



Growth of European beech recovered faster than that of Norway spruce after a five-year experimental drought in a mixed forest stand

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Abstract

Key Message Beech growth acclimated better during severe drought and recovered faster than spruce after drought ended. This was associated with a shift in performance along relative tree size towards small trees.

Abstract The effects of several consecutive drought years and the recovery reaction of mature trees in particular after a long-term drought have been poorly studied so far. In this study, we demonstrate the growth reactions of mature trees during and after a five-year treatment of extended summer droughts, followed by controlled irrigation in a very productive mixed forest stand. We exposed 70-year-old Norway spruce (*Picea abies* [L.] Karst) and 90-year-old European beech (*Fagus sylvatica* [L.]) trees to reduced precipitation using automatic throughfall exclusion (TE) roofs during the growing seasons from 2014 to 2018, irrigated the trees in early summer 2019 and removed the roofs thereafter. From 2009 to 2022, we monitored annual tree growth and precipitation on 6 plots with throughfall exclusion and on 6 plots with ambient Control conditions (CO) of the KROOF canopy experiment. Norway spruce lost significant growth during drought, with some trees dying and others remaining at a low growth level without significant recovery from the effects of drought stress. European beech also significantly reduced growth at the beginning of the drought but emerged stronger in growth from the drought than the Control group. Spruce and beech showed a non-significant trend of increased inter-specific growth compared to intra-specific growth during drought. We found that spruce benefitted more from mixture than beech in the recovery phase after drought than during the drought phase itself. Most importantly, we observed a shift in growth performance along the relative tree size towards smaller trees in the TE plots for both species. This change in the relationship between diameter increment and tree size during and after drought is a major finding of our study and suggests a possible response mechanism to prolonged drought. This key observation requires further investigation and should be considered in future forest management strategies under changing climatic conditions.

Keywords KROOF throughfall exclusion experiment · Tree growth · Inter · Intra-specific competition · Relative tree size · Acclimation · *Picea abies* · *Fagus sylvatica*

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Introduction

Global climate change is affecting forests worldwide through altered water and carbon cycles (Breshears et al. 2005; Ciais et al. 2005; Zhao and Running 2010) and through more frequent and intensified drought years, as well as extended arid periods (Allen et al. 2010; IPCC 2014). Drought can disrupt important physiological processes in trees such as water transport and carbon allocation (Adams et al. 2017; Choat et al. 2012, 2018; Hesse et al. 2019), cause various stress symptoms and negatively affect plant growth (Anderegg et al. 2012; Ciais et al. 2005; Gupta et al. 2020; Rais et al. 2021; Walthert et al. 2021). Many studies show that single dry years can reduce growth of Norway spruce (*Picea abies* [L.] Karst), European beech (*Fagus sylvatica* [L.]), and other tree species by up to 50% (Bosela et al. 2021; Leuzinger et al. 2005; Lloret et al. 2011; Zang et al. 2012). Recent large-scale studies with large data sets have highlighted even more clearly the effects of climatic variables on spruce and beech growth, with certain variables identified as particularly influential for spruce (Hlásny et al. 2017). A study conducted in the Czech Republic found that severe drought in 2017 and 2018 resulted in a significant decrease in annual radial stem growth of spruce compared to measurements in the wetter year 2016 of 78% and 61%, respectively (Krejza et al. 2021). Rohner et al. (2021) reported about growth reductions for beech trees of up to 100% during the severe spring–summer drought in 2018. Climate change, particularly extended and intensified droughts, causes severe abiotic stress and increases the risk of biotic stress to trees (Allen and Breshears 1998; Bauhus et al. 2017; Dale et al. 2001; Lindner et al. 2010) which may result in increased tree mortality or large-scale disturbance of forests (Allen et al. 2010, 2015; Anderegg et al. 2012; Choat et al. 2018; Hartmann et al. 2018; McDowell et al. 2008; Pretzsch et al. 2020a; Schuldt et al. 2020; Seidl et al. 2017). The partitioning of the stand-level growth results from the partitioning of resources among the individual trees in a stand. To date, there has been little analysis of interindividual growth partitioning and, in particular, the effects of long-term and repeated droughts on the contribution of different population fractions within the stand structure to total stand growth (Pretzsch et al. 2018b; Trouvé et al. 2014). In the long term, the functionality and further persistence of forest stands will be determined by their ability to resist such disturbances or to recover after non-lethal disturbances (Ibáñez et al. 2019). Especially the recovery of mature trees from stress, which is fundamental to understanding the stress resilience of forests, has been far too little addressed (Ruehr et al. 2019).

In recent years, knowledge of the growth effects of mixing complementary tree species has increased (Bosela et al. 2015; del Río et al. 2014a; Pretzsch et al. 2015b;

Pretzsch et al. 2017). Pretzsch and Zenner (2017) gave a broad review of the most important mixing effects, illustrated the role of models in the research on mixed-species stands, and pointed out remaining knowledge gaps. Many studies have specifically investigated tree responses to drought stress, showing differences between monocultures and mixed stands (Bréda et al. 2006; Ding et al. 2017; Grams et al. 2021; Kolář et al. 2017; Pretzsch et al. 2014). In many cases, an increase in growth has been confirmed when trees grow in mixed stands (Ammer 2019; Pretzsch et al. 2013, 2020a). The impact of mixture on forest stability and productivity was recently highlighted by del Río et al. (2022), who showed that adding just one more tree species to monocultures increased forest growth productivity and stability (overyielding: + 6%; temporal stability: + 12%). Pardos et al. (2021) found in a large-scale study on 13 trials across nine European countries that mixed forests, especially those combining conifer and deciduous species, have higher resilience and resistance to drought events than monospecific stands. However, this advantage of mixtures could not be generalized. Indeed, these benefits of species mixing can vary according to stand density (Pretzsch and del Río 2020), site conditions (Lévesque et al. 2016; Steckel et al. 2020b), tree species combination (Grossiord et al. 2014; Grossiord 2018; Steckel et al. 2020a), and mix proportion, among other factors (Pretzsch et al. 2020b). When the stress factor is reduced, the advantages can reverse to a disadvantage (Pretzsch et al. 2015a, 2017). Therefore, the influence of species mixing, respectively, intra- and interspecific competition has not been clarified.

Mixed spruce-beech forests cover large areas in Central Europe and are one of the preferred mixtures in actual silviculture (Grams et al. 2021). Both species, Norway spruce and European beech, exhibit species-specific differences in growth, stress reactions, and recovery after stress (Bréda et al. 2006; Bréda et al. 2006; Zang et al. 2012) and promote stand stability under poor conditions (Pretzsch et al. 2010). Reasons for such stabilization might be that Norway spruce and European beech differ in terms of their hydrological anatomy and physiology (Ellenberg and Leuschner 2010). Spruce with tracheids and few stem parenchyma cells is considered to be a very drought-sensitive tree species (Lévesque et al. 2013) with a more isohydric strategy, while beech with xylem vascular elements and higher proportions of xylem parenchyma has an anisohydric strategy (Hartmann 2011; Krupkova et al. 2019; McDowell et al. 2008; Pretzsch et al. 2013). From these two strategies, isohydric plants are often assumed to be more affected by carbon starvation under extended drought (Kannenbergh and Phillips 2020). Conversely, anisohydric plants are assumed to be more affected by hydraulic failure and thus water stress, especially during short periods of extreme drought (Grams et al. 2021).

Further complementary factors between spruce and beech are obvious. Spruce is an evergreen gymnosperm with needles and a mostly shallow-rooting system, whereas beech is a deciduous angiosperm with foliage and a heart-root system with coarse roots spreading horizontally and vertically (Grams et al. 2021). The maximum vertical fine root distribution for beech is below that of spruce (Ellenberg and Leuschner 2010). The different strategic approaches to hydraulic function and carbon assimilation, together with complementarity lead to a spatial and temporal offset in resource demands and thus may be checked if they can be considered as an explanation of different response patterns to changing environmental conditions (del Río et al. 2014b).

Although growth partitioning in light-limited temperate forests has been well studied, there is a lack of research on growth partitioning under water-limited conditions, with many studies on drought stress reaction focusing on the growth of dominant trees assuming that these trees reflect the response patterns of the entire stand. Pretzsch et al. (2018b) referred to studies that have investigated the effect of drought stress at different levels of organization (dominant trees vs. whole stand) and suggest that trees with different relative tree sizes respond differently to drought, to not neglect that dominant trees may continue to benefit from their achieved tree size (correlating with their social position), or, as recent results suggest, may show a particular vulnerability to drought (Bennett et al. 2015; Lebourgeois et al. 2014; McGregor et al. 2021; Stovall et al. 2019). For example, Ding et al. (2017) and Zang et al. (2012) report that growth reaction to drought varies as a function of tree size. Accordingly, a distinction can be made between completely symmetric, over size-symmetric to strongly size-asymmetric inter-individual partitioning patterns (Aldea et al. 2021; Pretzsch and Biber 2010). Relative reductions in growth are often more severe on sites previously well supplied with water than on sites that are intrinsically dry (Rukh et al. 2020; Stovall et al. 2019), but may be mitigated by factors such as stand density and tree species mixture (Aussenac et al. 2019; Pretzsch et al. 2015a, 2017; Pretzsch and del Río, 2020). Smaller trees in the stand could have a stabilizing function under dry conditions by partially compensating the losses of their dominant neighbors (Pretzsch and Biber 2010; Wichmann 2001). Studies showed that the correlation between tree size and growth is strong in wet years and weak in dry years. Findings at wet sites compared to dry sites show an analogous pattern. Thus, variation occurs at the temporal scale as well as at the spatial scale (Pretzsch et al. 2018b). Latte et al. (2016) have shown that in addition to such effects of drought on growth distribution in whole stands, there are also changes in growth distribution within trees (along the stem to the crown).

Controlled experiments in greenhouses or phytotrons can only provide limited answers to the mentioned

knowledge gaps. To gain new insights, theories need to be tested in natural and mature stands (Grams et al. 2021; Hartmann et al. 2018). So far, field manipulation studies on an ecosystem scale are still very rare but would contribute substantially to the understanding of tree reactions in complex environmental networks (Englund and Cooper 2003; Pretzsch et al. 2018a). Field manipulation studies that ensure both a prolonged drought and recovery through irrigation are even more rare (Gao et al. 2021). First insights into the growth losses in connection with drought stress and possible acclimation and recovery reactions are provided by the KROOF canopy experiment setup in the Kranzberg Forest near Freising (Bavaria) (Grams et al. 2021; Pretzsch et al. 2014, 2020a). Because the experiment in Kranzberg is unique in its design so far, this study is one of the first to present possible recovery reactions of mature spruce and beech trees after five years of drought stress under field conditions and enables to analyze the growth reactions of forests under extreme and extended drought. In this study, we investigated the influence of an extended five-year experimentally induced drought on the growth of mature trees in a stand of Norway spruce and European beech under intra- and inter-specific competition. We studied the possible recovery of growth following irrigation after a long-term drought-period and analyzed whether the relative tree size of individual trees had an effect on growth during drought and on recovery after irrigation. For this study, we concentrated on the following questions and null hypotheses:

Q1: Do Norway spruce and European beech recover in their growth rate after extended (5-year-long) experimentally induced drought and subsequent irrigation?

H₀1: Both, Norway spruce and European beech show full growth recovery to the unstressed growth upon irrigation after an extended drought period. Growth recovery is similar for Norway spruce and European beech.

Q2: What influence does intra- or inter-specific competition have on the recovery reaction?

H₀2: Growth recovery is independent of intra- and inter-specific environments. Intra-specific responses do not differ from inter-specific responses and all trees in a stand react similarly.

Q3: What are the effects of an extended drought and a subsequent irrigation on the growth reaction along the relative size of trees in a stand?

H₀3: Drought stress reaction and growth reaction after drought are independent of relative tree size within the population. All trees irrespective of their relative size in a stand react similarly.

Materials and methods

Site

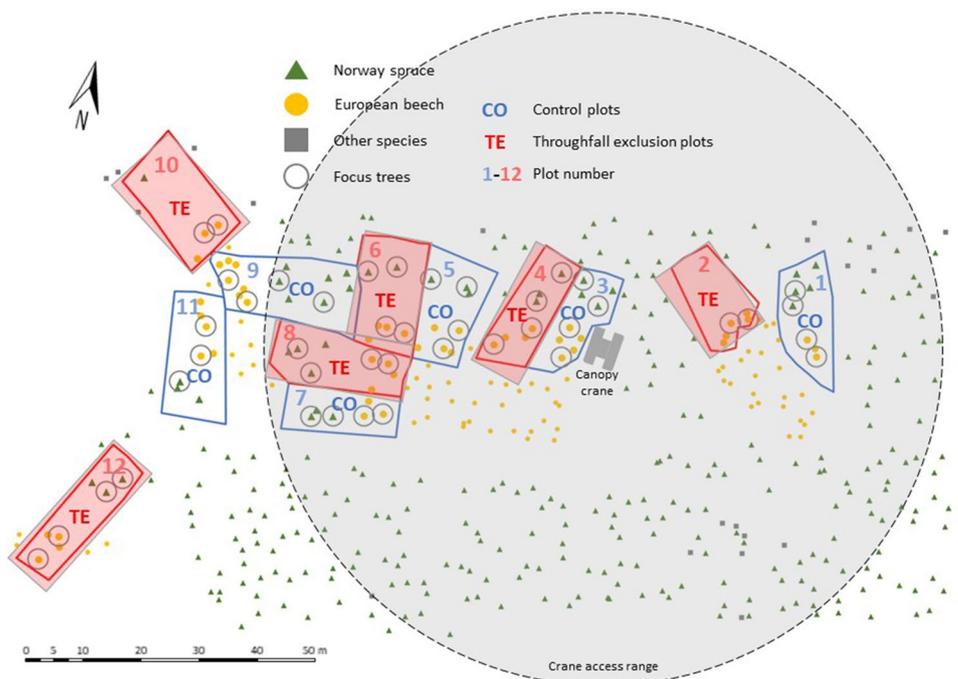
In our study, we used the KROOF design to show, if spruce and beech growth responds to extended drought, if species mix modifies growth reactions, if both species recover with subsequent irrigation, and if growth collapse and recovery vary along relative tree size. Kranzberg Forest (longitude: 11° 39' 42" E, latitude: 48° 25' 12" N, altitude 490 m a.s.l.) is located in Southern Germany, approximately 35 km North-east of Munich. At the site, mono-specific and mixed-species stands of Norway spruce and European beech stock on luvisol originating from loess over Tertiary sediments that provide a high nutrient and water supply (Göttlein et al. 2012; Pretzsch et al. 2014). Depending on soil depth, the water holding capacity for plant available water ranges between 17 and 28% of volumetric soil water content, while soil $\text{pH}_{\text{H}_2\text{O}}$ varies between 4.1 and 5.1.

Treatments

At the approximately 0.5 ha KROOF experimental site, a total of 12 experimental plots were installed (Fig. 1). Each plot includes a group of 3 to 7 beech and spruce trees at opposing ends of the plot (as of 2014 at the start of the experiment). To examine mixing effects, the plots were designed to create areas of intra-specific competition at each end of each plot and an area for inter-specific

competition in the middle. One tree of each species represented the intra-specific competition, and the other tree in the middle of the plot represented the inter-specific competition. In 2010 (four years before starting the drought experiment) the 12 plots were trenched to 1 m soil depth. Below this soil depth, a layer of sandy/silty loam inhibits deeper root growth of the trees. To prevent lateral root growth and lateral water flow between the plots, the trench was lined with a plastic tarp (Grams et al. 2021). After the trees have recovered from trenching for four years, five years of drought were conducted from 2014 to 2018. The precipitation during the growing season (April to October) was excluded using automatically closing and opening throughfall exclusion roofs for half of the 12 experimental plots (6 *TE* plots). The second half of the plots served as the *Control* (6 *CO* plots). To eliminate the influence of small-scale factors like soil properties, each *Control* plot was matched with a throughfall exclusion plot (Fig. 1). Over winter, precipitation on the *TE* plots was allowed to replenish soil water storage (SI-Fig. 1). To ensure that the possible water uptake of the trees from outside the plots could be excluded, deuterated water was injected in deep soil layers outside the trench. The tests showed that neither the deep-rooted beech trees nor the shallow-rooted spruce trees took up labelled water. It is important to note that the experimental plots were selected randomly, taking into account the species composition. This design was chosen to ensure that the study results are as representative as possible. However, due to their species composition and other factors, a complete

Fig. 1 Map of the KROOF experimental site in Kranzberg, Bavaria



randomisation of the plots was not possible. Therefore, some experimental plots are adjacent to control plots. Despite this spatial proximity, all necessary preparations were made to maintain the independence of the *TE* and *CO* plots.

Starting in June 2019, the plots were irrigated and the roofs were permanently opened (Grams et al. 2021). Irrigation (*CO* + 15 mm, *TE* + 90 mm) in June and July 2019 and the subsequent roof opening resulted in a rapid convergence of precipitation levels on the *TE* and *CO* plots (Fig. 2). Since 2014 throughfall is different for *CO* and *TE* (SI-Fig. 1). From 1998 until 2014, the year of the throughfall exclusion, temperature and precipitation were on average 8.1 °C and 841 mm year⁻¹, respectively. Particularly humid years in this time span were 2001 and 2002 (precipitation > 1000 mm year⁻¹). A particularly dry year (precipitation < 700 mm year⁻¹) was 2003. Since the start of the throughfall exclusion, temperatures have shown a slightly increasing trend (9.4 °C on average). Precipitation from 2014 onwards was slightly lower than the previous average (753 mm year⁻¹). With the beginning of the throughfall exclusion in 2014, the reduced precipitation on the *TE* plots amounted to approximately a quarter of the precipitation observed on the *CO* plots (Fig. 2). The *CO* plots also faced natural droughts in 2015 and 2022, and soil water content decreased significantly during the growing seasons (SI-Fig. 1). For further information about the KROOF experimental site, plot design and dehydration technique, see (Göttlein et al. 2012; Grams et al. 2021; Häberle et al. 2012; Pretzsch et al. 1998, 2014, 2016, 2018b).

Measurements

The individual plots are similar in size, stand density, range of diameters, and mixing ratios (Table 1). On average, the *CO* plots have a similar plot size of 143.1 ± 34.1 m² to the *TE* plots of 145.4 ± 22.4 m². Mean diameter at breast height is close between tree species as well as between treatment groups, similarly to the mean tree heights (Table 2). However, clear differences between the tree species and especially between the different treatment groups could be observed considering the annual increment of basal area in the three periods. Here, the *TE* spruce and beech trees showed similar increments as the respective *CO* trees at the beginning of the experiment, but then during the drought the difference is clear, but not significant ($iba_{2014-2018}$; spruce 14.2 ± 9.8 cm² in *CO*, 4.7 ± 4.1 cm² in *TE*; beech 9.0 ± 9.8 cm² in *CO*, 5.1 ± 6.2 cm² in *TE*). Apart from the *TE* plots, the site conditions in the Kranzberg forest provide almost maximum productivity for the 70-year-old spruces and the 90-year-old beeches on the experimental plots. This becomes visible by site indices of O40 according to the yield table of (Assmann and Franz 1963) for spruce, and site class I according to (Schober 1995) for beech (Fig. 3). For more information about stand and plot characteristics, as well as tree and stand growth, see (Grams et al. 2021; Pretzsch et al. 2014, 2018b, 2020a).

To measure stem diameter, dendrometer bands with a resolution of 0.01 cm (Permanent-Baummessband D1, UMS GmbH, München, Deutschland) were installed at a height of 1.30 m (DBH) on each tree. Stem diameters were measured several times a year since 1998. In our study, diameters at

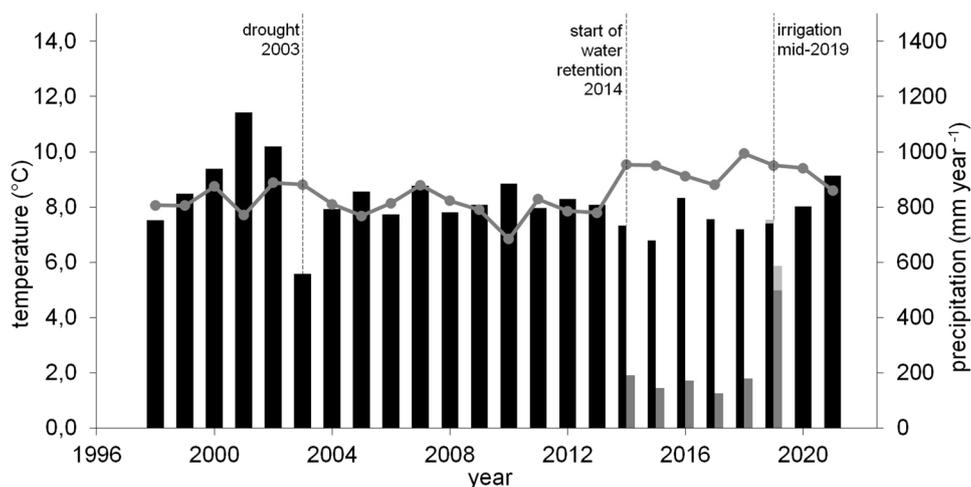


Fig. 2 Mean annual temperature (gray line), and annual precipitation received on *CO* plots (black columns) and on *TE* plots (dark-gray columns), respectively, at the KROOF experimental site since 1998. The drought in 2003, the beginning of the experimental drought in 2014 and the end of it with onsetting irrigation and the removal of roofing

in mid-2019 are highlighted by vertical lines. The additional irrigation (*CO* + 15 mm, *TE* + 90 mm) beginning in June and July 2019 are highlighted by light-gray shading stacked on top of the bar representing 2019. Meteorological data from the nearby Forest Climate Station Freising were provided by the Bavarian State Institute of Forestry

Table 1 Plot characteristics of the KROOF throughfall exclusion experiment with plot size (Area), number of trees on the plot (*N*) in 2014 and 2022 and diameter at breast height (*DBH*, mean ± 1 SD)

Plot	Area (m ²)	Norway Spruce					European Beech				
		<i>N</i> _{2014 (2022)}		<i>min</i>	<i>DBH</i> ₂₀₂₂ (cm)	<i>max</i>	<i>N</i> _{2014 (2022)}		<i>min</i>	<i>DBH</i> ₂₀₂₂ (cm)	<i>max</i>
1	131,8	5	(5)	32,7	36,9 ± 3,9	42,7	5	(3)	26,5	32,7 ± 10,5	44,8
3	109,8	4	(4)	32,1	38,7 ± 6,8	48,1	6	(5)	23,4	31,1 ± 7,6	43,4
5	142,1	3	(3)	33,4	39,6 ± 6,3	45,9	5	(5)	18,9	29,6 ± 7,9	41,1
7	111,3	3	(3)	32,0	39,8 ± 7,7	47,3	3	(3)	28,0	38,8 ± 12,2	52,1
9	199,0	7	(7)	16,8	39,6 ± 14,0	62,5	7	(7)	18,4	29,3 ± 8,3	40,4
11	164,3	4	(3)	29,7	39,2 ± 12,6	53,5	5	(5)	19,0	33,3 ± 14,4	54,6
CO total	858,3	26	(25)				31	(28)			
2	115,2	6	(0)	NA	NA	NA	5	(5)	15,9	26,7 ± 8,3	38,6
4	127,6	3	(3)	27,5	37,6 ± 9,2	45,5	4	(4)	27,7	33,4 ± 6,5	40,4
6	161,7	4	(2)	38,8	39,2 ± 0,6	39,6	4	(4)	14,5	35,4 ± 17,5	50,1
8	156,2	5	(4)	30,5	34,0 ± 3,2	38,0	5	(4)	23,0	28,5 ± 3,7	31,0
10	174,3	4	(1)	14,7	14,7 ± NA	14,7	3	(3)	24,1	33,6 ± 11,3	46,1
12	137,1	4	(3)	24,7	33,6 ± 14,0	49,8	4	(4)	24,0	28,9 ± 7,3	39,7
TE total	872,1	26	(13)				25	(24)			

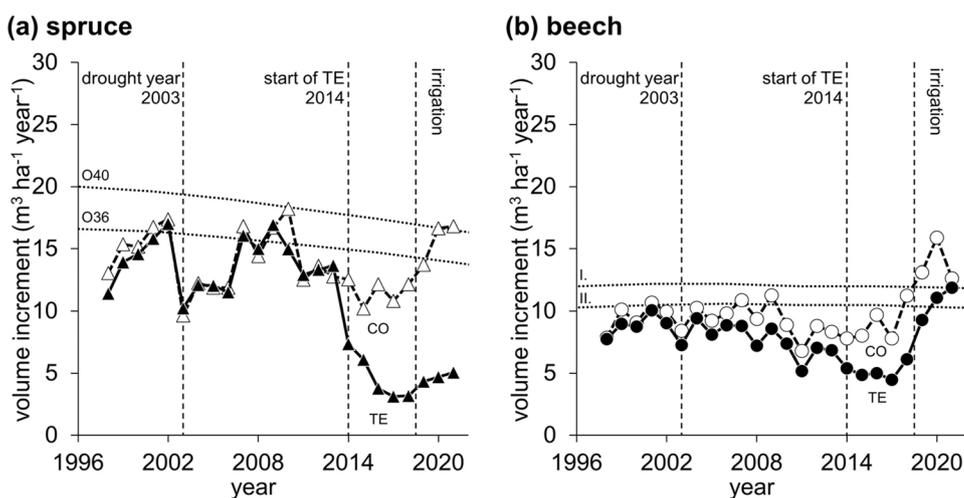
Plots 1, 3, 5, 7, 9 and 11 are the control plots (CO), throughfall exclusion (TE) was conducted on the plots 2, 4, 6, 8, 10 and 12

Table 2 Characteristics of spruce and beech trees studied during the three phases of the throughfall exclusion experiment from 2009 to 2022

Species	Group	<i>N</i>	<i>DBH</i> ₂₀₂₂ (cm)	<i>h</i> ₂₀₁₈ m	<i>iba</i> _{2009–2013} (cm ² year ⁻¹)	<i>iba</i> _{2014–2018} (cm ² year ⁻¹)	<i>iba</i> _{2019–2022} (cm ² year ⁻¹)	<i>iba</i> _{2019–2022} / <i>iba</i> _{2014–2018}
N. spruce	CO	25	38,9 ± 8,9	32,8 ± 2,39	21,7 ± 13,9	14,2 ± 9,8	21,2 ± 13,8	1,49
N. spruce	TE	13	34,1 ± 9,4	31,6 ± 2,25	21,2 ± 14,9	4,7 ± 4,1	11,6 ± 11,0	2,48
E. beech	CO	28	31,8 ± 9,6	29,5 ± 4,00	8,7 ± 10,3	9,0 ± 9,8	15,8 ± 14,0	1,76
E. beech	TE	24	30,8 ± 9,4	29,2 ± 3,81	7,5 ± 9,2	5,1 ± 6,2	14,4 ± 17,3	2,85

Throughfall exclusion was conducted from beginning of 2014 to end of 2018, number of trees (*N*), mean diameter at breast height in 2022 (*DBH*₂₀₂₂, mean ± 1 SD), mean height in 2018 (*h*₂₀₁₈), annual basal area increment (*iba*) for Preperiod, Droughtperiod, and Postperiod, respectively, ratio between *iba* in 4-year Postperiod and the 5-year Droughtperiod represents the recovery

Fig. 3 Current annual volume increment (m³ ha⁻¹ year⁻¹) at stand-level of spruce (a) and beech (b) on TE plots (solid line, filled marks) compared to the CO plots (dashed line, empty marks). The drought in 2003, the beginning of throughfall exclusion in 2014 and the end of the experimental drought-period with irrigation in mid-2019 are highlighted by vertical lines



the end of the growing season of each year from 2009 to 2022 were included. Then, radial stem growth and basal area growth were calculated for each year. Starting from the basal area, we have calculated the relative growth rate of each tree for our further analyses.

Data analysis

The relative growth rate (RGR) is a standard for describing the growth rate of an organism or a population over a certain period of time. According to plant physiology, we can assume that the increase in the dimension of a plant is more or less proportional to the already existing plant dimension. Different from absolute growth indicators, RGR allows us to compare the growth rates of different organisms or populations, even if they grow under different conditions or with different initial sizes. This makes it possible to compare growth rates of different locations or to assess the effects of environmental factors, e.g. changes in temperature or precipitation on growth rates. To evaluate ecological responses to disturbance, it can also be applied, allowing comparison of the magnitude and duration of the effects on growth. RGR is defined as the natural logarithm of the difference between the final value (e.g. biomass or size) and the initial value, divided by the time interval between the two measurements. In the case of plant growth from one year to the next, RGR can be calculated as follows, according to (Harper 1977):

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where \ln is the natural logarithm and W_1 and W_2 indicate plant biomass at the times t_1 and t_2 . In our case W_1 and W_2 are defined as the trees basal area from last year and from the actual year divided by 1. Based on the annual RGR values from 2009 to 2020, the following models have calculated the mean periodic RGR for each individual tree of the *CO* and the *TE* plots for each of the three different experimental periods (*Preperiod*, *Droughtperiod* and *Postperiod*) separately. When we talk about RGR in the following text, we always refer to RGR on the basis of basal area and use the unit $\text{mm}^2 \text{year}^{-1}$.

A general index for assessing tree growth reaction after drought is Recovery, $\text{Rc} = \text{PostDr}/\text{Dr}$ (Lloret et al. 2011). Recovery describes the tree growth response after the drought. This approach to measure the recovery is well suited to study singular, naturally occurring drought years. In our case, this index was less suitable for a drought period. Here, we fixed and distinguished different effects (1. general period effect and 2. pure drought stress effect due to a five-year extended drought) and then compared them with the *CO*. Therefore, we have chosen a post hoc test method to prove the recovery of *TE* spruce from the general period

effect of *Droughtperiod* and to show that there was no recovery from the effect of throughfall exclusion.

Mixed linear models for quantification of the growth effects and the recovery after extended experimentally induced drought and subsequent irrigation (Q1)

The analysis of possible improvement in growth (recovery) after throughfall exclusion and subsequent irrigation was performed separately for spruce and beech (Q1, H₀1). In order to test for significant effects, we fitted a mixed linear model that describes the dependency of the RGR on the experimental period and group affiliation (*CO*, *TE*) of a tree:

$$\begin{aligned} \text{RGR}_{ijk} = & a_0 + a_1 \times \text{Treat}_i + a_2 \times \text{Droughtperiod}_{ijk} \\ & + a_3 \times \text{Postperiod}_{ijk} + a_4 \times \text{Treat}_i \\ & \times \text{Droughtperiod}_{ijk} + a_5 \times \text{Treat}_i \\ & \times \text{Postperiod}_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned} \quad (1)$$

The indices i , j and k represent the nesting levels of the plot, the tree within the plot and the experimental period (*Preperiod*, *Droughtperiod*, *Postperiod*), respectively. *Droughtperiod* and *Postperiod* are dummy variables that have the value 1 in *Droughtperiod* and *Postperiod* and 0 otherwise. The variable *Treat* is also a dummy variable which is 1 for all *TE* plots and 0 for the *CO* plots. As described in Eq. 1, the dependency of the RGR in the periods (*Preperiod*, *Droughtperiod* or *Postperiod*) and treatment groups (*CO* or *TE*) as well as the interactions of these attributes was investigated. This approach allowed us to distinguish periodic effects that occurred on the *CO* plots as well as on the throughfall exclusion plots from the actual effects of drought stress. In other words, the fixed effect parameters a_0 to a_5 contain the information required to reconstruct the expected RGR's of the *CO* and *TE* trees in the different periods of the experiment and to test them and their differences post hoc for significance. As correlations of the observations on the plot level, and also on the tree level have to be taken into account, the model includes the random effects b_i and b_{ij} ($b_i \sim N(0, \tau_1^2)$, $b_{ij} \sim N(0, \tau_2^2)$). The term ε_{ijk} represents independently and identically distributed errors ($\varepsilon_{ijk} \sim N(0, \sigma^2)$). Using simultaneous post-hoc tests for general linear hypotheses (Hothorn et al. 2008), we tested whether recovery from drought stress had occurred.

Mixed linear models for Quantification of the effects of intra- and inter-specific competition (Q2)

To detect the differences in growth and recovery between trees growing in inter-specific and intra-specific competition, the analyses were conducted for both tree species and

treatment groups separately (Q2, H₀2). This was also tested for the *CO* trees due to the coincidental occurrence of a natural drought in 2015 during the *TE* period. To test for significant effects, we fitted a mixed linear model similar to the first one. The model describes the dependency of the RGR on the experimental period and group affiliation of a tree, as well as the interaction of these attributes:

$$\begin{aligned} RGR_{ijk} = & a_0 + a_1 \times Mix_{ij} + a_2 \times Droughtperiod_{ijk} \\ & + a_3 \times Postperiod_{ijk} + a_4 \\ & \times Droughtperiod_{ijk} \times Mix_{ij} + a_5 \\ & \times Postperiod_{ijk} \times Mix_{ij} + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned} \quad (3)$$

The indices and the period variables are defined the same as in Eq. 1. The variable *Mix* is a dummy variable that is 1 for all trees that grew in inter-specific competition and 0 for those that grew in intra-specific competition. By separately applying this model to the *CO* and *TE* trees of the two species, we were able to distinguish the periodic effects that occurred within the treatment groups from the effects of the intra-specific or inter-specific competition. The procedure for determining the expected RGRs is the same as described for Eq. 1. Correlations of observations on the plot level and also on the tree level have been considered by including the random effects b_i and b_{ij} ($b_i \sim N(0, \tau_1^2)$, $b_{ij} \sim N(0, \tau_2^2)$). The term ε_{ijk} represents independently and identically distributed errors ($\varepsilon_{ijk} \sim N(0, \sigma^2)$).

Mixed linear models for Quantification of the shift in growth performance depending on the relative size of trees (Q3)

To determine a possible influence of the tree's relative size on their growth reaction during the three experimental periods and to compare the growth in *Droughtperiod* and *Postperiod* regarding a possible growth improvement, the analyses for both tree species and treatment groups were conducted separately (Q3, H₀3). Relative tree size was chosen as an appropriate measure for a stable social tree classification throughout all observation periods. It includes on the one hand the information on the diameter, which correlates well with the social position of a tree in the stand (Pretzsch 2021), but also eliminates the absolute diameter change that the trees underwent over the three periods. By calculating the periodic diameter percentile of each tree within its species and treatment group, each tree was given a value between 0 (smallest diameter) and 1 (largest diameter) for each of the three periods. Assuming that an inert measure such as diameter is barely affected by short-term fluctuations between “top and bottom performers”, we have chosen the percentile of the periodic mean of the diameter. Hence, we considered the relative tree size in

the long run. Using this concept to contrast the growth of trees of different social positions before, during, and after the drought-period, we fitted the following model that describes the dependency of the diameter increment on the experimental period and the relative tree size (percentile 0 to 1), as well as the interaction of these variables:

$$\begin{aligned} id_{ijk} = & a_0 + a_1 \times Perc_{ij} + a_2 \times Droughtperiod_{ijk} \\ & + a_3 \times Postperiod_{ijk} + a_4 \times Perc_{ij} \\ & \times Droughtperiod_{ijk} + a_5 \times Perc_{ij} \\ & \times Postperiod_{ijk} + b_i + b_{ij} + \varepsilon_{ijk} \end{aligned} \quad (3)$$

The indices and the period variables are defined the same as in Eqs. 1 and 2. The variable *Perc* is the diameter percentile that takes values between 0 and 1. A look at the variables in our model shows both: on the one hand, how the increment level changes due to the treatment in the different periods, and with regard to the interaction of diameter percentile (*Perc*) and the two periods (*Droughtperiod* and *Postperiod*) on the other hand, whether the slope changes significantly. This provided a way to determine the growth reaction in the three experimental periods and also made it possible to assign this reaction to trees of different relative tree size. In our model, the parameters a_0 , a_2 and a_3 provide the information about the increment of the smallest trees during *Preperiod*, *Droughtperiod* and *Postperiod*. The parameters a_1 , a_4 and a_5 reflect the growth of the trees with the highest relative tree size in the three experimental periods. Correlations of tree diameter increment on the plot level and also on the tree level have been considered by including the random effects b_i and b_{ij} ($b_i \sim N(0, \tau_1^2)$, $b_{ij} \sim N(0, \tau_2^2)$). The term ε_{ijk} represents independently and identically distributed errors ($\varepsilon_{ijk} \sim N(0, \sigma^2)$).

The statistical programming language R 4.0.2 (R Core Team 2020) was used for all calculations, in particular we used the *lme* function for regression analyses from the package *nlme* (Pinheiro et al. 2021) and *glht* from the package *multcomp* (Hothorn et al. 2008).

Results

Description of the reaction patterns at the stand and tree level

The annual volume increment at the stand level showed a notable decrease on the *TE* plots for spruce and beech (Fig. 3). Over *Droughtperiod* a loss of growth of 34.4 m³ ha⁻¹ for spruce and 18,7 m³ ha⁻¹ for beech accumulated at the stand level. This corresponds to a loss in increment of 59% for *TE* spruce and 42% for *TE* beech to their respective *CO*. Upon drought release due to irrigation, *TE* beech trees in particular showed a clear increase in volume growth. *TE*

spruces did not show a clear upward trend in volume growth (Fig. 3a) and did not reach the level of *CO*. The growth of the *TE* beech stand almost reached the level of the *CO* plots after irrigation (Fig. 3b).

In the years before throughfall exclusion, the diameter increments of the trees, which were later assigned to the *TE* and the *CO*, were almost the same. Throughfall exclusion resulted in a noticeable decrease in the diameter increment of spruce and beech trees on *TE* plots (Fig. 4, solid line) compared to the *Control* (dashed line). With the beginning of the throughfall exclusion, the diameter increments of spruce fell on average steeply below the level of the *Control* and then stabilized at a low level of about 34% of the diameter increment of the *CO* group. With the start of irrigation, *TE* spruces noticeably recovered but remained clearly behind the *CO* trees. In 2022, both the *TE* and *CO* spruces experienced a natural drought. Despite this, the *TE* spruces showed an increase in growth, while the *CO* spruces showed a decrease. Consequently, the growth differences between *TE* and *CO* spruces were not significant in this year, indicating a recovery of the *TE* group. The diameter growth of

the *TE* beech trees decreased to about 56% of the diameter increment of *CO* beeches. As a clearly recognizable acclimation, the growth recovery of *TE* beeches began even before irrigation started in 2019 and the diameter increment of the *TE* beech almost reached the level of the *Control* already in 2019.

Growth reaction to extended drought and recovery after irrigation (Q1)

The regression model (Eq. 1) shows the growth reaction during and after the drought (SI-Table 1 upper part, SI = Supplementary Information; Fig. 5). The estimated mean RGR indicated a decline of tree growth on the *TE* plots (Fig. 5, solid lines) for both tree species and became evident as the experimental drought set in. Before the beginning of the throughfall exclusion, the periodic RGR for *CO* (dashed lines) and *TE* spruces was almost identical (Fig. 5a). In the case of beech trees (Fig. 5b), the two groups were also close during *Preperiod* and did not differ significantly (SI-Table 1 upper part). The *TE* spruces grew

Fig. 4 Mean annual diameter increment (mm year⁻¹) at tree-level of spruce (a) and beech (b) on the *TE* plots (solid line, filled marks) compared to the *CO* plots (dashed line, empty marks) ± CI (error bars). The drought in 2003, the beginning of throughfall exclusion in 2014 and the end of the experimental drought-period with irrigation in mid-2019 are highlighted by vertical lines and gray shading. The years of the periods that showed significant differences in the post-hoc tests are marked with asterisks

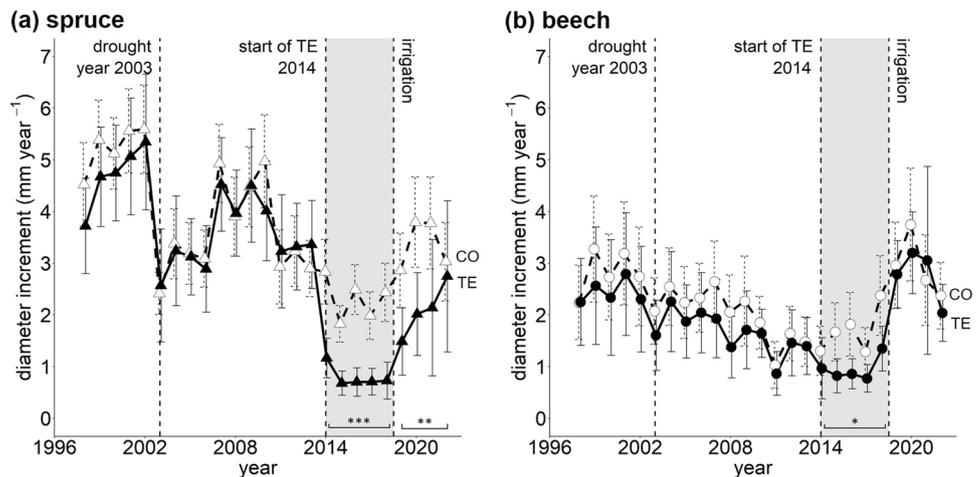
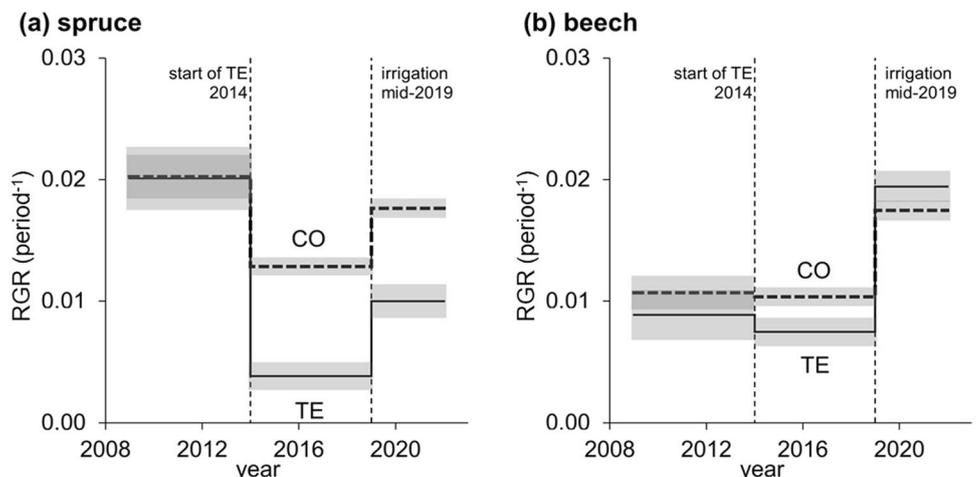


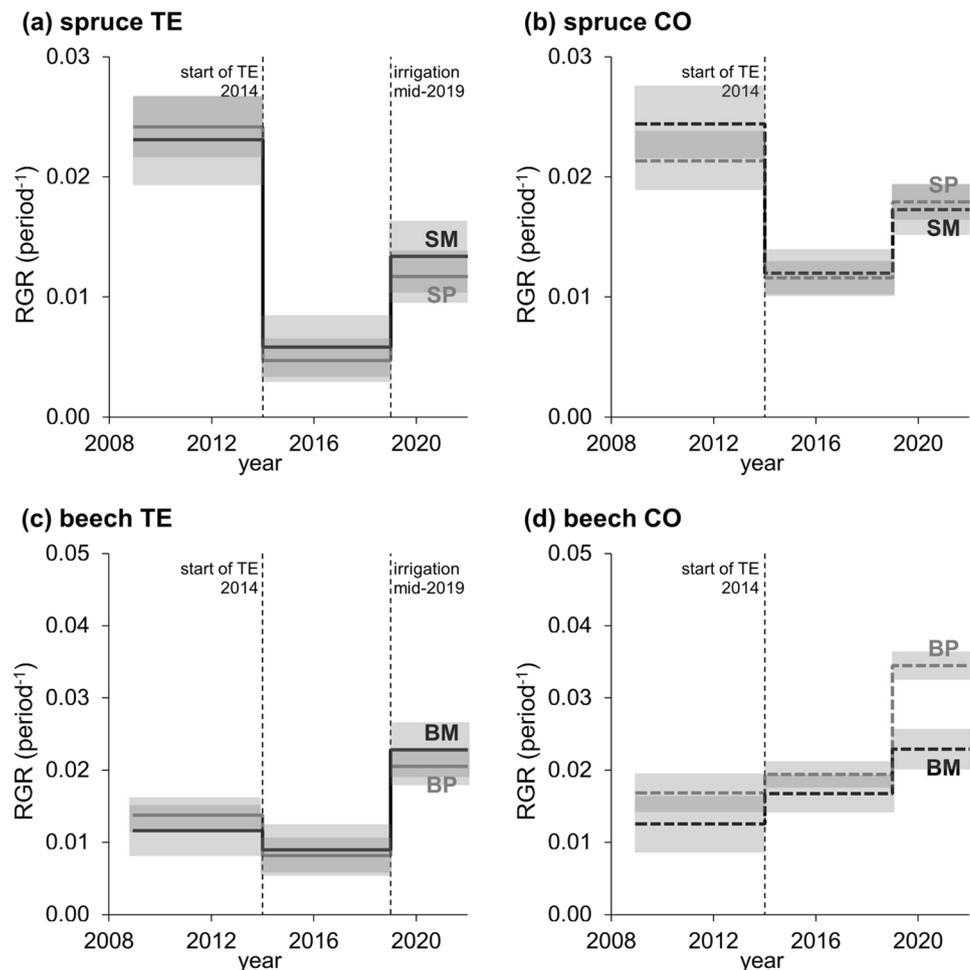
Fig. 5 Periodic relative growth rate (RGR) ± 1 SE (gray shading) estimated by the mixed-linear model shown in Eq. 1 Spruce (a) and beech (b) on the *TE* plots (solid line) compared to the *CO* plots (dashed line). The beginning of throughfall exclusion in 2014 and the end of the drought-period with irrigation in mid-2019 are highlighted by vertical lines



significantly less ($p < 0.05$) during the drought as well as after the irrigation ($n = 95$, mean 0.0038 ± 0.0012 ; $n = 53$, mean 0.0100 ± 0.0015), than the *CO* trees in the same periods ($n = 130$, mean 0.0128 ± 0.0008 ; $n = 102$, mean 0.0176 ± 0.0009). Thereby, the growth of the *TE* trees fell far below the level of *CO*, however, due to subsequent irrigation in mid-2019, spruce showed a recovery reaction in relative growth on the *TE* and *CO* plots (Fig. 5a). In the lower part of SI-Table 1, we show the results of the Simultaneous Tests for General Linear Hypotheses which were performed post hoc. Relative growth of the *TE* spruces deviated significantly from the *CO* spruces during the throughfall exclusion ($\Delta Droughtperiod = -0.0092 \pm 0.0027$). The deviation from *TE* to *CO* was less distinct in *Postperiod* ($\Delta Postperiod = -0.0078 \pm 0.0028$). Even though the relative growth of *TE* spruces showed a slight recovery compared to the *CO* spruces, this response was not significant. In relative terms, during *Droughtperiod*, the *TE* spruces lost 70% of relative growth (RGR) compared to the *Control*. In *Postperiod*, the relative growth loss was 43% compared to the *Control*. Beech *TE* trees in *Droughtperiod* ($n = 125$, mean 0.0075 ± 0.0012)

had significantly reduced growth ($p < 0.05$) compared to the *CO* trees ($n = 151$, mean 0.0104 ± 0.0008). The relative growth rate of *TE* beech trees differed significantly from *CO* beeches during the throughfall exclusion ($\Delta Droughtperiod = -0.0047 \pm 0.0021$) but no longer in *Postperiod*. Therefore, the *TE* beech trees showed significant recovery after irrigation compared to the *CO* group ($\Delta Droughtperiod - \Delta Postperiod = 0.0049 \pm 0.0013$). The *Control* beeches showed an increase of 69% in their growth performance in 2019–2022 (Fig. 5b). Beech on the *TE* plots slightly decreased in RGR during the throughfall exclusion (compared to *CO* -28%), increased impressively by 160% compared to its own growth performance during *Droughtperiod* and overtook beech on the *CO* plots by 11% due to its subsequent strong recovery in *Postperiod*. A direct comparison of spruce and beech (Fig. 5a and b) shows the obvious difference in the *Preperiod* between the two tree species in terms of growth performance. During *Droughtperiod*, spruce on the *TE* plots already fell below the level of beech. In contrast, the beech trees on the *TE* plots and the *CO* plots were able to catch up with spruce

Fig. 6 Periodic relative growth rate (RGR) ± 1 SE (gray shading) estimated by the mixed-linear model shown in Eq. 2. Spruce (a and b) and beech (c and d) on the *TE* plots (solid line) and on the *CO* plots (dashed line) separately. The growth of both species in inter-specific competition (black line; for spruce = SM, for beech = BM) is compared to intra-specific competition (grey line; reference for spruce = SP, reference for beech = BP). The beginning of throughfall exclusion in 2014 and the end of the drought-period with irrigation in mid-2019 are highlighted by vertical lines



in growth rate due to their strong recovery responses in the four years following irrigation.

Effects of intra- and inter-specific competition on tree growth and recovery (Q2)

The results of our regression model fits (Eq. 2) show the intra- and inter-specific response patterns during and after the drought period, respectively (SI-Table 2; Fig. 6). The *TE* spruce trees showed significant decreases in RGR for *Droughtperiod* and *Postperiod*. It should be noted here that when fitting the model to the *TE* group alone, these effects obviously include information about experimental through-fall exclusion. The model fit for the *CO* trees showed the effect of *Droughtperiod* and *Postperiod* due to a significant but less pronounced decrease in RGR. In both groups, intra- and inter-specific competition showed no effect on the relative growth of spruce. Effects in *Droughtperiod* and *Postperiod* also affected the growth of the *TE* beech trees as shown by a significant decrease of RGR in *Droughtperiod*

and a subsequent significant increase in *Postperiod*. For the *CO* beech trees, the model fit fixed an effect in *Postperiod* that was due to a significant increase in relative growth. Only beech trees of the *CO* group showed a significant effect in growth ($p < 0.05$), caused by the inter-specific competition (Fig. 6d). In *Postperiod*, beech mixed with spruce (*Mix = BS*) grew significantly less ($n = 48$, mean 0.0229 ± 0.0029) than beech next to beech ($n = 48$, mean 0.0345 ± 0.0021). Even though the model showed almost no significant differences between inter- (*SM = spruce mixed, BM = beech mixed*) and intra-specific (*SP = spruce pure, BP = beech pure*) competition, the model fits gave a good indication of trends on how the mean RGR estimated by the mixed-linear model is distributed among the groups (Fig. 6).

Growth reaction and shift of the growth performance depending on the relative tree size during the three experimental periods (Q3)

SI-Table 3 shows the results of fitting the regression models for absolute growth response in diameter increment before

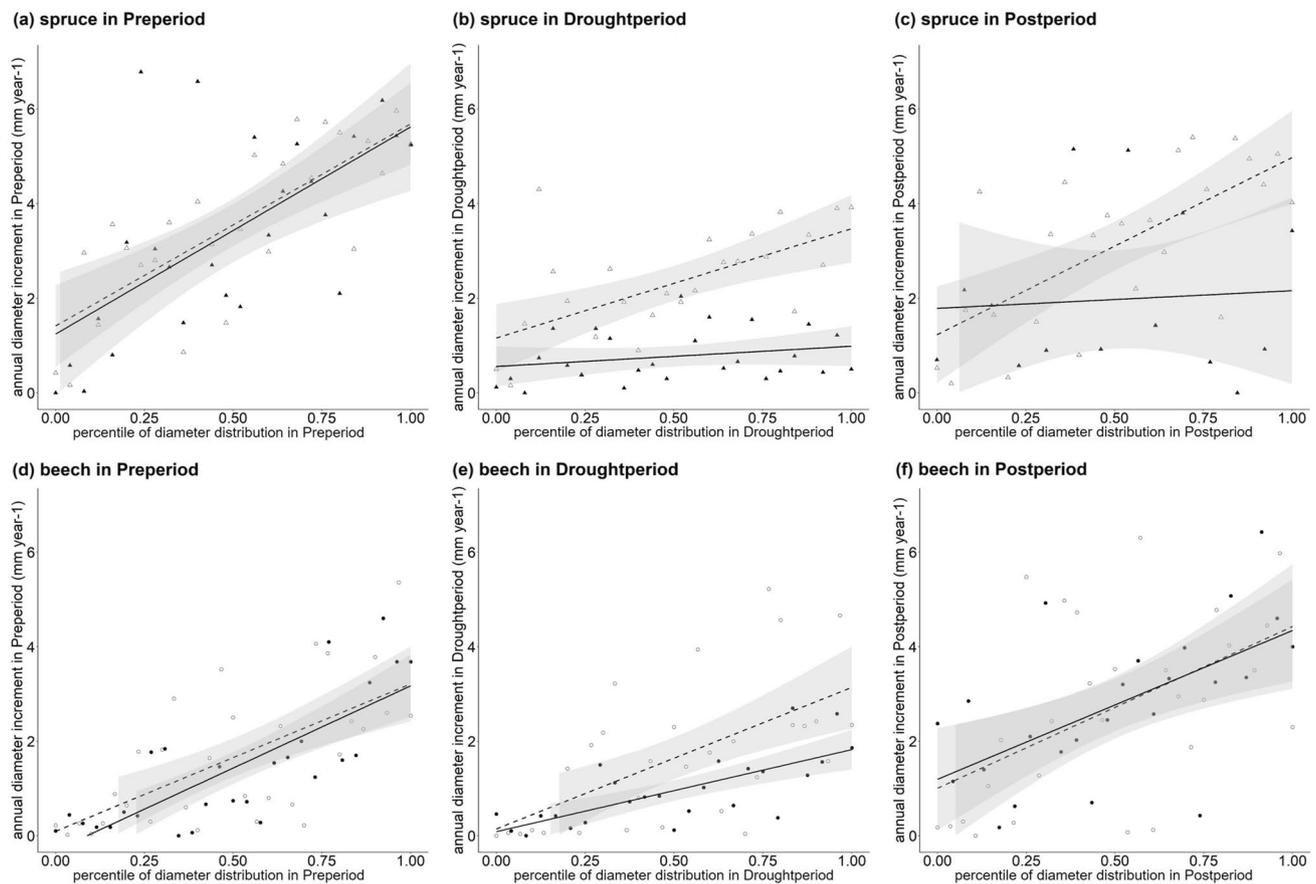


Fig. 7 Mean periodic diameter increment (mm year⁻¹ period.⁻¹) plotted over the percentile of stem diameter in the three experimental periods (*Preperiod* 2009–2013, *Droughtperiod* 2014–2018 and *Post-*

period 2019–2022) for spruce (a, b, c) and beech (d, e, f), on the *TE* plots (solid line, filled marks) and the *CO* plots (dashed line, empty marks) ± 1 SE (gray shading)

and after the drought period depending on the relative tree size (Eq. 3). By applying the model fit to the *TE* trees of the two species, the variables *Droughtperiod* and *Postperiod* showed how the growth level changed during and after the drought as a result of the treatment. The interaction with the variable *Perc* provided additional information on whether the slope of the regression in *Perc*, and thus the increment distribution changed over the relative tree size. The growth reaction along the relative tree size in Kranzberg confirmed that *TE* spruce lost growth during and after extended drought stress (Fig. 7a, b and c; intercept on the y axis, solid line, filled marks). Moreover, the significant decrease in slope indicated that the trees with a high relative size were most striking in this growth reaction. This decrease became evident from the interaction of the variables *Droughtperiod* and *Postperiod* with the variable *Perc* (a_4 and a_5 in SI-Table 3). During *Droughtperiod*, the diameter increments of the *TE* spruce tree with the highest relative tree size (1.6571 ± 0.7249) decreased compared to *Preperiod* (5.5127 ± 0.7871). Similarly, during *Postperiod* (1.2821 ± 0.9023), the diameter increments of the tree with the highest relative tree size decreased even more compared to *Preperiod*. Spruce trees with a low relative tree size did not lose much growth during the drought period, slight deviations (n. s.) were compensated after the drought. Thus, the flattening of the curves for *TE* (Fig. 7 b and c) must mainly be attributed to a decrease in the increment of the dominant spruce trees in the stand. For *CO* spruce the slope of the curves, and thus the distribution of increment performance across the relative tree size remained largely the same (Fig. 7a, b and c; dashed line) and trees showed no significant deviations in *Droughtperiod* and in *Postperiod* (SI-Table 3). Beech *TE* showed a slight decrease (n. s.) in the growth of the individuals with a high relative tree size during extended drought stress (Fig. 7e; solid line). Beech trees with a low relative tree size also did not deviate much in growth during extended drought but increased their growth after the drought period (Fig. 7f; solid line), as evidenced by a significant increase in overall growth level (a_3 in SI-Table 3). That is why the *TE* beech tree with the lowest relative tree size showed a significant higher diameter increment in *Postperiod* (2.3312 ± 0.5347) than in *Preperiod* (-0.4876 ± 0.4626). The tree with the highest relative tree size increased little but significantly in diameter growth from *Preperiod* (3.2802 ± 0.7929) to *Postperiod* (3.2556 ± 0.9077 ; a_5 in SI-Table 3). The apparent flattening of the curve is mainly due to the increase in growth among the smaller beech trees in the stand. In other words, the strong recovery of *TE* beech from *Droughtperiod* to *Postperiod* is characterized by a slight increase in growth for individuals with a high relative tree size but mainly by a strong increase in growth of trees with a low relative tree size. This is also reflected in Fig. 7d–f. Here we have seen

that in *Preperiod* mainly the dominant beech trees showed an increase in diameter, and many small beech trees showed a zero-growth. In *Postperiod*, more individuals achieved a measurable growth, the number of individuals with zero-growth decreased, and especially the *TE* beech trees with a low relative tree size became "high performers" in the stand. In contrast, many *CO* beech trees with low relative tree size remained at the bottom end of diameter increment. The *CO* beech tree with the lowest relative tree size showed a significant deviation from *Preperiod* (-0.1823 ± 0.4793) to *Postperiod* (1.0244 ± 0.3883 ; a_3 in SI-Table 3). Thereby, the growth level of all *CO* beeches increased. However, the slope of the curves and thus the distribution of the growth performance along the relative tree size did not change for *CO*.

Finally, our results can be summarized as follows: During 5 years of experimentally drought, beech suffered less than spruce in tree growth and recovered faster than spruce trees under controlled irrigation after the drought period. Spruce trees subjected to experimental drought continued to deteriorate compared to *Control* even after irrigation. During the drought period, but also after irrigation, we did not detect significant differences in growth due to throughfall exclusion, depending on intra- or inter-specific competition, but were able to see trends. Due to a shift in the growth performance along the relative tree size in the stand, growth reductions of the previously best-performing trees were partly compensated by an increased growth of the trees with lower relative tree size.

Discussion

Growth reaction and acclimation to extended drought and recovery after irrigation (Q1)

A five-year extended drought caused significant growth losses in both, spruce and beech (Fig. 5), but after irrigation spruce showed a delayed recovery (n.s.) while beech showed a strong and early recovery in the first two years (SI-Table 1, Fig. 4b). This may be interpreted as better acclimation of beech to drought, and as an indicator for serious damage on spruce, as described in recent studies (Arend et al. 2021; Bottero et al. 2021). In 2022, both *CO* and *TE* spruce and beech trees experienced a natural drought (see materials and methods section, SI-Fig. 1) which did not reduce the growth of *TE* spruce, while *TE* beech growth declined continuously, following the first year of recovery, as did *CO* spruce and beech trees (Fig. 4a). In summary, our null hypothesis H_0 1 was rejected as we showed species-specific growth and recovery from drought upon irrigation for spruce and beech. Our insights on the different drought response of spruce and

beech align with recent research that highlighted the role of nutrient regime, drought frequency, and hydraulic conditions in previous and subsequent years as critical factors in the drought response of these species (Schmied et al. 2023). This study linking higher drought frequency with increased resistance and resilience of spruce and beech provides an additional perspective that complements our focus on the effects of a prolonged five-year drought.

Kannenberg et al. (2019b), Kannenberg et al. (2019a) and Ruehr et al. (2019) discussed that drought stress responses may persist beyond the drought itself. Ovenden et al. (2021) showed that those responses did not solely negatively affected growth if longer post-drought periods were chosen or, as in our study, another drought event followed. Based on the different hydraulic functions introduced by McDowell et al. (2008), spruce (isohydric) and beech (anisohydric), two abiotic mechanisms i.e. carbon starvation and hydraulic failure are discussed as the causes of growth decline and tree mortality under drought (Adams et al. 2017; Hartmann 2011; McDowell et al. 2008, 2019; Sevanto et al. 2014), which also can occur in combination (Adams et al. 2017) and possibly even relate to each other (Kannenberg et al. 2019b).

Spruce, with its more conservative isohydric strategy, reduces acute water loss by closing its stomata (Vogel et al. 2017; Zavadilová et al. 2023). This mechanism can cause carbon starvation and occurs more frequently in gymnosperms than in angiosperms, which can also be associated with the hydraulic vulnerability of the xylem, thereby playing a role in reducing hydraulic function (Adams et al. 2017) and may also inhibit the long-term growth of new supply structures. It is possible that spruce thereby was unable to recover quickly when water became available again (Choat et al. 2018; Wu et al. 2018).

But delayed recovery after disturbance does not necessarily imply impaired function, and may also be a sign of acclimation reactions at the expense of growth (Gessler et al. 2020). Possible mechanisms of spruce may be hydraulic acclimations of leaves and branches, due to an increased hydraulic safety and decreased productivity (Tomasella et al. 2018). Such negative growth legacies were also discussed by Gessler et al. (2020) as possible positive acclimation responses and thus as long-term survival strategies of the tree with regard to future drought events. Also acclimations of root growth (Brunner et al. 2015; Gao et al. 2021), or crown morphology might fall under such mechanisms. We assume that the Norway spruce *TE* trees benefit from their xeromorphic needles and bark built in the years of the experimental drought period. Those needle cohorts are still maintained several years after the end of the experimental drought, whereas in the case of beech the newly built leaves and branches do not have this morphological acclimation (Pretzsch et al. 2021). In addition, the leaf area reduction,

shortening and xeromorphic anatomy of needles (Gebhardt et al. 2023) and xylem vessels with small diameters (Levionnois et al. 2021) built by the dried-out Norway spruces may have reduced the risk of embolism in the natural drought period 2022.

Beech follows the more "risky" anisohydric strategy regarding water consumption by leaving the stomata open, even when the water supply decreases, which can lead to hydraulic failure already after short periods of intense stress (Hesse et al. 2023; Petřík et al. 2022). Hydraulic failure can occur during a drought when the tree loses more water through its leaves than can be replenished by the roots (Brodribb et al. 2020; Choat et al. 2012).

In line with the anisohydric strategy, Nikolova et al. (2009) showed that under drought, beech was able to assimilate more carbon and invest it in stem and root growth than spruce. Our research confirms the advantage of beech in terms of relative stem growth not only under mild to moderate drought but also under severe and prolonged (five years) drought. This could be a possible explanation for the specific recovery reaction of beech and also the interesting detail that its recovery was already indicated during the drought period, even before the opening of the roof and the start of irrigation (Fig. 4b). Beech suffered less within the experimental drought period, probably took up deeper water than spruce, reduced probably less the xylem vessel diameters and thus is more prone to xylem failure under repeated drought events (Petit et al. 2022). The increased die-off of spruce on some *TE* plots during the drought period and the associated reduced stand density may also have contributed to the strong recovery of beech (Pretzsch et al. 2020a). The mortality of neighbors allowed more soil water to be used by the remaining individuals (SI-Fig. 1). This may have caused the two systems of beech and spruce to diverge, as spruce no longer absorbed water and the soil actually became wetter (especially in the plots where trees died). SI-Fig. 1 indicates that from 2017 onwards, the soil water content increased as well on the *TE* plots. The beeches may have shown fewer stress symptoms during the experimental drought, possibly due to the spruces no longer taking up water or the beech trees rooting deeper.

In addition, also more indirect drought effects such as a change in the composition of the microbiome may be considered as acclimation (Gao et al. 2021). As the stands have not been thinned for more than 20 years silvicultural interventions may be excluded as possible causes for a modified resistance and recovery under drought stress (Pretzsch 2022).

It should be mentioned that Fig. 5 shows an increased growth rate for both beech groups from 2019 onwards. This increase, also for *CO*, is likely due to a coincidental accumulation of relatively dry years during the experimental *Droughtperiod* 2014–2018 (see the temperature to

precipitation ratio in Fig. 2). In consequence, both groups experienced increased growth from 2019. Both spruce groups, including *CO*, suffered significant growth losses between 2014 and 2018, so a recovery phase was required after 2019 to compensate for these losses. One possible explanation could be that beech is benefiting from spruce's competitive weakness in the medium to long term. While spruce struggles in the *Postperiod*, beech could gain an advantage by using nutrients and water that would have otherwise been consumed by spruce. This could lead to an increase in growth for beech, which would indicate a shift in growth from spruce to beech. From this perspective, the naturally dry conditions between 2014 and 2018 may have resulted in less resource consumption by spruce, potentially favoring beech due to increased resource availability.

Effects of intra- and inter-specific competition on tree growth and recovery (Q2)

Spruce and beech tended to grow more in inter-specific than in intra-specific competition (n. s.) during a five-year extended drought (Fig. 6a and c) and tended to grow less in inter-specific competition than in the intra-specific competition under *CO* conditions with only beech showing significant differences (Fig. 6b and d). We observed a trend that for spruce the mixture appears to be more important during recovery after the extended drought stress than during the actual drought period itself. Thus, our null hypothesis H_02 was clearly rejected for the *TE* trees, but we showed tendencies of specific effects of competition (inter- vs. intra-specific) on the recovery from drought which was in addition tree-species-specific.

Previous studies have addressed species-specific stress reactions of trees in monocultures compared to mixed stands (Bello et al. 2019; Pardos et al. 2021; Schwarz and Bauhus 2020; Vergarechea et al. 2021). In many cases, an improved stress response has been confirmed by an increased growth in tree mixture (Ammer 2019; Pretzsch et al. 2013). Such benefits of mixture may depend on stand density, site conditions (Lévesque et al. 2016; Steckel et al. 2020b), species combination (Grossiord et al. 2014; Grossiord 2018; Steckel et al. 2020a), and mixture proportion, among other factors (Pretzsch et al. 2020b), and may be reversed to a disadvantage when the stress factor is diminished (Pretzsch et al. 2015a). Temporal complementarity in water uptake may explain the slight reduction of stress reaction in Kranzberg for *TE* spruce and beech in mixture (Rötzer et al. 2017), which could benefit both tree species by avoiding simultaneous water demand of conspecifics that occurs in the pure stand (Thurm et al. 2016). Relatively, spruce benefited slightly more from the mixture than beech during the drought (Fig. 6a and c), as it started transpiration earlier and used soil water first under inter-specific competition,

which was partially replenished in winter (Pretzsch et al. 2020a). By the end of the throughfall-exclusion and start of irrigation, soil water was able to recover from mid-2019, about three months earlier than during the five-year drought. Thus, in relative terms, spruce was better able to exploit its advantage of earlier water uptake in the following spring. The shallow fine roots of the spruces probably enabled them to access winter precipitation, but also irrigation in summer 2019, earlier than the deeper-rooted beeches. At least in the mixed zone of plots, Zwetsloot and Bauerle (2021) were able to verify that there was increased production of fine roots, whereas drought drastically reduced fine root production by spruce in the species-pure zone. Thus, the species complementarity could explain why spruce in the SM constellation continued to benefit more than beech in the BM constellation during and after the drought, even though these differences were not significant and could only be assumed visually. To prevent the spruces against bark beetle attack we started in 2015 annually spraying of the spruce crowns and stem surfaces with the contact insecticide Karate Forst liquid using the canopy crane. Without this measure, the drought damages on the plots may had been worse as drought can increase the susceptibility of spruce to insect attacks (Netherer et al. 2019). However, many studies (Jactel 2017; Skatulla 1989; Wermelinger 2004) show that tree species mixing can increase the resistance of Norway spruce against biotic disturbances e.g., bark beetle (*Ips typographus* L.) or gregarious spruce sawfly (*Pristiphora abietina* (Christ.) (Hym., Tenthredinidae)). And according to the growth-differentiation balance hypothesis (Matyssek et al. 2012) the continuous drought on the *TE* plots may have increased the trees' resistance against biotic disturbances (Nardi et al. 2023).

Growth reaction and shift of the growth performance depending on the relative tree size of trees during the three experimental periods (Q3)

In Kranzberg spruce trees with high relative tree size were most affected by growth losses during and after an extended drought, while beech trees with a high relative tree size showed just a slight decrease in growth during the extended drought. Spruce trees with low relative tree size did not lose much growth at all, while beech trees with low relative tree size increased their growth after the drought period. Now we can better assign the basic growth patterns we checked with H_01 to the relative tree size within the two tree species. The strong decrease in the growth of spruce was mainly caused by the dominant trees, while the strong recovery of beech was mainly caused by a strong growth increase of trees with low relative tree size (Fig. 7a–f). Our null hypothesis H_03 was distinctly rejected as we showed specific effects of the relative tree size (social position)

on growth performance during and recovery from drought which also was tree-species-specific.

Most studies dealing with growth reactions under drought stress are limited to the evaluation of the dominant trees in a stand. Consistent with recent studies like Ding et al. (2017); Pretzsch (2021) and Zang et al. (2012) we have shown that the growth reaction to drought can vary depending on tree size (diameter percentile). In line with other studies like Grote et al. (2016); Pretzsch et al. (2018b) and Pretzsch (2022) we showed that there was a significant shift in growth performance that favoured the smaller trees in the stand which has led to a more size-symmetric distribution of increment across diameter classes. The causal explanation might be that cooler microclimate and less transpiration demand can be expected in the shade-tolerant species, protecting from heat damage and decreasing drought stress (Grote et al. 2016). In dry years, small trees may benefit indirectly from the reduced water consumption of the tall trees, which are more exposed to heat, drought and stomata closure. Thus the growth partitioning may become more size-symmetric in dry years (Schwinning and Weiner 1998; Wichmann 2001) and on dry sites (Pretzsch and Dieler 2011). Under moist conditions, after ending of the experimental drought, large trees can make again use of their preferential access to light, increase their growth and water consumption and thus reduce the growth of smaller neighbors (Grote et al. 2016). This enables a change in competition mode from a more size-symmetric competition during drought to size-asymmetric competition under sufficient soil water supply as also described by Zang et al. (2012). Pretzsch and Biber (2010) and Pretzsch et al. (2022) showed that this may result in more heterogeneous stands under dry conditions or in periods with drought events and more homogeneous stands under moist conditions where the large trees can pre-empt the light and outcompete small neighbors. We observed that this shift occurred not only during drought stress but also in the post-drought period, where mostly the larger spruces lost growth performance, while mainly the small-sized beeches benefited. This is in itself an interesting species-specific redistribution of growth. With regard to the results from H₀I, we saw how the initial growth depression of spruce two years after the drought period occurred primarily in the large trees, and the remarkably good growth in the natural drought year of 2022 was achieved by the smaller trees (Fig. 4a). We also saw that some of the lost growth potential may be transferred to the small sized beech trees after the drought. Therefore, we concluded that in a spruce-beech stand under extended drought stress, the sequence of stress reaction and recovery reaction may lead to a reversal of the previous growth distribution among individuals and thus may have an effect on the vertical structure of future forest stands. Such a relative advantage of small trees results in lower mortality and an accumulation of previously subdominant trees

in the understory (Pretzsch et al. 2018b). Our results are in line with other studies (Chakraborty et al. 2021; Grote et al. 2016) and show that water availability can have a great influence on the structure and dynamics of forest stands. This is not only important for dry ecosystems but is already a common issue in temperate regions and is supposed to get more important under a climate with longer drought periods.

Functional and structural diversification as risk prevention

Under the experimental drought stress, in the phase of stress release, and also under the subsequent natural drought the two species reacted very differently (Figs. 5 and 6). We also found very different reactions on drought stress and stress release in different size classes (Fig. 7). This suggests a functional diversification that may stabilize the function and growth of forest stands (Bauhus et al. 2017; Larsen 1995; Pardos et al. 2021). However, Haberstroh and Werner (2022) recently reported that under extreme drought any synergistic inter-specific interactions may fail.

A silvicultural approach that promotes structural and genetic diversity may not achieve maximum productivity under normal conditions, i.e. without disturbances (Assmann 1970). However, with increasing frequency of disturbances the resistance and resilience by structural and genetic diversification may achieve advantageous productivity, stability and other ecosystem functions and services (Biber et al. 2015; del Río et al. 2022; Dieler et al. 2017). Thus silvicultural may prefer prescription that favour tree species mixture and structural layering, e.g. selection forest systems with 3 or 4 species as risk prevention (Pretzsch and Zenner 2017; Schütz 2001).

The recent commentary by Ulrich and Grossiord (2023) highlights the complexity of tree responses to drought, particularly regarding species-specific strategies for stomatal regulation along the iso-anisohydric continuum. They point out that while anisohydric species are often considered as more drought resistant, this may not always be the case, and that even anisohydric species with higher embolism resistance and hydraulic safety margins may have higher mortality rates than isohydric species that co-occur. Therefore, it is possible that classification of tree species along the iso-anisohydric continuum is not sufficient to fully capture drought vulnerability.

Moreover, Ulrich and Grossiord (2023) describe the potential role of water availability in shaping the structure and dynamics of forest ecosystems. They point out that even in temperate regions, water availability may become a critical factor, which could affect our forest composition. This

evaluation is consistent with our findings on the different responses of spruce and beech to extended drought.

This adds complexity to our understanding of functional diversification and species-specific drought response and underscores the need for a nuanced approach to predicting future forest dynamics under changing climatic conditions.

Considerations and perspectives

In our study, we discussed acclimation in *TE* beech before irrigation, and recovery in *TE* beech and the small *TE* spruce trees after irrigation. A possible, but in our study not considered cause for a recovery reaction might be the sudden availability of nutrients that could not be dissolved in soil water during the drought and suddenly became plant available with the onset of precipitation and irrigation (Gessler et al. 2017). Such mechanism and the question why this then primarily favored the beech trees would have to be further investigated.

Furthermore, it was not certain if the growth reactions were actual acclimation and recovery response or a simple shift of released resources from more suffering individuals to favored individuals. In this scenario, the delayed pattern of benefiting could be explained by the need for favored individuals to access the released resources first.

It should be measured whether crucial parts of hydraulic conduits may occluded by gas emboli and if the trees could not compensate by building up new tissue (Brodrribb et al. 2010). The remaining portion of water-conducting tissue after a drought might also determine how well a tree recovers (Bréda et al. 2006; Choat et al. 2018). A possible advantage of the anisohydric strategy is that beech can still assimilate carbon during drought to form new conductive vessels. Later this may become an additional risk, as these vessels can increase the tree's vulnerability to recurrent droughts (Gessler et al. 2020). Deeper research on the microscale, such as analysis of wood anatomy, would provide further insight.

Besides the limitations discussed, we want to mention that the design of our study did not allow for complete randomisation of the experimental plots due to the species composition. Some control and treatment plots were close to each other, which might affect the generalisability of our results. Despite our efforts to randomly select experimental plots taking into account species composition, future research should aim for even better randomisation to minimise possible bias.

Especially for the study of acclimation effects under drought, long-term experimental manipulation studies like those in Kranzberg are essential and may be useful to complement studies along natural precipitation gradients that taken place before. Together, the Kranzberg through-fall exclusion experiment and the associated precipitation

gradient from the KROOF project may allow us to distinguish drought acclimation effects from long-term adaptations to generally dry site conditions. To date, such field manipulation studies at an ecosystem level as the KROOF experiment are still very rare, but provide new and important evidence on how spruce and beech might respond to future climate. Even if such large-scale experiments are very costly, they contribute significantly to the understanding of trees responses in complex environmental networks.

Conclusion

An important highlight and new insight of our study is a more comprehensive picture of recovery reactions in the growth of mature spruce and beech after a long-term drought for the latitudes of Central Europe. With five years of drought followed by four years of recovery, a complete growth trajectory consisting of pre-, during-, and post-periods has been quantified. We considered not only possible differences in growth reactions in intra- and inter-specific competition of the trees but also differences between dominant and small trees.

In summary, growth reactions to drought are specific to tree species and mixture can influence this reaction, even though in our case only tendencies were observed. Furthermore, the structuring of small to dominant trees has a clear influence on the response of the stand as a whole. A redistribution pattern has emerged in favour of the smaller trees and at the expense of the dominant trees.

According to our results, we assume that spruce is significantly more drought-sensitive than beech during and also after prolonged droughts. Due to the superior recovery response of beech, the generally high productivity of spruce may face increased competitive pressure. This could particularly occur if consecutive drought years became more frequent and the Beech could play out its ability to recover. In conclusion, this could lead to a sustained decrease in the proportion of spruce in future forest ecosystems and its importance in silviculture could decline accordingly. However, its surprisingly good radial growth in the natural drought year 2022 indicated that spruce still has potential due to acclimation, apart from the general recovery. Nevertheless, the volume growth of the *TE* spruce trees remains far below the *CO* trees and the O40 site index line (Fig. 3a), indicating that spruce growth is still limited. Summarizing we conclude that spruce and beech can acclimate to a changed climate with an associated change in water supply even during prolonged drought stress.

Mixing economically valuable spruce with more drought-resistant tree species like beech might balance the needs of economics and ecology. The frequently reported drought stress relief of spruce in mixture is an argument for a

transition to mixed forest stands. Size-symmetric partitioning patterns along the relative tree size due to drought could result in a more even growth distribution and in the long term more heterogeneous stand structures under recurring and persistent drought stress. This may cause and accelerate changes in the distribution, species composition, and vertical structure of forests.

Author contributions statement FM and HP conceptualized the study. FM evaluated the data and wrote the paper. HP and KP initiated the project where the study at hand is embedded in. TR, KP, and HP developed and established the experimental design. HP, PB, EU and TR contributed to evaluating the data and writing the manuscript. HP, PB, EU, TR and KP revised the manuscript and contributed to the interpretation of the results.

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Availability of data and material The materials described in the manuscript including all relevant raw data will be freely available upon request from the corresponding author.

Code availability The R-codes described in the manuscript and designed for statistical analysis are freely available on request from the corresponding author.

Declarations

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

Ethics approval Not applicable.

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Consent for publication Not applicable.

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