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Structural and compositional acclimation of forests to extended drought: results of the KROOF throughfall exclusion experiment in Norway spruce and European beech

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Abstract

Drought effects on tree growth and mortality are widely studied, but scant knowledge exists on its impact on stand density, size variation, or mixing proportions. Grasping drought's influence on structural and compositional diversity is crucial for stand dynamics, ecosystem services, and silvicultural adaptation. We relied on KROOF, a 5-year throughfall exclusion experiment in a mature Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) stand, to analyze its impact on structural and compositional attributes, including Stand Density Index (SDI), Growth Dominance Coefficient (GDC), and species mixing proportion. Our study demonstrates that drought-induced growth reduction and tree loss decreased SDI by 27%, mixing proportion by 41% at Norway spruce's expense, and homogenized stand structure. Furthermore, we reveal that stand density, mixing proportion, and structural diversity were more affected in Norway spruce, stabilizing growth at the stand level. Extended drought significantly altered growth partitioning in favor of smaller trees, with a 70% reduction in growth-size relationship slope and a 157% decrease in GDC. Species-level analysis indicated a stronger partitioning shift towards smaller trees, particularly in Norway spruce. We discuss that longer drought periods may trigger acclimation at tree and stand levels, potentially underestimated when based solely on individual drought years. Sustained stress could induce acclimation across various levels, from the stand to the species cohort, tree, and organ. Maintaining structural and compositional diversity may mitigate future drought stress effects on growth, mortality, and stand structure, as exemplified by the extended experimental drought. We suggest silvicultural approaches better attuned to natural processes amid climate change.

Keywords Extended drought stress · Response of structural and species diversity · Inter-individual growth partitioning · Growth dominance · Mortality · Gini coefficient of tree size distribution · Recovery

Introduction

This study analyzes how extended drought modifies the species and structural diversity of forest stands of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). Knowledge about how drought stress alters the composition in terms of tree species and space occupation of trees of different social classes is essential for understanding and modeling ecosystem dynamics under climate change. For forest management, this knowledge is important to adapt forests to climate change or to stabilize drought-damaged forest stands by silvicultural interventions.

Structural and compositional forest stand diversity has many advantages (Dieler et al. 2017). It matters especially in view of climate change as it implies stabilization and risk distribution (Lindner et al. 2010; Bolte et al. 2009). Diversification of species composition and stand structure are promoted by forest management as they adapt stands to climate change and can also improve other ecosystem services, such as biodiversity, recreational value, or productivity (Hilmers et al. 2020; Schwaiger et al. 2019; Brockerhoff et al. 2017). Many studies show the detrimental effect of drought stress on tree growth (Zang et al. 2011), stand productivity (Rukh et al. 2020), and mortality (Van Mantgem and Stephenson 2007). Much less is known about how drought

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modifies the compositional and structural diversity (but see, e.g., Clark et al. 2016). According to the intermediate disturbance hypothesis (Connell 1978; Fox 1979), drought may promote diversity by reducing the dominance of trees in the upper layer in favor of subdominant con-species or by slowing down the most competitive species in favor of a higher diversity of other species in the same stand. However, drought-induced mortality may also cause a loss of tree species and a reduction of stand density that may promote demixing and homogenization of the stand (Hanberry et al. 2012; Moser et al. 2010).

Key aspects of compositional and structural stand diversity are the stand density, the mixing proportion, the growth partitioning between the trees, and the resulting size distribution. All these characteristics may be modified by drought-induced growth reduction or mortality. Stand density is an essential stand characteristic (del Río et al. 2016). In fully stocked stands, density results from growth and mortality (Dean et al. 2021, Zeide et al. 1991). Stand density co-determines stand growth (Assmann 1970), the available growing space and competition among different species and stand layers (Pretzsch 2014), and thus the growth partitioning between the trees and their mortality (Trouvé et al. 2014). The relationship between stand density and productivity is unimodal (Pretzsch 2005; Zeide 2004); e.g., for Norway spruce and European beech, Assmann (1970) showed that a reduction of the maximum stand density by 10–20% can increase the productivity by about 20%. Reductions beyond this growth-optimal stand density lead to linear productivity losses (Pretzsch 2020). Stand density in terms of SDI, stand basal area, or standing volume decreases along site gradients with decreasing water supply, because growth is lower and mortality rate is higher at sites with low water supply (Allen et al. 2010). This further suggests that drought periods may reduce stand density by lowering growth and increasing mortality (Bradford et al. 2022; Pretzsch and Grote 2023; Rais et al. 2014). A few studies quantify the decrease of stand density due to drought; they highlight that drought-induced mortality and stand density reduction can cause major ecosystem reorganization in the coming decades (Batllori et al. 2020; Clark et al. 2016). However, most of the studies consider individual drought years and neglect the interplay between stand density and productivity that may operate in longer drought periods. Mortality may reduce stand density and subsequently alter growing conditions for the remaining trees (Klos et al. 2009; Van Mantgem and Stephenson 2007). Thus, stand density losses may partly be buffered by individual growth acceleration (Bradford et al. 2022).

Drought may modify mixing proportions to the disadvantage of the species that is growing at the border of its natural distribution. For instance, the KROOF plots are located in the pre-alpine lowlands where Norway spruce grows at the dryness and warmth border of its fundamental niche and can suffer from abiotic (scarce water supply and high temperature) and biotic stress (bark beetle and sawfly), especially in dry years. Furthermore, drought tolerance is species-specific (Niinemets and Valladares 2006). Norway spruce, for instance, is more drought sensitive than European beech (Zang et al. 2014). In mixed stands, one species can mitigate the drought stress of another (Grossiord 2020; Pretzsch et al. 2013), although this cannot be generalized (Forrester et al. 2016). Finally, the mixing proportion (e.g., in terms of stand basal area or SDI proportion) represents the net effect of stand growth and mortality of a species (Pretzsch et al. 2023). Growth may be reduced, and mortality increased, either directly by drought stress or indirectly by pathogens that are promoted by stress and reduce a species' growth and survival (Jactel et al. 2012). Although Norway spruce grows at the border of its natural range on the KROOF plots (Grams et al. 2021; Pretzsch et al. 2014), it was artificially established and kept as an admixture of 30–50% in the stands as it is a fast and straight growing species with high timber quality and economic value under normal growing conditions; the future of this mixture may become questionable under extended drought (Paul et al. 2019).

Understanding how drought alters the growth partitioning between small and large trees is essential to determine its impact on stand structure (Schwinning and Weiner 1998). For Norway spruce, European beech, and common oak, several studies found a greater growth reduction of large than small trees due to summer drought (Zang et al. 2012; Rötzer et al. 2017; Pretzsch et al. 2018, 2022b; Bose et al. 2022). Studies by Pretzsch and Dieler (2011) and Carl et al. (2018) revealed flatter slopes of the growth–size relationships on nutrient-poor than on fertile sites; this suggests that water scarcity may have a similar effect on the growth partitioning between the trees in a stand along spatial gradients of water stress as on temporal changes of water supply. This may result in the frequently found higher structural stand heterogeneity on nutrient-poor compared to fertile sites (Aber et al. 1982; Gracia and Retana 1996; Pretzsch et al. 2022a). Under dry conditions, the growth of large trees is slowed down, which may allow smaller trees to benefit from better light conditions (Pretzsch et al. 2018), causing more heterogeneous stand structures in the long term.

We established our structural analyses on a set of metrics developed for quantification of growth partitioning between trees (Binkley et al. 2006; Wichmann 2001a, b; Pretzsch and Dieler 2011) and structural characteristics of forest stands (del Río et al. 2016; Pommerening 2002; Pretzsch 1997; Gadow et al. 2012). Using such metrics, Binkley et al. (2006) was able to show that in young stands, large trees are dominant in growth; in advanced stand development phases, however, the partitioning can change in favor of small trees. Studies along spatial gradients of decreasing water supply

by Pretzsch et al. (2022a) revealed a partitioning in favor of small trees at the expense of large trees, resulting in a more heterogeneous size distribution within the stand. Under dry condition, this altered partitioning might be attributed due to higher hydraulic stress of larger trees (Grote et al. 2016). The growth partitioning has been quantified by, e.g., growth–size relationships (Wichmann 2001a, b), Gini coefficient of growth, or the Growth Dominance Coefficient (West 2014; Binkley et al. 2006) for individual tree species (Pretzsch and Schütze 2016) and individual drought events (Wichmann 2001a, b). How growth partitioning between trees in a stand is altered by extended drought, how different species respond to prolonged stress and stress release, and how the partitioning is affected by drought-induced mortality is poorly understood.

To find out how extended drought changes stand structure and species composition and how this was caused by drought-related changes in growth partitioning and mortality of the trees, we utilized the throughfall exclusion experiment KROOF. This experiment is located in mature stands of Norway spruce (*Picea abies* [*L.*] Karst.) and European beech (*Fagus sylvatica* [*L.*]) in the Kranzberg Forest in southern Bavaria, Germany (Grams et al. 2021; Pretzsch et al. 2014, 2020). We posed the following three questions:

Q1: How did extended drought modify the compositional and structural characteristics (e.g., the stand density, mixing proportion, growth partitioning between trees, tree size distribution) at the stand level?

Q2: How did extended drought modify the compositional and structural characteristics at the species level (e.g., growth partitioning, tree size equality, growth dominance)?

Q3: How did extended drought modify the growth partitioning between trees of different sizes?

Finally, we discuss the consequences for ecosystem dynamics and forest management. Silvicultural measures, such as thinning from above or mixing regulation, may counteract the drought-induced compositional and structural homogenization and promote stand stabilization against future disturbances.

Materials and methods

The throughfall exclusion experiment KROOF as the empirical base

Here, we introduce only the main characteristics of our study site; for more detailed information, see Grams et al. (2021), and Pretzsch et al. (2020). The Kranzberg Forest (longitude: 11° 39′ 42″ E, latitude: 48° 25′ 12″ N, altitude 490 m a.s.l) is located in Southern Germany, 35 km Northeast of Munich. Here, stands of Norway spruce and European beech grow on luvisols, originating from loess over Tertiary sediments with high nutrient and water supply (Pretzsch et al. 2014; Göttlein et al. 2012). In the Kranzberg Forest, we established the approximately 0.5 ha KROOF experiment with a total of 12 experimental plots (Supplementary Fig. 1). The average plot size was 144 m². Each plot covers Norway spruce and European beech in a mixture. Four years before starting the throughfall exclusion experiment, in 2010, 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. The trenches were lined with a plastic tarp to prevent lateral root growth and lateral water flow between plots (Grams et al. 2021).

After the trees had recovered from trenching for 4 years (Pretzsch et al. 2016), 5 years of throughfall exclusion were conducted from 2014 to 2018 (Grams et al. 2021). For this purpose, the precipitation during the growing season (April to October) was excluded by automatically closing and opening throughfall exclusion roofs for half of the 12 experimental plots (treatment plots). The other six plots served as control (control plots). To replenish soil water storage of the six treatment plots, their roofs were kept open over winter. The throughfall exclusion period ended in 2018. In June 2019, the plots were irrigated, and the roofs were permanently opened (Grams et al. 2021). Irrigation (on control plots + 15 mm, treatment plots + 90 mm) in June and July 2019 and the subsequent roof opening resulted in a rapid convergence of precipitation levels on all plots.

Figure 1 shows that from 1998 until 2013, the year when the throughfall exclusion on the treatment plots started, temperature and precipitation were, on average, 8.1 °C and 841 mm year^{-1}, respectively. Within this time span, the years 2001 and 2002 were rather humid with annual precipitation amounts of more than 1000 mm year^{-1} followed by the particularly dry year 2003 with an annual precipitation amount of less than 700 mm year^{-1}. Since the start of the throughfall exclusion period in 2014, temperatures have shown a slightly increasing trend (9.4 °C on average), whereas precipitation from 2014–2018 (753 mm year^{-1}) was lower than in the previous period, 1998–2013. With the beginning of the throughfall exclusion period in 2014, the precipitation on the treatment plots was only a quarter of the precipitation on the control plots (Fig. 1).

Measurements at the tree and stand level

On the 12 plots, we measured the stem diameter with dendrometer bands at a resolution of 0.01 cm (UMS GmbH, Munich, Germany). The dendrometer bands were installed at a height of 1.30 m (DBH) on each tree. Stem diameters have been measured several times a year since 1998. In our
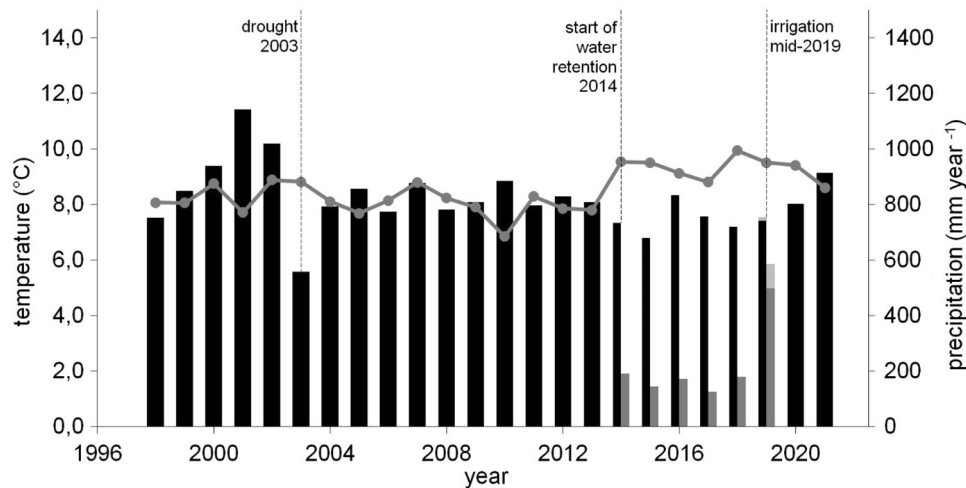
Fig. 1 Mean annual temperature (grey line) and annual precipitation at the KROOF site for 1998 to 2013 and for 2020 to 2021 (black columns). For the throughfall exclusion period from 2014 to 2019, the grey columns mark the precipitation of the treatment plots, while the black columns show the values for the control plots. The vertical lines show (from left to right) the natural drought in 2003 and the beginning and end of the throughfall exclusion from 2014 to 2018. In mid-2019, after the end of the throughfall exclusion period, a slight irrigation started, indicated by the light grey section on top of the bars representing the precipitation in 2019. Meteorological data were available from the nearby Forest Climate Station Freising (LWF 2022)

study, diameters at the end of the vegetation period of each year from 2009 to 2022 were included. Then, radial stem growth and basal area growth were calculated for each year.

The stand-level characteristics (see Table 1) were derived from the successive measurements by the dendrometer bands, additional tree height measurements, and records of the dropout trees. We used standard evaluation methods according to the DESER-norm recommended by the German Association of Forest Research Institutes (Biber 2013; Johann 1993). The results encompassed the quadratic mean tree diameter, stand basal area, and stand volume. The remaining stand basal area or stem volume at the first survey (BA1remain, V1remain), the total stand basal area or stem volume at the second survey (BA2remain, V2total), and the remaining stand basal area or stem volume at the second survey (BA2remain, V2remain) were used to calculate the annual stem volume gross growth, net growth, and dropout as follows: annual gross growth = (BA2total–BA1remain), mean annual net growth = (BA2remain–BA1remain) and mean annual stem volume dropout = (BA2total–BA2remain). The gross growth, net growth, and dropout of the stand volume were calculated analogously.

Tree and stand characteristics

The site conditions in the Kranzberg forest provide almost maximum productivity for the 71-year-old Norway spruces and the 91-year-old European beeches on the experimental plots. This is indicated by site indices of O40 according to the yield table of Assmann and Franz (1963) for Norway spruce and site class I according to Schober (1975) for European beech. For more information about stand and plot characteristics, as well as tree and stand growth, see Grams et al. (2021) and Pretzsch et al. (2014, 2018, 2020).

Table 1 summarizes the main dendrometric stand characteristics for the surveys in 2013, 2018, and 2022. We quantified the growth and yield in terms of stand basal area (m^2 ha^{-1} $year^{-1}$) and stem volume (m^3 ha^{-1} $year^{-1}$). The mean annual mortality rate calculations were based on the tree numbers, stand basal area, and stem volume at the beginning and at the end of the survey periods 2011–2013, 2014–2018, and 2019–2022 respectively.

The initial conditions concerning tree numbers, mixture proportions, stem diameters, tree heights, stand basal area, and stem volume were strikingly similar between the control and treatment plots, which were subsequently subjected to throughfall exclusion during the period 2011–2013. The productivity in the last period prior to the throughfall exclusion was also comparable between the control and treatment plots. On average, the control plots exhibited a volume increment of 10.49 m^3 ha^{-1} $year^{-1}$, while the treatment plots had an average volume increment of 9.37 m^3 ha^{-1} $year^{-1}$. There was no mortality observed within the control plots during this timeframe. The treatment plots, however, experienced minor mortality rates.

Throughout the 5-year throughfall exclusion period from 2014 to 2018, productivity (volume growth) was slightly higher on the control plots than during the 2011–2013 period, reaching 12.97 m^3 ha^{-1} $year^{-1}$. In contrast, productivity within the treatment plots for the 2014–2018 throughfall

Table 1 Stand characteristics (mean ± standard deviation) of the six control and the six treatment plots for the surveys (a) in 2013, before the start of the throughfall exclusion, (b) in 2018, after the throughfall exclusion ended, and (c) in 2022, the last survey

Group		N ha^{-1}	mix l. N.sp.	dq cm	hq m	BA m^2 ha^{-1}	V m^3 ha^{-1}	N_{loss} ha^{-1} yr^{-1}	BA_{loss} m^2 ha^{-1} yr^{-1}	V_{loss} m^3 ha^{-1} yr^{-1}	IBA m^2 ha^{-1} yr^{-1}	IV m^3 ha^{-1} yr^{-1}
(a) Survey in autumn 2013, growth relates to mean annual growth in the period 2011–2013 (3 years)												
contr	mean	670	0.54	33.41	30.45	58.20	886.98	0.00	0.00	0.00	0.61	10.49
	sd	149	0.07	2.39	0.66	10.31	156.31	0.00	0.00	0.00	0.09	1.64
treat	mean	604	0.59	33.31	31.56	52.21	814.72	9.18	0.13	1.58	0.56	9.37
	sd	190	0.10	2.43	0.50	16.07	244.59	14.24	0.23	2.80	0.09	1.32
(b) Survey in autumn 2018, growth relates to mean annual growth in the period 2014–2018 (5 years)												
contr	mean	643	0.55	34.86	30.87	61.11	941.06	5.56	0.16	2.15	0.74	12.97
	sd	112	0.08	2.22	0.58	10.26	158.50	8.67	0.35	4.93	0.13	2.59
treat	mean	445	0.35	31.86	31.23	36.49	577.80	31.86	3.39	51.72	0.25	4.33
	sd	115	0.26	4.22	0.89	14.47	234.91	37.33	4.60	70.56	0.05	0.92
(c) Survey in autumn 2022, growth relates to mean annual growth in the period 2019–2022 (4 years)												
contr	mean	620	0.55	36.61	31.36	64.88	1011.37	5.70	0.23	3.05	1.17	20.63
	sd	122	0.09	2.07	0.50	11.10	168.77	8.91	0.37	4.98	0.16	2.76
treat	mean	434	0.33	32.85	31.45	37.38	597.30	2.58	0.35	5.47	0.58	10.34
	sd	119	0.25	3.90	0.81	13.55	216.34	6.31	0.87	13.39	0.14	1.99

N tree number ha^{-1}, *mix* basal-area-related mixing proportion of Norway spruce, *dq* quadratic mean stem diameter, *hq* height of the tree with the quadratic mean stem diameter, *BA* stand basal area, *V* standing stem volume (merchantable volume > 7 cm at the smaller end), N_{loss}, BA_{loss}, and V_{loss} the annual loss of tree numbers, basal area, and standing volume in the previous survey period, *IBA*, *IV* mean annual basal area and volume increment in the previous survey period

exclusion period amounted to 4.33 m³ ha⁻¹ year⁻¹. Mortality rates were strongly elevated compared to the prior period and in relation to the control plots. An average of 2.15 m³ ha⁻¹ year⁻¹ of standing volume was lost on the control plots, whereas the treatment plots expierenced an average loss of 51.72 m³ ha⁻¹ year⁻¹. During the period after the throughfall exclusion (2019–2022), the growth rates on the treatment plots returned to inital levels, averaging an stand volume increment value (IV) of 10.34 m³ ha⁻¹ year⁻¹. However, stand volume increment on the control plots was higher than those of the previous periods (20.63 m³ ha⁻¹ year⁻¹).

Characterizing the compositional and structural stand diversity and the growth partitioning among differently sized trees

In our analysis, we used the annual stand basal area growth and the annual mortality rate (see the section "Tree and stand characteristics") as the main variables for quantifying the drought-induced disturbances on the treatment plots compared with the control plots. We relied on the Stand Density index (SDI), the mixing proportion (mix), the slope of the growth–size relationship (slope a_1), the Growth Dominance Coefficient (GDC), and Gini Coefficient of the stem diameter (GC) on all 12 plots over the period from 2010 to 2022 to characterize the effects of extended drought on compositional and structural stand diversity.

SDI: Stand density index according to Reineke (1933), calculated with exponents of $\alpha_{N,d} = -1.664$ for Norway spruce and $\alpha_{N,d} = -1.789$ for European beech, according to Pretzsch and Biber (2005).

Mixing proportion, mix: The mixing proportions were based on the SDI values. The mixing proportions m_1 and m_2 reflect the area proportions of the two species in the observed mixed stands (Dirnberger et al. 2017). We applied the equivalence factors introduced by Pretzsch and Biber (2016) to standardize the density and calculate the unbiased area-related mixing proportions. The equivalence factors adjust for the species-specific differences in the growing space requirement when calculating area-related mixing proportion.

Gini coefficient of stem diameter, GC: The Gini coefficient for a cumulative stock of trees is generally calculated as follows $GC = \frac{\sum_{i-1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n(n-1) \times \bar{x}}$ (see Camino 1976; Kramer 1988, p 82). Variables x_i and x_j denote size or growth (or other tree characteristics) for the i'th and the j'th tree in the stand with $i = 1 \dots n$ trees. Small GC values indicate equality, and large values close to $GC = 1$ a maximum inequality of size distribution (see Fig. 2a for further explanation).

Slope a_1 of the annual diameter growth-diameter relationship, slope: the slope of the plotwise linear regression $id = a_0 + a_1 \times d$, with id being the stem diameter increment in a given year and d being the stem diameter at the beginning of the year (Fig. 2b). The slope a_1 of the size growth-size relationship ($id = a_0 + a_1 \times d$) reflects how the growth rate of individual trees depends on their size (size-effect).

Growth dominance coefficient, GDC: To evaluate the growth partitioning among trees, we used the growth dominance coefficient (GDC) proposed by Binkley et al. (2006) and formulated in detail by West (2014). The GDC describes the partitioning of the annual or periodic size growth of n
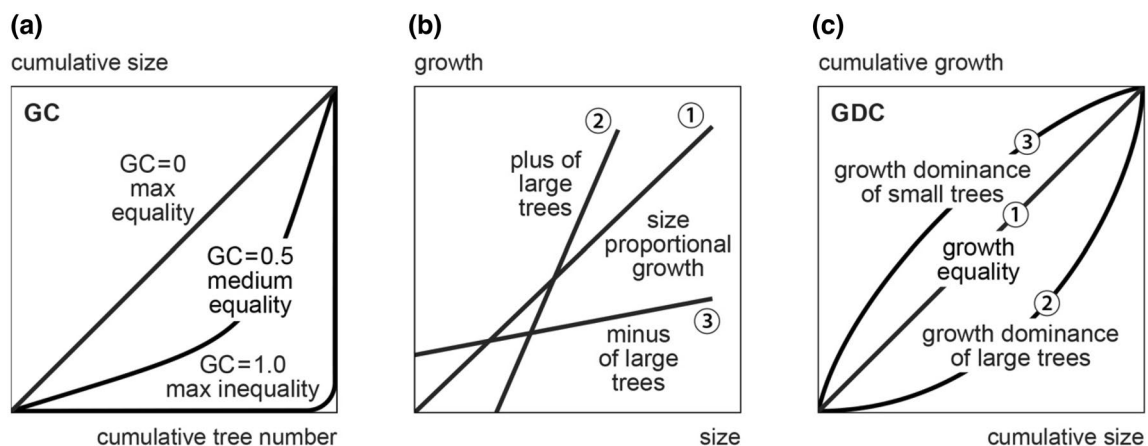

Fig. 2 Visualization of the approaches and applied metrics to quantify the effect of drought stress on size structure, growth partitioning, and mortality in forest stands. **a** The Gini coefficient, GC, of stem diameter reflects the degree of equality of the stem diameter distribution. **b** The growth-size relationship reflects the growth partitioning between large and small trees. Shown are proportional partitioning (line 1), plus of large (line 2), and plus of small trees (line 3). **c** The Growth Dominance coefficient, GDC, indicates equality of growth partitioning (curve 1, GDC = 0) and the growth dominance of large (curve 2, GDC > 0) or small trees (curve 3, GDC < 0)

individual trees (e.g., stem diameter growth, id) relative to their size at the beginning of the growth period (Fig. 2c). Thus, it provides a measure of the growth dominance within forest stands. For the calculation of the GDC, the following statistic was used:

$$GDC = 1 - \sum_{k=1}^{n} \left(cd_k - cd_{k-1} \right) \times \left(cid_k - cid_{k-1} \right),$$

where n is the number of trees, and k is the relative position (rank) of a tree in ascending order of tree volumes, whereas cd_k and cid_k denote the cumulative proportion of trees ranked 1 to k in the total stand volume and in the total stand volume increment, respectively. If the coefficient value is 0, all trees contribute proportionally to the total growth relative to their stem size. If the value is negative (GDC < 0), smaller trees contribute over-proportionately high to the total growth; if GDC > 0, larger trees contribute over-proportionally.

Any changes of the GDC indicate that trees of different sizes react differently to the variation of water supply, so that the growth partitioning pattern among the population changes. If water supply would affect the growth of all trees in a population in the same way, GDC would remain constant. However, an increase of GDC would mean an increasing growth of larger trees in relation to their share of the stand volume, i.e., the relation growth/size of the larger trees increase. In contrast, a decreasing GDC would indicate an increasing growth/size ratio of the smaller trees relative to their larger neighbors.

We used metrics for quantifying the size structure, growth partitioning, and mortality to trace drought stress effects from the tree to the size distribution and stand level. In Fig. 2, we briefly present the approach and main variables that we later use for the quantification the size structure of the stands and its modification by drought-induced changes of growth partitioning among trees and drought-induced mortality.

The Gini coefficient, GC, of tree size (e.g., based on stem diameter) can be used for quantification of whether a tree size distribution is homogeneous and equal (GC = 0), maximal unequal (GC = 1), or in between (e.g., GC = 0.5). It can be visualized by plotting the cumulative tree diameter over the cumulative tree number after ranking the trees according to their diameter (Fig. 2a). In Fig. 1a, we show the curve for GC = 0.50 that might be found in mature, even-aged forest stands. This size structure can be modified by growth, mortality, and regeneration (the latter is not considered in the following).

The size growth depends strongly on tree size; in Fig. 2b, we show some possible patterns. Line 1 represents growth proportional to size, line 2 an over-proportional growth of tall trees, and line 3 an over-proportional growth of small trees.

How these three size–growth relationships modify the growth partitioning between the small and large trees is reflected by the GDC in Fig. 2c. GDC = 0 applies if tree growth is proportional to size and leaves the size structure unmodified (Fig. 2c). In the case of over-proportional growth of larger trees (GDC > 0), the structure becomes more unequal; an under-proportional growth of large trees and over-proportional growth of small trees (GDC < 0) equalize the size structure. GDC = 0 will keep the Gini coefficient constant, whereas GDC > 0 will shift the Gini coefficient towards 1.0 in the long run (structural diversification). In contrast, GDC < 0 will shift the Gini coefficient towards zero (structural homogenization) (see Fig. 2a).

Statistical evaluation

To quantify the modification of the structural characteristics (e.g., SDI) due to drought, we calculated their mean characteristic in the pre-throughfall exclusion period 2010–2013 (e.g. $SDI_{pre-drought}$), their mean at the end of the drought period ($SDI_{drought}$), and their associated decrease (e.g. $SDI_{loss} = 1 - SDI_{drought}/SDI_{pre-drought}$). These loss values were calculated analogously for $slopea_1$, GC, GDC, Mix, etc. We refer to these loss values when presenting the stand and species-level results.

To determine the drought effects on compositional and structural diversity at the stand and species level (Q1 and Q2), we used OLS regression with a categorical variable (0/1) for the differentiation between control and treatment plots. For analyzing the interaction between the stand structure and the drought effects (Q3), we applied multiple linear OLS regression. For the revelation of any effects of the throughfall exclusion on the compositional and structural stand characteristics, we used models with the level of the respective variables in the pre-throughfall exclusion period and the treatment (control vs. treatment) as follows:

$$y = a_0 + a_1 \times pre_{drought} + a_2 \times treatment.$$

We included the pre-throughfall exclusion, $pre\_drought$, information as a co-variable to eliminate any initial differences between the plots. Treatments are coded by treatment = 0 for control and treatment = 1 for throughfall excluded plots. All models were fitted for each species and the total stand separately. When reporting the results, regression coefficients with marginal ($p < 0.10$) or higher significance levels are printed in bold letters.

All fitted models were subject to visual residual diagnostics. For all models, the residuals were plotted against the fitted values. In no case, the plots suggested a violation of variance homogeneity. Likewise, the normality of errors was verified by making normal q–q plots of the residuals.

For all calculations, we used the statistical software R 3.6.3 (R Core Team 2022).

Results

Drought-induced changes of structure and growth partitioning at the stand level (Q1)

Table 2 gives a general overview of all considered compositional and structural characteristics (mean ± standard deviation) on the 12 KROOF experimental plots in the last year before the throughfall exclusion started (2013) and in the last year of the survey (2022). On average, it reflects a reduction in stand density and mixing proportion (SDI, Mix), a decrease in size heterogeneity (GC), and a change towards a more size-symmetric growth partitioning among trees (a_1 and GDC).

Figure 3 (a and b) shows how stand basal area growth decreased and mortality increased on the treatment plots (red) compared to the control (green) due to the throughfall exclusion in 2014–2018. Stand basal area growth decreased by approximately 60% from 2010–2013 to 2014–2018, and the drought-induced mortality was sixfold that of the reference period (2010–2013). We show these trends (mean ± standard error), because they are important for understanding the development of the stand structure in Fig. 3c–e. For more details about growth and mortality in the KROOF experiment, see Pretzsch et al. (2020) and Grams et al. (2021).

While SDI continuously increased on the control plots, it decreased simultaneously with the drought-induced growth decrease and mortality on the treatment plots (Fig. 3c). Overall, SDI decreased by an average of 27% from the

Table 2 Mean (±standard deviation) of selected structural and compositional characteristics on the 12 KROOF experimental plots in the last year before the throughfall exclusion started (2013) and in the last year of the survey (2022)

Variable	Unit	Year 2013 mean	Year 2022 mean
Age	years, range	62–82	71–91
d	cm	31.6 ± 9.7	33.8 ± 9.6
SDI	ha^{-1}	1033 ± 247	979 ± 312
Mix	./.	0.55 ± 0.08	0.47 ± 0.16
GDC	./.	0.16 ± 0.07	0.09 ± 0.09
Slope a_1	cm cm^{-1}	0.015 ± 0.006	0.011 ± 0.005
GC	./.	0.17 ± 0.03	0.14 ± 0.04

Age = stand age; d = stem diameter; SDI = Stand Density Index; Mix = mixing proportion of Norway spruce based on SDI values; GDC = Growth Dominance Coefficient based on stem diameter; slope a_1 = slope of the regression $id = a_0 + a_1 \times d$; GC = Gini coefficient based on stem diameter

pre-throughfall exclusion period (2011–2013) to the end of the throughfall exclusion period (2018). Stand density losses occurred primarily in the middle of the throughfall exclusion period, and until now, the stands have not returned to the initial stand density levels. The mixing proportion of Norway spruce remained constant on the control plots but decreased from 0.57 in the pre-throughfall exclusion period to 0.34 in the throughfall exclusion period, i.e., by 41% (Fig. 3d). The decline was most pronounced in the middle of the throughfall exclusion period but continued until now. The decline of the Gini coefficient, GC, in the first two-thirds of the observation (Fig. 7e) indicates a homogenization of the stand structure in terms of the stem diameter distribution. Again, we found a general decline of the GC during the observation period, but the decrease was more substantial under throughfall exclusion. The decrease from the pre-throughfall exclusion period to 2018 was 15%, indicating a trend towards size equality and stand structure homogenization. The GC slightly increased in the last third of the observation period since 2019.

The statistical evaluation (Table 3a) showed for the Stand Density Index, SDI, and the mixing proportion a significant reduction by the throughfall exclusion. The Gini Coefficient, GC, depended significantly on the level of the pre-throughfall exclusion period but not on the treatment.

Drought-induced changes of the stand structure at the species level (Q2)

The stand basal area growth and mortality of Norway spruce and European beech reacted very differently to the extended drought (Fig. 4). Norway spruce (Fig. 4a and c) showed a much stronger growth reduction and mortality on the treatment compared to the control plots than European beech (Fig. 4c and d). From the pre-throughfall exclusion period 2011–2013 until the end of the throughfall exclusion period in 2018, Norway spruce growth decreased by 82% and European beech growth by only 3%. The mortality rate of Norway spruce changed from 0% in the pre-throughfall exclusion phase to 9.5% in the throughfall exclusion period and the mortality rate of European beech from 1.5% to 1%. Given a normal mean annual background mortality of 2% at medium stand ages (Pretzsch et al. 2023), Norway spruce mortality increased far above the normal level, whereas European beech remained normal.

The combination of growth reduction and mortality during the extended drought caused a strong and long-lasting reduction of stand density in the case of Norway spruce (Fig. 5a); compared to the density level before the throughfall exclusion, the SDI decreased by 40%. In the case of European beech (Fig. 5b), the SDI increased by 2% from the pre-throughfall exclusion to the throughfall
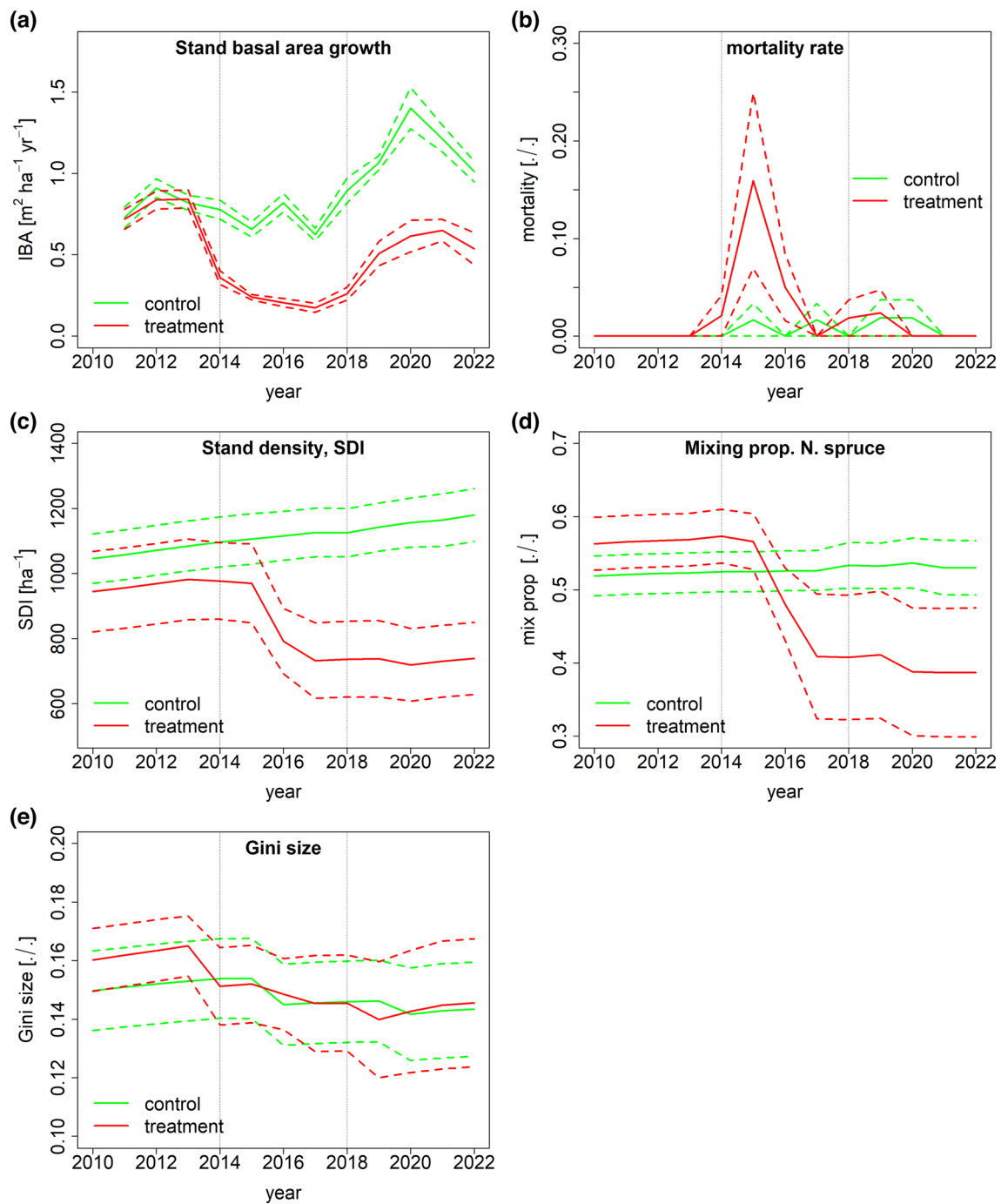
Fig. 3 Stand basal area growth, mortality, and structural characteristics of the treatment (red lines) versus control plots (green lines) in the period before, during, and after throughfall exclusion (from 2014–2018). Development of mean ± standard error of **a** Stand basal area growth, **b** tree mortality rate, **c** Stand density index, SDI, **d** mixing proportion of Norway spruce, and **e** Gini coefficient, GC, based on stem diameter. Solid lines indicate the mean, and broken lines indicate the standard error

exclusion period. Both the control and treatment plots showed a continuous slight increase from 2010 to 2022.

The drought decreased the Gini coefficient of Norway spruce from GC = 0.12 to GC = 0.09 by 29% and the Gini coefficient of European beech from GC = 0.15 to GC = 0.13 by 17% (Fig. 5c and d). The drought-induced decline of the GC indicates that the drought reduces the size variation and increases the size equality; this means a homogenization of the size distribution and stand structure within the throughfall exclusion period. The termination of the throughfall

Table 3 Statistical characteristics of the models for estimation of structure and partitioning in the throughfall exclusion period 2014–2018 for (a) the total stand, (b) Norway spruce, and (c) European beech

(a) Total stand

Coefficients	Characteristics	SDI	Mix prop	GC	Slope a_1	GDC
a_0	est	1126	0.53	0.02	0.006	0.015
intercept	se	85	0.07	0.05	0.002	0.032
	p tail	**<0.001**	**<0.001**	0.63	**0.015**	0.647
a_1	est	–	–	0.77	0.251	–
Pre-drought	se	–	–	0.30	0.128	–
	p tail	–	–	**0.028**	**0.082**	–
a_2	est	−389	−0.19	–	−0.007	−0.08
Treatment	se	121	0.10	–	0.001	0.04
	p tail	**0.009**	**0.087**	–	**<0.001**	**0.084**
Total model	R^2	**0.46**	**0.20**	0.34	**0.73**	**0.20**

(b) Norway spruce

Coefficients	Characteristics	SDI	GC	Slope	GDC
a_0	est	657	−0.015	0.005	0.023
Intercept	se	287	0.034	0.004	0.043
	p tail	**0.007**	0.675	0.260	0.611
a_1	est	−0.09	1.177	0.218	0.569
Pre-drought	se	0.30	0.319	0.242	0.278
	p tail	0.77	**0.008**	0.391	**0.070**
a_2	est	−328	−0.043	−0.006	−0.104
Treatment	se	110	0.021	0.003	0.047
	p tail	**0.016**	**0.098**	**0.072**	**0.098**
Total model	R^2	**0.39**	**0.58**	**0.20**	**0.30**

(c) European beech

Coefficients	Characteristics	SDI	GC	Slope	GDC
a_0	est	41	0.052	0.006	0.072
Intercept	se	60	0.041	0.003	0.042
	p tail	0.512	0.237	**0.061**	0.122
a_1	est	0.94	0.610	0.563	0.357
Pre-drought	se	0.11	0.246	0.195	0.286
	p tail	**<0.001**	**0.035**	**0.018**	0.243
a_2	est	−13	−0.009	−0.007	−0.019
Treatment	se	23	0.021	0.002	0.050
	p tail	0.58	0.663	**0.028**	0.708
Total model	R^2	**0.89**	**0.29**	**0.45**	**0.01**

We applied models with the level of the respective variables in the pre-period, the treatment, and the tree species according to the model $y = a_0 + a_1 \times pre\_drought + a_2 \times treatment$. Regression coefficients with marginal ($p<0.10$) or higher significance levels are printed in bold letters. Treatments are coded by treatment=0 for control and treatment=1 for throughfall excluded plots. Species are coded by species=0 for European beech and species=1 for Norway spruce

est Estimate, *se* standard error, *p tail* indicators of significance levels

exclusion did not significantly reverse this trend (see Fig. 5, c and d, time span 2019–2022).

The statistical evaluation showed a significant dependency on the treatment for the Stand Density Index, SDI, and the Gini Coefficient, GC, of Norway spruce (Table 3b). The corresponding reactions of European beech were not significant (Table 3c). Consequently, the GC decreased and indicated a trend towards structural homogenization, especially for Norway spruce (Fig. 5c, e and f).
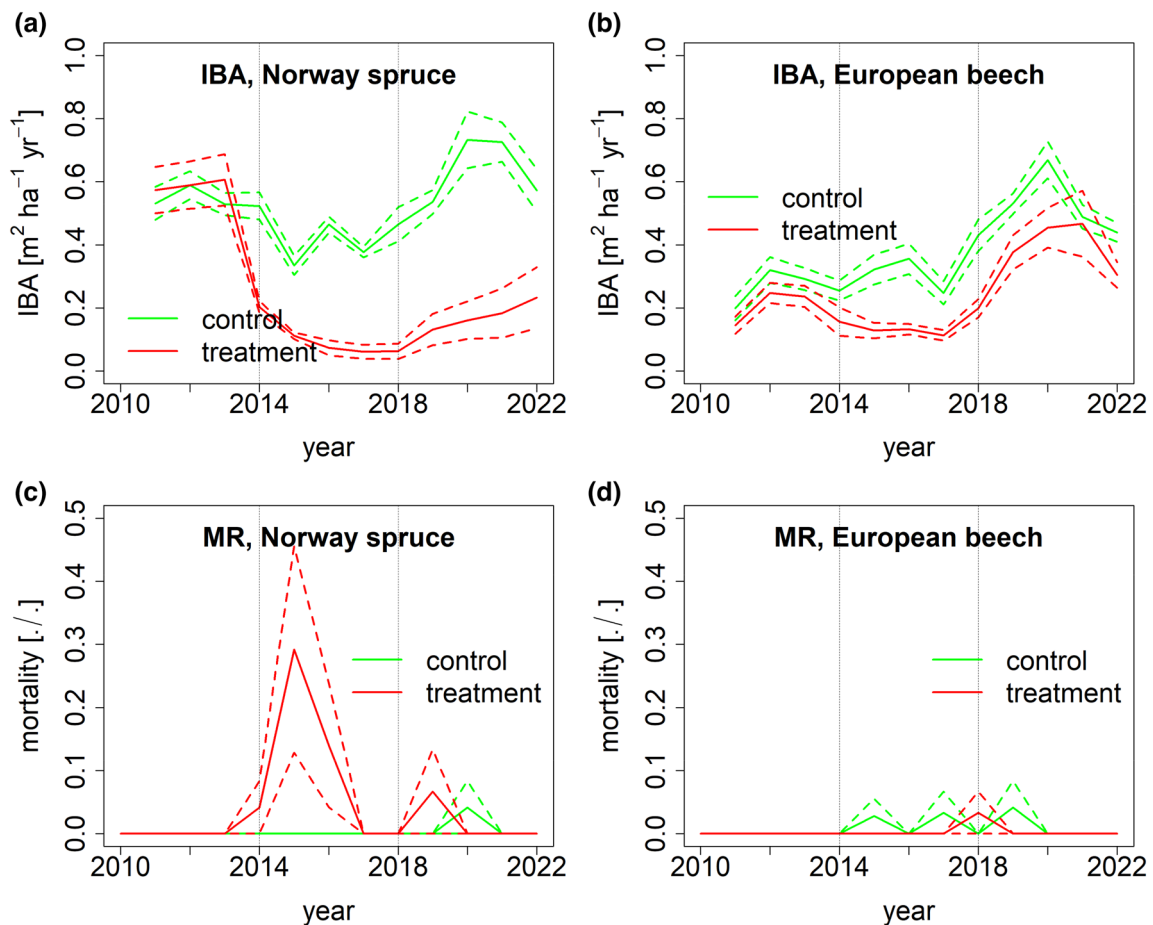
Fig. 4 Stand basal area growth and mortality of Norway spruce (**a** and **b**) and European beech (**c** and **d**) of the treatment (red lines) versus control plots (green lines) in the period before, during, and after throughfall exclusion (from 2014 to 2018). Development of mean ± standard error of the annual stand basal area growth and annual tree mortality rate. Solid lines indicate the mean, and broken lines indicate the standard error

Analyzing the growth partition among differently sized trees (Q3)

We first analyzed the common $id - d$ relationship for the two species (Norway spruce and European beech) together (Fig. 6). The upper range of the $id = a_0 + a_1 \times d$ relationships in the period 2010–2022 was very similar on the control and treatment plots (Fig. 6, a and b). However, in the lower range, some treatment plots had much lower and flatter $id - d$ lines than the control plots (Fig. 6b). Figure 6c shows that during the throughfall exclusion period (2014–2018), all $id - d$ lines were flatter on the treatment plots than on the control plots; this indicates a greater growth reduction of larger compared to small trees and a more size-symmetric growth partitioning. Figure 6d shows that in the post-throughfall exclusion period 2019–2022, the growth partitioning on the treatment resembles again that on the control plots; this suggests a fairly rapid recovery towards the initial partitioning pattern.

The development of the slope a_1 of the regression $id = a_0 + a_1 \times d$ and the growth dominance coefficient, GDC, from 2010 to 2022 confirms a growth partitioning in favor of smaller trees (size-symmetric partitioning) during the throughfall exclusion period in 2014–2018 and a switch back to partitioning in favor of larger trees (size-asymmetric partitioning) in the post-throughfall exclusion period (Fig. 7). The development of the slope a_1 (Fig. 7a) reflects that the relationship between growth and size was modified due to the throughfall exclusion (size-effect). The mean of the slope decreased by 70% from $a_1 = 0.014$ in the pre-throughfall exclusion period to $a_1 = 0.004$ in the throughfall exclusion period. The development of GDC (Fig. 7b) reflects that the relative growth contribution of trees of different sizes to the stand growth was also modified by the throughfall exclusion (combined size and frequency effect). The mean of GDC decreased by 157% from GDC $= 0.144$ in the pre-throughfall exclusion period to GDC $= -0.083$ in the throughfall exclusion period. The statistical evaluation
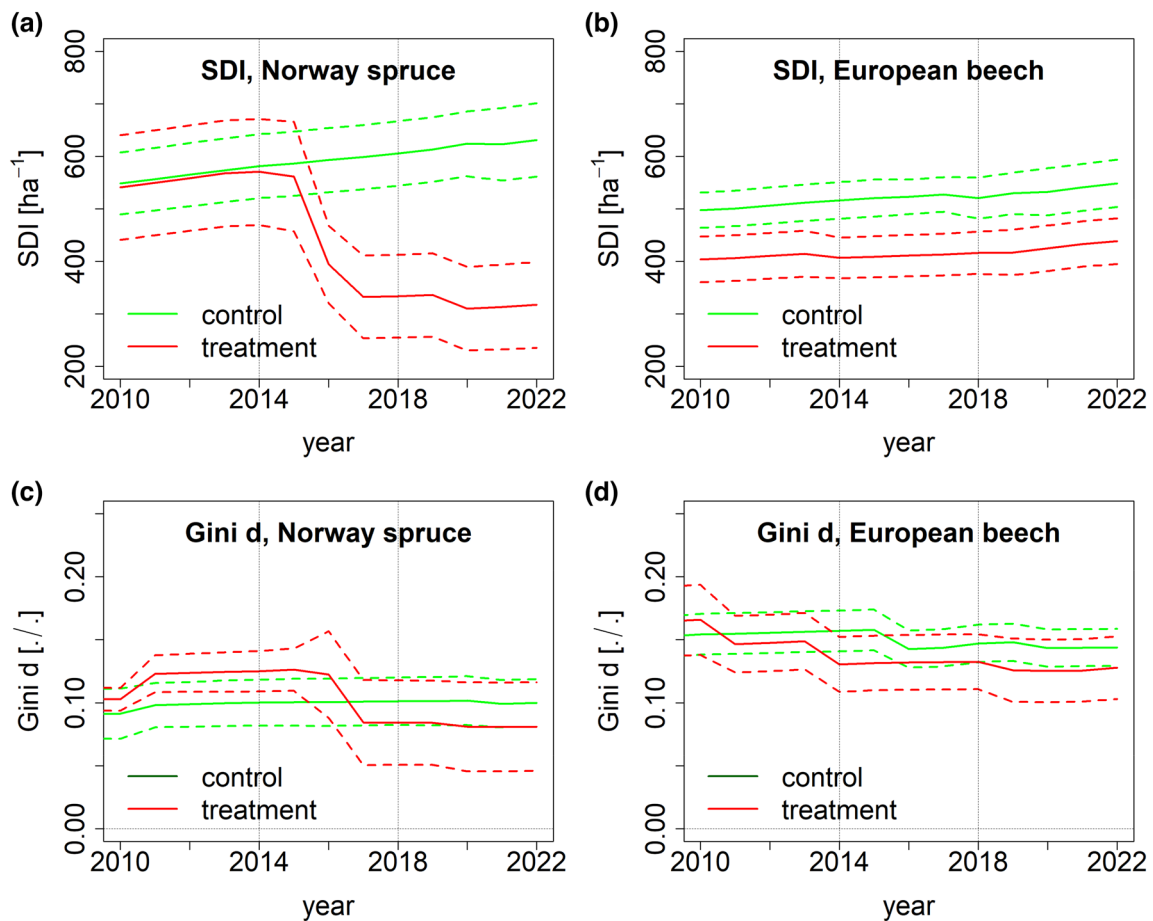
Fig. 5 Structural characteristics of Norway spruce (left column) and European beech (right column) on treatment (red) versus control plots (green) in the period before, during, and after throughfall exclusion (from 2014 to 2018). Development of mean ± standard error of (**a** and **b**) Stand density index, SDI, (**c** and **d**) Gini coefficient, GC, based on stem diameter, (**e** and **f**) growth dominance coefficient, GDC, based on stem diameter and stem diameter growth, and (**g** and h) mixing proportion. Solid lines indicate the mean, and broken lines indicate the standard error

showed for the slope a_1 and the GDC at the total stand level a significant effect of throughfall exclusion (Table 3a).

Figures 8 and 9 visualize how the throughfall exclusion modified the growth partitioning for Norway spruce and European beech. On the control plots, the annual id–d relationships were rather similar for Norway spruce and European beech in the period 2010–2022 (Fig. 8a and b). The treatment modified the annual id–d relationships of Norway spruce stronger than of European beech (Fig. 8c and d). In the years 2014–2018, the id–d relationships of Norway spruce were lower and much flatter on the treatment plots than on the control plots (Fig. 8e). For European beech, we found a smaller reduction in the slope and level of the id–d relationships due to throughfall exclusion (Fig. 8f).

Compared with the pre-throughfall exclusion period, the slopes of the annual id–d relationships became much flatter during the throughfall exclusion period 2014–2018, especially in the case of Norway spruce (Fig. 9a and b). The

mean of the slope decreased by 90% from $a_1 = 0.014$ in the pre-throughfall exclusion period to $a_1 = 0.002$ in the throughfall exclusion period for Norway spruce. The decrease for European beech was 49% from $a_1 = 0.013$ in the pre-throughfall exclusion period to $a_1 = 0.007$ in the throughfall exclusion period. After 2018, the slopes became steeper again. This indicates a trend towards reduced growth of primarily large trees, which partially favors small trees. The development of the GDC corroborates this growth partitioning in favor of small trees (Fig. 9c and d). The GDC strongly decreased during the throughfall exclusion period; we found a decrease of 238% from GDC = 0.072 to GDC = − 0.100 for Norway spruce and a reduction of 130% from 0.217 to GDC = − 0.065 for European beech. This means that the growth was partitioned in favor of the small trees.

Table 3b shows that the effects of the throughfall exclusion on the slope a_1 and GDC were marginally significant in the case of Norway spruce. Table 3c confirms a significant
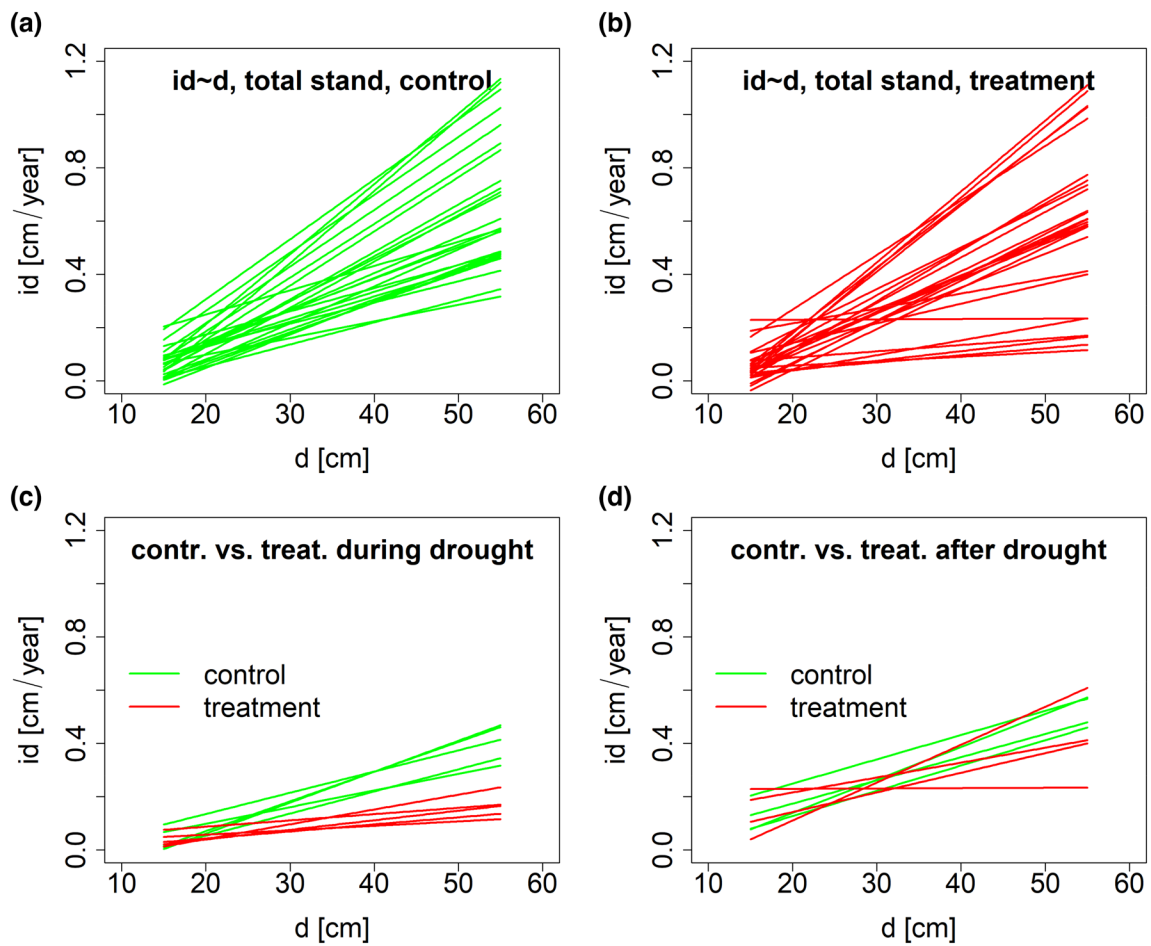
Fig. 6 Visualization of the regression lines id = $a_0 + a_1 \times$ d for the total stand (Norway spruce and European beech) from 2010 to 2022 for control (green) and treatment plots (red). **a** and **b** id–d relationships on the control and treatment plots from 2010 to 2022. **c** and **d** Comparison between the id–d relationships on control plots (green) and treatment plots (red) during the throughfall exclusion period 2014–2018 and the post-throughfall exclusion period 2019–2023
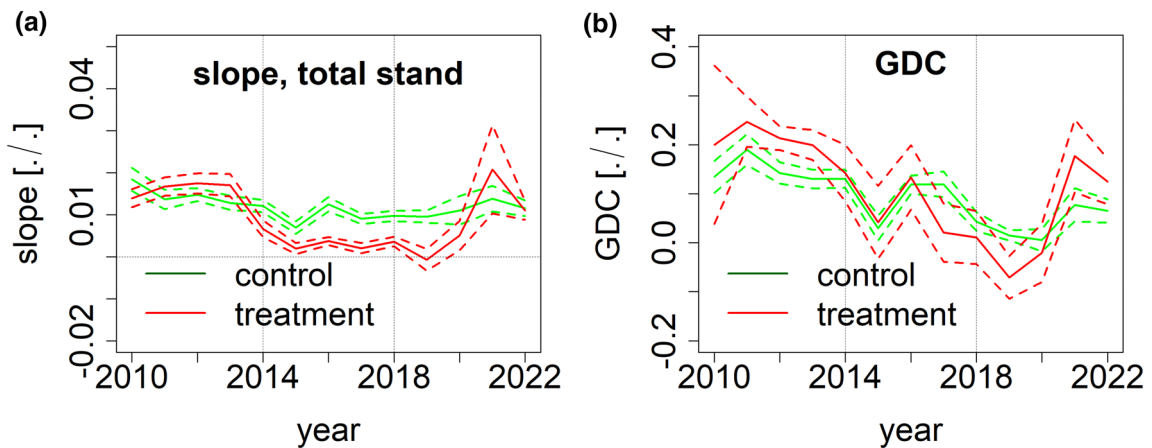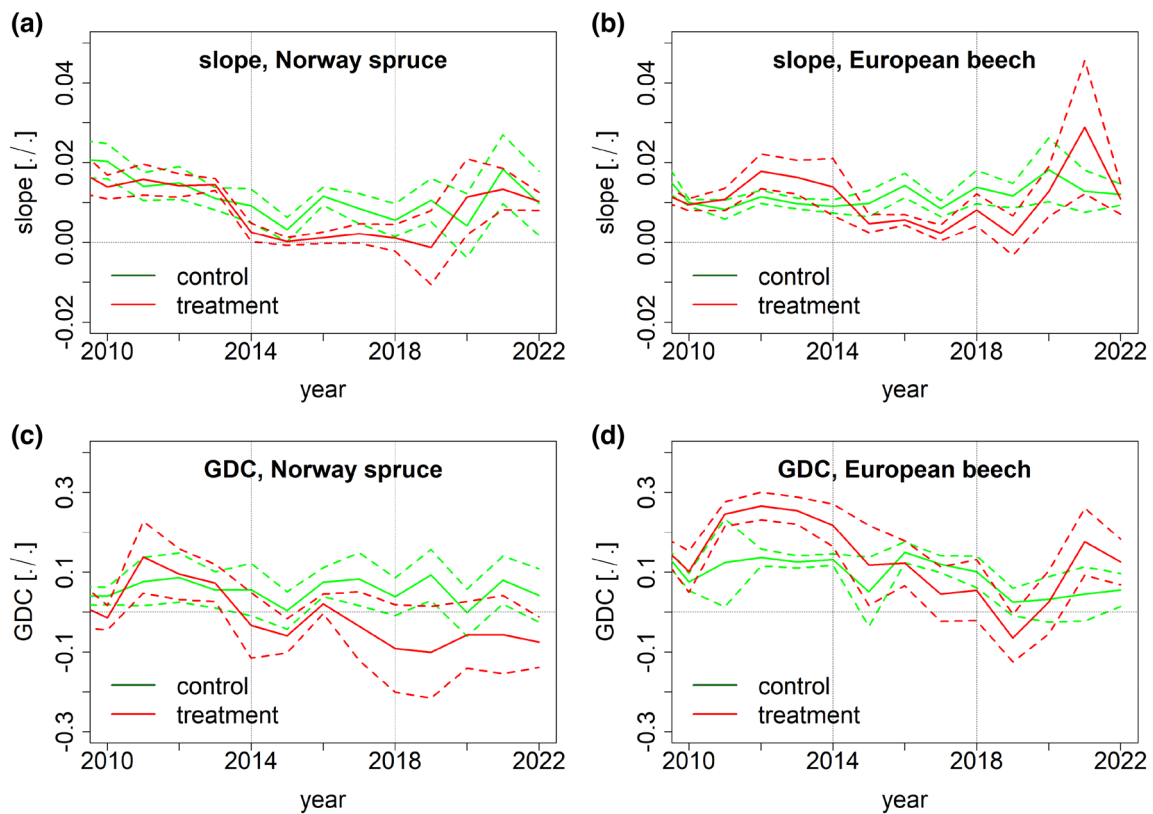

Fig. 7 Development of **a** slope a_1 of the regression id = $a_0 + a_1 \times$ d and **b** growth dominance coefficient, GDC, (mean ± standard error) at the total stand level on the treatment versus control plots (red versus green lines) in the period before, during, and after throughfall exclusion (from 2014 to 2018). Solid lines indicate the mean, and broken lines indicate the standard error
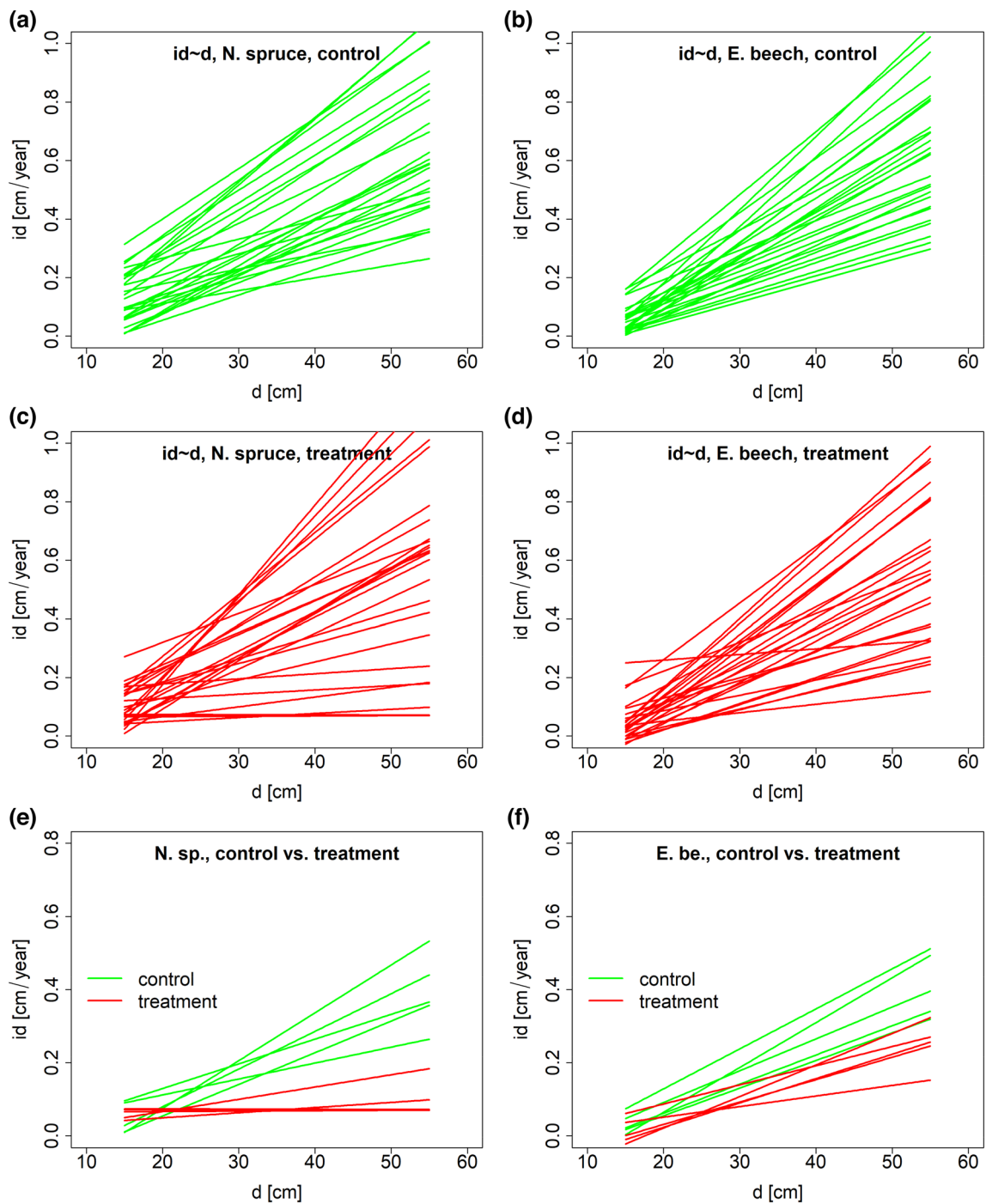
Fig. 8 Relationship between stem diameter growth and stem diameter (id–d relationship) for each year 2010–2022 represented by a regression line (id $= a_0 + a_1 \times$ d) for Norway spruce (left) and European beech (right). **a** and **b** id–d relationships on the control plots, **c** and **d** id–d relationships on the treatment plots, and **e** and **f** comparison between the id–d relationships on control plots (green) and treatment plots (red) in the throughfall exclusion period 2014–2018

Fig. 9 Development of slope a_1 of the regression $id = a_0 + a_1 \times d$ and growth dominance coefficient, GDC, (mean $\pm$ standard error) for Norway spruce (**a** and **c**) and European beech (**b** and **d**) on the treatment versus control plots (red versus green lines) in the period before, during, and after throughfall exclusion (from 2014 to 2018). Solid lines indicate the mean, and broken lines indicate the standard error

effect of the throughfall exclusion on slope a_1 but not on GDC in the case of European beech.

Discussion

Acclimation of stand structure to drought: resume and answering the research questions

Our study provides new insights into forests' structural and compositional acclimation to extended drought. The species composition and structure may determine the extent of drought damages regarding growth and tree loss. The effects of stand structure on damages have been frequently studied, e.g., for mitigating damages by adaption of species composition or stand density (Bradford et al. 2022; Steckel et al. 2020; Sohn et al. 2016). On the other hand, drought-induced growth and tree losses modify stand growth and structure. These relationships have been largely neglected (Batllori et al. 2020; Klos et al. 2009), although any drought-induced changes of the compositional and structural diversity may shape the stability of a stand under future disturbances.

The throughfall exclusion in our study was long-lasting and caused severely dry conditions. For 5 years, precipitation on the treatment plots was only a one-quarter that of control plots, and the reduced precipitation was concentrated in the winter months when roofs were open (Fig. 1). The throughfall exclusion reduced the total stand growth and increased the tree mortality, so that the SDI decreased by 27%, while the mixing proportion of Norway spruce decreased by 41%. The decrease of the Gini coefficient based on the stem diameter indicated a drought-induced structural stand homogenization within the throughfall exclusion period (Q1). Our finding that drought can significantly reduce stand growth, increase mortality, and thus reduce the stand density is in line with the other studies (Birdsey and Pan 2011; Choat et al. 2018; Adams et al. 2017).

The throughfall exclusion affected Norway spruce much more than European beech. The throughfall exclusion almost halved the stand density of Norway spruce and did not affect the SDI of European beech. The Gini coefficient of Norway spruce strongly decreased, but not the one of European beech. This means that the stand-level response in terms of density reduction, demixing, and homogenization can be

attributed mainly to Norway spruce. European beech hardly reacted and thus had a stabilizing effect regarding growth, mortality, density, and structure (Q2). Synchronously to the density reduction, we found a reduction of the mixing proportion of Norway spruce and a species demixing. This is consistent with several studies showing stronger drought resilience and resistance for European beech than for Norway spruce (Zang et al. 2011; Pretzsch et al. 2013; Niinemets and Valladares 2006) because of the anisohydric, respectively, isohydric, behavior of these species (Pardos et al. 2021; Grams et al. 2021; Hartmann 2011).

The slope of the growth–size relationship and GDC at the stand level indicated that the growth partitioning changed in favor of small and at the expense of large trees. For Norway spruce, we found strong growth losses of large trees and a growth partitioning in favor of small trees, which caused a shift to size homogeneity. European beech exhibited smaller changes in growth partitioning during the throughfall exclusion period and recovered more quickly after throughfall exclusion ended. In combination, the different species-specific responses caused a stabilization of growth and structure at the stand level (Q3). Wichmann (2001a, b) also showed a drought-induced partitioning in favor of small trees for Sitka spruce, while Schwarz and Bauhus (2019) observed this for silver fir, and Martín-Benito et al. (2008) for European black pine. In contrast, the trees in stands of Scots pine and European larch reacted differently (Zang et al. 2012; Pretzsch et al. 2022b). Here, we showed that extended drought stress caused a compositional and structural homogenization in stands of Norway spruce and European beech.

Since the throughfall exclusion experiment was carried out in a period with low rainfall and two particularly dry years (2015, 2018), its effect on growth was probably lower than under normal conditions. This is supported by our finding that the structure became more homogeneous on all plots, while the pattern on the treatment plots was more distinctive than on the control plots. On the treatment plots, the 5-year long throughfall exclusion started to change the compositional and structural diversity, but this trend was interrupted by the end of the throughfall exclusion. The strong recovery after the end of the throughfall exclusion is in line with the other studies. The more a species' growth is temporarily reduced by above-ground damages, the more it regrows afterwards. Following Körner (2002), we hypothesize that low-growth periods reduce resource uptake and accumulate them in the soil. The lower the nutrient consumption during the low-growth period, the better the supply in the following years and the stronger the overshoot of growth (Pretzsch et al. 2013), as shown in Fig. 3a.

Stabilization effect of compositional and structural diversity

The 5 years of throughfall exclusion did neither severely destroy the stand nor endanger its integrity in terms of its ability to maintain a forest structure, store carbon, protect biodiversity, and provide social and economic benefits (Tierney et al. 2009). The initial compositional and structural diversity caused that the reduced growth and increased mortality of one species was buffered by the persistence of the other; it caused that the growth loss of dominant trees was counterbalanced by the growth of smaller trees and that the drought-induced density reduction improved the growth and survival of the remaining trees. Similar water stress in homogeneous, monospecific stands of Norway spruce would probably have damaged the stand integrity (Gomez-Gallego et al. 2022, Thiele et al. 2017). Especially, the mixture, the size heterogeneity, and the different species-specific reaction patterns to the beginning and the end of the throughfall exclusion may have stabilized the growth and productivity.

We hypothesize that the initial density reduction improved the water supply of the remaining trees (Andrews et al. 2020; Giuggiola et al. 2013) and, in combination with their physiological and morphological acclimation (Hesse et al. 2023; Grams et al. 2021), stabilized their growth and survival in the second half of the throughfall exclusion period. Schaffner (1997) found by CT scanning of Norway spruces and European beeches in the Kranzberg Forest that stems of 30–35 cm in diameter had a water content of 518–614 L. The trees were felled near the KROOF plots and had stem sizes similar to our sample trees. When trees of this size die due to drought, they reduce the evapotranspiration and water consumption on the one hand, and on the other hand, some of the water stored within them may be relocated to the soil. Both effects may have improved soil moisture and stabilized the growth of the remaining stand (Fig. 3a) already during the throughfall exclusion period.

The 5-year stress caused a change in mixing proportion, stand density, and structure. However, the stands acclimated to the dry conditions by reducing stand density and water consumption, changing species composition towards the more drought resistance European beech, and changing growth dominance in favor of smaller trees with less hydraulic stress. In this way, the drought transformed the stands into a more drought-resistant state due to a lower stand density, higher proportion of drought adapted tree species, and more open canopy, so that other species can survive and enrich the diversity. This tendency towards a higher drought resistance corroborates the intermediate disturbance hypothesis (Connell 1978; Fox 1979). This hypothesis suggests that

neither too rare nor too frequent occasional stress may acclimate ecosystems to extended stress. Local species diversity is maximized when ecological disturbance happens occasionally (Seidl et al. 2014).

Compared to the harsh losses of Norway spruce (growth decreased by 82%, and mortality increased from 0% in the pre-throughfall exclusion period to 9.5% in the throughfall exclusion period), the mortality of European beech was much less affected by the throughfall exclusion. Although the growth partitioning changed in favor of smaller and at the expense of larger trees, the stand growth decreased by only about 3%. As a result, the mixing proportion of European beech and its SDI increased. This means that European beech maintained the stand integrity, stabilized the growth, and perpetuated structural diversity. Thus, European beech counteracts the stand disintegration that drought may cause in monocultures of Norway spruce (Vitali et al. 2017).

Whereas European beech has a deep-reaching heart root, Norway spruce has a more shallower and only occasionally deeper reaching tap root system (Ellenberg and Leuschner 2010). It is likely that the deeper rooting of European beech than Norway spruce in both monospecific and mixed species stands (Bolte and Villanueva 2006; Wiedemann 1942) contributes to the higher drought resistance and resilience of beech. Although Rötzer et al. (2009) found that, in dry years, European beech reduces the ratio of below- to above-ground growth partitioning more than Norway spruce, Schmid and Kazda (2001, 2002) found a higher belowground competitive ability of European beech due to a shift in beech fine roots from upper to lower soil layers compared to Norway spruce. The combination of both superior above and below ground morphological plasticity may be essential for the growth stabilizing effect of European beech in mixed species stands under drought stress.

Implications for silviculture

Most studies that focus on drought effects on trees or forest stands are based on selected individual drought years or on a series of drought years interspersed with normal years. In such cases, stands were acclimated to sufficient water and nutrient supplies, perhaps even to additional eutrophic deposition, prior to the drought and then suddenly faced drought stress. However, they may not be acclimated to sudden changes in stand density, species composition, size distribution, or root–shoot allometry. And in the case of a succession of drought years interspersed with normal years, they also may have a lack of acclimation, as they may have returned to previous stand density, physiology, morphology, and allometry in between. From our experiment, we learned that longer drought periods could trigger acclimation to drought at the tree and stand level already after 2–3 years due to stand density reduction (Fig. 3), change of growth

partitioning between large and small trees, as well as physiological and morphological acclimation (Fig. 6). Certainly, less drought-resistant tree species, especially when cultivated beyond their natural range, such as Norway spruce in our study, will lose in the mixing proportion (Fig. 5). Due to the reduced stand and canopy density, more acclimated species may establish in the understorey. They may replace the less acclimated species that were lost in the canopy. Our results suggest that the ability of forest stands to acclimate to drought stress may be underestimated if we deduce our knowledge only from individual drought years and that continuous stress triggers acclimation at different levels from stand to species cohort, tree, and organ level. The results indicate that the initial structurally and compositionally diverse stands can somewhat buffer drought-induced growth losses, as one species has a potential to replace another, and smaller trees can partly compensate for the growth losses of larger trees (Bennett et al. 2015).

Mixtures of broadleaved tree species within their natural range with conifers beyond their natural range are common in Central Europe (Brus et al. 2012). The mixed stands of the KROOF experiment with European beech (within natural range) and Norway spruce (beyond natural range) are a typical example for this. In such stands, Norway spruce is artificially established and kept as an admixture of 30–50%, because it is a fast and straight growing species with high timber quality and is economically important under normal growing conditions. Our results show that this mixture has a future even under extended drought. After 2–3 years of tree losses, density reduction, and structural, physiological, and morphological acclimation, the stand stabilized on a new level. Interestingly, the trend towards structural homogenization was attenuated already during the throughfall exclusion period and further mitigated by a strong recovery in the years after the throughfall exclusion. The initial mixing and tree size variation had a stabilizing effect on the growth, mortality, and stand structure under drought. Mixing both species may even mitigate the drought stress of Norway spruce (Pretzsch et al. 2020, 2013). This underpins the relevance of risk distribution and stabilization effect by tree species mixing (del Río et al. 2017, 2022; Hilmers et al. 2019; Jucker et al. 2014; Yachi and Loreau 1999). The relevance of tree size variation under dry conditions is further highlighted by recent findings that low and asymmetric competition is beneficial for tree vitality and growth in drought-damaged forest stands of European beech (Pretzsch and Zenner 2017; Schmied et al. 2023). We suggest that the compositional and structural diversity should be promoted to buffer future disturbances.

The drought-induced stand density and growth reduction of mainly large trees may pave the way to a stronger structuring of the stands in the long-term. A reduction in stand density and associated reduction of upper layer shading may

result in smaller trees having better conditions to survive in the medium and lower layers of the canopy and expand the size distribution, as is typical for stands under harsh conditions (Pretzsch et al. 2022a). The understory requires a thinning and mixing regulation to keep a reasonable number of survivors in all diameter classes and of various species to keep the potential of diverse stand in the future. Thus, extended drought may, in the long-term, enable higher structural diversity. Opening up of the upper layer improves the living conditions, i.e., the growth and survival of smaller trees and enhances the variety of light conditions, which may also promote species diversity, e.g., the ingrowth of a combination of light demanding and shade tolerant trees, as headed for in many silvicultural prescriptions for diversified forests. Indeed, future crop tree systems that concentrate the growth and value of a restricted number of large trees may be called into question by the mortality and growth reduction of preferentially large trees. However, thinning, and mixing regulation of the strengthened trees in the lower layers may prepare the transition to multi-layered and mixed stands. In this way, silviculture might incorporate drought-induced disturbances. Thus, the disturbance caused by drought stress suggests silvicultural approaches that are more aligned with natural processes under climate change (Bowditch et al. 2020; Messier et al. 2013; Puettmann et al. 2012).

Conclusion

Whereas individual tree growth showed a strong decrease during throughfall exclusion followed by a remarkable acclimation and recovery afterwards, stand-level analyses of compositional and structural diversity revealed a severe and longer lasting effect of drought on the stand dynamics. Thus, our results emphasize that the widespread drought stress analyses at the tree level need to be complemented by stand-level research. Most importantly, drought reduced stand density and tree species mixing and modified the growth partitioning between small and large trees. Small trees showed a relative benefit from drought compared to their larger neighbors, implying a restriction in size distribution and structural homogenization. The revealed compositional and structural changes will continuously affect the stand productivity and other ecosystem services, such as biodiversity, stability, or carbon sequestration. Our analyses suggest that the capacity of structural and compositional acclimation of forests to extended drought may be underestimated and that species mixing and size variation contribute to risk distribution and mitigation of drought stress compared with more homogeneous stands. However, the drought-induced mortality of Norway spruce and growth partitioning in favor of smaller trees requires structuring silvicultural measures to maintain the initial heterogeneity of the stand, which limited the drought stress damages by species and structural diversity.

Declarations

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