European beech reproduction is not reduced by drought, including the 2003, 2018, and 2022 extremes

Jakub Szymkowiak[1,2], Michał Bogdziewicz*[1], Dave Kelly[3], Jessie Foest[1], Sabine Braun[4], Burkhard Beudert[5], Francesco Chianucci[6], Andrea Cutini[6], Rachel Gaulton[7], Georg Gratzer[8], Angelika Kölbl[5], Georges Kunstler[9], Jonathan G. A. Lageard[10], Henning Meesenburg[11], Francesco Mezzavilla[12], Martina Mund[13], Anita Nussbaumer[14], Mario B. Pesendorfer[8], Wolfgang Schmidt[15], Anne Thimonier[14], Peter A. Thomas[16], Stanislav Vacek[17], Zdeněk Vacek[17], Arne Verstraeten[18], Markus Wagner[11], Andrew Hacket-Pain*[19]

[1]Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland.

[2]Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland.

[3]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand.

[4]Institute for Applied Plant Biology, Witterswil, Switzerland.

[5]Department of Conservation and Research, Bavarian Forest National Park, Grafenau, Germany.

[6]CREA – Research Centre for Forestry and Wood, Arezzo, Italy.

[7]Fera Science Ltd, York Biotech Campus, Sand Hutton, York, YO41 1LZ, United Kingdom.

[8]BOKU University, Institute of Forest Ecology, Department of Ecosystem Management, Climate and Biodiversity, Peter-Jordan-Strasse 82, A-1190 Vienna, Austria

[9]Université Grenoble Alpes, INRAE, LESSEM, Saint-Martin-d'Hères, France.

[10]Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, United Kingdom.

[11]Department of Environmental Control, Northwest German Forest Research Institute, Göttingen, Germany.

[12]Via Malviste 4 – 31057 Silea (TV), Italy.

[13]Forestry Research and Competence Centre Gotha, Gotha, Germany.

[14]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.

[15]Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany.

[16]School of Life Sciences, Keele University, Staffordshire ST5 5BG, United Kingdom.

[17]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic.

[18]Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium.

[19]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.

*corresponding authors: michalbogdziewicz@gmail.com; Andrew.Hacket-Pain@liverpool.ac.uk

Abstract

Climate change is intensifying drought stress in temperate forests, but its effects on tree reproduction, central to forest regeneration and migration capability, remain poorly understood. Here, we analyse 221 time series of beech (*Fagus sylvatica*) seed production across Europe to test whether drought reduces seed output. We isolate drought exposure during the flowering, pollination and seed maturation phases of reproduction, and test for legacy effects on future reproduction. Seed production was not impaired by summer drought, and dry spring conditions were associated with increased output, likely via enhanced pollen dispersal. Thus, once initiated, beech reproduction is not reduced by drought, with no suppression of reproduction the following year. Reproduction was not reduced at the driest sites during exceptional European summer droughts in 2003, 2018 and 2022. Considered alongside prior evidence that drought suppresses forest growth and elevates mortality, these findings indicate that vital rates can respond in opposite directions to the same stressor. Such contrasts may sustain forest reproduction during heat–drought events yet shift demographic balance toward higher mortality and turnover as climatic extremes intensify.

Classification

Biological sciences: Ecology

Significance Statement

Forest resilience to climate change depends not only on whether trees survive droughts, but also on whether they can still reproduce. Long-term seed production records from across Europe reveal that European beech continues to produce seeds even during the most severe recent summer droughts, including the 2003, 2018, and 2022 extremes. This resilience of reproduction sharply contrasts with the drought-induced declines in growth and increases in mortality observed in the same species and regions. Our results demonstrate that tree demographic rates respond differently to drought, with implications for predicting forest regeneration, turnover, and long-term responses to a warmer, drier climate.

Key words

Climate change, Climatic extremes, Drought, Seed production, Tree demography, Forest resilience

Introduction

Global change is altering average climatic conditions and their variability, leading to more frequent and intense extremes such as heatwaves and severe droughts (IPCC, 2023). Observations across continents reveal consistent trends with increasing rates of forest disturbance, elevated tree mortality, and changing growth dynamics in adult trees and seedlings (Johnstone *et al.*, 2016; McDowell *et al.*, 2020; Hartmann *et al.*, 2022; Klesse *et al.*, 2024; Mantgem *et al.*, 2009). In Europe, recent summer droughts have reached intensities without precedent in the past two millennia (Buras *et al.*, 2020; Büntgen *et al.*, 2021), exerting mounting pressure on forest demography (Senf *et al.*, 2018; McDowell *et al.*, 2020). For instance, tree canopy mortality trends have accelerated in response to prolonged drying (Senf *et al.*, 2020). The 2018–2020 European drought sharply illustrates the magnitude of current climatic pressures: stem growth declined by approximately 40% at sites in German forests (Thom *et al.*, 2023; Sachsenmaier *et al.*, 2024), and widespread dieback and mortality occurred among adult trees and saplings (Schuldt *et al.*, 2020; Beloiu *et al.*, 2022; Knutzen *et al.*, 2025). Yet while there are published data on the demographic consequences of drought through growth and mortality, much less is known about how drought influences reproduction, despite its key importance for long-term forest dynamics (Johnstone *et al.*, 2016; Seidl & Turner, 2022).

The resilience of forests to disturbance, including the potential reorganisation to non-forest, depends on the magnitude and consistency of tree reproduction and subsequent regeneration (Johnstone *et al.*, 2016; Brodribb *et al.*, 2020; Seidl & Turner, 2022; Davis *et al.*, 2023). In forests, tree reproduction is realised through seed production, a multi-stage process from floral initiation through pollination to seed maturation, which ultimately determines the potential for regeneration (Clark *et al.*, 2021; Hanbury-Brown *et al.*, 2022; Bogdziewicz *et al.*, 2025). Despite its central role, our understanding of how climate extremes, particularly drought, affect reproduction remains fragmentary (McDowell *et al.*, 2020; Seidl & Turner, 2022). In contrast to mortality, where extensive evidence and mechanistic theory link drought to hydraulic failure, carbon starvation, and biotic attack (Hartmann & Trumbore, 2016; McDowell *et al.*, 2022; Netherer *et al.*, 2024; Leuschner, 2020), reports of reproductive responses are sparse (Dohrenbusch *et al.*, 2002; Pérez-Ramos *et al.*, 2010; Zamorano *et al.*, 2018; Wright *et al.*, 2021; Zhang & Brodribb, 2017). Currently, we lack not only a physiological framework for interpretation, but also the basic knowledge of whether drought effects on reproduction are typically positive, negative, or neutral. This uncertainty is consequential: the direction and magnitude of reproductive responses will determine the regeneration potential of forests under drought (Martínez-Vilalta & Lloret, 2016), the capability of trees to track moving climate envelopes (Svenning & Skov, 2007; Nathan *et al.*, 2011), and, through the costs of reproduction, changes in the mortality risk to adult trees (Lauder *et al.*, 2019).

Drought is expected to influence tree seed production through multiple pathways. Drought can directly constrain photosynthesis and water uptake (McDowell *et al.*, 2008; Sevanto *et al.*, 2014), reducing the resources available for reproductive investment. Such resource limitation has been linked to declines in seed production in Scots pine (Vilà-Cabrera *et al.*, 2014), and is well-documented in herbaceous systems (Sage *et al.*, 2024). However, the consequences for seed output depend not only on resource availability, but also on how trees allocate those resources under stress. Reproduction can be prioritised or deprioritised under drought, relative to growth and other functions, including defence (Hacket-Pain *et al.*, 2017; Lauder *et al.*, 2019; Gonzalez *et al.*, 2023). For example, Lauder *et al.* (2019) suggested that trees may respond to drought by either allocating resources toward survival-related functions such as growth and defence, or by maintaining investment in reproduction at the potential cost of reduced survival. In support, in *Pinus ponderosa, Picea abies, and Quercus ilex, drought makes the trade-off between reproduction and growth or defence more pronounced* (Bogdziewicz *et al.*, 2020a; Hesse *et al.*, 2021; Gonzalez *et al.*, 2023). Drought can also reduce pollen viability or fertilisation rates (Tushabe & Rosbakh, 2025). However, not all effects are negative: warm and dry spring conditions may improve pollen dispersal and enhance pollination efficiency (Fleurot *et al.*, 2024), potentially increasing seed set under some circumstances. Moreover, maintaining reproduction under drought may confer selective advantages if stress signals favourable post-disturbance conditions for recruitment or if completing reproduction carries lower short-term costs than reallocating resources (Ascoli *et al.*, 2013; Lauder *et al.*, 2019). Because these mechanisms can act at different stages of reproduction and can operate in opposite directions, inference from short records or single drought events is limited. Long-term seed production datasets spanning multiple drought and non-drought years are needed to separate drought effects occurring during flowering and pollination from those during seed maturation, and to test for lagged effects on subsequent reproduction.

Here, we analyse 221 time series (5362 population-level, annual observations) of European beech reproduction to test whether drought disrupts seed production. Reproduction in beech varies strongly among years (masting), largely the result of temperature cues which regulate annual flowering effort (Vacchiano *et al.*, 2017; Journé *et al.*, 2024). Thus, we ask whether drought (climatic water balance, CWB) reduces seed output in years when trees are already committed to reproduce. By explicitly modeling the temperature cues that govern annual flowering effort, we separate cue-driven commitment from drought acting as a climatic veto during subsequent reproductive processes. We partitioned drought exposure into two phenological phases: flowering and pollination (spring, April–May) and fruit maturation (summer, June–September) and also tested for lagged effects of summer drought on seed production the following year. We hypothesised that spring drought could enhance seed production by promoting pollen dispersal under dry conditions in this wind-pollinated species (Schermer *et al.*, 2020; Fleurot *et al.*, 2024). In contrast, summer drought was expected to reduce seed production if trees allocate limited resources to competing sinks such as stem or root growth or storage under stress (Lauder *et al.*, 2019; Chuste *et al.*, 2020). Alternatively, reproductive output could be maintained despite summer drought if finalising seed maturation under stress is selectively advantageous (Wiley *et al.*, 2017). Two mechanisms could support such selective benefits. First, a form of reproductive persistence, akin to a "flight" strategy, where trees maintain reproduction at the expense of growth and survival-related functions (Lauder *et al.*, 2019). Second, reproduction may be favoured under stress as an adaptive response to environmental signals (Piovesan & Adams, 2005; Ascoli *et al.*, 2020): drought-induced canopy opening may signal favourable conditions for seedling establishment (Ascoli *et al.*, 2013; Maringer *et al.*, 2020), thus favouring investment in current seed maturation. In addition to analysing seed production responses

Table 1: Results of the Generalised Linear Mixed model testing for the effects of seasonal drought on European beech reproduction. Drought in spring had a positive effect, while drought in summer had no effect. The model included seed production (scaled between 0 and 1 at the site level) as a response, while masting cue (ΔT, i.e., the difference between summer temperatures two and one year before flowering), spring (April-May) and summer (June-September) climatic water balance (CWB, negative values indicate water deficit), summer CWB in year T-1, and previous year seed production (seeds T-1), were fixed effects. The model included siteID as a random intercept and was fitted with a Tweedie error distribution and logit link function.

Term	Estimate	SE	z	p
Intercept	-1.37	0.039	-35.51	**<0.001**
ΔT	0.72	0.024	30.48	**<0.001**
Spring CWB	-0.16	0.018	-8.60	**<0.001**
Summer CWB	0.01	0.020	0.47	0.637
Summer CWB T-1	-0.17	0.022	-7.70	**<0.001**
Seeds T-1	-0.58	0.021	-27.73	**<0.001**
Spring CWB * ΔT	0.05	0.022	2.34	**0.019**

across the full range of drought conditions represented in our dataset, we also test whether recent exceptional spring/summer drought events in Europe (in 2003, 2018, and 2022) (Gharun *et al.*, 2024) were associated with declines in seed production, paralleling established responses of tree growth and survival to these events.

Results

European beech reproduction was not suppressed by seasonal drought during reproduction, with no evidence that spring or summer climatic water deficits suppressed seed production (Fig. 1, Table 1 consistent results when using VPD to quantify drought, see Methods and TableS2). Once trees were committed to flowering, as indicated by strong responses to the flowering cue (ΔT, i.e., the difference between June-July temperatures one and two years before seedfall, see Methods) (Fig. 1), seed production increased under spring drought (Fig. 1). The positive effect of spring drought was slightly more pronounced when the ΔT cue was weaker (Spring CWB and ΔT interaction, Table 1, Fig. 1). Seed production was insensitive to summer drought conditions irrespective of the ΔT cue (Fig. 1). The positive effect of ΔT on seed production was 5 times stronger than the effect of spring drought (climatic water balance, CWB), underscoring that reproductive output in beech is primarily governed by sensitivity to its masting cue. Residual analyses showed no systematic patterns with summer drought intensity, indicating that no additional effects were overlooked at the extremes (Fig. 1f). Summer CWB did not suppress reproduction the following year; a weak significant effect indicated seed production was in fact slightly higher in the year following summer drought.

A complementary analysis of extreme drought years in 2003, 2018, and 2022 corroborated these findings (Fig. 2). At a continental scale, these three droughts are the most severe European events of recent decades, and possibly of the last two millennia (Gharun *et al.*, 2024; Büntgen *et al.*, 2021; Buras *et al.*, 2018; Schuldt *et al.*, 2020). Nevertheless, their severity varied across our network sites (Fig. S1). Sites experiencing the most severe drought conditions in these years did not have lower than expected seed production, based on the ΔT weather cue (Fig. 2). Indeed, in 2018 and 2022, it was the wettest sites that had lower than expected seed production, rather

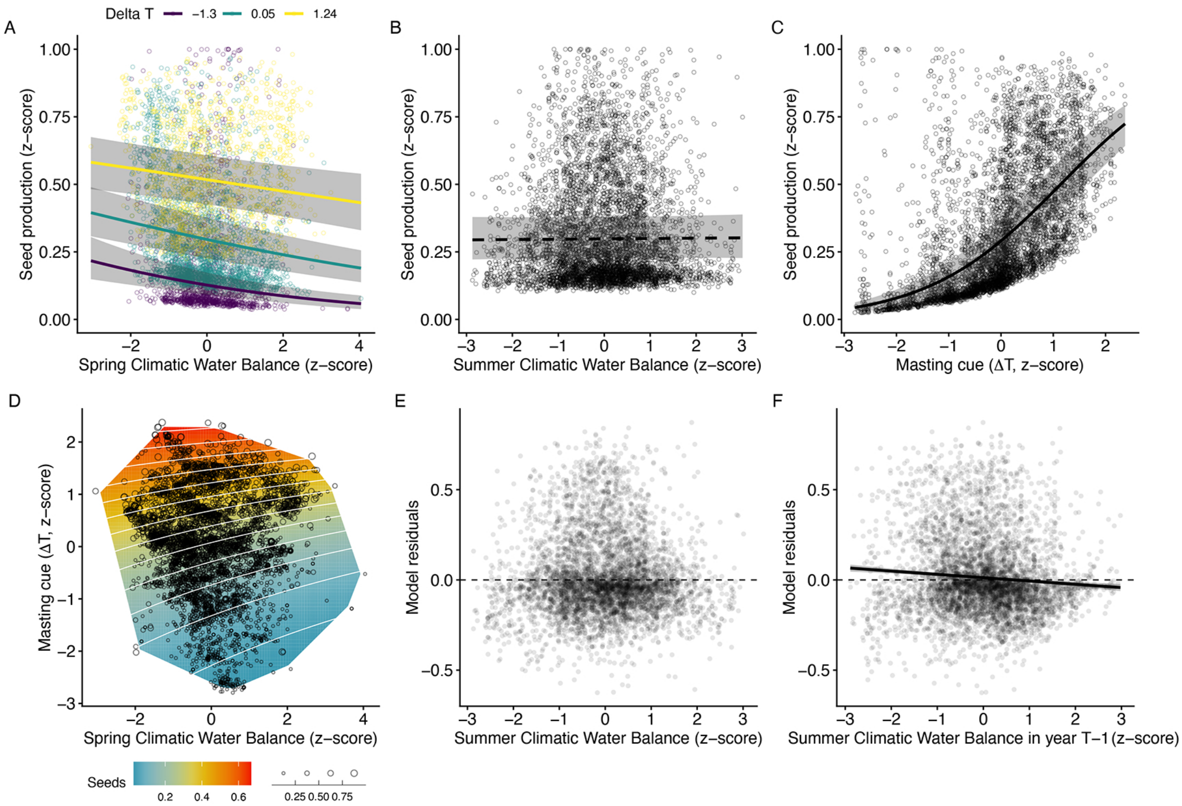

Figure 1: European beech reproduction is not suppressed by seasonal drought. Estimated relationships between A) masting cue (ΔT, i.e., difference between summer temperatures two and one year before flowering, see Methods), B) spring (April-May) climatic water balance (CWB, negative values indicate water deficit), and C) summer (July-September) CWB on population-level seed production in European beech. The dashed line at B) highlights a non-significant effect. Points on A-C show partial residuals of a model including the ΔT masting cue, spring CWB, summer CWB and prior year seed production (see Methods). D) Surface plot shows estimated population-level seed production effort across combinations of masting cue and spring CWB, with the convex hulls (parameter space across which predictions are computed) defined by observations (black circles). Points show population-level annual seed production. E) The model residuals plotted against summer CWB highlight the lack of overlooked effects at extremes. F) The model residuals plotted against summer CWB in year T-1 showing the weak negative effect of past-year drought on seed production. Estimates are derived from a GLMM that included site as a random intercept (N sites = 221, N observations = 5362).

than the driest where seed production was close to that predicted (negative residuals at wet sites, Fig. 2). In other words, sites that experienced the most severe conditions in these exceptional European summer droughts did not have lower-than-predicted seed production.

Discussion

Our findings demonstrate that once European beech trees are committed to reproduction, following favourable masting cues, drought does not impair the quantity of seeds produced, even under extreme conditions. Across 221 time series, we found no evidence that drought during fruit maturation reduced seed output in the year of drought or the following year. Instead, seed production was maintained or slightly increased, including in years of severe summer drought such as 2003, 2018 and 2022. These patterns indicate that, at the stand level, reproductive output

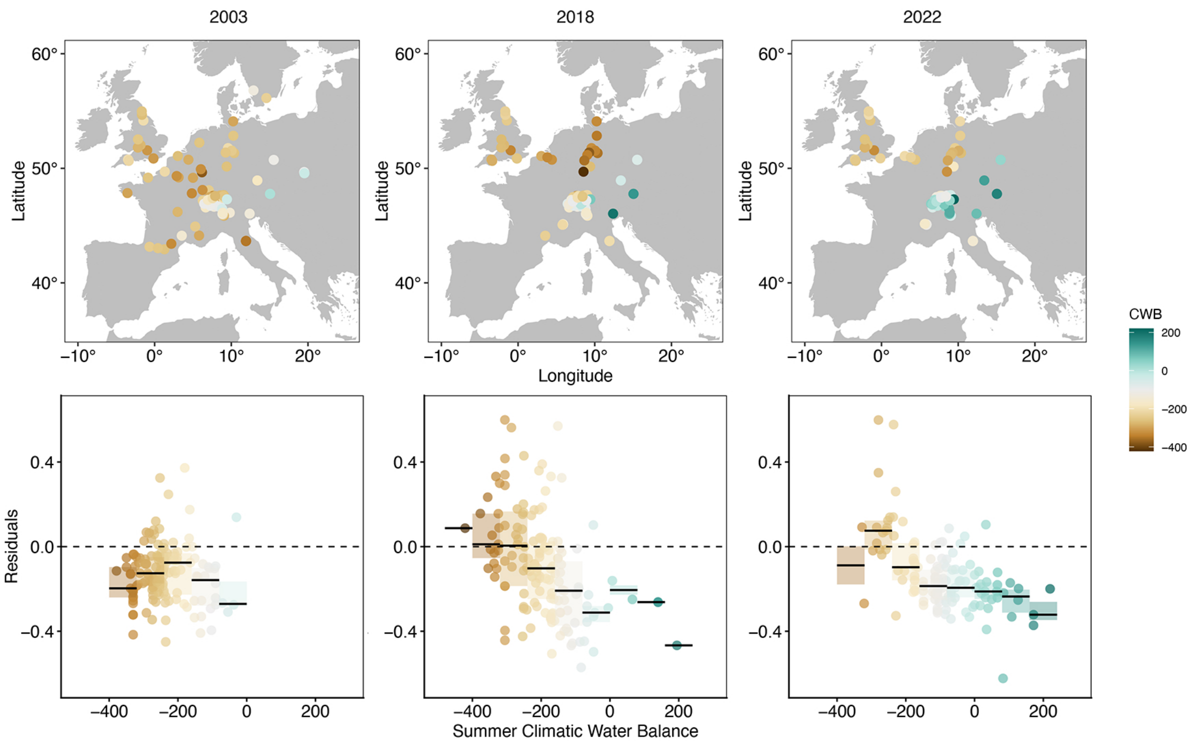

Figure 2: **Seed production response to climatic water deficit during the severe droughts in 2003, 2018, and 2022.** Points on top panels show the location of sites available in MASTREE+ and Swiss Intercantonal Forest Observation databases (N = 151 for 2003, N = 143 for 2018, and N = 127 for 2022). Bottom panels show the relationships between the residuals from a GLMM predicting seed production as a function of masting cues and spring drought, but keeping the effect of summer drought fixed at its median value (see Methods, Table 1), versus summer climatic water balance of each site in a given year (CWB). Negative residuals show reproduction was lower than predicted based on cues and spring drought conditions. The bins highlight the median and interquartile range (25th and 75th) for given CWB values. The density plots of summer CWB values in 2003, 2018, and 2022 in the context of all other years in our data are shown in Fig. S1.

is maintained even at drought intensities that simultaneously suppress growth and elevate mortality within the same forests (Buras *et al.*, 2020; Brun *et al.*, 2020; Schuldt *et al.*, 2020; Braun *et al.*, 2025), including at our study sites.

Our results suggest that reproduction in beech is resilient to drought, resulting from high resistance in the year of flowering and seed maturation (neutral or even positive effects of drought on seed production) , and an absence of lagged suppression of reproduction the following year. The positive association between dry spring conditions and seed production is likely explained by enhanced pollen dispersal and improved pollination efficiency under low humidity, as previously observed in oak populations, where airborne pollen concentrations increased during dry conditions (Schermer *et al.*, 2020; Fleurot *et al.*, 2024). This effect is strongest when the weather cues of masting are weaker. We interpret this effect as representing greater benefits of weather-enhanced pollen dispersal in years when conspecific flowering effort is lower, and pollen limitation is otherwise greater. In beech, airborne pollen abundance has been shown to correlate with seed production (Bogdziewicz *et al.*, 2017; Nussbaumer *et al.*, 2020), supporting the interpretation that dry springs may facilitate higher reproductive success via improved pollen transfer.

We also found no effect of summer drought on seed production. This result suggests that, once reproduction has been initiated by prior-years temperature cues, trees continue to allocate resources to seeds even under water stress. The mechanisms governing carbon allocation among competing sinks under drought remain unresolved (Dietze *et al.*, 2014; Hartmann & Trumbore, 2016; McDowell *et al.*, 2022), and our findings indicate that developing fruits are not downregulated relative to other functions during short-term drought. Indeed, several lines of evidence suggest how beech could maintain carbon supply to developing fruits, even under severe drought. Drought limits photosynthesis via stomatal closure, which serves to avoid hydraulic failure, but does not necessarily translate immediately into carbon limitation (McDowell *et al.*, 2008; Leuschner, 2020; Chuste *et al.*, 2020). A delayed onset of carbon limitation may especially be the case in anisohydric species such as beech, as stomata tend to remain open for longer under drought, increasing hydraulic risk, but allowing continued gas exchange under stress (McDowell *et al.*, 2008; Leuschner, 2020). Furthermore, trees possess substantial non-structural carbon reserves (Hoch *et al.*, 2003; Hartmann *et al.*, 2020; Trugman & Anderegg, 2025), and there is little evidence that single-year droughts cause acute carbon limitation (McDowell *et al.*, 2008; Hartmann & Trumbore, 2016; Leuschner, 2020; Chuste *et al.*, 2020; Peltier *et al.*, 2023). Growth reduction under short-term drought is thought to result from low water potential and turgor-driven inhibition of cell expansion, alongside hormonal signalling that suppresses cambial activity—not from a lack of available carbon (Buras *et al.*, 2018; Cabon *et al.*, 2020; Chuste *et al.*, 2020). In fact, increased concentration of secondary metabolites (defences) may follow drought, likely due to decreased growth sink activity (Hartmann & Trumbore, 2016). Under such conditions, trees may draw on stored reserves to sustain seed maturation (Wiley *et al.*, 2017), especially if doing so offers a selective advantage. Continued investment in seeds may thus reflect both the low immediate cost of reproduction under short-term drought and the potential long-term benefit of successful recruitment in drought-disturbed environments (Ascoli *et al.*, 2015; Vacchiano *et al.*, 2021).

Similar responses have been documented in other species. In *Quercus ilex*, *Pinus ponderosa*, and *Picea abies*, drought has been shown to intensify trade-offs between growth and reproduction, with reproductive effort maintained despite reductions in growth (Dohrenbusch *et al.*, 2002; Bogdziewicz *et al.*, 2020a; Gonzalez *et al.*, 2023), but see Le Roncé *et al.* (2021). While negative effects of drought on seed production have been reported in several systems (Clark *et al.*, 2011; Rowland *et al.*, 2018), including *Pinus sylvestris* (Vilà-Cabrera *et al.*, 2014), and Mediterranean oaks (Pérez-Ramos *et al.*, 2010; Gavinet *et al.*, 2019), positive or neutral responses have also emerged. For example, genus-level analysis by Wright *et al.* (2021) found that seed production in fir and pine species in the Sierra Nevada was not negatively affected by drought (*Pinus*), and in some cases even increased (*Abies*). Reduced rainfall was linked to enhanced reproductive output in *Sorbus aucuparia* (Żywiec *et al.*, 2012; Zamorano *et al.*, 2018), and seed production in tropical communities also showed resilience to drought (O'Brien *et al.*, 2018). These findings point to a broader pattern where reproduction may be buffered against short-term drought stress. Future studies combining drought manipulations with carbon budget tracking and reproductive monitoring are needed to clarify the mechanisms (Gavinet *et al.*, 2019; Le Roncé *et al.*, 2021). This will include understanding how the response of seed production to drought varies among species, and how this fits within broader physiological and ecological drought strategies (McDowell *et al.*, 2022). Whether reproductive investment remains stable under multi-year droughts also remains unclear, including the potential for chronic drought or more frequent or recurrent climatic extremes to gradually erode internal carbon reserves (Chuste *et al.*, 2020; Peltier *et al.*, 2023).

Although drought does not disrupt seed production once reproductive commitment has occurred, this does not imply that beech reproduction is broadly resilient to climate change. Other pathways threaten reproduction, particularly the increasing frequency of masting cues under warming (Bogdziewicz *et al.*, 2021). Warmer summers induce flowering more often, but frequent reproduction can outpace resource accumulation (Kelly *et al.*, 2025; Hacket-Pain *et al.*, 2025), reducing reproductive efficiency and growth (Bogdziewicz *et al.*, 2020b; Hacket-Pain *et al.*, 2025). In the UK, the resulting breakdown of masting has lowered flowering synchrony, pollination success, and increased seed predation, cutting viable seed output by over 50% despite mean reproductive effort slightly increasing (Bogdziewicz *et al.*, 2023). Similar declines in variability are emerging elsewhere across the range (Foest *et al.*, 2024). Thus, the absence of drought effects does not indicate resilience of seed production to climate change overall.

Moreover, reproductive resilience at the seed production stage does not guarantee successful regeneration (Rodman *et al.*, 2020; Davis *et al.*, 2023). Recruitment processes, including seed viability, seedling establishment and survival, are sensitive to moisture availability and are likely to be strongly affected by climate extremes (Andrus *et al.*, 2018; Conlisk *et al.*, 2018; Davis *et al.*, 2019; Pawłowski *et al.*, 2024). Extreme droughts can eliminate seedling banks, sharply reducing future recruitment potential (Schuldt *et al.*, 2020). Evidence from other forest systems shows that seed availability alone is insufficient to ensure regeneration: when soil moisture falls below critical thresholds, recruitment may fail even if seeds are available (Davis *et al.*, 2019). These effects are speciesspecific. Experimental heating crossed with watering in North American forests demonstrated strong contrasts: seedling survival of *Picea engelmannii* declined drastically under warming, whereas *Pinus flexilis* showed little response, resulting in simulated rapid range contraction of the former but not the latter (Kueppers *et al.*, 2017; Conlisk *et al.*, 2017). Water additions ameliorated these effects, highlighting the pivotal role of drought. How these dynamics operate in beech and European forests more broadly remains poorly understood, and further work is needed to assess the sensitivity of recruitment to drought (Leuschner, 2020) and the interaction between seed supply and post-dispersal climatic conditions.

Our analysis isolates the response of seed production to summer drought during the seed maturation phase and demonstrates that once flowering has been triggered, European beech maintains reproductive output even under extreme water deficits. While our data prevents analysis of spatial variation in fecundity, differences across moisture regimes may exist and could reflect local adaptation of reproductive strategies to prevailing hydrological conditions (Felton *et al.*, 2022; Stemkovski *et al.*, 2025). Identifying such patterns could help clarify whether reproductive resilience is uniform across the species' range or shaped by long-term environmental constraints, with implications for predicting demographic responses under future climates (Perret *et al.*, 2024; Stemkovski *et al.*, 2025). Likewise, while our study focuses on short-term drought events, understanding how beech reproduction responds to chronic or multi-year water stress remains an important next step. Evidence from other systems indicates that prolonged drought can depress reproductive output over time (Wion *et al.*, 2025). With climate projections indicating increasing frequency and severity of dry periods, assessing reproductive responses to long-term stress should be a research priority (Serra-Maluquer *et al.*, 2025). Notably, while our dataset does not include the southernmost range margin of the species where moisture limitation is most severe, our dataset includes well-characterised episodes of extreme drought, including the record European droughts of 2003, 2018, 2022, with sites within our network experiencing summer climatic water balances deficits below –300 mm, and where abundant evidence of strong effects on tree physiology and forest functioning have previously been documented (Fig. 2) (Buras *et al.*, 2020; Braun *et al.*, 2025; Gharun *et al.*, 2024; Schuldt *et al.*, 2020), ensuring that our results reflect tree responses under genuine drought conditions. The resilience of reproduction potentially comes at the cost of increased drought-related mortality, if sustained reproduction speeds up carbon depletion (Martínez-Vilalta *et al.*, 2016; Hacket-Pain *et al.*, 2025). Further work is needed to assess responses under chronic drought, variation across moisture regimes, and the demographic consequences of sustained reproduction under stress.

Methods

Data

Seed production Annual observations of European beech seed production were obtained from MASTREE+, an open-access database of annual records of population-level reproductive effort (Hacket-Pain *et al.*, 2022; Foest

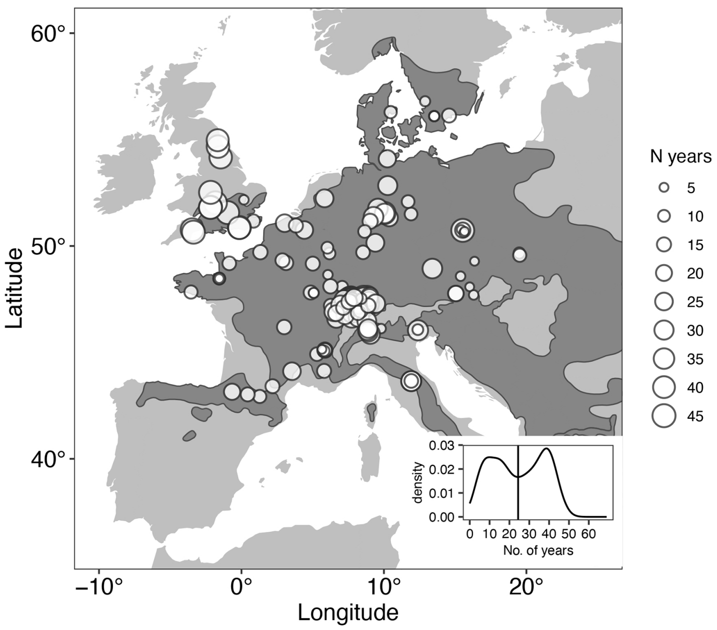

Figure 3: Map of study sites. Locations of the 221 time series of annual seed production of European beech (*Fagus sylvatica*) used in this study (N = 5362, average N per site = 24, see the inset plot for how sample size was distributed across sites). Size of points is scaled to the number of observations at the focal site. The shaded area highlights the species range, based on EUFORGEN (Caudullo *et al.*, 2017).

et al., 2024). We selected European beech because its masting cues are well studied and consistently linked to the summer solstice (Journé *et al.*, 2024), providing a clear temporal reference point that facilitates alignment of reproductive cues with climatic drivers across populations throughout the species' range. Only continuous time series longer than 5 years and beginning in 1952 or later were included, ensuring both sufficient length and overlap with climatic records. Pollen-based, ordinal, and regional-scale records were excluded. For several sites with ongoing monitoring, we supplemented MASTREE+ records with additional observations, extending coverage beyond 2019. Additionally, we added 105 sites from the Swiss Intercantonal Forest Observation network, where annual fruit production is estimated using fruit counts and fruit scars (Braun *et al.*, 2025). Thus, in total, our dataset included 221 series, with an average length of 24 years and a total of 5362 observations (Fig. 3). The sample for the three exceptional drought years (2003, 2018, 2022) was 151, 143, and 127 observations, respectively.

Climate We extracted daily climate data for each study site from the corresponding 0.1° grid cell of the E-OBS dataset (Cornes *et al.*, 2018). From these records, we derived daily temperature and precipitation. We quantified drought as the climatic water balance (CWB), calculated as monthly precipitation sum minus potential evapotranspiration, summed for April–May (spring) and June–September (summer). Potential evapotranspiration was estimated using the Thornthwaite method. CWB reflects the balance between water supply and demand but does not simulate local soil moisture availability. We also quantified drought using the vapour pressure deficit (VPD), a measure of atmospheric dryness, calculated from daily mean temperature and relative humidity following Duursma (2015), and aggregated to monthly means for the same seasonal windows.

Analysis To test the effects of drought on annual seed production, we fitted a generalised linear mixed model (GLMM) with a Tweedie distribution and logit link, including site ID as a random intercept. The Tweedie distribution was chosen because it accommodates zero-inflation and overdispersion, both of which are common features of seed production data. The response variable was annual, site-level observations of population seed production. To account for differences in monitoring methods among sites in MASTREE+, seed production values were standardised within each site to range between 0 and 1 (Journé *et al.*, 2024, 2025).

Fixed effects included spring climatic water balance (CWB; April–May), summer CWB (June–September), and the difference in mean maximum summer temperatures between the year one and two years prior to seedfall (ΔT). The latter captures the established cueing system of European beech reproduction: low June–July temperatures two years before seedfall (T2) followed by high temperatures one year before seedfall (T1) (Kelly *et al.*, 2025). Because these cues are anchored to the summer solstice and are consistent across the species' range (Journé *et al.*, 2024), ΔT provides a parsimonious representation of masting drivers, combining T1 and T2 into a single parameter (Szymkowiak *et al.*, 2024). We also included lagged effect of summer CWB (CWB_{T-1}) to test for lagged effects of summer drought on seed production. We included seed production in the previous year (T–1), following standard practice in masting studies, to account for short-term legacy effects associated with resource depletion (Crone *et al.*, 2009). The full model included two interactions, between ΔT and spring CWB, and between ΔT and summer CWB. We removed non-significant interactions from the final model.

To ensure comparability across sites and to separate within-site temporal variation from among-site spatial differences, all predictors were standardised by subtracting their site-level mean and dividing by the site-level standard deviation (z-transformation) (Buras *et al.*, 2018). Working with anomalies provides the advantage of accounting for local adaptation and acclimation, as site-specific means capture baseline climatic conditions while highlighting deviations relevant to physiological responses. However, because CWB was standardised within sites, years that are relatively dry compared to local averages may be classified as negative anomalies even if absolute CWB remains positive (i.e., precipitation still exceeds potential evapotranspiration). Thus, anomaly-based drought metrics can reflect relative dryness rather than absolute water deficit. (Buras *et al.*, 2020). Thus, we additionally tested an alternative approach, in which CWB was entered as observed, and supplemented with site-level mean CWB to avoid mixing within- and among-site level variation (van de Pol & Wright, 2009). In these models, we also added an interaction term between site-level mean and annual variation in CWB, to test whether the responses to drought vary with local moisture norms. That interaction was not significant in the case of summer CWB (Table S1); thus, the response to summer drought was consistent across space. In the case of spring CWB, the driest sites were characterized by the strongest positive responses to dry springs (Table S1). Nonetheless, we report the simpler z-transformed models in the main text. Models using vapour pressure deficit (VPD) instead of CWB produced qualitatively similar outcomes (Table S2). Model validation by graphical exploratory inspection of residual patterns indicated normality and homogeneity. We also estimated VIF values for our models which indicated lack of collinearity issues. Residual spatial autocorrelation was checked and was absent.

In a complementary analysis, we examined the effects of extreme summer droughts (2003, 2018, and 2022). The growth, vitality and mortality response of European forests to these events has been the subject of intense prior investigation (Braun *et al.*, 2025; Brun *et al.*, 2020; Buras *et al.*, 2020; Gharun *et al.*, 2024; Knutzen *et al.*, 2025; Sachsenmaier *et al.*, 2024; Schuldt *et al.*, 2020; Thom *et al.*, 2023). The spatial extent and severity of summer CWB varied across Europe for each event, and sites in our network experienced a range of conditions including sites with strong summer CWB deficits Fig. S1). For each year, we compared observed seed production to model predictions holding summer CWB at each site's median conditions. We examined how model residuals varied with local summer CWB to test if seed production was overestimated in sites experiencing the most severe drought in these years, in comparisons to sites n our network that did not experience drought in those years.

We conducted our analysis in R version 4.2.3 (R Core Team, 2024), using *glmmTMB* package to fit the model (Brooks *et al.*, 2017), *SPEI* package to calculate climatic water balance (Beguería & Vicente-Serrano, 2023), and *plantecophys* package to calculate vapour pressure deficit (Duursma, 2015).

Acknowledgements

We are grateful to the many colleagues, students, family and friends who have contributed to the English Beech Mast Survey and other long-term monitoring efforts on which this work is based. This study was funded by the European Union (ERC, ForestFuture, 101039066). Views and opinions expressed are however, those of the authors only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them. AHP and JL acknowledge institutional support and funding from The University of Liverpool and Manchester Metropolitan University respectively (2004 to present). JF was supported by the Foundation for Polish Science (FNP). GG and MBP acknowledge support by the projects 'Forest dynamics in old growth spruce-fir-beech forests', P14583. 'Sporadic seed production in mast seeding trees', P30381 of the Austrian Science Fund (FWF) and 'FORSEE: Seeds for Austria's Climate-Fit Forests' (WF 101656) of the Austrian Ministry of Agriculture, Forestry, Environment, Climate, Regions and Water Management (BMLUK). GK was funded for seed monitoring by REGE-ADAPT of the research program FORESTT through the Agence Nationale de la Recherche under the France 2030 program, grant ANR-24-PEFO-0006. MM knowledges support from the Integrated project CarboEurope-IP, European Commission, Directorate-General Research, Sixth Framework Programme, Priority 1.1.6.3: Global Change and Ecosystem (Contract no. GOCECT-2003-505572); Max Planck Institute for Biogeochemistry, Germany; German Research Foundation (DFG) (INST 186/1118-1 FUGG); German Federal Ministry of Education and Research (BMBF; research infrastructure ICOS); Georg-August-University Göttingen, Germany. As the French part of the ICP Forests intensive (Level II) monitoring programme, the RENECOFOR network has benefited from its scientific framework and shared expertise. The surveys on the Swiss ICP Forests Level II plots (LWF) are financed by WSL and the Swiss Federal Office for the Environment (FOEN), with some financial support from the Canton of St. Gallen and the City of Lausanne. We thank Allan Buras for useful discussions during the initiation of this project.

Author Contributions Statement

AHP conceived the study and AHP, MB, and JS designed the study. JS analysed the data. MB and AHP drafted the manuscript. All authors contributed data and contributed critically to data interpretation and manuscript revisions.

Declaration of interests

No competing interests to declare.

References

Andrus, R.A., Harvey, B.J., Rodman, K.C., Hart, S.J. & Veblen, T.T. (2018). Moisture availability limits subalpine tree establishment. *Ecology*, 99, 567–575.

Ascoli, D., Castagneri, D., Valsecchi, C., Conedera, M. & Bovio, G. (2013). Post-fire restoration of beech stands in the southern alps by natural regeneration. *Ecological Engineering*, 54, 210–217.

Ascoli, D., Hacket-Pain, A., LaMontagne, J.M., Cardil, A., Conedera, M., Maringer, J. *et al.* (2020). Climate teleconnections synchronize picea glauca masting and fire disturbance: Evidence for a fire-related form of environmental prediction. *Journal of Ecology*, 108, 1186–1198.

Ascoli, D., Vacchiano, G., Maringer, J., Bovio, G. & Conedera, M. (2015). The synchronicity of masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and Management*, 353, 126–135.

Beguería, S. & Vicente-Serrano, S.M. (2023). *SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index*. R package version 1.8.1.

Beloiu, M., Stahlmann, R. & Beierkuhnlein, C. (2022). Drought impacts in forest canopy and deciduous tree saplings in central european forests. *Forest Ecology and Management*, 509, 120075.

Bogdziewicz, M., Fernández-Martínez, M., Espelta, J.M., Ogaya, R. & Penuelas, J. (2020a). Is forest fecundity resistant to drought? Results from an 18-yr rainfall-reduction experiment. *New Phytologist*, 227, 1073–1080.

Bogdziewicz, M., Hacket-Pain, A., Kelly, D., Thomas, P.A., Lageard, J. & Tanentzap, A.J. (2021). Climate warming causes mast seeding to break down by reducing sensitivity to weather cues. *Global Change Biology*, 27, 1952–1961.

Bogdziewicz, M., Kelly, D., Tanentzap, A.J., Thomas, P., Foest, J., Lageard, J. *et al.* (2023). Reproductive collapse in European beech results from declining pollination efficiency in large trees. *Global Change Biology*, 29, 4595–4604.

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A. & Hacket-Pain, A. (2020b). Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nature Plants*, 6, 88–94.

Bogdziewicz, M., Kelly, D., Zwolak, R., Szymkowiak, J. & Hacket-Pain, A. (2025). Dynamics, mechanisms, and consequences of mast seeding. *Annual Reviews in Ecology, Evolution, and Systematics*.

Bogdziewicz, M., Szymkowiak, J., Kasprzyk, I., Grewling, , Borowski, Z., Borycka, K. *et al.* (2017). Masting in wind-pollinated trees: System-specific roles of weather and pollination dynamics in driving seed production. *Ecology*, 98, 2615–2625.

Braun, S., Tresch, S., Hopf, S.E. & Schindler, C. (2025). *Four Decades of Forest Development in the Context of Nitrogen Eutrophication and Climate Change*, Springer, Berlin, Heidelberg, pp. 1–57.

Brodribb, T.J., Powers, J., Cochard, H. & Choat, B. (2020). Hanging by a thread? forests and drought. *Science*, 368, 261–266.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Brun, P., Psomas, A., Ginzler, C., Thuiller, W., Zappa, M. & Zimmermann, N.E. (2020). Large-scale early-wilting response of central european forests to the 2018 extreme drought. *Global Change Biology*, 26, 7021–7035.

Buras, A., Rammig, A. & Zang, C.S. (2020). Quantifying impacts of the 2018 drought on european ecosystems in comparison to 2003. *Biogeosciences*, 17, 1655–1672.

Buras, A., Schunk, C., Zeitrg, C., Herrmann, C., Kaiser, L., Lemme, H. *et al.* (2018). Are scots pine forest edges particularly prone to drought-induced mortality? *Environmental Research Letters*, 13.

Büntgen, U., Urban, O., Krusic, P.J., Rybníček, M., Kolář, T., Kyncl, T. *et al.* (2021). Recent european drought extremes beyond common era background variability. *Nature Geoscience*, 14, 190–196.

Cabon, A., Peters, R.L., Fonti, P., Martínez-Vilalta, J. & Cáceres, M.D. (2020). Temperature and water potential co-limit stem cambial activity along a steep elevational gradient. *New Phytologist*, 226, 1325–1340.

Caudullo, G., Welk, E. & San-Miguel-Ayanz, J. (2017). Chorological maps for the main european woody species. *Data in Brief*, 12, 662–666.

Chuste, P.A., Maillard, P., Bréda, N., Levillain, J., Thirion, E., Wortemann, R. *et al.* (2020). Sacrificing growth and maintaining a dynamic carbohydrate storage are key processes for promoting beech survival under prolonged drought conditions. *Trees*, 34, 381–394.

Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C. *et al.* (2021). Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications 2021 12:1*, 12, 1–11.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011). Climate change vulnerability of forest biodiversity: Climate and competition tracking of demographic rates. *Global Change Biology*, 17, 1834–1849.

Conlisk, E., Castanha, C., Germino, M.J., Veblen, T.T., Smith, J.M. & Kueppers, L.M. (2017). Declines in low-elevation subalpine tree populations outpace growth in high-elevation populations with warming. *Journal of Ecology*, 105, 1347–1357.

Conlisk, E., Castanha, C., Germino, M.J., Veblen, T.T., Smith, J.M., Moyes, A.B. *et al.* (2018). Seed origin and warming constrain lodgepole pine recruitment, slowing the pace of population range shifts. *Global Change Biology*, 24, 197–211.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J. & Jones, P.D. (2018). An ensemble version of the e-obs temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123, 9391–9409.

Crone, E.E., Miller, E. & Sala, A. (2009). How do plants know when other plants are flowering? resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters*, 12, 1119–1126.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T. *et al.* (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences*, 116, 6193–6198.

Davis, K.T., Robles, M.D., Kemp, K.B., Higuera, P.E., Chapman, T., Metlen, K.L. *et al.* (2023). Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western united states. *Proceedings of the National Academy of Sciences*, 120, e2208120120.

Dietze, M.C., Sala, A., Carbone, M.S., Czimczik, C.I., Mantooth, J.A., Richardson, A.D. *et al.* (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, 65, 667–687.

Dohrenbusch, A., Jaehne, S., Bredemeier, M. & Lamersdorf, N. (2002). Growth and fructification of a norway spruce (picea abies l. karst) forest ecosystem under changed nutrient and water input. *Annals of Forest Science*, 59, 359–368.

Duursma, R.A. (2015). Plantecophys - An R Package for Analysing and Modelling Leaf Gas Exchange Data. *PLoS ONE*, 10, e0143346.

Felton, A.J., Shriver, R.K., Stemkovski, M., Bradford, J.B., Suding, K.N. & Adler, P.B. (2022). Climate disequilibrium dominates uncertainty in long-term projections of primary productivity. *Ecology Letters*, 25, 2688–2698.

Fleurot, E., Keurinck, L., Boulanger, V., Debias, F., Delpierre, N., Delzon, S. *et al.* (2024). Reconciling pollen limitation theories: Insights from temperate oak masting. *Ecology Letters*, 27.

Foest, J., Bogdziewicz, M., Ascoli, D., Pesendorfer, M., Cutini, A., Nussbaumer, A. *et al.* (2024). Widespread breakdown in masting in European beech due to rising summer temperatures. *Global Change Biology*, 30, e17307.

Gavinet, J., Ourcival, J.M. & Limousin, J.M. (2019). Rainfall exclusion and thinning can alter the relationships between forest functioning and drought. *New Phytologist*, 223, 1267–1279.

Gharun, M., Shekhar, A., Xiao, J., Li, X. & Buchmann, N. (2024). Effect of the 2022 summer drought across forest types in europe. *Biogeosciences*, 21, 5481–5494.

Gonzalez, A.D., Pearse, I.S. & Redmond, M.D. (2023). Increased aridity is associated with stronger tradeoffs in ponderosa pine vital functions. *Ecology*, 104, e4120.

Hacket-Pain, A., Foest, J.J., Pearse, I.S., LaMontagne, J.M., Koenig, W.D., Vacchiano, G. *et al.* (2022). Mastree+: Time-series of plant reproductive effort from six continents. *Global Change Biology*, 28, 3066–3082.

Hacket-Pain, A., Szymkowiak, J., Journé, V., Barczyk, M.K., Thomas, P.A.., Lageard, J.G.A. *et al.* (2025). Growth decline in european beech associated with temperature-driven increase in reproductive allocation. *PNAS*, 122, e2423181122.

Hacket-Pain, A.J., Lageard, J.G. & Thomas, P.A. (2017). Drought and reproductive effort interact to control growth of a temperate broadleaved tree species (*Fagus sylvatica*). *Tree Physiology*, 37, 744–754.

Hanbury-Brown, A.R., Ward, R.E. & Kueppers, L.M. (2022). Forest regeneration within earth system models: current process representations and ways forward. *New Phytologist*.

Hartmann, H., Bahn, M., Carbone, M. & Richardson, A.D. (2020). Plant carbon allocation in a changing world – challenges and progress: introduction to a virtual issue on carbon allocation: Introduction to a virtual issue on carbon allocation.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J. *et al.* (2022). Climate change risks to global forest health: Emergence of unexpected events of elevated tree mortality worldwide. *Annual Review of Plant Biology*, 43, 22.

Hartmann, H. & Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates in forest trees - from what we can measure to what we want to know. *The New phytologist*, 211, 386–403.

Hesse, B.D., Hartmann, H., Rötzer, T., Landhäusser, S.M., Goisser, M., Weikl, F. *et al.* (2021). Mature beech and spruce trees under drought – higher c investment in reproduction at the expense of whole-tree nsc stores. *Environmental and Experimental Botany*, 191.

Hoch, G., Richter, A. & Körner, C. (2003). Non-structural carbon compounds in temperate forest trees. *Plant, Cell and Environment*, 26, 1067–1081.

IPCC (2023). Climate change 2023: Synthesis report. contribution of working groups i, ii and iii to the sixth assessment report of the intergovernmental panel on climate change. *Intergovernmental Panel on Climate Change*. Core Writing Team: Lee, H. and Romero, J. (eds.).

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E. *et al.* (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14, 369–378.

Journé, V., Kelly, D., Hacket-Pain, A., Pearse, I.S., Szymkowiak, J., Foest, J.J. *et al.* (2025). Weather drivers of reproductive variability in perennial plants and their implications for climate change risks. *Nature Communications*, 16, 9226.

Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D. & Bogdziewicz, M. (2024). Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature Plants*, 10, 367–373.

Kelly, D., Szymkowiak, J., Hacket-Pain, A. & Bogdziewicz, M. (2025). Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues. *New Phytologist*.

Klesse, S., Peters, R., Alfaro-Sánchez, R., Badeau, V., Baittinger, C., Battipaglia, G. *et al.* (2024). No future growth enhancement expected at the northern edge for european beech due to continued water limitation. *Global Change Biology*, 30.

Knutzen, F., Averbeck, P., Barrasso, C., Bouwer, L.M., Gardiner, B., Grünzweig, J.M. *et al.* (2025). Impacts on and damage to european forests from the 2018–2022 heat and drought events. *Natural Hazards and Earth System Sciences*, 25, 77–117.

Kueppers, L.M., Conlisk, E., Castanha, C., Moyes, A.B., Germino, M.J., de Valpine, P. *et al.* (2017). Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology*, 23, 2383–2395.

Lauder, J.D., Moran, E.V. & Hart, S.C. (2019). Fight or flight? potential tradeoffs between drought defense and reproduction in conifers. *Tree Physiology*, 39, 1071–1085.

Le Roncé, I., Gavinet, J., Ourcival, J.M., Mouillot, F., Chuine, I. & Limousin, J.M. (2021). Holm oak fecundity does not acclimate to a drier world. *New Phytologist*, 231, 631–645.

Leuschner, C. (2020). Drought response of European beech (*Fagus sylvatica* L.)—a review. *Perspectives in Plant Ecology, Evolution and Systematics*, 47, 125576.

Mantgem, P., Stephenson, N., Bryne, J., Daniels, L., Franklin, J., Fule, P. *et al.* (2009). Widespread increase of tree mortality rates in the western united states. *Science*, 323, 521–524.

Maringer, J., Wohlgemuth, T., Hacket-Pain, A., Ascoli, D., Berretti, R. & Conedera, M. (2020). Drivers of persistent post-fire recruitment in european beech forests. *Science of the Total Environment*, 699.

Martínez-Vilalta, J. & Lloret, F. (2016). Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global and Planetary Change*, 144, 94–108.

Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S. *et al.* (2016). Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. *Ecological Monographs*, 86, 495–516.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. *et al.* (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L. *et al.* (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, 368.

McDowell, N.G., Sapes, G., Pivovaroff, A., Adams, H.D., Allen, C.D., Anderegg, W.R. *et al.* (2022). Mechanisms of woody-plant mortality under rising drought, co2 and vapour pressure deficit. *Nature Reviews Earth and Environment*, 3, 294–308.

Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M. & Katul, G.G. (2011). Spread of north american wind-dispersed trees in future environments. *Ecology Letters*, 14, 211–219.

Netherer, S., Lehmanski, L., Bachlehner, A., Rosner, S., Savi, T., Schmidt, A. *et al.* (2024). Drought increases norway spruce susceptibility to the eurasian spruce bark beetle and its associated fungi. *New Phytologist*, 242, 1000–1017.

Nussbaumer, A., Meusburger, K., Schmitt, M., Waldner, P., Gehrig, R., Haeni, M. *et al.* (2020). Extreme summer heat and drought lead to early fruit abortion in european beech. *Scientific Reports 2020 10:1*, 10, 1–11.

O'Brien, M.J., Peréz-Aviles, D. & Powers, J.S. (2018). Resilience of seed production to a severe el niño-induced drought across functional groups and dispersal types. *Global Change Biology*, 24, 5270–5280.

Pawłowski, T.A., Suszka, J., Mucha, J., Zadworny, M., Alipour, S., Kurpisz, B. *et al.* (2024). Climate legacy in seed and seedling traits of european beech populations. *Frontiers in Plant Science*, 15.

Peltier, D.M.P., Carbone, M.S., McIntire, C.D., Robertson, N., Thompson, R.A., Malone, S. *et al.* (2023). Carbon starvation following a decade of experimental drought consumes old reserves in pinus edulis. *New Phytologist*, 240, 92–104.

Perret, D.L., Evans, M.E. & Sax, D.F. (2024). A species' response to spatial climatic variation does not predict its response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 121, e2304404120.

Piovesan, G. & Adams, J.M. (2005). The evolutionary ecology of masting: Does the environmental prediction hypothesis also have a role in mesic temperate forests?

van de Pol, M. & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, 77, 753–758.

Pérez-Ramos, I.M., Ourcival, J.M., Limousin, J.M. & Rambal, S. (2010). Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*, 91, 3057–3068.

R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rodman, K.C., Veblen, T.T., Chapman, T.B., Rother, M.T., Wion, A.P. & Redmond, M.D. (2020). Limitations to recovery following wildfire in dry forests of southern colorado and northern new mexico, usa. *Ecological Applications*, 30.

Rowland, L., da Costa, A.C., Oliveira, A.A., Almeida, S.S., Ferreira, L.V., Malhi, Y. *et al.* (2018). Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics. *Journal of Ecology*, 106, 1673–1682.

Sachsenmaier, L., Schnabel, F., Dietrich, P., Eisenhauer, N., Ferlian, O., Quosh, J. *et al.* (2024). Forest growth resistance and resilience to the 2018–2020 drought depend on tree diversity and mycorrhizal type. *Journal of Ecology*, 112, 1787–1803.

Sage, R.F., Quesada, M., Brunet, J. & Aguilar, R. (2024). An introduction to the special issue on global change and plant reproduction. *Annals of Botany*, 135, 1–8.

Schermer, E., Bel-Venner, M.C., Gaillard, J.M., Dray, S., Boulanger, V., Roncé, I.L. *et al.* (2020). Flower phenology as a disruptor of the fruiting dynamics in temperate oak species. *New Phytologist*, 225, 1181–1192.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A. *et al.* (2020). A first assessment of the impact of the extreme 2018 summer drought on central european forests. *Basic and Applied Ecology*, 45, 86–103.

Seidl, R. & Turner, M.G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences of the United States of America*, 119.

Senf, C., Buras, A., Zang, C.S., Rammig, A. & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across europe. *Nature Communications 2020 11:1*, 11, 1–8.

Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M. *et al.* (2018). Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications*, 9, 1–8.

Serra-Maluquer, X., Astigarraga, J., Morales-Molino, C. & Ruiz-Benito, P. (2025). Non-stationary forest responses to hotter droughts: a temporal perspective considering the role of past legacies. *Ecography*.

Sevanto, S., Mcdowell, N.G., Dickman, L.T., Pangle, R. & Pockman, W.T. (2014). How do trees die? a test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell and Environment*, 37, 153–161.

Stemkovski, M., Bernhardt, J.R., Blonder, B.W., Bradford, J.B., Clark-Wolf, K., Dee, L.E. *et al.* (2025). Ecological acclimation: A framework to integrate fast and slow responses to climate change. *Functional Ecology*.

Svenning, J.C. & Skov, F. (2007). Could the tree diversity pattern in europe be generated by postglacial dispersal limitation? *Ecology Letters*, 10, 453–460.

Szymkowiak, J., Foest, J., Hacket-Pain, A., Journé, V., Ascoli, D. & Bogdziewicz, M. (2024). Tail-dependence of masting synchrony results in continent-wide seed scarcity. *Ecology Letters*, 27.

Thom, D., Buras, A., Heym, M., Klemmt, H.J. & Wauer, A. (2023). Varying growth response of central european tree species to the extraordinary drought period of 2018 – 2020. *Agricultural and Forest Meteorology*, 338, 109506.

Trugman, A.T. & Anderegg, L.D. (2025). Source vs sink limitations on tree growth: from physiological mechanisms to evolutionary constraints and terrestrial carbon cycle implications. *New Phytologist*, 245, 966–981.

Tushabe, D. & Rosbakh, S. (2025). Patterns and drivers of pollen temperature tolerance. *Plant, Cell and Environment*, 48, 1366–1379.

Vacchiano, G., Hacket-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M. *et al.* (2017). Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist*, 215, 595–608.

Vacchiano, G., Pesendorfer, M.B., Conedera, M., Gratzer, G., Rossi, L. & Ascoli, D. (2021). Natural disturbances and masting: from mechanisms to fitness consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200384.

Vilà-Cabrera, A., Martínez-Vilalta, J. & Retana, J. (2014). Variation in reproduction and growth in declining scots pine populations. *Perspectives in Plant Ecology, Evolution and Systematics*, 16, 111–120.

Wiley, E., Casper, B.B. & Helliker, B.R. (2017). Recovery following defoliation involves shifts in allocation that favour storage and reproduction over radial growth in black oak. *Journal of Ecology*, 105, 412–424.

Wion, A.P., Pearse, I.S., Broxson, M. & Redmond, M.D. (2025). Mast hindcasts reveal pervasive effects of extreme drought on a foundational conifer species. *New Phytologist*, 246.

Wright, M.C., van Mantgem, P., Stephenson, N.L., Das, A.J. & Keeley, J.E. (2021). Seed production patterns of surviving sierra nevada conifers show minimal change following drought. *Forest Ecology and Management*, 480.

Zamorano, J.G., Hokkanen, T. & Lehikoinen, A. (2018). Climate-driven synchrony in seed production of masting deciduous and conifer tree species. *Journal of Plant Ecology*, 11, 180–188.

Zhang, F.P. & Brodribb, T.J. (2017). Are flowers vulnerable to xylem cavitation during drought? *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162642.

Żywiec, M., Holeksa, J. & Ledwoń, M. (2012). Population and individual level of masting in a fleshy-fruited tree. *Plant Ecology*, 213, 993–1002.

Supplementary Material

Table S1: Results of the Generalised Linear Mixed model testing for the effects of site-level mean climatic water balance (CWB) in spring and summer on the effects of drought-reproduction relationship in European beech. The model included seed production (scaled between 0 and 1 at the site level) as a response, while site-level mean CWB in spring (April-May) in interaction with annual spring CWB, and mean summer (June-September) CWB in interaction with annual summer CWB, were fixed effects. The model included also masting cue (ΔT, i.e., the difference between summer temperatures two and one year before flowering) and previous year seed production (seeds T-1) as fixed effects, while siteID was random intercept. The model was fitted with a Tweedie error distribution and logit link function. The interaction between site-level mean summer CWB and summer CWB was not significant ($z = -0.78$, $p = 0.436$), therefore dropped from the model.

Term	Estimate	SE	z	p
Intercept	-1.017	0.08	-13.02	**<0.001**
Mean Spring CWB	-0.004	0.001	-3.50	**<0.001**
Spring CWB	-0.003	0.0004	-7.34	**<0.001**
Mean Summer CWB	0.002	0.0006	3.87	0.160
Summer CWB	-0.0003	0.0002	-1.40	**<0.001**
ΔT	0.530	0.01	46.54	**<0.001**
Seeds T-1	-0.001	0.00006	-10.73	**<0.001**
Mean Spring CWB * Spring CWB	0.00001	0.000004	2.67	**0.008**

Table S2: Results of the Generalised Linear Mixed model testing for the effects of seasonal drought on European beech reproduction. Drought in spring had a positive effect, while drought in summer had no effect. The model included seed production (scaled between 0 and 1 at the site level) as a response, while masting cue (ΔT, i.e., the difference between summer temperatures two and one year before flowering), spring (April-May) and summer (June-September) Vapour Pressure Deficit (VPD), and previous year seed production (seeds T-1), were fixed effects. The model included siteID as a random intercept and was fitted with a Tweedie error distribution and logit link function. The interaction between ΔT and summer VPD was not significant ($z = 0.72$, $p = 0.474$), therefore dropped from the model.

Term	Estimate	SE	z	p
Intercept	-1.38	0.0387	-35.76	**<0.001**
ΔT	0.80	0.0216	37.04	**<0.001**
Spring VPD	0.27	0.0198	13.59	**<0.001**
Summer VPD	-0.11	0.0203	-5.50	**<0.001**
Seeds T-1	-0.53	0.0203	-26.27	**<0.001**
Spring VPD * ΔT	-0.16	0.0247	-6.28	**<0.001**

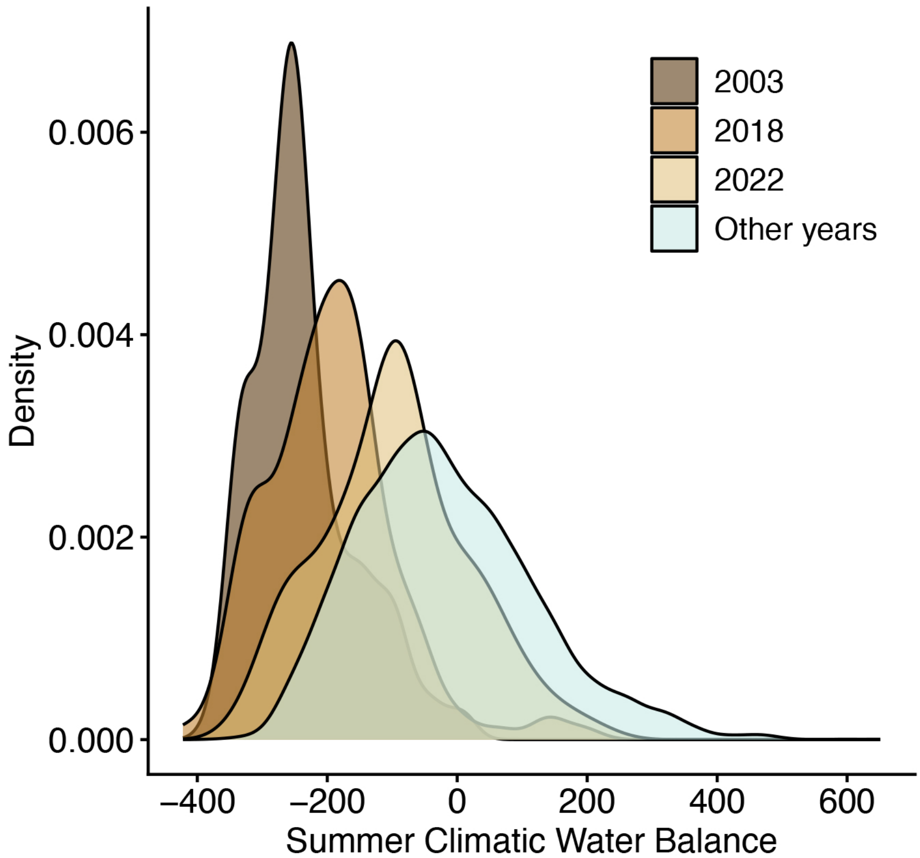

Figure S1: **Drought severity in the 2003, 2018, and 2022**. Density plots showing variation in drought severity as measured by Climatic Water Balance (CWB) in 2003 (n = 151), 2018 (n = 143), and 2022 (n = 127) in the context of all other years in the data (1967 to 2023).