ring width and element concentrations in beech (*Fagus sylvatica* L.) from a periurban forest in central Belgium. For. Ecol. Manage. 113, 23–33. https://doi.org/10.1016/S0378-1127(98)00412-5.
Pinheiro J, Bates D, DebRoy S et al (2017) Nlme: Linear and Nonlinear Mixed Effects Models.
Pretzsch, H., Bielak, K., Block, J., et al., 2013a. Productivity of mixed versus pure stands of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) and European beech (*Fagus sylvatica* L.) along an ecological gradient. Eur. J. Forest Res. 132, 263–280. https://doi.org/10.1007/s10342-012-0673-y.
Pretzsch, H., Rötzer, T., Matyssek, R., et al., 2014. Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. Trees 28, 1305–1321. https://doi.org/10.1007/s00468-014-1035-9.
Pretzsch, H., Schütze, G., Uhl, E., 2013b. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. Plant Biol. 15, 483–495. https://doi.org/10.1111/j.1438-8677.2012.00670.x.
R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24, 505–514. https://doi.org/10.1016/j.tree.2009.03.018.
Saurer, M., Siegenthaler, U., Schweingruber, F., 1995. The climate-carbon isotope relationship in tree rings and the significance of site conditions. Tellus B 47, 320–330. https://doi.org/10.1034/j.1600-0889.47.issue3.4.x.
Scharnweber, T., Manthey, M., Criegee, C., et al., 2011. Drought matters – declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in northeastern Germany. For. Ecol. Manage. 262, 947–961. https://doi.org/10.1016/j.foreco.2011.05.026.
Schmid, I., 2002. The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. Basic Appl. Ecol. 3, 339–346. https://doi.org/10.1078/1439-1791-00116.
Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. https://doi.org/10.1038/nmeth.2089.
Schuldt, B., Knutzen, F., Delzon, S., et al., 2016. How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? New Phytol. 210, 443–458. https://doi.org/10.1111/nph.13798.
Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. Soil Sci. 66, 77.
Toïgo, M., Perot, T., Courbaud, B., et al., 2018. Difference in shade tolerance drives the mixture effect on oak productivity. J. Ecol. 106, 1073–1082. https://doi.org/10.1111/1365-2745.12811.
Van der Werf, G.W., Sass-Klaassen, U.G., Mohren, G.M.J., 2007. The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. Dendrochronologia 25, 103–112. https://doi.org/10.1016/j.dendro.2007.03.004.
Verheyen, K., Bulteel, H., Palmborg, C., et al., 2008. Can complementarity in water use help to explain diversity-productivity relationships in experimental grassland plots? Oecologia 156, 351–361. https://doi.org/10.1007/s00442-008-0998-x.
Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2009. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1.
WRB IWG (2014) World Reference Base for soil resources 2014: International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Report.
Zapater, M., Hossann, C., Bréda, N., et al., 2011. Evidence of hydraulic lift in a young beech and oak mixed forest using ^{18}O soil water labelling. Trees 25, 885–894. https://doi.org/10.1007/s00468-011-0563-9.