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ORIGINAL ARTICLE

Tree species diversity improves beech growth and alters its physiological response to drought

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Abstract

Key message **Beech trees growing in biodiverse patches in Belgium have higher radial growth and are less physiologically sensitive to drought than those in monocultures. Forest diversification therefore alleviates the negative effects of drought on beech.**

Abstract Common beech, a widespread and economically important tree species in Europe, is known to be drought sensitive. For ensuring its survival under increasing future drought conditions, we need to advance our understanding on the relationships between drought and its growth performance. Diversifying forests has been proposed as a management strategy to mitigate the effects of drought, because a more complete use of the available water is expected. We made use of a tree species diversity gradient in Belgium to study if beech trees growing in diverse forest patches are more resistant and resilient to drought than beech trees in monocultures. Combining dendrochronological and stable carbon ($\delta^{13}C$) and oxygen isotope ($\delta^{18}O$) data allowed for studying the effect of tree species diversity on the response of beech growth to drought regarding stem radial growth and physiological performance. Up to 62% enhanced stem radial growth strongly increased growth stability, and higher resistance to drought was observed for beech trees in diverse forest patches. Beech performs best in three-species mixtures, particularly those with oak and maple. In drought years, beech growth is more reduced in monocultures than mixtures. During these drought years, $\delta^{13}C$ values increased, and the increase was weaker in beech trees of diverse stands compared to monospecific stands, indicating enhanced stomatal conductance and growth continuation in mixtures. $\delta^{18}O$ patterns did not indicate a clear effect of diversity or the response of beech trees to drought. Overall, our results indicate that until now, still the positive effects of diversity on beech growth outperform the negative effects induced by drought.

Keywords *Fagus sylvatica* · Stable isotopes · Tree ring · Complementarity effects · Resilience · Recovery

Introduction

Common beech (*Fagus sylvatica* L.) is one of the most important broadleaved tree species in Europe. Owing to its rather wide ecological range, it covers a vast area in Europe and delivers important provisioning and regulating ecosystem services (Dittmar et al. 2003; Tegel et al. 2014). However, drought, especially in early summer, can have a serious

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impact on the growth of beech (Scharnweber et al. 2011; Houston Durrant et al. 2016), and, hence, the species may be at risk under further climate change, especially in the southern and lowland parts of its range (Hanewinkel et al. 2013). The last decade has been the warmest on record in Europe with several summer heatwaves (e.g., 2003, 2010 and 2018) and almost a doubling of the number of warm days since 1960 (EEA 2012). Temperatures and the incidence of dry periods are expected to further increase in the future (IPCC 2013). It is thus important to improve our understanding of the effects of drought on the growth performance of beech, to develop effective forest management strategies to mitigate potential negative effects on forest growth.

The effect of drought on the growth performance of beech depends on the characteristics of the drought event (duration, timing and severity), but also on stand characteristics such as the stand structure and species mixture (Zang et al. 2014; Metz et al. 2016). The functioning of ecosystems is considered to benefit from biodiversity, that is, the diversity of species, genetic material and functional traits (Loreau and Hector 2001; Isbell et al. 2009). Several studies have demonstrated that biodiversity results in higher tree growth and lower growth variability (Pretzsch and Schütze 2009; Mölder and Leuschner 2014; Metz et al. 2016). In a drought context, complementarity effects observed in species mixtures, comprising niche differentiation and facilitation effects, may play a prominent role in the causal relationship between biodiversity and ecosystem functioning (Verheyen et al. 2008). A better exploitation and more efficient use of available soil water resources in a more diverse system are an example of niche differentiation. Increased availability of water due to hydraulic redistribution (i.e., deep rooting tree species move water from deeper soil layers upward) is an example of the facilitation effect (Hafner et al. 2017). During drought, niche differentiation and facilitation effects can result in a more complete use of the available water resulting in less drought-stressed trees in diverse forests (Loreau and Hector 2001). These biodiversity mechanisms are complex and influenced by spatial and temporal variations of resource availability and climate conditions (Morin et al. 2011; Forrester 2014). Previous studies demonstrated on the one hand that diverse forests can be more resilient to drought compared to monospecific forests (Perot et al. 2013; Jucker et al. 2014; Metz et al. 2016). On the other hand, however, neutral to negative effects of biodiversity on drought stress also have been reported (Grossiord et al. 2014a, b; Forrester et al. 2016). Considering the contradictory findings of existing research, it is important to gain deeper insight into the underlying physical and biological mechanisms that drive diversity effects during drought (Grossiord 2019).

A combination of dendrochronological and stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope analyses can allow to evaluate the effect of drought on stem radial growth and the underlying physiological mechanisms. The $\delta^{13}C$ signature of tree rings strongly depends on isotopic fractionation (1) during diffusion of atmospheric CO_2 into the leaf, and, hence, on stomatal conductance (Farquhar et al. 1989), and (2) during carbon assimilation at the enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) and, hence, on photosynthetic activity (Gessler et al. 2014). Overall (in drought and non-drought conditions), higher $\delta^{13}C$ values primarily result from lower stomatal conductance or higher photosynthetic activity, but may be modified by post-photosynthetic biochemical fractionation and possible re-mobilization of carbon reserves (Gessler et al. 2014). During drought, trees tend to close their stomata to reduce water loss (i.e., stomatal conductance is reduced), which can result in an increase in $\delta^{13}C$ (Farquhar et al. 1989). Also, the photosynthetic activity is reduced under stress conditions such as drought; however, the decrease in stomatal conductance is larger than the decrease in photosynthetic activity resulting in higher $\delta^{13}C$ under drought conditions (Gessler et al. 2014). In addition, the use of stored carbon reserves from previous years during drought can modify the $\delta^{13}C$ measured in tree rings, as the stored carbohydrates are imprinted with the isotopic signal from previous years; and during storage and remobilization of the carbohydrates, fractionation may occur (Helle and Schleser 2004; Gessler et al. 2014). In a study on biodiversity effects in a drought context, Schäfer et al. (2017) found that the increase in $\delta^{13}C$ during the 2003 drought was higher for beech trees growing in monocultures compared to beech trees growing in mixtures on moist sites. Grossiord et al. (2014b) found the same effect of diversity during drought on $\delta^{13}C$, but only for trees growing in drought-prone environments. Tree-ring $\delta^{18}O$ may reflect: (1) the isotopic ratio of the water taken up by the tree at the time of wood formation, (2) evaporative leaf water ^{18}O enrichment, mainly controlled by vapor pressure deficit (Barbour 2007; Treydte et al. 2014). Post-photosynthetic biochemical fractionation and oxygen atom exchange between xylem water and phloem assimilates can further modify the signal (Gessler et al. 2013, 2014; Treydte et al. 2014). Despite the complexity of fractionation processes generating its signature, tree-ring $\delta^{18}O$ can nevertheless be useful to disentangle effects of stomatal conductance and photosynthesis, when interpreted carefully (Roden and Siegwolf 2012).

The aim of this study was to investigate whether beech trees growing in diverse patches are more resilient [i.e., capable of maintaining functioning throughout a disturbance, Hodgson et al. (2015)] to drought and grow better when compared to those in monospecific patches. For this purpose, a targeted observational platform was established in Belgium, with beech trees growing in forest patches of different tree species diversity levels and different tree species composition (i.e., the combination of particular tree species). The design of the platform allowed for differentiating effects of tree species diversity, as well as tree species identity on the performance of beech. Tree species identity effects refer to the effect a particular species can have on the performance of beech trees in the mixture. To characterize the short-term effects of a disturbance, such as drought, on ecosystem stability, the indices resistance, resilience and recovery are often used (Lloret et al. 2011; Pretzsch et al. 2013; Metz et al. 2016). Resistance defines the reduction in ecological performance during a disturbance, resilience indicates to what extent the original ecological performance is reached after a disturbance, and recovery indicates the ability of an ecosystem to recover from the damage experienced during a disturbance (Lloret et al. 2011).

The specific objectives of this study were to investigate (1) the impact of tree species diversity and composition on average stem radial growth and growth variability, (2) the performance of stem growth, δ^{13}C and δ^{18}O in drought versus non-drought years as a function of tree species diversity level, and (3) the impact of tree species diversity on the resistance, resilience and recovery of stem growth, δ^{13}C and δ^{18}O to drought. Our main hypotheses were that beech trees growing in mixtures have (1) increased radial growth and lower growth variability, (2) lower growth decline and higher stomatal conductance (indicated by lower δ^{13}C values and increased δ^{18}O values) during drought, and (3) higher resistance, resilience and recovery to drought compared to beech trees growing in monospecific patches.

Methods

Study area and plot description

The study area of this research is located in the loamy region (loam and sandy-loam soils) of Belgium and comprises two mixed forests, Meerdaal and Zoniën, where a total of 27 plots were selected (18 plots in Zoniën and 9 plots in Meerdaal) (Fig. 1a). Both forests have not been under other land use since a long time [i.e., ancient forests (De Keersmaeker et al. 2013)] and have similar soil properties, with no significant differences in bulk density, pH, soil organic matter content and soil C/N ratio, but with a slightly higher loam fraction in Zoniën compared to Meerdaal; 79 ± 4 and 72 ± 5%, respectively (based on analysis of soil samples taken in the sampled plots). Annual precipitation is 829 mm year^{-1} (217 mm for June to August) and mean annual temperature is 10.7 °C (17.8 °C for June to August) for the period 1970–2006 (Fig. S1).

The maximum distance between plots from the two forests is 21.7 km, and 3.2 km and 8.7 km between plots within Meerdaal and Zoniën, respectively. Plots are circular (18 m radius) with a (co)dominant beech tree in the center. This center tree is the tree that was cored (further referred to as center tree). Plots were selected in a way that three species diversity levels were represented: monospecific beech plots (Isp), combination of beech with one other tree species (IIsp), and beech combined with two

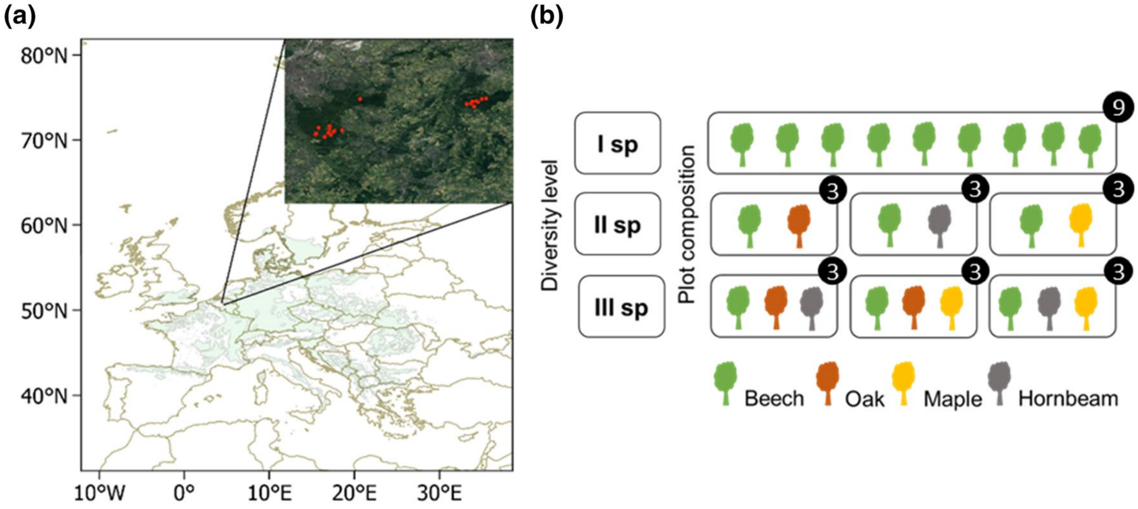

Fig. 1 Location of the plots (**a**) and sampling design (**b**). The study area comprises two forests: Meerdaal (50.77° N–50.82° N, 4.64° E–4.72° E) and Zoniën forest (50.71° N–50.85° N, 4.36° E–4.52° E). The distribution area of European beech is visualized in light green on the overview map of central Europe (EUFORGEN 2008). Diversity level: number of tree species present in the plot (circular plot with 18 m radius from thre center tree). (Isp): monoculture beech plot, (IIsp): combination of beech and one other tree species, and (IIIsp): beech combined with two other tree species. Species composition: tree species present in plot. The number of plots for each species composition level is indicated by the filled black circles. From each species composition level, three plots are selected, except for the monospecific beech plots where nine plots are selected

other tree species (IIIsp) (Fig. 1b). The considered tree species (other than beech) in the diverse plots are: oak (*Quercus robur*), maple (*Acer pseudoplatanus*) and hornbeam (*Carpinus betulus*) (see Fig. 1b). Due to its deeper rooting system, oak can withstand moderate droughts and is much more drought tolerant than beech (Zimmermann et al. 2015; Eaton et al. 2016). Maple is more drought sensitive and does not thrive in drought-prone regions; however, it is more drought tolerant than beech (Köcher et al. 2009; Zimmermann et al. 2015; Pasta et al. 2016). Hornbeam prefers deep moist and well-drained soils, and it is more drought tolerant compared to maple and beech (Köcher et al. 2009; Sikkema et al. 2016).

From each of the seven species composition combinations, three plots were selected, except for the monospecific beech plots, where nine plots were selected to ensure a balanced design. In the selection of the diverse plots (i.e., two and three species plots) the highest possible evenness in basal area between tree species, including beech, was pursued. Plots were selected in even aged stands to ensure that the center tree developed in a monospecific (i.e., Isp) or diverse environment (i.e., two and three species plots) over its whole life span. The admixture of admixed tree species, expressed as the percentage of trees that are not beech trees (based on number of trees), ranged between 23 and 80% in the diverse plots.

In each plot, the tree position, species identity, diameter at breast height (DBH), crown projection area (CPA, achieved by mapping the crown border in the four cardinal directions), and total tree height (H in meters) of all trees with a DBH > 15 cm were measured (Table 1). Moreover, the scaled Shannon diversity index (DivCPA) and structural diversity index (SD) were calculated. DivCPA quantifies the tree species diversity present in the plot based on their CPA and takes the evenness into account. CPA instead of basal area was used for the calculation of the Shannon diversity index to take possible crown competition effects into account. SD quantifies the structural heterogeneity of the plots, which itself is influenced by the number of tree species present in the plot. DivCPA and SD were calculated as follows:

$$\mathrm{Div}_{\mathrm{CPA}} = \exp\left(-\sum_{i=1}^{S} P_{\mathrm{CPA};i} * \ln\left(P_{\mathrm{CPA};i}\right)\right),$$

with $P_{\mathrm{CPA};i} = \frac{\mathrm{CPA}_i}{\mathrm{CPA}_{\mathrm{tot}}}$ and S is the total number of species present in the plot.

$$\mathrm{SD} = \frac{\mathrm{StDev}\left(H_i{*}\mathrm{CPA}_i\right)}{\mathrm{Mean}\left(H_i{*}\mathrm{CPA}_i\right)},$$

with StDev the standard deviation, H_i the height and CPA_i the crown projection area of the ith tree present in the plot (Van de Peer et al. 2017).

Selection of drought years

Monthly precipitation sums (P) and mean monthly temperatures (Tmean) of the climate station of Ukkel (Royal Meteorological Institute of Belgium, RMI) located at 5–26 km distance from the plots from 1970 to 2006 were used as the basis to identify drought years (Fig. 2). Moisture indices were calculated as the difference between precipitation and potential evapotranspiration (PET), with PET calculated after Thornthwaite (1948). For the selection of the drought years, we gave a score to the anomalies of precipitation, mean temperature and moisture indices for the summer period June–August (JJA) for the years from 1970 to 2006. The highest score was given to the year with the highest anomaly. Then, the scores of all the three climate variables were summed up to achieve a drought severity score for each year (Table S2). The years 1976, 1983 and 2003 turned out

Table 1 Characteristics of plots and center trees (a beech tree in the center of a 18 m radius circular plot) for each diversity levels: Isp (monoculture plots), IIsp (two species plots) and IIIsp (three species plots)

Diversity level	Plot					Center tree			
	Tree density (no of trees/ha)	BA (m^2/ha)	CPA (m^2/ha)	$\mathrm{Div}_{\mathrm{CPA}}$ (–)	SD (–)	DBH (cm)	CPA (m^2)	H (m)	ddg (–)
Isp	120 ± 60^{a}	35 ± 7	144 ± 30	1.00 ± 0^{c}	0.4 ± 0.1^{e}	68 ± 13	152 ± 38	36 ± 4	1.1 ± 0.2
IIsp	$170 \pm 40^{a,b}$	38 ± 4	167 ± 36	1.75 ± 0.19^{d}	0.8 ± 0.1^{f}	70 ± 14	147 ± 60	34 ± 3	1.4 ± 0.3
IIIsp	190 ± 40^{b}	36 ± 6	163 ± 25	2.46 ± 0.51^{d}	0.8 ± 0.2^{f}	67 ± 16	153 ± 77	33 ± 6	1.4 ± 0.2

Mean values and standard deviations are given. At the plot level, only trees with a DBH > 15 cm were considered. Diversity level groups without common letters differ significantly at $p < 0.05$ for the considered variable. For variables with no letters present, no significant differences were found between the diversity level groups. For tree density and SD, the parametric Tukey multiple comparison test is used, and for DivCPA the non-parametric Dunn test is used (see Table S1)

Tree density number of trees with DBH > 15 cm per hectare, *BA* total basal area, *CPA* total crown projection area, *DivCPA* scaled Shannon diversity index for CPA, *SD* structural diversity index, *DBH* diameter at breast height, *H* tree height, *ddg* ratio of DBH of center tree and average DBH of all trees in the plot

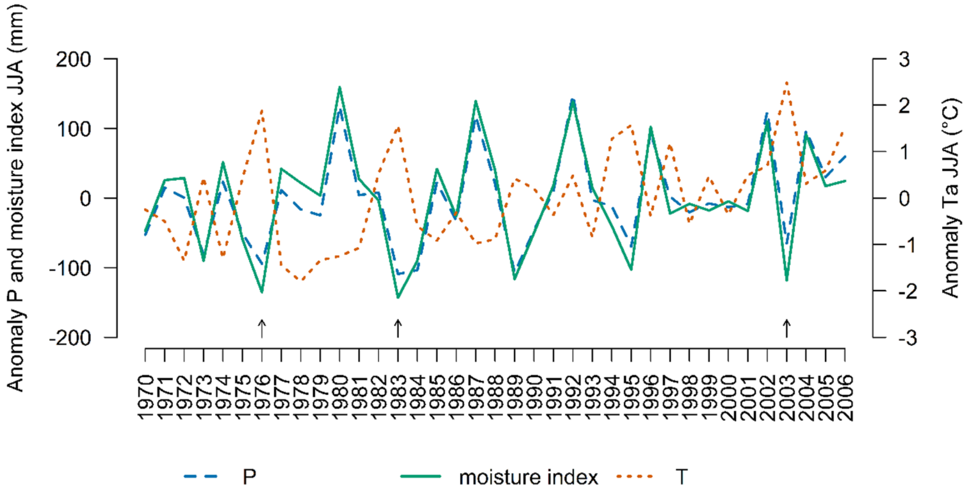

Fig. 2 P (precipitation), moisture index [calculated according to Thornthwaite (1948)] and Tmean (mean temperature) anomalies for the period June to August (JJA) as observed at the climatic station of Ukkel. Selected drought years (i.e., 1976, 1983 and 2003) are indicated with arrows

to be the years with the highest severity scores and were selected as drought years. These 3 years correspond well to drought years in Central Europe identified in previous studies (Pretzsch et al. 2013; Metz et al. 2016). In addition, the Standardized Precipitation Index for the growing period from April to October was lower than − 1.28 for all the three selected drought years, supporting severe drought conditions (Isbell et al. 2015) (Fig. S2).

The year 1976 is known as an exceptionally dry year across Europe, with mean temperature above the average of 1970–2006 during May to August and precipitation below the average of 1970–2006 during January–June and in August (Fig. S3). In 1983, drought occurred later in the growing season with mean temperature above the average of 1970–2006 from June to August, and P below the average of 1970–2006 from June to December (Fig. S3). Compared to the drought years 1976 and 1983, 2003 is ranked as the least severe drought year at our sites (Table S2) with high temperatures occurring late in the growing season. Mean temperature in August 2003 was 2.7 °C higher than the average of 1970–2006, while in 1976 and 1983 the increase was only 0.6 and 0.9 °C, respectively.

Tree cores

The center trees were cored in winter 2015 with 5 mm Suunto increment borers. Two cores (north and south direction) were taken at 1 m height. DBH and bark thickness at the coring location were measured. The cores were prepared with a core microtome to visualize the tree rings. Tree-ring widths (TRW) were measured using a Lintab measurement system with 1/100 mm resolution. The TSAP-Win and COFECHA software were used for tree-ring cross-dating.

For isotope analysis, tree rings of the three selected drought years, the 2 years before and 2 years after the drought were separated with a scalpel under a stereomicroscope and put into Teflon bags (Ankom Technology, Macedon, NY, USA) for subsequent cellulose extraction. Cellulose extraction was performed after Boettger et al. (2007), and cellulose was homogenized following Laumer et al. (2009). 1 ± 0.1 mg of cellulose was weighed into capsules (tin and silver for $\delta^{13}C$ and $\delta^{18}O$, respectively). Cellulose was combusted to CO_2 with an ANCA-SL for $\delta^{13}C$ measurements and pyrolyzed to CO for $\delta^{18}O$ measurements, respectively. The stable isotope ratios were measured with a SerCon 20–22 IRMS and 20–20 IRMS analyzer with a precision of 0.06 and 0.3‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. The $\delta^{13}C$ cellulose measurements were corrected for the decline in atmospheric $\delta^{13}C$ (Treydte et al. 2009) based on extrapolation of atmospheric $\delta^{13}C$ data published in McCarroll and Loader (2004). The number of measured tree rings is presented for the variables $\delta^{13}C$ and $\delta^{18}O$ in Table S3.

Statistical analysis

For the three diversity levels (i.e., Isp, IIsp and IIIsp) and the seven species composition levels, chronologies were constructed from both raw (referred to as TRW) and individually detrended (referred to as RWI) tree-ring width series by calculating a robust mean to remove extreme values (Mosteller 1977; Wigley et al. 1984). Detrending was applied using a 15-year cubic smoothing spline with a 50% frequency cutoff to remove non-climatic low-frequency variability, as for example age trends (Cook and Peters 1981). The chronologies of TRW and RWI allowed for the evaluation of the effect of diversity on the productivity and growth variability of beech. A Tukey multiple comparison test was used to test for significant differences between the TRW chronologies of the three diversity levels for the period 1970–2015. The effect of species composition on TRW (period 1970 and 2015) was tested with a mixed model in combination with a post hoc Tukey multiple comparison test with species composition as grouping variable. A mixed model with a random intercept for each tree was used to take the hierarchical structure of the data into account. With the same method, the effect of presence–absence of a particular tree species on the growth of beech was tested, providing insight into species identity effects (Zuur et al. 2009).

To evaluate the tree performance in drought versus non-drought years as a function of diversity level, mixed models for TRW, $\delta^{13}C$ and $\delta^{18}O$ with "drought year" (i.e., a variable indicating if the considered year is a drought year or not), diversity level, and their interaction as explanatory variables were developed. Adding a random intercept for each tree was needed due to more than one data point of each tree (i.e., drought year, 2 pre-drought years and 2 post-drought years). This model was applied to the 5-year periods centered around the three selected drought years. A post hoc Tukey multiple comparison test was used to test if TRW, $\delta^{13}C$ and $\delta^{18}O$ differed among the three diversity levels in (1) all years (drought and non-drought years) and (2) drought years. The effect of species composition on $\delta^{13}C$ and $\delta^{18}O$ was not tested because of the low number of observations for each species composition level.

Stability indices are mostly calculated for TRW, but in this study they were calculated for $\delta^{13}C$ and $\delta^{18}O$ as well. In addition, to evaluate the effect of diversity, the stability indices were calculated for the three diversity levels separately for the three considered event years (i.e., dry years 1976, 1983 and 2003). Resistance, recovery and resilience are defined as:

$$\text{Resistance} = \frac{X_{\text{event year}}}{\text{mean}X_{2\ \text{pre}\ -\ \text{event years}}},$$

$$\text{Resilience} = \frac{X_{\text{post}\ -\ \text{event year}}}{\text{mean}X_{2\ \text{pre}\ -\ \text{event years}}},$$

$$\text{Recovery} = \frac{X_{\text{post}\ -\ \text{event year}}}{X_{\text{event year}}},$$

where X is TRW, $\delta^{13}C$ or $\delta^{18}O$, and event year is 1976, 1983 or 2003 with their respective post-event years (i.e., 1977, 1984 and 2004) and their respective two pre-event years (i.e., 1974–1975, 1981–1982 and 2001–2002).

Since stability indices are calculated as ratios, the absolute values of TRW, $\delta^{13}C$ or $\delta^{18}O$ (further referred to as |TRW|, $|\delta^{13}C|$ and $|\delta^{18}O|$, respectively) need to be considered for the interpretation of the stability indices. During drought, a decrease in TRW (i.e., |TRW| decreases) and an increase in $\delta^{13}C$ (as $\delta^{13}C$ is negative for wood cellulose this means that $|\delta^{13}C|$ decreases) and $\delta^{18}O$ (i.e., $|\delta^{18}O|$ increases) is expected, if assimilate production and stomatal conductance are low (low TRW and high $\delta^{13}C$), and VPD is high ($\delta^{18}O$). Thus, stability indices of TRW or $\delta^{13}C$ that are smaller than one indicate that TRW or $\delta^{13}C$ is negatively impacted during drought, did not reach pre-drought conditions after drought, and did not recover from the drought event for resistance, resilience and recovery indices, respectively. For stability indices of $\delta^{18}O$, the opposite is true. Note that the stability indices for isotopes do not say something about tree growth, they say something about the temporal patterns of $\delta^{13}C$ and $\delta^{18}O$ in drought years, pre-drought years and post-drought years. The stability indices for isotopes need to be interpreted in their statistical meaning as described above.

To test if the calculated stability indices are smaller (for TRW and $\delta^{13}C$) or greater than one (for $\delta^{18}O$) as expected during drought, a mixed model with a random intercept for each tree was used (cp. Zang et al. 2012; Metz et al. 2016). To identify significant differences in resistance, resilience and recovery between the three considered diversity levels (i.e., Isp, IIsp and IIIsp), a post hoc Tukey multiple comparison test on a mixed model with diversity level as a fixed effect and a random intercept for each tree was used.

All statistics were performed in R (version 3.2.5) with packages "nlme", "dplr" and "multcomp" (Bunn 2008; Pinheiro et al. 2016). For all statistical tests, the significance level was set to $p < 0.05$.

Results

Stem radial growth and growth variability as a function of tree diversity and species composition

In general, beech trees growing in plots with two or three tree species have higher stem radial growth compared to monospecific beech plots (Fig. 3a and Table 2). As also confirmed by the Tukey multiple comparison test, TRW is 16%, 39% and 62% higher for two species versus monoculture plots, three species plots versus two species plots, and three species plots versus monoculture plots for the period 1970 to 2015 (Table S4), respectively. The RWI chronologies show higher growth variability of beech trees growing in monospecific beech plots compared to those growing in plots with two or three tree species (Fig. 3b), which is also represented by the autocorrelation (i.e., higher autocorrelation in more diverse plots Table 2). Note that the EPS of the trees growing in the three species plots is rather low, indicating a more heterogenous growth behavior, compared to that of trees from the less diverse plots.

As to tree composition, beech trees growing in beech–maple–oak mixtures have significantly higher TRW compared to beech, beech–hornbeam, beech–oak and beech–oak–hornbeam combinations (Fig. 4, for chronologies of TRW and RWI see Fig. S4 and Table S5). When the

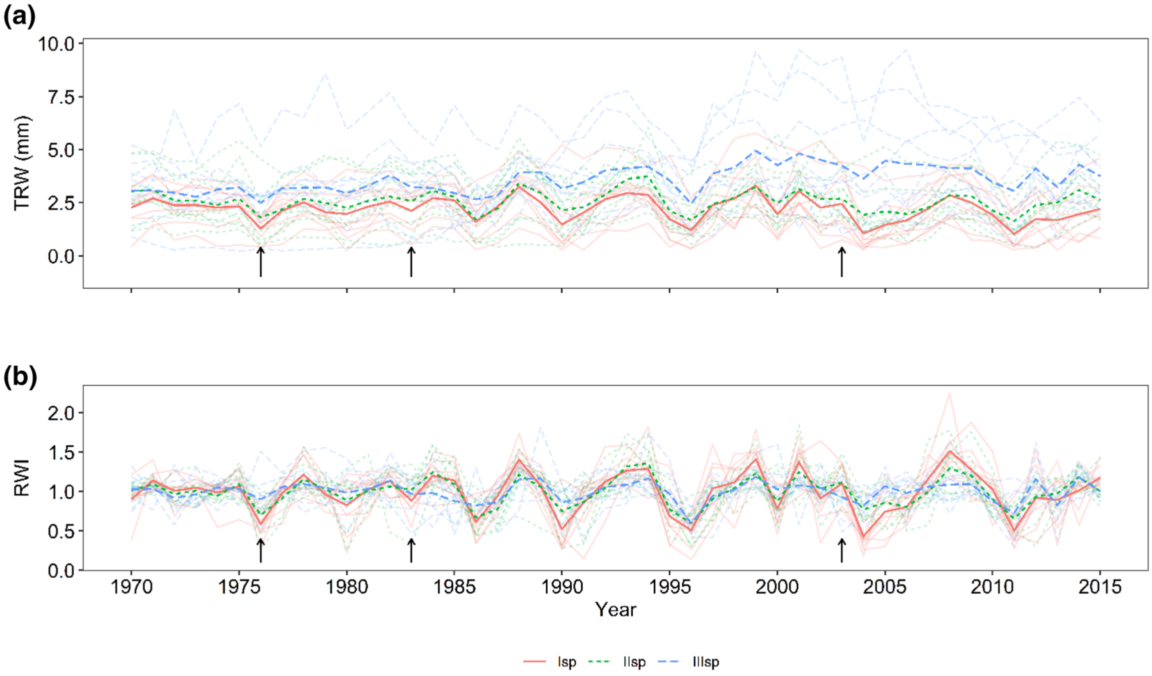

Fig. 3 Chronologies of TRW (**a**) and RWI (**b**) for beech trees growing in plots with three diversity levels Isp (monoculture plots), IIsp (two species plots) or IIIsp (three species plots). Thin lines represent the series of individual trees, and thick lines the corresponding mean. Selected drought years (i.e., 1976, 1983 and 2003) are indicated with arrows. Sample size: 9 trees per diversity level

Table 2 Characteristics of beech TRW chronologies for the three diversity levels Isp (monoculture plots), IIsp (two species plots) or IIIsp (three species plots) during the period 1970–2015

Diversity level	Rbar[a]	EPS[a]	AGR (mm)	Lag-1
Isp	0.480	0.893	2.155	0.246
IIsp	0.347	0.827	2.501	0.314
IIIsp	0.199	0.691	3.483	0.503

Rbar interseries correlation, *EPS* expressed population signal, *AGR* average growth rate, *lag-1* first year autocorrelation

[a] Referring to detrended TRW-data. Sample size: nine trees per diversity level

presence–absence of a particular tree species is used as a grouping variable, TRW of beech is found to be significantly higher in plots where maple or oak is present, but no effect of hornbeam presence or absence is found.

TRW, δ^{13}C and δ^{18}O in drought versus non-drought years as a function of diversity level

No significant correlation between TRW and climate variables precipitation, moisture index and mean temperature for the summer period June to August is found (Table S6), suggesting a relatively low sensitivity of beech growth to these climate indices in normal years. In all three drought years, however, stem growth is reduced. In 1976, a clear decrease in TRW is visible for the three diversity levels (Fig. 5) compared to the two previous years, whereas for 1983 this is only the case for beech trees growing in monospecific beech plots. In 2003, however, TRW is not reduced except for beech trees growing in monospecific plots. Growth in 2004 is, however, lower compared to 2003 (Fig. 5). In all three drought years, the reduction in stem radial growth is more pronounced for beech trees growing in monospecific plots compared to beech trees growing in plots with two or three tree species. The post hoc Tukey multiple comparison test indicates that TRW of beech trees growing in three species plots is significantly higher compared to trees growing in the monoculture plots, both overall (in drought and non-drought years) as well as in drought years alone (Table S7).

Overall, δ^{13}C values of beech trees growing in monoculture plots are higher compared to those growing in mixtures. In 1976, δ^{13}C values increased for all diversity levels, while in 1983, δ^{13}C values were higher for monoculture plots only, and no clear increase in δ^{13}C was found for the diverse plots. In 2003, only a weak δ^{13}C increase was found for all diversity levels compared to the pre-drought years.

Interestingly, tree-ring δ^{18}O does not show any systematic differences either between diversity levels in general or in drought years specifically, which is also confirmed with the post hoc Tukey multiple comparison test (Table S7). The only exception is 1976 with a slight δ^{18}O increase of the trees from the monoculture and the two-species plots.

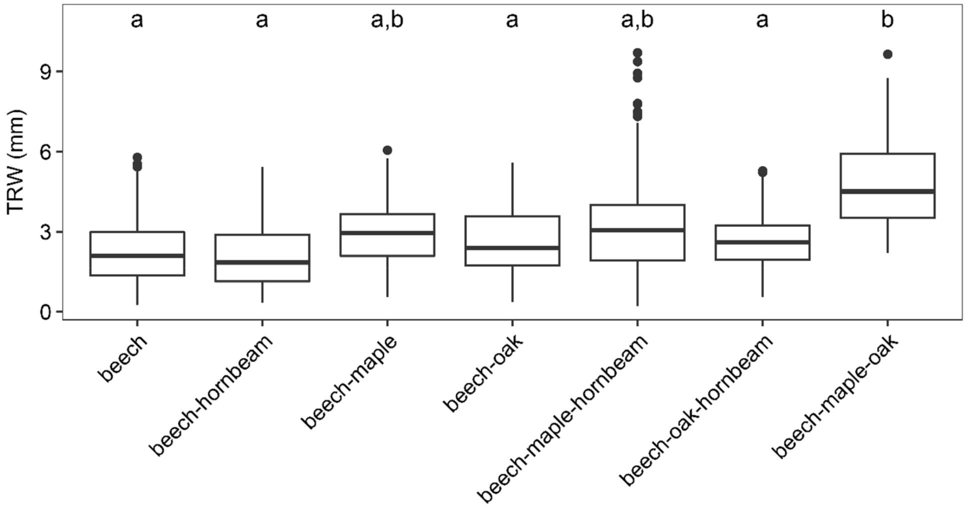

Fig. 4 Box plots of TRW of beech growing in plots with different species composition for the period 1970–2015. Species composition groups without common letters differ significantly at $p < 0.05$. Sample size: nine trees for beech plots and three trees for other species composition levels

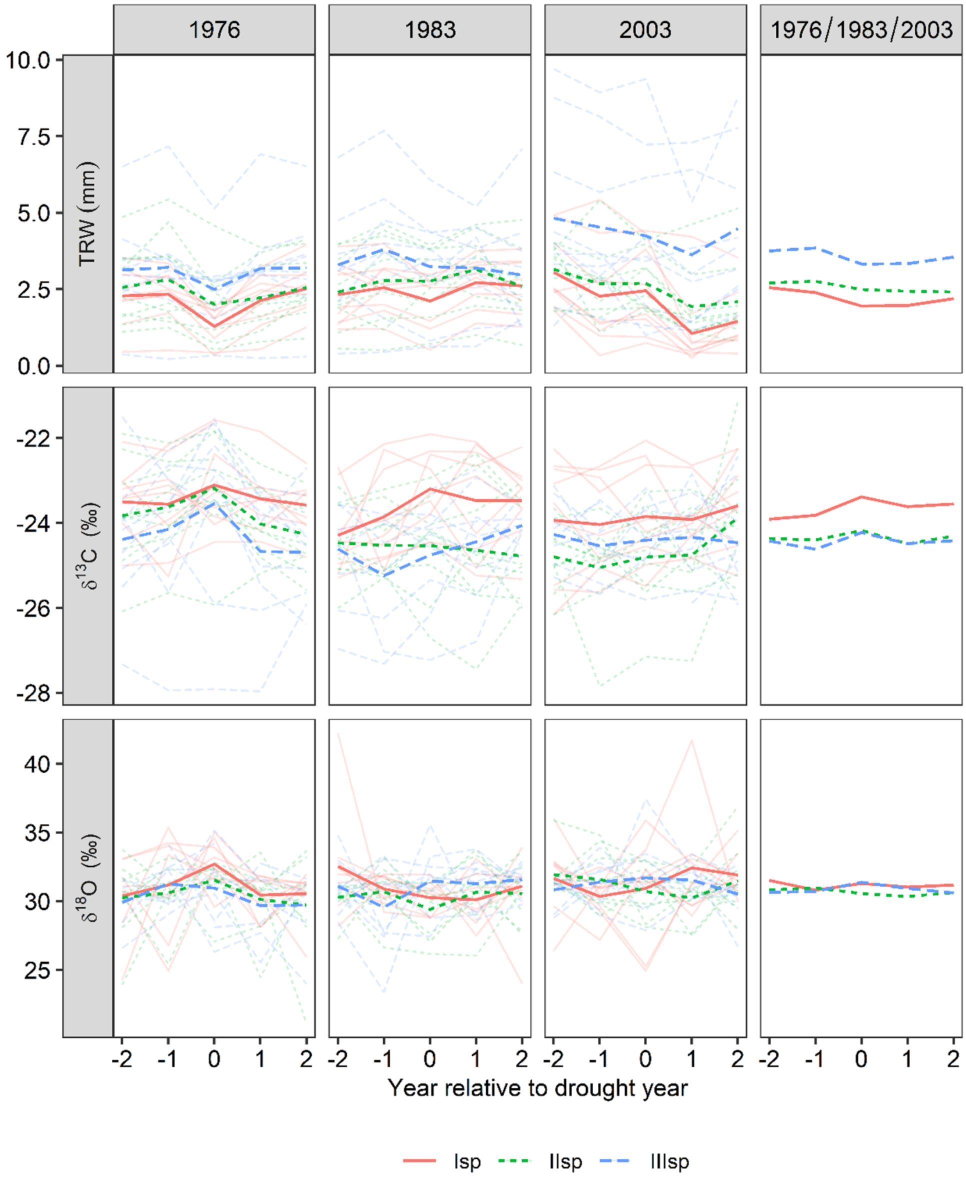

Fig. 5 Mean (thick lines) and individual tree (thin lines) TRW, δ^{13}C and δ^{18}O values for the drought years 1976, 1983, 2003 and their combination for beech trees growing in Isp (monoculture plots), IIsp (two species plots) and IIIsp (three species plots) diversity level plots. Values for 2 years before drought, 1 year before drought, drought year, 1 year after drought and 2 years after drought are shown (i.e., − 2, − 1, 0, 1, 2 year relative to drought year, respectively). Sample size: 9 trees per diversity level

Resistance, resilience and recovery

For stem growth, expressed by TRW, the resistance increases from monoculture plots and two species plots to the three species plots, although the differences are not significant (Fig. 6). Only for the monoculture plots, the resistance is significantly lower than one, indicating that TRW in the drought year is lower when compared to the mean value of 2 years before the drought year. Resilience of TRW is significantly lower than one in the monoculture and three species plots. This indicates that stem radial growth does not reach pre-drought growth levels in the year after drought. For the recovery of TRW after drought, no significant differences are found between the different diversity levels. TRW seems to respond differently in the drought years 1976 and 1983 on the one hand and 2003 on the other. In the drought year 2003, the reaction to drought appears to be postponed to the next year (i.e., 2004, see Fig. 5). Because of this difference, the calculated stability indices for TRW are quite different between the drought years 1976 and 1983 when compared to the drought year 2003 (Fig. S5).

In this research we are interested in the immediate reaction to drought in monospecific versus diverse plots. When a post-event period of two years is used instead of 1 year for the calculation of TRW resistance, resilience and recovery the results of resistance and recovery remain the same (Fig. S6b). The resilience of TRW in monoculture and three species plots is, however, no longer smaller than one. This is likely related to the drought year 2003 (Fig. S5), because, the postponed reaction of TRW to drought in 2004 is alleviated by the TRW in 2005 (Fig. S6) when a post-event period of two years is used. Because of this, the significant low resilience in the year after drought of the monoculture and three species plots is not further discussed in the discussion section.

$\delta^{13}C$ values do not show any significant differences in either resistance, resilience or recovery among the different diversity levels. For the monoculture plots, however, the resistance of $\delta^{13}C$ is significantly lower than one, meaning that $\delta^{13}C$ in the drought year is higher when compared to the mean value of two years before the drought year.

Resistance, resilience and recovery calculated for $\delta^{18}O$ do not indicate any significant effects of drought, and there are also no significant differences between the diversity levels. This indicates that $\delta^{18}O$ values are not negatively impacted during drought (i.e., resistance), do reach pre-drought values after drought (i.e., resilience), and do

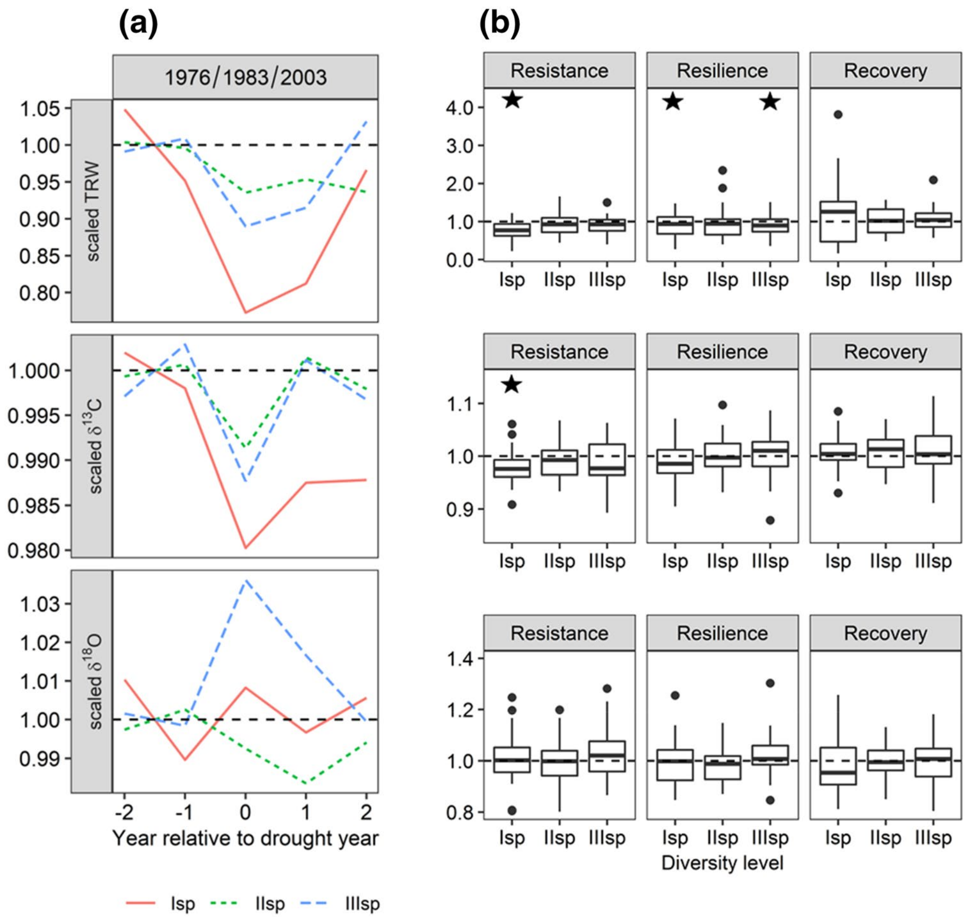

Fig. 6 **a** Mean of scaled TRW, $\delta^{13}C$ and $\delta^{18}O$ values for Isp (monoculture plots), IIsp (two species plots) and IIIsp (three species plots) diversity level plots for the years − 2, − 1, 0, 1 and 2. Values for each year are scaled to the two pre-drought years (i.e., years − 2 and − 1). Value in the drought year (i.e., year 0) indicates the resistance to drought. Value in the post-drought year (i.e., year 1) indicates the resilience to drought. Recovery = resilience/resistance. **b** Box plots visualize the resistance, resilience and recovery to drought for the variables TRW (top), $\delta^{13}C$ (middle) and $\delta^{18}O$ (bottom). Stars indicate the significant deviations from 1 as tested with a post hoc test on a mixed model with a random intercept for each tree ($p < 0.05$). Sample size: nine trees per diversity level

recover from the drought event (i.e., recovery) among the different diversity levels.

Discussion

Impact of tree species diversity and composition on beech growth, $\delta^{13}C$ and $\delta^{18}O$

Beech trees in more diverse plots grow significantly better (based on TRW) and show lower year-to-year growth variability (i.e., lower variability and higher first-order autocorrelation of RWI for beech trees growing in diverse plots) when compared to monospecific plots for the period 1970–2015 (Fig. 3, Table 2, Table S4). This indicates a positive relationship between biodiversity and productivity at the individual tree level for beech trees. Previous studies have already demonstrated such positive effects of species diversity on beech growth (Pretzsch and Schütze 2009; Mölder and Leuschner 2014; Metz et al. 2016) and growth variability (Metz et al. 2016).

More efficient use of the space in diverse patches both above- (crown complementarity) and belowground (root complementarity), and more efficient use and redistribution of resources have been shown to result in higher growth in diverse compared to monospecific forests (Kelty, 2006; Richards et al. 2010; Morin et al. 2011; Dieler and Pretzsch 2013; Pretzsch 2014). A more efficient use of the aboveground space is suggested by the higher structural diversity values of the more diverse plots with a higher vertical layering of crowns (Table 1). In our study, water availability seems to be a key factor of diversity effects on beech growth. This is suggested by the high growth rates in combination with low $\delta^{13}C$ values, indicating high stomatal conductance, at the diverse site and—vice versa—low growth rates in combination with high $\delta^{13}C$ values at the monoculture. In addition, well-known belowground differences in root structure between the involved species may play a role (Rosengren et al. 2005; Schwendenmann et al. 2015). Compared to beech, oak has a deeper rooting system and, at least under controlled conditions, it has been shown that oak is able to move water from deeper soil layers upwards (i.e., hydraulic redistribution) (Hafner et al. 2017), resulting in increased soil moisture in the upper soil layer potentially accessible for beech.

Complementarity effects increase when species in diverse stands have more distinct functional traits (Metz et al. 2016). This may be the reason why in our study the presence of hornbeam does not influence beech radial growth significantly, while the presence of maple or oak resulted in significantly higher growth. Positive effects of the presence of maple on the growth of beech was also reported in Mölder and Leuschner (2014), where it was linked to reduced crown competition in maple–beech mixtures in comparison to oak–beech mixtures, as both beech and maple are rather shade tolerant in contrast to oak.

No systematic relationships between diversity and tree-ring $\delta^{18}O$ patterns (Fig. 5 and Table S7) are found. Since also $\delta^{13}C$ and $\delta^{18}O$ patterns are not interrelated at our sites, we assume that the source water isotopic signature (Roden et al. 2000) plays a key role for the tree-ring signature and is mixed with the signal generated at the leaf level. This may particularly hold for situations when water from deeper soil layers with low $\delta^{18}O$ signatures is used (e.g., due to hydraulic lift) and at the same time high evaporative enrichment occurs (Sarris et al. 2013; Gessler et al. 2014; Treydte et al. 2014). However, as soil water uptake was not measured in this study, we cannot draw sound conclusions about this.

Note that the productivity of only one tree species is considered, and, hence, other tree species in the mixture may not experience positive biodiversity effects. It may thus happen that when a community level focus is used (i.e., considering all tree species present in the plot) no or negative effects of biodiversity are observed (Pretzsch 2017). In addition, despite selecting plots in even aged stands to ensure that the studied trees developed in a particular tree species diversity environment over their whole life span, we cannot guarantee this. Since nutrient availability, competition level, tree density, and stand structure (evaluated by the soil C:N value, ddg and SD, respectively) and also tree DBH or height are not significantly different between the three diversity level groups (Table 1, Table S8), their effects on TRW, $\delta^{13}C$ and $\delta^{18}O$ can most probably be excluded. Particularly for $\delta^{13}C$ and, although less distinct for, $\delta^{18}O$, however, it is known that tree height and DBH explain more of the stable isotope variability compared to tree age itself (Brienen et al. 2017; Klesse et al. 2018). Finally, as indicated by the low EPS of the beech trees growing in the three species plots, the sample size is rather small (i.e., 9 trees per diversity level). Therefore additional research is needed to confirm our observations.

Effects of drought on TRW, $\delta^{13}C$ and $\delta^{18}O$

While beech stem radial growth is clearly affected by drought in the 3 years of interest (Fig. 5), yet with some delayed effects in 2003, the $\delta^{13}C$ and $\delta^{18}O$ responses to drought are less consistent. The different reaction is related to differences in the duration, timing and severity of the studied drought years (Helle and Schleser 2004; Skomarkova et al. 2006). $\delta^{13}C$ values are known to be modified by carryover effects from previous years, since stored carbohydrates may be preferably used for wood production at the beginning of the growing season (Zeng et al. 2017). Since the peak in storage of non-structural carbohydrates occurs in late summer for beech (August–September), summer drought can therefore delay the storage and increase the isotopic signature of the stored non-structural carbohydrates which will be carried over to the next year (Scartazza et al. 2013). These carryover effects may have occurred in 1984 and 2004, because droughts of 1983 and 2003 occurred relatively late in the growing season (Fig. S3) and δ^{13}C did not decrease that much in 1984 and 2004 as expected (c.f. the decrease in δ^{13}C in 1977, Fig. 5). This pattern is not observed in the δ^{18}O values, indicating that δ^{18}O values are less influenced by carryover effects, but rather depend on the isotopic signature of soil water and evaporative leaf water enrichment (Zeng et al. 2017).

In the drought year 2003, no change in TRW was found. Limited beech growth reduction to the 2003 drought was also observed by Latte et al. (2016) and van der Werf et al. (2007) in Belgium and the Netherlands, respectively. For 2004, a decrease in TRW was visible. We interpret this as a lagged drought effect of 2003's drought, since precipitation, moisture index and mean temperature for the period June–August in 2004 we are not unusual (Fig. 2 and Fig. S3). Lagged response to drought is a well-known phenomenon, as drought can cause: (1) loss of leaf area and/or non-structural carbohydrates impeding growth in subsequent years, (2) vulnerability to pest and pathogens, (3) hydraulic dysfunction caused by stress induced shifts in xylem anatomy or (4) drought-induced xylem cavitation influencing water transport and thus affecting growth (Anderegg et al. 2015).

A lagged effect to drought is also often observed when the year following the drought year is a masting year (mass seed production) (Hacket-Pain et al. 2017), as the year 2004 was for beech in Belgium (Nussbaumer et al. 2016). Dry years with high temperature and low precipitation may trigger masting in the next year, which results in prolonged or delayed growth reduction (Hacket-Pain et al. 2017). Several studies indicate that fruit production is dependent on recently assimilated carbon and that stored carbon does not decline during masting years; therefore, reduced growth is often observed during masting years as tree growth and fruiting compete for the same assimilated carbon (Hacket-Pain et al. 2017). It is difficult to disentangle masting and drought effects on growth as they interact. The observed growth decrease in 2004 is likely the combined effect of masting and lagged drought effects.

Effect of diversity on TRW, δ^{13}C and δ^{18}O during drought

Combining TRW, δ^{13}C and δ^{18}O values of beech trees growing in plots with different tree species diversity provides more insight into the potential effect of biodiversity on the tree's physiological response to drought stress. The lower decrease in growth (i.e., resistance of TRW is not significantly lower than the one in diverse plots opposed to monoculture plots) in combination with the smaller increase in δ^{13}C values (i.e., resistance of δ^{13}C is not significantly lower than the one in diverse plots opposed to monoculture plots) and the higher δ^{18}O values (although not significant) of three species plots in drought years suggest a smaller reduction in stomatal conductance, likely resulting from higher water availability in two and three species mixtures compared to monospecific plots (Table S7, Figs. 5, 6) (Leavitt and Long 1989; Saurer et al. 1995). A lower decrease in stomatal conductance for beech trees growing in mixtures during drought will result in water loss through transpiration, but allow enhanced CO_2 uptake and assimilate production, resulting in minimal decrease in stem radial growth in two and three species plots during drought (Fig. 5). The high transpiration will result in high evaporative leaf water ^{18}O enrichment (Barbour et al. 2004), and as a consequence in assimilates with relatively high isotope values that are finally incorporated into cellulose (McCarroll and Loader 2004; Gessler et al. 2014; Treydte et al. 2014). This is suggested by the findings of this study with higher δ^{18}O values (although not significant) during drought years of beech trees growing in the three species diversity plots when compared to beech trees growing in monospecific plots (Fig. 6), but unexpectedly not for beech trees growing in two species plots. This is possibly caused by the source water signature, which can compensate for evaporative enrichment as discussed above.

Effect of diversity on resistance, resilience and recovery of beech trees to drought

The lower variability in stem radial growth of beech trees growing in more diverse plots (Fig. 3 and Table 2) suggests an overall stabilizing effect of diversity (Pretzsch and Schütze 2009; Jucker et al. 2014). Resistance, resilience and recovery are useful descriptors when looking specifically at growth reactions of trees during and after drought events. The low resistance of TRW and δ^{13}C values of beech trees growing in monospecific plots indicates that stem radial growth declines and δ^{13}C increases during drought. Similar findings are revealed when using RWI data for calculation of resistance (Fig. S6a). For beech trees growing in mixtures, resistance of TRW and δ^{13}C is not significantly lower than one. Thus, drought does not influence beech growth and does not markedly alter stomatal conductance, as discussed in the previous section. The lower resistance to drought of monoculture beech trees could lead to future mortality as demonstrated by DeSoto et al. (2020) that drought-related mortality risk is related to low drought resistance in angiosperms.

Metz et al. (2016) also reports lower resistance in stem growth expressed by TRW for beech trees growing in monospecific plots when compared to mixtures, but Forrester et al. (2016) consider the lower stand densities in diverse patches of the mentioned study as the possible cause of this low resistance rather than the effect of species diversity itself. In the present study, we can exclude that lower stand density caused higher resistance in the diverse plots, since stand density is higher for the diverse plots (Table 1).

Conclusion

The findings of this study indicate that beech trees in monospecific plots grow slower and more irregular in terms of stem radial growth, and suffer more from drought. Beech trees growing in diverse plots have more soil water available than beech trees in monospecific plots, evidenced by lower δ^{13}C values (although not significant) and a lower increase in δ^{13}C in drought years compared to previous years (i.e., resistance is not significantly lower than one for diverse plots plots). Higher water availability allows higher stomatal conductance, even in dry years, which can result in higher growth rates. However, this overriding effect of biodiversity on beech stem radial growth and drought resistance might diminish in the future with increasing drought intensity and frequency. We acknowledge that the findings of this study result from a relatively moderate sample size (i.e., nine beech trees per diversity level); therefore, additional research is required to further explore the interactions between the clearly observed effects of diversity on beech tree growth and its physiological response to drought.

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Author contribution statement AV collected and analysed the data and was a major contributor in writing the manuscript. KT povided guidance on sample preparation for isotope analysis and interpretation of data. KT, PB, VK, QP, KV and BM made substantial contributions to the conception and design, the interpretation of data and writing of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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