379

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Stem and root diameter growth of European beech and Norway spruce under extreme drought

T. Rötzer*, P. Biber, A. Moser, C. Schäfer, H. Pretzsch

Technical University München, Chair for Forest Growth and Yield Science, Germany

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ABSTRACT

Current and future climate change will be accompanied by more frequent and more severe drought events, with potential impacts on tree growth and forest stand productivity. Tree growth response may depend on its water status and on the competition or facilitation of the neighbouring trees. We analysed inter- and intra-annual diameter increments of European beech and Norway spruce trees within a mixed forest stand for two treatments, i.e., with and without rainfall exclusion and for two neighbourhood competition situations of the two climatically contrasting years 2014 and 2015. Rainfall exclusion by roofs at about 3 m height induced soil drought under 116 trees, particularly supported in the year 2015 by hot and dry weather conditions. The effects of extreme drought was examined at three levels, i.e. at two stem heights and at the main coarse root of 48 trees with inter- and intraspecific neighbourhood. We found species specific diameter growth performances during the year at all three levels. Compared to beech trees annual diameter increments of spruce trees were in most cases significantly higher in the year 2014, while in the drought year 2015 no significant differences between the two species were obvious. Under the heavy drought by the rainfall exclusion experiment and by the hot year 2015 diameter increments were significantly smaller for spruce trees at all three levels whereas for beech trees at all levels no significant differences were obvious. The diameter growth differences between inter- and intraspecific neighbourhood were in most cases small and not significant. In the drought year 2015 beech trees in intraspecific neighbourhood grew better at all levels compared to interspecific neighbourhood, with a significantly higher growth rate at the upper stem level. Reasons for the species specific reactions patterns on drought were discussed (phenology, water balance, species specific physiological reactions).

1. Introduction

Declining tree vitality and tree growth found in different European regions can be traced back to a severe reduction of the water availability (ICP-Forests, 2004). Tree mortality of forests at the edge of their bio-geographical distribution may rise if temperature is increased, particularly in Southern and Central Europe (e.g. Schröter et al., 2004; Camarero et al., 2015). On the other hand, climate and other environmental changes such as precipitation patterns, length of growing season, CO_2-concentration, or nitrogen deposition can stimulate forest growth (e.g. Pretzsch et al., 2014a), which is a major component of the forest biomass changes through time since recruitment and mortality also influence the turnover times of forest biomass (Körner, 2017). In recent years the number of studies increased which report an acceleration and a rise of tree and stand growth of temperate and boreal forests within the last 50 years (e.g. Innes, 1991; Spiecker et al., 1996; Pretzsch et al., 2014a; Kauppi et al., 2014; Fang et al., 2014; Aertsen et al., 2014). The higher growth rates of the last decades can be

explained by temperature increase (IPCC, 2007), by extended growing seasons (e.g. Chmielewski and Rötzer, 2001) and by the rise of N-depositions (e.g. Churkina et al., 2010) and of the atmospheric CO_2-concentration (e.g. Churkina et al., 2010) within the last century (Pretzsch et al., 2014a).

In future water availability which is an essential parameter for tree growth will become more and more critically with longer and more frequent drought periods (Leuschner, 2009; Allen et al., 2010). While drought adapted forest types show mortality during long-lasting water shortage, less drought adapted forest types like temperate broadleaved forests show highest mortality rates during short-term (seasonal) water shortage (Allen et al., 2010). The influence of water shortage on tree and stand growth is closely linked with the environment of the tree individuals and the forest stand as a whole (Rötzer et al. 2017), i.e. with tree age (e.g. Peterken and Mountford, 1996), social classes of the trees (e.g. Orwig and Abrams, 1997; Dohrenbusch et al., 2002), site and soil conditions (e.g. Orwig and Abrams, 1997; Modrzynski and Eriksson, 2002; Pichler and Oberhuber, 2007) but also tree species (e.g. Orwig

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and Abrams, 1997; Leuschner et al., 2001) and tree genotype (e.g. Hamanishi and Campbell, 2011). Further on, species mixing could change the stand water balance (e.g. Pretzsch et al., 2012).

For mixed stands of Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) which are the most relevant mixture in Central Europe, actual evapotranspiration rates were found to be clearly different from the corresponding monospecific stands and thus also stand productivity and resource use efficiency (Pretzsch et al., 2012). And even forest mixing structure, i.e. the spatial distribution of the species within the stand, change the resource supply of water and light and in consequence tree growth (e.g. Rötzer, 2013). The responses of beech and spruce trees to the long and intensive drought of the exceptionally hot and dry summer of 2003 in Central Europe brought new knowledge in tree growth reactions on drought stress (Leuzinger et al., 2005; Breda et al., 2006; Löw et al., 2006; Nikolova et al., 2009; Pretzsch et al. 2012). Forest growth and primary production was reduced in this year which was closely linked to water availability (e.g. Ciais et al., 2005; Pichler and Oberhuber, 2007; Reichstein et al., 2007; Pretzsch et al. 2013). However, there is still a lack of knowledge how different tree species behave under extreme drought conditions, particularly in mixed forests, and what are the consequences for stand growth.

Many studies about mixed spruce beech stands in Central Europe showed a significant overyielding of mixed versus monospecific stands of 10–30% in terms of volume growth (Kennel, 1965; Pretzsch et al., 2010a; Rothe, 1997). Growth superiority of mixed versus monospecific stands, mostly referred to as overyielding, can amount to 10–30% in 2-species stands (Pretzsch et al., 2016a) and increases degressively with species richness (Liang et al., 2016). For the age series of a long term forest experiment (Pretzsch et al., 1998) which includes the Kranzberg Forest the long-term overyielding at the stand level amounts to 1.18 (Pretzsch et al., 2010a, Pretzsch and Schütze, 2009). Under normal conditions the mixed stand is by 18% more productive than the weighted mean of the two monocultures; both Norway spruce and European beech contribute approximately the same to this overyielding. The better below and above ground resource access of mixed stands as reasons for overyielding have been studied rather extensively, e.g., regarding the tree morphology (Kennel, 1965: Petri, 1966), canopy layering (Pretzsch, 2014), and root stratification (Wiedemann, 1942).

The higher growth stability of mixed-species stands compared with monocultures can be quantified by comparing the inter-annual growth oscillation of mixed stands with the monocultures at the stand or species level (Río et al., 2017). The main reason for their more stable growth is an asynchronous growth behaviour of the associated species (Jucker et al., 2014). Río et al. (2017) showed that asynchrony can closely correlate with stability and overyielding. The species' complementarity known from monocultures may even increase in mixture due to their phenotypical plasticity. E.g., crown extension and thereby light interception of European beech can exceed beyond its behaviour known from monocultures (Dieler and Pretzsch, 2013). Such temporal diversification was studied at the long-term inter-annual scale (von Lüpke and Spellmann, 1997: Pretzsch et al., 2010a:, Rothe, 1997) but hardly at the intra-annual level (seasonal development).

Plant allocation theory states that biomass allocation to aboveground or belowground tree compartments follows the principle of maximizing the capture and minimizing the limitation of resources (e.g. Chapin, 1980). Consequently, decreasing water supply or increasing drought conditions may result in enhanced root growth. This is reported in numerous articles (e.g. Cienciala et al., 1994; Polomski and Kuhn, 1998; Leuschner et al., 2001; Frank, 2007; Noguchi et al., 2007) as well as shown by simulation studies (Rötzer et al., 2009; Rötzer et al., 2012). Thus, water uptake of trees in periods with low water availability can be ensured by carbon allocation to the roots (Leuschner et al., 2001). Extreme drought, however, may reduce root biomass, particularly for less drought adapted species like spruce (Polomski and Kuhn, 1998; Rötzer et al., 2009). Further, species mixing can change

share and distribution of roots in forests. For example spruce in inter-specific neighborhood or in mixed stands with beech showed lower root biomasses respectively lower fine root production compared to spruce trees in intra-specific neighborhood or in monospecific stands (Goisser et al., 2016; Bolte et al., 2013).

In this study we analyse any annual growth differences between Norway spruce and European beech. We examine whether stem diameter growth is equal in inter- and intra-specific neighborhood, i.e., whether it is modified by species mixing under normal and extremely dry conditions. We further scrutinize whether the diameter increments of the upper stem and of the main roots are similar to the increments at breast height under normal conditions and also under extremely dry conditions. Extreme drought conditions were induced by a rainfall exclusion experiment (Pretzsch et al., 2014b). This way, the following research questions arise

(1) How do spruce and beech trees differ in their growth reaction on drought stress (2014 vs. 2015 and control vs. drought treatment)?
(2) Are there differences in the stress reaction on drought between trees in intra- and inter-specific neighborhood?
(3) To which extent do drought periods modify the growth development of the stem (diameter at breast height (1.3 m) and 50% height) and the main roots of spruce and beech trees?

2. Material and methods

2.1. Study area Kranzberg forest

Located in Southern Germany, about 35 km Northeast of Munich the study site Kranzberg Forest (longitude: 11°39′42″E, latitude: 48°25′12″N, elevation 490 m a.s.l) has an average annual precipitation of 750–800 mm yr^{-1} and of 460–500 mm during the growing season (May - September), both for the period 1971–2000. The average air temperature is at 7.8 °C on annual average and 13.8 °C on a seasonal basis (Hera et al., 2011). The forest stand has a size of 0.5 ha and stocks on a luvisol originating from loess over Tertiary sediments and providing high nutrient and water supply (Göttlein et al., 2012; Pretzsch et al., 1998). Depending on soil depth the water holding capacity for plant available water ranged between 17% and 28%, while soil pH pH_{H2O} varied between 4.1 and 5.1. The mixed stand comprises groups of beech trees surrounded by spruce trees. By coring each tree to the heart wood in a height of 30 cm tree age was assessed as 63 ± 2 years for spruce and 83 ± 4 years for beech for the year 2014.

2.2. The KROOF rainfall exclusion experiment

The Kranzberg Forest is part of the age series of a long term forest experiment (Pretzsch et al., 1998). Within the Kranzberg Forest site 12 experimental plots were established. Already in spring 2010 trenching was performed to avoid effects on tree growth in the study phase (Pretzsch et al., 2016b). Lined by a heavy-duty plastic tarp which is impermeable to water and root growth soil was trenched to about 1 m deep. Afterwards it was refilled with the original soil material. A dense clay layer of tertiary sediments prevented further downward-rooting at a depth of app. 1 m (Haberle et al., 2015).

Each plot as well as the entire site consist of intra-specific zones with only spruce and beech trees and a mixed transition zone with both spruce and beech trees. Six of the 12 plots are serving as control plots. At another six plots roofs were built underneath the stand canopy at about 3 m height to induce soil drought, with the first drying cycle being started in April 2014. To induce experimental drought the automated rain exclusion roofs only close during rainfall to exclude unintended micro-meteorological and physiological effects (Pretzsch et al., 2014b).
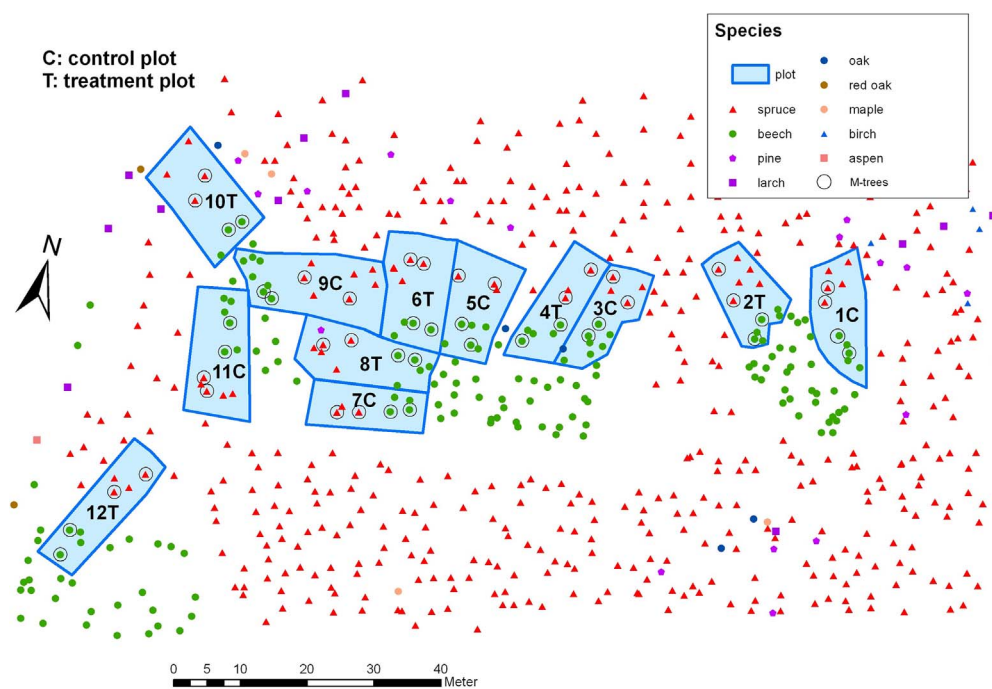
Fig. 1. Map of the site Kranzberger Forst; measurement-trees (M-trees) are highlighted by black circles.

2.3. Description of plots

The sizes of the plots range between 110 and 200 m², amounting to 868 m² and 862 m² in total for the control and drought treatment plots, respectively (Fig. 1). Each plot consists of 4 - 6 beech trees at one side of the plot and the same number of spruce trees at the other side, with a broad contact zone in-between. The comparability of the control and drought treatment plots is shown by the stand characteristics in Table 1. Edge effects are minimized as trees used for detailed measurements (M-trees) are far enough away from the plot edges (Pretzsch et al., 2016b).

The total area of the twelve plots is 1730 m² with a mean stocking density of 659 trees per ha and a mean basal area of 52 m² per ha. The plots comprise 63 beech trees with an average height of 26.1 m and an average diameter at breast height of 28.9 cm. The 53 spruce trees have an average height of 29 m and an average diameter at breast height of 34.3 cm.

2.4. Soil water content and climate data

Starting in 2013 volumetric soil water content SWC was measured at each of the 12 plots by using time domain reflectometry (TDR 100, Campbell Scientific, Inc., Logan, Utah, USA). Probes are installed in four depths in the centre of each plot representing the volumetric soil water content for the soil layers of 0–7 cm, 10–30 cm, 30–50 cm and 50–70 cm. All probes were assessed weekly during the entire year.

Daily meteorological data (air temperature, humidity, wind speed, radiation, and precipitation) were provided by the forest climate station "Freising" which is about 1.5 km away from the study site and part of the European Level 2 programme (LWF, 2016).

2.5. Dendrometrical measurements

Overall, at each plot 2 spruce and 2 beech trees with intra- and interspecific neighborhood were chosen for detailed measurements (M-trees). Automatic point dendrometers (Deslauriers et al., 2003) of the

Table 1
Characteristics of the 12 plots (N: number of trees per ha; BA: basal area per ha; V: total stem volume per ha; hq: mean height; dq: quadratic mean diameter at 1.3 m breast height).

Area (m²)	Spruce					Beech					Total		
	N	BA (m²)	V (m³)	hq (m)	dq (cm)	N	BA (m²)	V (m³)	hq (m)	dq (cm)	N	BA	V
Control plots													
1	132	379	33.1	454	28.6	33.4	379	23.4	312	25.9	28.0	758	56.5	766
3	110	364	35.8	501	29.3	35.4	545	31.5	421	25.7	27.1	909	67.3	922
5	142	211	19.5	271	28.9	34.3	352	20.5	271	25.8	27.3	563	40.0	542
7	199	352	40.3	571	30.1	38.1	302	18.4	245	25.9	27.9	654	58.7	816
9	111	270	27.2	416	29.4	32.5	359	29.7	416	26.7	32.4	629	56.9	832
11	174	230	22.4	316	29.2	35.3	172	13.7	188	26.6	31.8	402	36.1	504
mean	**145**	**301**	**29.7**	**422**	**29.3**	**34.8**	**352**	**22.9**	**309**	**26.1**	**29.1**	**653**	**52.6**	**730**
Treatment plots													
2	115	520	58.2	827	30.0	37.7	520	24.6	316	25.2	24.5	1040	82.8	1143
4	128	235	23.1	322	29.3	35.4	392	26.0	351	26.1	29.0	627	49.1	673
6	162	185	15.9	220	28.5	33.1	247	24.8	355	27.1	35.7	432	40.7	575
8	156	320	29.3	405	28.8	34.1	320	15.6	199	25.3	24.9	640	44.9	604
10	164	305	24.6	336	28.1	32.0	366	27.7	385	26.5	31.1	671	52.3	721
12	137	292	21.6	290	27.6	30.7	292	17.0	223	25.8	27.2	584	38.6	513
mean	**144**	**310**	**28.8**	**400**	**28.7**	**33.8**	**356**	**22.6**	**305**	**26.0**	**28.7**	**666**	**51.4**	**705**

DR-type (Ecomatik, Dachau, Germany) were used for constant measurements of stem growth in breast height (1.3 m) dbh and 50% tree height H50. Before the installation of dendrometers, the outermost bark of the spruce trees was removed to reduce the swelling and shrinking effect of the bark. The dendrometers consist of aluminium frames and are fixed with special screws on the tree stem. Measurements are based on a precision linear variable transducer. The transducers are placed directly in contact with the bark.

To measure the root's diameter increment of the 48 M-trees circumference dendrometers of the DC2 type were used and fixed on one main root. The tension is applied in radial direction. Slide rings reduce the friction between the wire cable and the tree bark. Dendrometers were installed, if applicable, in NW-direction, to avoid environmental influences.

Variations of radial growth were determined in 10 min intervals. Consequently both, the irreversible tree growth and the reversible swelling and shrinking of stem and root can be recorded.

2.6. Statistical analysis of annual increments

We used linear mixed effect models for relating annual dbh-, H50, and root diameter increments to the four factors of the experiment, which are tree species (Norway spruce, European beech), treatment (control, drought treatment), local competition (intraspecific, interspecific), and year (2014, 2015). These analyses were done separately for the increments of dbh, H50 diameters, and root diameters with the diameter increments as goal variables and with the above-mentioned factors as predictors. Due to the nested data structure, random effects on plot and tree level were included in the models' intercepts.

When fitting the models, we started with a version that included all four fixed effects variables, including all possible interactions. We used Wald tests on the fitted models to identify significant fixed effects and stepwise omitted non-significant ones in line with a procedure suggested by Zuur et al. (2009). Hereby, we prioritized the omission of more complex terms (interactions) to less complex ones. If an interaction was significant, the corresponding main effects and contained lower-level interactions were kept in the model even in case they were not significant themselves. Following this procedure, we ended up with fairly simple models. The lowest significance level we accepted for keeping variables in such a model was $p < 0.1$. This high tolerance was chosen because we did not want to risk an undue premature constriction of the variable set to be used in the final step of the analysis: From the parameter estimates of the final models we estimated diameter increments and corresponding standard errors for all combinations of fixed effects in the final models. As these diameter increment estimates are linear combinations of the model parameter estimates, they could in turn be tested against each other for significant differences. I.e. if their pair-wise differences deviate significantly from zero, they are significantly different.

2.7. Statistical analysis of inter-annual growth patterns

Based on the dendrometer-equipped trees we scrutinized the intra-annual dbh-, H50-, and root diameter growth patterns for differences by species (spruce, beech), treatment (control, drought treatment), local competition (intraspecific, interspecific), and year (2014 = normal climate, 2015 = extreme dry year). As diurnal diameter variation was not in focus of this analysis, we only used the diameter values reached at the end (11:50 p.m.) of each day. While 2015 was covered with measurements from 1st January to 31st December, measurements in 2014 started on April 1st (day 90). During the statistical analyses reported below it turned out that the 2015 data had to be clipped to the same starting date in order to obtain plausible results. At that time (April 1st) tree growth has not yet started.

For the statistical analysis there were some frame conditions we had to keep: (i) Classic s-shaped growth models (like the Logistic or the Gompertz function) could not be used for describing the intra-annual diameter growth, because many trees pronouncedly showed non-s-shaped development. (ii) due to the nesting levels tree and tree in plot, the single measurements could not be taken as statistically independent.

This lead us to the following approach, based on a Generalized Additive Mixed Model (GAMM; Wood, 2011; Zuur et al., 2009):

$$\ln(RD_{ijkl}) = f(DAY_l, \mathbf{cat}_{ijk}) + \mathbf{cat}'_{ijk} \cdot \boldsymbol{\beta} + \beta_0 + b_i + b_{ij} + \varepsilon_{ijkl} \qquad (1)$$

The indexes i, j, k, l represent the plot, tree, year (2014, 2015) and day-in-year (1–365) level. *RD* is a variable we call relative diameter, for a given day in a given year it calculates as dividing a tree's diameter on that day by the tree's diameter on the first day in the year (in our case 1st April). Thus, the first RD value of each tree in both years is 1. The function *f()* is a non-linear smoothing function which describes the course of ln(*RD*) over the days of a year. This function is a allowed to be different for each specification of **cat**, which is a vector of categorial variables of interest (see below). The vector **β** corresponds to the fixed linear effects connected to each specification of **cat**, and β_0 is the model's intercept. The random effects on plot level, b_i, and on tree-in-plot level b_{ij} are assumed to be normally distributed with an expectation of zero, and the same assumption is made for the i.i.d. errors ε_{ijkl}.

For understanding the variable **cat** it is important to clarify the explanatory variable combinations to test against each other. The connection of species, treatment, local competition, and year leads to $2 \times 2 \times 2 \times 2 = 16$ possible specifications. As our statistical software didn't allow to have more than one categorial variable for specifying the smoother function *f()*, the variable **cat** was designed, which represents each of the 16 specifications as one category (see supplementary Table 1 for the design of **cat**).

The logarithmic transformation of *RD* has an important property for the purpose of this study as it allows to fit a model with an additive error structure to data which in reality have a multiplicative error structure. The idea is to have the smoother $f(DAY_l, \mathbf{cat}_{ijk})$ in Eq. (1) to describe the category-specific average course of ln(RD) and to have the term $\mathbf{cat}'_{ijk} \cdot \boldsymbol{\beta} + \beta_0$ to adjust the population level prediction of ln(RD) at values sufficiently near to zero for the first included day of the year for each category. This means the (delogarithmized) prediction of RD = exp(ln(RD)) being sufficiently near to 1. In the delogarithmized form of Eq. (1) exp(b$_i$) and exp(b$_{ij}$) are multiplicative random effects which means that they influence small RD values less than higher ones, in other words, for a normally growing tree they influence more the amount of cumulative growth during the year than its level.

We visually tested for significant differences between the effects of different specifications of **cat** by plotting the delogarithmized corresponding population level predictions together with their 95 % confidence intervals. All statistical analyses were performed with the software R (R Core Team, 2014), namely the package mgcv (Wood, 2011).

3. Results

3.1. Climate and water supply of the years 2014 and 2015

The climate of the two analysed years 2014 and 2015 reveal clear differences. For 2014 air temperature (15.2 °C), potential evapotranspiration (506 mm) and precipitation amount (423 mm) of the growing season were close to the respective long term means from 2001 to 2015 (15.5 °C, 539 mm, 446 mm; data: LWF, 2016). In 2015, the air temperature was 1.1 °C above the average, the potential evapotranspiration sum 27 mm above the average and precipitation sum with 328 mm clearly below the respective long term mean of the growing season. The strong drought period of the growing season 2015, however, was exceeded considerably by the drought of the year 2003 (temperature 18.0 °C, potential evapotranspiration 647 mm, precipitation 282 mm; all values for the growing season).
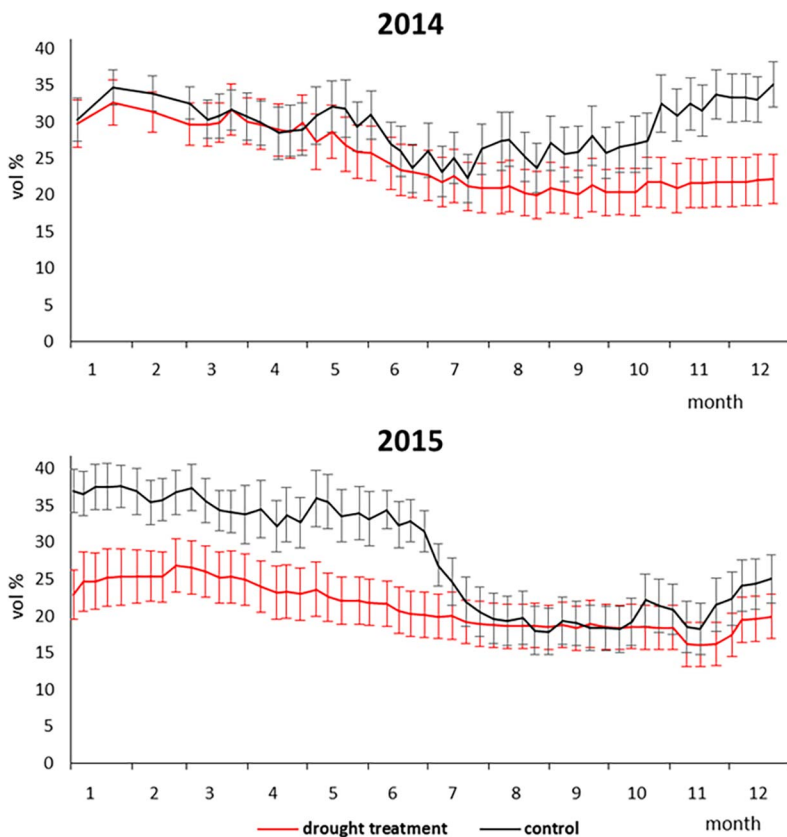
2014

2015

A good indicator of the trees' water supply are the soil water content measurements for the control and the treatment plots, at which rain fall was excluded from the 6th May 2014 to the 9th December 2014 and from the 10th March 2015 to the 21st November 2015 (Fig. 2, data: Kallenbach et al., 2017).

The soil water content (SWC) of the control plots reveal a stronger drop for the year 2015 compared with 2014, particularly in July. At the drought treatment plots in both years lowest soil water content levels can be seen, with minimum values in September and October 2015. The soil water contents of the treatment plots for the year 2015 displayed low values already in January and stayed below the corresponding values of the year 2015: This denotes high water stress for the trees. Interestingly, SWC of the control and the drought treatment plots were almost equal in late August and September of the year 2015.

Based on these climate and water balance conditions the development of the diameter increment of spruce and beech trees differs between the years 2014 and 2015 as well as between the control and the drought treatment plots at the H50, dbh and root level (Fig. 3).

Already with the beginning of April (> doy 100) a steep increase of stem and root growth of the evergreen tree species spruce can be seen, while stem increment of the deciduous tree species beech was delayed for app. 2–4 weeks. In this period (April to June) soil water content was at a high level. With beginning of May, however, the SWC under the drought treatment trees decreased stronger than the SWC under the control trees, resulting in lower growth rates for both species but more pronounced for the spruce trees (Fig. 2).

3.2. Annual diameter increments

3.2.1. Annual diameter increment at breast height

The final statistical model for the annual diameter increment at breast height IDBH can be written as

$$IDBH_{ijk} = \beta_0 + \beta_1 \cdot Species_{ij} + \beta_2 \cdot Treat_i + \beta_3 \cdot Year_k + \beta_4 \cdot Treat_i \cdot Year_k$$
$$+ \beta_5 \cdot Species_{ij} \cdot Year_k + \beta_6 \cdot Species_{ij} \cdot Treat_i + b_i + b_{ij} + \varepsilon_{ijk} \quad (2)$$

The indexes i, j, and k represent the plot, tree and year level, respectively. The variable $Species$ is a dummy-coded variable which is 0 if the tree of interest is a European beech (reference) and 1 if it is a Norway spruce. Likewise, the variable $Treat$ is 0 if the plot of interest is a control plot and 1 in case it is a drought treatment plot. The variable $Year$ was coded in the same way with the "normal" year 2014 as the reference ($Year = 0$) and the drought year 2015 represented as 1. The corresponding fixed effects' coefficients are $\beta_0, \dots \beta_5$. Random effects on plot and tree level are noted as b_i and b_{ij} ($b_i \sim N(0,\tau_1^2)$, $b_{ij} \sim N(0,\tau_2^2)$), while ε_{ijk} represents i.i.d. errors ($\varepsilon_{ijk} \sim N(0,\sigma^2)$).

Intra- and interspecific neighborhood did not show any significant relation with $IDBH$, thus, the corresponding fixed effect variable was left out of the final model which is limited to the three main explanatory variables species, treatment, year and the three possible two-way-interactions with significant effects (Table 2a). The parameter estimates for the fitted Eq. (2) are shown in supplementary Table S2.

Drought treatment and year as main effects had significant ($p < 0.01$ and $p < 0.001$) effects on dbh increment (supplementary Table S3). A tree's species did not have a significant influence as a main effect, but its significant interactions with year and treatment ($p < 0.001$, $p < 0.05$) show that the growth reactions on climatically different years and on treatment are species specific. Linear combinations of the parameters of the fitted model (supplementary Table S2) allow to quantify these effects (supplementary Table S3). **Highest dbh increment for Norway spruce was found for the control plots in 2014 (2.4 mm/yr).** With one exception, the estimated IDBH are significantly different from zero ($p < 0.001$). This exception is Norway spruce on the drought treatment plots in 2015, where the estimated increment (0.24 mm/yr) does not significantly deviate from zero. The increment estimates shown in supplementary Table S3 were pairwise contrasted against each other in order to test for differences due to species,
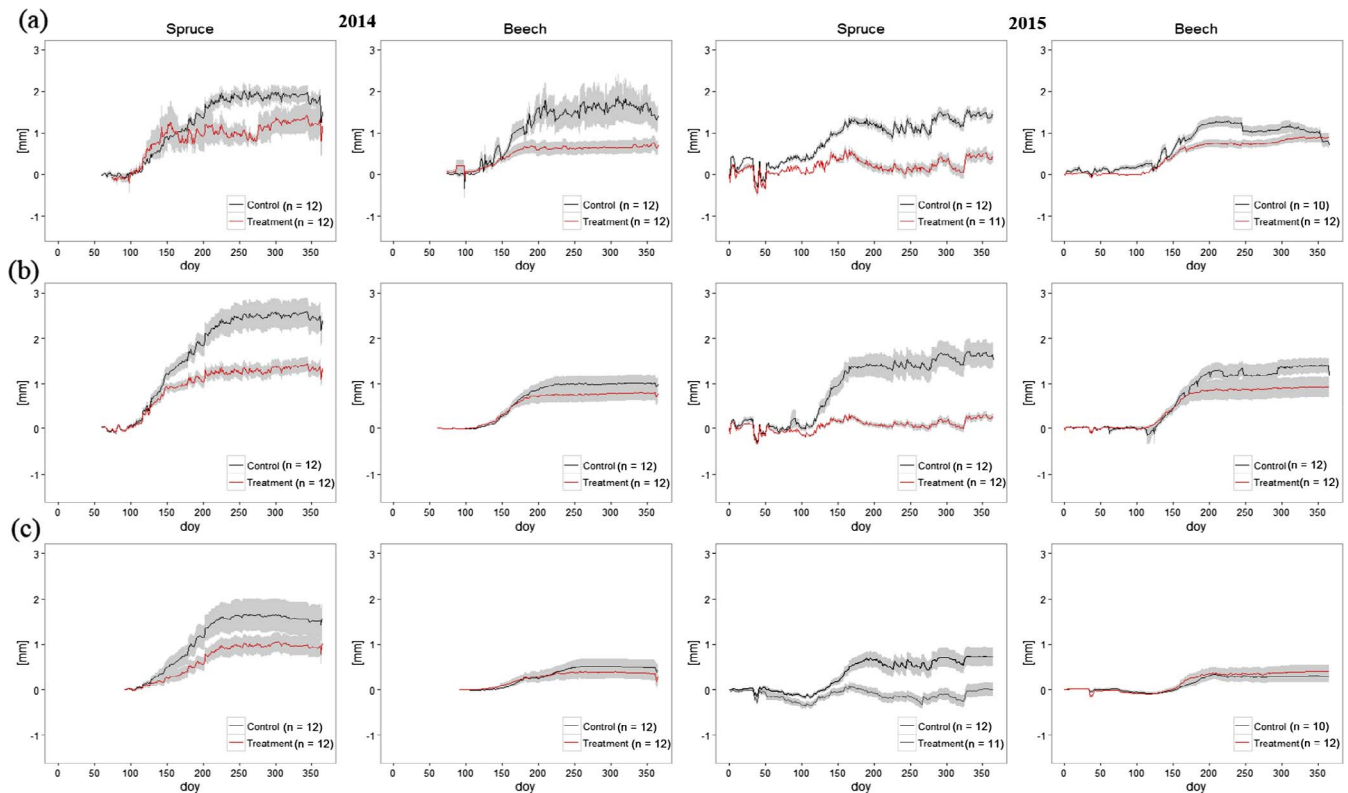
Fig. 3. Diameter increment of spruce and beech trees at the H50 (a), dbh (b) and root (c) level of the control (black) and drought treatment plots (red) with standard error (grey) for the years 2014 and 2015.

treatment, and year (Table 3).

Neither in the year 2014 nor in the year 2015 drought treatment affects the annual diameter increment of beech significantly (Table 3, lines 1, 2), while the dbh increment of spruce trees under drought treatment was significantly reduced in both years (Table 3, lines 3, 4). Compared to 2014, beech trees on the control plots show a significant higher increment in 2015, while for those on the drought treatment

plots no significant difference is evident (Table 3, lines 5, 6). On both, drought treatment and control plots the diameter increment of spruce was significantly lower in 2015 compared to 2014 (Table 3, lines 7, 8). Spruce trees on the control plots had a higher annual dbh increment than beech in the year 2014 (Table 3, lines 9, 10). On the drought treatment plots IDBH of both species did not differ significantly in 2014, while in 2015, however the dbh increment of spruce trees is

Table 2
Influence variables on *IDBH (a), IH50 (b) and ICR (c)* in the mixed linear model from Eqs. (2)–(4), and their significance. A Wald test was performed on the fitted model after Eqs. (2)–(4) and Supplementary Table S2, S3 and S4. As explained in the methods section, non-significant variables and interactions were kept in the model if they were part of a significant higher-level interaction. Significance symbols: '.': $p < 0.1$, '*': $p < 0.05$, '**': $p < 0.01$, 'a': $p < 0.001$.

Fixed Effect	Numerator DF	Denominator DF	F-Value	p	Significance
(a)					
Species	1	35	3.5444	0.0681	.
Treat	1	10	13.8452	0.0040	**
Year	1	44	18.9472	0.0001	***
Treat x Year	1	44	3.7465	0.0594	.
Species x Year	1	44	60.0644	< 0.0001	***
Species x Treat	1	35	5.6475	0.0231	*
(b)					
Species	1	30	0.9254	0.3437	
Treat	1	10	8.4069	0.0158	*
Year	1	40	7.2201	0.0105	*
Treat x Year	1	40	0.0752	0.7854	
Species x Year	1	40	2.0867	0.1564	
Species x Treat	1	30	2.2040	0.1481	
Species x Treat x Year	1	40	8.8639	0.0049	=
(c)					
Species	1	32	10.1675	0.0032	**
Treat	1	10	2.6509	0.1345	
CSpecies	1	32	0.7771	0.3846	
Year	1	42	14.9602	0.0004	***
Treat x CSpecies	1	32	5.6270	0.0239	*
Species x Year	1	42	17.5211	0.0001	***
Species x Treat	1	32	3.6326	0.0657	.

Table 3

Pair-by-pair comparisons of the dbh increment estimates shown in supplementary Table S3 for beech (B) and spruce (S) of the control (C) and drought treatment plots (T) for the years 2014 and 2015. Significance symbols: '.': p < 0.1, '*': p < 0.05, '**': p < 0.01, '***': p < 0.001. Estimates with significance levels of p < 0.05 and higher are printed in bold.

Table Line #	Contrasted factor combinations	Estimated DBH increment difference [mm/yr]	Std. Error	p	Significance
1	B T 2014 – B C 2014	−0.1755	0.2941	0.5506	
2	B T 2015 – B C 2015	−0.4994	0.2938	0.0892	.
3	S T 2014 – S C 2014	**−1.0776**	0.2971	0.0003	***
4	S T 2015 – S C 2015	**−1.4014**	0.2971	0.0000	***
5	B C 2015 – B C 2014	**0.4413**	0.1358	0.0012	**
6	B T 2015 – B T 2014	0.1174	0.1320	0.3737	
7	S C 2015 – S C 2014	**−0.7558**	0.1325	0.0000	***
8	S T 2015 – S T 2014	**−1.0796**	0.1325	0.0000	***
9	S C 2014 – B C 2014	**1.4091**	0.2825	0.0000	***
10	S C 2015 – B C 2015	0.2120	0.2809	0.4504	
11	S T 2014 – B T 2014	0.5070	0.2760	0.0662	.
12	S T 2015 – B T 2015	**−0.6901**	0.2774	0.0128	*
13	(T 2015 – C 2015) – (T 2014 – C 2014) (Species overarching comparison of treatment effect 2015 vs. 2014)	**−0.3238**	0.1538	0.0353	*

Table 4

Pair-by-pair comparisons of the diameter-in-50%-tree-height increment estimates shown in Supplementary Table S5 for beech (B) and spruce (S) of the control (C) and drought treatment plots (T) for the years 2014 and 2015. Significance symbols: '.': p < 0.1, '*': p < 0.05, '**': p < 0.01, '***': p < 0.001. Estimates with significance levels of p < 0.05 and higher are printed in bold.

Table Line #	Contrasted Factor Combinations	Estimated increment difference [mm/yr]	Std. Error	p	Significance
1	B T 2014 - B C 2014	−0.6233	0.3370	0.0644	.
2	B T 2015 - B C 2015	0.0980	0.3370	0.7712	
3	S T 2014 - S C 2014	−0.4470	0.3220	0.1650	
4	S T 2015 - S C 2015	**−1.2384**	0.3220	0.0001	***
5	B C 2015 - B C 2014	**−0.5268**	0.2659	0.0476	*
6	B T 2015 - B T 2014	0.1945	0.2535	0.4430	
7	S C 2015 - S C 2014	−0.1371	0.2427	0.5723	
8	S T 2015 - S T 2014	**−0.9284**	0.2535	0.0003	***
9	S C 2014 - B C 2014	0.2584	0.3303	0.4340	
10	S C 2015 - B C 2015	**0.6481**	0.3303	0.0497	*
11	S T 2014 - B T 2014	0.4346	0.3289	0.1864	
12	S T 2015 - B T 2015	**−0.6883**	0.3289	0.0364	*
13	(B T 2015 – B C 2015) – (B T 2014 – B C 2014) (Comparison of Treatment Effect Beech 2015 vs. 2014)	**0.7213**	0.3674	0.0496	*
14	(S T 2015 – S C 2015) – (S T 2014 – S C 2014) (Comparison of Treatment Effect Spruce 2015 vs. 2014)	0.1762	0.4661	0.7054	

clearly lower than it is for beech (Table 3, lines 11, 12).

As the interaction species-treatment-year had to be excluded from the mixed linear model (Eq. (2)) due to non-significance, differences in the drought treatment effects of 2015 and 2014 could be tested only as averaged over the tree species (Table 3, line 13). We observed a significantly stronger increment reduction (-0.3 mm/yr) for the drought treatment plots in 2015 compared to 2014.

3.2.2. Annual diameter increments at 50% tree height

The final model for the annual diameter increment at 50% tree height IH50 was:

$$
\begin{aligned}
IH50_{ijk} = {} & \beta_0 + \beta_1 \cdot Species_{ij} + \beta_2 \cdot Treat_i + \beta_3 \cdot Year_k + \beta_4 \cdot Treat_i \cdot Year_k \\
& + \beta_5 \cdot Species_{ij} \cdot Year_k + \beta_6 \cdot Species_{ij} \cdot Treat_i + \beta_7 \cdot Species_{ij} \cdot Treat_i \cdot \\
& Year_k + b_i + b_{ij} + \varepsilon_{ijk}
\end{aligned}
\tag{3}
$$

This model has almost exactly the same structure as the one for dbh increment (Eq. (2)). In addition to the IDBH model, the three-way interaction of species, treatment, and year was significant and was thus kept in the equation (Table 2b). Similar as for IDBH, there was no significant relation with intra- or interspecific neighborhood (supplementary Table S4). As can be taken from Table 2b, IH50 was significantly different by treatment and year, but not for species. However, due to the corresponding significant three-way-interaction, there is a species- and year-specific treatment effect. Linear combinations of the parameters of the fitted model (supplementary Table S4) were used for quantifying these effect (supplementary Table S5). Similar as for IDBH, highest IH50 was found for spruce on the control plots in 2014 (1.6 mm/yr; supplementary Table S5, line 1). In parallel, also the 2015 IH50 of spruce on the drought treatment plots (0.2 mm/yr) is the only one which is not significantly different from zero. The increment estimates shown in supplementary Table S5 were pairwise contrasted against each other in order to test for differences due to species, treatment, and year (Table 4).

Neither in 2014, nor in 2015 did beech trees' diameter in 50% of the tree height grow significantly different under drought treatment compared to the control plots (Table 4, lines 1, 2). For spruce trees a significant reduction of the increment due to drought treatment could only

be seen in 2015 (Table 4, lines 3, 4). In year the 2015 IH50 of beech trees of the control plots was significantly reduced compared to the year 2014, while at the drought treatment plots no significant difference is evident (Table 4, lines 5, 6). The annual diameter increment of spruce trees at the control plots did not differ significantly between the years 2014 and 2015. For the drought treatment a clear and significant reduction of the increment for 2015 in comparison to 2014 can be seen (Table 4, lines 4, 8). Compared to beech trees the IH50 of spruce trees on the control plots is not significantly different in 2014. However, on the same plots in 2015 spruce trees grew significantly more than beech trees (Table 4, lines 9, 10). For the drought treatment plots a significant higher diameter increment of beech compared to spruce can be seen in 2015, while for 2014 no such difference is obvious (Table 4, lines 11, 12). No significant difference between drought treatment and control can be seen for spruce when comparing the years 2014 and 2015. For beech, in contrast, the drought treatment effect was significantly lower in 2015 (Table 4, lines 13, 14).

3.2.3. Effects on diameter increments for main coarse roots

The final model for the annual coarse root diameter increment ICR was

$$
\begin{aligned}
ICR_{ijk} = {} & \beta_0 + \beta_1 \cdot Species_{ij} + \beta_2 \cdot Treat_i + \beta_3 \cdot CSpecies_{ij} + \beta_4 \cdot Year_k \\
& + \beta_5 \cdot Treat_i \cdot CSpecies_{ij} + \beta_6 \cdot Species_{ij} \cdot Year_k + \beta_7 \cdot Species_{ij} \cdot Treat_i \\
& + b_i + b_{ij} + \varepsilon_{ijk}
\end{aligned}
\tag{4}
$$

All variables and notations have the same meaning as in Eqs. (2) and (3). In addition, the variable *CSpecies* allows to distinguish between intra, and interspecific neighborhood. This variable is 0, if the tree of interest's competitors are European beeches and 1, if they are Norway spruces. With the four main effects species, treatment, year, intra-/interspecific competition, only 3 out of the 6 possible 2-way -interactions

Table 5
Estimated increments of the coarse root diameter increments from the fitted model after Eq. (4) and Supplementary Table S6. Species names in parentheses indicate the species that dominates a tree's competitive environment. Significance symbols: '.': p < 0.1, '*': p < 0.05, '**': p < 0.01, '***': p < 0.001.

Table line #	Factor combination	Estimated increment [mm/yr]	Std. Error	p	Significance
1	Beech (Beech) Control 2014	0.6244	0.2190	0.0044	**
2	Beech (Beech) Control 2015	0.6292	0.2190	0.0041	**
3	Beech (Beech) Treat 2014	0.2007	0.2207	0.3632	
4	Beech (Beech) Treat 2015	0.2054	0.2207	0.3519	
5	Beech (Spruce) Control 2014	0.0821	0.2190	0.7079	
6	Beech (Spruce) Control 2015	0.0868	0.2190	0.6919	
7	Beech (Spruce) Treat 2014	0.4639	0.2207	0.0355	*
8	Beech (Spruce) Treat 2015	0.4686	0.2207	0.0337	*
9	Spruce (Beech) Control 2014	1.8914	0.2210	0.0000	***
10	Spruce (Beech) Control 2015	0.9421	0.2210	0.0000	***
11	Spruce (Beech) Treat 2014	0.8186	0.2226	0.0002	***
12	Spruce (Beech) Treat 2015	−0.1306	0.2378	0.5828	
13	Spruce (Spruce) Control 2014	1.3490	0.2210	0.0000	***
14	Spruce (Spruce) Control 2015	0.3998	0.2226	0.0705	.
15	Spruce (Spruce) Treat 2014	1.0818	0.2226	0.0000	***
16	Spruce (Spruce) Treat 2015	0.1326	0.2378	0.5772	

and no higher order interactions have been significant (Table 2c). However, in contrast to IDBH and IH50 intra- and interspecific competition have a different effect on ICR (Table 2c). This effect is not due to *CSpecies* as a main effect but in interaction with treatment, which indicates that drought treatment effects on root diameter growth were different in intra- and interspecific neighborhood.

A tree of interest's species, i.e., .the local competition, has a significant influence on ICR, while a species-specific drought treatment effect is just not significant on the level of p < 0.05. The calendar year (2014, 2015) has a significant stand-alone influence, but also a species specific one (supplementary Table S6).

In the same way as for IDBH and IH50, we used linear combinations of the parameters of the fitted model (supplementary Table S6) for quantifying these effect (Table 5). ICR of beech in intraspecific neighborhood displays neither for the year 2014 nor for 2015 a significant increment under drought treatment (Table 5, lines 3, 4). The same is obvious for beech trees in interspecific neighborhood for the control plots (Table 5, lines 5, 6), while at the drought treatment plots in both years a significant increment of beech is evident (Table 5, lines 7, 8). ICR of spruce trees in intra- as well as in interspecific neighborhood was significant and high in 2014 under drought treatment, but not in 2015 (Table 5, lines 11, 12, 15, 16). At the control plots coarse roots of spruce in interspecific neighborhood grew well in both years (Table 5, lines 9, 10), spruce in intraspecific neighborhood, however, only in 2014 (Table 5, lines 13, 14).

The increment values given in Table 6 were contrasted against each other; due to the structure of the ICR model (Eq. (4)), there were less meaningful combinations to test (e.g. testing for calendar year specific treatment effects would make no sense). No effect of the drought treatment on the ICR of beech trees in intra- and interspecific neighborhood is evident (Table 6, lines 1, 2). Spruce trees in interspecific neighborhood showed a significant effect under the drought treatment with a strong reduction of ICR, while in intraspecific neighborhood this effect was not apparent (Table 6, lines 3, 4). The general annual diameter increment (including drought treatment and control, intra- and interspecific competition) of the beech coarse roots is not differing significantly between the two years (Table 6, line 5). Coarse roots of spruce trees, on the other hand, grew significantly better in 2014 compared to 2015 (Table 6, line 6).

3.3. Statistical model for the diameter increment of spruce and beech trees under extreme drought

The course of the daily diameter increments of spruce and beech trees for the years 2014 and 2015 under control and the drought treatments are displayed in Fig. 4 as results of GAMM modelling. No overlapping of green and red areas indicate significant differences in the growth curves. While in 2014, the diameter increments of spruce and beech trees at the H50 level and of spruce trees at the dbh was significantly different, there were no significant differences in the growth course of beech trees at dbh level as well as of spruce and beech trees at the root level. In 2015, the diameter increment course of spruce of the control plots differed significantly at all three level from trees of the drought treatment plots. For beech trees, on the other hand, no differences in the growth patterns at control and drought treatment plots are obvious. No differences at all were found between interspecific and intraspecific competition.

4. Discussion

Within this study we analysed annual diameter increments of trees within a forest stand. Differences based on the tree species spruce and beech, on inter- and intraspecific neighborhood and at different levels of the stem (dbh and 50% height) and at one main coarse root, were studied. Our focus was on annual tree diameter growth under extreme drought conditions established by a rainfall exclusion experiment and within the hot and dry year 2015.

4.1. Effects of tree species on stem and root growth

Studies of Norway spruce and European beech under drought showed that spruce decreases stronger in growth compared with beech in drought years like in 1976 or 2003 (Pretzsch, 2005; Pretzsch et al., 2013). This can also be seen when comparing the diameter increments of beech and spruce for the drought year 2015 with the year 2014
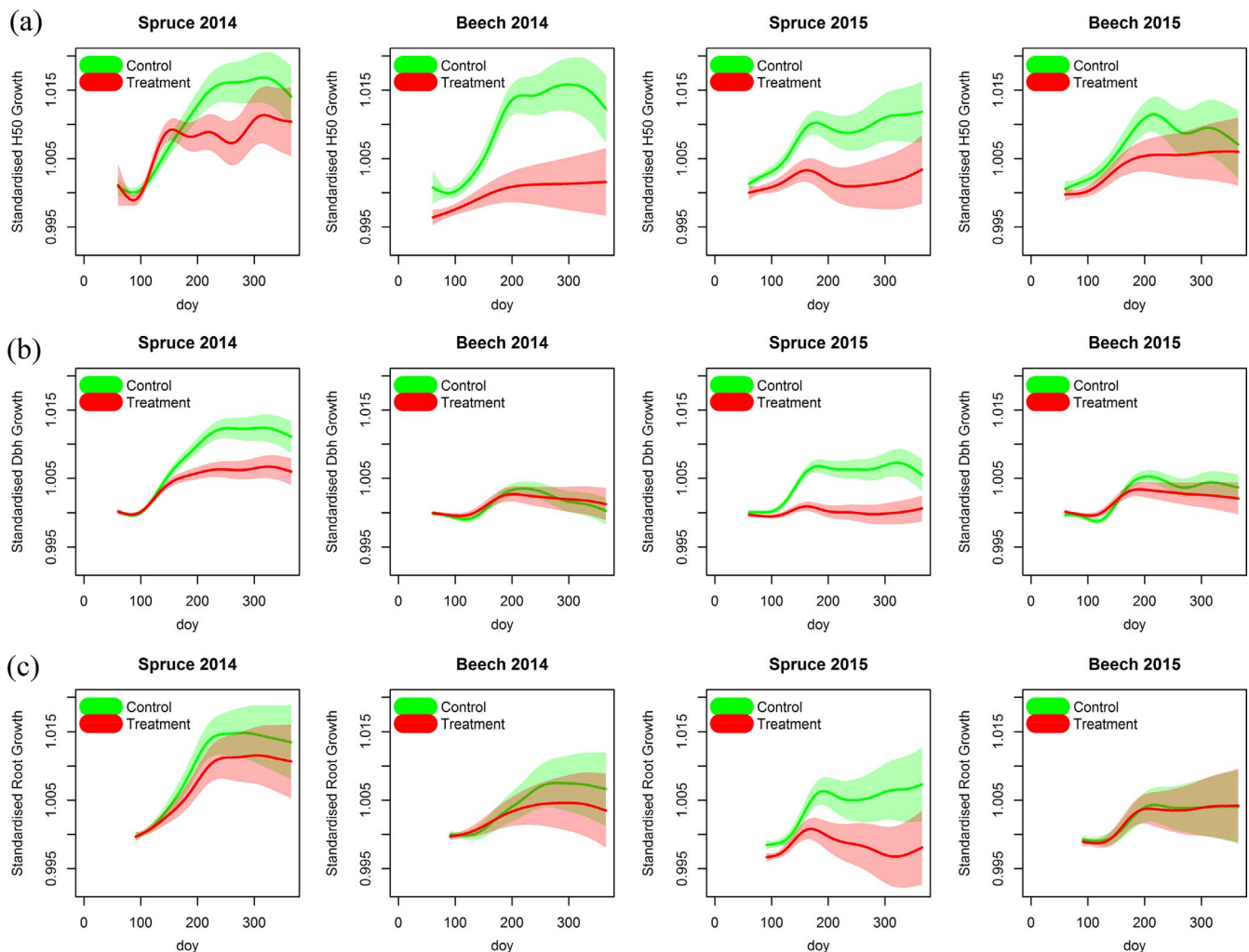
Table 6
Pair-by-pair comparisons of the coarse root diameter increment estimates shown in Table 5 for beech (B) and spruce (S) of the control (C) and drought treatment plots (T) for the years 2014 and 2015, and inter- and intraspecific competition (species abbreviation in parentheses). Significance symbols: '.': p < 0.1, '*': p < 0.05, '**': p < 0.01, '***': p < 0.001. Estimates with significance levels of p < 0.05 and higher are printed in bold.

Table line #	Contrasted Factor Combinations	Estimated increment difference [mm/yr]	Std. Error	p	Significance
1	B (B) T - B (B) C	−0.4238	0.2916	0.1462	
2	B (S) T - B (S) C	0.3818	0.2916	0.1905	
3	S (B) T - S (B) C	**−1.0728**	0.2976	0.0003	***
4	S (S) T - S (S) C	−0.2672	0.2976	0.3693	
5	B 2015 - B 2014	0.0047	0.1524	0.9752	
6	S 2015 - S 2014	**−0.9492**	0.1634	0.0000	***

Fig. 4. Generalized additive mixed model on the standardized daily diameter increments of spruce and beech trees at the H50 (a), dbh (b) and root (c) level for the years 2014 and 2015.

(Fig. 3). Particularly in the summer months soil water content under the trees of the drought treatment plots decreased stronger than under the trees of the control plots, which lead to lower growth rates for both species however more pronounced for the spruce trees (Fig. 2). The strong drop in the SWC in 2015 at the end of June with remaining very low available water for the next months (control, Fig. 2) are responsible for the low or no diameter growth rates in the summer months. This reaction pattern was stronger for the spruce trees and even more distinct under the drought treatment (Fig. 3).

The found species differences in the growth of beech and spruce under drought can also be explained with their different water conservation strategies. Isohydric species like spruce close their stomata immediately during a drought event (Pretzsch et al., 2014b; del Río et al., 2014) to maintain a consistent minimum leaf water potential and prevent the tree from high water losses and disruptions of the water balance. However, this stomata response can reduce carbon dioxide and finally leaf carbon uptake which leads to carbon starvation (Roman et al., 2015; Klein, 2014, McDowell et al., 2008). Under the rainfall exclusion experiment and particularly in the hot year 2015, the growth patterns of spruce revealed typical responses of an isohydric species to drought. The quick stomatal response maintained a minimum leaf water potential (Goisser et al., 2016), while carbon uptake and thus stem and coarse root growth diminished strongly compared to the control trees in 2015 and to the growth in the year 2014. Moreover, preserved photosynthesis under low water status can cause stem shrinkage due to low water status of cells as observed for spruce under

drought treatment and in 2015. When water availability increases again, stomata open, cells saturate with water and tree stems swell again.

On the contrary, anisohydric species like beech close their stomata slowly during droughts, therefore the leaf water potential decreases markedly with changes in evaporative demands (Klein, 2014). Hence, anisohydric species are under the risk of hydraulic failure and cavitation (McDowell et al., 2008), though gas exchange and photosynthesis can still continue (Kolb and Stone, 2000). Stem and root growth of the analysed beech trees in 2015 were not significantly different compared to the growth in the year 2014. In addition, the growth differences between control and drought treatment were markedly smaller compared to spruce. These reactions are a consequence of the anisohydric water management strategy of beech that high levels of stomatal conductance preserve carbon uptake and stem and root growth.

Trees species have different adaption strategies to drought stress. Recent research found that some species accumulate more non-structural carbohydrates (NSC) during drought stress, leading to a better maintenance of osmoregulation and hydraulic function (O'Brien et al., 2014). Consequently, species with more NSC have a higher drought resistance. NSC accumulation in trees is important for survival under stress since they indicate a trade-off between photosynthesis (carbon availability, growth) and respiration (Chapin et al., 1990; Dietze et al., 2013; O'Brien et al., 2014). This highlights that species can react different to drought stress concerning their water management.

4.2. Tree growth reaction pattern under drought stress in inter- and intra-specific neighborhood

Studies showed that in mixed stands both species rather keep to their behaviour like in monocultures. Independent of species no evidence was found for a significant stress increase or decrease for trees when comparing mixed and monospecific stands (Pretzsch et al., 2013: Thurm et al., 2016). However, studies so far analysed the annual increment in total rather than its course within the year. Our study shows in some cases clear differences in the radial increment between spruce and beech in intra- as well as in inter-specific environment, however only the differences of the ICR were significant. This asynchrony in growth means a temporal diversification of resource uptake which can result in a stress release. For instance, spruce may profit from a released competition for water in early spring when beech is still leafless and lives from the reserves of the previous year. In this period water consumption, photosynthesis and growth of spruce may profit from higher temperature and light supply until beech sprouts in April/May (Rötzer et al. 2017). Afterwards beech in mixture may profit in relation to the monospecific stands, as the admixed spruces are rooting less deeply, so that beeches neighboured by spruce have better growing conditions due to their deeper rooting and lower intra-specific competition for water by neighbouring beeches.

Several studies (e.g. Augusto et al., 2002; Wiedemann, 1942; Block, 1997) prove that differences in tree growth of spruce and beech in mixed versus monospecific stands may be caused by better below-ground resource exploitation, by better litter decomposition and turnover of mineral nutrients. The combination of the rather fast growing and light demanding spruce with slower growing and shade tolerant beech in the lower canopy layer may further increase the capture und use-efficiency of light and thereby the stand productivity (Kelty, 1992; Pretzsch, 2014). In a mixture of a shallow-rooting and light demanding species with a deep-rooting and shade tolerant species water and light may be better exploited than in stands which are more homogeneous in space occupation (Dǎnescu et al., 2016; Pretzsch et al., 2016a). These may result in an overyielding of mixed stands compared to the corresponding monospecific stands (e.g. Pretzsch et al., 2010a; Pretzsch et al., 2012; Rothe, 1997).

In this study, however, no significant differences on stem diameter growth both at the H50 and dbh level in inter- and intraspecific neighborhood for the beech and spruce trees was found. Only the annual diameter increments of the coarse roots were affected by inter- and intraspecific competition. For the same study site Goisser et al. (2016) also found no influence of inter- and intraspecific neighborhood when measuring leaf gas exchange during a drought period in summer 2013 and analyzing the stem diameter growth of the drought year 2003. Reasons of these results could be due to the seasonal timing of drought periods and their intensity and duration (Rötzer et al., 2012) which could compensate the above mentioned positive effects of species mixture. Another possible reason might be the grouped mixing pattern of the site, i.e., that the spruce trees are subject to direct competition with beech trees only along the edges of the group. In consequence, the supposed negative effect of beech trees on the soil water availability of spruce trees in mixture is small.

4.3. Growth partitioning between stem and coarse root as acclimation to drought stress

The large variation in the root-shoot relationship of trees growing under different site conditions (Fogel, 1983; Santantonio et al., 1977) can be explained by the theory that the limitation of a resource leads to the promotion of growth of the plant organ responsible for supplying that critical resource (Comeau and Kimmins, 1989; Keyes and Grier, 1981). Limitation of nutrients and water supply causes a partitioning in favour of roots. Limitation of energy supply raises the investment of biomass into shoots (Kimmins, 1993). In addition to this acclimation to

spatial variation of site conditions trees modify their root-shoot relationship also in dependence on the temporal variation of their growing conditions (Pretzsch et al., 2014c). For instance, water limitation in dry years can drive up the root growth as a measure of acclimation to drought stress. Hagedorn et al. (2016) found that after drought trees preferably allocate carbon to the roots, probably for recovering. In our study coarse root growth under drought stress (Fig. 3c) was not enhanced compared to the control trees. Only, under heavy drought, i.e. for the rainfall exclusion experiment in the year 2015 the coarse roots of beech trees showed higher increments than the control trees (Table 2c, 5–6). We assume that initially fine root growth is promoted while coarse root growth will be intensified afterwards.

Of special interest are the species specific behaviour and differences in the intra- and inter-specific interactions. The isohydric character of Norway spruce, and the anisohydric behaviour of European beeches might modify the diameter growth behaviour and allocation of carbon into the stem, the branches and the roots depending on species in mixed compared with monospecific stands (Pretzsch and Rais, 2016).

Stress caused by low soil water conditions may change not only diameter growth at breast height but also allocation patterns and stem form. Pretzsch et al. (2010b) found that stress caused by ozone fumigation of Norway spruce and European beech induced a shift in resource allocation into height growth at the expense of diameter growth leading to rather cone-shaped stem forms. This way, stress could alter diameter increment differently at different stem heights. Within this study, the patterns of the diameter increment for spruce and beech trees under drought stress were also dependent on the level of measurement (H50, dbh, root; Fig. 4).

5. Conclusions

Diameter growth performance of beech and spruce trees was species specific during the year at all three measurement levels (coarse root, breast height, 50% height). Competition between neighbouring trees revealed in most cases no significant differences in stem and root growth of individual trees. No significant differences in the diameter increment between the two species were found under the conditions of the hot and dry year 2015. However, rainfall exclusion in addition to the hot climate of the year 2015 caused significantly smaller diameter increments for spruce trees at all three levels, while beech trees showed no significant differences. In years without heat and water stress (e.g. 2014) spruce trees grew significantly stronger than beech trees. Thus, different growth reactions of conifers (e.g. spruce) and of deciduous tree species (e.g. beech) in dry and/or hot years as well as in 'normal' or 'favourable' years may result in stabilizing effects on the growth of conifers growing in broadleaved stands which supports the maintenance of a reasonable portion of conifers despite trends and events towards warmer and drier growing conditions. Tree species mixing can also increase stand heterogeneity, survival of less drought tolerant species, and thereby tree species richness and diversity, which in general increases level and stability of stand productivity (Liang et al., 2016). This way, the mixture of tree species despite the ongoing transition to more close-to-nature broadleaved forests is important as it guarantees forestry a sustainable supply of high quality timber (Pretzsch and Rais, 2016). The different phenological development (coniferous vs. deciduous), the different water availability in the course of the year of the two species (Rötzer et al., 2017) and the species-specific physiological reaction patterns (aniso- vs. isohydric) may be responsible for these growth increments. This way, intra- and inter-annual growth pattern analysis of spruce and beech trees in mixed stands can help to uncover not only the quantity of growth changes under drought but also the possible reasons of these changes which might be useful for mitigating drought stress in forest stands.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.070.

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