



## Heading for a fall: The fate of old wind-thrown beech trees (*Fagus sylvatica*) is detectable in their growth pattern

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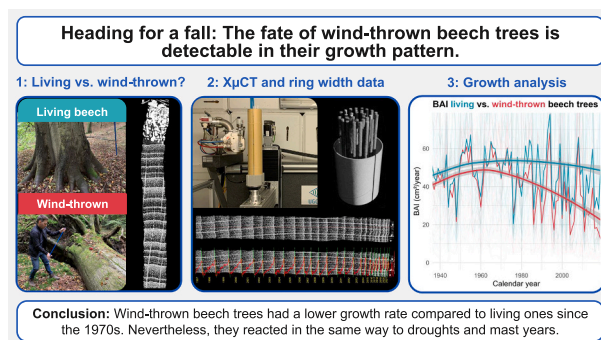
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### HIGHLIGHTS

- Tree ring data from living and recently wind-thrown beech trees were analyzed.
- Recently wind-thrown trees showed a lower growth rate compared to living trees.
- Wind-thrown and living trees reacted equally to droughts, heatwaves, and mast years.
- All beech trees at this site were sensitive to droughts but recovered quickly.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Common beech (*Fagus sylvatica*) is one of the most important deciduous tree species in European forests. However, climate-change-induced drought may threaten its dominant position. The Sonian Forest close to Brussels (Belgium) is home to some of the largest beech trees in the world. This UNESCO world heritage site is famous for its high density of very large beech trees as a result of its climatic suitability, fertile soil conditions, and past management. Here we utilized tree-ring data from increment cores to investigate the growth of these old and monumental beech trees, evaluating their growth trends, response to past climate, and the effect of mast years on 39 living and 16 recently wind-thrown trees. Our analysis reveals that the sampled trees were generally sensitive to spring and summer droughts but recovered quickly after such an extreme climatic event. The growth trend of living trees has remained high and only shows a slight, statistically insignificant, decline over the past

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50 years. Although the overall growth rate remains strong (BAI 50 cm<sup>2</sup>/year), the past five decades have shown strong inter-annual growth variations due to frequent and more intense droughts combined with an increased frequency of mast years. We also found notable differences in growth patterns between the living trees and those that had recently been wind-thrown. While there were no significant differences between living and wind-thrown trees in response to droughts, heatwaves, or mast years when examining year-to-year growth changes, the wind-thrown trees did exhibit considerably lower overall growth rates and a significant downward trend in growth (BAI -0.57 cm<sup>2</sup>/year). This difference in growth trends has been apparent since at least the 1980s. Overall, the findings of this study can provide valuable insights for understanding the long-term dynamics of lowland beech forests and their responses to climate change.

## 1. Introduction

Beech (*Fagus sylvatica* L.) is one of the most common deciduous tree species in European forests and is naturally the dominant tree species in most of Western Europe. About a hundred beech forests in 18 European countries (including part of the Sonian Forest) are protected as UNESCO World Heritage sites because of their unique natural and heritage value. However, climate change puts pressure on the dominant position of beech in central and southern Europe (Allen et al., 2015; Reyer et al., 2013). Many studies highlight the drought sensitivity of beech (Brinkmann et al., 2019; Cavin and Jump, 2017; Köcher et al., 2009; Leuschner, 2020; Leuschner et al., 2019; Scharnweber et al., 2011; Scherrer et al., 2011) while other sources emphasize the resilience of beech or put this impact into perspective, making it highly dependent on the followed climate scenario and the specific stand characteristics (Dyderski et al., 2018; Leuschner, 2020; Martínez del Castillo et al., 2022).

In addition to higher average temperatures, climate models for Western Europe also predict a less uniform distribution of rain, resulting in wetter winters and drier summers (Capioli et al., 2012; Termonia et al., 2018). Extreme climatic events such as droughts and heat waves will also become more frequent and intense (Capioli et al., 2012; Termonia et al., 2018). These predicted conditions can have major consequences for the vitality and growth of beech as it is sensitive to prolonged drought, especially in spring and summer (Giagli et al., 2016; van der Werf et al., 2007). Moreover, extreme seed production events are becoming more frequent due to increased summer heat waves and sustained atmospheric nitrogen deposition (Drobyshev et al., 2010; Hacket-Pain et al., 2018; Latte et al., 2015; Müller-Haubold et al., 2015; Nussbaumer et al., 2021; Vacchiano et al., 2017; Vanhellemont et al., 2019). This production of seeds can use up to half of the net photosynthetic production in a mast year (Drobyshev et al., 2010; Müller-Haubold et al., 2013), which leaves less energy for growth and for the repair of damaged tissues.

Old-growth beech stands in lowland forests are a rare and understudied forest ecosystem. One of these stands in the Sonian Forest in Belgium is remarkable as it contains some of the largest beech trees in the world (Vandekerkhove et al., 2018). The growth of the large beech trees in this UNESCO World Heritage site is the subject of this paper. The oldest stand in this reserve is known for its extraordinary densities and sizes of very large beech trees, which is the result of a suitable climate, favorable soil, and intensive former management. The soil at this site is of exceptionally high quality for beech as it is a unique combination of loess that is deep and well-drained but has good water storage and a subsoil with a high base saturation. This results in remarkably high canopy heights (45+ m) and diameter increments (4.75 mm/year) for 250-year-old beech trees (Langohr and Sanders, 1985; Vandekerkhove et al., 2018).

In this study, we used tree-ring data from these monumental trees to evaluate their growth trends, response to climate fluctuations, and the effect of mast years. Moreover, we investigated whether there is a difference in growth and growth fluctuation between living and recently wind-thrown beech trees. Windthrow is an important cause of mortality in older beech trees due to their large size and shallow rooting system (Schütz et al., 2006). Understanding if this is a random process or if

certain individuals are more prone to windthrow than others is thus of importance to understanding beech forest dynamics. Our hypothesis is that wind-thrown beeches have a different growth trend and react more negatively to droughts, heat waves, and mast years in the years before their fall (DeSoto et al., 2020). Studies by Holzwarth et al. (2013), Gillner et al. (2013), Hülsmann et al. (2016) and Dulamsuren et al. (2022) already found that long-term slow growth is a good predictor for mortality in beech. They, however, mainly looked at standing dead trees, which occurs more frequently for small to mid-sized individuals and has different causes than mortality by windthrow.

We investigated the growth patterns of large beech trees in the Sonian forest by addressing the following research questions: 1) What is the growth rate of large beech trees in the Sonian forest, and how has it changed over time? 2) How do climate fluctuations, extreme droughts, and mast years affect the growth of these large beech trees? 3) Is there a difference in growth rate and climate response between living and recently wind-thrown beech trees? Our corresponding literature-based hypotheses are that 1) these trees have a high growth rate but show a recent slowdown, 2) droughts and mast years have a big impact on growth, and 3) recently wind-thrown trees show a stronger growth decline and higher sensitivity to climate extremes than living trees. The novelty here lies in investigating the link between growth and the windthrow-susceptibility of large beech trees in European lowland forests. We also extensively investigate the drivers of growth variability and the potential effects of climate change on this unique UNESCO World Heritage site. A better understanding of these mechanisms is important as it provides valuable insights into the long-term dynamics of beech forest ecosystems and their responses to climate change.

## 2. Material and methods

### 2.1. Study area and fieldwork

The study area is the core research plot of the Joseph Zwaenepoel Forest Reserve (50.7514 N, 4.4224 E, 10.06 ha), located within the Sonian forest in Belgium. This site is a prime example of a lowland old-growth beech forest and is included in the UNESCO World Heritage site 'Primeval Beech Forests of the Carpathians and Other Regions of Europe' (Vandekerkhove et al., 2018). The old beech trees in this plot are all of the same age: they were planted in 1775 and were managed intensively during the first 200 years of their life by means of regular thinning and possibly some pruning early on. Underneath and between the old trees, a new generation of beech trees is developing, gradually filling the gaps. These trees have however not reached the upper canopy yet, and thus do not compete for light with the old stand. The stand became part of a forest reserve in 1995 and has been left unmanaged since 1983 (Baeté et al., 2002). For DBH > 5 cm, this stand is characterized by a tree density of 286.5 trees/ha, a total basal area of 39.05 m<sup>2</sup>/ha, and a quadratic mean diameter of 41.6 cm (census data from 2020). When only considering the original 250-year-old beech population (by excluding trees with DBH < 50 cm), which dominates this stand and is the subject of this paper, this results in 45.2 trees/ha, 31.65 m<sup>2</sup>/ha, and a quadratic mean diameter of 94.3 cm. The sampled area is on a plateau that is relatively flat and has an elevation of 113 m ± 2 m. The

microtopography is slightly undulating, but slopes rarely exceed 5 %. Some small valleys are present but were not sampled. Soil conditions are also homogeneous with a thick niveo-aeolian loess layer on top of tertiary calcareous sands. The plot mainly consists of silt-loam soils that are well-drained and have a mottled and discontinuous clay illuviation horizon (Abc soils) (De Keersmaecker et al., 2003; Dondeyne and Deckers, 2019) which is the most common soil type in the Sonian forest. The climate is characterized by a total annual rainfall of 849 mm and a mean annual temperature of 10.7 °C (1991–2020) (KMI, 2022).

Thirty-nine old living trees from the original regeneration were randomly selected and sampled in October 2021. For each tree, two perpendicular cores were collected with a 2-threaded 5.15 mm haglöf increment borer. During the same campaign, all recently wind-thrown beech trees in the plot were also sampled ( $n = 16$ ). Due to the poor rot resistance of beech wood, only the recently fallen trees (fallen between 2016 and 2020) proved suitable for dendrochronological sampling with an increment borer. All sampled trees were growing on the same type of Abc soil. Trees on other soil types at the edges of the research plot were not sampled. Due to their age, optimal soil conditions, and historic management (Vandekerckhove et al., 2018), all sampled trees were very large and can be considered dominant or co-dominant. The average DBH of the sampled trees is respectively 98.5 cm (SD = 23.9) and 93.8 cm (SD = 15.6) for living and wind-thrown trees (overview in Table A.1). Hegyi's competition index - a tree size and position-related competition index (Hegyi, 1974) - was determined for each sampled tree based on census data from 2009, as they were all still alive at that time. This was done using the *pairwise* function from the *splab* R-package (García, 2014).

## 2.2. Sample-preparation, X $\mu$ CT, and tree-ring measurements

The 110 collected increment cores were soaked for 20 h in an 80 °C heated water bath and subsequently extracted with a Soxhlet-extraction for 6 h using a 0.43 to 1 toluene - ethanol mixture (Schweingruber, 1988). The samples were then dried, stored in paper straws, and conditioned in a climate chamber at 65 % RH and 20 °C. We used X-ray micro-Computed Tomography (X $\mu$ CT) to visualize and measure the tree rings in 3D. The main advantages of using X $\mu$ CT over more traditional techniques are that it is non-destructive and that the data can be used for tree ring densitometry studies (Van den Bulcke et al., 2014). The cores were scanned using the HECTOR X $\mu$ CT scanner (Masschaele et al., 2013) from UGCT (Centre for X-ray Computed Tomography of the Ghent University) at a resolution of 50  $\mu$ m. Reconstruction was performed using *Octopus Reconstruction* (Dierick et al., 2004; Vlassenbroeck et al., 2007) and the stacked scans per sample holder were stitched and merged afterward using a custom-written routine in *Fiji* (Schindelin et al., 2012; Schneider et al., 2012) based on the stitching algorithm of Preibisch et al. (2009). All tree-ring boundaries were indicated and visually crossdated using the *XCT toolchain* (De Mil et al., 2016; De Ridder et al., 2011; Van den Bulcke et al., 2014; Van den Bulcke et al., 2019) (software packages available on [www.dendrochronomics.ugent.be](http://www.dendrochronomics.ugent.be)). An additional check of the crossdating quality was performed with the *COFECHA* software (Holmes, 1983) and in *R* (R Core Team, 2020) using the *dplR*-package (Bunn, 2008). The total mean inter-series correlation (RBAR) and expressed population signal (EPS) (Wigley et al., 1984) were calculated as well using the *dplR*-package (Bunn, 2008).

## 2.3. Data analysis

Tree productivity within this paper is quantified as the Basal Area Increment (BAI) as it is a better indicator of long-term growth variations than radial growth (Biondi and Qeadan, 2008; Kint et al., 2012). Yearly BAI per tree was calculated with the *bai.in* function from the *dplR* R-package (Biondi and Qeadan, 2008; Bunn, 2008). The double bark thickness, needed for accurate BAI calculations, was estimated using the allometric relationship from Lojo et al. (2021). All BAI series were

averaged in each of the two classes (living and wind-thrown) resulting in two BAI chronologies. To check for absolute differences in growth between living and wind-thrown trees, a linear mixed-effects model was fitted to the BAI data of all trees using a moving window of 10 years. This was done using the *lmer* function from the *lme4* R-package (Bates et al., 2015) with the formula *BAI LivingOrWindthrown* + (1|TreeID) + (1|Year). The *p*-value was estimated using the *lmerTest* R-package (Kuznetsova et al., 2017). The slope of the growth trend from the individual trees and two BAI chronologies was quantified with the Sen's slope coefficient (Sen, 1968; Weigel et al., 2022) by regressing BAI against the calendar year using the *sens.slope* function from the *trend* R-package (Pohlert, 2020). Testing for significance ( $p < .05$ ) was done within the same function using a Mann-Kendall trend test (Libiseller and Grimvall, 2002).

Ring width index (RWI) chronologies were calculated using the *dplR* R-package (Bunn, 2008). First, the two tree-ring width series per tree were averaged. Then, the RWI series per tree were calculated by detrending and standardizing the ring-width series. The *detrend* function was used (Bunn, 2008) with a smoothing spline and a spline length of 50 years (Klesse, 2021). This was done to remove low-frequency variations and emphasize year-to-year variation. All remaining RWI series were then averaged to get two RWI chronologies: one for living and one for wind-thrown trees. The correlation between these RWI chronologies and the three-monthly average temperature and precipitation during spring (March–May) and summer (June–August) between 1970 and 2020 was calculated using the *dcc* function from the *treeclim* R-package (Biondi and Waikul, 2004; Zang and Biondi, 2015). The correlations were tested with the 95 % percentile range method (Dixon, 2006). As suggested by Carrer (2011) and Galván et al. (2014), each individual tree RWI series was also correlated to the climate in the same way as the chronologies. 1970 to 2020 was chosen as 1970 is the start of strong differentiation between the two groups (see Results) and 2020 is the last ring present in the data set of wind-thrown trees. Three-monthly averages of climate data were chosen to strengthen the signal of individual drought and heatwave events. 50-year moving correlations with monthly climate data between 1834 and 2020 were also performed within the same package to check the stability of the found correlations between 1970 and 2020. The effect of late spring frost was also evaluated using the lowest recorded temperature in April and May. Additionally, the standard deviation and first-order autocorrelation of each RWI chronology were calculated using the *rwl.stats* function, as these can tell us something about growth variance and legacy effects (Klesse et al., 2022a). Climate data is available from the Uccle weather station, located 7 km from the study area, where monthly average air temperature and total precipitation are being recorded since 1833.

The effect of strong droughts was estimated by evaluating each individual tree's detrended and standardized RWI value during and after several drought events. This is an alternative approach to Lloret et al. (2011) resistance, recovery, and resilience indices. Using detrended RWI values accounts better for general growth trends and allows more for analysis of lagged effects. The 10 strongest spring and summer droughts from 1970 till 2020 were respectively identified as the lowest SPEI3 values (Vicente-Serrano et al., 2010) in May (drought from March till May) and August (drought from June till August). For spring these years ended up being 1976, 1990, 1993, 1996, 2004, 2007, 2011, 2014, 2017, and 2018. For summer they were 1973, 1976, 1983, 1984, 1989, 1995, 2003, 2013, 2015, and 2018. The SPEI3 values were calculated with the *SPEI* R-package (Vicente-Serrano et al., 2010). Differences between living and wind-thrown trees were tested with linear mixed-effects models using the *lmer* function from the *lme4* R-package (Bates et al., 2015) as *RWI LivingOrWindthrown* + (1|TreeID) + (1|Year). The *p*-value was estimated using the *lmerTest* R-package (Kuznetsova et al., 2017).

Seed production data from the Sonian Forest is available since 1999 via standardized seed collection within the ICP Forests Level II network (de Vries et al., 2003) in a beech stand a few hundred meters from the study area. Mast years (years with large amounts of seed production)

were defined as years in which seed production exceeded 500 seeds/m<sup>2</sup> (LaMontagne and Boutin, 2009; Nussbaumer et al., 2016; Overgaard et al., 2007; Paar et al., 2011). The use of this data is possible as we only look at the presence or absence of mast years, and not the absolute amount of seed production. The effect of mast years was evaluated on the detrended and standardized RWI values of individual trees before, during, and after mast years. Differences between living and wind-thrown trees were tested with linear mixed-effects models as before. Additionally, two linear mixed-effects models were made to check if adding seed data to climate-based growth models has a positive effect on model fit (Nussbaumer et al., 2021). The first model fitted yearly BAI to the mean BAI of the previous ten years, tree type (living or wind-thrown), and all significant temperature and precipitation variables. This included precipitation during the previous April–May, previous August–September, previous October–November, current April–May, and temperature of the previous July–September. The lowest recorded temperature during the previous and current April–May was also included to account for late spring frost. The precipitation data from April–May and July–August two years ago were also added as these can have an effect on mast behavior (Bajocco et al., 2021). All variables were standardized before model construction and BAI values were log-transformed (Martinez del Castillo et al., 2022). Tree ID and year were added as random effects. The second model was identical to the first but added a categorical variable indicating the presence or absence of a mast year event. A chi-square difference test was used to test if the model with mast year data performed significantly better than the model without. Marginal and conditional R<sup>2</sup> values were calculated with the *r.squaredGLMM* function from the *MuMIn* R-package to estimate model performance (Nakagawa and Schielzeth, 2013).

### 3. Results

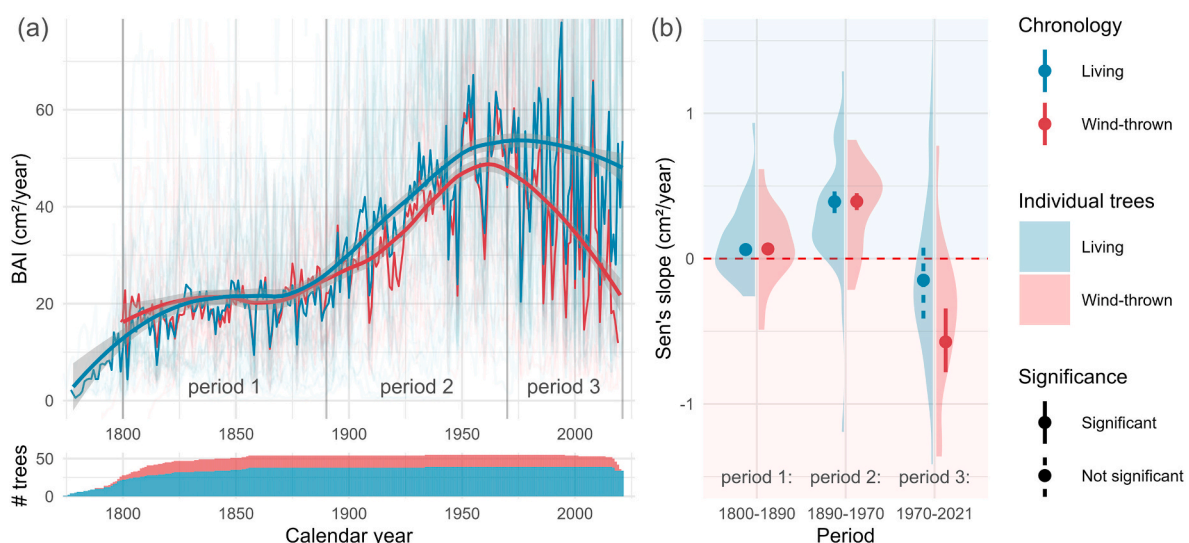
#### 3.1. Tree-ring data set

The tree ring records span from 1775 until 2021 and consist of 21,428 ring width measurements from 39 living and 16 wind-thrown even-aged trees. The distribution of sampling depth through time is shown in Fig. 1a. The average ring width is 1.93 mm (SD = 1.16) and 1.84 mm (SD = 1.06) for living and wind-thrown trees respectively. Strong pointer years from 1970 onward were 1976, 1986, 1990, 1995,

2000, 2002, 2004, 2011, and 2016. The RBAR/EPS values for living and wind-thrown RWI chronologies between 1970 and 2020 (the climate analysis period) are respectively 0.418/0.966 and 0.393/0.912, which indicates a good crossdating quality and high growth synchrony among these trees. Within that same period, the standard deviation of the RWI chronologies from living and wind-thrown trees respectively is 0.266 and 0.322. The first-order autocorrelation is 0.041 and 0.130. This suggests that wind-thrown trees have a greater variation in very positive and very negative growth years and that these years have a longer legacy effect in comparison with trees that are still alive. The sampled trees had an average competition index of 7.89 (SD = 2.16) and 7.77 (SD = 2.03) for living and wind-thrown trees respectively. Hence, no significant above-ground competition differences between these two groups were found. All sampled trees are in locations between 112 m and 115 m above sea level. The plot is thus relatively flat.

#### 3.2. Growth trends

The growth (defined as BAI) of the living and wind-thrown beech trees is shown in Fig. 1a. The two groups have a very similar growth trajectory with a significant growth increase between 1890 and 1970. In this period, the mean BAI doubled from 25 cm<sup>2</sup>/year to >50 cm<sup>2</sup>/year. From the 1980s onward, the recently wind-thrown trees grew less than the trees that are still alive. This is significant ( $p < .05$ ) in the periods 1982–1998 and 2009–2020. In most of the remaining 10-year periods since 1980, only marginally significant differences were found (see Table B.1 for test results). The growth of the wind-thrown beech trees also had a significant ( $p < .05$ ) negative slope (i.e. downward growth trend) of on average  $-0.57$  cm<sup>2</sup>/year between the years 1970 and 2020 (see Fig. 1b). This same slope was less steep ( $-0.15$  cm<sup>2</sup>/year) and not significantly different from zero in the living trees. Hence, the recently fallen beech trees showed a remarkable decrease in growth rate for at least 40 years before their actual fall whereas the living trees had no significant decrease in growth rate during that same period. In both groups, 1970 to 2020 is characterized by increased inter-annual variability of growth, where years with high average growth are followed by years with very little growth.



**Fig. 1.** (a) Basal area increment (BAI) of the living (blue) and wind-thrown (red) beech trees in the study area. Both the individual trees, mean chronologies, and general trends (loess smoothed curve) are shown. The growth series is subdivided into three distinct periods: 1800–1890 (period 1), 1890–1970 (period 2), and 1970–2021 (period 3). For each year, the number of available trees is plotted below. (b) The Sen's slope of the BAI trend (cm<sup>2</sup>/year change) in each of the 3 distinct growth periods. The slope and corresponding 95 % confidence intervals of the two mean chronologies are shown as point range plots. The violin plots represent the average slopes of the individual trees.

### 3.3. Effect of climate fluctuations on growth

The growth of the beech trees, as expressed by the detrended and indexed ring-width series, between 1970 and 2021 was positively correlated with precipitation in the previous summer and current spring (see Fig. 2). The temperature of the previous summer was negatively correlated with growth. Thus, a dry or warm previous summer or a dry current spring negatively affects tree growth. These correlations were all significant ( $p < .05$ ) when evaluating the RWI chronology of wind-thrown beech trees. The growth of living trees had the same average correlation values with climate but these correlations were not significant. The two groups, therefore, seem to respond in the same way to precipitation and temperature fluctuations, but the reaction of the wind-thrown trees is more pronounced. Both groups also showed a strong positive correlation between RWI and the precipitation of the previous fall (see Fig. C.1 and C.2). We also detected a negative correlation between RWI and current summer precipitation (see Fig. 2). This would mean that a dry summer would lead to higher growth that same year. We checked the consistency of this correlation between 1834 and 2020 using a moving correlation analysis and found that this effect is only present between 1970 and 2020, and was absent between 1833 and 1970 (see Fig. C.2). The other correlations presented in Fig. 2 were present and consistent between 1833 and 2020. Significant factors negatively affecting growth that are not shown in the figures are low precipitation during the previous October–November, and late spring frost in the previous and current year.

The effect of the strongest spring and summer droughts (lowest SPEI3 values) since 1970 is shown in Fig. 3. The largest impact is seen during spring droughts, where it adversely affects growth in that same growing season ( $p < .001$ ), resulting in a mean RWI of 0.85. Although summer droughts also have a negative impact on growth ( $p < .001$ ), the strongest effects are only visible in the following year, resulting in a mean RWI of 0.88. No significant differences between the growth response of living and wind-thrown beech trees to these drought events were found. The recovery of these trees after a strong drought is fast. One year after a spring drought, the growth has returned to normal levels. The same is true for summer droughts when accounting for the 1-

year lag effect on growth.

### 3.4. Effect of seed production on growth

Seed production and corresponding growth before, during, and after mast years are shown in Fig. 4. Of the years between 1999 and 2020 (22 years), 9 years could be considered mast years. The mean RWI during a mast year was 0.77. During non-mast years, it was 1.14. The presence of a mast year had a significant ( $p < .001$ ) negative effect on growth but no significant differences between the response of living and wind-thrown beech trees were found.

The model fitting BAI to climate data had a decent fit (marginal  $R^2 = 0.61$ , conditional  $R^2 = 0.78$ , AIC = 1491.3). However, the model performed significantly better when adding mast year data as a predictor (marginal  $R^2 = 0.66$ , conditional  $R^2 = 0.77$ , AIC = 1487.2, Chisq = 6.11,  $p = .013$ ). Additional model output can be found in Appendix D. Hence, mast year data is a good predictor for tree growth, even with limited data availability.

## 4. Discussion

Overall, the sampled trees displayed sensitivity to droughts in spring and summer but were able to recover quickly after these extreme climatic events. The growth trend of living trees has remained high and shows a slight, statistically insignificant, decline over the past 50 years. However, while their general growth trend remains high (BAI 50 cm<sup>2</sup>/year), these past five decades have been marked by strong year-to-year growth variations. Although no significant differences between living and wind-thrown trees in response to droughts, heatwaves, or mast years were found when examining year-to-year growth changes, the wind-thrown trees did exhibit considerably lower overall growth rates and a significant downward trend in growth. This difference in growth patterns has been apparent since at least the 1980s.

The beech trees in this plot show a strong increase in growth between 1890 and 1970, during which the BAI more than doubled (Fig. 1a). Other studies which found similar growth increases, attributed this to size effects, management, rising atmospheric CO<sub>2</sub> concentration, and

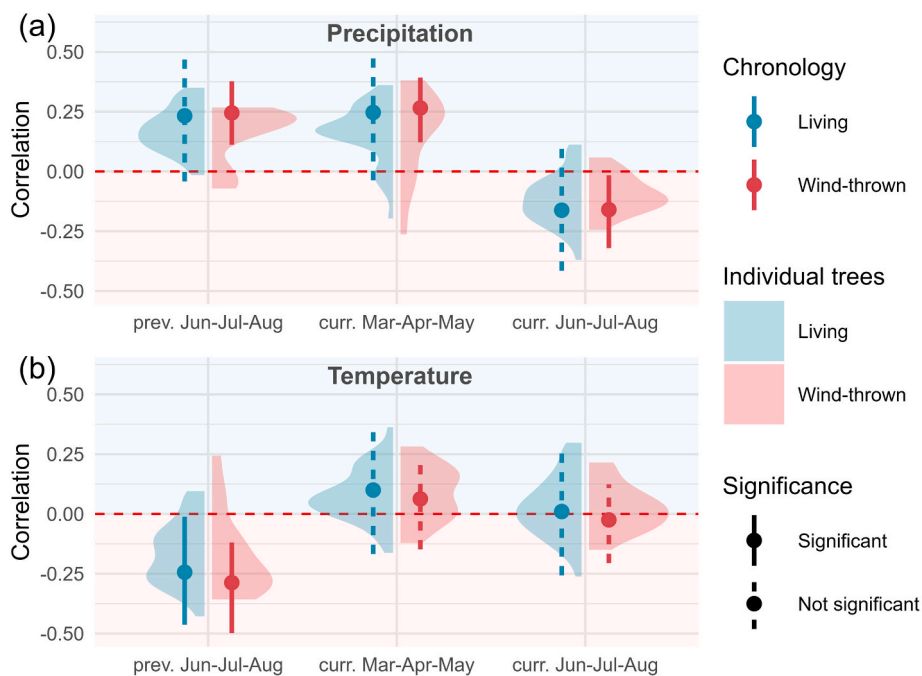


Fig. 2. Correlation between the ring width index (RWI) and (a) total monthly precipitation, and (b) mean monthly air temperature during the previous summer and the current spring and summer. The correlation is from 1970 to 2020. The correlations from average RWI chronologies (point range plots) and individual tree RWI series (violin plots) are shown. Statistical significance (95 % percentile range) is shown as a full line.

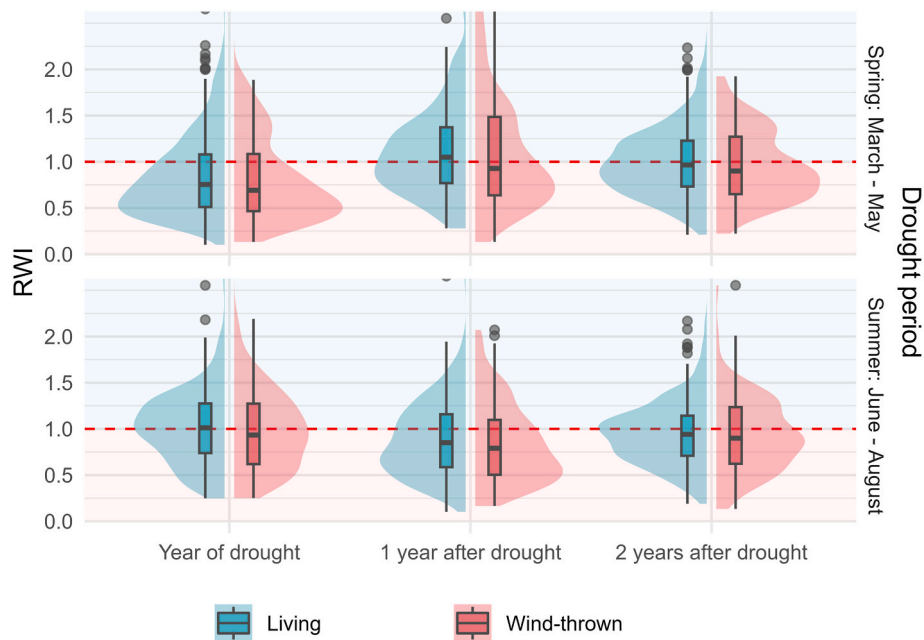


Fig. 3. Ring width index (RWI) of individual trees during and after the 10 strongest spring (above) and summer (below) droughts between 1970 and 2020.

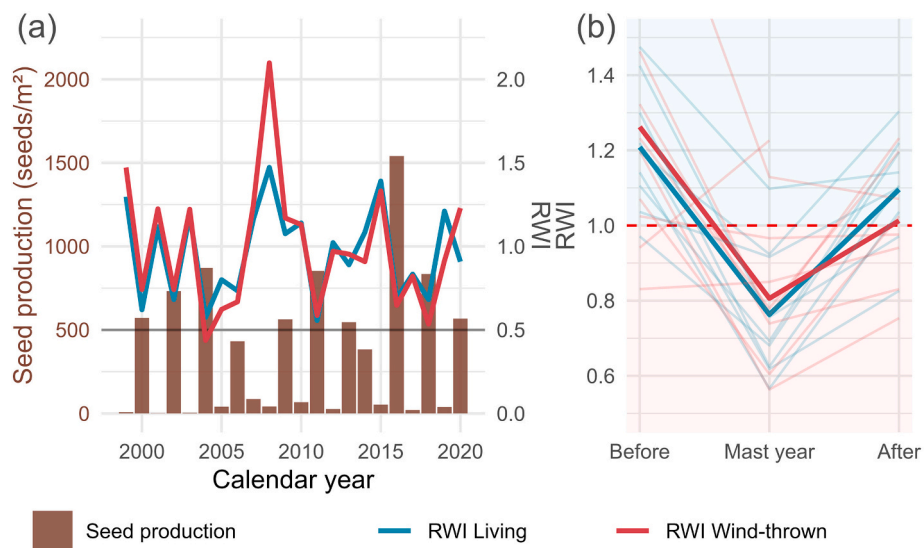


Fig. 4. (a) The seed production in a nearby seed sampling plot (brown bars) and the mean ring width index (RWI) chronologies of living (blue) and wind-thrown (red) beech trees. In this paper, mast years are defined as years with >500 seeds/m<sup>2</sup> (indicated by the horizontal line). (b) Average RWI before, during, and after individual mast years and an overall average line for both living and wind-thrown beech trees.

the high levels of atmospheric nitrogen deposition in forests during that period. Forests became richer in nutrients and grew stronger as a result (de Vries et al., 2009; Kint et al., 2012; Laubhann et al., 2009). In accordance with other studies on western-European beech by Kint et al. (2012), Latte et al. (2015) and Scharnweber et al. (2011), we also found an increase in inter-annual growth variability since 1970 (Fig. 1a). These sharp fluctuations in growth since 1970 (Fig. 1a) can generally be attributed to the occurrence of more frequent and more intense droughts in combination with an increased frequency of mast years (Fig. 4a). The occurrence of a mast year is a strong predictor for the growth of the studied trees. As was shown by this study, including this type of data in climate-based growth models significantly improves their performance. However, the limited time frame with available seed production data in this forest (20 years) makes it unsuitable for long-term growth models. Future studies where long-term seed production data is available should

make sure to include it in their growth analysis and modeling efforts. The recently wind-thrown trees at this site had a strongly decreasing growth trend since the 1970s, a trend that is not significantly present in trees that are still alive (Fig. 1b). This result suggests that mortality by windthrow in old-grown beech forests is not a random process (Cailleret et al., 2017) but is biased towards trees that are already in growth decline. A study by Holzwarth et al. (2013) did not find a significant link between growth rate and mortality due to uprooting. That study, however, was performed using census data, which had a smaller temporal range (1999–2007) and is generally less precise than tree-ring data. A bias in mortality towards trees with a decreasing growth trend is a well-known factor for standing dead beech trees (Cailleret et al., 2017; Dulamsuren et al., 2022; Gillner et al., 2013; Holzwarth et al., 2013; Hülsmann et al., 2016), which is a more common form of mortality for small to mid-sized trees. Our results expand this to large wind-thrown

beech trees.

Regarding inter-annual growth variation, we did not find a difference in climate-growth correlation (Fig. 2), reaction to droughts (Fig. 3), or growth during mast years (Fig. 4) between living and wind-thrown beech trees. This suggests that the decline in growth, and eventual death by windthrow, is not caused by an inherent difference in drought resistance or seed production, but more a general decline in reserves, productivity, and root repair potential. The sampled trees were all very large (Table A.1) and were managed intensively during the first 200 years of their life by means of regular thinning, resulting in similar competition index values between the two groups. This makes above-ground competition a less likely cause for the observed growth decline of wind-thrown trees. This, combined with the fact that it was specifically a support failure of the root system that led to their death, could indicate that the observed decline in growth is a result of below-ground processes. Possible explanations for the difference in growth between living and wind-thrown trees are differences in assimilate reserves to repair the root system after a stress event (Hagedorn et al., 2016), general below-ground competition (Lang et al., 2010), and root pathogen susceptibility and subsequent (absent) repair. Moreover, the wind-thrown trees may have been situated in areas characterized by limited access to deeper soil horizons due to a scarcity of fissures within the dense fragipan horizon (Latte et al., 2015). The high number of mast years, combined with increased climatic extremes, depletes the reserves of these trees faster than in the past (Cailleret et al., 2017; Hackett-Pain et al., 2018). Possibly, trees that are slower at replenishing their reserves get into a negative growth spiral. These trees do not have enough reserves to repair the root system after a drought or pathogen attack and the reserves are not replenished fast enough due to dieback of the root system, a negative spiral that also affects the growth potential of these trees. This is supported by the higher temporal autocorrelation found in the RWI chronology of wind-thrown trees and thus a higher legacy effect of extreme years (Klesse et al., 2022a). This hypothesis could be tested in future studies by examining the differences in storage tissue, like ray parenchyma cells, between the two groups of trees. Root-based dendrochronology could also shed light on the relationship between stem growth and root growth during and after extreme events and if these two follow similar trends and patterns.

The living beech trees recovered very quickly after a drought (Fig. 3). One year after a drought event, growth is back to pre-drought levels. Also, only a very small overall growth decrease with an insignificant negative slope of the growth trend was found in the living trees (Fig. 1a). These findings are similar to a study on beech trees from the Meerdaal forest and Sonian forest by Vannoppen et al. (2018). However, most studies on beech in Western Europe find a growth decline in the last few decades (Bontemps et al., 2010; Charru et al., 2017, 2010; Dittmar et al., 2003; Kint et al., 2012; Latte et al., 2015; Martinez del Castillo et al., 2022; Vannoppen et al., 2018), largely attributed to the effects of climate change. The same is true for the southern range limit of beech like Spain and Italy, where climate conditions are sub-optimal (Jump et al., 2006; Peñuelas et al., 2008; Piovesan et al., 2008; Rozas et al., 2015; Rubio-Cuadrado et al., 2021; Serra-Maluquer et al., 2019). The key to the better performance of the beech trees in the Sonian forest is probably its soil. The rich loamy soil on this site is of exceptionally high quality for beech and can store high amounts of water to buffer the effects of droughts (Klesse et al., 2022b; Schmied et al., 2023). Future studies could look into specific micro-site soil properties of individual trees to determine if this can be correlated with individual tree performance or mortality. In addition to unique the soil is this stand centrally located in a relatively large forest complex. As a result, heatwaves and droughts are buffered more strongly than in small forest patches or at the edge of the forest (De Frenne et al., 2021).

In the future, we can expect further mortality, mainly of individual trees in growth decline, in this stand. However, the strong recovery and current high growth rates in living trees suggest that the dominant position of beech in the Sonian forest is probably not at stake, mainly

thanks to its uniquely favorable soil. Nevertheless, it is probable that a continued increase in climate extremes will mean a change to a more downward general growth trend in the future (Martinez del Castillo et al., 2022).

## 5. Conclusions

We compared tree ring patterns between living and recently wind-thrown large beech trees in a lowland old-growth beech forest and found that the predisposition of beech trees to windthrow is already detectable in their growth pattern many decades before their fall. Wind-thrown trees show a negative growth trend starting 4 decades before their fall, which on average, is absent in trees that are still alive. However, climate-growth correlation, reaction to droughts, and growth during mast years exhibited no differences between living and wind-thrown beech trees. The sampled trees displayed sensitivity to droughts in spring and summer but were able to recover quickly after these extreme climatic events. Wind-thrown trees displayed a higher temporal autocorrelation in their growth which could hint at a more prolonged legacy effect of extreme years. Overall, the findings of this study can provide valuable insights for understanding the long-term dynamics of beech forest ecosystems and their responses to climate change.

## CRedit authorship contribution statement

**Louis Verschuren:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Tom De Mil:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **Pieter De Frenne:** Methodology, Writing – review & editing. **Kristof Haneca:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **Joris Van Acker:** Writing – review & editing. **Kris Vandekerckhove:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **Jan Van den Bulcke:** Conceptualization, Methodology, Validation, Resources, Data curation, Writing – review & editing, Supervision, Funding acquisition.

## Declaration of competing interest

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

## Data availability

Data will be made available through the International Tree-Ring Data Bank (ITRDB) upon acceptance.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166148>.

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