Growth decline in European beech associated with temperature-driven increase in reproductive allocation

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Abstract

Climate change is impacting forests in complex ways, with indirect effects arising from interactions between tree growth and reproduction often overlooked. Our 43-year study of European beech (*Fagus sylvatica*), showed that rising summer temperatures since 2005 have led to more frequent seed production events. This shift increases reproductive effort but depletes the trees' stored resources due to insufficient recovery periods between seed crops. Consequently, annual tree ring increments have declined by 28%, dropping from a stable average of 1.60 mm y^{-1} between 1980 and 2005 to 1.16 mm y^{-1} thereafter. Importantly, this growth decline occurred without an accompanying trend in summer drought, indicating that altered reproductive patterns—not moisture stress—are driving the reduction. This creates a "perfect storm": increased reproductive effort drains resources, viable seed output falls due to the loss of mast-seeding benefits via pollination and lower seed predation, and the ongoing growth decline reduces current carbon uptake and future reproductive potential. These compounding factors threaten the sustainability of Europe's most widespread forest tree. Our findings unveil a critical yet underrecognized indirect mechanism by which climate change endangers forest ecosystems, emphasizing the need to consider interactions between demographic processes when assessing species vulnerability to climate change.

Significance Statement

Climate change effects on forest growth and reproduction are widely reported, but indirect effects from their interactions are rarely demonstrated. In a 43-year study of European beech (*Fagus sylvatica*), rising summer temperatures led to more frequent seed production (masting) which unexpectedly also increased total reproductive investment. This increased reproductive effort depletes stored resources, causing a 28% reduction in annual growth rates, even without increased drought stress. Diminished growth will further reduce future reproductive potential, creating a negative feedback loop. This "perfect storm" of decreased growth and reduced viable seed output threatens the sustainability of Europe's most widespread forest tree. Our findings reveal a novel indirect mechanism by which climate change endangers forests, highlighting the need to consider interactions between demographic processes when assessing species sensitivity to climate change.

Introduction

The influence of climate change on global forest demographics is now evident, often characterized by increased mortality rates (Senf *et al.*, 2018; Hartmann *et al.*, 2022), shifts in growth rates (del Castillo *et al.*, 2022), and changes in fecundity (Redmond *et al.*, 2012; Bogdziewicz *et al.*, 2023). While the direct impacts of climate on these metrics have been extensively examined, the interaction between demographic rates suggests the possibility of indirect effects (Clark *et al.*, 2014, 2021). For instance, mortality rates can increase when extreme weather events coincide with reproductive phases that deplete plant reserves (Lauder *et al.*, 2019; Corona *et al.*, 2022). This is particularly pertinent for species that mast, i.e. forgo regular reproduction in favor of concentrating seed production into sporadic, large-scale events, resulting in strong resource depletion (Sala *et al.*, 2012; Han & Kabeya, 2017; Lauder *et al.*, 2019). For example, in the tree *Distylium lepidotum*, masting depletes stored starch, resulting in slower regrowth or increased susceptibility to dieback following drought conditions (Nakamura *et al.*, 2021). Consequently, alterations in reproductive patterns due to climate change, which are now increasingly documented (Hacket-Pain & Bogdziewicz, 2021; Foest *et al.*, 2024), may indirectly affect mortality and growth rates. These indirect effects remain largely unexplored, primarily due to the scarcity of long-term data on both seed production and subsequent impacts on growth or mortality (Clark *et al.*, 2021). Nonetheless, acknowledging their existence is essential. These indirect effects can shape trends in demographic rates, even without the expected changes in climatic conditions that are known to directly influence these rates.

Weather effects on growth are typically understood in terms of photosynthesis and wood formation processes, yet weather also affects resource allocation, such as between growth and reproduction (Norton & Kelly, 1988; Lauder *et al.*, 2019; Leuschner, 2020). In masting plants, allocation to reproduction can vary dramatically between years; for example, in European beech (*Fagus sylvatica*), allocation to fruit production can vary 34-fold among years, from 508 g m^{-2} y^{-1} to 15 g m^{-2} y^{-1}, which negatively correlates with growth allocation (Müller-Haubold *et al.*, 2015). In years of high seed production, more carbon may be invested in reproduction than aboveground growth (Genet *et al.*, 2009; Müller-Haubold *et al.*, 2013). Besides resource trade-offs, indirect effects such as the replacement of leaf buds with flower buds also affect growth (Müller-Haubold *et al.*, 2015; Vergotti *et al.*, 2019). These processes might exacerbate whole-tree shortages in carbon supply during high seed years, especially in the early growing season when carbon demand is high (Mund *et al.*, 2020).

The strong links between masting and weather render masting potentially sensitive to climate change (Bogdziewicz *et al.*, 2024). For instance, masting in Japanese oak (*Quercus crispula*) is correlated with warm springs, resulting in shortened intervals between mast years from a 4-year cycle to a 2-year cycle as temperatures rise (Shibata *et al.*, 2020). In European beech, masting is triggered by summer temperature cues (Vacchiano *et al.*, 2017; Journé *et al.*, 2024). Elevated summer temperatures in recent decades have increased the frequency of weather cues, leading to more frequent initiation of reproduction, and dampening interannual variability of masting; a trend now detected across Europe (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024). In principle, masting only affects how a constant reproductive allocation (RA, the fraction of all plant resources devoted to reproduction) is distributed among years to increase reproductive efficiency (Kelly, 2020), but it is possible that changing cue frequency might also lead to changes in RA. To the extent that changed reproductive investment limits resources allocated to growth, such disrupted temporal allocation to reproduction has the potential to impact growth patterns and long-term growth trends (Leuschner, 2020). However, the indirect effects of climate change on growth, through effects on reproduction, have not yet been investigated.

Beech is considered a highly drought-sensitive species, and defoliation, dieback and mortality responses to recent severe summer droughts have raised concerns about the species' long-term future under climate change (Geßler *et al.*, 2007; Leuschner, 2020; Buras *et al.*, 2020). In addition to the response to individual extreme droughts, growth declines are occurring across the species distribution, driven by increased summer aridity, with stronger declines at drier sites (del Castillo *et al.*, 2022; Weigel *et al.*, 2023). Nonetheless, while the link between European beech masting and interannual variation in growth is well established (Müller-Haubold *et al.*, 2015; Hacket-Pain *et al.*, 2018), the potential for longer-term changes in masting to influence growth trends remains untested (Leuschner, 2020). In this study, we explore the potential effects of warming-driven disruptions in masting patterns on radial growth using populations of European beech (*Fagus sylvatica*) in which seed production has been monitored annually for 43 years (1980 - 2022).

To untangle how the coupled growth-reproduction system has responded to climate warming, we cored 57 individuals in which seed production has been monitored as a part of the English Beech Mast Survey since 1980 (Bogdziewicz *et al.*, 2020b). Tree rings offer annual measures of radial tree growth. They are widely used to study long-term changes in growth patterns (Jump *et al.*, 2006; del Castillo *et al.*, 2022), and allow us to match individual-level seed production data with growth variation. We first tested how tree-level annual growth rate, as measured by tree ring increments, is correlated with tree-level seed production in the current and previous year, and with summer drought. Seed production in the previous year was included as strong masting-driven depletion of resources could produce a carry-over effect and reduce growth the following year (Hacket-Pain *et al.*, 2017). Next, we evaluated the temporal trends in growth and attributed the trend to variations in seed production and drought, all in the context of changes in tree size. We predicted that more regular reproduction caused by a warming climate (Bogdziewicz *et al.*, 2020b, 2021) will reduce growth through the existence of a trade-off between masting and growth, even if the UK is not currently experiencing increasing summer drought due to climate change (Environment Agency, 2023). To better evaluate the impact of reproduction on each tree's remaining resources (including nitrogen, which is important for reproductive resource dynamics: (Abe *et al.*, 2016)), we estimated net plant resources each year following Rees *et al.* (2002). For each tree, this estimated unspent resources as that year's residual from a regression of cumulative seed production against time (a proxy for cumulative resource gain), thereby integrating the impact of all recent reproduction. Next, we tested for the temporal change in the negative association between radial growth and summer temperatures in the preceding year. That correlation arises through indirect effects, as high summer temperatures trigger masting the following year, diminishing growth (Hacket-Pain *et al.*, 2018; Leuschner, 2020). As warming has reduced the sensitivity of seed production to summer temperatures (Bogdziewicz *et al.*, 2021), we expected that to translate into weaker effects of summer temperatures on growth increments.

Results

Despite no change in summer drought (May-July water deficit) over the most recent four decades, European beech annual radial growth has declined by 28%. During the period 1980-2005, estimated growth rate was a relatively stable average of 1.6 mm per year, but this progressively declined to 1.16 mm per year by 2022 (Fig 1), after accounting for the effect of increasing tree size over the study period. The onset of this growth decline coincided with the timing of the shift in European beech masting at our site, which changed state to more regular and less synchronized reproduction ("masting breakdown") as a result of warming temperatures (Fig. S1) (Bogdziewicz *et al.*, 2020b, 2023). Concurrently, and in agreement with UK Environment Agency analysis of summer precipitation and hydrological records, we detected no trends in summer drought, as measured as the ratio of precipitation to potential evapotranspiration (P-PET) for the period May-July (Fig. S2, Table S1).

As expected, masting was an important driver of high-frequency growth variation, with narrower growth rings following high-seed years (Fig. 2). Summer drought and allocation to reproduction combined to determine annual radial growth, which included a lagged effect of the previous year's reproduction on growth. Growth was reduced most strongly when high seeding co-occurred with drought (Fig. 2). For example, in years when seeding failed, the estimated growth rate was 2.2 mm y^{-1}, but less than 1 mm y^{-1} when mast years co-occurred with drought. The effect of seed production on growth (β = -0.10, SE = 0.03) was similar to that of drought (β = 0.13, SE = 0.03) during the pre-breakdown period (1980-2005). While the effect of drought on growth remained largely unchanged over the last four decades, the effect of the current and previous year reproduction of growth has decreased in the last two decades (post-breakdown, 2006-2022) (Fig. 2).

Trend attribution analysis showed that the beech growth decline was explained mainly by

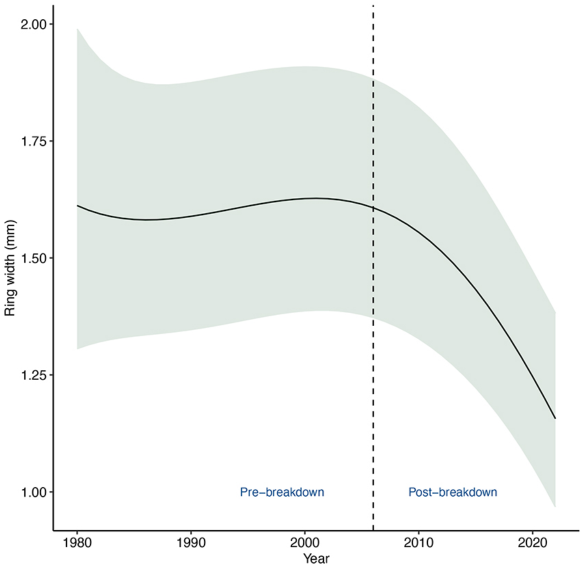

Figure 1: **Decline in European beech growth over the last four decades** A) Estimated annual tree ring increments; estimate derived from a generalized additive mixed model that included tree ID (N = 57) and site (N = 7) as random intercepts, and year and tree DBH (diameter at breast height) as predictors. Shading shows a 95% confidence interval. The dashed vertical line shows the year 2006, at which masting at our populations changed the state into more regular and desynchronised seed production, called "masting breakdown" (Fig. S1).

allocation to reproduction (Fig. 3). Allocation to seed production was the only significant contributor to the trend in annual growth rate, with the sensitivity of growth to increasing allocation to reproduction -0.002 (mm y^{-1} ring increment reduction per additional seed counted). In turn, consistent with a lack of trend in drought, summer water deficit was not a contributor to growth trends (Fig. 3).

Reconstruction of tree-level stored resources from seed production data, following the method of Rees *et al.* (2002), indicates that more frequent reproduction associated with masting breakdown has led to progressive resource depletion (Fig. 4). In the first two decades of monitoring, mean stored resources fluctuated stably above zero (bin averages: 14.2 - 21.7). However, frequent and greatly synchronized low-seed years (Fig. S1) in the 2002-2006 period appear to have caused an initial increase in stored resources ($\bar{x}$ = 84.6). After 2006, when more frequent weather cues caused plants to flower more often and less in synchrony, resources progressively declined, with negative averages recorded in 2012-2016 ($\bar{x}$ = -34.5) and 2017-2022 ($\bar{x}$ = -39) (Fig. 4, Fig. S3). That analysis suggests that a change in seed production pattern to more regular masting depleted plant resources due to insufficient recovery periods between seed crop production.

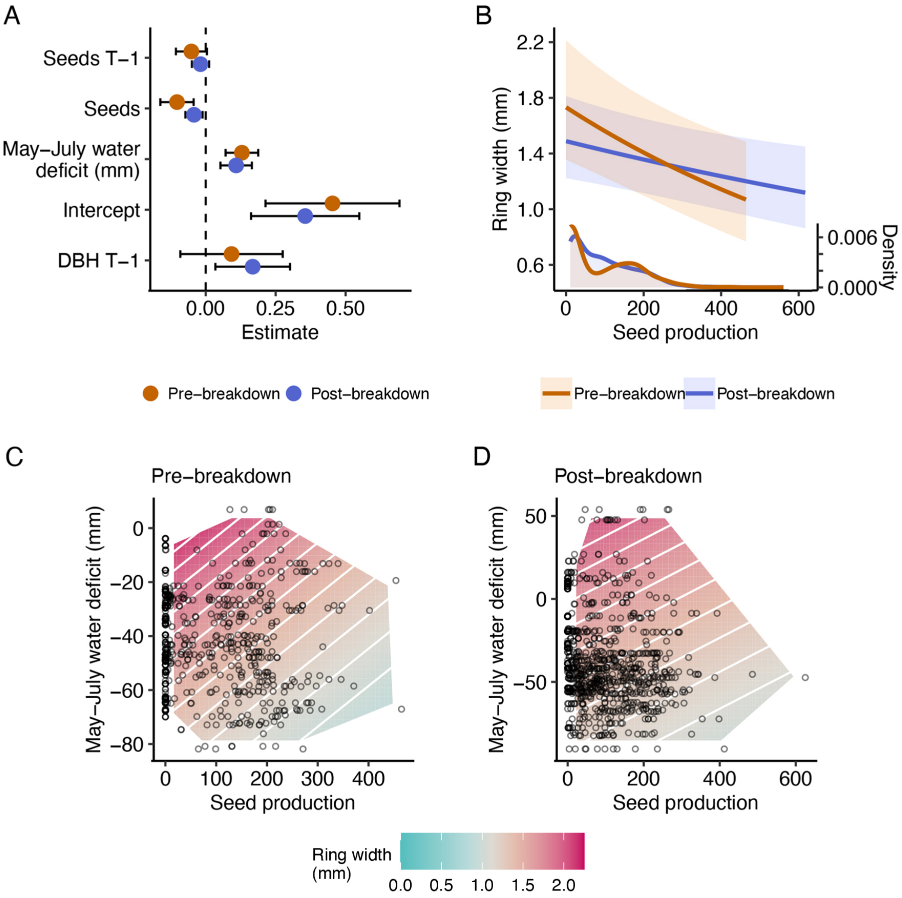

Figure 2: High-frequency variation in growth rate is related to summer drought and allocation to reproduction. A) Effect sizes of lagged seed production, production in the current year, summer drought, and previous year DBH on annual growth rates. Slopes and associated standard errors are estimated with a GLMM model with Gamma family error distribution that included tree ID (N = 57) and site (N = 7) as random intercepts. B) Relationship between the tree ring width and seed production pre-2006 (red) and post-2006 (blue); estimates and associated 95% CI are derived from the same model as presented at A). The inset density plot shows the distribution of observations. Surface plots at C) and D) show estimated growth rates across combinations of current-year seed production and summer water deficit, with the convex hulls defined by observations (black points). Predictions are derived from the same GLMM model as slopes presented at A). The y-axis range at D) may suggest that post 2006 period was less dry compared to before 2006, but we detected no trends in summer water deficit (Table S1), and that shift in y-axis range is largely driven by unusually wet 2007 (Fig. S2).

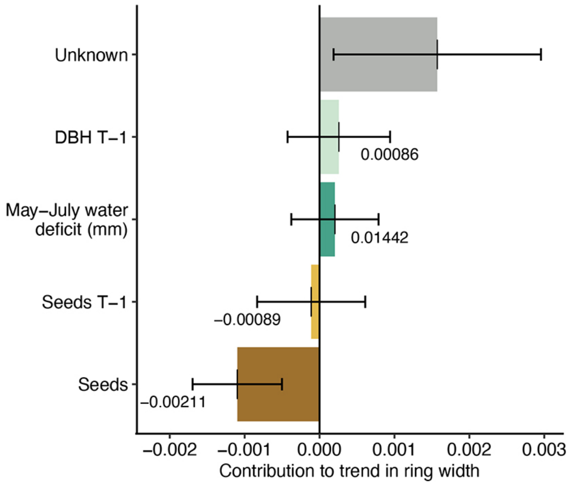

Figure 3: Contribution of the predictor variables to European beech growth trend. The analysis, based on 7 sites and 57 trees (1980–2022), indicated that change in patterns of seed production is the main contributor to the observed decrease in European beech annual growth rate (tree ring increments). The difference between the modeled contributions and the observed trend was considered an unknown contribution to the temporal variation of annual growth. The numbers alongside the bars show the sensitivity of ring width to predictor changes (see Methods: Trend attribution). Error bars for associated contributions indicate standard errors. See Methods for information about the methodology used to calculate the contributions.

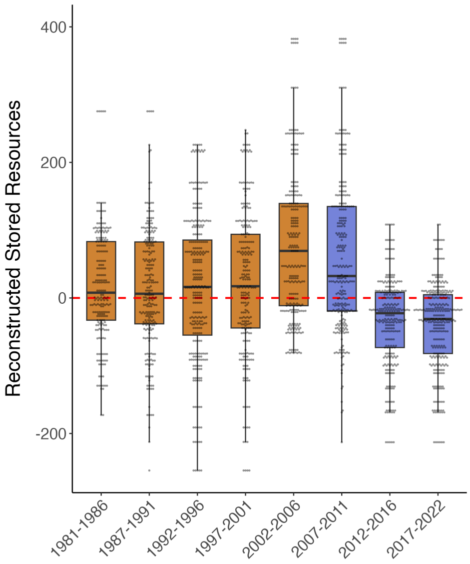

Figure 4: Temporal decline after 2006 in the reconstructed stored plant resources suggests an increase in relative reproductive allocation post-breakdown (blue bins). Resources are estimated from individual-level seed production data, following the Rees *et al.* (2002) method, see text. Boxplots are based on tree-level averages in each bin (shown as swarmed grey points), while the non-binned data is presented in Fig. S3. Resources in 2002-2006 and in 2007-2011 were significantly higher than in all other groups, while in 2012-2016 and 2017-2022 were significantly lower than in all other groups. Colors show periods before (red) and after (blue) 2006, when masting changed the state to less interannually variable and synchronized reproduction ("masting breakdown"; Fig. S1).

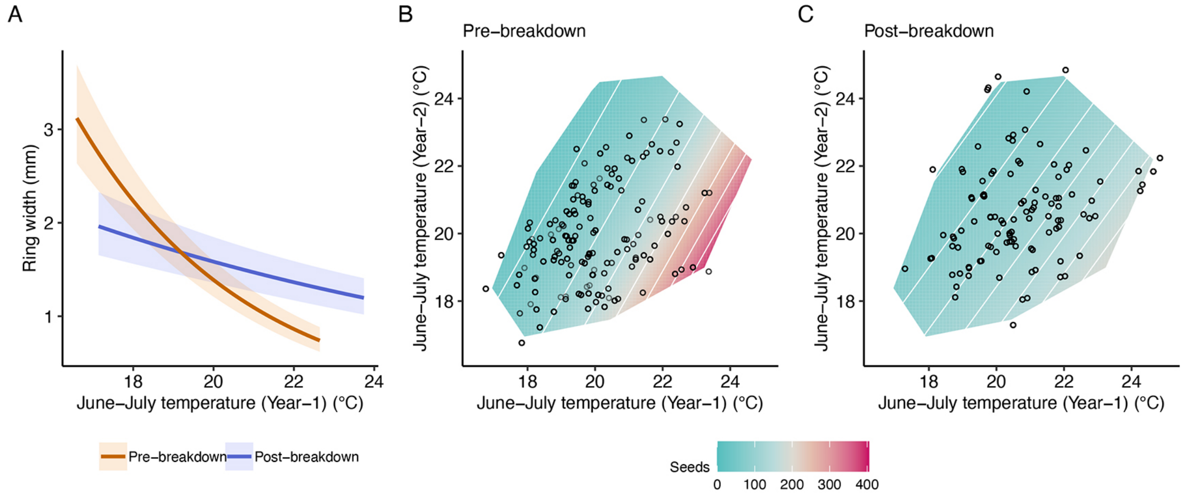

Figure 5: Weakening sensitivity of annual growth rate to previous year summer temperatures mirrors the similar pattern in association between seed production and summer temperatures. A) Association between annual tree ring increments and June-July mean max temperatures in the previous year, predicted for the period before (red) and after (blue) 2006, when masting changed the state to less interannually variable reproduction. Prediction lines are derived from a GLMM model with tree ID (N = 57) and site (N = 7) as random intercepts, shading shows associated 95% confidence intervals. Surface plots at B) and C) show estimated seed production across combinations of summer (June-July) temperatures one (T1) and two years (T2) before seed fall, with the convex hulls defined by observations (black points). Predictors are derived from zero-inflated negative binomial GLMM with tree ID and site used as random intercepts.

The strength of the relationship between growth and the previous year's summer temperature declined by two-thirds over time, with effect size -0.33 (SE = 0.02) before 2006, and -0.12 (SE = 0.02) after that year (Fig. 5A). Annual growth was estimated as 2.7 mm for temperatures below 18 °C in the pre-breakdown period, which is reduced by 30% to 1.91 mm in the post-breakdown period. At the same time, at a temperature of 22 °C, growth was estimated as 0.85 mm, which increased 1.6-fold to 1.36 mm (Fig. 5A). This is consistent with the observation that warming has broken the link between seed production and previous years' summer temperature (Fig. 5B,C), and a weakening of the relationship between growth and seed production (Fig. 2A,B). Cool summer temperatures in the previous year are no longer strongly associated with seeding failure (Fig. 5C), when growth is highest. Pre-2006, seed production was largely concentrated in years that followed a sequence of cold and hot summers ((Fig. 5B). Post-breakdown (2006-2022), seed production was weakly associated with previous summer temperatures (Fig. 5C).

Discussion

Evidence gathered in this study indicates that climate-driven shifts to more frequent reproduction may explain the observed decline in European beech growth rate. Consequently, we show a previously unidentified and indirect mechanism for climate change-driven growth decline in European beech, that may be operating covertly alongside a direct drought-driven decline already reported in other populations (Jump *et al.*, 2006; del Castillo *et al.*, 2022). The role of reproduction in mediating the response of growth to warming is consistent with the proposal of Leuschner (2020) that shifts in allocation to reproduction may contribute to reported growth responses to nitrogen deposition in Europe. It is also consistent with an observation that under experimentally-induced drought, holm oak (*Quercus ilex*), strawberry tree (*Arbutus unedo*), beech and spruce (*Picea abies*) maintain fecundity at the expense of reduced growth (Bogdziewicz *et al.*, 2020a; Hesse *et al.*, 2021). In our case, growth decline occurs despite no long-term trend in summer drought stress, because climate warming changes the temporal allocation of resources to reproduction. While this can explain the recent growth decline in the absence of increased summer drought stress in UK beech forests, we suspect that this driver may also be contributing to the reported growth declines across Europe (del Castillo *et al.*, 2022), where consistent warming-driven changes in masting are also occurring (Foest *et al.*, 2024). A priority for future research is understanding how the reproduction-driven growth decline mechanism reported here operates in conjunction with increases in summer drought stress.

Growth decreased in our populations because reproductive effort increased. Typically, variations in masting — the allocation of seeds across years — are assumed not to affect the long-term mean reproductive allocation (RA; Kelly (2020)). However, changes in RA are seldom tested, particularly in masting species, due to high interannual and interindividual variability. Previous studies on the English Beech Mast Survey initially reported a recent increase in mean seed production (Bogdziewicz *et al.*, 2020b), but this was later attributed mainly to a gradual increase in tree sizes over time (Bogdziewicz *et al.*, 2021). Our method that estimates an individual plant's reserves based on its cumulative seed production is more sensitive because it is less affected by short-term variability and allows the effects of large seed crops to persist over several years. Hence, the observed decrease in plant reserves from higher reproductive investment post-breakdown plausibly explains the growth declines. Importantly, our findings provide a rare demonstration in a mast-seeding tree that changes in the frequency of weather cues can alter both the temporal pattern of reproduction and the mean level of investment (RA). Although increased RA under climate change was initially considered a potential issue (McKone *et al.*, 1998), resource-based models Satake & Iwasa (2000); Rees *et al.* (2002) later suggested that changes in RA were unlikely. Our results challenge this notion, highlighting a novel mechanism by which climate change can impact tree growth through altered reproductive strategies.

Shifting allocation to reproduction is an important contributor to the observed decline in growth, despite the weakening of the growth-reproduction trade-off. Post masting breakdown, the positive growth response to low-to-medium seed production (0-150 seeds) weakens compared to the pre-breakdown period, i.e. years of low seed production are no longer associated with such a large positive growth response. We interpret this as a consequence of increasingly resource-limited conditions, caused by more frequent reproduction. Strong depletion of carbon and other nutrients in association with masting is widely documented (Sala *et al.*, 2012; Han & Kabeya, 2017; Roncé *et al.*, 2023), and fruit removal experiments in trees prove that reproduction depletes resources (Sala *et al.*, 2012; Roncé *et al.*, 2023). We hypothesize that more frequent reproduction is depleting internal resource reserves, inhibiting the strong positive growth response to low seed production. This effect is not offset by the corresponding dampening of growth response to peak seed production because high seed production years are rare, particularly post-breakdown.

The transition in masting patterns toward more consistent reproduction, and the weaker effects of seed production on growth, paralleled a diminishing correlation between growth and the previous summer temperature. This lagged correlation is ubiquitous in European beech tree ring chronologies, and results from an indirect effect of summer temperature-cued masting and a growth-reproduction trade-off (Piovesan & Schirone, 2000; Hacket-Pain *et al.*, 2018). The correlation is typically stronger in older or larger trees Hacket-Pain *et al.* (2016), probably because investment in reproduction increases with age (Genet *et al.*, 2009; Pesendorfer *et al.*, 2020). In contrast, we found the opposite trend. The decline in correlation over time resulted from the weakening of the growth reproduction trade-off, combined with the reduced sensitivity of seed production to summer temperatures. These effects are likely due to shortened intervals between seeding events, limiting the accumulation of reserves for substantial seeding efforts (Rees *et al.*, 2002; Bogdziewicz *et al.*, 2021). Our findings align with this narrative; historically, a strong association between summer weather and masting led to predictable and synchronized peak seed production years following warm summers, accompanied by significant negative growth anomalies. However, currently, such warm summers are less reliably linked to high seed production, resulting in less predictable growth responses. That suggests that the breakdown in masting is linked to "signatures" in tree-ring chronologies, i.e. weakened correlations between growth and previous summer temperatures, which might help identify effects described here even in the absence of direct monitoring of both seed production and growth.

The indirect effects of altered reproductive patterns on growth rates can vary depending on the reproductive biology of the species under consideration. In European beech, and other species where masting is triggered by high temperatures (Fernández-Martínez *et al.*, 2017; Zamorano *et al.*, 2018; Pesendorfer *et al.*, 2020), warming which exceeds the capacity of the species to adapt or acclimate could potentially amplify annual allocation to reproduction and decrease its inter-annual variation (Bogdziewicz *et al.*, 2024; Foest *et al.*, 2024), resulting in declining radial growth. Conversely, in species where reproduction is stimulated by low temperatures or suppressed by high temperatures, warming may reduce the frequency of high-seed years, enabling higher investment in growth. For instance, in *Beilschmiedia tawa*, reduced frequency of low winter and summer temperature cues resulted in reproductive failure in warmer sites (Yukich-Clendon *et al.*, 2023). On the other hand, masting in other species like North American conifers seems to be largely insensitive to weather trends, which could render their reproductive patterns resistant to climate change (LaMontagne *et al.*, 2021). Consequently, as the climate warms, reproduction frequency may decrease or increase, depending on the masting mechanisms in operation (Bogdziewicz *et al.*, 2024), with potentially predictable responses of growth. The growth response to a change in reproductive allocation will also depend on the strength of trade-offs between seed production and growth (Thomas, 2011; Patterson *et al.*, 2023). Tree ring measurements offer the potential to reconstruct growth patterns in populations in which seed production has been monitored for decades (Hacket-Pain *et al.*, 2022), opening the avenues for testing these hypotheses.

In summary, the breakdown of masting within our populations correlates with a decline in growth, even without concurrent trends in summer aridity (del Castillo *et al.*, 2022). This reveals a previously unrecognized indirect pathway by which climate change can influence growth trends — through its effect on tree reproduction. The documented decline in growth presents a concerning scenario for European beech populations, which now face a cascade of negative effects under warming temperatures. Declining growth indicates reduced vitality, reduced future reproduction due to smaller plant size, lower carbon uptake, increased vulnerability to future climate extremes, and could serve as a precursor to dieback and mortality (Dobbertin, 2005; Gillner *et al.*, 2013; Neycken *et al.*, 2022). Moreover, despite increased reproductive effort, the breakdown in masting means the trees actually produce fewer viable seeds. Reduced flowering synchrony and decreased interannual variability lead to higher seed predation and decreased pollination efficiency, resulting in up to an 80% decrease in viable seed production (Bogdziewicz *et al.*, 2020b, 2023). While life history theory predicts that long-lived plants should avoid reproduction that lowers survival (Obeso, 2002; Thomas, 2011), an abruptly changed environment may render the regulation of reproduction maladaptive, with broad consequences for demographic rates. Thus, European beech faces a "perfect storm" under climate change: lower growth, lower carbon uptake, higher flowering effort, and lower viable seed production, all at a time when robust regeneration and carbon uptake are crucial for forests across Europe.

Materials and Methods

Study system and data collection

European beech is a major forest-forming species in temperate Europe, with high economic and ecological importance (Leuschner & Ellenberg, 2017). Beech is a model masting species, with seed production characterized by large interannual variation and synchrony (Nilsson & Wastljung, 1987; Mund *et al.*, 2020). High seed production negatively correlates with above-ground productivity (Müller-Haubold *et al.*, 2013, 2015; Hacket-Pain *et al.*, 2017). Across the species range, annual growth is mainly driven by early summer moisture availability (Dorado-

Liñán *et al.*, 2022; Weigel *et al.*, 2023).

The English Beech Mast Survey was established in 1980, with seed production sampled at 15 sites across England annually (Bogdziewicz *et al.*, 2023). The ground below each tree was searched for seeds for 7 minutes, and the collected seeds were later sorted and counted in the laboratory. Our past studies on these beech populations have shown that interannual variability and among-trees synchrony of beech seed production declined by 3̃0% over the past four decades, which includes less frequent reproductive failures (Bogdziewicz *et al.*, 2020b). The state of masting changed abruptly after 2005, the last highly synchronized year. Post-2005, masting switched to more regular and less synchronized reproduction, termed "masting breakdown" (Bogdziewicz *et al.*, 2021). Interannual variation of seed production associated with masting increases reproductive efficiency through reduced seed predation and improved pollination efficiency (Kelly, 1994; Pearse *et al.*, 2016). Consequently, masting breakdown decreased pollination efficiency and increased seed predation, reducing viable seed production by 50-80%, depending on tree size (Bogdziewicz *et al.*, 2023). Trend attribution analysis suggested that temperature that rose $\sim 1^{\circ}$C over the last four decades was responsible (Bogdziewicz *et al.*, 2020b). Proximally, the masting breakdown is caused by increased frequency of weather cues that trigger flowering (Bogdziewicz *et al.*, 2021). Recurrent cueing increased the fraction of years when flowering is triggered, which has led to less frequent failures and more regular reproduction (Bogdziewicz *et al.*, 2020b, 2021), a trend now reported over the majority of European beech range (Foest *et al.*, 2024).

In 2022, we cored 57 trees across 7 sites. Cores were extracted using an increment corer, at 1.3m above ground level, and perpendicular to any slope to avoid tension wood. 1-2 cores were sampled per trees, air-dried, and then prepared using standard dendrochronological methods. Polished cores were imaged using a flatbed scanner, and ring width was measured using CooRecorder v9.8.1 (Maxwell & Larsson, 2021).

We extracted daily weather data for each site from the corresponding 0.1° grid cell of the E-OBS dataset (Cornes *et al.*, 2018). The summer water deficit was calculated as $P - PET$, with P standing for precipitation and PET for potential evapotranspiration, summed from May 1st to July 31st del Castillo *et al.* (2022); Weigel *et al.* (2023). Evapotranspiration PET was calculated based on the Thornthwhaite equation (Thornthwaite, 1948) using the R package SPEI (Beguería & Vicente-Serrano, 2017).

Data analysis

Trends in annual growth. We have started our analysis by testing for the temporal trends in annual tree ring increments in sampled trees. To this end, we have fitted a generalized linear mixed model (GLMM) that included tree ID (N = 57) and site (N = 7) as random intercepts. We used the Gamma family error and log link. Tree ring chronologies typically contain low-frequency trends associated with changes in tree size and competition. All our sampled trees were reproductively mature and at least canopy co-dominant when first added to the masting survey, so we did not statistically detrend ring width. Instead, our model included year and tree diameter at breast height (DBH) in the year prior to growth as predictors. The year effect was fitted with a B-spline to allow for non-linear trends.

High-frequency variation in growth increments. To test for the relationship between annual tree ring increments, summer drought, and seed production, we have fitted a GLMM, with a Gamma family error term and log link. Tree ID and site ID were used as random intercepts, while drought (May-July water deficit), seed production in the current year (T), and seed production in the previous year (T-1), and tree size (DBH) in the previous year (T-1) were used as fixed effects.

Trend attribution analysis. To attribute the temporal trends in annual tree ring increments to its possible drivers, we used the temporal contribution method (Fernández-Martínez & Maspons, 2019; Pesendorfer *et al.*, 2020). First, using the tree ID and site as the random intercepts, we modeled annual growth as a function of drought (May-July water deficit), seed production (current and past, T and T-1), and tree size. We then used the full model to predict the change in ring increments during the study period (1980–2022). We first calculated the observed trend (slope estimate ± standard error of the slope estimate) in our data using GLMMs with random intercepts. We then calculated the trend predicted by the full model and the trends predicted by the same model but maintaining the predictors constant one at a time (for example, drought is held constant, using the mean values per site, while all other predictors change according to the observations). The difference between the trend predicted by the full model and when one variable was controlled was the contribution of that predictor variable to the change in the response variable. The difference between all individual contributions and the observed trend was considered to be unknown contributions. Finally, we calculated the average ring width sensitivities to predictor changes by taking the differences between the full model trend and the trends from the models with the predictors held constant, and dividing it by the trends of the predictor variables. All errors were calculated using the error-propagation method (Fernández-Martínez & Maspons, 2019).

Reconstructing stored resources To estimate how change in masting patterns affected relative allocation to reproduction, we reconstructed individual tree stored resources from seed production data, following the approach developed by Rees *et al.* (2002). In short, this analysis includes fitting a linear model of cumulative reproduction (summed seed count) vs cumulative years (as a surrogate of resource acquisition over time). We used generalized linear mixed models (GLMMs) implemented via the 'lme4' package (Bates *et al.*, 2015) with plant ID and site ID as random intercept and year as random slope. The random effect structure allowed fitting a unique intercept for each plant which estimates stored resources of a plant at the beginning of the monitoring period (Rees *et al.*, 2002), while random slope allowed heterogeneous resource acquisition of individuals over time (Crone *et al.*, 2005). Because that analysis requires long-term, continuous observations, we used a subset of trees from the English Beech Mast Survey that have been monitored for at least 30 years (N = 56).

To test whether estimated stored resources, and therefore relative allocation to reproduction, have changed over time, we have binned the stored resources into 5-year-long bins, and calculated the tree-level mean for each bin. That was done to smooth over the large year-to-year variation associated with masting (Bogdziewicz *et al.*, 2020b, 2023). We adjusted the bins to have 2006 as one of the bin borders; in consequence, the first and last bins have 6 years. The differences among bins were tested with an LMM model that included tree and site ID as random intercepts.

Growth and seed production sensitivity to weather cues. We tested for the temporal change in the association between radial growth and summer temperatures in the preceding year with a Gamma family, log link GLMM model. The model included tree ID and site ID as random intercepts and the previous year's mean maximum summer (June-July) temperature as a fixed effect and tree size (DBH) as a covariate. A similar model was constructed for seed production. Here, we used zero-inflated negative binomial GLMM with log-link, and two fixed factors: seed production in the previous year (T-1) and two years before seed fall (T-2). That is because the relationship between the T1 summer temperature is conditional on the T2 summer temperature; cold T2 summer enhances the response to T1 temperature (Vacchiano *et al.*, 2017; Journé *et al.*, 2024). In addition, we included individual-level seed production in T1 as a covariate. Both models (with growth and seeding as a response) were fitted to two data subsets; 1980 - 2005, and 2006-2022. 2006 is the year when European beech masting at our site changed state to more regular and less synchronized reproduction (Fig. S1) (Bogdziewicz *et al.*, 2020b, 2023).

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Author Contributions Statement

AHP, MB, JSz, DK designed the study, AHP, JL and PT collected the tree ring samples, AHP measured the samples, JSz ran the analysis, all authors contributed to the data interpretation, AHP and MB wrote the first draft of the manuscript, all authors revised the text.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are available at

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Supporting Information

Hacket-Pain et al. Growth decline in European beech associated with temperature-driven increase in reproductive allocation.

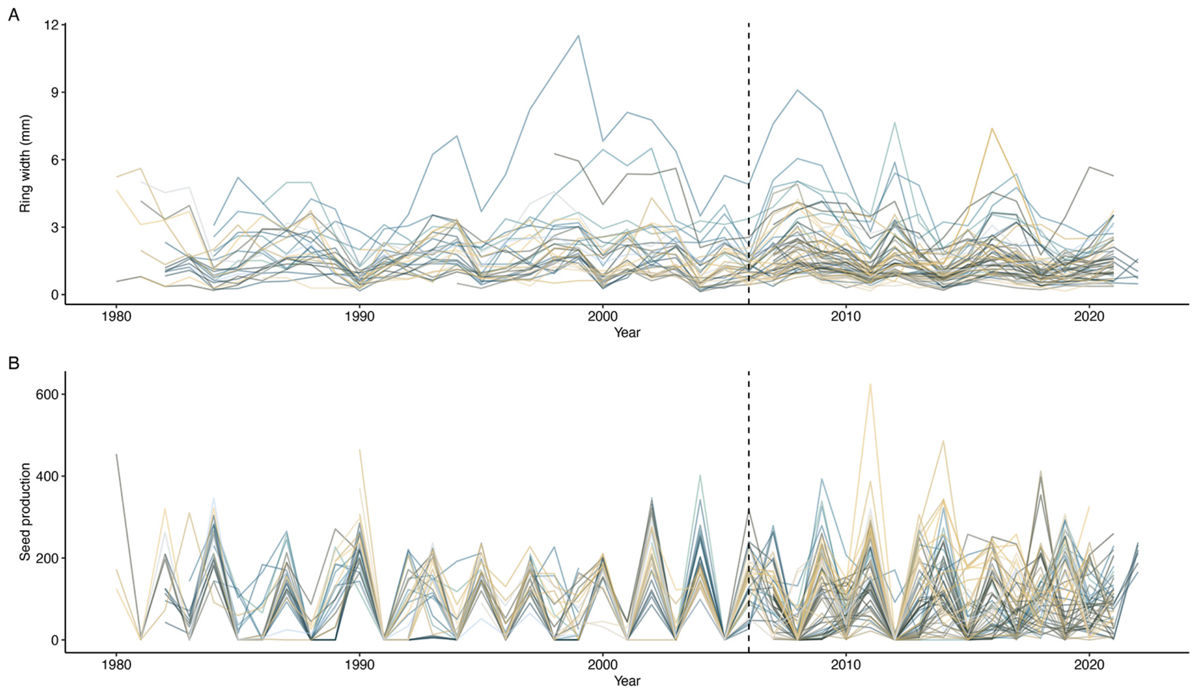

Figure S1: Individual-level temporal patterns of A) growth rates as measured by tree ring increments and B) seed production, measured across 7 sites and 57 trees. Each line shows one tree. The dashed vertical line shows the year 2006, at which masting at our populations changed the state into more regular and desynchronised seed production, called "masting breakdown.

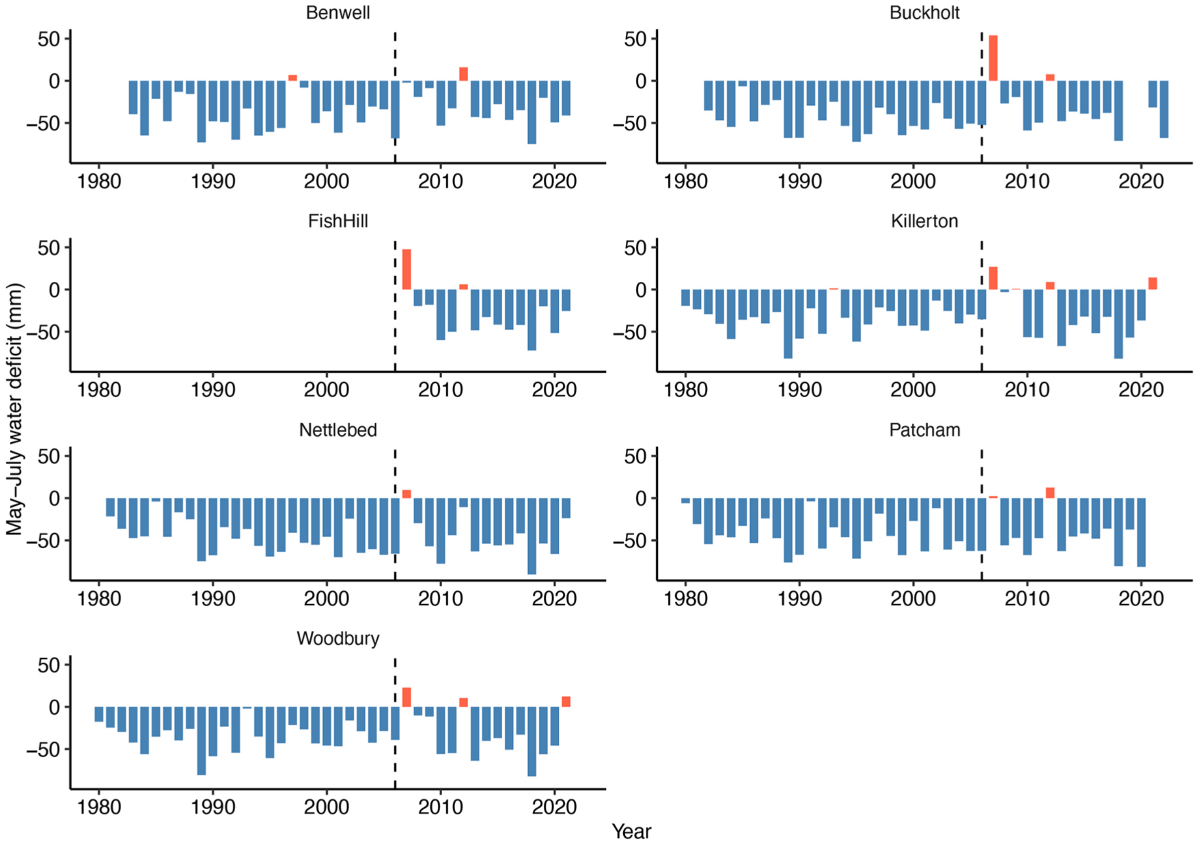

Figure S2: Annual variation in May-July water deficit (mm) at 7 study sites as measured by the difference between precipitation and potential evapotranspiration ($P - PET$). The bars are colored blue for drought and red for wet conditions. The dashed vertical line shows the year 2006, at which masting at our populations changed the state into more regular and desynchronised seed production (Fig. S1). Range of annual observations is trimmed to the observations of growth rates and seed production for each site.

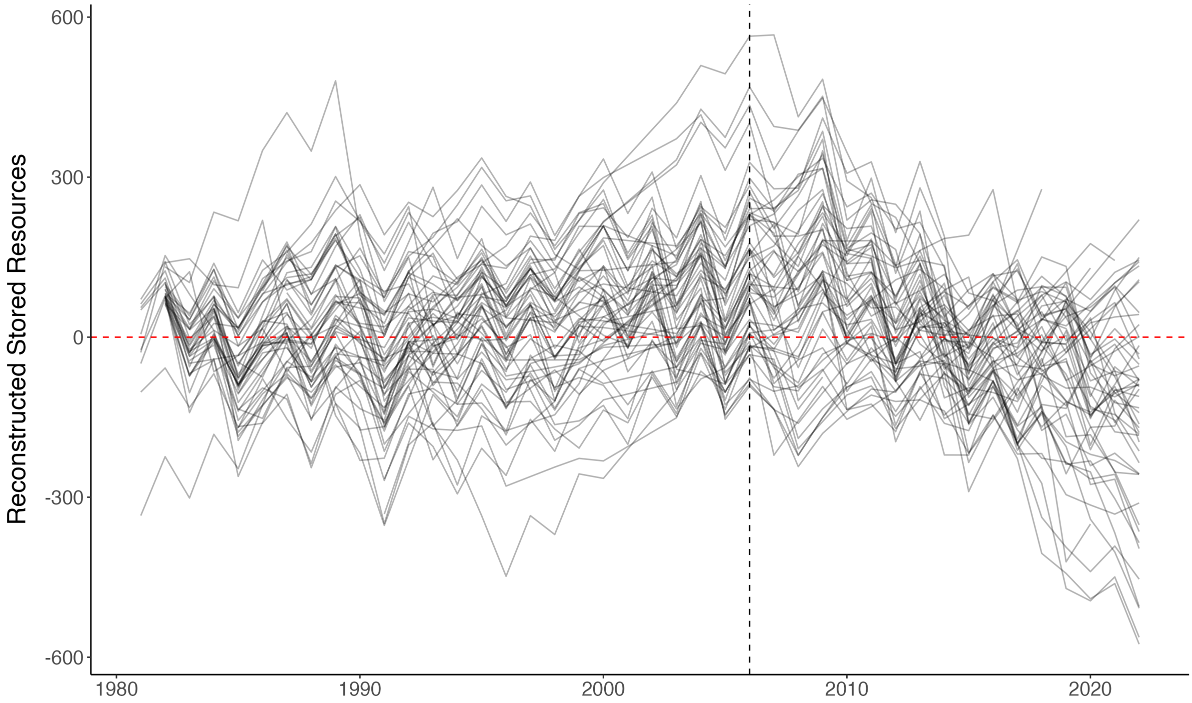

Figure S3: Temporal variation in the reconstructed stored resources. Each line shows one tree (N = 51). Resources are estimated from individual-level seed production data, following the Rees *et al.* (2002) method. In short, these are residuals of the linear relationship between cumulative seed production and cumulative time. The horizontal dashed line highlights 0, while the vertical year 2006, i.e. the year when masting changed the state to more regular and less synchronized reproduction (see Fig. S1).

Table S1: Results of model selection based on Akaike Information Criterion for models testing the temporal trends in May-July water deficit. We tested for the temporal trends using a set of GLMMs, with each model including water deficit as a response and site as a random intercept. The null model was intercept-only model and assumed no temporal trend in water deficit. In the other models, we included ranked year as a predictor fitted either as a linear effect (i.e., assuming linear trend) or via natural cubic spline to test for non-linear trends. Moreover, in the subset of trend models we included also the AR(1) covariance structure to account for a possible temporal autocorrelation of the water deficit time series. The models were fitted using water deficit data trimmed to the years with observations of growth rates and seed production at each site, and compared using Akaike Information Criterion following (Burnham *et al.*, 2011). Note that in the models that included the year effect, and which scored relatively well (Δ = 1.9), the year effect was not significant (p > 0.7)

Model	AICc	ΔAICc	weight
null model (intercept-only)	2371.0	0.0	0.537
non-linear trend	2372.9	1.9	0.205
linear trend	2372.9	1.9	0.205
linear trend + AR(1)	2377.0	6.0	0.027
non-linear trend + AR(1)	2377.0	6.0	0.027