



Slower growth prior to the 2018 drought and a high growth sensitivity to previous year summer conditions predisposed European beech to crown dieback

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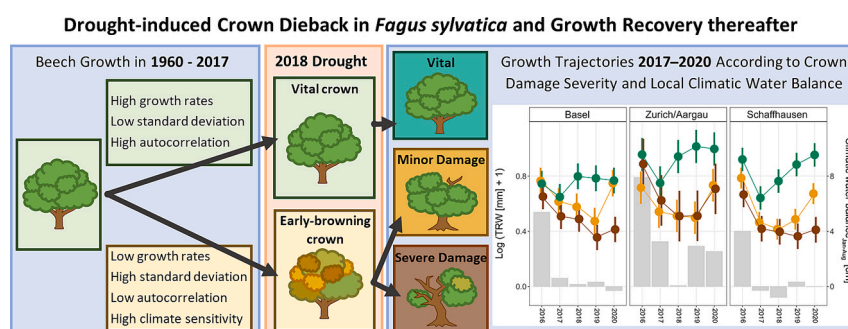
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HIGHLIGHTS

- We analyzed growth factors predisposing beech to drought-induced crown dieback.
- Slow growth prior to the 2018 drought predisposes to crown vitality loss.
- Trees with crown vitality loss were sensitive to past summer climate conditions.
- Recent competition played a minor role in the predisposition to crown vitality loss.
- Growth recovery potential depended on crown damage and site water availability.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Manuel Esteban Lucas-Borja

Keywords:

Climate sensitivity
Crown damage
Fagus sylvatica
Forest dieback
Tree rings
Recovery

ABSTRACT

The record-breaking drought in 2018 caused premature leaf discoloration and shedding (early browning) in many beech (*Fagus sylvatica* L.) dominated forests in Central Europe. However, a high degree of variability in drought response among individual beech trees was observed. While some trees were severely impacted by the prolonged water deficits and high temperatures, others remained vital with no or only minor signs of crown vitality loss. Why some beech trees were more susceptible to drought-induced crown damage than others and whether growth recovery is possible are poorly understood. Here, we aimed to identify growth characteristics associated with the variability in drought response between individual beech trees based on a sample of 470 trees in northern Switzerland. By combining tree growth measurements and crown condition assessments, we also investigated the possible link between crown dieback and growth recovery after drought. Beech trees with early browning exhibited an overall lower growth vigor before the 2018 drought than co-occurring vital beech trees. This lower vigor is mainly indicated by lower overall growth rates, stronger growth declines in the past decades,

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<https://doi.org/10.1016/j.scitotenv.2023.169068>

Received 7 August 2023; Received in revised form 21 November 2023; Accepted 1 December 2023

Available online 2 December 2023

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and higher growth-climate sensitivity. Particularly, warm previous year summer conditions negatively affected current growth of the early-browning trees. These findings suggest that the affected trees had less access to critical resources and were physiologically limited in their growth predisposing them to early browning. Following the 2018 drought, observed growth recovery potential corresponded to the amount of crown dieback and the local climatic water balance. Overall, our findings emphasize that beech-dominated forests in Central Europe are under increasing pressure from severe droughts, ultimately reducing the competitive ability of this species, especially on lowland sites with shallow soils and low water holding capacity.

1. Introduction

Global warming and the ongoing increase in the frequency and severity of drought events pose a major challenge for forest ecosystems around the globe (Allen et al., 2015). Prolonged periods of dry and hot weather conditions can have detrimental effects on tree growth, productivity, carbon sequestration and spatial distribution of tree species (Anderegg et al., 2013; Neycken et al., 2022; Trotsiuk et al., 2020). Long-lasting droughts might thus jeopardize the provision of ecosystem services by triggering tree dieback and widespread mortality (Schuldt et al., 2020; Senf et al., 2020).

Following the record-breaking drought year of 2018 in Central Europe, lasting declines in tree vitality were observed (Hermann et al., 2023). European beech (*Fagus sylvatica* L.), which is one of the most widespread and economically important broadleaf tree species in Europe (Bolte et al., 2010), was among the severely impacted (Rathgeb et al., 2020). Due to extremely elevated temperatures and high precipitation deficits, many beech trees showed early leaf discoloration and shedding, giving the forest an autumnal appearance in the middle of summer (Brun et al., 2020; Frei et al., 2022; Rohner, 2020). Although it has been hypothesized that early leaf discoloration and premature leaf shedding (hereafter early browning) could be adaptive traits to reduce further water loss and the risk for cavitation (Bréda et al., 2006), recent work suggests that acute hydraulic failure is the primary cause of the deterioration of the crown condition in beech trees (Walthert et al., 2021). This is underlined by the fact that in the years following the exceptional summer drought of 2018, many trees exhibited partial or complete dieback of their crown (Frei et al., 2022). In addition, the degree of crown dieback remained relatively stable in 2019 and 2020 with only minor signs of crown biomass recovery (Frei et al., 2022).

Yet, individual beech trees within the same stand showed a high degree of variability in their response to the 2018 drought (Frei et al., 2022). While some beech trees were severely impacted, others remained vital with no or only minor signs of crown dieback (Klesse et al., 2022; Neycken et al., 2022; Wohlgemuth et al., 2020). Consequently, the question arises which past growth characteristics and climate factors predispose some beech trees to early browning and others not when both experienced the same climate conditions.

Crown vitality assessments and tree-ring width (TRW) measurements can provide valuable information on changes in tree vitality (Cailleret et al., 2017). TRW is especially interesting because it provides a long-term retrospective growth record of tree vigor and environmental conditions at an annual resolution. Drought-induced crown dieback was reported to be more prevalent in beech trees with lower growth rates and continuously declining long-term growth trends in the last decades compared to beech trees without crown damage (Neycken et al., 2022; Rukh et al., 2023). It is unclear which environmental factors might lead to the shift in growth trends, but long-term tree competition levels might be a key driver (Schmied et al., 2023). Trees under high competition usually have limited access to critical resources (e.g., light, water, nutrients), leaving them in an inferior state compared to trees with less competition. The weaker trees could be limited in their capacity to buffer adverse effects of unfavorable climate conditions and thus respond more sensitively to climate variability (Stovall et al., 2019). The higher climate sensitivity can be mirrored in tree growth as a larger growth standard deviation and an increasing effect of the growing

conditions of the previous year on the growth of the current year (Camarero et al., 2015; Scheffer et al., 2009). On top of the enhanced growth sensitivity to seasonal climate, increased investments into seeds could further diminish the capacity of beech trees to grow and form new leaves (Nussbaumer et al., 2021; Wohlgemuth et al., 2020). Thus, a shift of the carbon allocation from secondary growth (growth in thickness) toward reproduction could predispose already weakened trees further to early browning and dieback under adverse climatic conditions.

Yet, most beech trees with early browning in 2018 survived at least until 2020 despite extensive crown dieback (Frei et al., 2022). Whether the early-browning trees can recover their growth after drought-induced crown dieback or whether crown biomass loss can indicate the growth recovery potential is still unclear. This information is, however, crucial for forest managers confronted with declining tree crown vitality due to increased drought stress and the task of deciding on the suitable management options to guarantee forest ecosystem services under climate change.

Our study aimed to identify differences in secondary growth characteristics that could explain the variability in crown dieback between individual beech trees following the exceptionally hot and dry summer of 2018 in Central Europe. Further, we explored the impact of the 2018 drought on tree growth and the possibility of growth recovery in the subsequent years by combining tree growth measurements and crown condition assessments.

Specifically, the following hypotheses were tested:

- (i) Past growth patterns (mean tree-ring width, long-term growth trend, first-order autoregressive coefficient, growth variance) are good predictors of drought-induced early browning in beech. A high degree of competition from neighboring trees can further increase the risk of early browning.
- (ii) On the one hand, the radial growth (tree-ring width) of the early-browning trees is highly sensitive to the climate conditions of the year preceding tree-ring formation. In addition, masting enhances the climate sensitivity of early-browning beech trees. On the other hand, the vital trees show a low climate sensitivity and retain high radial growth rates despite high temperatures and low precipitation sums in current and previous summer.
- (iii) Severe crown dieback after the 2018 drought leads to low recovery of stem growth.

2. Materials & methods

2.1. Study sites and tree selection

In this study, we used a subset of mature beech trees that were continuously observed after the 2018 summer drought (Frei et al., 2023, 2022; Wohlgemuth et al., 2020). The trees were located in three regions in northern Switzerland, i.e., Baselland (hereafter BL), Zurich/Aargau (hereafter ZH/AG), and Schaffhausen (hereafter SH), where beech exhibited early browning in the summer 2018 (Fig. 1). The sampled stands originate from natural regeneration and have been moderately managed according to close-to-nature practices since their establishment (Wohlgemuth et al., 2020).

The original dataset included 963 mature dominant or co-dominant beech trees sampled in groups of up to five vital or early-browning trees

during August and September 2018. Out of the 963 beech trees, 824 trees showed early leaf browning of at least 50 % of their crown and/or premature leaf shedding after the summer drought in August 2018 (hereafter early-browning trees). The remaining 139 beech trees shed their leaves at the normal time at the beginning of fall and/or exhibited only minor signs of a reduction in crown condition (hereafter vital trees). More details about the original sampling design can be found in [Frei et al. \(2022\)](#). From this dataset we selected in total 118 vital beech trees (in BL and ZH/AG) and 278 nearby early-browning trees (in BL, ZH/AG, and SH) so that diameter at breast height (DBH) distribution between the two vitality groups were similar ([Table 1](#), Fig. S1). Thereby, we excluded all early-browning tree groups that deviated too far from the DBH range of the vital tree groups.

As the original dataset did not include any vital beech trees within the region SH, we used a combination of Sentinel-2-based NDWI (Normalized Difference Water Index) and NDVI (Normalized Difference Vegetation Index) images ([Baltensweiler, 2020](#)) to identify forest areas in this region where no early-browning trees could be detected between the 25th of August 2018 and the 20th of September 2018 (Fig. S2). From those areas, we selected 74 additional co-dominant or dominant vital beech trees with a similar DBH located in the same forest as the previously sampled early-browning tree groups in August 2021. In total, we analyzed 278 early-browning beech trees and 192 vital trees in 127 tree groups distributed over three regions in northern Switzerland that included the Jura and Swiss Plateau biogeographic regions ([Fig. 1](#)). The average distance between vital and early-browning tree groups was ca. 72 m in BL, 283 m in ZH/AG and 162 m in SH. The soil within the three regions is relatively shallow and is comparable between the vitality classes (Fig. S3).

2.2. Crown condition monitoring and tree individual data

For the selected trees, the tree-specific crown condition data collected during summer 2020 was used for further analysis. Specifically, crown dieback was estimated as the volume proportion of dead (branches with no living tissue) and lost branches (%DB) compared to the potential full

Table 1

Number and characteristics of the sampled beech trees in the three study regions BL, ZH/AG and SH. Different letters (a, b) in the columns DBH (diameter at breast height in 2018, Fig. S1), estimated age (Fig. S1) and CI (competition index in 2021) indicate a significant difference ($\alpha < 0.05$) between the two vitality classes per region (Wilcoxon rank sum test). Number of trees represents the individuals with available tree-ring data. The CI was calculated for 76 vital and 101 early-browning in the region BL, 74 vital and 96 early-browning trees in SH, and 41 vital and 48 early-browning trees in ZH/AG.

Region	Vitality class	Number of cored trees	DBH in cm (range)	Estimated age (range)	CI (range)
Basel (BL)	Early-browning	112	43.1 (23–73) a	115 (67–208) a	1.17 (0.04–4.05) a
	Vital	76	45.8 (24–77) a	114 (74–179) a	1.29 (0.16–3.99) a
Schaffhausen (SH)	Early-browning	116	40.8 (22–66) a	110 (59–204) a	1.12 (0.12–2.99) a
	Vital	74	43.4 (26–69) a	98 (55–150) b	0.80 (0.17–1.68) b
Zurich/Aargau (ZH/AG)	Early-browning	50	53.0 (28–78) a	121 (72–190) a	1.25 (0.22–3.79) a
	Vital	42	48.8 (26–80) a	105 (69–184) b	1.03 (0.21–3.08) a

crown ([Dobbertin et al., 2016](#)). Moreover, crown transparency (%CT) was estimated as the percentage of total leaf loss compared to a fully foliated reference beech tree using field reference photographs ([Eichhorn et al., 2016](#)). For the crown transparency assessment, dead branches were not considered. Both crown parameters were taken in 5 %-steps where 0 % signifies the absence of crown dieback/leaf loss and 100 % total crown loss. Based on these two crown assessment parameters, we determined the percentage of total crown biomass loss (%CBL) following [Frei et al. \(2022\)](#):

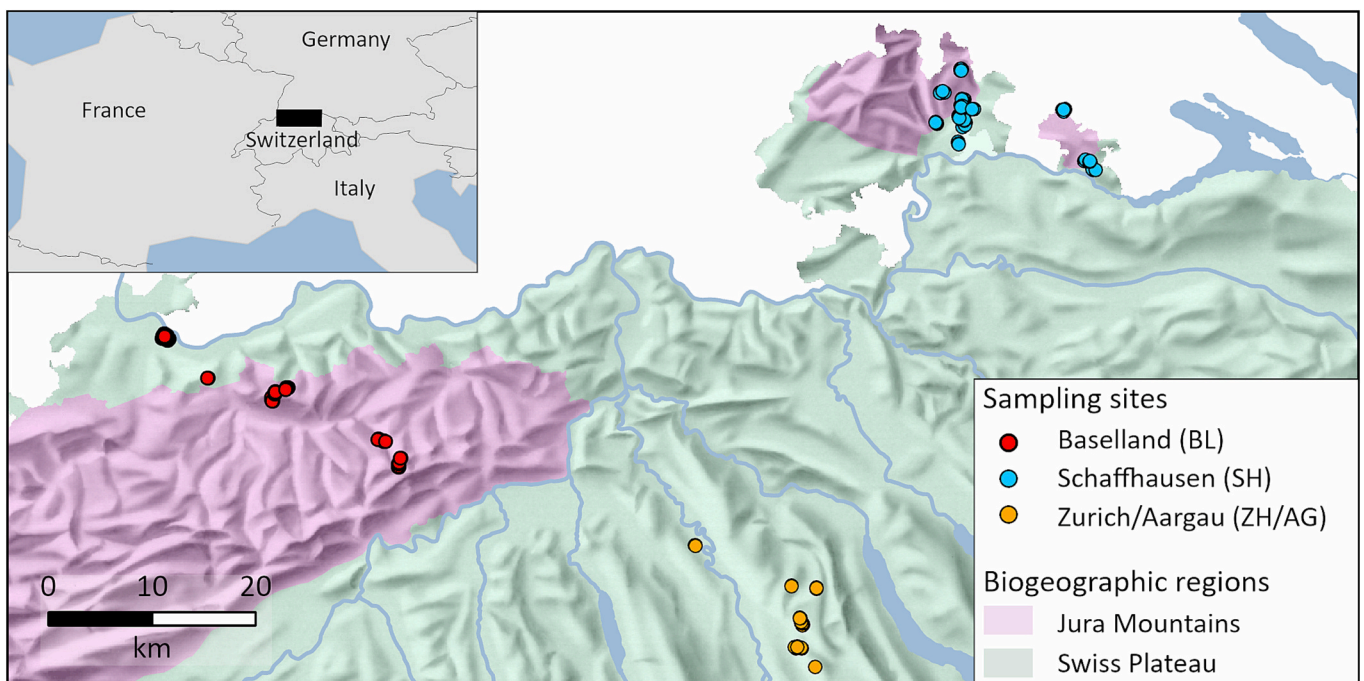


Fig. 1. Location of the sampling sites over the three study regions BL (red dots), ZH/AG (yellow dots) and SH (blue dots) in northern Switzerland (inset map). The trees were sampled in groups of up to five trees per vitality class (vital or early-browning). The background colors indicate the biogeographical regions after [Gonseth et al. \(2001\)](#).

$$\%CBL = \%DB + (100 - \%DB) * \%CT / 100$$

A tree was considered dead if no living branches and leaves could be observed in the crown and along the stem. For the vital trees in SH, the crown parameters could only be assessed in summer 2021. Thus, we used the observations from 2021 as an approximation for %CBL in the year 2020. All trees that died or were harvested until 2020 (20 trees), and trees with incomplete crown data (2 trees) were omitted from the analysis. In total, %CBL was available for 256 early-browning and 192 vital beech trees (Table S1).

2.3. Tree-ring data

For each tree, except for the vital trees in SH, two increment cores were extracted at breast height (1.30 m) perpendicular to the slope in September/October 2020. The DBH was measured with a DBH tape in August/September 2018. For the vital trees in SH, the extraction of the increment cores and the DBH measurements were performed in September 2021.

The tree cores were air-dried, and their surfaces were prepared with a core microtome (Gärtner and Nievergelt, 2010). Subsequently, the cores were scanned using an Epson Expression 10,000 XL scanner at 2400 dpi or with a digital camera (Canon EOS 5DSR) equipped with a 100 mm macro lens (Skipky, WSL, 2021) at a resolution of 5950 dpi. TRW was measured to the nearest 0.01 mm with the program Coorecorder 9.5 (Cybis Elektronik and Data AB, www.cybis.se). When the pith was missing from the increment core, the age of each tree was assessed by estimating the distance to the pith based on the curvature of the last rings and dividing this distance by the mean TRW of the last 20 rings on the core. The individual tree-ring series were visually crossdated in Coorecorder and statistically verified with the program COFECHA (Holmes, 1983). All trees could be successfully crossdated (Table 1). Then, the two ring-width series (cores) per tree were averaged using a biweight robust mean to build individual tree chronologies (data available in Neycken et al. (2023)). The analysis considered the period 1960–2020 and excluded all TRW measurements outside this period.

For the analysis of the growth characteristics prior to the 2018 drought, we calculated the first-order autoregressive coefficient (AR1) and standard deviation of the TRW series (1960–2017) for each tree (Eqs. (S1) & (S2)). For this purpose, the TRW chronologies were detrended using an additive modelling framework (Wood, 2017) which related $\log(\text{TRW} + 1)$ to the change in DBH over time. The DBH time series was derived for each tree by subtracting twice the cumulative sum of TRW per year from the DBH measured in 2018 or 2021. To calculate the cumulative DBH time series for trees that were cored in 2020 but for which their DBH was measured in 2018, the TRW of 2019 and 2020 was added twice to the 2018 DBH measurements. The detrending model was run for each tree separately between 1960 and 2020. DBH was modeled as a flexible cubic regression spline with a maximum of six degrees of freedom (Eqs. (S3) & (S4)). Differences in DBH and age between vital and early-browning trees per region were assessed using a Wilcoxon rank sum test.

2.4. Competition index

To estimate the competition level experienced by each target tree, we measured the DBH of all neighbor trees with a DBH ≥ 20 cm within a 10 m radius of each target tree and their distances to the target tree in the summer 2021 (Frei et al., 2022). These measurements were taken with a DBH tape and a Vertex clinometer (Haglöf Vertex 3). Then, we calculated a competition index (CI) following Hegyi (1974):

$$CI_i = \sum_{k=1}^N \frac{DBH_k}{DBH_i \times dist_{ik}}$$

where CI_i is the competition experienced by the target tree i , DBH_k is the DBH of the competitor k , DBH_i indicates the DBH of the target tree i and $dist_{ik}$ signifies the distance between the target tree i and the competitor

k . High CI values indicate high competition experienced by the target tree. Differences in CI between the two vitality classes were tested with a Wilcoxon rank sum test.

2.5. Climate and masting events data

We used monthly mean air temperature (hereafter temperature) and precipitation sum (hereafter precipitation) interpolated data (100 m resolution) based on the MeteoSwiss weather stations measurements (Swiss Federal Office of Meteorology and Climatology) and calculated with the DAYMET algorithm of Thornton et al. (1997). The data was derived for each tree and for the period 1959–2020. For the quantification of the water deficit prior to and during the growing period, we calculated the average climatic water balance between January and August ($CWB_{\text{Jan-Aug}}$) by subtracting the monthly potential evapotranspiration (Thornthwaite, 1948) from the monthly precipitation sum and subsequently taking the mean over the January–August period. Overall, the region of Basel (mean annual temperature: 9.3 °C, mean annual precipitation sum: 999 mm, mean $CWB_{\text{Jan-Aug}}$ 24 mm) and Schaffhausen (mean annual temperature: 9 °C, mean annual precipitation sum: 923 mm, mean $CWB_{\text{Jan-Aug}}$ 18 mm) were drier than Zurich/Aargau (mean annual temperature: 8.9 °C, mean annual precipitation sum: 1223 mm, mean $CWB_{\text{Jan-Aug}}$ 48 mm).

Masting events can influence carbon allocation and, thus, secondary growth and tree-ring width when they occur (Hackett-Pain et al., 2018; Nussbaumer et al., 2021). For this reason, we estimated the likelihood of beech masting in a given year according to three levels: 0 – low likelihood, 1 – medium likelihood, 2 – high likelihood (Fig. S4). For that, we compiled beech pollen or masting data from different sources (beech pollen count data from the Swiss Federal Office of Meteorology and Climatology (Fig. S5), mast data from Ascoli et al., 2017 and Jenni, 1987) and then aggregated and harmonized the data. We assume that beech pollen count is a viable predictor for masting intensity (Kasprzyk et al., 2014) and that beech masting has high spatial synchronicity (Vacchiano et al., 2018).

2.6. Statistical analysis

2.6.1. Predisposing growth characteristics prior to 2018

To investigate if tree growth differed between vital and early-browning trees before the 2018 summer drought, we calculated several TRW metrics for each beech tree that describe their respective growth properties. The mean TRW for 1960–2017 was computed as a measure of overall growth performance during the period. In addition, for describing the long-term growth trend of each tree, we used the linear regression coefficient relating the TRW ($\log+1$ transformed) to year for the period 1960–2017. The transformation was applied so that the residuals of the models were normally distributed. We also computed the AR1 and growth standard deviation of the detrended TRW index series for each tree for the period 1960–2017 (Eqs. (S3) & (S4)). We chose to use the detrended TRW data to minimize the effect of the changes in tree size over time on the time series metrics. AR1 and the growth standard deviation can be used to describe the stability of the growth of a tree and its sensitivity to external influences such as climate, pests and disturbances (Beck and Heußner, 2012; Cailleret et al., 2019; Scheffer et al., 2009). To test whether the tree-ring variables differ between both vitality classes, we used four linear mixed effects models. In each model, a factor variable describing the vitality class (vital or early browning) of a tree and the DBH of 2018 was included (Eq. (S5)). DBH was added to each model to account for the growth differences due to tree size. Tree size is thus accounted twice (during detrending and in the linear mixed effects models with DBH). All linear models were fitted with restricted maximum likelihood (REML) using the R package lme4 (Bates et al., 2015) in R 4.2.1 (R Core Team, 2022).

Table 2

Summary of the fitted linear mixed-effects models estimating the effect of the vitality class (vital vs. early-browning trees) and DBH (diameter at breast height) on a set of variables describing the long-term tree radial growth following Eq. (S5). The estimate, standard error (std. error) and *p*-value (*p*) are given for each term. Significant results are in bold. TRW stands for tree-ring width.

		Estimate	Std. error	p
Mean raw TRW 1960–2017				
	Intercept	1.918	0.049	<0.001
	Vitality class [Vital]	0.290	0.085	<0.001
	DBH 2018	0.369	0.022	<0.001
Observations		470		
Marginal R ²		0.36		
Conditional R ²		0.73		
Linear regression coefficient 1960–2017				
	Intercept	−0.005	0.001	<0.001
	Vitality class [Vital]	0.004	0.001	<0.001
	DBH 2018	−0.002	0.001	<0.001
Observations		470		
Marginal R ²		0.08		
Conditional R ²		0.35		
Log (Standard deviation of TRW indices 1960–2017)				
	Intercept	−1.429	0.020	<0.001
	Vitality class [Vital]	−0.192	0.033	<0.001
	DBH 2018	−0.079	0.011	<0.001
Observations		470		
Marginal R ²		0.22		
Conditional R ²		0.51		
First-order autoregressive coefficient of TRW indices 1960–2017				
	Intercept	0.154	0.013	<0.001
	Vitality class [Vital]	0.065	0.022	0.004
	DBH 2018	−0.035	0.008	<0.001
Observations		470		
Marginal R ²		0.07		
Conditional R ²		0.33		

2.6.2. Climate sensitivity before 2018

The growth response of each vitality class to the interannual variability in climate conditions (i.e., variation in temperature and precipitation) was assessed using distributed time lag models in combination with flexible penalized regression splines incorporated in additive models (Nothdurft, 2020; Nothdurft and Vospernik, 2018; Pedersen et al., 2019; Wood, 2017). This hierarchical framework was applied to investigate the climate sensitivity of vital and early-browning trees in 10 different time periods (lag) ranging from the current year to the previous year of ring formation. These 10 climate lags were defined as the temperature and precipitation of two consecutive months, starting with July/August of the current year and ending with January/February of the previous year. We did not include current September, October, November and December in the model because radial growth typically ends in late summer in the study regions (Etzold et al., 2022). The DBH change of each individual tree was included as splines in the model to account for size-dependent long-term trends. Moreover, the masting index was added as a parametric term. We included tree ID and group as random intercepts to account for the repeated measurements per tree and possible differences between tree groups (Eqs. (S6) & (S7)). The climate response of both vitality classes was assessed by predicting log (TRW +1) based on all possible temperature and precipitation combinations, excluding the most extreme 5 % of the data at the upper and lower end for each lag, while all other climate variables and DBH were kept at their respective mean. We only predicted 90 % of the data distribution to reduce the impact of extreme values. The masting index was set to no or weak mast. ID and group effects were set to zero because we were interested in the mean population response. Afterwards, the predicted TRW values, which resulted from each model when all climate parameters were set to the mean, were subtracted from the climate response prediction to obtain the relative TRW change for each temperature, precipitation, and lag period combination. The relative TRW

change was back-transformed by exponentiating the values and subtracting 1.

2.6.3. Growth after 2018 in relation to crown condition and regional water deficits

We compared the growth response of vital and early-browning trees during and after the severe drought year 2018 in relation to the amount of crown loss in each region. The analysis was conducted separately for each region to investigate the effect of regional differences in CWB during and after 2018 on the growth recovery potential. Accordingly, we separated the early-browning trees into two groups based on the observed %CBL in 2020: early-browning trees with %CBL ≤ 58 % were classified as “early-browning with minor damage”, while early-browning trees with %CBL > 58 % were grouped as “early-browning with severe damage”. The vital trees were not re-classified into the vitality classes because only nine trees in total reached %CBL > 58 % in 2020. These nine trees were excluded from the analysis because of the small sample size. The threshold of 58 % biomass loss was chosen following Chakraborty et al. (2017) which found that beech trees exceeding this value have a high likelihood to die. Trees that died until 2020 or for which crown data was missing were excluded from the analysis (20 trees died, 2 trees with incomplete crown data). The difference in %CBL between the vital trees and the other two vitality classes was tested per region using a Wilcoxon rank sum test ($\alpha < 0.05$). In total, the analysis included 183 vital trees (BL: 68, ZH/AG: 41, SH: 74), 103 early-browning trees with severe damage (BL: 52, ZH/AG: 11, SH: 40) and 153 early-browning trees with minor damage (BL: 49, ZH/AG: 37, SH: 67).

A linear mixed-effects model was used to test the annual growth differences between the three vitality classes in each region. We included the log+1 transformed TRW data for the period 2016–2020 of all sampled trees. In addition, we substituted missing tree rings with the

Table 3

Summary of the fitted additive model for early-browning (A) and vital (B) beech trees estimating the effect of the masting, diameter at breast height (DBH), precipitation sum (PrecSum), mean temperature (Tmean) and lag period (lag) onto tree-ring width (TRW) following Eq. (2) & Eq. (S2). The effective degrees of freedom (edf), F-value and p-value of the tree-individual DBH-smooths (278 for early-browning trees, 192 for vital trees) were omitted in the table for brevity. Tree ID (ID) and tree group (Group) were added as grouping variables for the random intercept. For the parametric terms, the estimate with the standard error (std. error) and the associated p-values (p) are shown. Significant p-values are in bold.

Log(tree-ring width + 1)					
A. Early-browning trees					
	Component	Term	Estimate	Std. error	p
	Parametric	Intercept	0.629	0.104	<0.001
		Masting	−0.019	0.003	<0.001
	Component	Term	edf	F-value	p
	Smooth terms	DBH	2.991	142.953	<0.001
		DBH × ID	~	~	~
		Tmean × lag	5.667	7.878	<0.001
		PrecSum × lag	17.678	20.308	<0.001
		Tmean × PrecSum × lag	45.671	18.098	<0.001
		Group	55.021	102.442	<0.001
		ID	156.182	14.383	<0.001
Observations			16,056		
Adjusted R ²			0.678		
Deviance explained			69.4 %		
B. Vital trees					
	Component	Term	Estimate	Std. error	p
	Parametric	Intercept	1.032	0.097	<0.001
		Masting	−0.021	0.003	<0.001
	Component	Term	edf	F-value	p
	Smooth terms	DBH	2.984	93.745	<0.001
		DBH × ID	~	~	~
		Tmean × lag	16.762	9.104	<0.001
		PrecSum × lag	4.276	4.796	<0.001
		Tmean × PrecSum × lag	39.590	9.151	<0.001
		Group	28.076	93.375	0.056
		ID	107.348	6.495	<0.001
Observations			11,090		
Adjusted R ²			0.672		
Deviance explained			68.9 %		

value 0.001 mm to include them in the analysis of the short-term growth response. The years 2016 and 2017 were added to the model as reference years to facilitate the assessment of the growth response to the 2018 drought and the growth recovery after that. ID nested in tree group was added as a grouping variable for the random intercept to account for the sampling design (Eq. (S8)).

3. Results

3.1. Factors predicting the likelihood of early-browning

The early-browning trees were slightly yet significantly older than the vital trees in ZH/AG (mean difference 16 years) and SH (mean difference 12 years, Table 1, Fig. S1). Moreover, competition was slightly higher for the early-browning trees in SH than for the vital trees. For the other two regions, CI did not differ between early-browning and vital trees (Table 1).

Between 1960 and 2017, vital trees had wider tree rings compared to early-browning trees (Table 2, Fig. S6). Both tree groups reduced their growth between 1960 and 2017, but the early-browning trees had a stronger reduction than the vital trees. Overall, the standard deviation of the detrended TRW series was higher for early-browning trees than for vital trees (Table 2, Fig. S7). Early-browning trees showed lower ARI values compared to vital trees.

3.2. Effects of DBH, climate and masting on tree growth

Masting intensity had a negative effect on the TRW of vital and early-browning trees (Table 3). The effect was, however, small and within a comparable range for both classes. In addition, the population-wide size trend for the period 1960–2017 had a slight positive effect on the growth

of vital and early-browning trees (Fig. S8). The tree-individual size-growth trends varied strongly between trees (Fig. S9).

The significant tensor products for the climate parameters showed the additive and, in many cases, the interactive influence of temperature, precipitation, and lag on annual tree growth of both vitality classes (Table 3). Regarding the climate response per lag, vital and early-browning trees exhibited similar patterns (Figs. 2 & S10).

The growth of the vital trees was mainly affected by the current spring and summer climate (May–August). Warm and dry conditions led to strong growth reductions. However, high precipitation sums could counteract the negative temperature effect in spring and summer. The TRW of the vital trees was enhanced with summer temperatures of up to 19 °C when the precipitation sum was sufficiently high. The other analyzed lag periods influenced the growth of the vital trees only to a small degree, with cold and dry fall and winter conditions leading to less growth.

The growth of the early-browning trees responded the strongest to previous summer (July/August) and current spring and summer (May–August) climate. High temperatures and low precipitation had a strong negative effect on the growth of early-browning trees, especially in previous summer. This negative effect was also visible in the lag periods previous May/June and previous September/October, although less pronounced. Current summer temperatures above 18 °C had a negative effect on TRW even with high precipitation values.

3.3. Growth after 2018 in relation to crown condition and regional water deficits

The selected vital trees exhibited significantly less crown dieback in 2020 than the early-browning trees (Fig. S11). Concerning the growth shortly before and after 2018, 2016 was a relatively wet year with high

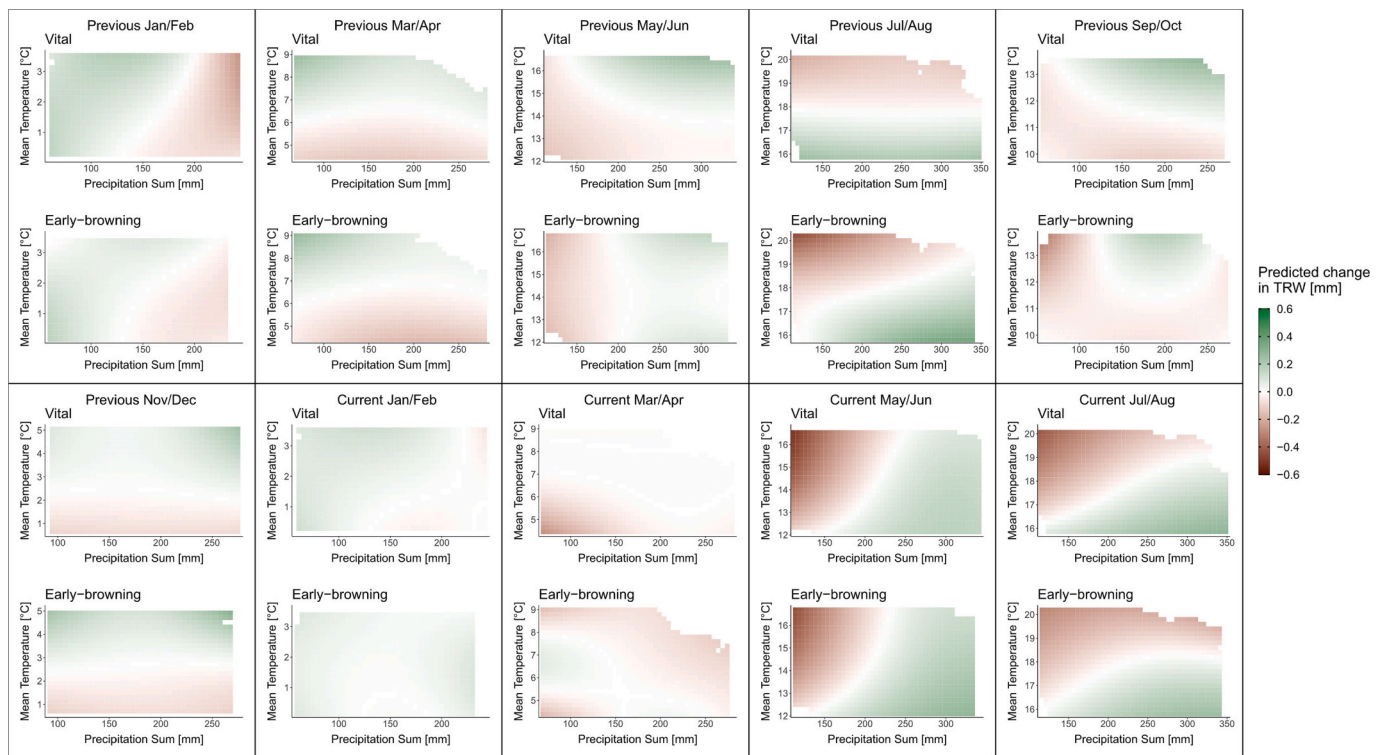


Fig. 2. Predicted change in tree-ring width (TRW) of vital and early-browning beech trees in function of mean temperature and precipitation sum of the previous and current year for two-months periods from previous year January to current year August following Eqs. (S6) & (S7) and calculated for the period 1960–2017. The months are abbreviated by the first three letters. Brown signifies narrower TRW values compared to mean conditions and green indicates larger TRW values.

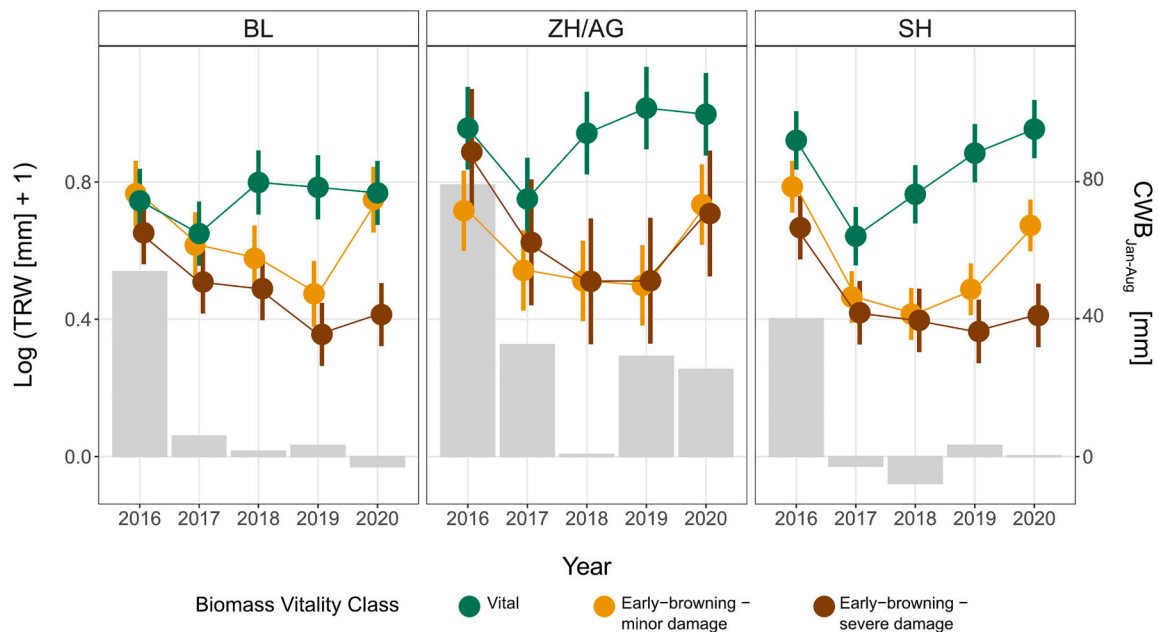


Fig. 3. Predicted log +1 transformed tree-ring width (TRW) including 95 % confidence intervals for the period 2016–2020 for vital (green), early-browning with minor crown damage (orange) and early-browning with severe crown damage (brown) beech trees for each region separately (BL, ZH/AG, SH) following Eq. (S8). The gray bars indicate the average climatic water balance between January and August ($CWB_{Jan-Aug}$) per year and region.

$CWB_{Jan-Aug}$ (Fig. S12) and high growth rates in all three regions (Fig. 3). In 2017, $CWB_{Jan-Aug}$ dropped to low values mediated by a dry winter and warm spring (Fig. S12), leading to growth reductions for all tree vitality classes in the three regions (Fig. 3, Tables S2–S4). While trees with minor and severe crown damage had similar growth rates in 2018 compared to 2017, the vital trees grew more despite the drought

conditions. The climate conditions (water availability) became favorable again in 2019 and 2020 in Zurich/Aargau, while conditions remained dry in the other two regions (Figs. S12 & S13). The trees with minor crown damage in BL and SH could recover to their pre-drought growth rate in 2020 (Tables S2 & S4). The trees with severe damage did only slightly but not significantly increase their growth except in

ZH/AG where they reached higher growth levels in 2020 than in 2019 (Table S3).

4. Discussion

We showed that beech trees that exhibited early browning during the extreme drought year 2018 were characterized by lower overall growth rates, steeper growth declines and higher climate sensitivity prior to 2018 than co-occurring beech trees with normal leaf fall. The competition experienced by individual trees could not predict the observed differences in response to the 2018 drought. Growth recovery after the drought was possible but depended on crown dieback severity and regional post drought water availability.

4.1. Low tree vigor predisposes beech trees to early browning

Our results show that lower growth performance, indicated by slower mean growth rates and a steeper growth decline in the last decades, predisposed beech trees in northern Switzerland to early browning induced by the severe drought in 2018. Similar growth reductions have been found in trees of multiple broadleaf and conifer species before severe drought-related crown dieback occurred (e.g., Camarero et al., 2015, 2021; Klesse et al., 2022; Marqués et al., 2022). Slower growth over an extended period can indicate an overall low tree vigor mediated by prolonged environmental stress and slow-acting processes, e.g., competition and resource limitation (Das et al., 2011). However, in two of the three regions studied (i.e., BL, ZH/AG), we did not find significant differences in the recent competitive environment between beech trees that showed early browning and those that remained vital. This result suggests that recent competition alone cannot explain the observed difference in drought response.

Similar findings were reported by Neycken et al. (2022) in northern Switzerland, where competition during the last 20 years could not predict the occurrence of crown dieback in beech-dominated forests. Minor competitive disadvantages in earlier decades that could potentially lay back decades might have weakened the trees, but several adverse effects had to accumulate in our case to cause a higher susceptibility to drought-induced crown dieback (Manion, 1990). For example, innate unfavorable physiological traits (Dounavi et al., 2016), as well as negative biotic (e.g., competition (Young et al., 2017)), herbivory (Brück-Dyckhoff et al., 2019), pests (Langer and Bußkamp, 2023), masting (Nussbaumer et al., 2021) and abiotic interactions (e.g., climate warming (Martinez del Castillo et al., 2022)), low soil water holding capacity (Klesse et al., 2022), air pollution (Braun et al., 2017) and nitrogen deposition (Braun et al., 2020) can exacerbate the effects of drought predisposing the weaker beech trees to decline and dieback (Griffin-Nolan et al., 2021).

4.2. Early-browning trees were highly sensitive to past summer climate

The results from the distributed lag model confirm previous studies which reported that beech growth is positively influenced by moist and mild conditions in spring and summer in Central Europe (e.g., Etzold et al., 2022; Klesse et al., 2022; van der Maaten, 2012). Overall, higher precipitation amounts during the growing season could compensate for higher temperatures, though to a limited extent. Overly high temperatures in July and August led to a reduction in growth rates. Early-browning trees were particularly affected because they additionally carried over stronger adverse effects from poor growing conditions of previous summer to the following year's growth. Future drought stress (IPCC, 2021) might thus push beech in our study regions out of its climatic comfort zone (Walthert et al., 2021), leading to widespread growth declines as already predicted for other European beech forests (Knutzen et al., 2017; Martinez del Castillo et al., 2022).

The higher climate growth sensitivity of the early-browning trees confirmed by the higher standard deviation and lower growth stability

together with the overall lower growth rates could point toward shallower rooting depth and reduced water uptake from deeper soil layers (Ripullone et al., 2020). Unfavorable microsite conditions leading to generally lower water availability or below-ground competition, which cannot be measured by the competition index we used, could hamper fine root development and distribution, making early-browning trees more dependent on top-soil water and recent moisture conditions than vital trees (Gessler et al., 2022; Schmied et al., 2023). The resource limitation could force the trees closer to their physiological tipping points, rendering them more sensitive to climate variations and hydraulic failure in the short term (McDowell et al., 2008).

Declining beech trees have been shown to reduce their water use efficiency several years before crown dieback (Camarero et al., 2021; Michelot-Antalik et al., 2019). It is thus possible that early-browning trees were less effective in regulating their stomatal conductance to prevent excessive water loss due to high temperatures. In years with sufficient precipitation during the growing season, the inefficient stomatal control of early-browning trees could be compensated by higher water uptake, while during drought years, the excessive evaporation could lead to xylem cavitation and early browning (Walthert et al., 2021). Recent studies suggest that the drought tolerance observed on some beech individuals could be related to different genotypes (Cuervo-Alarcon et al., 2021; Müller et al., 2017; Pfenninger et al., 2021) and/or gene expression pathways (Petrik et al., 2022). To which degree genetic factors regulate the observed lower tree vigor and different drought responses is unknown for our stands. Further studies are needed to clarify the genetic effect of drought resistance in beech.

Besides the climate response of beech trees, we also investigated if masting intensity, i.e., seed production, influenced tree growth of early-browning trees more negatively compared to the vital trees. The increased investments of resources into seed production in mast years often lead to reduced foliage mass and the formation of smaller tree rings (Braun et al., 2017; Nussbaumer et al., 2021). Our study confirms this negative effect of masting on radial growth. However, the effect was relatively small. Nussbaumer et al. (2021) showed that adverse climatic conditions that negatively influence tree growth could also trigger masting. In other words, climatic conditions and masting cumulatively alter radial growth. Therefore, the effect of masting might be masked by the effect of the climate variables in our model. In addition, the occurrence of masting was not directly recorded at our sites, but we based the masting probability on pollen data from measurement stations in Switzerland and other historical sources (Ascoli et al., 2017; Jenni, 1987). The derived masting index might thus underestimate the amount of seed production or be too estimative to generate significant statistical evidence.

Overall, the distributed lag model has shown to be an interesting new tool to model the climate sensitivity of beech during various time frames. The approach allowed us to model simultaneously the tree-individual size trend and growth-climate relationships without detrending the tree-ring or climate data a priori (Ols et al., 2023). On the downside, it was impossible to directly compare and test the linear predictors between classes with this method. Therefore, we could not ascertain if the detected growth differences in response to variations in temperature and precipitation were significantly different between the vital and the early-browning trees. Another critical point to consider is that we used the distributed lag model only to predict deviations from the mean tree-ring width due to variations in mean climate conditions. Responses to extreme weather conditions (e.g., drought years, extremely wet years, cold spells) were not predicted because they still occur too rarely to be represented correctly in our model framework (Gao and Shen, 2007).

4.3. Diverging growth trajectories after 2018

The summer drought in 2018 did not lead to consistently narrower tree rings in 2018 compared to 2017 in the 439 analyzed beech trees.

The lack of growth response to the 2018 drought has already been documented in other studies (Klesse et al., 2022; Mathes et al., 2023; Salomón et al., 2022) and can be explained by the timing of the heat-wave and drought conditions. The soil water potential reached low critical values only after mid-July (Walthert et al., 2021), a period of the growing season when most of the annual tree ring was already formed (Etzold et al., 2022). Moreover, the unusually warm winter and spring in 2017 and the late frost in spring 2017 (MeteoSchweiz, 2018) had already led to considerable growth decreases in the same year from which the trees could not recover in 2018. Nonetheless, the increase in growth of the vital trees in 2018 compared to 2017 in all three regions is surprising but might be related to the overall higher tree vigor incited by higher resource access and carbon reserves (as discussed above) compared to the trees with crown dieback. In contrast to the early-browning trees the vital trees could profit from the relatively mild winter and spring conditions in 2018 and recovered from the growth depression in 2017 before the drought in August 2018 led to a growth cessation.

The observed differential growth trajectories of the vitality classes after 2018 may be related to the extent of the hydraulic damage caused by the drought (Ruehr et al., 2019). Early browning and xylem embolism in beech start occurring at high drought stress levels when the leaf water potential drops below -1.3 MPa and water uptake is severely reduced (Walthert et al., 2021). Early browning occurs due to hydraulic failure and the resulting undersupply of the crown with moisture. When the hydric stress rises further, reaching very high levels (leaf water potential below -2.1 MPa), severe tissue damage can occur, causing crown dieback in the following year (Walthert et al., 2021). Secondary growth in the stem and branches is crucial for restoring hydraulic functioning because beech cannot repair embolized xylem vessels (Arend et al., 2022). According to Ruehr et al. (2019), higher stress levels are related to greater functional tissue damage and higher carbon costs to re-establish tree functioning. The reduced growth recovery combined with the high crown biomass loss observed for early-browning trees with severe crown damage compared to the ones with minor or no crown damages might thus indicate the occurrence of a higher proportion of non-reversible tissue damage. The trees might not be able to recover as efficiently due to the continuing depletion of their carbon reserves, which the remaining crown foliage mass cannot refill completely. We also found an important impact of local climate on growth recovery. Mild climate conditions in 2019 and 2020 in Zurich/Aargau enabled even the beech trees with severe crown damage to increase their growth levels again in 2020, although the variance in the growth response between trees was large. This finding suggests that beech can slowly recover from drought-induced hydraulic damage when the hydric stress level does not exceed critical limits and the climatic conditions return to less extreme levels again (Frei et al., 2022; Ruehr et al., 2019). Accordingly, previous studies have shown that beech can rapidly respond to rewetting of the topsoil after drought and restore the root water uptake within weeks (Gessler et al., 2022). Moreover, in a controlled rain exclusion experiment with mature beech trees, Hesse et al. (2023) found that beech could recover stem sap flow to the level of the control trees within two years after watering.

5. Conclusion

Our large-scale growth analysis of beech trees with and without drought-induced crown vitality loss in 2018 found that affected beech trees were characterized by an overall lower tree vigor in the past, indicated by lower overall growth, steeper recent growth declines and higher climate sensitivity compared to beech trees that remained vital. These findings suggest that unfavorable microsite conditions may have weakened the affected trees over several decades, by limiting their ability to access critical resources, e.g., water and light, and forced them to function closer to their physiological tipping points. The severe water deficits and high temperatures in summer 2018, which were

exacerbated by the dry conditions in 2017 led to hydraulic failure of these weakened trees and crown dieback in the following years. We also found evidence that, despite crown dieback, growth recovery within two years after the 2018 drought was possible. However, the level of growth recovery depended on crown dieback severity and the water availability in the following years.

Overall, our findings suggest that severe droughts are increasing the pressure on beech-dominated forests, especially on lowland sites with shallow soils and low water holding capacity. At such sites, drought-induced crown dieback and enhanced mortality rates can reduce the competitive ability of beech, which could favor the co-occurrence of more light-demanding and drought-tolerant species such as *Acer* spp. and *Quercus* spp. in the long term.

Aknowledgements

We thank Magdalena Nötzli, Anne Verstege and Loïc Schneider for the technical support in the laboratory. We also thank Eva Samblás Vives, Ide Uitenhuis, Maurice Moor and Ulrich Wasem for conducting the fieldwork and helping with the lab work. Additionally, we thank Flavian Stocker for the help with the tree-ring measurements. We thank all forest managers and owners for allowing us to conduct our study in their forests, as well as the three reviewers for their valuable comments on an earlier version of this manuscript.

This research was funded by ETH Zurich and the WHFF-CH fund (Project 2019.15). Stefan Klesse was supported by the SwissForestLab (Research Grant SFL20 P5), and by the Federal Office for the Environment FOEN.

CRediT authorship contribution statement

Anna Neycken: Formal analysis, Investigation, Methodology, Writing – original draft. **Thomas Wohlgenuth:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – original draft. **Esther R. Frei:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – original draft. **Stefan Klesse:** Methodology, Writing – original draft. **Andri Baltensweiler:** Methodology, Writing – review & editing. **Mathieu Lévesque:** Funding acquisition, Methodology, Supervision, Writing – original draft.

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

Dendrological data are archived in the environmental data portal and repository EnviDat doi: [10.16904/envi.dat.427](https://doi.org/10.16904/envi.dat.427) (Neycken et al., 2023) and crown data are archived in the EnviDat data portal doi: [10.16904/envi.dat.422](https://doi.org/10.16904/envi.dat.422) (Frei et al., 2023). All other data generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.169068>.

References

- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 1–55.

- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* 3, 30–36. <https://doi.org/10.1038/nclimate1635>.
- Arend, M., Link, R.M., Zahnd, C., Hoch, G., Schuldt, B., Kahmen, A., 2022. Lack of hydraulic recovery as a cause of post-drought foliage reduction and canopy decline in European beech. *New Phytol.* 234, 1195–1205.
- Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R., Cirolli, M., Kantorowicz, W., Zang, C., Schueler, S., Croisé, L., Piussi, P., Berretti, R., Palaghianu, C., Westergren, M., Lageard, J.G.A., Burkart, A., Gehrig-Bischel, R., Thomas, P.A., Beudert, B., Overgaard, R., Vacchiano, G., 2017. Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology* 98, 1473. <https://doi.org/10.1002/ecy.1785>.
- Baltensweiler, 2020. Räumliche Analyse von Trockenheitssymptomen im Schweizer Wald mit Sentinel-2-Satellitendaten. *Schweiz. Z. Forstwes.* 171, 298–309. <https://doi.org/10.3188/szf.2020.0298>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Beck, W., Heußner, K., 2012. Increased sensitivity in ring width series of common beech after 1990-climatic impact or normal patterns due to ageing? *TRACE-Tree Rings Archaeol. Climatol. Ecol.* 10, 13–19.
- Bolte, A., Hilbrigg, L., Grundmann, B., Kampf, F., Brunet, J., Roloff, A., 2010. Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce-beech forest. *Eur. J. For. Res.* 129, 261–276. <https://doi.org/10.1007/s10342-009-0323-1>.
- Braun, S., Schindler, C., Rihm, B., 2017. Growth trends of beech and Norway spruce in Switzerland: the role of nitrogen deposition, ozone, mineral nutrition and climate. *Sci. Total Environ.* 599–600, 637–646. <https://doi.org/10.1016/j.scitotenv.2017.04.230>.
- Braun, S., Schindler, C., Rihm, B., 2020. Foliar nutrient concentrations of European beech in Switzerland: relations with nitrogen deposition, ozone, climate and soil chemistry. *Front. For. Glob. Chang.* 3, 33. <https://doi.org/10.3389/ffgc.2020.00033>.
- Bréda, N., Huc, R., 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. <https://doi.org/10.1051/forest:2006042>.
- Brück-Dyckhoff, C., Petercord, R., Schopf, R., 2019. Vitality loss of European beech (*Fagus sylvatica* L.) and infestation by the European beech splendour beetle (*Agrilus viridis* L., Buprestidae, Coleoptera). *For. Ecol. Manag.* 432, 150–156. <https://doi.org/10.1016/j.foreco.2018.09.001>.
- Brun, P., Psomas, A., Ginzler, C., Thuiller, W., Zappa, M., Zimmermann, N.E., 2020. Large-scale early-wilting response of Central European forests to the 2018 extreme drought. *Glob. Chang. Biol.* 26, 7021–7035. <https://doi.org/10.1111/gcb.15360>.
- Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, 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., Heres, A., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanić, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., 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., Vode, 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>.
- Cailleret, M., Dakos, V., Jansen, S., Robert, E.M.R., Aakala, T., Amoroso, M.M., Antos, J.A., Bigler, C., Bugmann, H., Caccianiga, M., Camarero, J.-J., Cherubini, P., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Heres, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanić, T., Linares, J.-C., Lombardi, F., Mäkinen, H., Mészáros, I., Metsaranta, J.M., Oberhuber, W., Papadopoulos, A., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Smith, J.M., Stan, A.B., Stojanović, D.B., Suarez, M.-L., Svoboda, M., Trotsiuk, V., Villalba, R., Westwood, A.R., Wyckoff, P.H., Martínez-Vilalta, J., 2019. Early-warning signals of individual tree mortality based on annual radial growth. *Front. Plant Sci.* 9, 1964. <https://doi.org/10.3389/fpls.2018.01964>.
- 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>.
- Camarero, J.J., Colangelo, M., Gazol, A., Azorín-Molina, C., 2021. Drought and cold spells trigger dieback of temperate oak and beech forests in northern Spain. *Dendrochronologia* 66, 125812. <https://doi.org/10.1016/j.dendro.2021.125812>.
- Chakraborty, T., Saha, S., Matzarakis, A., Reif, A., 2017. Influence of multiple biotic and abiotic factors on the crown die-back of European beech trees at their drought limit. *Flora* 229, 58–70. <https://doi.org/10.1016/j.flora.2017.02.012>.
- Cuervo-Alarcon, L., Arend, M., Müller, M., Sperisen, C., Finkeldey, R., Krutovsky, K.V., 2021. A candidate gene association analysis identifies SNPs potentially involved in drought tolerance in European beech (*Fagus sylvatica* L.). *Sci. Rep.* 11, 2386. <https://doi.org/10.1038/s41598-021-81594-w>.
- Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. *For. Ecol. Manag.* 261, 1203–1213. <https://doi.org/10.1016/j.foreco.2010.12.035>.
- Dobbertin, M., Hug, C., Schwyzler, A., Borer, S., Schmalz, H., 2016. Kronenansprachen auf den Sanasilva- und den LWF-Flehen.
- Dounavi, A., Netzer, F., Celepirovic, N., Ivanković, M., Burger, J., Figueroa, A.G., Schön, S., Simon, J., Cremer, E., Fussli, B., Konner, M., Rennerberg, H., 2016. Genetic and physiological differences of European beech provenances (*F. sylvatica* L.) exposed to drought stress. *For. Ecol. Manag.* 361, 226–236. <https://doi.org/10.1016/j.foreco.2015.11.014>.
- Eichhorn, J., Roskams, P., Potočić, N., Timmermann, V., Ferretti, M., Mues, V., Szepesi, A., Durrant, D., Seletković, I., Schröck, H.-W., Nevalainen, S., Bussotti, F., García, P., Wulff, S., 2016. Visual assessment of crown condition and damaging agents. In: Manual Part IV. UNECE ICP Forests Programme Co-ordinating Centre: Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Thünen Institute of Forest Ecosystems, Eberswalde, Germany, p. 49.
- Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Kahmen, A., Peters, R.L., Vitasse, Y., Walthert, 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>.
- 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., Uitentuis, I., von Arx, G., Wohlgemuth, T., 2022. European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. *Plant Biol. J.* 24, 1132–1145. <https://doi.org/10.1111/plb.13467>.
- Frei, E.R., Gossner, M.M., Vitasse, Y., Queloz, V., Neycken, A., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., Wohlgemuth, T., 2023. Data on multi-year drought impacts on European beech in northern Switzerland. *EnviDat*. <https://doi.org/10.16904/enviDat.422>.
- Gao, S., Shen, J., 2007. Asymptotic properties of a double penalized maximum likelihood estimator in logistic regression. *Statist. Probab. Lett.* 77, 925–930. <https://doi.org/10.1016/j.spl.2007.01.004>.
- Gärtner, H., Nievergelt, D., 2010. The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28, 85–92. <https://doi.org/10.1016/j.dendro.2009.09.002>.
- Gessler, A., Bächli, L., Rouholahnejad Freund, E., Treyde, K., Schaub, M., Haeni, M., Weiler, M., Seeger, S., Marshall, J., Hug, C., Zweifel, R., Hagedorn, F., Rigling, A., Saurer, M., Meusburger, K., 2022. Drought reduces water uptake in beech from the drying topsoil, but no compensatory uptake occurs from deeper soil layers. *New Phytol.* 233, 194–206. <https://doi.org/10.1111/nph.17767>.
- Gonseth, Y., Wohlgemuth, T., Sansonnens, B., Buttler, A., 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard, Umwelt-Materialien. Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern.
- Griffin-Nolan, R.J., Mohanbabu, N., Araldi-Brondolo, S., Ebert, A.R., LeVonne, J., Lumsden-Pinto, J.I., Roden, H., Stark, J.R., Tourville, J., Becklin, K.M., Drake, J.E., Frank, D.A., Lamit, L.J., Fridley, J.D., 2021. Friend or foe? The role of biotic agents in drought-induced plant mortality. *Plant Ecol.* 222, 537–548. <https://doi.org/10.1007/s11258-021-01126-4>.
- Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M., Drobyshev, I., Liñán, I.D., Friend, A.D., Grabner, M., Hartl, C., Kreyling, J., Lebourgeois, F., Levanić, T., Menzel, A., van der Maaten, E., van der Maaten-Theunissen, M., Muffler, L., Motta, R., Roibu, C.-C., Popa, I., Scharnweber, T., Weigel, R., Wilking, M., Zang, C.S., 2018. Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecol. Lett.* 21, 1833–1844. <https://doi.org/10.1111/ele.13158>.
- Hegyi, F., 1974. A Simulation Model for Managing Jack-pine Stands. *Growth Models for Tree and Stand Simulation* 30. Royal College of Forestry, Stockholm, Sweden, pp. 74–90.
- Hermann, M., Röthlisberger, M., Gessler, A., Rigling, A., Senf, C., Wohlgemuth, T., Wernli, H., 2023. Meteorological history of low-forest-greenness events in Europe in 2002–2022. *Biogeosciences* 20, 1155–1180. <https://doi.org/10.5194/bg-20-1155-2023>.
- Hesse, B.D., Gebhardt, T., Hafner, B.D., Hikino, K., Reitsam, A., Gigl, M., Dawid, C., Häberle, K.-H., Grams, T.E.E., 2023. Physiological recovery of tree water relations upon drought release—response of mature beech and spruce after five years of recurrent summer drought. *Tree Physiol.* 43, 522–538. <https://doi.org/10.1093/treephys/tpac135>.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- IPCC, 2021. Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, 1st ed. Cambridge University Press. <https://doi.org/10.1017/9781009157896>.
- Jenni, L., 1987. Mass concentrations of bramblings *Fringilla montifringilla* in Europe 1900–1983: their dependence upon beech mast and the effect of snow-cover. *Ornis Scand.* 18, 84. <https://doi.org/10.2307/3676843>.
- Kasprzyk, I., Ortyl, B., Dulski-Jez, A., 2014. Relationships among weather parameters, airborne pollen and seed crops of *Fagus* and *Quercus* in Poland. *Agric. For. Meteorol.* 197, 111–122. <https://doi.org/10.1016/j.agrformet.2014.05.015>.
- Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., Neycken, A., Braun, S., Dubach, V., Gessler, A., Ginzler, C., Gossner, M.M., Hagedorn, F., Queloz, V., Samblás Vives, E., Rigling, A., Frei, E.R., 2022. Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in *Fagus sylvatica*. *Sci. Total Environ.* 851, 157926. <https://doi.org/10.1016/j.scitotenv.2022.157926>.
- 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/10.1007/s10021-017-0128-x>.

- Langer, G.J., Bußkamp, J., 2023. Vitality loss of beech: a serious threat to *Fagus sylvatica* in Germany in the context of global warming. *J. Plant Dis. Prot.* <https://doi.org/10.1007/s41348-023-00743-7>.
- Manion, P.D., 1990. *Tree Disease Concepts*, 2nd ed. Prentice-Hall.
- Marqués, L., Ogle, K., Peltier, D.M.P., Camarero, J.J., 2022. Altered climate memory characterizes tree growth during forest dieback. *Agric. For. Meteorol.* 314, 108787 <https://doi.org/10.1016/j.agrformet.2021.108787>.
- Martinez del Castillo, E., Zang, C.S., Buras, A., Hacket-Pain, A., Esper, J., Serrano-Notivol, R., Hartl, C., Weigel, R., Klesse, S., Resco de Dios, V., Scharnweber, T., Dorado-Liñán, I., van der Maaten-Theunissen, M., van der Maaten, E., Jump, A., Mikac, S., Banzragch, B.-E., Beck, W., Cavin, L., Claessens, H., Čada, V., Čufar, K., Dulamsuren, C., Gričar, J., Gil-Pelegrín, E., Janda, P., Kazimirovic, M., Kreyling, J., Latte, N., Leuschner, C., Longares, L.A., Menzel, A., Merela, M., Motta, R., Muffler, L., Nola, P., Petritan, A.M., Petritan, I.C., Prislan, P., Rubio-Cuadrado, Á., Rydval, M., Stajić, B., Svoboda, M., Toromani, E., Trotsiuk, V., Wilmking, M., Zlatanov, T., de Luis, M., 2022. Climate-change-driven growth decline of European beech forests. *Commun. Biol.* 5, 163. <https://doi.org/10.1038/s42003-022-03107-3>.
- Mathes, T., Seidel, D., Annighöfer, P., 2023. Response to extreme events: do morphological differences affect the ability of beech (*Fagus sylvatica* L.) to resist drought stress? *Forestry*, cpac056. <https://doi.org/10.1093/forestry/cpac056>.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yezzer, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>.
- MeteoSchweiz, 2018. *Klimabulletin Jahr 2017*. Zürich.
- Michelot-Antalik, A., Granda, E., Fresneau, C., Damesin, C., 2019. Evidence of a seasonal trade-off between growth and starch storage in declining beeches: assessment through stem radial increment, non-structural carbohydrates and intra-ring δ13C. *Tree Physiol.* 39, 831–844. <https://doi.org/10.1093/treephys/tpz008>.
- Müller, M., Seifert, S., Lübke, T., Leuschner, C., Finkeldey, R., 2017. De novo transcriptome assembly and analysis of differential gene expression in response to drought in European beech. *PLoS One* 12, e0184167. <https://doi.org/10.1371/journal.pone.0184167>.
- Neycken, A., Scheggia, M., Bigler, C., Lévesque, M., 2022. Long-term growth decline precedes sudden crown dieback of European beech. *Agric. For. Meteorol.* 324, 109103 <https://doi.org/10.1016/j.agrformet.2022.109103>.
- Neycken, A., Wohlgemuth, T., Frei, E.R., Lévesque, M., 2023. Tree-ring data of European beech with premature leaf discoloration in 2018 and beech with normal leaf fall. *EnviDat*. <https://doi.org/10.16904/envidat.427>.
- Nothdurft, A., 2020. Climate sensitive single tree growth modeling using a hierarchical Bayes approach and integrated nested Laplace approximations (INLA) for a distributed lag model. *For. Ecol. Manag.* 478, 118497 <https://doi.org/10.1016/j.foreco.2020.118497>.
- Nothdurft, A., Vospernik, S., 2018. Climate-sensitive radial increment model of Norway spruce in Tyrol based on a distributed lag model with penalized splines for year-ring time series. *Can. J. For. Res.* 48, 930–941. <https://doi.org/10.1139/cjfr-2018-0027>.
- Nussbaumer, A., Gessler, A., Benham, S., de Cinti, B., Etzold, S., Ingerslev, M., Jacob, F., Lebourgeois, F., Levanic, T., Marjanović, H., Nicolas, M., Ostrogović Sever, M.Z., Privitzer, T., Rautio, P., Roskams, P., Sanders, T.G.M., Schmitt, M., Šrámek, V., Thimonier, A., Ukonmaanaho, L., Verstraeten, A., Vesterdal, L., Wagner, M., Waldner, P., Rigling, A., 2021. Contrasting resource dynamics in mast years for European beech and oak—a continental scale analysis. *Front. For. Glob. Chang.* 4, 689836 <https://doi.org/10.3389/ffgc.2021.689836>.
- 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, 126094. <https://doi.org/10.1016/j.dendro.2023.126094>.
- Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7, e6876. <https://doi.org/10.7717/peerj.6876>.
- Petrik, P., Petek-Petrik, A., Kurjak, D., Mukarram, M., Klein, T., Gömöry, D., Strelcová, K., Frýdl, J., Konopková, A., 2022. Interannual adjustments in stomatal and leaf morphological traits of European beech (*Fagus sylvatica* L.) demonstrate its climate change acclimation potential. *Plant Biotechnol. J.* 24, 1287–1296. <https://doi.org/10.1111/plb.13401>.
- Pfenninger, M., Reuss, F., Kiebler, A., Schönnenbeck, P., Caliendo, C., Gerber, S., Cocchiarraro, B., Reuter, S., Blüthgen, N., Mody, K., Mishra, B., Bálint, M., Thines, M., Feldmeyer, B., 2021. Genomic basis for drought resistance in European beech forests threatened by climate change. *eLife* 10, e65532. <https://doi.org/10.7554/eLife.65532>.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rathgeb, U., Bürgi, M., Wohlgemuth, T., 2020. Waldschäden wegen Dürre von 1864 bis 2018 in der Schweiz und insbesondere im Kanton Zürich. *Schweiz. Z. Forstwes.* 171, 249–256. <https://doi.org/10.3188/szf.2020.0249>.
- Ripullone, F., Camarero, J.J., Colangelo, M., Voltas, J., 2020. Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of Mediterranean oaks. *Tree Physiol.* 40, 591–604. <https://doi.org/10.1093/treephys/tpaa026>.
- Rohner, 2020. Kronenzustand und Zuwachs in Schweizer Buchenwäldern während der Trockenheit 2018. *Schweiz. Z. Forstwes.* 171, 298–309. <https://doi.org/10.3188/szf.2020.0298>.
- Ruehr, N.K., Grote, R., Mayr, S., Arneith, A., 2019. Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiol.* 39, 1285–1299. <https://doi.org/10.1093/treephys/tpz032>.
- Rukh, S., Sanders, T.G.M., Krüger, I., Schad, T., Bolte, A., 2023. Distinct responses of European beech (*Fagus sylvatica* L.) to drought intensity and length—a review of the impacts of the 2003 and 2018–2019 drought events in Central Europe. *Forests* 14, 248. <https://doi.org/10.3390/f14020248>.
- Salomón, R.L., Peters, R.L., Zweifel, R., Sass-Klaassen, U.G.W., Stegehuis, A.I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B.J.W., Lindner, M., Martínez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bär, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiller, D., Blaženc, M., Čada, V., Carraro, V., Cecchini, S., Chan, T., Conedera, M., Delpierre, N., Delzon, S., Dittmarová, L., Dolezal, J., Dufrêne, E., Edvardsson, J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Güney, A., Heinrich, L., Hentschel, R., Janda, P., Ježík, M., Kahle, H.-P., Knüsel, S., Krejza, J., Kuberski, L., Kučera, J., Lebourgeois, F., Mikoláš, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbell, I., Rathgeber, C.B.K., Salmon, Y., Saunders, M., Scharnweber, T., Sitková, Z., Stangler, D.F., Stereńczak, K., Stojanović, M., Strélová, K., Světlík, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavřík, H., Vejpustková, M., Walthert, L., Wilmking, M., Zin, E., Zou, J., Steppe, K., 2022. The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. *Nat. Commun.* 13, 28. <https://doi.org/10.1038/s41467-021-27579-9>.
- Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461, 53–59. <https://doi.org/10.1038/nature08227>.
- Schmid, G., Pretzsch, H., Ambs, D., Uhl, E., Schmucker, J., Fähr, J., Biber, P., Hoffmann, Y.-D., Šeho, M., Mellert, K.H., Hilmers, T., 2023. Rapid beech decline under recurrent drought stress: individual neighborhood structure and soil properties matter. *For. Ecol. Manag.* 545, 121305 <https://doi.org/10.1016/j.foreco.2023.121305>.
- Schuldt, B., Buras, A., Arend, M., Vitasé, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hilbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübke, 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.* <https://doi.org/10.1016/j.baae.2020.04.003> (S1439179120300414).
- Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently linked to drought across Europe. *Nat. Commun.* 11, 6200. <https://doi.org/10.1038/s41467-020-19924-1>.
- Stovall, A.E.L., Shugart, H., Yang, X., 2019. Tree height explains mortality risk during an intense drought. *Nat. Commun.* 10, 4385. <https://doi.org/10.1038/s41467-019-12380-6>.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55–94. <https://doi.org/10.2307/210739>.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190, 214–251. [https://doi.org/10.1016/S0022-1694\(96\)03128-9](https://doi.org/10.1016/S0022-1694(96)03128-9).
- Trotsiuk, V., Hartig, F., Cailleret, M., Babst, F., Forrester, D.I., Baltensweiler, A., Buchmann, N., Bugmann, H., Gessler, A., Gharun, M., Minunno, F., Rigling, A., Rohner, B., Stihlhard, J., Thürig, E., Waldner, P., Ferretti, M., Eugster, W., Schaub, M., 2020. Assessing the response of forest productivity to climate extremes in Switzerland using model–data fusion. *Glob. Chang. Biol.* 26, 2463–2476. <https://doi.org/10.1111/gcb.15011>.
- Vacciano, G., Ascoli, D., Berzaghi, F., Lucas-Borja, M.E., Caignard, T., Collalti, A., Mairota, P., Palaghianu, C., Rey, C.P.O., Sanders, T.G.M., Schermer, E., Wohlgemuth, T., Hacket-Pain, A., 2018. Reproducing reproduction: how to simulate mast seeding in forest models. *Ecol. Model.* 376, 40–53. <https://doi.org/10.1016/j.ecolmodel.2018.03.004>.
- van der Maaten, E., 2012. Climate sensitivity of radial growth in European beech (*Fagus sylvatica* L.) at different aspects in southwestern Germany. *Trees* 26, 777–788. <https://doi.org/10.1007/s00468-011-0645-8>.
- Walthert, L., Ganthaler, A., Mayr, S., Saurer, M., Waldner, P., Walser, M., Zweifel, R., von Arx, G., 2021. From the comfort zone to crown dieback: sequence of physiological stress thresholds in mature European beech trees across progressive drought. *Sci. Total Environ.* 753, 141792 <https://doi.org/10.1016/j.scitotenv.2020.141792>.
- Wohlgemuth, T., Kistler, M., Aymon, C., Hagedorn, F., Gessler, A., Gossner, M.M., Queloz, V., Vögeli, I., Wasem, U., Vitasé, Y., Rigling, A., 2020. Früher Laubfall der Buche während der Sommertrockenheit 2018: Resistenz oder Schwächesymptom? *Schweiz. Z. Forstwes.* 171, 257–269. <https://doi.org/10.3188/szf.2020.0257>.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R*, 2nd ed. CRC press.
- WSL, 2021. Skippy - The new high-resolution image capturing system for tree rings developed at WSL [WWW document]. URL: <https://www.wsl.ch/en/services-and-products/research-instruments/skipky.html>.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecol. Lett.* 20, 78–86. <https://doi.org/10.1111/ele.12711>.