



A warmer climate impairs the growth performance of Central Europe's major timber species in lowland regions

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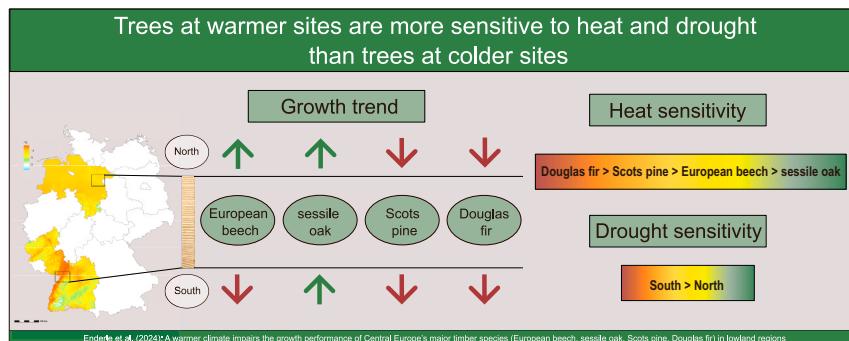
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HIGHLIGHTS

- All species except sessile oak show growth declines, especially less vital trees.
- Trees in the warmer region show higher climate sensitivity.
- Conifers display higher heat sensitivity than broadleaf trees.
- All species showed fast recovery after hot and dry years.

GRAPHICAL ABSTRACT



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ABSTRACT

Recent hot droughts have caused tree vitality decline and increased mortality in many forest regions on earth. Most of Central Europe's important timber species have suffered from the extreme 2018/2019 hot drought, confronting foresters with difficult questions about the choice of more drought- and heat-resistant tree species. We compared the growth dynamics of European beech, sessile oak, Scots pine and Douglas fir in a warmer and a cooler lowland region of Germany to explore the adaptive potential of the four species to climate warming (24 forest stands). The basal area increment (BAI) of the two conifers has declined since about 1990–2010 in both regions, and that of beech in the warmer region, while oak showed positive BAI trends. A 2 °C difference in mean temperatures and a higher frequency of hot days (temperature maximum >30 °C) resulted in greater sensitivity to a negative climatic water balance in beech and oak, and elevated sensitivity to summer heat in Douglas fir and pine. This suggests to include hot days in climate-growth analyses. Negative pointer years were closely related to dry years. Nevertheless, all species showed growth recovery within one to three years. We conclude that all four species are sensitive to a deteriorating climatic water balance and hot temperatures, and have so far not been able to successfully acclimate to the warmer climate, with especially Douglas and beech, but also Scots pine, being vulnerable to a warming and drying climate.

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1. Introduction

Recent climate change is advancing faster than many plants can adapt, which exposes especially long-lived organisms such as trees to growing stress (Jump and Peñuelas, 2005; Petit and Hampe, 2006). During the last two decades, reports of large-scale tree vitality loss and forest dieback have rapidly increased worldwide, which mostly were attributed to the direct or indirect impact of climate warming (Allen et al., 2010; Hammond et al., 2022; Van Mantgem et al., 2009). In the temperate forests of Central Europe, widespread crown damage and tree dieback has been observed, especially after the severe hot droughts of 2003, 2015 and 2018/2019, which primarily hit drought-sensitive Norway spruce (*Picea abies* Karst.), but other major timber species like European beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and the introduced Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) were affected as well (Bigler et al., 2006; Braun et al., 2021; Schultdt et al., 2020; Sergent et al., 2014; Thonfeld et al., 2022).

Reports about crown damage and mortality were complemented by dendrochronological findings that showed in recent decades continued growth decline of several major timber species in various Central European temperate forest regions (Debel et al., 2021; Knutzen et al., 2017; Leuschner et al., 2023; Scharnweber et al., 2011; Weigel et al., 2023). Negative growth trends may be an indicator of climate stress-related vitality loss, when other possible drivers of growth decline such as competition or biotic agents can be excluded (DeSoto et al., 2020), and they are frequently a precursor of subsequent tree death (Cailleret et al., 2017; Camarero et al., 2015; Neycken et al., 2022). Thus, by combining dendrochronological time-series analysis with visually assessed canopy health, a more comprehensive picture of climate change impacts on tree and forest vitality can be achieved. Such information is urgently needed for informing foresters about the drought and heat sensitivity of the main timber species during the transformation process to 'climate-smart forestry', i.e. the establishment of forests with higher resistance and resilience to climate warming and drying (Bowditch et al., 2020; Verkerk et al., 2020).

European beech is known since long to be fairly drought-sensitive (Gessler et al., 2020; Leuschner, 2020; Zimmermann et al., 2015). In accordance, the species has shown recent growth decline in many regions of Central Europe and beyond, especially in warmer lowland regions and on shallow soils (Charru et al., 2010; Dulamsuren et al., 2017; Härdtle et al., 2013; Kasper et al., 2022; Knutzen et al., 2017; Scharnweber et al., 2011; Weigel et al., 2023). After the extreme 2018/2019 hot drought episode, beech was also affected by canopy defoliation and increased mortality at various sites in the lower mountain ranges of Central Europe, for example in central and southern Germany and northern Switzerland (Frei et al., 2022; Neycken et al., 2022; Obladen et al., 2021). In the lowlands of northern Central Europe, damage was less severe and crown dieback and mortality rate have only slightly increased after this extreme drought, with a focus in low-precipitation regions such as the German state of Saxony-Anhalt (NW-FVA, 2021).

Sessile oak is widely plagued by herbivore and pathogen attack (Thomas et al., 2002), but the species' radial growth is usually less sensitive to hot and dry summers compared to other species (Cavin et al., 2013; Friedrichs et al., 2009a; Kunz et al., 2018; Mérien et al., 2011; Scharnweber et al., 2011; Vitasse et al., 2019; Zimmermann et al., 2015). However, a higher drought vulnerability was observed at dry sites (Friedrichs et al., 2009b) and at the species' distribution edges (Bose et al., 2021), suggesting that the species' climate sensitivity will likely increase in Central Europe in the coming decades. Nevertheless, most authors categorize sessile oak due to its growth performance as less vulnerable to climatic stress than beech (Friedrichs et al., 2009a; Kasper et al., 2022; Leuschner et al., 2024; Zimmermann et al., 2015).

Scots pine is after Norway spruce the economically most important timber species in Central Europe, which is planted in large areas especially in the lowlands (Fürster et al., 2021). It has long been assessed as

an undemanding species that tolerates nutrient-poor and dry sites (Roloff, 2008; Schütt and Stimm, 2014) and thus was assumed to cope well with climate warming. However, recent reports of stand-level dieback in southern and central Europe raise concerns about the species' resistance to climate stress, in particular as it is often planted on soils with low water-holding capacity, making it more vulnerable to heat and drought (Bose et al., 2024). In fact, Scots pine growth is sensitive to drought and heat (Buras et al., 2018; Martínez-Vilalta et al., 2008; Michelot et al., 2012a), and results from northern Bavaria indicate an even higher drought sensitivity of pine than of Norway spruce (Debel et al., 2021). In accordance, pine growth in the North German Lowlands was found to be sensitive to summer drought and heat, but no consistent growth decline has so far been reported (Bauwe et al., 2016, 2013; Diers et al., 2022; Stolz et al., 2021). Here, the species' mortality is still fairly low, despite local dieback due to Diplodia infection and insect pests (NW-FVA, 2022).

The introduced Douglas fir has generally been assessed as drought-resistant (Lévesque et al., 2014; Thomas et al., 2022), and its high productivity makes it a favored timber species in many Central European regions (Nicoleescu et al., 2023; Thomas et al., 2022). However, dendrochronological studies demonstrate that Douglas fir growth is sensitive to summer water deficits and high vapor pressure deficits (Restaino et al., 2016; Vejpustková and Čihák, 2019), and the species has suffered crown damage and dieback after severe hot droughts in several European regions such as France (Sergent et al., 2014) and SW Germany (Delb et al., 2023; MKUEM-RP, 2021). A direct comparison to Scots pine growth dynamics indicates that Douglas fir is less drought sensitive than pine and recovers faster (Eilmann and Rigling, 2012; Lévesque et al., 2014; Rais et al., 2014; Sergent et al., 2014). While recent growth trends of Douglas fir in mountainous, precipitation-rich regions of southern Central Europe were found to be stable (Lévesque et al., 2014; Stangler et al., 2022; Vitali et al., 2017, 2018), not much is known about the species' growth performance in Central European lowland regions, where it is increasingly planted.

A crucial question is to what extent trees can adapt to increasing drought and heat stress through acclimation and heritable adaptation. Central European tree species have shown in the past variable responses to climatic gradients across regions. In European beech, for example, a comparison of the growth performance of central and southern, marginal populations revealed higher growth resistance to dry years and fewer negative pointer years at the drier and warmer sites (Cavin and Jump, 2017; Muffler et al., 2020), which may point to successful adaptation under extremer growth conditions. In contrast, beech and pine populations showed negative basal area increment (BAI) trends at various drier locations (Martínez-Vilalta et al., 2008; Weigel et al., 2023), which is no support for successful adaptation under more stressful climatic conditions. The climate sensitivity of sessile oak and Scots pine growth was in several studies greater at drier sites (Friedrichs et al., 2009a; Stolz et al., 2021; Diers et al., 2024). On the other hand, oak growth recovered faster at drier sites, suggesting successful adaptation (Trouvé et al., 2017). It appears that our understanding of the acclimation and adaptation potential of the major timber species is still incomplete. Some insight into the adaptive capacity and the tolerance of tree species to climate warming may be gained from comparing the species' growth patterns at sites differing in mean temperature.

Here, we examine the radial growth patterns of European beech, sessile oak, Scots pine and Douglas fir in two lowland regions of Germany, which differ markedly in mean annual temperature (MAT), the Upper Rhine Valley (southern region) and the North-west German Lowlands (northern region). The Rhine Valley is the hottest region in Germany with about 2 °C higher MAT than in the northern lowlands. The current thermal regime in the Upper Rhine Valley may roughly resemble the MAT to be expected in large parts of the German lowlands at the end of the 21st century, when mean temperature might have increased by 2–2.5 °C, if greenhouse gas emission reductions are not very ambitious (IPCC, 2023). In this descriptive dendrochronological

study, we compare the long-term growth trends, the climate sensitivity of growth, and the growth response to extreme drought and heat events of the four species between the two regions in monospecific, mature stands on relatively nutrient-poor, predominantly sandy soils without groundwater influence. We use the comparison of the cooler and the 2 °C-warmer region to get an idea, how the trees may respond to a warmer climate at the end of the 21st century. We tested the hypotheses that (i) the most important growth-controlling climatic factors are in all four species the climatic water balance and high temperatures in the growing season, (ii) growth declines in recent decades are more frequent in the presumably more sensitive species beech and pine than in Douglas fir and oak, and (iii) growth declines and negative pointer years are in all species more frequent in the southern than in the northern region due to insufficient local adaptation.

2. Methods

2.1. Study regions and climatic conditions

The study sites are located in two regions of Northern and Southern Germany with a difference in mean annual temperature (MAT) of about 2 °C. The northern region is centered in the Lüneburg Heath in the North German Lowlands (federal state of Lower Saxony) near the village of Unterlüess (52.76 to 52.85°N, 10.27 to 10.52°E), the southern region in the Upper Rhine Valley near the city of Karlsruhe (federal state of Baden-Württemberg) (48.80 to 49.07°N, 8.13 to 8.42°E) (Fig. 1). The climate is cool-temperate with a more oceanic character in the north and a more sub-continental character in the south. The MAT of the southern region ranges between 11.2 °C and 11.4 °C, that of the northern region between 9.1 °C and 9.4 °C (mean of 1991–2020 period; German Weather Service, DWD). The Rhine valley is the warmest region in Germany with the highest number of hot days (Alexander, 2003; Buth et al., 2015). According to regional climate models, the current thermal regime of this region resembles that to be expected for much of the lowlands of Germany at the end of the 21st century in the course of climate warming

(Buth et al., 2015). Mean annual precipitation (MAP, 1991–2020) varies between 731 and 810 mm in the North and between 667 and 1006 mm in the South. Local precipitation differences in the southern region are largely the consequence of the vicinity of the Black Forest mountain ridge, which causes precipitation to peak at its foothills.

In both study regions, we selected 12 mature, monospecific forest stands, each three per tree species, i.e. 24 plots in total. The six plots per species (three in the north, three in the south) were selected to be sufficiently comparable in terms of tree height and diameter at breast height (Table 1). Apart from oak, where the stands in the north are older, the age within a species is similar between the two regions (Table 2). The conifers are in the study regions generally younger than the broadleaf species, reflecting faster growth rates in the former. All plots were selected in forest patches with a crown closure of >50% (Table 1). The soils were nutrient-poor sandy to sandy-loamy soils (Dystric Cambisols to Podzols) (Table S1). All study plots are managed by forestry authorities, but the timing and type of management is not precisely known. Maximum distance between plots was 20 km in the north and 40 km in the south.

2.2. Tree-ring data analysis and metadata

We sampled tree cores from at least 20 dominant or co-dominant trees per plot in March 2021 in the northern region and in March 2022 in the southern region. The focus on dominant trees likely increases the climate signal in the growth rings and reduces the influence of competition effects (Cook and Kairiukstis, 1990). Even though we attempted to sample only the most vital trees, some trees showed noticeable signs of crown damage, especially in the southern plots, where tree health was generally worse than in the north. To quantify this damage, tree vitality was evaluated visually in winter 2022/23. The trees were assigned to four vitality classes based on their crown morphology, and in case of the conifers, additionally according to the number of annual needle cohorts being present, following the methodology of Roloff (2018).

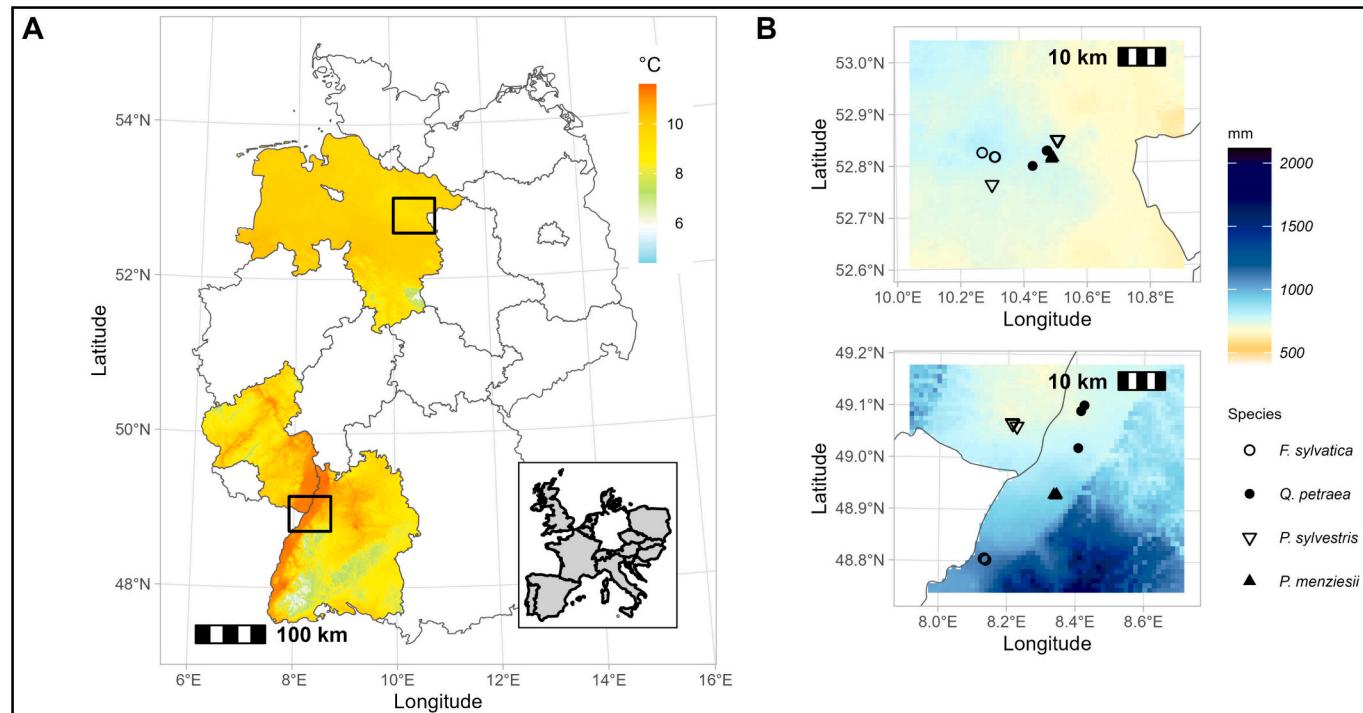


Fig. 1. Location of the two study regions in Germany (A) and of the 24 study plots in the two regions (B). Variation in mean annual temperature is indicated by different colors in fig. A, variation in mean annual precipitation in fig. B. Climate data are means of the 1991–2020 period (German Weather Service, DWD). The number of plot symbols in fig. B is smaller than 24, as several plots were located in close vicinity to each other.

Table 1

Location and site characteristics of the 24 study plots. Mean annual precipitation (MAP) and mean annual temperature (MAT) are averages for the 1991–2020 period (DWD). Mean height and diameter at breast height (DBH) (standard errors) refer to the cored trees, while canopy cover, basal area and stems per hectare refer to the whole forest plot including all trees with a diameter > 10 cm.

Species	Region	Latitude (°N)	Longitude (°E)	MAT	MAP	Mean tree height (m)	Mean DBH (cm)	Canopy cover (%)	Basal area (m ² /ha)	Stems (n/ha)
European beech	North	52.82	10.27	9.1	810	28.5 ± 0.4	50.6 ± 1.6	98	41.59	322.81
		52.82	10.32	9.1	793	31.4 ± 0.4	49.0 ± 2.0	85	39.99	345.09
		52.82	10.31	9.1	793	33.3 ± 0.3	51.5 ± 1.4	95	36.17	262.10
	South	48.81	8.13	11.2	994	26.3 ± 0.3	45.4 ± 1.8	95	33.78	225.81
		48.80	8.13	11.2	994	25.6 ± 0.4	47.4 ± 1.6	90	32.17	189.47
		48.80	8.14	11.2	1006	24.1 ± 0.5	39.3 ± 1.6	55	29.66	254.03
Sessile oak	North	52.83	10.48	9.1	773	27.9 ± 0.3	42.4 ± 1.2	80	26.85	184.56
		52.83	10.48	9.1	773	28.7 ± 0.3	46.7 ± 1.1	80	24.61	139.81
		52.80	10.43	9.3	760	31.3 ± 0.3	54.4 ± 1.5	95	53.23	238.50
	South	49.10	8.42	11.3	689	25.6 ± 0.4	34.9 ± 1.1	-	26.97	274.60
		49.10	8.41	11.3	687	25.2 ± 0.3	32.0 ± 1.0	70	20.41	263.44
		49.02	8.41	11.3	744	23.2 ± 0.4	31.8 ± 1.1	75	24.72	334.99
Scots pine	North	52.85	10.51	9.3	731	26.0 ± 0.3	32.0 ± 0.9	50	30.08	361.29
		52.85	10.52	9.3	731	27.5 ± 0.3	34.3 ± 0.9	50	36.99	388.89
		52.76	10.30	9.4	747	22.1 ± 0.2	26.9 ± 0.7	70	45.18	852.94
	South	49.07	8.21	11.4	679	31.5 ± 0.4	44.0 ± 1.1	50	33.66	254.03
		49.06	8.23	11.3	696	29.4 ± 0.4	39.9 ± 0.9	65	46.58	226.45
		49.07	8.21	11.4	676	25.8 ± 0.3	31.7 ± 0.7	80	65.15	893.14
Douglas fir	North	52.81	10.50	9.2	762	26.7 ± 1.4	35.3 ± 1.1	85	56.14	725.58
		52.81	10.50	9.3	745	25.9 ± 0.7	34.7 ± 1.3	80	45.83	555.90
		52.81	10.50	9.2	764	29.1 ± 0.4	41.5 ± 1.0	80	55.92	465.45
	South	48.93	8.34	11.2	834	35.3 ± 0.4	46.7 ± 1.2	65	35.72	215.05
		48.93	8.34	11.2	850	35.6 ± 0.5	51.9 ± 1.2	55	33.73	156.46
		48.93	8.34	11.2	839	35.1 ± 0.3	49.9 ± 0.9	60	33.36	172.41

Table 2

Statistics of the 24 tree ring chronologies. For series length, the mean and standard error are given. EPS (Expressed Population Signal (Wigley et al., 1984)) and Rbar (average pairwise Spearman correlation between all tree-ring series) refer to the period 1980–2020 (Douglas fir 1991–2020).

Species	Region	No. trees / no. cores	Series length (years)	EPS	Rbar
European beech	North	21/40	130.5 ± 1.9	0.98	0.66
		21/42	108.6 ± 2.1	0.98	0.69
		21/42	114.7 ± 1.9	0.98	0.66
	South	21/42	97.5 ± 1.5	0.97	0.59
		21/42	99.2 ± 1.2	0.98	0.67
		21/42	97.5 ± 1.3	0.96	0.52
Sessile oak	North	21/42	114.5 ± 1.8	0.98	0.73
		21/42	121.8 ± 1.4	0.99	0.77
		22/42	170.4 ± 3.0	0.98	0.67
	South	21/42	78.0 ± 0.9	0.95	0.48
		21/42	76.7 ± 1.1	0.96	0.53
		21/41	65.6 ± 1.0	0.97	0.62
Scots pine	North	21/42	59.5 ± 0.7	0.95	0.47
		21/42	63.6 ± 1.0	0.95	0.47
		21/42	58.7 ± 0.5	0.98	0.66
	South	21/42	81.0 ± 0.7	0.95	0.48
		21/42	64.2 ± 0.4	0.95	0.49
		21/42	42.5 ± 0.5	0.94	0.45
Douglas fir	North	22/44	37.5 ± 0.4	0.96	0.54
		22/43	36.7 ± 0.4	0.96	0.53
		24/48	35.7 ± 0.6	0.97	0.57
	South	20/40	46.7 ± 0.5	0.96	0.53
		21/42	45.4 ± 0.4	0.97	0.58
		21/42	42.1 ± 0.4	0.98	0.71

For analysing tree growth dynamics, two cores taken perpendicular to each other were extracted at breast height from each tree with a 5 mm-increment corer (Haglöf, Langsele, Sweden), resulting in 1011 cores in total. In the lab, the cores were dried, glued on wooden mounts, sanded (400 grit) and polished to prepare a smooth surface. The cores were scanned at 800 dpi (beech at 1200 dpi) (EPSON Expression 11,000 XL) and tree ring widths were measured with the software CooRecorder (v. 9.5, Cybis Elektronik & Data AB, 2020). Cross-dating was done with the program CDendro (v. 9.5, Cybis Elektronik & Data AB, 2020). The

quality of site chronologies was assessed through the expressed population signal (EPS), i.e. the alignment between a limited set of tree samples and a theoretical chronology created from an infinite number of trees. EPS values >0.85 were considered as reliable for a chronology (Wigley et al., 1984) (Table 2). The two ring series per tree were averaged to receive one ring series per tree. Detrending was done with a 20-year smoothing spline and low-frequency cut-off at 50 %, using the “detrend” function of the “dplR” package (Bunn, 2008), to largely remove age trends and reduce the influence of stand dynamics. This procedure results in dimensionless tree-ring index series that display the inter-annual fluctuation in ring width driven by climate variation. We first generated one chronology per plot (24 chronologies in total) and subsequently computed one chronology per species and region by averaging over all trees of the three plots in a region, resulting in eight chronologies (4 species × 2 regions). All statistical analyses were conducted with the software R version 4.0.2 (R Core Team, 2022).

2.3. Growth trends

To analyse long-term growth trends, we calculated annual basal area increment (BAI) from bark to pith based on the average ring width series of the two cores per tree and DBH, using the “bai.out” function of the “dplR” package (Bunn, 2008). DBH measured in the field was included with the aim to remove errors due to broken cores and/or skewed tree growth. In the analysis of growth trends, BAI is preferred over ring width, because it accounts for geometric tree characteristics and is better representing coarse wood production than ring width does (Schweingruber, 1983). The following equation was used to compute BAI in year t from the difference of the reconstructed tree radii r_t and r_{t-1} in the years t and t-1:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2)$$

The BAI curves were averaged over the 62 to 68 trees to form a single chronology per region and species using Tukey's bi-weight robust mean. By pooling the values of the three replicate plots, we aimed to minimize the influence of local management and competition effects, thereby emphasizing broader regional climate trends. We then used segmented regression analysis to detect changes in growth trends over the entire

length of the chronologies. The optimal breakpoints in growth trend direction were chosen according to the Bayesian information criterion (BIC) with the “segmented” function of the “segmented” R package (Muggeo, 2008). We limited the number of breakpoints to a maximum of three to focus on long-term growth trends. We then analyzed the significance and the direction of BAI trends for the identified periods using Sens's slope coefficient s at a significance level of $p < 0.05$, by regressing BAI against calendar year. A positive s value indicates a positive growth trend, and a negative one stands for a negative growth trend. The significance of trends was tested with a modified Mann-Kendall test with a variance correction approach for serially correlated data (Yue and Wang, 2004) (R package “modifiedmk”, Patakamuri and O'Brien, 2020). We additionally analyzed the trends of the individual trees in the last 20 years with the same method to compare growth trends between tree vitality classes.

2.4. Climate-growth relationships

To analyse relationships between annual growth and selected climate variables, we used monthly precipitation and temperature data provided by the German Weather Service (DWD, Offenbach, Germany) that are available in gridded datasets with 1 km mesh width. The data was detrended in the same way as done with the tree-ring data (Ols et al., 2023). To quantify the climatic water balance, we used the Standardized Precipitation-Evapotranspiration Index (SPEI), i.e. the locally-standardized difference between precipitation and potential evapotranspiration (as estimated with Thornthwaite's formula), calculated with the package “SPEI” (Beguería and Vicente-Serrano, 2023). Negative SPEI values are indicative of drier conditions, while positive values signal moister conditions, relative to the long-term SPEI average. We calculated the SPEI for 3-month periods (SPEI-3) to smoothen the SPEI curve. We then correlated the RWI values with monthly climate variables of the current and the previous year for each species and region in a 1000-fold bootstrapping procedure, using the “dcc” function of the “treeclim” package (Zang and Biondi, 2015). We chose therefore a 16-month window from previous June until current September. The analysis was performed first with all 24 chronologies and subsequently with the 8 chronologies that included all trees of the three plots per species and region. For the latter, the climate data of the three plots were averaged. Furthermore, we calculated the correlation between the number of hot days (daily maximum $>30^{\circ}\text{C}$) in the current and the previous year and RWI in a 1000-fold bootstrapping procedure using the “cor.ci” function of the “psych” package (Revelle, 2017). As the common observation period varies between the four species, we decided to focus in both analyses on the last 40 years (1981–2020) and to narrow it to the 1991–2020 period in case of Douglas fir to exclude the juvenile phase.

2.5. Pointer year analysis

To detect abnormal years with region-wide growth reductions (negative pointer years), we employed the bias-adjusted standardized growth change method (BSGC) of Buras et al. (2022) for each region and species. This new method examines both, how extreme the growth change in a given year is in comparison to the previous year, and how extreme this value is in comparison to all earlier RWI values (Buras et al., 2022). Previous methods compared growth only with one or a few earlier years, which has become problematic in recent time, when extreme drought years are happening consecutively. Further, this new method allows the calculation of a deflection period, which identifies the years after a pointer year until normally expected growth rates are reached again (Buras et al., 2022). To ascertain whether the identified pointer years coincided with drought events, we used the SPEI-3. The specific month was determined based on the results of the climate-growth correlation analysis for each species. The assumption of normally distributed growth changes was not met in case of the Douglas fir chronology in the southern region (Shapiro-Wilk test, $p = 0.005$). Hence,

the results for this particular site should be interpreted with caution. For all pointer years pooled, we calculated in a 1000-fold bootstrapping procedure the mean RWI, 95 % confidence intervals and percentage of tree individuals with growth halved ($\text{RWI} < 0.5$) during years with growth anomalies.

3. Results

3.1. Climate trends

From 1980 to 2020, mean annual temperature has significantly increased by $>1.5^{\circ}\text{C}$ in both regions, whereas between 1950 and 1980, no significant trend existed (Fig. 2A). The number of hot days per year (temperature maximum $>30^{\circ}\text{C}$) is generally higher in the south; the mean number has in both regions significantly increased from the first to the second period (Fig. 2B). The climatic water balance has deteriorated during the growing season (April to August), but has improved during the winter months in both regions (Fig. 2C). However, the winter increase in P-PET has not fully compensated the summer decrease, especially in the southern region, which results in an overall decrease in the annual climatic water balance by about 60 mm in that region. Mean annual precipitation has significantly decreased from 1980 to 2020 at all twelve study plots in the south, while the trend was not significant in the north (Fig. S1).

3.2. Long-term growth trends

The beech chronology from the northern region showed since >100 years a positive BAI trend that continues in the most recent decades (Fig. 3A). In contrast, the southern beech chronology followed positive growth trends over much of the 20th century but shifted to a negative growth trend in 2007 that continues until today.

Oak showed a continuous BAI increase since nearly 200 years in the northern stands and since nearly 100 years in the younger southern stands, which lasts until today (Fig. 3A). Pine has generally the lowest BAI rates of all species and showed less variation during the last 70 years (Fig. 3B). However, growth shifted from a positive to a negative BAI trend around the year 2000, which continues until today. The Douglas fir stands are younger than those of the other species, and they showed rapidly increasing BAI rates in their first 20–30 years to reach a growth peak between 1996 and 2010, when BAI started to decline again (Fig. 3B). Detailed information about dates of the growth periods including slope, significance and the percentage of trees displaying the trend can be found in Table S1.

In the majority of tree individuals of the four species, the growth trend during the past two decades (2001–2020) was significant ($\sim 64\%$ of stems, Fig. 4A). In beech, pine and Douglas fir, far more individuals showed a negative BAI trend in recent time than a positive, and the proportion of trees with a negative trend increased in the three species from crown vitality class 0 to classes with higher damage. Especially in the classes with low vitality (classes 2 and 3), a high proportion (64–76 %) of trees showed a significant BAI decline in the last two decades. Surprisingly, even some of the most vital trees (class 0) displayed negative growth trends; this fraction reached $>20\%$ in beech, oak and Douglas fir, and in pine even $>50\%$. Oak differed from the other species in that positive growth trends were more abundant than negative trends, even in the lower vitality classes. In the other three species, $<20\%$ of trees showed significant positive BAI trends. Across all species, the proportion of trees in higher vitality classes (higher damage) was greater in the southern region than in the northern one. This trend was more pronounced in beech and oak (Fig. 4B).

3.3. Climate sensitivity of growth

All four species showed a significant positive relationship between growth and SPEI-3 of the summer months, i.e. growth limitation by a

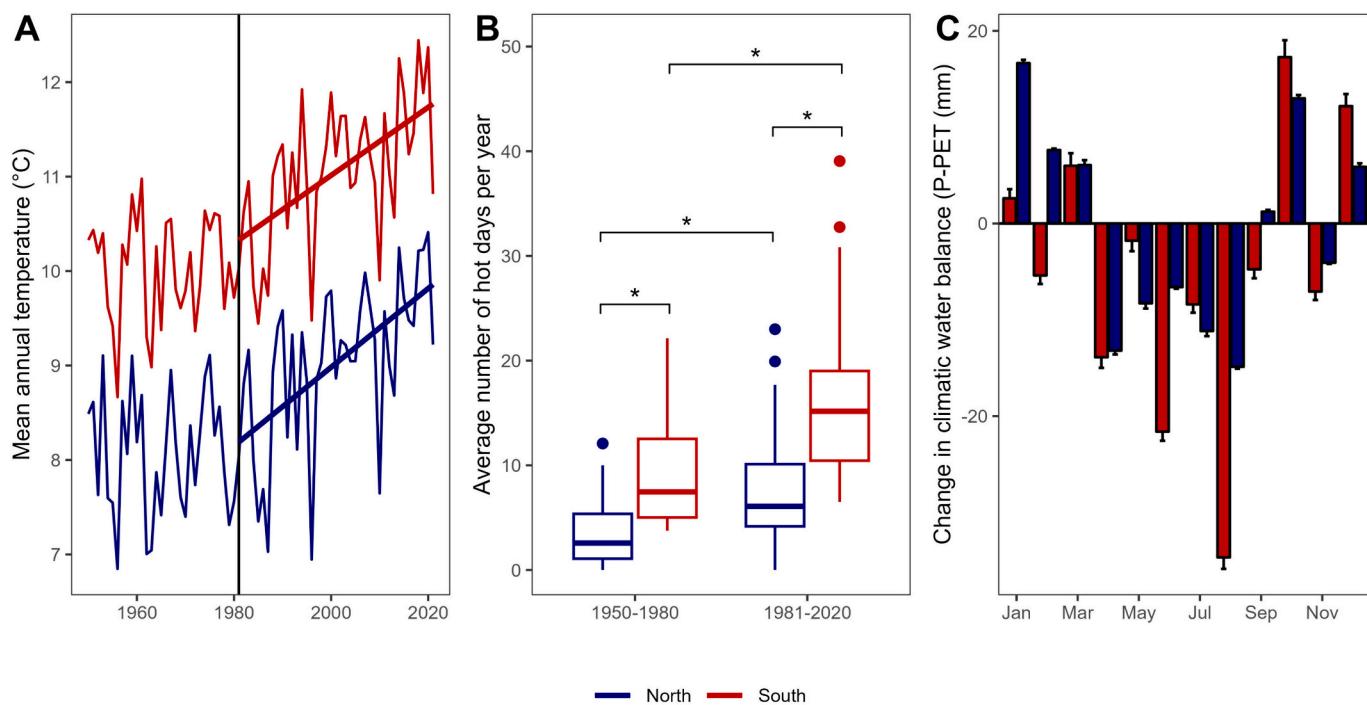


Fig. 2. Change in climatic conditions between 1950 and 2020 in the northern and southern study regions. A) Change in mean annual temperature with regression lines in the periods 1950–1980 and 1981–2020 in the two regions (solid lines: significant trend according to a Mann-Kendall test). B) Average number of hot days per year (temperature maximum $>30^{\circ}\text{C}$) in the two periods and two regions. Significant differences between means are indicated by horizontal lines ($p < 0.05$). C) Change in mean monthly climatic water balance (P-PET, in mm) \pm SE from the 1950–1979 to the 1980–2020 period in the two regions.

less favourable climatic water balance (in oak only significant in the southern region; Fig. 5). In addition, high temperatures in the current or previous summer had a significant negative effect on growth in all species. However, the species differed with respect to the sensitive months of the SPEI and temperature effects, and the trees of the same species in the northern and southern region differed in their responsiveness. Beech trees in the southern region were significantly impacted by water deficits in spring and summer of the current year (February to July), while in the northern region, water deficits in previous year's summer (July – September) were more important (Fig. 5: first panel). Previous year's water availability was less important in the other three species. In oak, water deficits in spring (February to May) were the main determining factor in the southern region, while growth in the northern region was not significantly dependent on SPEI, neither in spring nor in summer (Fig. 5: second panel). In contrast, both conifers exhibited growth sensitivity to late-summer water deficits of the current year (July – September), and pine in the southern region was additionally sensitive to spring water deficits (February – April) (Fig. 5: third panel). The sensitivity to spring moisture lacked in Douglas fir, but the trees in the southern region were additionally affected by water deficits in previous year's June (Fig. 5: fourth panel). The correlation between growth and monthly precipitation was similar to the correlation with SPEI in the four species (Fig. S3A). A significant negative temperature signal was detected in beech for previous summer's July (only northern region), and for oak in previous summer's August (northern region) (Fig. 5: first and second panel). In pine, high temperature in current July (southern region) limited growth, while this was found for current-year June (northern region) or previous year's June (southern region) in Douglas fir (Fig. 5: third and fourth panel). A similar pattern emerged, when the influence of monthly mean maximum temperature was investigated (Fig. S3D). Growth stimulation by mild winters was observed in oak, pine and Douglas fir, especially in the cooler northern region, but not in beech (Fig. 5). In addition, oak growth in the southern region was stimulated by a warm May. The more detailed analysis with three chronologies per species and region revealed that differences in the

climate-growth correlation between the replicate stands were generally small (Fig. S3).

The number of hot days (days with $>30^{\circ}\text{C}$ maximum temperature) significantly reduced the annual growth of beech, pine and Douglas fir, but not of oak (Fig. 6). In case of beech, the previous year was more influential in both regions, but this effect was more pronounced in the north, while the influence of current-year heat was much lower. In pine and Douglas fir, the current year influenced growth in both regions, while the previous-year heat had an additional effect only in the warmer southern region, but not in the northern. These heat effects were in the conifer species stronger than the average temperature signal in the ring-width series (Figs. 5 and 6).

3.4. Pointer-year analysis

Between two and five negative pointer years were identified per species and region during the 1981–2020 observation period, with beech in the northern region displaying the highest number, while beech in the southern region and Douglas fir (both regions) showing the fewest pointer years (Fig. 7). During this period, no change in pointer year frequency is recognizable. Douglas fir was the only species with identical pointer years in both regions (2003 and 2018), while in the other species, most pointer years differed between the regions. In the identified years, nearly every tree exhibited lower growth rates than usual ($\text{RWI} < 1$) (Fig. S4). Beech showed the largest growth anomalies among the species with no difference between the regions (Table 3). Oak and Douglas fir had larger growth anomalies in the north, whereas pine displayed slightly smaller growth anomalies in the north than in the south (Table 3). The majority of pointer years did not show a deflection period, and growth returned to normal rates in the first year after the pointer year. Pointer years often coincided with low SPEI values or, in some instances, occurred in the year after a dry period (Fig. 7). Pointer years also coincided with years with frequent hot days (or the subsequent year); this relation seems to be stronger in the conifers (Fig. S5).

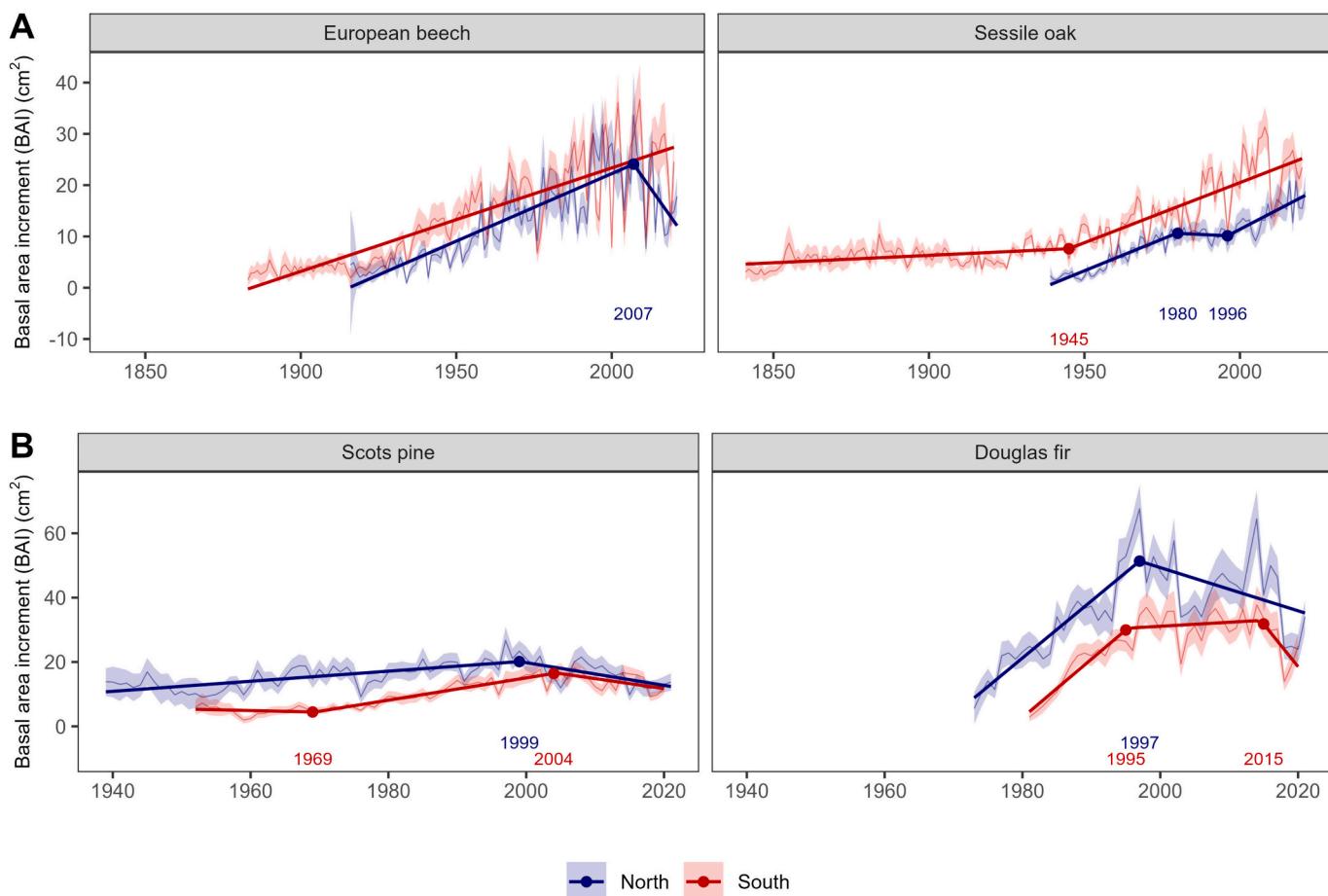


Fig. 3. Change in basal area increment over the length of the chronologies (when the number of trees was ≥ 10) with 99 % confidence interval in the northern and southern region for A) beech and oak and B) pine and Douglas fir. Straight lines represent segmented regression analyses for changes in growth trends, points mark the breakpoints detected by the algorithm (maximum of three breakpoints allowed).

4. Discussion

Our study provides valuable insights into the effects of climate warming on the growth dynamics of four major Central European timber species. While water availability in the growing season limited growth in all four species, beech, pine and Douglas fir showed predominantly negative BAI trends in recent decades, likely caused by recent increases in drought and heat stress. Since negative growth trends were more pronounced in the warmer, southern region, this might suggest absence of sufficient local adaptation to these conditions and that the trees could not acclimate in the past decades to the 2 °C warmer climate in order to prevent tree vitality decline.

4.1. Prevailing negative growth trends in beech, pine and Douglas fir since the 1980s

We found recent BAI declines in (co-)dominant trees not only in beech and pine, but also in Douglas fir, in contradiction to our second hypothesis. Sessile oak was the only species that showed for the large majority of tree individuals stable or increasing growth trends since the 1980s, supporting earlier dendrochronological studies from Central Europe that revealed a lower climate sensitivity of growth of oak than of beech and other broadleaf and coniferous trees (Friedrichs et al., 2009a; Fuchs et al., 2021; Maes et al., 2019). The contrast to the other three species is even more impressive, when the higher age of the oak trees (especially at the northern sites) is taken into account. Our data from the dominant trees may not be representative for the whole stand, as suppressed trees and individuals in lower strata can respond differently to

climate (Grote et al., 2016; Nehrbass-Ahles et al., 2014). However, the chosen trees are relevant for forestry, as they represent the trees selected for eventual harvest ('future trees').

It was unexpected that more oak trees with low vitality showed positive growth trends, while many trees assigned to the 'high vitality' category had negative growth trends. We speculate that healthier-looking oak trees might allocate more resources to maintain leaf area and crown functioning, which must reduce the carbohydrates that are available for stem growth. If valid, crown vitality would not be a reliable indicator of stem growth in oak trees. However, age could also have contributed to the observed patterns: the less vital trees are mostly located in the south and are younger, which could also contribute to their better growth and might have blurred the crown vitality-growth relationship. The observation of negative BAI trends for beech in our southern region matches reports from various other Central and Western European regions, where persistent growth reductions since about the 1980s have been detected in dominant mature beech trees, especially at submontane and lowland elevations (Belgium: Kint et al., 2012, Luxembourg: Härdtle et al., 2013, North-East France: Charru et al., 2010, Central Germany: Zimmermann et al., 2015, North-West Germany: Knutzen et al., 2017; North-East Germany: Scharnweber et al., 2011) in regions with $<\sim 650$ mm MAP (Leuschner et al., 2023; Weigel et al., 2023). Our findings of positive BAI trends in the northern region with 793–810 mm MAP fit to this picture, while the southern sites revealed negative BAI trends despite exceeding the 650 mm MAP threshold. A plausible explanation is that this threshold is only valid for the North German Lowlands, where it was derived, and needs adjustment especially in warmer regions as in the Upper Rhine Valley, where

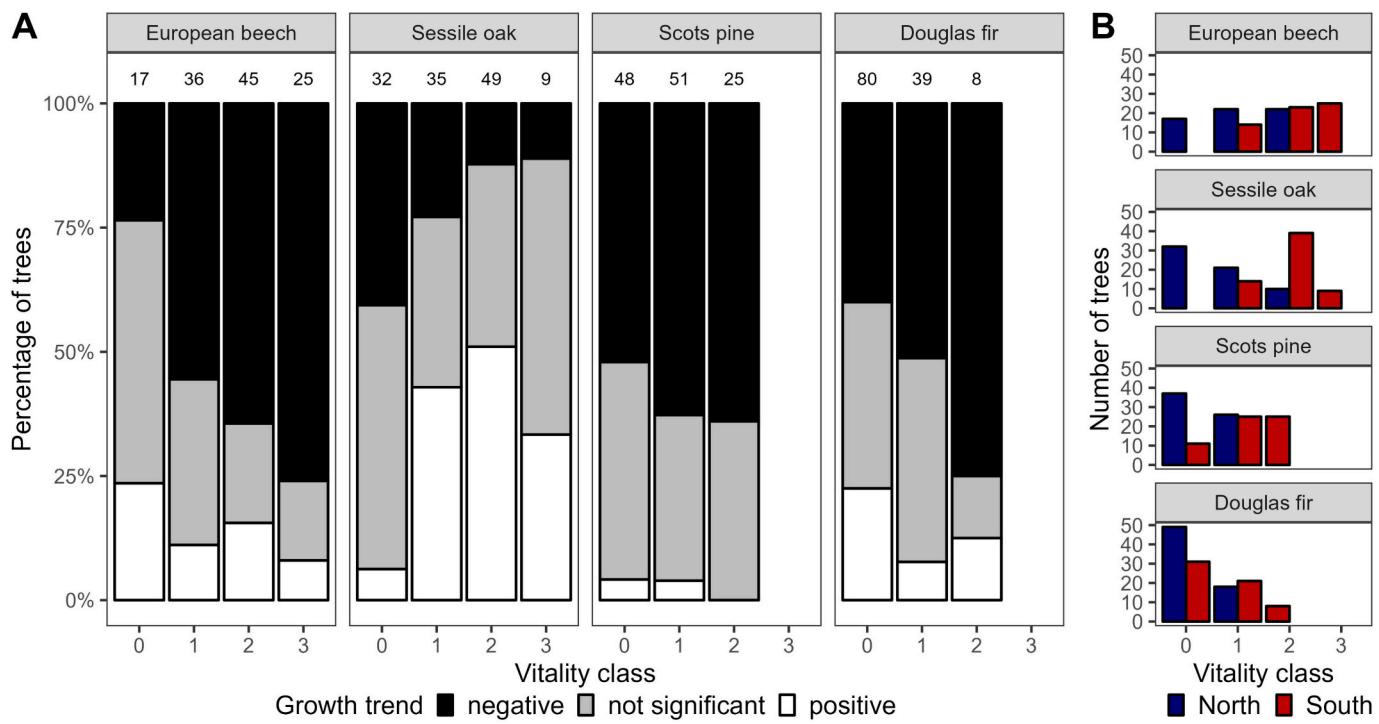


Fig. 4. A) Proportion of trees of the four species with significant positive or negative BAI trends or a non-significant trend during the period 2001–2020 in different canopy vitality classes (0 to 3) (100 % = all tree individuals of a species in the two regions). Numbers over bars give the number of trees per species and vitality class. Only classes with >5 individuals are displayed. B) Frequency of trees of the four species in the four vitality classes in the two regions.

evapotranspiration is higher and temperature extremes might play a more decisive role for beech health than further in the north.

The performance of Douglas fir with pronounced negative growth trends during the last 20–30 years in both study regions disproves our second hypothesis and contradicts the widely held assumption of a fairly high drought resistance of this species (Lévesque et al., 2014; Spellmann et al., 2015; Thomas et al., 2022). Since the transition from a positive (or stable) BAI to a negative growth trend occurred around 1997 in the south and 2015 in the cooler north in Douglas fir, it is plausible to assume a causal relation to the rapid warming trend since about 1980. We assume that this productive conifer likely has profited from favourable growing conditions in the second half of the 20th century, as has been observed in other species (Boisvenue and Running, 2006; Pretzsch et al., 2014). We speculate that the subsequent growth decline might partly be a consequence of structural over-shoot of trees that have produced large crowns with high needle surface areas in the past (Jump et al., 2017), which turned out to be mal-adaptations in a warmer and drier climate and therefore exposed the trees to severe stress. However, since we cannot entirely exclude that the BAI decline in our study is partly caused by increased competition in ageing stands, more dendrochronological and physiological studies in Central Europe are needed to identify hygric and thermal thresholds, below which the species is facing growth decline and vitality loss in recent time.

Comparative growth analyses in southern Central Europe have demonstrated a higher drought resistance of Douglas fir than Scots pine (Eilmann and Rigling, 2012; Lévesque et al., 2014). This finding is supported by our crown vitality evaluation, but, in contrast, our growth trends from lowland regions indicate a higher sensitivity of Douglas fir than of Scots pine in both studied regions. The pine stands showed generally lower BAI rates ($<25 \text{ cm}^2 \text{ year}^{-1}$) than Douglas fir and revealed only a slight growth decrease in recent decades in both regions. According to Diers et al. (2024) and Pretzsch et al. (2023), pine growth trends vary considerably across Europe, with northern European stands thriving under global warming, while southern European stands being mostly negatively affected. Central European pine stands (which

includes our stands) often take an intermediate position, and growth stimulation by warmer late-winter periods seems to compensate for growth impairment due to warmer and drier summers (Diers et al., 2022, 2024). Since our pine stands are regularly thinned, we cannot rule out that the slight decline in growth observed in recent decades is caused by an increase in competition (Sánchez-Salguero et al., 2015).

4.2. Water availability and heat are key drivers of radial growth in all four species

The growth correlation to climatic water balance (SPEI) in the summer months was in all species usually closer than to any other climatic variable tested here, exceeding the positive relation to summer precipitation and the negative one to summer temperature. This supports part of our first hypothesis. The only exception was the positive effect of winter (spring) temperature (December – March) in pine, Douglas fir and oak, which was similarly important as SPEI in these species. That SPEI exceeds the precipitation influence in most cases is a hint at the importance of VPD as an atmospheric driver of plant water status, which acts on growth in addition to precipitation and soil moisture availability (Grossiord et al., 2020; Williams et al., 2013). In agreement with expectations, the SPEI dependence of growth was in all species more consistent in the warmer southern region, where average VPD must be higher than in the northern region, even though precipitation was higher at the beech and Douglas fir sites.

The months with largest influence on growth varied among the species and largely corresponded to the species' growth phenology. In accordance with other dendrochronological studies, we found a spring sensitivity of oak growth (Friedrichs et al., 2009b; Fuchs et al., 2021). This is plausible, as the species completes most of its early-wood formation before and during bud burst in late spring and thus before the usual start of summer droughts in Central Europe (Etzold et al., 2022; Michelot et al., 2012b). While many studies report a fairly low climate sensitivity of oak (Cavin et al., 2013; Friedrichs et al., 2009b; Mérion et al., 2011; Walentowski et al., 2017), evidence exists that sensitivity is

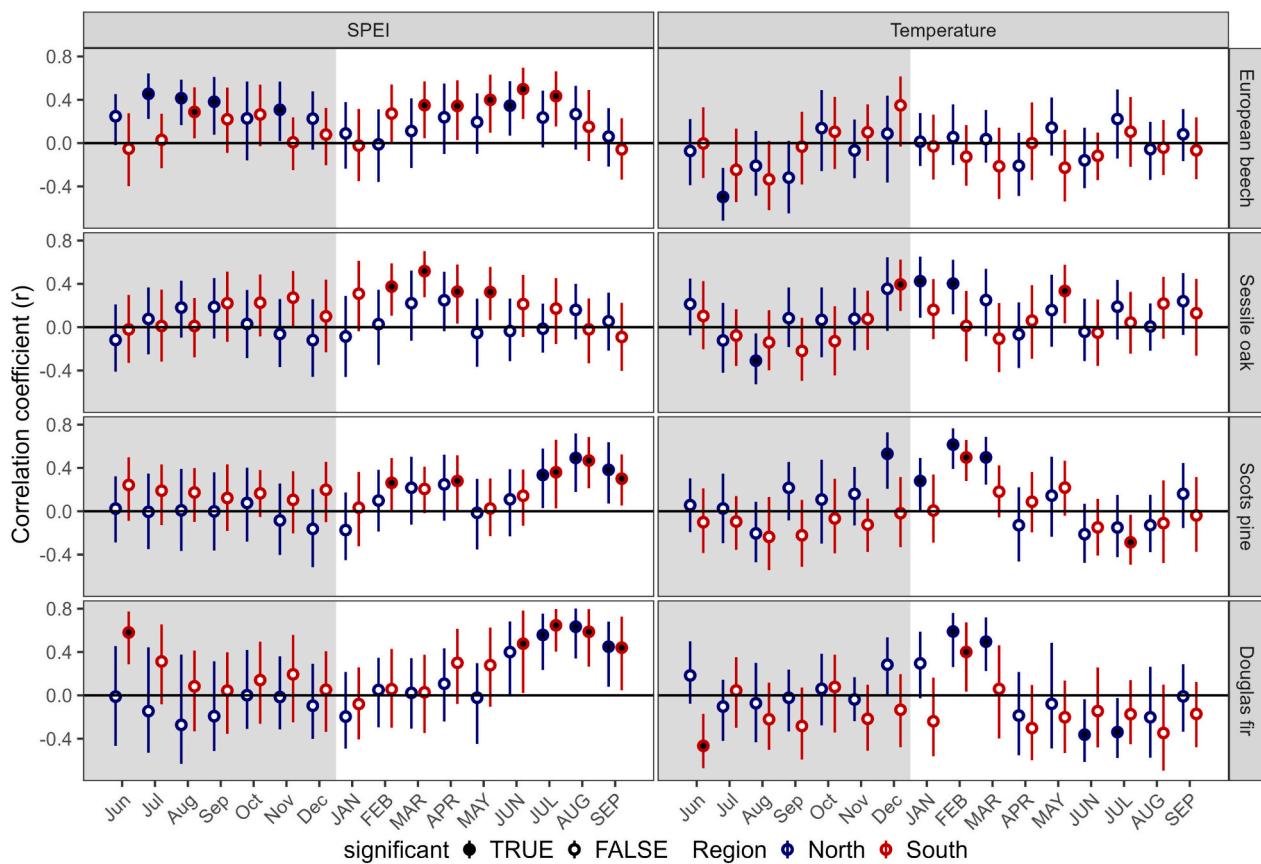


Fig. 5. Correlation coefficients (Pearson's r) of ring width index values and the SPEI-3 or mean temperature of selected current-year or previous-year months in the four species in the two regions during the observation period 1981–2020 (Douglas fir: 1991–2020). Shown are means \pm SE of r values for all stands of a species in a region pooled ($N = 3$ per region). Months of the previous year are written in lowercase letters, months of the current year in capital letters. Filled circles indicate significant correlations between climate parameters of the respective month and RWI.

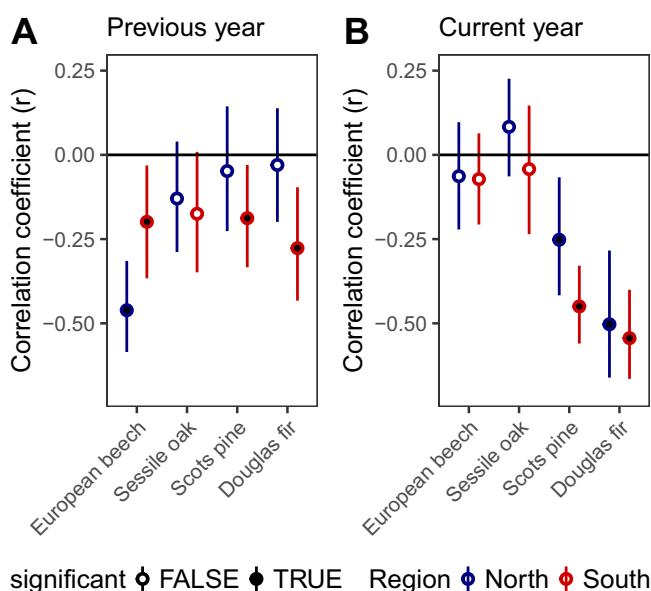


Fig. 6. Correlation coefficients (Pearson's r) for the relation between growth (RWI) and the number of hot days in A) the previous year or B) the current year in the four species and the two regions during the observation period 1981–2020 (Douglas fir: 1991–2020).

higher at warmer and drier sites (Bose et al., 2021; Friedrichs et al., 2009b). This matches our observations, where a significant spring drought sensitivity existed only in the southern region. This suggests that the drought sensitivity of oak growth likely will increase in future with climate warming in large parts of Central Europe.

Beech radial growth tends to peak later, in Central Europe in June (Čufar et al., 2008; Etzold et al., 2022). Consequently, beech growth was more sensitive to summer drought than that of oak. In addition, water deficits in the previous summer were more relevant than in the other species, especially in the northern region, which might relate to the mast-fruiting behavior of beech (Hacket-Pain et al., 2015; Müller-Haubold et al., 2015). Several dendrochronological studies in northern Germany show non-stationarity of climate-growth relationships of beech with either increases (Stolz et al., 2021) or decreases in climate sensitivity (Diers et al., 2022). Van der Maaten-Theunissen et al. (2016) observed a recent shift from current- to previous-year drought effects on growth, i.e. an increasing lag-effect. These results point at considerable spatial and temporal variability in the relevant climatic drivers of beech growth in the Central European lowlands, which partly is explained by the additional influence of edaphic (e.g. soil water storage capacity) and stand structural factors on growth dynamics (Weigel et al., 2023).

In contrast to the broadleaf species, the two conifers were more sensitive to late-summer water deficits, especially July–September SPEI, matching the results of other studies (Bose et al., 2020; Stolz et al., 2021; Vejpustková and Čihák, 2019), which may relate to the evergreen habit. The important role of atmospheric water status for the growth of conifers was demonstrated by Restaino et al. (2016) for Douglas fir in the western US, where radial growth is negatively related to VPD and this growth-controlling factor is more important than soil moisture. The

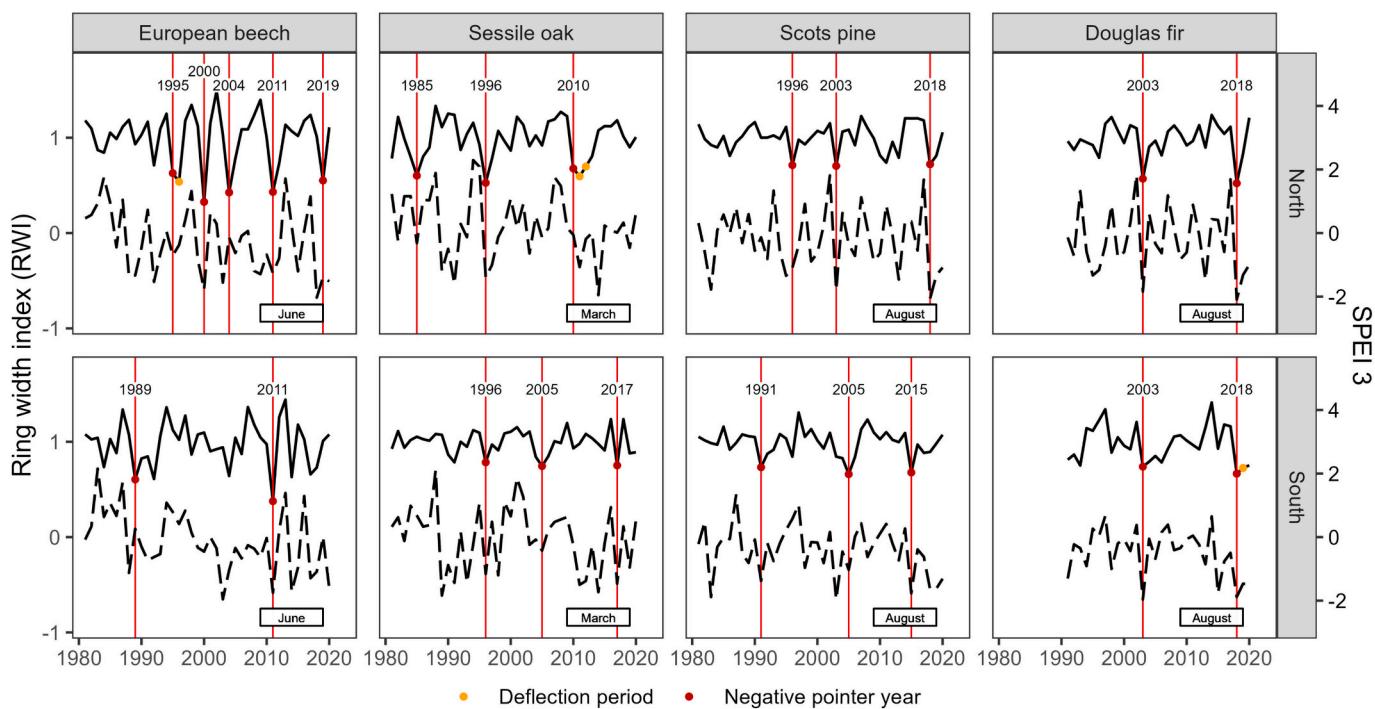


Fig. 7. Negative pointer years in the period 1981–2020 in the ring width index (RWI) chronologies (solid lines) of the four species in the two study regions (Douglas fir: 1991–2020). Also shown is the SPEI-3 (dotted lines; right y-axis) and the deflection period (the years after a pointer year until ordinary growth rates are reached again). Positive pointer years are not shown. The relevant SPEI months differ among the species and were chosen according to their importance for the species.

Table 3

Mean ring width index, 95 % confidence intervals (CI), and percentage of tree individuals with growth halved (RWI < 0.5) during years with growth anomalies.

Species	European beech		Sessile oak		Scots pine		Douglas fir		
	Region	North	South	North	South	North	South	North	South
Mean		0.48	0.49	0.61	0.76	0.71	0.69	0.54	0.70
95 % CI		0.46–0.50	0.46–0.52	0.59–0.63	0.75–0.78	0.69–0.73	0.67–0.71	0.52–0.57	0.68–0.73
% cases RWI < 0.5		60.00	61.10	24.00	1.06	5.82	9.68	35.90	5.65

more consistent correlation between SPEI in the summer months and growth in Douglas fir than in pine (see Fig. S4) seems to suggest that the VPD influence is indeed greater in the former species. In agreement with the BAI trends, the growth dependence on elevated summer precipitation and a higher SPEI tended to be greater in Douglas fir than in pine in both regions.

According to the climate-growth analysis, a negative effect of elevated summer temperatures on growth was less influential than hygric factors (precipitation and SPEI) in the four species. It is possible that our analysis, which bases on monthly temperature averages, has masked heat effects on tree growth. Experimental evidence shows that heatwaves have a greater impact on growth than uniform warming over extended periods (Bauweraerts et al., 2014), as high temperatures experienced over a few minutes to hours can already cause damage to the photosynthetic apparatus and other components of the leaf metabolism of trees (Teskey et al., 2015). However, most dendrochronological studies use monthly average or maximum temperature data, which do not adequately represent heatwaves, if the remaining days of the month are cooler than the average. We therefore conducted an additional correlation analysis with the number of hot days per year and could show that heat indeed negatively affects the growth of all species except oak. This demonstrates that heat effects on growth are probably underestimated in many dendrochronological climate sensitivity analyses. We therefore recommend adding the number of hot days as a climate variable in future growth sensitivity studies to better understand the role of heat as an independent driver of growth reductions in the

course of climate warming.

Our analysis suggests that Douglas fir is the most heat-sensitive species, which revealed in both regions the closest negative relation between hot days and growth among the four species. The heat effects on pine and beech were also significant in both regions, but less strong, while oak showed no significant heat effect. This is partly a consequence of differences in leaf and cambial phenology, with oak completing most of its early-wood growth before summer heat develops, while the other species show radial growth until later in summer (Michelot et al., 2012b). Moreover, the conifers flush their new needles only in mid-summer, when heat exposure is usually highest. This could be one explanation for the observation of Húdková et al. (2022) from heat stress experiments that the photosystem II of angiosperm trees is usually more heat-resistant than that of conifers. The 1-year lag in the heat effect on beech growth might relate to mast-fruiting which is stimulated by warm and dry summers (Müller-Haibold et al., 2015) or the regeneration of a drought-damaged fine root system (Hertel et al., 2013), in the consequence of which less carbon would be available for stem growth. Species differences in leaf temperatures and biochemical heat protection and repair mechanisms may offer further explanations for the apparently greater heat sensitivity of Douglas fir. More studies that compare root dynamics across regions are needed for understanding the complete picture of C-allocation under different climatic constraints.

Growth enhancement by a warmer spring, which has been observed in many studies on conifers (Castaldi et al., 2020; Diers et al., 2024; Seidling et al., 2012; Vejpustková and Čihák, 2019), was also found in

our study for both conifer species, especially for pine, probably due to an earlier start of photosynthetic activity. The effect was more pronounced in the cooler northern region, perhaps due to the more oceanic and thus humid climate there. A warmer winter was positively related to the growth of oak, but not of beech, which may relate to the higher winter frost resistance of diffuse-porous beech than of ring-porous sessile oak (Sakai and Larcher, 1987; Till, 1956). Winter-cold sensitivity of oak growth was also found in some other dendrochronological studies (e.g. Fuchs et al., 2021), but lacked in others (Bose et al., 2021).

Comparing the growth responses in our warmer and cooler regions indicates a generally higher climate sensitivity of the species in the southern region, in support of our third hypothesis. Here, the drought sensitivity of growth was higher in beech and oak (and less pronounced in pine), and the heat sensitivity of growth higher in pine and Douglas fir as compared to the northern region. This is reflected in the poorer growth performance (more negative growth trends, slower growth rates) and a less favourable crown vitality status in the southern region. While it is possible that differences in site quality or management could influence these results, we believe the primary driver is the variation in climatic conditions.

4.3. The number of pointer years does not differ between regions

An increase in negative pointer year frequency over time in consequence of the recent climate warming, as observed in other studies (e.g. Perkins et al., 2018; Vejpustková and Čihák, 2019), is not indicated by our data (a trend might exist for beech in the northern region, but the period is still too short). Moreover, oak, pine and Douglas fir showed no difference between the two regions in negative pointer year frequency, disproving our hypothesis (iii). However, these species showed larger growth anomalies in the north than in the south, except for pine, which exhibited slightly smaller anomalies in the north. Only beech showed a higher pointer year frequency in conjunction with greater inter-annual growth variation in the northern region, which might point at acclimation to the warmer climate in the southern region, as is also suggested by the results of Weber et al. (2013). Nevertheless, beech trees experienced in both regions larger growth reductions during pointer years than the other species.

Negative pointer years mostly coincided with dry and hot summers, or, in case of beech, partly were related to previous-year drought (Latte et al., 2016). The severe hot summer droughts of 2003 and 2018 caused negative pointer years in beech, pine and Douglas fir, but not in oak, due to the species' sensitivity to spring drought. However, most pointer years were followed by rapid growth recovery already in the next year, which may point to a vigorous recovery potential of the studied (co-)dominant trees. Exceptions are the multi-year growth depression of the northern oak trees after the combined cold and drought in March/April 2010, and of the southern Douglas fir trees after the 2018 summer drought. A likely explanation is consecutive droughts in more than one year, which can exhaust the resources needed for damage repair (Bréda et al., 2006; Gessler et al., 2020; Wu et al., 2018).

5. Conclusions

Our dendrochronological study that compared a cooler and a warmer region produced multiple evidence that beech, pine and Douglas fir are facing recent vitality declines in parts of the Central European lowlands, which likely are caused by increasing exposure to drought and heat. Oak was the best-performing species in both regions, even though its higher drought sensitivity in the warmer region is pointing at growing climate change vulnerability in the future. While some findings suggest acclimation to the warmer and drier climate in the southern region, those trees were generally more susceptible to heat and drought and thus suffered stronger vitality decline.

Given that the drought and heat exposure will most likely increase further in the course of the century, we expect that beech, pine and

Douglas fir will suffer under increasing climatic stress in many regions of the Central European lowlands, especially in more continental climates and at sites with reduced soil water storage capacity (such as sandy soils) and higher heat exposure. Except for regions near the coast, foresters planning production forests should consider more drought- and heat-resistant tree species such as sessile oak and several minor hardwood timber species (including Norway maple, little-leaved linden and hornbeam) that are more stress-tolerant than beech, pine and Douglas fir. More dendrochronological data and retrospective analyses of growth trials with different provenances are needed to better understand differences in the drought and heat resistance of the studied major timber species. Based on extended data sets, large-scale growth modeling approaches are also needed to help foresters calculating the risk of failure in a warming climate more reliably.

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CRediT authorship contribution statement

Lena Enderle: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Stella Gribbe:** Writing – review & editing, Investigation. **Lena Muffler:** Writing – review & editing, Supervision, Resources. **Robert Weigel:** Writing – review & editing, Supervision, Resources. **Dietrich Hertel:** Project administration, Funding acquisition, Conceptualization. **Christoph Leuschner:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.173665>.

References

- Alexander, J., 2003. Die heißesten und kältesten Gebiete, in: Bundesrepublik Deutschland Nationalatlas Band 3 - Klima, Pflanzen- Und Tierwelt. Spektrum Akademischer Verlag, pp. 36–37.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Fed.), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.

- Bauwe, A., Koch, M., Kallweit, R., Konopatzky, A., Strohbach, B., Lennartz, B., 2013. Tree-ring growth response of Scots pine (*Pinus sylvestris* L.) to climate and soil water availability in the lowlands of North-eastern Germany. *Balt. For.* 19, 212–225.
- Bauwe, A., Jurasiński, G., Scharnweber, T., Schröder, C., Lennartz, B., 2016. Impact of climate change on tree-ring growth of Scots pine, common beech and pedunculate oak in northeastern Germany. *IForest* 9, 1–11. <https://doi.org/10.3832/ifor1421-008>.
- Bauweraerts, I., Ameye, M., Werten, T.M., McGuire, M.A., Teskey, R.O., Steppe, K., 2014. Water availability is the decisive factor for the growth of two tree species in the occurrence of consecutive heat waves. *Agric. For. Meteorol.* 189–190, 19–29. <https://doi.org/10.1016/j.agrformet.2014.01.001>.
- Beguería, S., Vicente-Serrano, S.M., 2023. SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9, 330–343. <https://doi.org/10.1007/s10021-005-0126-2>.
- Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. *Glob. Chang. Biol.* 12, 862–882. <https://doi.org/10.1111/j.1365-2486.2006.01134.x>.
- Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J.J., Haenzi, M., Heresz, A.M., Hevia, A., Lévesque, M., Linares, J.C., Martínez-Vilalta, J., Matías, L., Menzel, A., Sánchez-Salguero, R., Saurer, M., Vennetier, M., Ziche, D., Rigling, A., 2020. Growth and resilience responses of Scots pine to extreme droughts across Europe depend on predrought growth conditions. *Glob. Chang. Biol.* 26, 4521–4537. <https://doi.org/10.1111/gcb.15153>.
- Bose, A.K., Gessler, A., Büntgen, U., Rigling, A., 2024. Tamm review: Drought-induced Scots pine mortality—trends, contributing factors, and mechanisms. *For. Ecol. Manag.* 561, 121873.
- Bose, A.K., Scherrer, D., Camarero, J.J., Ziche, D., Babst, F., Bigler, C., Bolte, A., Dorador-Liñán, I., Etzold, S., Fonti, P., Forrester, D.I., Gavinet, J., Gazol, A., de Andrés, E.G., Karger, D.N., Lebourgeois, F., Lévesque, M., Martínez-Sancho, E., Menzel, A., Neuwirth, B., Nicolas, M., Sanders, T.G.M., Scharnweber, T., Schröder, J., Zweifel, R., Gessler, A., Rigling, A., 2021. Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. *Sci. Total Environ.* 784, 147222 <https://doi.org/10.1016/j.scitotenv.2021.147222>.
- Bowditch, E., Santopuoli, G., Binder, F., del Río, M., La Porta, N., Kluvankova, T., Lesinski, J., Motta, R., Pach, M., Panzacchi, P., Pretzsch, H., Temperli, C., Tonon, G., Smith, M., Velikova, V., Weatherall, A., Tognetti, R., 2020. What is climate-smart forestry? A definition from a multinational collaborative process focused on mountain regions of Europe. *Ecosyst. Serv.* 43, 101113 <https://doi.org/10.1016/j.ecoser.2020.101113>.
- Braun, S., Hopf, S.E., Tresch, S., Remund, J., Schindler, C., 2021. 37 years of forest monitoring in Switzerland: drought effects on *Fagus sylvatica*. *Front. For. Glob. Chang.* 4, 1–10. <https://doi.org/10.3389/ffgc.2021.765782>.
- Bréda, N., Roland, H., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63, 625–644.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Buras, A., Schunk, C., Zeiträg, C., Herrmann, C., Kaiser, L., Lemke, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.J., Menzel, A., 2018. Are Scots pine forest edges particularly prone to drought-induced mortality? *Environ. Res. Lett.* 13 <https://doi.org/10.1088/1748-9326/aaa0b4>.
- Buras, A., Ovenden, T., Rammig, A., Zang, C.S., 2022. Refining the standardized growth change method for pointer year detection: accounting for statistical bias and estimating the deflection period. *Dendrochronologia* 74, 125964. <https://doi.org/10.1016/j.dendro.2022.125964>.
- Butz, M., Kahlenborn, W., Savelberg, J., Becker, N., Bubeck, P., Kabisch, S., Kind, C., Tempel, A., Tucciadelph, F., Greiving, S., Fleischhauer, M., Lindner, C., Lückenkötter, J., Kofler, C., 2015. 24/2015 Germany's vulnerability to climate change. *Clim. Chang.* 24 (2015), 62.
- Cailleret, M., Janssen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Cáda, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Heresz, A.M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. *Glob. Chang. Biol.* 23, 1675–1690. <https://doi.org/10.1111/gcb.13535>.
- Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S.M., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. *J. Ecol.* 103, 44–57. <https://doi.org/10.1111/1365-2745.12295>.
- Castaldi, C., Marchi, M., Vacchiano, G., Corona, P., 2020. Douglas-fir climate sensitivity at two contrasting sites along the southern limit of the European planting range. *J. For. Res.* 31, 2193–2204. <https://doi.org/10.1007/s11676-019-01041-5>.
- Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Glob. Chang. Biol.* 23, 362–379. <https://doi.org/10.1111/gcb.13366>.
- Cavin, L., Mountford, E.P., Peterken, G.F., Jump, A.S., 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct. Ecol.* 27, 1424–1435. <https://doi.org/10.1111/1365-2435.12126>.
- Charru, M., Seynave, I., Morneau, F., Bontemps, J.D., 2010. Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *For. Ecol. Manag.* 260, 864–874. <https://doi.org/10.1016/j.foreco.2010.06.005>.
- Cook, E.R., Kairiukstis, L.A., 1990. Methods of dendrochronology: applications in the environmental sciences. Springer Dordrecht. <https://doi.org/10.1007/978-94-015-7879-0>.
- Ćufar, K., Prislan, P., De Luis, M., Gričar, J., 2008. Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees - Struct. Funct.* 22, 749–758. <https://doi.org/10.1007/s00468-008-0235-6>.
- Debel, A., Meier, W.J.H., Bräuning, A., 2021. Climate signals for growth variations of *F. sylvatica*, *P. abies*, and *P. sylvestris* in Southeast Germany over the past 50 years. *Forests* 12. <https://doi.org/10.3390/f12111433>.
- Delb, H., Burger, M., Grüner, J., Kautz, M., Thomas, L., Wonsack, D., Wussler, J., 2023. Waldschuttsituation 2022/23 in Baden-Württemberg. *AFZ-DerWald* 09, 16–20.
- DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., Ćufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Heresz, A.M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanic, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nat. Commun.* 11, 1–9. <https://doi.org/10.1038/s41467-020-14300-5>.
- Diers, M., Weigel, R., Leuschner, C., 2022. Both climate sensitivity and growth trend of European beech decrease in the North German Lowlands, while Scots pine still thrives, despite growing sensitivity. *Trees - Struct. Funct.* <https://doi.org/10.1007/s00468-022-02369-y>.
- Diers, M., Leuschner, C., Dulamsuren, C., Schulz, T.C., Weigel, R., 2024. Increasing winter temperatures stimulate Scots pine growth in the north German lowlands despite stationary sensitivity to summer drought. *Ecosystems*. <https://doi.org/10.1007/s10021-023-00897-3>.
- Dulamsuren, C., Hauck, M., Kopp, G., Ruff, M., Leuschner, C., 2017. European beech responds to climate change with growth decline at lower, and growth increase at higher elevations in the center of its distribution range (SW Germany). *Trees - Struct. Funct.* 31, 673–686. <https://doi.org/10.1007/s00468-016-1499-x>.
- Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. *Tree Physiol.* 32, 178–187. <https://doi.org/10.1093/treephys/tps004>.
- Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters, R.L., Vitasse, Y., Walther, L., Ziemińska, K., Zweifel, R., 2022. Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecol. Lett.* 25, 427–439. <https://doi.org/10.1111/ele.13933>.
- Förster, A., Culmsee, H., Leuschner, C., 2021. Thinned northern German Scots pine forests have a low carbon storage and uptake potential in comparison to naturally developing beech forests. *For. Ecol. Manag.* 479, 118575 <https://doi.org/10.1016/j.foreco.2020.118575>.
- Frei, E.R., Gossner, M.M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Utentius, I., von Arx, G., Wohlgemuth, T., 2022. European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. *Plant Biol.* 24, 1132–1145. <https://doi.org/10.1111/plb.13467>.
- Friedrichs, D.A., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009a. Complex climate controls on 20th century oak growth in Central-West Germany. *Tree Physiol.* 29, 39–51. <https://doi.org/10.1093/treephys/tpn003>.
- Friedrichs, D.A., Troutet, V., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009b. Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees - Struct. Funct.* 23, 729–739. <https://doi.org/10.1007/s00468-009-0315-2>.
- Fuchs, S., Schuld, B., Leuschner, C., 2021. Identification of drought-tolerant tree species through climate sensitivity analysis of radial growth in Central European mixed broadleaf forests. *For. Ecol. Manag.* 494, 119287 <https://doi.org/10.1016/j.foreco.2021.119287>.
- Gessler, A., Bottero, A., Marshall, J., Arend, M., 2020. The way back: recovery of trees from drought and its implication for acclimation. *New Phytol.* 228, 1704–1709. <https://doi.org/10.1111/nph.16703>.
- Grossjord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226, 1550–1566. <https://doi.org/10.1111/nph.16485>.
- Grote, R., Gessler, A., Hommel, R., et al., 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees* 30, 1467–1482. <https://doi.org/10.1007/s00468-016-1446-x>.
- Hackett-Pain, A.J., Friend, A.D., Lagueard, J.G.A., Thomas, P.A., 2015. The influence of masting phenomenon on growth-climate relationships in trees: explaining the influence of previous summers' climate on ring width. *Tree Physiol.* 35, 319–330. <https://doi.org/10.1093/treephys/tpv007>.
- Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nat. Commun.* 13 <https://doi.org/10.1038/s41467-022-29289-2>.
- Härdtle, W., Niemeyer, T., Assmann, T., Baiboks, S., Fichtner, A., Friedrich, U., Lang, A.C., Neuwirth, B., Pfister, L., Ries, C., Schuld, A., Simon, N., von Oheimb, G., 2013. Long-term trends in tree-ring width and isotope signatures (δ¹³C, δ¹⁵N) of *Fagus sylvatica* L. on soils with contrasting water supply. *Ecosystems* 16, 1413–1428. <https://doi.org/10.1007/s10021-013-9692-x>.

- Hertel, D., Strecker, T., Müller-Haubold, H., Leuschner, C., 2013. Fine root biomass and dynamics in beech forests across a precipitation gradient - is optimal resource partitioning theory applicable to water-limited mature trees? *J. Ecol.* 101, 1183–1200. <https://doi.org/10.1111/j.1365-2745.12124>.
- Húdoková, H., Petrik, P., Petek-Petrik, A., Konópková, A., Leštianska, A., Strelcová, K., Kmeť, J., Kurjak, D., 2022. Heat-stress response of photosystem II in five ecologically important tree species of European temperate forests. *Biologia (Bratisl)* 77, 671–680. <https://doi.org/10.1007/s11756-021-00958-9>.
- IPCC, 2023. Climate Change 2023: Synthesis Report | UNEP - UN Environment Programme 35–115.
- Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8, 1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>.
- Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Chang. Biol.* 23, 3742–3757. <https://doi.org/10.1111/gcb.13636>.
- Kasper, J., Leuschner, C., Walentowski, H., Petritan, A.M., Weigel, R., 2022. Winners and losers of climate warming: declining growth in *Fagus* and *Tilia* vs. stable growth in three *Quercus* species in the natural beech-oak forest ecotone (western Romania). *For. Ecol. Manag.* 506, 119892. <https://doi.org/10.1016/j.foreco.2021.119892>.
- Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A., Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. *Clim. Chang.* 115, 343–363. <https://doi.org/10.1007/s10584-012-0465-x>.
- Knutzen, F., Dulamsuren, C., Meier, I.C., Leuschner, C., 2017. Recent climate warming-related growth decline impairs European beech in the center of its distribution range. *Ecosystems* 20, 1494–1511. <https://doi.org/10.1002/eet.017-0128-x>.
- Kunz, J., Löffler, G., Bauhus, J., 2018. Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *For. Ecol. Manag.* 414, 15–27. <https://doi.org/10.1016/j.foreco.2018.02.016>.
- Latte, N., Lebourgeois, F., Claessens, H., 2016. Growth partitioning within beech trees (*Fagus sylvatica* L.) varies in response to summer heat waves and related droughts. *Trees - Struct. Funct.* 30, 189–201. <https://doi.org/10.1007/s00468-015-1288-y>.
- Leuschner, C., 2020. Drought response of European beech (*Fagus sylvatica* L.)—a review. *Perspect. Plant. Ecol. Evol. Syst.* 47, 125576. <https://doi.org/10.1016/j.pees.2020.125576>.
- Leuschner, C., Weithmann, G., Bat-Enerel, B., 2023. The future of European beech in northern Germany — climate change vulnerability and adaptation potential. *Forests* 14. <https://doi.org/10.3390/f14071448>.
- Leuschner, C., Fuchs, S., Wedde, P., Rüther, E., Schultdt, B., 2024. A multi-criteria drought resistance assessment of temperate *Acer*, *Carpinus*, *Fraxinus*, *Quercus*, and *Tilia* species. *Perspect. Plant. Ecol. Evol. Syst.* 62, 125777. <https://doi.org/10.1016/j.pees.2023.125777>.
- Levesque, M., Rigling, A., Bugmann, H., Weber, P., Brang, P., 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. *Agric. For. Meteorol.* 197, 1–12. <https://doi.org/10.1016/j.agrformet.2014.06.001>.
- Trouvé, R., Bontemps, J.D., Collet, C., et al., 2017. Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. *Trees* 31, 517–529. <https://doi.org/10.1007/s00468-016-1479-1>.
- van der Maaten-Theunissen, M., Bümmertede, H., Iwanowski, J., Scharnweber, T., Wilmking, M., van der Maaten, E., 2016. Drought sensitivity of beech on a shallow chalk soil in northeastern Germany – a comparative study. *For. Ecosyst.* 3 <https://doi.org/10.1186/s40663-016-0083-6>.
- Maes, S.L., Perring, M.P., Vanhellemont, M., Depauw, L., Van den Bulcke, J., Brumelis, G., Brunet, J., Decocq, G., den Ouden, J., Hardtke, W., Hédi, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Máliš, F., Wulf, M., Verheyen, K., 2019. Environmental drivers interactively affect individual tree growth across temperate European forests. *Glob. Chang. Biol.* 25, 201–217. <https://doi.org/10.1111/gcb.14493>.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L., Ninyerolas, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Glob. Chang. Biol.* 2868–2881. <https://doi.org/10.1111/j.1365-2486.2008.01685.x> Twentieth.
- Mérian, P., Bontemps, J.D., Bergès, L., Lebourgeois, F., 2011. Spatial variation and temporal instability in climate-growth relationships of sessile oak (*Quercus petraea* [Matt.] Liebl.) under temperate conditions. *Plant Ecol.* 212, 1855–1871. <https://doi.org/10.1007/s11258-011-9959-2>.
- Michelot, A., Bréda, N., Damesin, C., Dufrêne, E., 2012a. Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *For. Ecol. Manag.* 265, 161–171. <https://doi.org/10.1016/j.foreco.2011.10.024>.
- Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., Damesin, C., 2012b. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 32, 1033–1045. <https://doi.org/10.1093/treephys/tpz052>.
- MKUEM-RP, 2021. Waldzustandsbericht 2021 Rheinland-Pfalz. Ministerium für Klimaschutz, Umwelt, Energie und Mobilität.
- Muffler, L., Weigel, R., Hackett-Pain, A.J., Klisz, M., van der Maaten, E., Wilmking, M., Kreyling, J., van der Maaten-Theunissen, M., 2020. Lowest drought sensitivity and decreasing growth synchrony towards the dry distribution margin of European beech. *J. Biogeogr.* 47, 1910–1921. <https://doi.org/10.1111/jbi.13884>.
- Muggeo, V., 2008. Segmented: an R package to fit regression models with broken-line relationships. *R News* 8, 20–25.
- Müller-Haubold, H., Hertel, D., Leuschner, C., 2015. Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts. *Ecosystems* 18, 1083–1100. <https://doi.org/10.1007/s10021-015-9885-6>.
- Nehrbaß-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M., Frank, D., 2014. The influence of sampling design on tree-ring-based quantification of forest growth. *Glob. Chang. Biol.* 20 (9), 2867–2885. <https://doi.org/10.1111/gcb.12599>.
- Neycken, A., Scheggia, M., Bigler, C., Lévesque, M., 2022. Long-term growth decline precedes sudden crown dieback of European beech. *Agric. For. Meteorol.* 324 <https://doi.org/10.1016/j.agrformet.2022.109103>.
- Nicolae, V.N., Mason, W.L., Bastien, J.C., Vor, T., Petkova, K., Podrázský, V., Dodan, M., Perić, S., La Porta, N., Brus, R., Andrašev, S., Slávik, M., Modranský, J., Pástor, M., Rédei, K., Cvjetkovic, B., Sivacioglu, A., Lavnyy, V., Buzatu-Goană, C., Mihăilescu, G., 2023. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in Europe: an overview of management practices. *J. For. Res.* 34, 871–888. <https://doi.org/10.1007/s11676-023-01607-4>.
- NW-FVA, 2021. Waldzustandsbericht 2021 für Sachsen-Anhalt. Ministerium für Wirtschaft, Tourismus, Landwirtschaft und Forsten des Landes Sachsen-Anhalt. <https://doi.org/10.5281/zenodo.5588321>.
- NW-FVA, 2022. Waldzustandsbericht 2022 für Niedersachsen. Niedersächsisches Ministerium für Ernährung, Landwirtschaft und Verbraucherschutz. <https://doi.org/10.5281/zenodo.7276926>.
- Obladen, N., Decherig, P., Skiadaresis, G., Tegel, W., Keßler, J., Höllerl, S., Kaps, S., Hertel, M., Dulamsuren, C., Seifert, T., Hirsch, M., Seim, A., 2021. Tree mortality of European beech and Norway spruce induced by 2018–2019 hot droughts in central Germany. *Agric. For. Meteorol.* 307 <https://doi.org/10.1016/j.agrformet.2021.108482>.
- Ols, C., Klesse, S., Girardin, M.P., Evans, M.E.K., DeRose, R.J., Trouet, V., 2023. Detrending climate data prior to climate-growth analyses in dendroecology: a common best practice? *Dendrochronologia* 79. <https://doi.org/10.1016/j.dendro.2023.126094>.
- Patakanuri, S.K., O'Brien, N., 2020. Modifiedmk: Modified Mann Kendall and Spearman's Rho Trend Tests. R Packag. Version 1.6. <https://doi.org/10.1023/B>.
- Perkins, D., Uhl, E., Biber, P., du Toit, B., Carraro, V., Rötzer, T., Pretzsch, H., 2018. Impact of climate trends and drought events on the growth of oaks (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) within and beyond their natural range. *Forests* 9, <https://doi.org/10.3390/f9030108>.
- Petit, R.J., Hampe, A., 2006. Some evolutionary consequences of being a tree. *Annu. Rev. Ecol. Evol. Syst.* 37, 187–214. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110215>.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 1–10. <https://doi.org/10.1038/ncomms5967>.
- Pretzsch, H., del Rio, M., Arcangeli, C., Bielak, K., Dudzinska, M., Forrester, D.I., Klädtke, J., Kohlne, U., Ledermann, T., Matthews, R., Nagel, J., Nagel, R., Ningre, F., Nord-Larsen, T., Biber, P., 2023. Forest growth in Europe shows diverging large regional trends. *Sci. Rep.* 13, 1–12. <https://doi.org/10.1038/s41598-023-41077-6>.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing.
- Rais, A., van de Kuilen, J.W.G., Pretzsch, H., 2014. Growth reaction patterns of tree height, diameter, and volume of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) under acute drought stress in Southern Germany. *Eur. J. For. Res.* 133, 1043–1056. <https://doi.org/10.1007/s10342-014-0821-7>.
- Restaino, C.M., Peterson, D.L., Littell, J., 2016. Increased water deficit decreases Douglas fir growth throughout western US forests. *Proc. Natl. Acad. Sci. U. S. A.* 113, 9557–9562. <https://doi.org/10.1073/pnas.1602384113>.
- Revelle, W.R., 2017. psych: Procedures for Personality and Psychological Research.
- Roloff, A., 2008. Baum des Jahres 2007: die Wald-Kiefer (*Pinus sylvestris* L.) – Biologie, Ökologie, Verwendung, Schäden, in: Beiträge Aus Der NW-FVA, Band 2.
- Roloff, A., 2018. Vitalitätsbeurteilung von Bäumen. Aktueller Stand und Weiterentwicklung, Haymarket Media, Braunschweig.
- Sakai, A., Larcher, W., 1987. Frost survival of plants. In: Responses and Adaptation to Freezing Stress, in: Ecological Studies, vol. 62. Springer, Berlin. <https://doi.org/10.1007/978-3-642-71745-1>.
- Sánchez-Salgado, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A., Sánchez-Miranda, Á., Rigling, A., 2015. Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine. *For. Ecol. Manag.* 358, 12–25.
- Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., Wilmking, M., 2011. Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *For. Ecol. Manag.* 262, 947–961. <https://doi.org/10.1016/j.foreco.2011.05.026>.
- Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl. Ecol.* 45, 86–103. <https://doi.org/10.1016/j.baae.2020.04.003>.
- Schütt, P., Stimm, B., 2014. *Pinus sylvestris*. In: Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie. John Wiley & Sons, Ltd, pp. 1–32.
- Schweingruber, F.H., 1983. Der Jahrring: Standort, Methodik, Zeit und Klima in der Dendrochronologie. Bern, Stuttgart: Haupt.
- Seidling, W., Ziche, D., Beck, W., 2012. Climate responses and interrelations of stem increment and crown transparency in Norway spruce, Scots pine, and common beech. *For. Ecol. Manag.* 284, 196–204. <https://doi.org/10.1016/j.foreco.2012.07.015>.

- Sergent, A.S., Rozenberg, P., Bréda, N., 2014. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. Ann. For. Sci. 71, 697–708. <https://doi.org/10.1007/s13595-012-0220-5>.
- Spellmann, H., Weller, A., Brang, P., Michiels, H.-G., Bolte, A., 2015. Douglasie (*Pseudotsuga menziesii* (Mirb.) Franco), in: Potenziale Und Risiken Eingeführter Baumarten. Baumartenportraits Mit Naturschutzfachlicher Bewertung, pp. 187–198.
- Stangler, D.F., Miller, T.W., Homer, H., Larysch, E., Puhlmann, H., Seifert, T., Kahle, H.P., 2022. Multivariate drought stress response of Norway spruce, silver fir and Douglas fir along elevational gradients in Southwestern Germany. Front. Ecol. Evol. 10, 1–15. <https://doi.org/10.3389/fevo.2022.907492>.
- Stoltz, J., van der Maaten, E., Kalanke, H., Martin, J., Wilmingking, M., van der Maaten-Theunissen, M., 2021. Increasing climate sensitivity of beech and pine is not mediated by adaptation and soil characteristics along a precipitation gradient in northeastern Germany. Dendrochronologia 67. <https://doi.org/10.1016/j.dendro.2021.125834>.
- Teskey, R., Wertiau, T., Bauweraerts, I., Ameye, M., McGuire, M.A., Steppe, K., 2015. Responses of tree species to heat waves and extreme heat events. Plant Cell Environ. 38, 1699–1712. <https://doi.org/10.1111/pce.12417>.
- Thomas, F.M., Blank, R., Hartmann, G., 2002. Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. For. Pathol. 32, 277–307. <https://doi.org/10.1046/j.1439-0329.2002.00291.x>.
- Thomas, F.M., Rzepecki, A., Werner, W., 2022. Non-native Douglas fir (*Pseudotsuga menziesii*) in Central Europe: ecology, performance and nature conservation. For. Ecol. Manag. 506, 119956. <https://doi.org/10.1016/j.foreco.2021.119956>.
- Thonfeld, F., Gessner, U., Holzwarth, S., Kriese, J., da Ponte, E., Huth, J., Kuenzer, C., 2022. A first assessment of canopy cover loss in Germany's forests after the 2018–2020 drought years. Remote Sens. 14 <https://doi.org/10.3390/rs14030562>.
- Till, O., 1956. Über die Frosthärtung von Pflanzen sommergrüner Laubwälder. Flora oder Allg. Bot. Zeitung, 143, pp. 499–542. [https://doi.org/10.1016/s0367-1615\(17\)33134-8](https://doi.org/10.1016/s0367-1615(17)33134-8).
- Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. Science 323, 521–524. <https://doi.org/10.1126/science.1165000>.
- Vejpustková, M., Čihák, T., 2019. Climate response of Douglas fir reveals recently increased sensitivity to drought stress in Central Europe. Forests 10, 1–17. <https://doi.org/10.3390/f10020097>.
- Verkerk, P.J., Costanza, R., Hetemäki, L., Kubiszewski, I., Leskinen, P., Nabuurs, G.J., Potočnik, J., Palahí, M., 2020. Climate-smart forestry: the missing link. Forest Policy Econ. 115 <https://doi.org/10.1016/j.forepol.2020.102164>.
- Vitali, V., Büntgen, U., Bauhus, J., 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. Glob. Chang. Biol. 23, 5108–5119. <https://doi.org/10.1111/gcb.13774>.
- Vitali, V., Buntgen, U., Bauhus, J., 2018. Seasonality matters—the effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. Dendrochronologia 48, 1–9. <https://doi.org/10.1016/j.dendro.2018.01.001>.
- Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., Wohlgemuth, T., 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob. Chang. Biol. 25, 3781–3792. <https://doi.org/10.1111/gcb.14803>.
- Walentowski, H., Falk, W., Mette, T., Kunz, J., Bräuning, A., Meinardus, C., Zang, C., Sutcliffe, L.M.E., Leuschner, C., 2017. Assessing future suitability of tree species under climate change by multiple methods: case study in southern Germany. Ann. For. Res. 60, 101–126. <https://doi.org/10.15287/afr.2016.789>.
- Weber, P., Bugmann, H., Pluess, A.R., Walther, L., Rigling, A., 2013. Drought response and changing mean sensitivity of European beech close to the dry distribution limit. Trees - Struct. Funct. 27, 171–181. <https://doi.org/10.1007/s00468-012-0786-4>.
- Weigel, R., Bat-Enerel, B., Dulamsuren, C., Muffler, L., Weithmann, G., Leuschner, C., 2023. Summer drought exposure, stand structure, and soil properties jointly control the growth of European beech along a steep precipitation gradient in northern Germany. Glob. Chang. Biol. 29, 763–779. <https://doi.org/10.1111/gcb.16506>.
- Wigley, T.M., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Appl. Meteorol. Climatol. 23 (2), 201–213.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Chang. 3, 292–297. <https://doi.org/10.1038/nclimate1693>.
- Wu, X., Liu, H., Li, X., Ciaias, P., Babst, F., Guo, W., Zhang, C., Magliulo, V., Pavelka, M., Liu, S., Huang, Y., Wang, P., Shi, C., Ma, Y., 2018. Differentiating drought legacy effects on vegetation growth over the temperate Northern Hemisphere. Glob. Chang. Biol. 24, 504–516. <https://doi.org/10.1111/gcb.13920>.
- Yue, S., Wang, C.Y., 2004. The Mann-Kendall test modified by effective sample size to detect trend in serially correlated hydrological series. Water Resour. Manag. 18, 201–218.
- Zang, C., Biondi, F., 2015. Treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography (Cop.) 38, 431–436. <https://doi.org/10.1111/ecog.01335>.
- Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in central European mixed forests. Ecosystems 18, 560–572. <https://doi.org/10.1007/s10021-015-9849-x>.