Higher drought sensitivity of radial growth of European beech in managed than in unmanaged forests

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HIGHLIGHTS

- Climate sensitivity of beech is strongly related to forest management history.
- Drought-induced growth decline is critically higher in managed stands.
- Management legacies have long-lasting impacts on climate-growth relationships.
- Trade-off between maximum individual tree growth and drought resistance.
- Management legacies and climate change drivers are interacting.

GRAPHICAL ABSTRACT
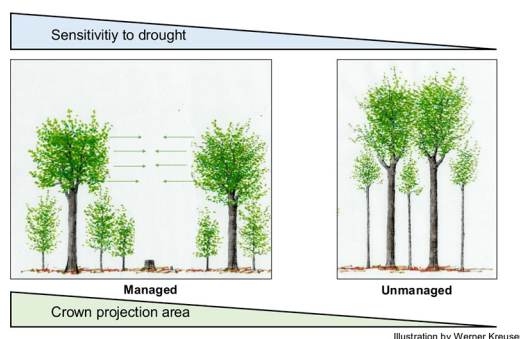
ABSTRACT

Climate extremes are predicted to become more frequent and intense in future. Thus, understanding how trees respond to adverse climatic conditions is crucial for evaluating possible future changes in forest ecosystem functioning. Although much information about climate effects on the growth of temperate trees has been collected in recent decades, our understanding of the influence of forest management legacies on climate-growth relationships is still limited. We used individual tree-ring chronologies from managed and unmanaged European beech forests, located in the same growth district (i.e. with almost identical climatic and soil conditions), to examine how forest management legacies (recently managed with selection cutting, >20 years unmanaged, >50 years unmanaged) influence the radial growth of *Fagus sylvatica* during fluctuating climatic conditions. On average, trees in managed stands had higher radial growth rate than trees in unmanaged stands during the last two decades a 50%. However, the beech trees in the unmanaged stands were less sensitive to drought than those in the managed stands. This effect was most pronounced in the forest with longest management abandonment (>50 years), indicating that the drought sensitivity of mature beech trees is in these forests the lower, the longer the period since forest management cessation is. Management-mediated modifications in crown size and thus water demand are one likely cause of the observed higher climate sensitivity of beech in the managed stands. Our results indicate a possible trade-off between radial growth rate and drought tolerance of beech. This suggests that reducing stem density for maximizing the radial growth of target trees, as is common practice in managed forests, can increase the trees' drought sensitivity. In the prospect of climate change, more information on the impact of forest management practices on the climate-growth relationships of trees is urgently needed.

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1. Introduction

Forests dominated by European beech (*Fagus sylvatica*; hereafter: beech) represent the natural vegetation of large parts of Central Europe (due to its oceanic to sub-oceanic climate; Leuschner and Ellenberg, 2017) and they play an important role for Europes' forestry sector. The increasing variability of climate and the more frequent occurrence of climatic extremes such as heat waves and severe droughts (IPCC, 2013), however, will impact tree growth in future (Easterling et al., 2000; Anderegg et al., 2015). Specifically, there is increasing evidence that beech is more sensitive to climatic extremes than most other Central European broadleaf tree species (Köcher et al., 2009; Zang et al., 2014; Zimmermann et al., 2015; Kunz et al., 2018), and the species shows a recent growth decline at sites even in the core of its distribution range, which was attributed to climate warming (Cavin and Jump, 2017; Knutzen et al., 2017). In this context, various forest management practices have been proposed to reduce the climate change impact on temperate forests, e.g. reducing stand density, promoting structural diversity and tree species richness or introducing drought-tolerant tree species or genotypes (Keenan, 2015; Ammer, 2017). For example, numerous studies have shown that thinning can mitigate the impact of drought on tree growth due to a reduced water demand at the stand level (e.g. D'Amato et al., 2013; Bosela et al., 2016; Sohn et al., 2016). Other studies, however, indicate that the short-term benefits of thinning may in the longer term enhance the trees' susceptibility to drought due to altered tree architecture and physiological constitution (e.g. leaf area/sapwood area ratio) (McDowell et al., 2013; Clark et al., 2016; Jump et al., 2017). Given that trees are long-lived organisms which may have an 'ecological memory' (Johnstone et al., 2016), legacy effects of land-use and silvicultural treatments should have an important influence on the trees' climate sensitivity (Perring et al., 2016). Recent research has provided evidence that the drought sensitivity of beech depends partly on the type of former land-use (i.e. farmland vs. forest) and forest continuity (Mausolf et al., 2018). However, studies investigating legacy effects of forest management in paired managed and unmanaged forests remain rare. Although Bosela et al. (2018) found recently in a cross-European study that the climate sensitivity of beech seems not to depend on forest management, as the long-term response of the trees to adverse climatic conditions was similar in unmanaged and managed forests, our understanding of legacy effects of forest management on climate-growth relationships at the local neighbourhood level remains rudimentary.

Here, we use individual tree-ring chronologies (i.e. the tree-ring series of individual trees) from managed and long-term (>50 years) and short-term (>20 years) unmanaged European beech forests to explore, how forest management history affects the radial growth of *F. sylvatica* during fluctuating climatic conditions. To examine the link between forest management and climate sensitivity, we applied a local neighbourhood approach to model climate-growth relationships of target trees in response to neighbour removal. Specifically, we asked the following questions: (i) Are there legacy effects of forest management which modulate the growth of individual trees in response to climate extremes? (ii) Is drought sensitivity mediated by the length of abandonment of forest management? and (iii) What are the underlying mechanisms driving possible differences in climate-growth relationships in managed and unmanaged forests?

2. Material and methods

2.1. Study design and stand characteristics

The study was conducted in Baltic beech forests (Galio-Fagetum community) of the forest district Stadtwald Lübeck (53°47′ N, 10°37′ E; total forest area: 4657 ha), which is located in the moraine landscapes of south-eastern Schleswig-Holstein, Northwest Germany (Fig. S1). Elevation ranges from 0 to 90 m asl. The study area is characterised by a sub-oceanic climate with a mean annual precipitation of 789 mm and a mean annual temperature of 8.3 °C (DWD, 2017). Edaphic conditions of the beech forests investigated are characterised by moderately moist to moist moraine soils originating from the last (Weichselian) glaciation. Soil texture consists of till (clay/sandy loam) with varying carbonate content in the deeper layers of the mineral soil, providing an optimal nutrient and water supply for tree growth.

We selected four stands in European beech forests located at four different study sites (Fig. S1). The study stands reflect a gradient of forest management history that ranged from long-term (>50 years; U50-SZ) and short-term (>20 years; U20-HEV) unmanaged (U) to managed (M; M-BKS, M-RIZ; abbreviations of localities see Table 1) beech forests. M-BKS and M-RIZ are managed according to a low-impact approach (e.g. single-tree harvest with minimal thinning interventions and the development of high growing stocks) based on the protection of natural disturbance regimes within managed stands (for more detailed information see Sturm, 1993). Since differences in the forest continuity of a site can modulate tree growth responses to climate extremes (Mausolf et al., 2018), we chose study sites that had a forest continuity for at least 200 years according to Glaser and Hauke (2004) to allow a meaningful comparison between managed and unmanaged stands. Moreover, to avoid confounding effects between forest management history and stand or site characteristics, we restricted the analyses to stands that were similar in tree species composition, stand age, topography and soil type, but differed in their management history. All stands were dominated by *F. sylvatica* (>95%), were located in level terrain and had (pseudogleyic) Luvisols as the predominant soil type (Table 1). Tree age of the canopy trees ranged between 105 and 120 years (Table 2).

To characterise stand structure, we selected a representative 40 × 40 m plot within each stand. All trees with a diameter at breast height (DBH; at 1.30 m) larger than 7.5 cm were measured, and for each measured tree, species identity and DBH were recorded. Tree height was measured for ten randomly selected trees of the upper canopy. Structurally, the studied stands are multi-layered and uneven-aged and developed from natural regeneration (Fig. S2). Mean stem density amounted to 281 trees ha^{-1} in the unmanaged stands, and to 172 trees ha^{-1} in the managed stands, reflecting the harvest of target trees. Correspondingly, mean stand basal area was 37% larger in unmanaged compared to managed stands (U: 46.4 m^2 ha^{-1}, M: 33.9 m^2 ha^{-1}). Soil chemical properties were analysed based on four randomly selected soil samples of the upper mineral soil horizon (A-horizon). Within each stand, soil samples were taken using a metallic corer (volume: 100 cm^3). Analyses were performed following the detailed protocol described by Leuschner et al. (2014). Total carbon (C), nitrogen (N) and resin-extractable phosphorus (P$_{resin}$), base saturation (BS), cation exchange capacity (CEC) and pH-values (measured in H$_2$O) were determined from sieved and homogenised soil samples. Soil carbonate content was estimated through the evolution of CO$_2$ after adding HCl, showing that all topsoil samples were free of carbonate. Therefore, all measured soil carbon was assumed to represent soil organic carbon (SOC). Stand characteristics and soil properties are summarized in Table 1. Soil chemical properties did not significantly vary between managed and unmanaged stands (PERMANOVA: $F = 1.28$, $P = 0.292$; Fig. S3). However, there was a trend towards slightly higher soil fertility at the U50-SZ and M-BKS sites than at U20-HEV and M-RIZ (Table 1).

2.2. Tree data

Within each study stand, we randomly selected 30 beech trees from the upper canopy with similar DBH (57–62 cm; Table 2) resulting in a total of 120 target trees. For each target tree, DBH, tree height and crown projection area (CPA) were determined in spring 2016. CPA was calculated as the area of a disc derived from averaging over four crown diameter measurements. Wood volume was calculated based on DBH and tree height measurements using the allometric function

Table 1

Summary statistics of structural and edaphic properties of the study stands. Values are means and their standard error (in brackets). Different superscript letters indicate significant (Tukey-HSD: $P_{adj.} < 0.05$) differences between study sites. DBH: diameter at breast height, H/D-ratio: height/diameter-ratio, C: carbon, N: nitrogen, P_{resin}: resin extractable phosphorus, CEC: cation exchange capacity, BS: base saturation. Average harvested timber volume since 1994: M-BKS 30.73 $m^3 ha^{-1}$; M-RIZ 55.07 $m^3 ha^{-1}$.

	Schattiner Zuschlag (U50-SZ)	Hevenbruch (U20-HEV)	Berkenstrücken (M-BKS)	Ritzerau (M-RIZ)
Stand characteristics				
Management history	Unmanaged >50 years	Unmanaged >20 years	Managed	Managed
Tree species composition				
Beech (%)	100	100	100	96
Oak (%)	0	0	0	4
Stand volume ($m^3 ha^{-1}$)[1]	903	690	652	613
Stand basal area ($m^2 ha^{-1}$)	58.83	33.97	39.40	28.48
Stem density ($n ha^{-1}$)	368.75	193.75	187.50	156.25
DBH (cm)	43.96 (1.31)[n.s.]	44.50 (2.90)[n.s.]	46.51 (4.20)[n.s.]	45.05 (3.48)[n.s.]
Tree height (m)[2]	40.94 (0.14)[a]	36.33 (0.29)[b]	39.29 (0.23)[c]	36.72 (0.28)[b]
H/D-ratio[B]	0.77 (0.01)[a]	0.64 (0.01)[b]	0.61 (0.01)[b]	0.63 (0.01)[b]
Soil properties[3]				
Soil type	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol	(pseudogleyic) Luvisol
pH (H_2O)	4.10 (0.07)[a]	3.71 (0.08)[b]	4.42 (0.21)[a]	3.57 (0.03)[b]
C_{total} (%)	4.35 (0.47)[ab]	8.60 (1.44)[a]	3.69 (0.42)[b]	6.86 (1.53)[ab]
N_{total} (%)	0.28 (0.03)[ab]	0.49 (0.07)[a]	0.26 (0.02)[b]	0.38 (0.07)[ab]
C:N	15.87 (0.34)[ab]	17.57 (0.32)[a]	14.31 (0.58)[b]	17.81 (0.69)[a]
P_{resin} ($mg\ g\ d \cdot m.^{-1}$)	0.10 (0.02)[n.s.]	0.13 (0.03)[n.s.]	0.08 (0.03)[n.s.]	0.16 (0.03)[n.s.]
$C:P_{resin}$	453.26 (63.65)[n.s.]	689.19 (82.68)[n.s.]	513.90 (118.98)[n.s.]	471.87 (98.26)[n.s.]
CEC ($\mu mol_c\ g\ d \cdot m.^{-1}$)	97.41 (10.08)[ab]	123.36 (7.93)[b]	77.51 (11.45)[a]	82.16 (11.76)[ab]
BS%	23.72 (3.93)[n.s.]	11.75 (2.47)[n.s.]	30.91 (7.52)[n.s.]	16.74 (3.42)[n.s.]

1: values refer to the data obtained from the permanent sample plot inventory in 2013.

2: values refer to ten randomly selected canopy trees.

for European beech of Bergel (1973). Tree volume was then converted in aboveground biomass (AGB, in MgC) by applying the wood density value of beech for monocultures (665.43 kg m⁻³; Zeller et al., 2017) and the standard conversion of 0.5 gC per gram of biomass.

To assess the impact of forest management on climate-growth relationships, all selected target trees in the managed stands were located north to a management-induced gap created by single tree harvesting, and defined by the closest cut stump (target stump) of a crop tree. Mean estimated target stump diameter was 72 cm, and mean distance between target tree and cut target stump amounted to 7 m. Mean number of cut stumps within the local neighbourhood (i.e. closest neighbours) of a target tree amounted to 2.8. All stumps were associated with later decay stages, meaning that the estimated stump age was >10 years. To ensure meaningful comparisons between managed and unmanaged stands, selected target trees growing in unmanaged stands were surrounded by neighbours to avoid effects of natural gaps.

2.3. Wood coring and tree ring analysis

For each target tree, we collected one bark-to-pith increment core at 1 m height above the ground in spring 2016. Cores were taken from the cardinal points west to east using an increment borer (Suunto 400, Vantaa, Finland, 0.5 cm diameter and 40 cm length). Each core was air-dried in the laboratory and annual tree-ring width (TRW) was measured from bark to pith with 0.01 mm resolution (see Mausolf et al., 2018 for more detailed information). To minimise measurement errors, cross-dating of single tree chronologies was performed by using site chronologies from former studies conducted in the same study region as a reference (Mausolf et al., 2018). Cross-dating was done following Mausolf et al. (2018). Due to incomplete and broken wood cores, we omitted two trees from subsequent analyses. To minimise the effect of tree age on annual growth rates, TRW data of individual tree chronologies were standardized. Standardization was performed in TSAP-Win by first

Table 2

Differences in target tree characteristics and tree-ring statistics of European beech growing in stands with different management history. Values are means and their standard error (in brackets). Different superscript letters indicate significant (Tukey-HSD: $P_{adj.} < 0.05$) differences between study sites. DBH: diameter at breast height; BAI: Basal area increment; TRW: Tree-ring width; AC (TRW): AC: first-order autocorrelation, expressing the interannual TRW persistence.

	Schattiner Zuschlag (U50-SZ)	Hevenbruch (U20-HEV)	Berkenstrücken (M-BKS)	Ritzerau (M-RIZ)
Target tree characteristics[1]				
Management history	Unmanaged >50 years	Unmanaged >20 years	Managed	Managed
Tree age (years)[2]	107.77 (1.86)[a]	119.97 (1.82)[b]	103.59 (2.03)[a]	104.93 (1.52)[a]
Diameter at 1.30 m (cm)	57.45 (0.65)[a]	59.60 (0.67)[b]	61.81 (0.71)[b]	61.23 (0.68)[b]
Basal area (cm^2)	2602.18 (59.99)[a]	2799.81 (64.27)[ab]	3011.41 (68.95)[b]	2954.67 (64.95)[b]
Tree height (m)	41.74 (0.10)[a]	36.39 (0.36)[b]	37.28 (0.40)[b]	34.97 (0.45)[c]
Crown projection area (m^2)	75.01 (3.78)[a]	91.21 (4.05)[b]	117.11 (4.34)[c]	127.21 (4.72)[c]
Aboveground biomass (MgC)	1.87 (0.05)[n.s.]	1.74 (0.05)[n.s.]	1.92 (0.05)[n.s.]	1.77 (0.06)[n.s.]
Tree-ring statistics[3]				
BAI ($cm^2\ year^{-1}$)	20.86 (0.73)[a]	21.77 (0.89)[a]	27.93 (1.21)[b]	28.28 (1.24)[b]
TRW (mm)	2.48 (0.05)[a]	2.40 (0.06)[a]	2.92 (0.07)[b]	2.92 (0.08)[b]
Maximum TRW (mm)	5.12 (0.15)[a]	5.09 (0.17)[a]	5.44 (0.14)[b]	5.70 (0.17)[b]
Minimum TRW (mm)	0.39 (0.03)[a]	0.48 (0.03)[ab]	0.74 (0.07)[c]	0.58 (0.04)[bc]
AC (TRW)	0.70 (0.02)[a]	0.66 (0.02)[ab]	0.65 (0.02)[ab]	0.60 (0.02)[b]
Number of target trees	30	29	29	30

1: values refer to the date of sampling (2016).

2: tree age is related to cambial age at coring height.

3: values refer to tree chronologies (mean across the entire lifespan of each tree), note that 'Hevenbruch' was managed until 1994.

calculating the five-year moving average trend of each chronology. In a second step, measured tree-ring series were divided through the five-year moving average trends, resulting in a dimension-less index of tree-ring width (TRI) (for more information see Dulamsuren et al., 2017). As TRI is centred around zero, negative values indicate growth decline, whereas positive values indicate growth stimulation. Radial growth measurements were performed using IML software T-Tools Pro (Version 1.4, Instrumenta Mechanik Labor GmbH, Wiesloch, Germany). Descriptive dendrochronological statistics were based on individual tree chronologies and calculated using TSAP-Win (Table 2). For further analyses we used individual tree rather than site chronologies (i.e. pooled tree-ring chronologies of a given site) to account for the variability in individual growth responses, which has been shown to be crucial, when assessing the response of forest ecosystems to climate change (Carrer, 2011; Zang et al., 2014).

2.4. Climate data

To quantify changes in climatic conditions, we used the standardized precipitation-evapotranspiration index (SPEI), which is a climatic water balance index that considers precipitation and potential evapotranspiration (Vincente-Serrano et al., 2010) and allows to study the effects of climate change for varying time scales (Bhuyan et al., 2017). Following Bhuyan et al. (2017) describing the SPEI of different timescales to show best explanatory power in climate-growth analyses of beech we decided to use SPEI for further analyses. SPEI data were extracted from the Global SPEI database (http://spei.csic.es/database.html, accessed 14.09.2017) for the nearest 0.5 grid cell (54°45′ N, 10°45′ E), meteorological data were achieved from the nearest weather station (DWD, 2017). We selected climate indices for spring, summer and previous summer conditions, as beech has been shown to be most sensitive to climatic variations during these periods (Lebourgeois et al., 2014; Hacket-Pain et al., 2015). We calculated SPEIs for different time scales (ranging from one to six months), and selected those periods that showed the strongest correlation (Pearson correlation) with TRIs (across all target trees and study stands) during the analysed timespan (1995–2014). The following SPEIs, based on a three-month time scale, were used in the climate-response analysis: seasonal values for current spring (March, April, May; SPEI-spring; $r = 0.33$; $P < 0.001$), summer (June, July, August; SPEI-summer, $r = 0.22$; $P < 0.001$) and previous summer (June, July, August; SPEI-previous summer, $r = 0.15$; $P < 0.001$), based on a three-month period.

2.5. Data analysis

We used linear mixed-effects models to test whether climate-growth relationships vary with forest management history. We limited our analysis to the recent (1995–2014) climate regime for several reasons: First, the study site 'Hevenbruch' (U20-HEV), our short-term unmanaged stand, was managed until 1994. Second, detailed information on management history was only available for this period. Third, climatic fluctuations were strongest during recent decades (IPCC, 2013). Thus, effects of management history are assumed to be most relevant during this period. TRI was used as response variable, and climate indices (SPEI-spring, SPEI-summer, SPEI-previous summer), tree size (using basal area) and management type (managed vs. unmanaged forest) were used as explanatory variables. To test for a potential dependence of climate effects on forest management history, we additionally considered all possible two-way interaction terms between management type and climate indices. To account for differences in abiotic site conditions, the studied stand was used as a random effect. Moreover, we used a first-order autoregressive covariance structure (AR-1) to account for temporal autocorrelation in observations among years (tree nested within stand; Zuur et al., 2009). Different competing models were evaluated by sequential comparison (backward selection) based on the Akaike Information Criterion (AIC) and maximum

likelihood (ML) estimation, using the *stepAIC* function in R. We further simplified the model with the lowest AIC value by removing all terms that were not significant according to likelihood ratio tests. Parameter estimates of the final model were fitted using the restricted maximum likelihood (REML) method (Zuur et al., 2009). All continuous predictors were standardized (mean = 0; SD = 1) before analysis.

We used Hedges' *d* effect size as a standardized measure to quantify the mean difference of the effects of forest management legacies on TRI during climate extremes (Hedges and Olkin, 1985). We defined extreme climate events (extremely dry or extremely wet) as those periods with the lowest and highest SPEI during the last two decades (1995–2014), respectively (Table S1). Note that negative values of SPEI indicate periods with water deficit, and vice versa. Hedges' *d* effect size was calculated based on observed TRI values. Positive values of Hedges' *d* indicate stronger responses, meaning growth stimulation (positive TRI values) or growth reduction (negative TRI values), of beech growing in managed compared to unmanaged beech forests, and vice versa. Hedges' *d* values of 0.2, 0.5 and 0.8 indicate a small, moderate and large effect, respectively (Koricheva et al., 2013).

Differences in stand, soil and target tree characteristics among the study stands were analysed using analysis of variance (ANOVA) followed by a post-hoc test (Tukey-HSD). Data exploration was performed prior to all analyses, following Zuur et al. (2010). Furthermore, model assumptions were visually checked and confirmed according to Zuur et al. (2009). All analyses were performed in R (version 3.3.1.) using the packages MASS (Venables and Ripley, 2002), nmle (Pinheiro et al., 2016) and vegan (Oksanen et al., 2016).

3. Results

On average, radial growth rates were 27% to 83% higher in managed (BKS: 43.41 ± 2.42 cm^2 year^{-1}, RIZ: 42.26 ± 2.36 cm^2 year^{-1}) than in unmanaged stands (HEV: 33.33 ± 2.32 cm^2 year^{-1}, SZ: 23.61 ± 1.46 cm^2 year^{-1}) during the last two decades ($P_{adj.} < 0.05$; Fig. S3). The best-fitting growth model included positive effects of tree basal area and SPEI (i.e. climatic conditions in spring, summer and previous summer), with climatic effects on TRI being strongest for variation in spring (Table 3). For SPEI-summer, the climate-growth relationship was consistent across managed and unmanaged stands. The sensitivity of beech growth to climatic conditions in spring and previous summer, however, depended on forest management history, as indicated by the significant interaction between management type and SPEI-spring and SPEI-previous summer, respectively (both: $P < 0.01$; Table 3). Results based on SPEI were qualitatively the same compared to those using precipitation and temperature data separately, meaning that TRI of trees in managed stands was more strongly related to changes in current year spring precipitation as well as previous year summer temperature than those growing in unmanaged stands (Table S2).

Growth stimulation (i.e. positive TRI-values) was higher in managed stands during years with ample water supply (i.e. positive SPEI-values; Fig. 1), but the benefit of trees growing in managed stands during

Table 3
Regression coefficients from the best-fitting mixed-effects model for tree-ring width index (TRI) of European beech (*Fagus sylvatica*). Predictor estimates were standardized, hence their magnitude is proportional to the effect size. Note that the intercept refers to the response of unmanaged stands, while 'M' indicates managed stands. BA: basal area, SPEI: standardized precipitation-evapotranspiration index, SE: standard error.

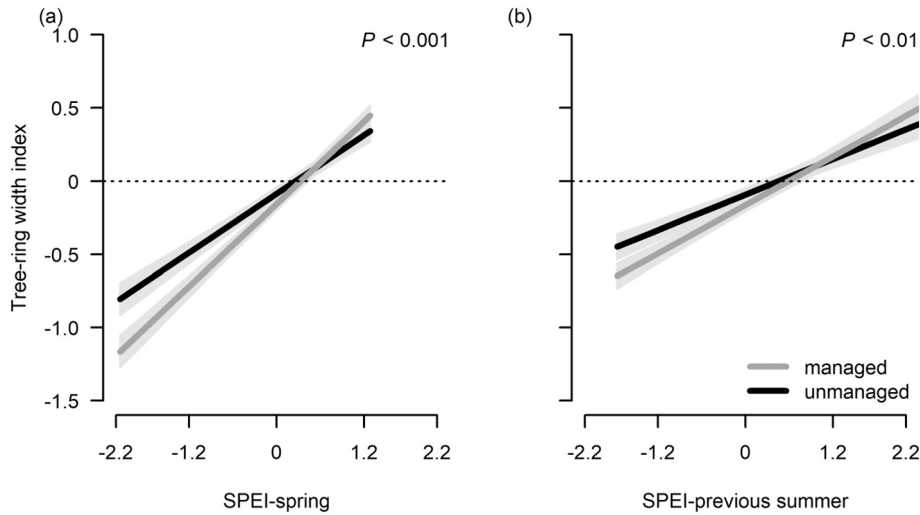| Fixed effects	Estimate	SE	P-value
Intercept	−0.064	0.022	0.005
BA	0.054	0.016	<0.001
SPEI-spring	0.320	0.022	<0.001
SPEI-summer	0.260	0.015	<0.001
SPEI-previous summer	0.226	0.022	<0.001
Managed stands (M)	−0.060	0.032	0.207
SPEI-spring × M	0.129	0.031	<0.001
SPEI-prev. summer × M	0.082	0.031	0.008

Fig. 1. Effects of forest management history (managed versus unmanaged forests) on the growth (tree-ring width index, TRI) responsiveness of European beech (*Fagus sylvatica* L.) to interannual fluctuations in climate during the last two decades (1995–2014) considering (a) the response to the climatic water balance during spring and (b) the response to the climatic balance during the previous summer. Periodic water surplus or deficits are estimated by the standardized precipitation-evapotranspiration index (SPEI) in a seasonal (three month) resolution. Negative values of SPEI indicate a water deficit, positive values a positive climatic water balance. Lines correspond to the predicted response based on mixed-effects models and shaded areas indicate the 95% confidence interval. The basal area and SPEI-summer parameter estimate were fixed at their mean values.

climate extremes (extremely wet) was not significant (Hedges' *d*: 0.29; Fig. 2a). In contrast, trees in unmanaged stands showed considerably lower growth reduction (i.e. negative TRI-values) during years with a water deficit (i.e. negative SPEI-values) compared to those growing in managed stands, with effects being stronger for drought events in spring (Fig. 1a) than in previous summer (Fig. 1b). Particularly, during severe drought, trees in unmanaged stands exhibited significantly lower growth decline compared to those in managed stands (Hedges' *d*: 0.94; *P* < 0.05; Fig. 2b). Such effects of forest management history became even stronger when considering the length of forest management abandonment. Values of Hedges' *d* increased from 0.46 (short-term unmanaged vs. managed stands; *P* < 0.05) to 1.42 (long-term unmanaged vs. managed stands; *P* < 0.05). Moreover, growth reduction during extreme drought in spring was positively related to crown projection area (*P* < 0.01; Fig. 3), meaning that trees with large-sized crowns were prone to drought events in particular (highest negative values of TRI). Due to lower stem density, average crown size was greater in the

managed stands (means of 117 and 127 m^2) than in the unmanaged ones (75 and 91 m^2, Table 2), and growth decline was greater in the former.

4. Discussion

We found that legacy effects of forest management modulate the response of beech to climate extremes. Specifically, trees growing in managed stands showed a larger growth decline during severe drought in spring than trees in unmanaged beech forests. This finding contrasts the common belief that thinning and thus canopy release improves the water status of remaining broad-leaved trees (Breda et al., 1995; Sohn et al., 2016; Diaconu et al., 2016).

Beech has been identified as being relatively sensitive to summer drought and elevated summer temperatures (Geßler et al., 2007; Köcher et al., 2009; Packham et al., 2012), which may relate to its large shade crown and comparably high water consumption
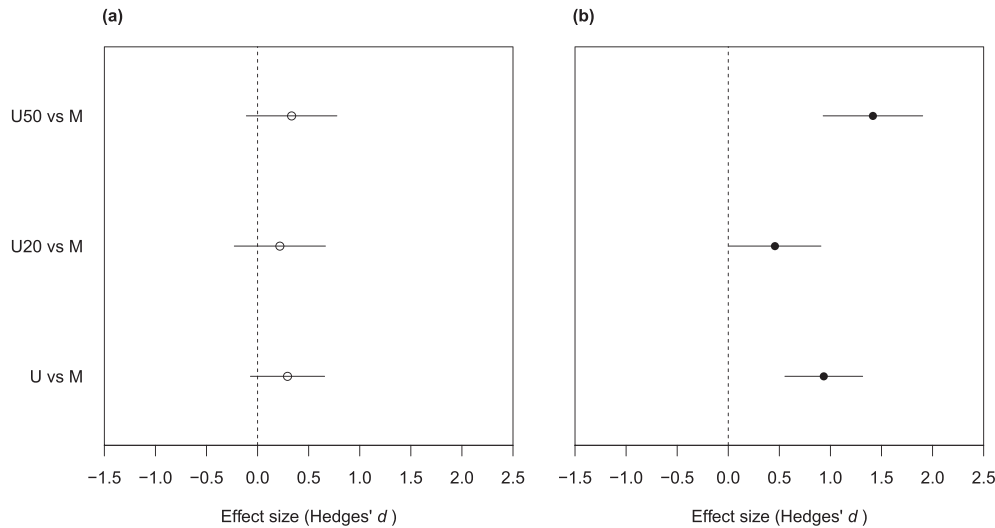

Fig. 2. Effects of forest management history on (a) growth stimulation (i.e. positive tree-ring width indices) and (b) growth reduction (i.e. negative tree-ring width indices) of European beech (*Fagus sylvatica*) during climate extremes in spring (extremely dry or extremely wet events). Error bars denote the 95% confidence intervals. Closed circles indicate significant (*P* < 0.05) and open circles indicate non-significant (*P* > 0.05) effect sizes. Positive values indicate stronger responses (growth stimulation or reduction) of beech growing in managed compared to unmanaged beech forests, and vice versa. M: managed, U50: unmanaged >50 years, U20: unmanaged >20 years; U: U50 + U20.
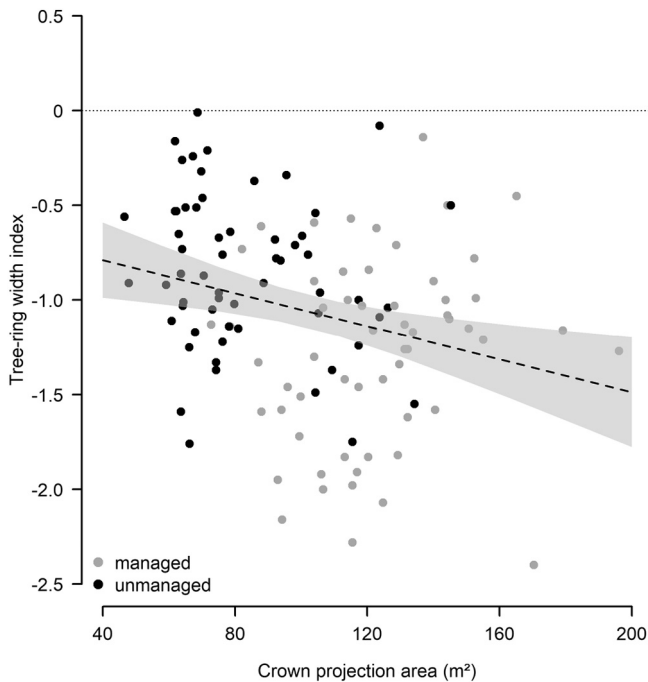
Fig. 3. Relationship between tree-ring width index (TRI) and crown projection area (CPA) of European beech (*Fagus sylvatica*). Negative values of TRI indicate growth decline. The black line is a linear model fit ($P = 0.003$) and the shaded area indicates the 95% confidence interval. Points represent observed values of TRI for extreme climate events (extremely dry) in spring (2011) and crown projection area (2016) for trees growing in managed (grey) and unmanaged (black) beech forests.

(Leuschner and Ellenberg, 2017), and a relatively high vulnerability to cavitation due to a less negative P_{50} value than in other broadleaf trees (Choat et al., 2012). In accordance, high temperatures and low precipitation during current and previous year growing seasons, particularly during May to July, were identified as main factors driving the observed recent growth decline in various regions of Europe (Zimmermann et al., 2015; Hacket-Pain et al., 2016; Knutzen et al., 2017). This is consistent with our finding of overall decreasing radial growth rates of beech in northern Germany under elevated climatic water deficits in spring and current and previous years' summer. In contrast to other studies on beech growth decline (e.g. Knutzen et al., 2017), we found that early-season drought (March to May) was decisive and not summer (June to August) water shortage. Our results match with those of Bosela et al. (2016) and Mausolf et al. (2018), where early-season water shortage was also found to be the main driver of declining radial growth rates in beech. Importantly, our results also show that drought sensitivity of beech strongly depends on management history with trees growing in unmanaged forests being less sensitive to drought events during spring and previous summer. The influence of current and previous year water deficits on radial growth is explained by the phenology of cambial activity. A large part (~75%) of annual tree-ring formation in beech is completed until the end of June (Packham et al., 2012). Thus, carbohydrates assimilated during previous summer and current spring likely contribute most to the current-year tree-ring, whereas the C gain of the current summer should play a minor role. This is in line with the fact that early growing season conditions and remobilization processes rather than current summer conditions significantly influence tree-ring width in beech when assessing the whole tree-ring (Hentschel et al., 2016). Moreover, up to 20% of a tree-ring of European beech in spring can be built from remobilized storage compounds (Skomarkova et al., 2006). Furthermore, water deficits are often associated with high summer temperatures, which may negatively affect the radial growth of beech in the next year through a stimulation of mass fruiting. Full masting can

consume >50% of annual C gain (Hacket-Pain et al., 2015; Müller-Haubold et al., 2015), thereby reducing radial growth in the subsequent year.

Crown size is considered a key tree trait controlling the radial growth of trees due to its relation to leaf area and thus photosynthetic carbon gain and transpirative water loss (Niinemets, 2010). Crown size may also reflect the tree's past competitive strength (Fichtner et al., 2013). The removal of competitive neighbours in thinning operations typically leads to enhanced growth of the remaining trees through rapid crown expansion, which is a characteristic response of *F. sylvatica* (Lebourgeois et al., 2014). In the managed stands, the beech trees had on average an about 50% larger crown size than in the denser unmanaged stands, which must have increased carbon gain after having cut the neighbours, but sap flux density in the stem xylem should also have increased due to growing canopy water loss. Trees will adapt their hydraulic architecture to an expanding crown and growing water consumption, but the critical question is, whether the increase in hydraulic efficiency with radial sapwood expansion through the formation of new tree rings keeps pace with the growing evaporative demand on the leaf side. Noyer et al. (2017) showed that trees released from intense competition in managed stands increase their vessel diameter, which will increase hydraulic conductance, but larger vessels in turn can lead to a higher risk of hydraulic failure and embolism during drought. Thus, it is likely that the higher water demand of trees with light-exposed and expanding crowns in the direct neighbourhood of tree cutting-gaps will increase the trees' susceptibility to severe drought, at least for several years until hydraulic adaptation is completed. Although the branch hydraulic architecture of beech acclimates sufficiently fast after canopy opening to avoid hydraulic dysfunction (Lemoine et al., 2002), this acclimation potential at the canopy level seems insufficient. A related phenomenon was recently described by Jump et al. (2017) as structural overshoot, meaning that the promotion of tree growth by favourable environmental conditions (via management) can enhance the risk of a temporal mismatch between water demand and water supply in times of drought. Structural overshoot may explain our finding of increasing drought-induced growth decline with increasing crown size, when the hydraulic system and/or the root system are not able to meet the water demand of the expanding crown.

Other factors which could be responsible for the higher drought sensitivity of beeches in the managed stands are differences in stand microclimate and in the soil biological activity and mycorrhizal net. In the absence of selective cutting, stem density and canopy closure were higher in the unmanaged forests, which must have resulted in reduced light transmission to the ground and a higher air humidity level in the stands (Rambo and North, 2009; Latif and Blackburn, 2010). High-resolution radial increment measurements on beech stems have shown that the cambial activity of this species is in the peak growing phase less dependent on high rainfall amounts than on high air humidity (Köcher et al., 2012). This highlights the importance of a closed canopy for the vitality of late-successional beech, which likely is more sensitive to abrupt changes in the microclimate and air humidity, as resulting from forest management activities (Aussenac, 2000), than other temperate broadleaf trees. Moreover, it might be conceivable that absorbing roots of trees in densely-stocked unmanaged stands had migrated to deeper soil layers to avoid belowground competition for water (Schenk, 2005). Therefore, sensitivity to drought stress during climate extremes should be lower, because water uptake can occur from deeper soil layers. In contrast, trees growing in managed stands might develop fine roots primarily in upper soil layers due to reduced belowground competition for water uptake after thinning. Given that upper soil layers are prone to soil drying, trees in managed stands could exhibit higher sensitivity to extreme drought. In addition, management-induced compaction of forest soils has been found to result in long-lasting impact on the soil microbial community (Hartmann et al., 2014), which could influence the drought susceptibility of the trees.

5. Conclusion

Our findings highlight the relevance of understanding how legacy effects interact with drivers of global environmental change. We found a strong effect of forest management legacies on the climate sensitivity of beech and could show that drought-induced growth declines during spring are less severe in the unmanaged stands. Overall, our results suggest that management practices conducted to promote the growth of target trees, such as neighbour removal, can result in increased drought sensitivity of the remaining trees. The different responsiveness of stands with 20 years or 50 years of management abandonment suggests that the length of the period since management cessation plays a crucial role in determining the trees' susceptibility to drought. Among the factors that could explain the variable responsiveness of beech trees in managed and unmanaged stands, we discuss differences in canopy size which could affect the water status of the trees, microclimate alteration, and putative management-induced effects on the soil. We obtained evidence of a trade-off between high radial growth rates and high drought tolerance in beech, which deserves further study. The results of our study may be of high relevance for the management of beech forests in a warming climate, but it has to be kept in mind, that local site conditions such as soil moisture regime and soil fertility likely are influencing the climate-growth relationship. Managed and unmanaged beech stands growing under deviating environmental conditions and management regimes could thus behave differently. Further research is needed to improve our understanding of the interactive effects between management legacies and drivers of global environmental change.

Author contributions

CL, DH, BS, KS, and AF designed the research; PW collected and compiled the data. KM and AF analysed the data. KM wrote the first draft of the manuscript. All authors substantially contributed to revisions and gave final approval for publication.

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Data accessibility

In case of publication, data will be archived in in the Dryad Digital Repository.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.06.065.

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