

# Did stand opening 60 years ago predispose a European beech population to death?

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## ARTICLE INFO

### Keywords:

climate change  
drought  
early-warning signal of tree death  
land use legacy  
logging  
short-term ring width variation  
stand history  
tree-ring analysis

## ABSTRACT

Widespread increases in tree mortality have fueled the debate on the mechanisms of heat- and drought-related tree death. While much research focused on the immediate causes of tree death, the role of predisposing factors for death is not well understood. We employed tree-ring and climate sensitivity analysis of growth to study the importance of legacy effects of past disturbances for growth patterns and a recent mortality burst in a protected European beech (*Fagus sylvatica*) forest, comparing groups of live and recently died trees in the same stand. Live and dead trees showed a decade-long decrease in radial growth since the severe 1976 drought, which indicates that the high mortality in the last two decades is not solely caused by recent drought spells, but that trees were apparently predisposed by previous events to death decades later. An even more distant event than the 1976 drought that has imprinted on the chronologies is the severe 1947 drought in combination with extensive logging at that time. It appears that stand opening 60 and 40 years ago due to high immediate drought mortality in conjunction with heavy logging resulted in much higher inter-annual ring width variability with more extreme negative and positive pointer years in the subsequent years, and led to permanent reduction in tree health. We identified the first derivative of the ring width curve as the most reliable early-warning signal of a predisposition to drought-induced death, while inter-annual growth variability and growth resistance and resilience to drought were less suited. We suggest that the causes of recent climate warming-related dieback of beech and other temperate hardwood forests may only be fully grasped, when the imprint of past stress events on growth and vitality is understood. The physiological mechanisms causing legacy effects with long delay of death require further study.

## 1. Introduction

Recent climate warming has triggered increases in drought- and heat-related tree mortality and forest dieback in many regions of the world (Allen et al., 2010; Schuldt et al., 2020). These reports are paralleled by dendrochronological studies demonstrating recent decline in the growth rates of major timber species, which have been related to increases in the frequency and severity of droughts (Jump et al., 2006; Dulamsuren et al., 2010; Scharnweber et al., 2011; Zimmermann et al., 2015). The mortality increase has triggered an intensive debate about the likely physiological mechanisms leading to drought-induced tree death (Anderegg and Callaway, 2012; McDowell et al., 2013; Anderegg et al., 2015a), while less is known about the drivers of long-term, non-lethal decline in radial stem growth, if not attributable to

senescence or competition effects (Cailleret et al., 2017). It is likely that long-term growth decline and death are often inter-related and caused by similar factors (Liang et al., 2016; Vanoni et al., 2016; Wang et al., 2020). Yet, this interaction is poorly understood and what we currently know represents a hypothesis. The study of the physiological and physical drivers of tree death and forest dieback is mostly concerned with the immediate causes of mortality, only rarely taking effects of the more distant past into account, while dendrochronological studies of growth declines predominantly address living trees and only exceptionally deal with tree death. However, increasing evidence suggests that many cases of tree death and forest dieback can only be fully understood, when a causal analysis of the growth patterns of the past is conducted (Bigler and Bugmann, 2004; Cailleret et al., 2017).

A multitude of dendroecological studies has investigated the growth

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<https://doi.org/10.1016/j.tfp.2022.100265>

Received 6 April 2022; Received in revised form 20 April 2022; Accepted 21 April 2022

Available online 26 April 2022

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response of temperate trees to droughts. Tree-ring chronologies often show growth recovery within a few years after a drought (Anderegg et al., 2015b; Merlin et al., 2015), but evidence of longer recovery periods and continued growth depressions for several decades also does exist (Aertsens et al., 2014; Dulamsuren et al., 2017; Leuschner, 2020). Much of the variation in tree growth resilience is explained by differences in drought severity and specific soil moisture patterns (Gazol et al., 2017), but tree age and size and species differences in the recovery potential are also influential. Peterken and Mountford (1996) found divergent recovery capacities of different tree individuals in an English beech forest after the severe 1976 drought, with some trees recovering fast, while others, especially large individuals, had not recovered even after 15 years. No doubt, disturbance events in the past can imprint on the growth patterns and vitality of trees for decades or even the whole lifetime (Johnstone et al., 2016; Mausolf et al. 2018).

Variation in annual stem increment is not only driven by climate, but also by changes in stand structure and stand density, which influence access to resources. Tree removal from a stand by natural disturbance or logging typically leads to sudden growth releases in the remaining trees, which imprints on tree-ring chronologies and allows tracking past logging events and even to assess their magnitude (Dulamsuren et al., 2014). Since reduced stand densities should increase the water availability for the remaining trees, thinning is often suggested as a silvicultural option for adapting managed forests to climate warming (Ammer et al., 2016; Zhang et al., 2019). While this approach may be suitable for stands of light-demanding trees such as pines and oaks, it remains unclear, whether stand thinning is reducing or increasing the overall stress level in closed stands of shade-tolerant late-successional species. For example, European beech (*Fagus sylvatica* L.), the most important tree species of Central Europe's natural forest vegetation and an important timber species (Leuschner and Ellenberg, 2017), is known to suffer from sudden light exposure by bark damage, which may predispose trees to death after a lag phase (Wohlgemuth et al., 2020). In correspondence, heavy thinning has been found to cause negative growth trends in beech forests (Bosela et al., 2016).

Several authors have examined tree-ring series with the aim to identify parameters suited for predicting drought-induced tree mortality. Vanoni et al. (2016), Cailleret et al. (2017, 2019) and Wang et al. (2020) reported abrupt or gradual decreases in the annual stem increment for variable time spans prior to death; however, such growth declines were not consistently found. Long-term growth declines seem to be more typical for dying gymnosperms, whereas angiosperms rather tend to show smaller growth reductions for short periods before death (Cailleret et al., 2017). DeSoto et al. (2020) suggested that low resilience of tree-ring width to drought events often indicates later mortality. Based on the assumption that temporal disorder in the carbon and water relations of trees should manifest in irregularities in annual stem wood formation, Camarero et al. (2015) and Cailleret et al. (2017, 2019) screened the descriptive statistics of tree-ring series for suitable early-warning signals of tree death, including the temporal first-order autocorrelation within ring series, the standard deviation from the mean in ring series, and growth synchronicity, but these approaches did not deliver clear results. Growth variance increased and synchronicity decreased 20 years before tree death in gymnosperms, but not in angiosperms, irrespective of the cause of death (Cailleret et al., 2019). First-order autocorrelation provided inconsistent results as well and was considered a poor early-warning signal (Cailleret et al., 2019). It is evident that progress in our understanding of the causes of tree mortality events can only be achieved when both the proximal mechanisms leading to death such as hydraulic failure and carbon starvation, as well as the pattern of pre-lethal growth decline are better known (Salmon et al., 2015).

We conducted a dendrochronological study in a protected mature *F. sylvatica* forest in the center of the species' distribution range, where beech is assumed to grow under optimal climatic conditions. In this stand, the mortality of dominant and sub-dominant beech trees

markedly increased after the severe 2003 drought and continued until today. This observation raised the question on the causes of increased death, as the climate is humid throughout the year, the soils are moderately deep, and the trees were not in the age of senescence. By comparing the tree-ring width chronologies of live and recently dead beech trees in relation to climatic extremes and major disturbance events in the past ~150 years, we attempted to (i) reconstruct the temporal development of the mortality event in the nearest past (i.e. for the not yet decayed deadwood stems), (ii) search for differences in growth patterns between dead and surviving trees in the past, and (iii) identify possible destabilizing events in the trees' life history that could have led to growth decline and death at mature age. Our main study goal was to better understand the influence of assumed legacy effects of the more distant forest history on present-day tree vitality. Based on published work on the impact of atmospheric and soil drought on tree health, we formulated the following hypotheses: (1) The increased recent mortality did not result from competitive inferiority of the dead trees, (2) death was preceded by long-term growth decline which is related to past drought events, and (3) stand thinning in the more distant past had a negative effect on tree vitality. Furthermore, we aimed at making a methodical contribution by identifying possible indicators of vitality loss, which could serve as early-warning signals of subsequent death. Therefore, we tested a variety of statistical parameters related to ring-width chronologies, including the widely used variables ring-width standard deviation, and growth resistance, resilience and recovery in response to selected droughts. As these parameters were not consistently found to be good predictors in other studies (Camarero et al., 2015; Cailleret et al., 2017, 2019; DeSoto et al., 2020), we tested the hypothesis (4) that the first derivative of a tree-ring series is a proper tool for quantifying variability in annual stem increment and is a useful early-warning signal for subsequent tree death. This hypothesis is based on the assumption that the tree-ring curve's slope, which is quantified by the first derivative, will increase with higher year-to-year variability of ring width.

## 2. Materials and methods

### 2.1. Study area

Field work was carried out in November/December 2015 in a nearly monospecific *F. sylvatica* forest (Luzulo-Fagetum community) in the Solling Mountains, central Germany, at lower montane elevation (400 m a.s.l.) on the mountain ridge Limker Strang (51°43' N, 9°41' E). The bedrock is Triassic sandstone (Middle Bunter); soils are acidic dystric Cambisols with relatively thick organic layers. The terrain is gently inclined to the northwest. The climate is humid throughout the year with a mean annual temperature of ~7.5°C and mean annual precipitation around 1000 mm.

The investigated stand is a single-layered age-class forest without a second canopy layer and shrub layer with most trees being ~165 years old at the time of sampling. It was under silvicultural management in the past, but was declared a forest reserve in 1972. The present tree layer originates from natural regeneration and planting activities in the mid-19<sup>th</sup> century. In 1948, the canopy was opened by heavy logging in the at that time roughly 100-year-old beech stand in order to harvest fuelwood; nearly a third (80–90 m<sup>3</sup> ha<sup>-1</sup>) of the stocking volume was felled. Damaged trees were also extracted after the severe 1959 drought (Meyer et al. 2015). Wind breakage occurred in 1972, 1976, 1990, and 2007. The stand survived several severe droughts, as the well-known transregional droughts in 1947, 1959, 1976, and 2003 (Rebetez et al., 2006; Brázdil et al., 2016). In many cases, severe summer droughts are related to heat waves in Central Europe. Since the mid-1990s, in particular since 2003, widespread mortality hit the mature beech trees.

## 2.2. Climate data

Local climate data were derived from modeled grid data of monthly temperature and precipitation with a mesh size of 1 km x 1 km, obtained from the German Weather Service network (DWD-CDC) for the period 1935–2015. Climatic aridity was assessed from the weather data for this period by calculating 3-monthly means of the Standardized Precipitation Evapotranspiration Index (SPEI3; Vicente-Serrano et al., 2010) for the months March to August using the R package SPEI version 1.6 and R 4.0.3 software. Potential evapotranspiration was calculated from monthly mean temperature and a coefficient derived from latitude to obtain day length (Thorntwaite, 1948) and related to measured monthly precipitation. This allowed computing climatic water balance. Bonnemann (1984) was used as a regional source for information on the occurrence of drought years in the period until 1935. He reported droughts for the years 1884, 1886, 1887, 1892, 1893, 1911, 1915, 1921, 1929, 1934, and 1935. Bonnemann's data refer to the Reinhardswald, a forest region about 20 km west of the Solling Mountains with very similar climate. Local trends of temperature, precipitation and SPEI are displayed in Figs. S1, S2 and S3 in the Supplementary Information.

## 2.3. Tree-ring analysis and age determination

Stem coring was conducted in 2015 in 200 living dominant or co-dominant *F. sylvatica* trees and 57 dead individuals of similar stem diameter to the living trees. Fifty-one of these dead trunks were still standing upright, the remaining six trunks were downed deadwood of a relatively low decomposition stage. Stem diameter at breast height (1.3 m) was measured in the standing trees with a measuring tape. Tree height was determined with a Vertex IV hypsometer (Haglöf, Langsele, Sweden). Assumed competitive interactions in the stem neighborhood of target trees were estimated with the Hegyi competition index (Hegyi, 1974) with the aim to detect possible differences in the competition pressure dead and living trees were exposed to. Wood cores were collected at 1.3 m height using an increment borer of 5 mm inner diameter. Ring width was measured with a precision of 10 µm using a Lintab 6 measuring table (Rinntech, Germany). Dendrochronological standard methods were used for cross-dating and quality assessment of the tree-ring chronologies (see Supplementary Information). Tree-ring series were standardized by dividing the observed tree-ring width through the expected annual increment by applying a spline function using the R package dplR ("Dendrochronology Program Library") version 1.7.1 (Bunn et al., 2020). The cubic spline function (with a 50% frequency-response cut-off at a wavelength of 30 yr) was chosen to reduce the influence of the long-term growth trend on the data, but to keep much of the inter-annual (high-frequency) growth variability (Klesse, 2021). This approach differs, for example, from a logarithmic transformation, as we were interested in examining the differences in inter-annual growth variability between live and dead trees (Cook et al., 1990).

Tree age refers to the age of the oldest tree ring ('cambial age') at the sampling height of 1.3 m. The trunks of several trees (especially of dead individuals) were already partly decayed in their core, so that age determination was not possible through tree-ring counting. This problem was overcome by two approaches: First, the number of decayed annual tree rings was estimated from the ring width of the subsequent years using the growth characteristics of nearby trees with intact pith as a reference, if only small parts of the inner heartwood close to the pith were rotten (applied to 155 (=78%) of the living trees and 6 (=11%) of the dead sample trees, adding 1 to 6 years (median: 4 years) to the age counts). Second, the age of trees with partly decayed heartwood was estimated by means of linear regression of dbh on tree age, established in living sample trees with intact trunk wood. Subsequently, the number of trees used for linear regression was narrowed to include only those trees, where linear regression yielded an age estimate that deviated by ≤5% from the counted age. The resulting linear regression equation based on

data from 57 trees ( $r = 0.87$ ,  $P < 0.001$ ) is

$$\text{Age (yr)} = 109.9601 + 0.8824 \times \text{dbh}$$

The expression was applied to estimate tree age in 28 (=14%) live and 50 (=88%) dead trees. We used these tree age estimates in our study only to ensure that the age of live and dead tree individuals was comparable. Thus, the inherent estimation error was acceptable.

## 2.4. Inter-annual ring width variability

Inter-annual ring width variation was explored by calculating the standard deviation of mean increment for the individual tree-ring series. The impact of previous-year growth on stem increment in the current year was examined by calculating first-order autocorrelation. Synchronicity in annual stem increment between tree individuals was examined analyzing linear Pearson correlation. For a closer look on ring width variation in short time intervals of a few years, the first derivative of the ring-width curve was calculated for the individual ring series as well, as it provides information on the slope of the curve in different life stages of a tree and thus may visualize inter-annual growth variation more clearly than the standard deviation of mean ring width or mean sensitivity. In addition to the original value of the first derivative (which includes – or + signs), we also analyzed its absolute value (i.e. without slope direction) for characterizing slope steepness, which might be lost when averaging over positive and negative values. We also calculated mean sensitivity in addition to the standard deviation of the tree-ring series, although we are well aware of the methodical concerns against this parameter (Bunn et al., 2013). This is because, at high first-order autocorrelation, mean sensitivity is strongly influenced by first-order autocorrelation. Mean sensitivity thus represents a bulk parameter that merges inter-annual growth variability and autocorrelation, with the influence of the latter varying. Nevertheless, we included mean sensitivity in our comparison of parameters that could serve as early-warning signals of later tree death, because mean sensitivity is still widely used in tree-ring studies (e.g. Camarero and Ortega-Martínez, 2021; Arzac et al., 2022; Crispín-DelaCruz et al., 2022; González de Andrés et al., 2022; Zhang et al., 2022; Zhou et al., 2022). Synchronicity was calculated with the R package dplR 1.7.1 (Bunn et al., 2020), whereas the remaining parameters, including the first derivative, were computed with TSAP software.

## 2.5. Pointer years and relative growth changes

Standardized tree-ring data were used for computing pointer years and relative growth changes. Pointer years were calculated to identify years with exceptional positive or negative growth responses. In general, various alternative methods are used for the calculation of pointer years (Jeschke et al., 2019; Buras et al., 2020), which result in different detection rates (i.e. in their thresholds for accepting a year as a pointer year). We analyzed tree-ring width in a given year  $i$  relative to the mean increment in the last 5 years prior to year  $i$  following the concept of abrupt growth changes of Schweingruber et al. (1990), which has been integrated into the approach of van der Maaten-Theunissen et al. (2015). These values were calculated separately for each tree individual and then averaged year-wise for all trees of a chronology. A year  $i$  was considered a pointer year when this mean value representing the standardized increment of all trees of the chronology in a given year  $i$  was more than 25% larger or smaller than the growth mean of the preceding 5 years in the mean curve of the chronology.

The relative growth (Jeschke et al., 2019) in a given year  $i$  was related to the growth in the preceding year  $i-1$  according to the expression:

$$\text{Relative growth change (\%)} = \left( \frac{\text{Growth in year}_i - \text{Growth in year}_{i-1}}{\text{Growth in year}_{i-1}} \right) \times 100$$

These analyses were done for all pointer years occurring simultaneously in dead and live trees; if trees reacted on a weather extreme in two consecutive years, only the first pointer year was considered.

## 2.6. Superposed epoch analysis

Superposed epoch analysis (SEA) was applied to examine whether droughts had the largest negative effect on growth in the same year or in subsequent years. SEA calculates the mean departure in growth performance of each year in the epoch (i.e. the drought year and subsequent years) from the mean of all analyzed epochs per chronology (Rao et al., 2019). Bootstrapping (1000-times) against randomly drawn epochs from the respective chronology was used for defining 95% confidence intervals of the departure. SEAs were calculated with the R package dplR for all spring and summer seasons for the drought year and the three subsequent years (mean of SPEI3 from March to August) with a meteorological drought, defined by SPEI values <-1. Spring droughts were included from the years 1938, 1942, 1953, 1959, 1963, 1971, 1974, 1991, 1996, 2011, 2012, and 2014, while summer droughts were from 1947, 1959, 1964, 1976, 1989, 1990, 2003, 2010, and 2015.

## 2.7. Growth resistance, resilience and recovery

Since SEA yielded the result that summer droughts reduced radial stem growth for 2 years after the drought (Ch. 3.3.), growth resilience ( $R_s$ ) was defined as the ratio of the standardized mean ring width in the 2 years after the drought ( $PostDr$ ) to the 2 years before the drought ( $PreDr$ ) ( $R_s = PostDr/PreDr$ ), resistance ( $R_t$ ) as the ring width in the drought year ( $Dr$ ) relative to the mean ring width in the 2 years before the drought ( $R_t = Dr/PreDr$ ), and recovery ( $R_c$ ) as the ratio of mean ring width in the 2 years after the drought relative to ring width in the drought year ( $R_c = PostDr/Dr$ ; Lloret et al., 2011). The selection of drought years for quantifying these indices was based on common negative pointer years in dead and live trees, marking either the drought year itself or the subsequent year, depending on the timing of the drought period.

## 2.8. Climate-response analysis

The R package treeclim 2.0.5.1 (Zang and Biondi, 2015) was used to examine correlations between tree-ring indices and monthly climate data. Climate data included in the analysis were mean temperature, precipitation sums, and SPEI3 values of the most relevant months (April to November in the previous year; April to August in the current year). The climate-response analysis was based on bootstrapped Pearson correlation analysis using moving windows of 10 years.

## 2.9. Statistical analyses

Arithmetic means and standard errors are given throughout the paper. We tested for normal distribution with the Shapiro-Wilk test and homoscedasticity with Fisher's  $F$ -test. The Mann-Whitney  $U$ -test was applied for pairwise comparisons of non-normally distributed data. The effect of tree vitality (live vs. dead) in the year of sampling and of different time periods on growth performance was analyzed with the Friedman test for data that were not normally distributed. For pairwise comparisons, we used the  $t$ -test (normally distributed data; Student's/ $t$ -test in case of equal/unequal variances) or the Mann-Whitney  $U$ -test (non-normally distributed data). Statistical testing was done with SAS 9.4 software.

## 3. Results

### 3.1. Mortality patterns

Most of the 57 sampled dead trees (91%) died after 2004 with mortality peaks observed in the relatively dry year 2011 (SPEI = -1.3),

but also in the moister years 2012-14 with SPEI -0.2 – -0.6 (Fig. S4). Death usually did not occur in a particular drought year, as inferred from the missing relation of tree mortality to the March-August SPEI of the respective year (Fig. S2).

Individual ring series from dead trees showed that the growth patterns prior to death were quite variable between different deceased tree individuals (Fig. 1). About 85% of the dead trees suffered decadal or multi-decadal growth reductions before death; examples of typical growth trajectories are compiled in Fig. 1b-f. In contrast, roughly 15% of the trees lacked any peculiarities in annual stem increment patterns before death. As shown for the tree in Fig. 1a, stem increment repeatedly passed through marked growth depressions due to previous droughts (e.g. in 1948, 1960, 1976, 1989, 1996, 2004), but growth always resumed rapidly. The tree suddenly died after the multi-annual drought starting in 2010 (Fig. S4) which caused a marked ring width reduction.

### 3.2. Growth history of the live and dead tree groups

The dead trees sampled in 2015 differed from the live trees by slightly higher age, tree height, and stem diameter (differences significant, Table 1). The Hegyi competition index showed lower values in the dead tree group (Table 1), suggesting that the trees have not died from inferior competitive ability.

For more than 100 years, the dead trees had a more than 10% greater annual ring width than the live trees (difference significant; Table 1). This difference disappeared after the severe 1976 drought, and the surviving trees showed after 2003 a slightly superior growth (Fig. 2). While inter-annual ring width variation of both the live and dead trees was only moderate until about 1945, variation greatly increased after the severe 1947 drought and intensive logging in these years, resulting in both more extreme low (e.g. in 1948, 1953, 1956, 1960, 1970, 1976), but also high, annual growth rates (e.g. 1951, 1955, 1958, 1967). This variation was greater in the dead than the live tree group. In the severe drought year 1976, tree-ring width was strongly reduced (similar to that in 1948), but it did not recover to the pre-drought level as had happened after 1947 (Fig. 2). Ring width and basal area increment more or less continuously declined from 1980 till very low values in the early 2000s (Fig. 2a and c), when mortality rate greatly increased in the dead tree group (Table 1).

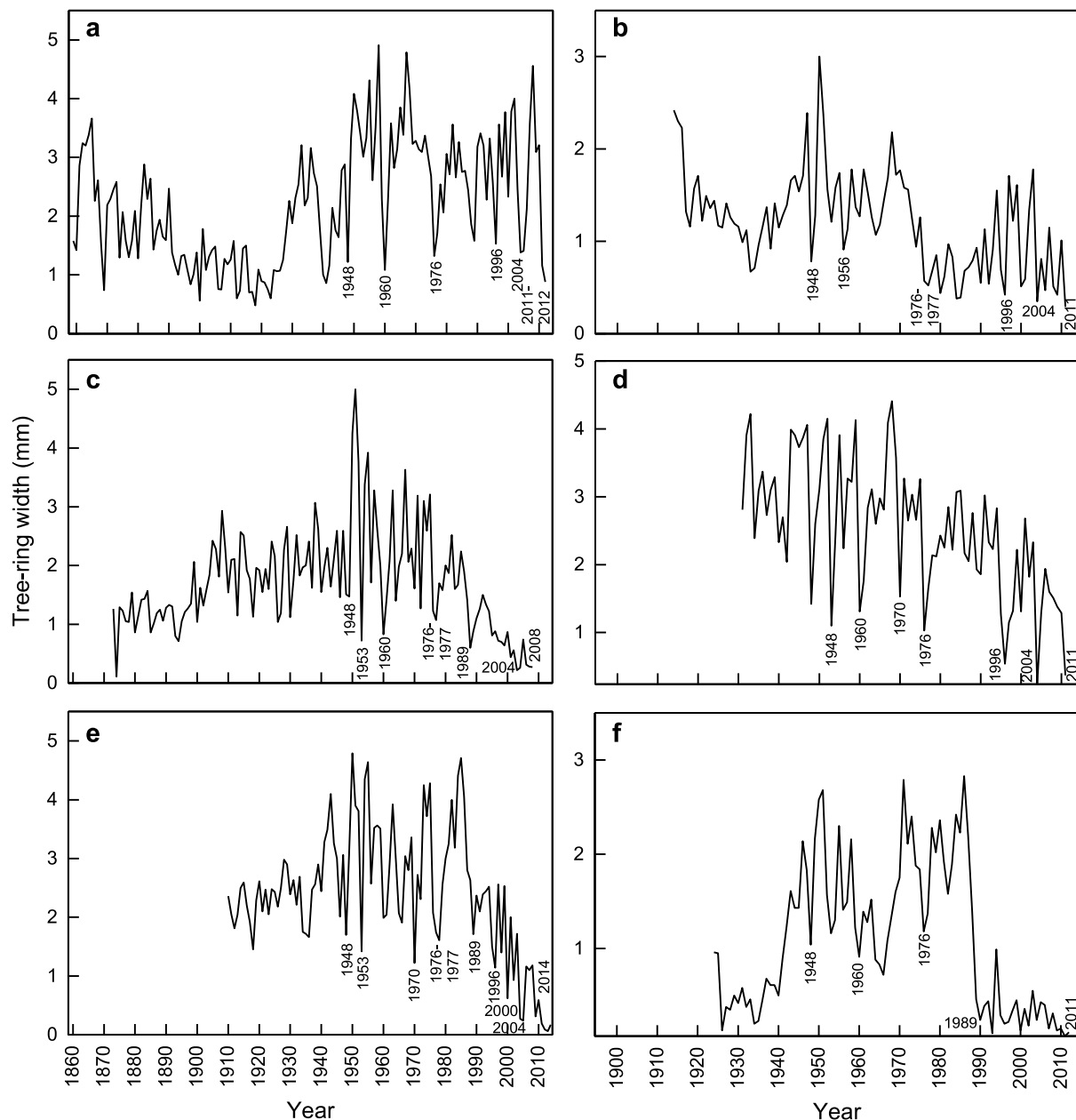
### 3.3. Depression and stimulation of growth and the potential for recovery

Pointer-year frequency increased after 1947 and this increase was greater in the dead than the live trees, boosting the number of pointer years per decade by a factor of 2.8 or 1.8, respectively (Fig. S5). Most negative pointer years were related to drought in the previous year (e.g. 2003) or in two consecutive dry years (1976, 2011; Table 2). Only in 1953 and 2000, negative pointer years were attributable to dry early-growing seasons of the current year (March to May in 1953 and June in 2000). This matches the SEA results, which show growth depressions after a summer drought usually in the two subsequent years, but a growth reduction in the same year only, when the drought occurred in spring (Fig. 3a, b).

The dead tree group responded to drought on average with a greater growth depression than the live tree group ( $-36.7 \pm 11.1\%$  vs.  $-27.8 \pm 8.4\%$  reduction in 11 negative pointer years, Fig. 4a). Correspondingly, the growth increase in response to favorable climatic conditions or competition release showed a trend for higher values in the dead tree group than the live trees ( $70.8 \pm 18.3\%$  vs.  $50.2 \pm 13.0\%$  increase in 15 events), but this difference was not significant ( $P \leq 0.05$ , Friedman test; Fig. 4b). Neither growth resilience to drought ( $0.94 \pm 0.06$  vs.  $1.00 \pm 0.03$ ) nor resistance ( $0.58 \pm 0.03$  vs.  $0.64 \pm 0.03$ ) or recovery ( $2.47 \pm 0.39$  vs.  $2.05 \pm 0.15$ ) differed significantly between the dead and live tree groups (Fig. 5).

Positive pointer years indicating growth releases due to favorable moisture conditions or reductions in stand density were even more





**Fig. 1.** Example chronologies of six beech trees that died between 2008 and 2014 and are representative for different growth trajectories in the studied population: (a) sudden death in 2012 without preceding long-term declining growth trend; (b) reduced growth after 1976, transient recovery from the 1990s till 2003, growth decline since 2003, death in 2011; (c) progressing growth decline since 1976, death in 2008; (d) pronounced negative growth departures since 1976 in or after drought years (1996, 2004), death in 2011; (e) progressing growth decline since 1989, death in 2014; (f) sudden persistent growth reduction in 1989, death in 2011.

frequent than negative pointer years caused by drought (Fig. S5). A series of three consecutive positive pointer years occurred from 1950–1952, likely as the result of reduced competition due to selective logging in the late 1940s, as weather conditions were not particularly favorable in these summers (Table 3). Positive pointer years were also observed in 1997, 2007, 2013, and 2015. However, these growth releases related to spontaneous reductions in stem density due to increased tree mortality, with the proximate cause being frequent fungal infections by *Fomes fomentarius* from 1997 onwards and subsequent stem breakage in many large-diameter trees.

### 3.4. Differences between live and dead trees in the climate response of growth

Linear regression of standardized annual ring-width on monthly

mean temperature and monthly precipitation for the whole data set from 1938–2015 exhibited positive correlations with previous year's June to September precipitation and SPEI as well as negative correlation with previous year's July and August and current year's April and July temperature (Fig. S6). Dividing the chronologies into the periods prior to and since 1948 showed that these correlations appeared only after the late 1940s (Fig. S6). The analysis of consecutive 10-year-intervals in the period 1938–2015 indicated a growing summer drought influence on growth over time (Fig. 6). From 1985 onwards, the ring index increased with increasing July precipitation of the previous year both for the live and dead tree group, an effect that was weaker or indifferent in the period before 1985. Furthermore, the negative correlation of growth to previous year's July temperature became more pronounced after 1975.

Trees that were dead at the time of sampling revealed a greater sensitivity to hot summers, visible in this group in a continuous negative

**Table 1**

Descriptive statistical parameters for the tree-ring chronologies from the live and dead beech trees. Arithmetic means  $\pm$  standard error over all years and all trees of a group.

	Dead trees	Live trees	$P^a$
Number of sample trees	57	200	
Mean cambial tree age (years) <sup>b</sup>	159 $\pm$ 2	149 $\pm$ 2	0.01
Mean diameter at breast height (cm)	57 $\pm$ 2	50 $\pm$ 1	0.006
Mean tree height (m)	32.1 $\pm$ 0.6	29.8 $\pm$ 0.4	0.02
Mean Hegyi index	0.44 $\pm$ 0.03	0.60 $\pm$ 0.03	0.01
Tree-ring width, mean (mm)	1.64 $\pm$ 0.07	1.49 $\pm$ 0.03	0.009
Tree-ring width, 1918 – 1947 (mm)	1.86 $\pm$ 0.05	1.55 $\pm$ 0.04	<0.001
Tree-ring width, 1948 – 1976 (mm)	2.08 $\pm$ 0.09	1.84 $\pm$ 0.07	0.02
Tree-ring width, 1977 – 2006 (mm)	1.27 $\pm$ 0.06	1.26 $\pm$ 0.05	n.s.
Standard deviation of tree-ring width	0.77 $\pm$ 0.03	0.73 $\pm$ 0.01	(0.07)
Mean sensitivity (%)	36.6 $\pm$ 1.0	35.0 $\pm$ 0.4	n.s.
First-order autocorrelation	0.56 $\pm$ 0.02	0.64 $\pm$ 0.01	0.001
Synchronicity (Pearson's $r$ )	0.52 $\pm$ 0.02	0.52 $\pm$ 0.01	n.s.
First derivative of ring width (mm yr <sup>-1</sup> )	-2.07 $\pm$ 0.27	-1.05 $\pm$ 0.07	<0.001
Absolute values of first derivative (mm yr <sup>-1</sup> )	52.0 $\pm$ 2.0	45.3 $\pm$ 0.8	<0.001
Standard deviation of first derivative	69.6 $\pm$ 2.6	60.9 $\pm$ 1.0	<0.001
Residuals of first derivative <sup>c</sup>	33.9 $\pm$ 2.2	25.8 $\pm$ 1.7	0.007

<sup>a</sup> Level of significance ( $P \leq 0.05$ , Mann-Whitney  $U$ -test); n.s., not significant

<sup>b</sup> Tree age at the year of sampling (2015, live trees) or tree death (dead trees)

<sup>c</sup> Residuals calculated from the derivatives of mean chronologies

correlation of growth to previous-year July temperature in the period 1975–2014. In contrast, this negative effect became significant in the live trees only in the period from 1975–1984 and disappeared thereafter. A negative influence of previous summer's drought on tree-ring formation was further indicated by a positive correlation of the July and August SPEI with the ring index in both live and dead trees. A year-wise shifting moving-window analysis confirmed that the radial growth of the dead trees was nearly continuously correlated with previous year's July SPEI since 1948; this relation became visible in the live tree group only  $\sim$ 15–20 years later (Figs. S7, S8).

### 3.5. The first derivative of the ring-width curve as a tool for detecting legacy effects

Inter-annual ring width variation in the 1948–1976 period was greater in the dead tree group than the live tree group, resulting in higher positive and lower negative growth extremes (Fig. 2). However, the greater variance was reflected neither in a significantly higher standard deviation of ring width in the dead trees (Table 1), nor in a greater mean sensitivity or reduced synchronicity of growth in this tree group (Fig. 7). Yet, mean first-order autocorrelation was higher in the live than the dead trees, indicating a greater moderating influence of previous year's growth on stem wood formation in the surviving trees (Table 1), but this difference became insignificant, when the decadal variation of first-order autocorrelation was analyzed (Fig. 7d). More informative was the mean value of the first derivative of the ring width curve, which reached significantly higher values ( $P < 0.001$ ,  $U$ -test) in the dead tree group (Table 1), indicating a steeper mean slope of the ring-width curve (Figs. 7 and 8). All measures of inter-annual ring width variability (standard deviation, the first derivative of the chronology and its residuals to the mean) exhibited relatively high values in the period 1948–1976 after the 1948 event, compared to much lower values in the decades before (Fig. 7).

## 4. Discussion

### 4.1. Chronology of growth decline and the role of droughts

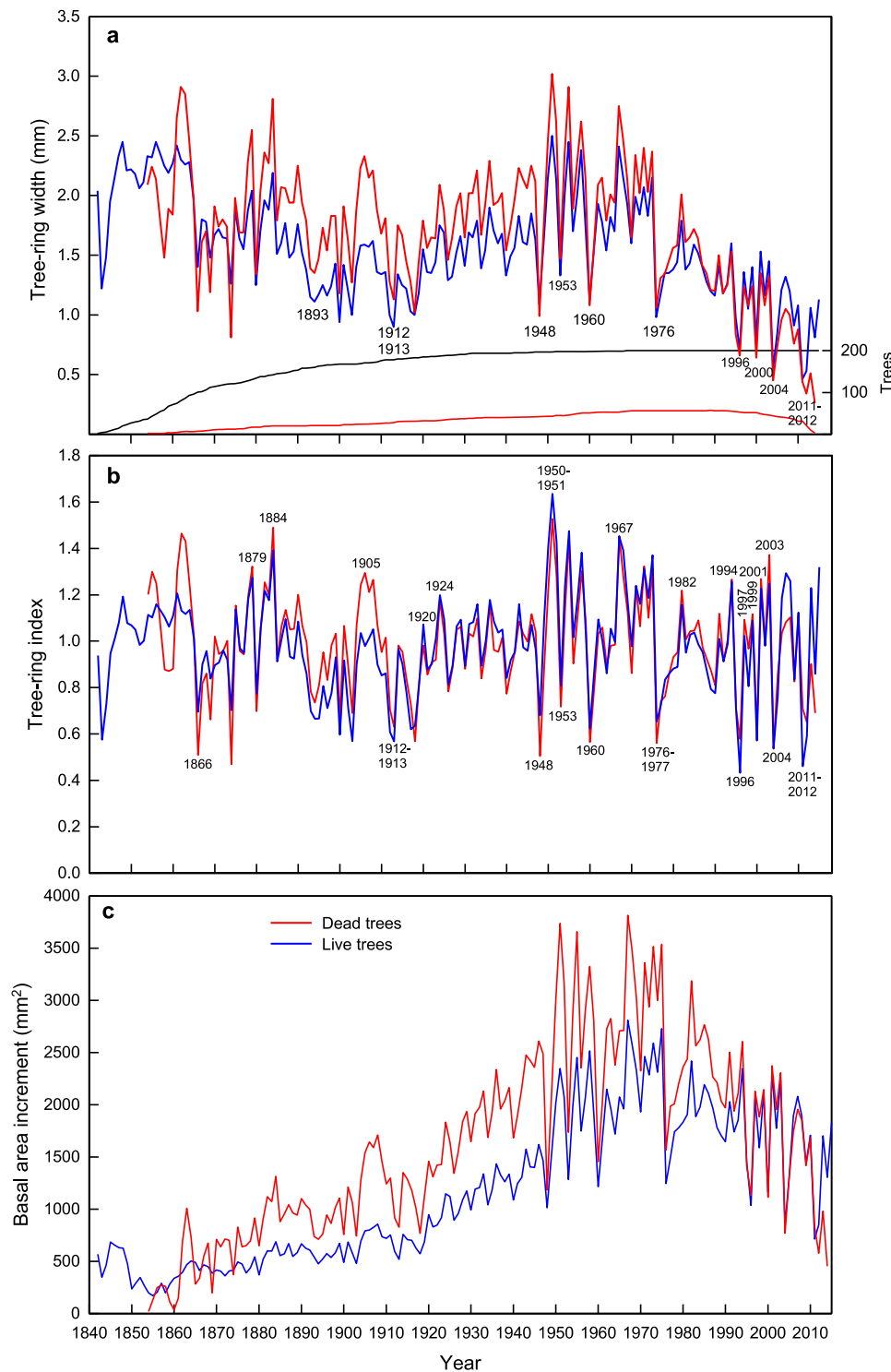
A key result of this analysis of recent dieback in a submontane beech forest is that death was preceded by decade-long growth decline in most

trees (hypothesis 2), as it has been observed in other temperate hardwood trees before (Cailleret et al., 2017). While the bulk of trees showed continued growth reductions after the severe 1976 drought, the same trees responded to the earlier, similarly severe 1947 drought only with transient growth reduction but increased growth variability. Since most trees have established between 1840 and 1860, the beeches had ages of about 100 or 125 years, when they were hit by the 1947 and 1976 events, respectively. Given that European beech trees grow in forest reserves well to 400 or even 500 years (Piovesan et al., 2003; Hobi et al., 2015), it is unlikely that the trees have died as a result of a natural senescence process. We can also exclude that asymmetric competition was a main cause of the high mortality, as has been reported e.g. by Becker et al. (1989) and Linares et al. (2009), because the dead trees were slightly larger than the surviving ones and were not suppressed by their neighbors according to the Hegyi index (hypothesis 1). This indicates that a few severe drought events must have played a key role, apparently in combination with abrupt harvest-related alterations in stand structure. Unexpected in the light of the current tree mortality debate is that the growth trend of the dead trees shifted from positive to negative already 40 years ago, and growth variability changed from moderate to high inter-annual variation already 65 years ago, which supports our hypothesis (2).

Both the 1947 and the 1976 drought episodes belong to the most extreme droughts and heat waves that hit Central Europe in the 20<sup>th</sup> century (Hanel et al., 2018). Both have strongly imprinted for many decades on the radial growth characteristics of the studied trees, suggesting that they have triggered the growth decline, as other triggers are not known from the well-documented disturbance history. The marked increase in inter-annual growth variation after 1947, more pronounced negative pointer years, the steeper ring width and BAI decline from the 1970s to the 2010s, and the greater sensitivity to previous year's July temperature in the dead tree group as compared to the live trees supports the assumption that the 1947 and 1976 droughts play a key role not only for the decade-long growth decline but also for the eventual mortality peak in the dead tree group.

While the immediate damage caused by the 1947 and 1976 droughts was not precisely recorded in our stands, it was in other European beech stands (e.g. Peterken and Mountford, 1996), demonstrating the exceptional severity of these past drought events. Our data show that these droughts in addition had a long-term after-effect on the surviving trees, visible in higher growth variation, a long-term negative growth trend and eventually increased mortality even after six decades.

Important information on the possible causes of tree death is also provided by a comparison of the growth rates of the dead and live tree populations in the distant past. The dead group had an on average 10% higher growth rate in the first half of the 20<sup>th</sup> century than the live tree group, i.e. faster growth was in this group associated with higher mortality in the consequence of the severe droughts of 1947, 1976 and afterwards. This finding is in line with the 'grow fast – die young' principle in biology and matches results from another dendroecological study on two conifer species that prove a negative association between radial growth rate and tree longevity (Voltas et al., 2013; Büntgen et al., 2019). Our analysis of short-term ring width variation further demonstrates a greater temporal fluctuation of growth rate in the faster growing, but earlier dying trees. With a slightly higher age, diameter and height, the population of dead trees probably occupied the uppermost canopy layer in the stand and thus was exposed to a greater atmospheric evaporative demand, likely causing higher water consumption than in the surviving trees. This should have increased the drought exposure of these trees. A greater mortality of these somewhat larger trees fits well to theoretical and empirical work that indicates an increased mortality risk of larger trees under drought stress (Fuentes et al., 2010; Sevanto et al., 2014; Stovall et al., 2019). It is also in agreement with Peterken & Mountford (1996), who found low growth resilience and delayed mortality in particular in large beech trees (dbh >15 cm) after the 1976 drought in England. However, the opposite has also been observed, i.e. a higher



**Fig. 2.** Tree-ring chronologies showing (a) mean tree-ring width, (b) mean tree-ring index values and (c) basal area increment of the dead and live beech tree samples. Dates in the upper panel (a) mark selected years with low growth extremes due to drought (according to Table S3 after 1947 or [Bonnemann 1984](#) for early droughts), dates in panel (b) mark common negative and positive pointer years of the dead and live tree samples.  $\text{EPS} \geq 0.85$  since 1861 (live trees) and 1865 (dead trees).

drought mortality risk of smaller trees, if access to water in deep soil layers is critical for survival ([Colangelo et al., 2017](#)).

#### 4.2. Possible causes of mortality

We can only speculate about the mechanisms that reduced the vitality of both the dead and live tree populations during and after the

1976 drought and caused continuous growth decline thereafter. Nevertheless, exploring the growth history of live and dead trees as done here can provide valuable information on vitality changes in the past, that may allow excluding some possible physiological mechanisms known to weaken tree health and to cause death. While it is undisputed that extreme drought events in combination with heat can lead to hydraulic failure in mature beech trees and cause partial or full canopy

**Table 2**

Meteorological events related to negative pointer years in the period 1947 to 2015.

Pointer year	Source <sup>a</sup>	Explanation <sup>b</sup>
1948	Prev.	Drought in 1947 (Jul., Aug., Sep., Oct.)
1953	Pres.	Drought in 1953 (Mar., Apr., May)
1956 <sup>c</sup>	Prev.	Dry fall in 1955 (Nov.)
1960	Prev.	Drought in 1959 (Mar. to Sep.)
1970 <sup>c</sup>	Prev./ Pres.	Dry winter (Nov., Dec. 1969, Jan. 1970)
1976	Prev./ Pres.	Drought in 1975 (Aug. to Sep.) and 1976 (Apr. to Sep.)
1977	Prev.	After-effect of 1976 drought despite wet year in 1977
1995 <sup>c</sup>	Prev.	Drought in 1994 (Jul., Aug.)
1996	Prev./ Pres.	Drought in 1995 (Aug., Dec.) and 1996 (Jan. to May)
2000 <sup>c</sup>	Pres.	Drought in 2000 (June)
2004	Prev.	Drought in 2003 (Apr. to Sep.)
2011	Prev./ Pres.	Drought in 2010 (Jun., Jul.) and 2011 (Mar. to Jul.)
2012	Prev.	Drought in 2011 (Mar. to Jul., Nov.) and early 2012 (Apr., May)

<sup>a</sup> Pointer year caused by meteorological event in previous (Prev.) or present (Pres.) year

<sup>b</sup> Specifications of dry months refer to low SPEI values

<sup>c</sup> Pointer year occurred only in dead trees

dieback, as it likely occurred in some Central European beech stands during the exceptionally hot and dry 2018/19 episode (Leuschner, 2020; Schuldt et al., 2020; Walthert et al., 2021), it becomes increasingly clear that the majority of recent cases of beech dieback can only be understood, when triggering events in the more distant past are also considered. That death often happens only after decades of low radial growth, has also been found in other Central European beech forests (Wunder et al., 2007; Gillner et al., 2013), suggesting that the factors predisposing the trees to death in the distant past may be critically important for forest health, in addition to the immediate causes of death, which are more in the focus of the recent debate.

Our findings provide some evidence for the assumption that a single (or two) severe drought (or logging) events 40 or even 65 years ago are sufficient to set a mature beech tree to a decade-long path to death. It appears that highly shade-tolerant European beech is sensitive to stand opening, in contrast to more light-demanding tree species, where stand health may profit from reduced stem density after logging or drought mortality, as competition for water is reduced among the remaining trees (Fernández-de-Uña et al., 2015; del Río et al., 2017; Lechuga et al., 2017). The fact that the 1947 event triggered a marked increase in inter-annual growth variability in combination with an initial increase in growth rate, excludes a lasting effect of hydraulic failure and carbon starvation in the trees that survived this severe drought. Why was the inter-annual growth variation increase greater in the faster-growing death-prone tree population? We assume that stand opening in the late 1940s, likely caused by immediate drought mortality and thinning, has increased the availability of light (and water) in the stand with the consequence that trees released from competition enlarged their leaf area, especially the already larger individuals of the death-prone tree group. Yet, drought vulnerability generally increases with tree size (McDowell and Allen, 2015). Larger leaf areas may increase the drought exposure in dry years also through 'structural overshoot' (Jump et al., 2017), which should have affected the faster-growing, death-prone tree population to a greater extent. This is supported by the greater increase in short-term growth variability in this group after 1947 (shown in the first derivative of ring width in Fig. 7f) as compared to the live tree population.

Interestingly, the severe 1976 drought, amplified by the hot and dry summer in 1975, obviously has had a different effect on tree vitality compared to the 1947 drought. After 1976, inter-annual growth

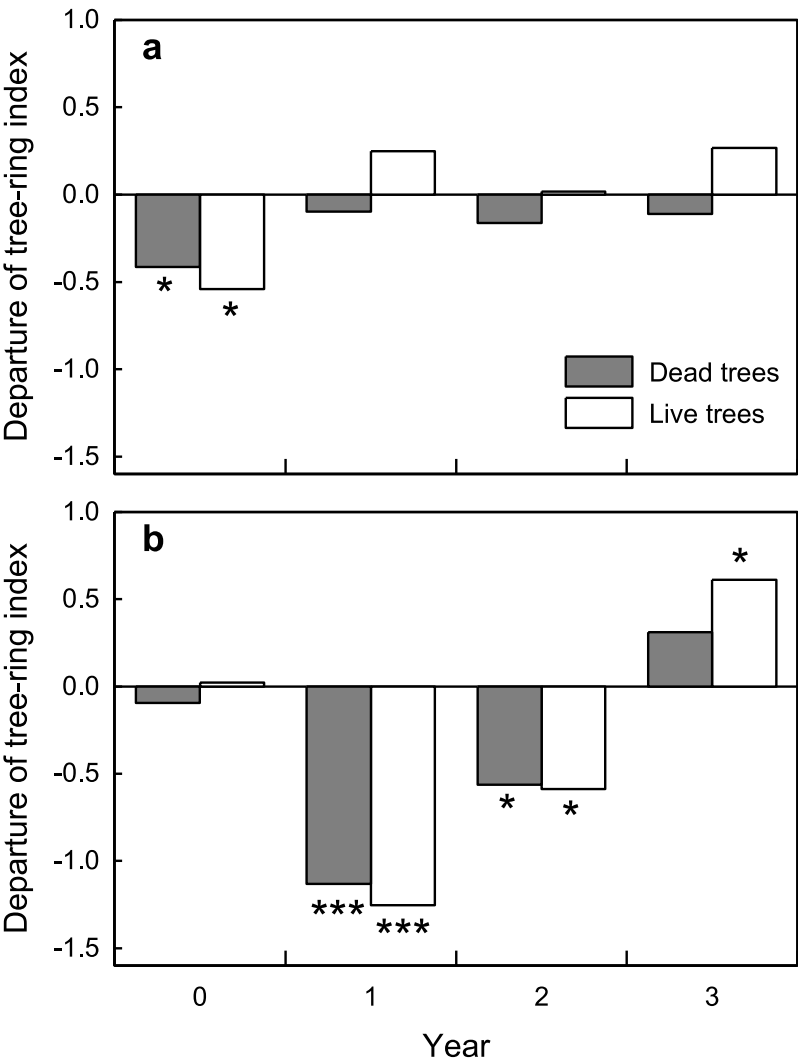
variability increased as after 1947, whereas average growth rate continuously declined in the decades following 1976. Clearly, the growth-promoting effect of thinning was absent in this event (apart from a few trees thrown in a storm in 1976; Meyer et al., 2015). Yet, the tree group with faster growth and higher inter-annual growth variability experienced in consequence of the logging event a steeper growth decline and eventually suffered death 15 to 28 years later. It is likely that advancing climate aridification since around 1975 has contributed to the recent growth decline, visible in a significant sensitivity of growth to summer precipitation (positive correlations) and to previous year's summer temperature (negative correlations) since 1975, which was absent before.

Some physiological mechanisms can be excluded in the explanation of the trees' response to the 1947 and 1976 droughts, notably critical hydraulic failure or carbon starvation that should have killed the trees within a few years. Yet, non-lethal hydraulic failure in branch and petiole conduits of certain crown sections and in part of the fine root system is possible, which could have permanently impaired the efficiency of the hydraulic system and the photosynthetic capacity of the crown (Schuldt et al., 2020). Nevertheless, most trees partially recovered from the 1976 drought, promoted by the moist period from 1978 to 1981, suggesting that any putative damage to the hydraulic system or foliage area has at least partly been repaired (Brodersen & McElrone, 2013). Yet, the legacy of the drought and heavy logging in the late 1940s and the 1976 drought apparently have hindered the trees to achieve full vitality again, as is indicated by the poor recovery after subsequent drought events, such as the multi-annual droughts in 1995/96 and 2011/12, and the dry summers of 2000 and 2003. We speculate that the faster growing, dead-prone tree group might have exhausted its potential for damage repair in the hydraulic system, root system or canopy and pathogen defense earlier than the live tree group. This could have favored infection by pathogenic fungi such as *Fomes fomentarius* and *Phytophthora* and *Nectria* species which is an important proximate cause of beech death in trees weakened by preceding drought events (Leak, 2006; Jung, 2009). Yet, drought-induced damage by pathogens or herbivores is of lower significance for tree mortality in *F. sylvatica* than in most temperate and boreal conifers (e.g. *Picea abies*, Netherer et al., 2021).

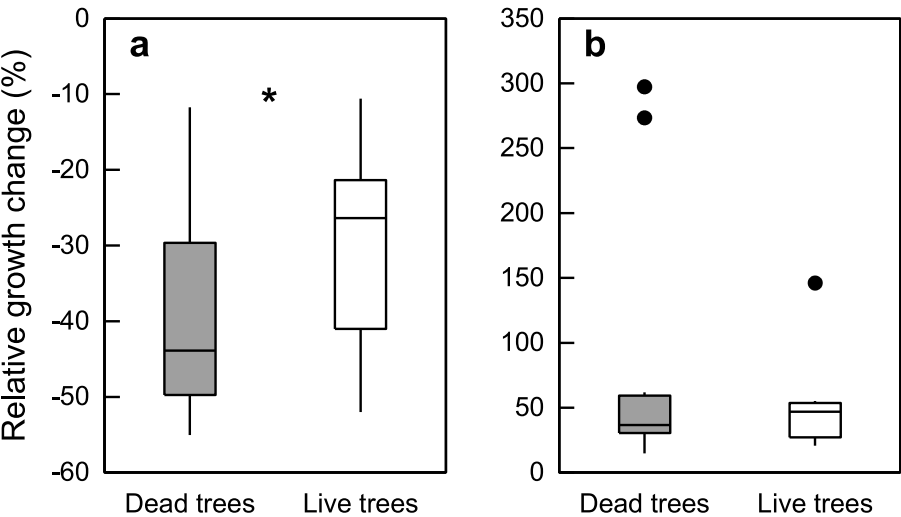
#### 4.3. The possible impact of logging

Some evidence suggests that heavy logging in the late 1940s has contributed to the subsequent vitality decline in this stand (hypothesis 3). After the expected growth depression in 1948, the year following the drought, beech growth reached high increment rates for three consecutive years (2-3 positive pointer years in sequence in 1950-52), even though climatic conditions were near to average. This makes it likely that the growth of the remaining trees was promoted by competitive release, which increased the average radial growth rate for more than two decades by about 10-20% and enabled in favorable years higher growth rates than have been observed in any year between 1880 and 1947. That not only negative, but also positive, pointer years have increased in frequency after 1947, makes it very likely that the thinning in the late 1940s has significantly contributed to the sudden change in growth patterns from 1950 onwards. Growth release after thinning is an intended silvicultural measure and well documented in dendrochronological studies on beech and other species (Pretzsch 2019). More recently, it has been found in *F. sylvatica* stands that heavy thinning can reduce tree vitality and cause negative growth trends in the remaining trees, likely enhanced by climate aridification, as observed in Slovakian beech forests, while unthinned stands showed growth increases (Bosala et al. 2016). A matching observation on the negative impact of historical logging on tree health has been made in *Abies alba* forests of the Pyrenees (Camarero et al. 2011). Analyzing forest inventory data of *F. sylvatica* forests from central Germany, Meyer et al. (2022) found a shift of tree mortality from suppressed to large tree individuals in response to the

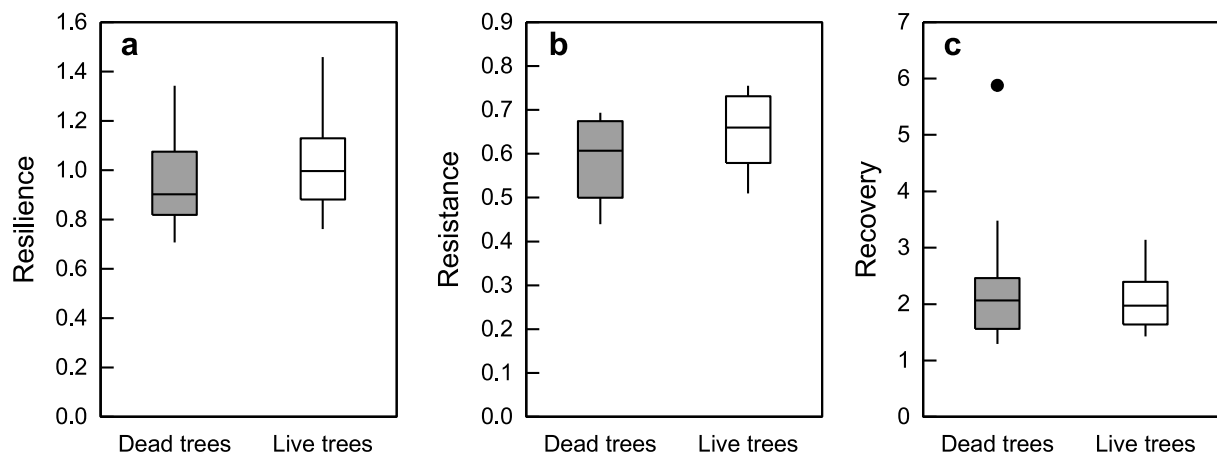




**Fig. 3.** Results of superposed epoch analysis (SEA) of the tree-ring index in drought seasons marked by SPEI3 values <-1 (1936–2015) for (a) spring droughts and (b) summer droughts (\* $P\leq0.05$ , \*\*\* $P\leq0.001$ ). Averaged over all selected drought events.



**Fig. 4.** Average growth changes in negative and positive pointer years relative to the annual stem increment in the previous year in dead trees and live trees: (a) negative pointer years (dry years) ( $N=10$  years), (b) positive pointer years (wet years) ( $N=13$  years). Data include only years in the 1936–2015 period when both dead and live trees exhibited pointer years; in case of two consecutive pointer years, only the first one was included. A significant difference between dead and live trees is indicated by an asterisk (Friedman test,  $P\leq0.05$ ). Dots represent far outside values.



**Fig. 5.** (a) Resilience, (b) resistance, and (c) recovery of annual radial stem increment in response to drought in the dead and live tree groups. Responses averaged over all negative pointer years occurring simultaneously in dead and live trees. No significant differences between dead and live trees ( $t$ -test,  $P \leq 0.05$ ). Dots represent far outside values.

**Table 3**

Meteorological events and changes in stand density due to anthropogenic or natural causes related to positive pointer years in the period 1947 to 2015.

Pointer year	Source <sup>a</sup>	Explanation <sup>b</sup>
1950 – 1951	Thinning	Intense selective logging in the late 1940s; positive pointer year in 1950 occurred despite dry Aug. and Sept. in 1949
1952 <sup>c</sup>	Thinning	Intense selective logging in the late 1940s
1955 <sup>c</sup>	Prev.	Wet phase in 1954 (Jul. to Nov.)
1958	Prev./ Pres.	Wet phase in 1957 (Sep. to Nov.) and 1958 (May to Aug.)
1967	Prev./ Pres.	Wet phase in the growing season of 1966 (Apr. to Aug.) in the winter of 1966/67 (Dec. to Feb.) and in the growing season of 1967 (May, Jun.)
1973 <sup>c</sup>	Prev.	Wet phase in 1972 (Jun. to Aug.), despite dry winter and early spring of 1973 (Dec. to Mar); windthrow due to heavy storm in Nov. 1973
1975 <sup>d</sup>	Prev./ Pres.	Wet winter 1974/75 (Dec. to Feb.)
1981 <sup>c</sup>	Prev./ Pres.	Wet phase in 1980 (Jun. to Sep.) and 1981 (Mar. to Aug.)
1982	Prev./ Pres.	Wet phase in summer 1981 (Mar. to Aug.) and autumn/winter 1981/82 (Oct. to Jan.)
1994	Prev./ Pres.	Wet phase in winter 1993/94 and spring 1994 (Dec. to May)
1997	Thinning	Reduction of stand density due to increased tree mortality (breakage of large-diameter stems, fungal infections by <i>Fomes fomentarius</i> )
1999	Prev.	Wet phase in fall and winter 1998 (Sep. to Dec.)
2001	Pres.	Wet phase in spring 2001 (Apr.)
2003	Prev./ Pres.	Wet winter 2002/03 (Nov. to Jan.); positive pointer year despite the strong drought of the summer 2003
2007 <sup>d</sup>	Thinning	Reduced stand density resulting from extensive windthrow and breakage due to cyclone Kyrill on 18 Jan. 2007
2013 <sup>d</sup>	Thinning	Reduced stand density from increased tree mortality
2015 <sup>d</sup>	Thinning	Reduced stand density from increased tree mortality

<sup>a</sup> Pointer year caused by meteorological event in previous (Prev.) or present (Pres.) year or thinning of the stand

<sup>b</sup> Specifications of wet months refers to high SPEI values

<sup>c</sup> Pointer year occurred only in dead trees

<sup>d</sup> Pointer year occurred only in live trees

2018/19 drought, which is also consistent with our results.

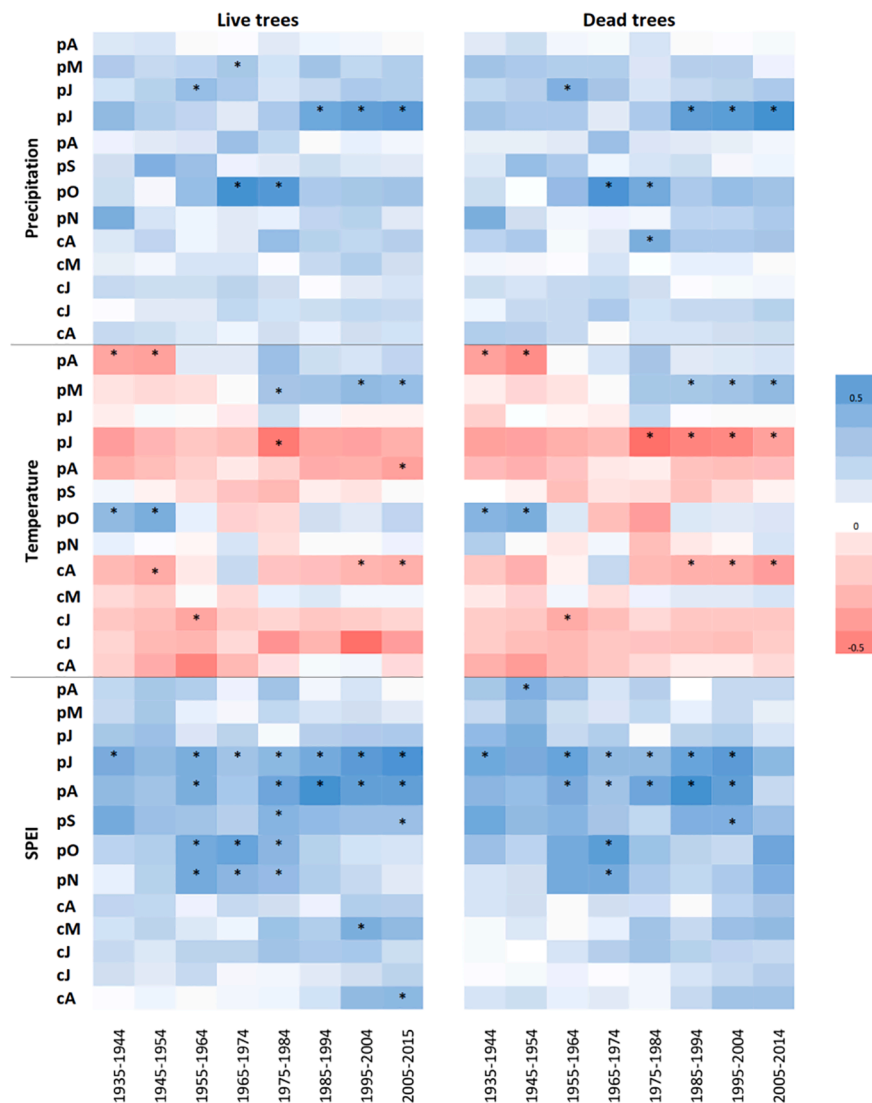
The heavy thinning in the late 1940s may well have increased the drought stress in our stand, especially of the faster growing larger trees, through a shift in growth strategy from a slower, risk-avoidance strategy to a faster and riskier canopy-expansion strategy. This contradicts an earlier dendrochronological study, which assumed a positive effect of

thinning on the drought tolerance of beech (Diaconu et al., 2017). The finding of that study may be explained by the fact that the authors investigated the short-term drought response (4 years), while Bosala et al. (2016) and we analyzed the long-term consequences of thinning. Our study thus suggests that the short-term growth resistance and resilience in response to a drought is not a suitable predictor of the mortality risk of beech in the long-term.

#### 4.4. Measuring short-term growth variation as an indicator of mortality risk

An interesting result is that the increased inter-annual ring width variability after the two severe droughts, in combination with stand thinning, did not only amplify growth minima, but also maxima, since the late 1940s. Intuitively, one would interpret growth bursts after drought-induced growth depressions as a sign of vigor and rapid and complete recovery (Lloret et al., 2011; Trouvé et al., 2017). Our finding that beech trees with more extreme negative and also positive ring width extremes are more vulnerable to eventual drought mortality, questions this view. Rather, the large inter-annual variation in ring width might reflect a temporal mismatch of resource allocation to foliage, hydraulic system and roots, probably caused by rapidly changing light and soil moisture conditions in the tree's direct vicinity, as an indication of increased stress.

The long time lag between likely predisposing events (1947 and 1976) and eventual mortality of up to 65 years, together with the diversity of individual growth trajectories, explains, why it has been difficult to derive simple mathematical expressions from tree-ring data, which can serve as early-warning signals of mortality (Camarero et al., 2015; Cailleret et al., 2017, 2019). We examined a broad set of descriptive parameters related to the tree-ring data, but several of them, albeit being well established, did not capture the higher variance in the annual stem increment of the dying trees. Mean sensitivity, synchronicity between individual tree-ring series as well as growth resilience, resistance and recovery to and after drought events did not differ significantly between dying and surviving trees and were, thus, not suited to identify trees with elevated mortality risk in our study. In our sample trees, mean sensitivity increased since the 1976 drought in both live and dead trees, which renders this parameter an unsuitable predictor of tree mortality, even though high mean sensitivity and drought stress have repeatedly been linked (Eilmann and Rigling, 2012; Navarro-Cerrillo et al., 2018). Further, mean sensitivity is known to increase also with tree age (Carrer and Urbinati, 2004; Gilner et al., 2013), largely independent of vitality. First-order autocorrelation was higher in surviving than dying trees, reflecting the stronger growth extremes in



**Fig. 6.** Results of bootstrapped climate-response analysis for consecutive moving 10 year-windows from 1935–2014 analyzing linear correlations of the tree-ring index with monthly (April to November or April to August) mean temperature, precipitation, and SPEI of the year prior to and of the year of tree-ring formation (p, previous year; c, current year; \* $P \leq 0.05$ ). Shown is the size and direction of the correlation coefficient.

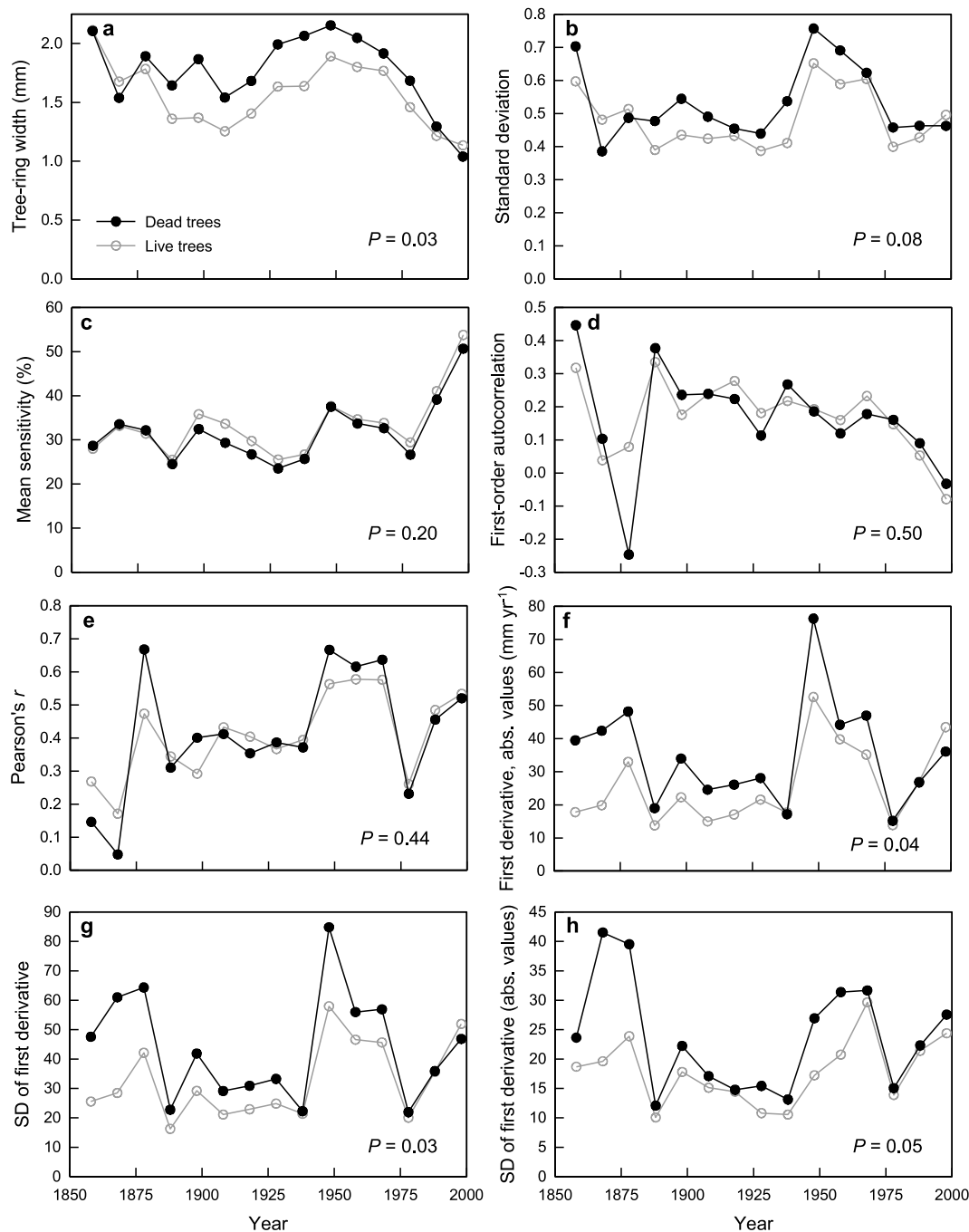
the latter group, but the relation of this parameter to the mortality risk was not close, in line with findings of [Cailleret et al. \(2019\)](#). Moreover, a significant difference did not occur, when the decadal variation of autocorrelation was analyzed. Growth resilience, recovery and resistance to individual droughts have been found in other studies to decrease prior to tree death ([Navarro-Cerrillo et al., 2018](#); [DeSoto et al., 2020](#)), but this is not supported by our data.

The most informative parameter for assessing the risk of mortality, which could be derived from the ring width data in our study, was the first derivative of the ring width series. Since the first derivative expresses the slope of each individual curve section, high inter-annual ups and downs (i.e. large high-frequency variation) in the ring series are clearly displayed in the curve of the first derivative, but are less influenced by the long-term (low-frequency) variability than e.g. the standard deviation of ring width. [Bigler and Bugmann \(2003, 2004\)](#) used linear regression of ring chronology sections of up to 40 years to quantify growth decline before death, but they did not employ the curve's slope systematically as a measure of growth variation. Given the principal differences in short-term ring width variability over time and between the live and dead tree groups, our results support the suggestion that this variability measure (and parameters describing its temporal variance such as the residuals of the first derivative or its standard

deviation) is a suitable tool for identifying trees with increased mortality risk. It is worth testing with other tree species and in other climatic regions, whether the first derivative of tree-ring width series can be used in a more general way as a reliable early-warning signal of tree mortality.

## 5. Conclusions

Our results suggest that severe droughts, probably exacerbated by heavy logging activities, may affect the drought tolerance of mature beech trees for as long as 40 years (1976 drought) or even 65 years (1947 drought and late-1940s logging), predisposing part of the population to eventual death. In our stand, tree death cannot be attributed to a single recent drought event alone, but the chronologies suggest that a many decades-old legacy has weakened the trees after the 1976 drought and reduced their potential to tolerate subsequent dry episodes including the 2003 event, which was followed by a wave of beech bark necrosis and tree dieback. We found evidence that abrupt stand opening due to heavy logging or high mortality (e.g. due to drought) is rendering the remaining beech trees more drought-vulnerable, despite immediate growth release due to reduced competition. In fact, faster radial growth was associated in our stand with higher growth variability and greater

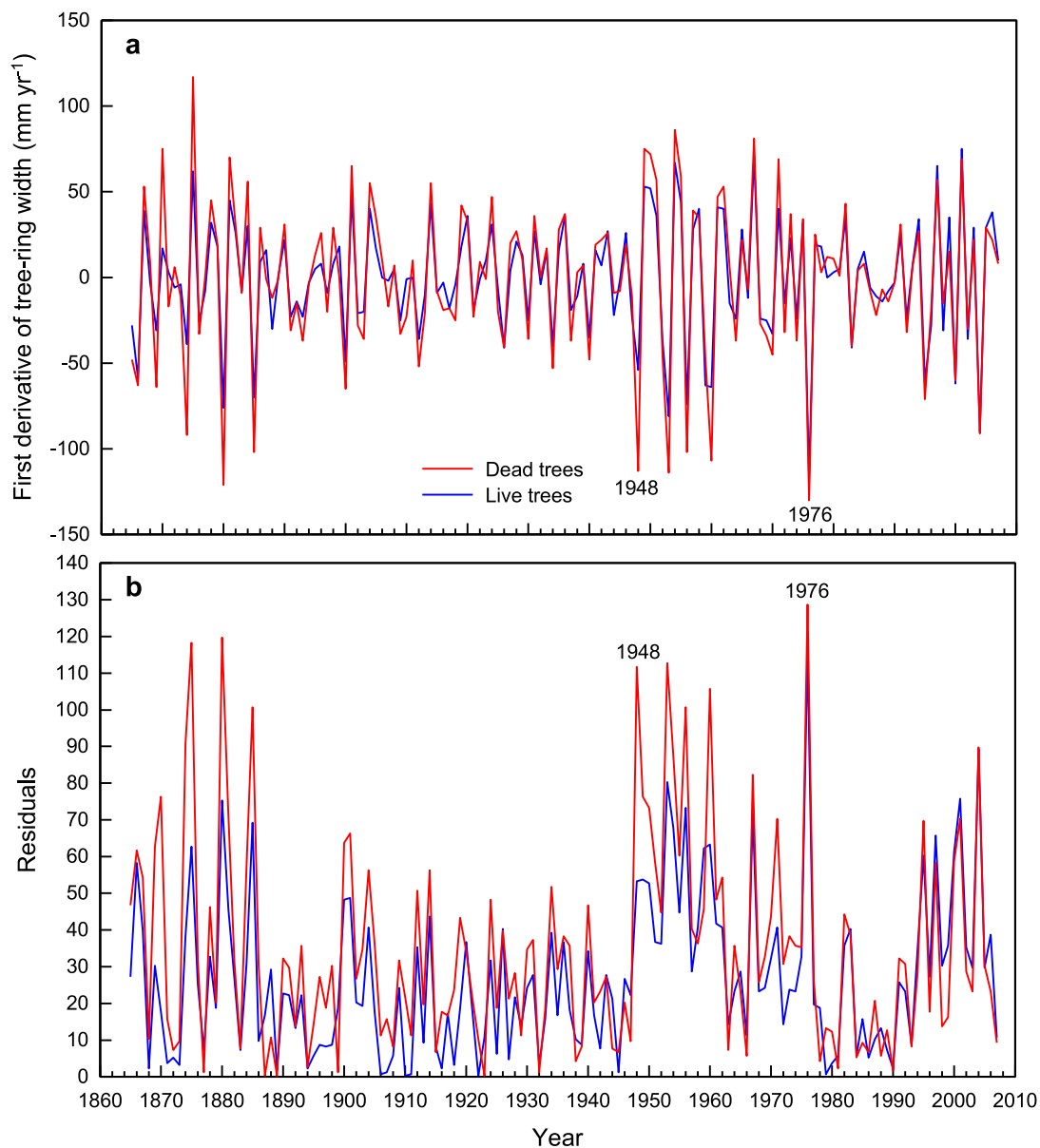


**Fig. 7.** Decadal variation (1858–2007) of (a) mean tree-ring width, (b) the standard deviation of mean tree-ring width, (c) mean sensitivity, (d) first-order autocorrelation, (e) growth synchronicity, (f) absolute values of the first derivative of tree-ring width, (g, h) the standard deviation of the first derivative's (g) original and (h) absolute values for dead and live trees. Years on the x-axis represent the respective first year of the different 10-year intervals; statistical testing is across these intervals ( $P \leq 0.05$ ; Mann-Whitney U-test).

overall tree size, attributes that often have been found to be linked to higher drought-induced mortality (Stovall et al., 2019). Our results suggest that abrupt stand opening, as caused by heavy logging or drought mortality events (or both in combination), increases the mortality risk of the remaining individuals in highly shade-tolerant European beech, which depends on a humid shaded forest-interior climate. The increasing aridification of climate since the 1970s with a rising atmospheric evaporative demand certainly has exacerbated the stress level. Attempts to understand the drivers of recent dieback should therefore consider the whole legacy of stress events instead of focusing on the last extreme events alone.

The fact that the surviving trees also show long-term (though less pronounced) growth decline and enhanced short-term growth variability, makes it plausible that mortality will remain high in the studied stand, and part of the surviving trees will die in the near future as well. Given that the 2018–2020 drought was even more extreme than the 1947 and 1976 events (Büntgen et al. 2021), we expect for the future a marked increase in beech mortality in Central Europe as a long-term after-effect of this exceptional event. High values of the first derivative of the ring width series may serve as better indicators of a high future drought mortality risk in beech than variables such as the standard deviation of ring width, many years of low ring width, mean sensitivity,





**Fig. 8.** (a) First derivative of ring width chronologies of the dead and live beech trees. (b) Residuals of the first derivative of ring width to its arithmetic mean. 1948 and 1976 represent the two most critical years with drought responses for tree growth and vitality in the stand between 1940 and 2015.

first-order autocorrelation, or short-term growth resilience.

#### Author contributions

CD, PM and CL conceived the idea. BB conducted field work, BB and CD carried out laboratory work and statistical analyses. CD and CL wrote the paper. All authors provided comments to the manuscript.

#### Conflict of interest

I declare no conflict of interest.

#### Acknowledgments

We thank Davaadorj Saindovdon and Yolk Yeruult for the help with wood core sampling for tree-ring analysis. We are grateful to Katja Lorenz and Christoph Tewes for supporting us with preparing the data on stand structure. Two anonymous reviewers helped to improve the manuscript with their critical comments.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.tfp.2022.100265](https://doi.org/10.1016/j.tfp.2022.100265).

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