Climate warming reduces seed mass in European beech through altered resource dynamics and drought

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keywords: climate change | *Fagus sylvatica* | drought | mast seeding | resource limitation | seed size | regeneration

Abstract

Seed mass is a key life-history trait that influences dispersal, seedling establishment, and plant fitness, yet its long-term response to climate change remains poorly understood. We used two long-term datasets of European beech (*Fagus sylvatica*) from the United Kingdom and the Netherlands (1976-2024) to test whether seed mass has changed over time and whether any decline can be attributed to changing climate or altered resource dynamics. Seed mass declined by 13% over the study period, with a non-linear decrease starting in the mid-2000s. Models of year-to-year variation showed that seeds were smaller in years with lower reconstructed stored resources and in years that were dry during the period of seed filling (May- June). Temporal contribution analysis indicated that the long-term decline in seed mass was driven primarily by declining resource availability, with increasing drought making an additional contribution. Climate warming affects seed size in beech by direct effects of drought on seed development, and indirectly by altering reproductive dynamics and shortening the intervals available for resource recovery between reproductive events. Because seed mass influences dispersal and survival of seeds and seedlings, declines in seed mass are likely to reduce regeneration potential. Our findings identify an indirect pathway by which climate change may weaken forest regeneration.

Introduction

Seed mass is a life-history trait that is strongly linked to plant fitness (Muller-Landau, 2010). While small seeds have a dispersal advantage, larger seeds produce larger seedlings with higher survival, faster early growth, and greater tolerance to environmental stress (Kidson & Westoby, 2000; Baraloto *et al.*, 2005; Muller-Landau, 2010). Because early establishment is a major demographic bottleneck in long-lived plants, variation in seed mass affects recruitment and population dynamics (Turnbull *et al.*, 1999; Clark *et al.*, 2007). Importantly, these effects also operate within species: larger seeds from the same species produce seedlings with larger cotyledons, taller hypocotyls, greater first-year biomass, and greater early height (Reich *et al.*, 1994; Muñoz *et al.*, 2014; Pawłowski *et al.*, 2024). Seed mass can also influence interactions with animals, including seed predation and animal-mediated dispersal rates (Lichti *et al.*, 2017; Dylewski *et al.*, 2020). Finally, because seed biomass contributes to resource availability for consumers (Ostfeld & Keesing, 2000; Dri *et al.*, 2025), changes in seed mass can influence their population dynamics. Because seed mass influences multiple stages of regeneration, from dispersal and survival to early seedling performance, environmentally driven variation in seed mass within populations can scale up to affect population dynamics (Clark *et al.*, 2007).

Seed mass varies substantially within species, including temporal fluctuations within populations. For example, in valley oak (*Quercus lobata*), mean acorn mass varied from 1.06 to 2.20 g among years (Koenig *et al.*, 2009). In European beech (*Fagus sylvatica*), the mean seed mass among years can vary 4-fold (Kondrat *et al.*, 2025). Part of the seed mass variation reflects environmental conditions during seed development (Frenne *et al.*, 2013; Lenzo *et al.*, 2025). Weather conditions such as temperature and precipitation influence the physiological processes that determine seed filling, including photosynthesis and the duration of developmental stages (Frenne *et al.*, 2013). For example, seed mass tends to be greater in warmer conditions and in wetter environments, particularly where precipitation occurs during the months of seed maturation (Gao *et al.*, 2023; Lenzo *et al.*, 2025). The effect of warming on seed size in trees is poorly understood, but experimental warming tends to increase seed size in perennial herbaceous species (WALCK *et al.*, 2011; Zi *et al.*, 2023). Temperature may affect seed mass indirectly through phenology: warmer springs can advance flowering and potentially extend the period of seed development (Frenne *et al.*, 2013; Bogdziewicz *et al.*, 2019). Drought during seed filling could affect seed mass as water limitation induces stomatal closure and reduces photosynthesis, limiting resources available for developing seeds, especially during late spring and summer when seeds are actively filling (Hoch, 2005; Han *et al.*, 2020). The effects have been shown in perennial herbaceous species in experimental manipulations (Vázquez-Ramírez & Venn, 2025). However, most work has focused on explaining variation among populations, while year-to-year variation associated with weather remains less well resolved. This temporal weather sensitivity is important because short-term weather effects can translate into directional changes under climate change.

Seed mass may also vary with seed number through allocation trade-offs (Smith & Fretwell, 1974; Qiu *et al.*, 2022). Under a fixed reproductive budget, increased seed production is expected to reduce investment per seed (Smith & Fretwell, 1974). In mast-seeding species, however, this expectation is complicated because reproductive allocation can vary strongly among years (Bogdziewicz *et al.*, 2025; Ward *et al.*, 2025). In years of high seed production, trees may shift resource allocation toward reproduction, at the expense of storage, growth, or defense (Han *et al.*, 2011; Lauder *et al.*, 2019; Gonzalez *et al.*, 2023), allowing seed number to increase without a decline in seed mass (Kondrat *et al.*, 2025). Such a pattern has been reported in European beech, valley oak, and holm oak (*Quercus ilex*) (Koenig *et al.*, 2009; Roncé *et al.*, 2021; Kondrat *et al.*, 2025). By contrast, lower seed mass in years when seed number was high has been found in Armand's pine (*Pinus armandii*) and Farges' chestnut (*Castanopsis* *fargesii*) (Wang & Ives, 2017; Huang *et al.*, 2021). These contrasting results suggest that trees can buffer the seed size-number trade-off by temporarily increasing reproductive allocation, but that buffering is not universal. Importantly, if climate warming makes high reproductive allocation more frequent, the resources that buffer other functions against increased reproductive investment may be replenished less completely between reproductive events (Hacket-Pain *et al.*, 2025).

In addition to short-term weather effects during seed development, seed mass may also vary through longer-term changes in plant resource levels. In mast-seeding species, temporal variation in reproduction is shaped by endogenous resource dynamics (Satake & Iwasa, 2000; Pearse *et al.*, 2016; Kelly *et al.*, 2025). Large reproductive events are typically followed by periods of depleted reserves, during which plants rebuild the carbohydrates and nutrients required for the next reproductive effort (Crone *et al.*, 2009; Sala *et al.*, 2012; Roncé *et al.*, 2023). Climate warming can disrupt these dynamics, leading to a breakdown of mast seeding characterized by more frequent but smaller reproductive events (Bogdziewicz *et al.*, 2020; Foest *et al.*, 2025b; Jantzen *et al.*, 2026). Specifically, warming can increase the frequency of weather events that trigger reproduction (weather cues, often high temperature), shortening the intervals available for resource recovery between reproductive events (Bogdziewicz *et al.*, 2024). Such warming-induced shifts in reproductive allocation in European beech have been associated with reduced secondary growth by 28% and indications of nutrient limitation (Hacket-Pain *et al.*, 2025), suggesting that repeated reproduction can constrain resource availability for other vital functions (Lauder *et al.*, 2019). Consequently, if resource pools are replenished less completely between reproductive events, the resources available per seed may decline, leading to reduced investment in individual seeds and, ultimately, lower seed mass.

Testing trends in seed mass, including the effects of weather variation and seed production, requires long-term records that include seed traits and number. Such datasets are rare because measuring both seed number and seed mass on the same individuals over decades is logistically demanding and rarely incorporated into long-term monitoring programs. Here, we use two long-term datasets: one from the United Kingdom, including 6 populations and 85 individual trees (1989-2024), and another from the Netherlands, including one population and 74 individuals (1976-2024). Importantly, in both systems, an increased frequency of warm summers that trigger mass flowering has been associated with reduced inter-annual variation in seed production (Bogdziewicz *et al.*, 2021; Jantzen *et al.*, 2026). In the UK dataset, where measurements of tree growth are also available, these changes in reproductive dynamics and increased frequency of reproductive allocation have been linked to a 28% decline in secondary growth (Hacket-Pain *et al.*, 2025). This provides a mechanistic basis to expect parallel changes in seed mass.

If more frequent reproduction leaves insufficient time for trees to replenish stored carbon and nutrients, then the resource pool available for seed filling should progressively decline.

Here, we tested for long-term changes in seed mass in European beech. We examined the effects of early spring temperature, which may extend the growing season and increase seed mass, and summer drought during the seed-filling period, which may constrain seed development and reduce seed mass. We also tested whether year-to-year variation in seed mass was associated with internal resource levels reconstructed from long-term seed-production records using the method of Rees *et al.* (2002). Finally, we asked whether the seed mass decline over time can be attributed to changing climatic conditions and altered resource dynamics caused by warming-induced shift in reproductive allocation (Hacket-Pain *et al.*, 2025).

Methods

Study species

European beech (*Fagus sylvatica* L.) is a major forest-forming broadleaved tree in temperate Europe of high ecological and economic importance (Leuschner, 2020). It is a wind-pollinated, mast-seeding species, characterized by strong inter-annual variation and high synchrony in seed production (Vacchiano *et al.*, 2017; Ascoli *et al.*, 2017). Masting in beech increases reproductive efficiency through economies of scale: large, synchronous flowering improves pollination, while intermittent large crops reduce losses to pre-dispersal seed predators (Nilsson & Wastljung, 1987; Pesendorfer *et al.*, 2024). Moreover, high-seeding years are associated with lower pilferage rates of seeds cached by rodents, which improves germination rates (Zwolak *et al.*, 2016; Mittelman *et al.*, 2024). High-seeding years are also associated with a shift in allocation from radial growth towards reproduction (Hacket-Pain *et al.*, 2015; Nussbaumer *et al.*, 2021).

Annual flower production is linked to summer temperature cues, particularly June-July temperature (Journé *et al.*, 2024), and recent warming has increased the frequency of those cues (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024). Both in the UK and the Netherlands, seed production shifted in mid-2000 from highly variable and synchronous to more regular and less synchronized (Bogdziewicz *et al.*, 2020; Jantzen *et al.*, 2026). The reduction in year-to-year variation in seed production and reduced synchrony, termed masting breakdown, is widespread across the species' range and is strongest where summer temperatures have increased most rapidly (Foest *et al.*, 2024, 2025b). As a consequence of reduced inter-annual variation and synchrony, the economies of scale have weakened, which has led to a decrease in pollination efficiency, increased pre-dispersal seed predation rates (Bogdziewicz *et al.*, 2023; Jantzen *et al.*, 2026), and consequently, a decline in viable seed production by more than 50% (Bogdziewicz *et al.*, 2023).

Data

Seed production In the UK, seed production was monitored using a timed count beneath the same set of 85 trees, distributed across 6 sites (site details in Packham *et al.* (2008); Bogdziewicz *et al.* (2023)). Shortly after seed fall (late-September or early October), the ground beneath each canopy was searched for seeds for 3.5 minutes. Collected seeds were bagged in the field and later air-dried for at least 24 hours, sorted, and counted in the laboratory. In a validation against quadrat-based ground counts, the timed count showed a strong loglinear relationship with area-based estimates of seed fall ($R^2 = 0.78$) (Foest *et al.*, 2025a). The sample size used here is smaller than in previous studies based on this monitoring program (Bogdziewicz *et al.*, 2020; Hacket-Pain *et al.*, 2025), because we restricted the analysis to trees for which seed mass data were also available. Mean seed mass was estimated by weighing all viable seeds from each tree (occasionally a random subsample), and dividing by the number of seeds.

In the Netherlands, seed production was monitored annually in mid-October at the National Park De Hoge Veluwe (52.038°N, 5.857°E) using the ground-plot method beneath the same set of 74 trees. Four metal quadrats (25 x 25 cm) were placed in a straight line of a fixed direction underneath each tree, with the first square being placed half a meter from the trunk, the outer square underneath the tip of the largest overhanging branch, and the remaining two squares at equal distance in between. All whole and partial seeds were collected within each square, bagged, and labeled. After air-drying for at least 24h, seeds were sorted and counted. Per sample, all sound nuts were weighed together, and a random subset of these nuts was weighed individually to determine the weight per nut. For a detailed description of the Dutch data collection, see Jantzen & Visser (2026).

Climate data We obtained high-resolution (0.1°) daily climate data for each study site from the E-OBS dataset (Cornes *et al.*, 2018), including mean temperature and precipitation. For each site, we quantified summer (May-June) climatic water balance (CWB), calculated as monthly precipitation sum minus potential evapotranspiration. Potential evapotranspiration was estimated using the Thornthwaite method. In addition, we quantified summer (May-June) vapour pressure deficit (VPD), an alternative drought index measuring atmospheric dryness, calculated from daily mean temperature and relative humidity following Duursma (2015).

Reconstructed stored resources To estimate annual variation in internal resources available for reproduction, we reconstructed stored resources from long-term seed-production records following the approach of Rees *et al.* (2002) (Fig. S1). For each tree, cumulative seed production was modeled as a function of cumulative time (in years), with time treated as a proxy for cumulative resource acquisition. Annual stored resources were then defined as the residual deviation from the expected cumulative seed production given time, such that positive values indicate greater-than-expected unspent resources and negative values indicate relative depletion. A detailed protocol is included as a supplementary file in (Kelly *et al.*, 2025). We used Tree ID and site ID as random intercept and year as random slope, which allowed fitting a unique intercept for each tree, which estimates stored resources of a tree at the beginning of the monitoring period (Rees *et al.*, 2002). Random slope allowed heterogeneous resource acquisition of individuals over time (Crone *et al.*, 2005; Bogdziewicz *et al.*, 2018). Because that data requires long-term observations, we used only trees with at least 10 years of monitoring and no more than 5 missing observations.

Note that this approach does not make assumptions on the nature of the limiting resource, i.e., whether that is carbon, nitrogen, or another limiting resource (Han & Kabeya, 2017). Because cumulative reproduction is on the Y axis, the units of resource reserves are seeds, including the combination of carbon, nitrogen, and other resources required for reproduction in that species (Kelly *et al.*, 2025).

Analysis

Temporal trend in seed mass We first tested for long-term changes in seed mass using a generalized linear mixed model (GLMM). Mean seed mass was modeled with a Gamma error distribution and log link. The Gamma distribution was appropriate because seed mass is a continuous, positive variable. Year was included as a smooth term to allow for a nonlinear trend, while tree identity and site were included as random-effect smooths. We also included the interaction term between year and country to test whether trends differ between datasets. That interaction was not significant ($P = 0.29$) and was removed from the model.

Year-to-year variation in seed mass To test which factors explained year-to-year changes in seed mass, we fitted a GLMM with a Gamma error distribution and log link. Tree identity and site were included as random intercepts. Fixed effects were spring temperature (mean January-April temperature), summer drought during seed filling (May-June), annual tree-level seed production in the focal year, reconstructed stored resources (see below), and country (United Kingdom/Netherlands). Summer drought was tested both as climatic water balance (CWB) and vapor pressure deficit (VPD); results were qualitatively the same (Table S1), and we report CWB in the main text. All continuous predictors were standardized prior to analysis by subtracting the mean and dividing by the standard deviation (z-transformation).

We have also tested for temporal trends in the above-listed predictors using Gaussian error, identity link GLMMs. Spring temperature, summer drought, seed production, or reconstructed stored resources (described below) were included as response variables in separate models, while year and country were included as predictors. Site was included as a random intercept in all models, while treeID was additionally included in the models that tested for trends in seed production and reconstructed resource levels. We inspected the model residuals, and if they suggested a non-linear relationship, we fitted a focal predictor using cubic splines.

Trend attribution To attribute the long-term change in seed mass to its potential drivers, we used the temporal contribution approach of Fernández-Martínez *et al.* (2019). The full year-to-year seed-mass model described above was used to predict annual seed mass across the study period. We then generated predictions in which one predictor at a time was held constant (median), while all other predictors were allowed to vary as observed. The contribution of a given predictor to the temporal change in seed mass was calculated as the difference between the change predicted by the full model and the change predicted when that predictor was held constant. The unexplained difference between the observed temporal change and the sum of predictor-specific contributions was treated as an unknown component, representing the residual temporal (year) effect not accounted for by the predictors included in the model. Uncertainty of contributions was quantified by error propagation.

Results

Seed mass declined over time (Fig. 1A), and temporal contribution analysis indicated that this decline was driven primarily by declining reconstructed stored resources, with an additional negative contribution from increasing summer drought (Fig. 2A).

We detected a significant nonlinear temporal trend in seed mass ($F = 10.78$, $P = 0.001$). Model predictions indicated that mean seed mass declined by 13% over the study period, from 0.26 g (95% CI:

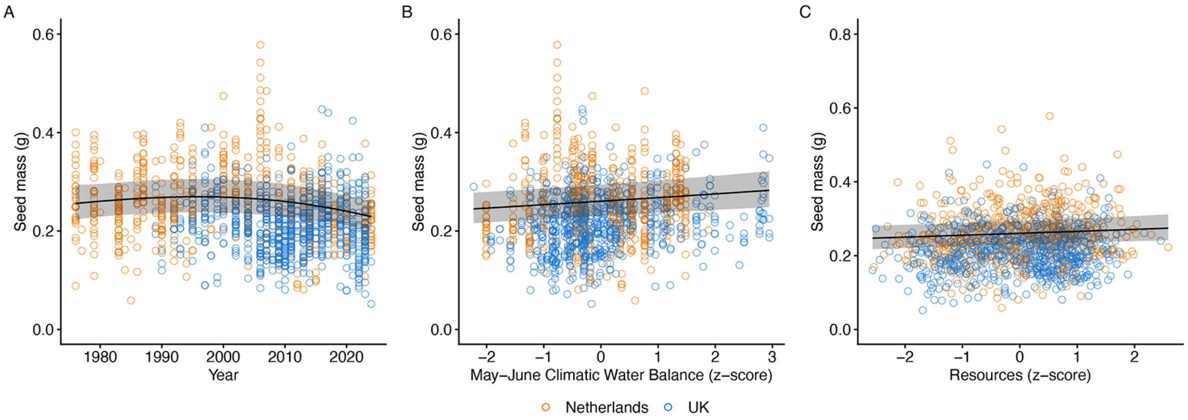

Figure 1: Seeds mass declined over time, was lower in dry years, and was lower when reconstructed resources were low. A) Seed mass over time, B) across summer (May-June) climatic water balance (CWB), and C) across reconstructed resource levels. Prediction lines are derived from a Generalized Mixed Models fitted with a Gamma error distribution and a log link function that included tree ID (N = 159 for A, N = 103 for B and C) and site ID (N = 7 for A-C) as random intercepts. Points show annual, tree-level measurements; colors show region (UK - 1989-2024; and Netherlands - 1976-2024). Resources are reconstructed using individual-level seed production, following the Rees *et al.* (2002) method, see text.

0.22-0.29) in 1976 to 0.23 g (95% CI: 0.20-0.26) in 2024 (Fig. 1a). The decline was non-linear, with seed mass generally stable until mid-2000 (Fig. 1A).

The model of year-to-year variation showed that seed mass was higher in years with greater reconstructed resource level ($\beta = 0.02 \pm 0.008$, $z = 2.64$, $P = 0.008$), corresponding to an estimated 11% change in seed mass across the observed range of the resource levels (Fig. 1). Seed mass was also higher in years with higher May-June climatic water balance ($\beta = 0.03 \pm 0.007$, $z = 3.73$, $P < 0.001$), indicating lower seed mass in drier years and corresponding to an estimated 15% change across the observed climatic gradient. Seed mass was unrelated to annual seed production ($\beta = 0.006 \pm 0.008$, $z = 0.79$, $P = 0.428$) and to January-April mean temperature ($\beta = 0.007 \pm 0.007$, $z = 0.97$, $P = 0.335$) (Table S1).

Consistent with these associations, temporal contribution analysis showed that declining reconstructed resources (Fig. 2B) explained the largest share of the long-term decline in seed mass, increasingly dry May-June conditions made an additional important contribution (Fig. 2), despite the underlying trend towards aridity being only modest ($P = 0.136$, Table S2). (Fig. 2A, C). In contrast, temporal changes in annual seed production and January-April temperature had negligible effects on the long-term trend (Fig. 2A). A substantial fraction of the temporal change remained unexplained by the predictors included in the model (Fig. 2A).

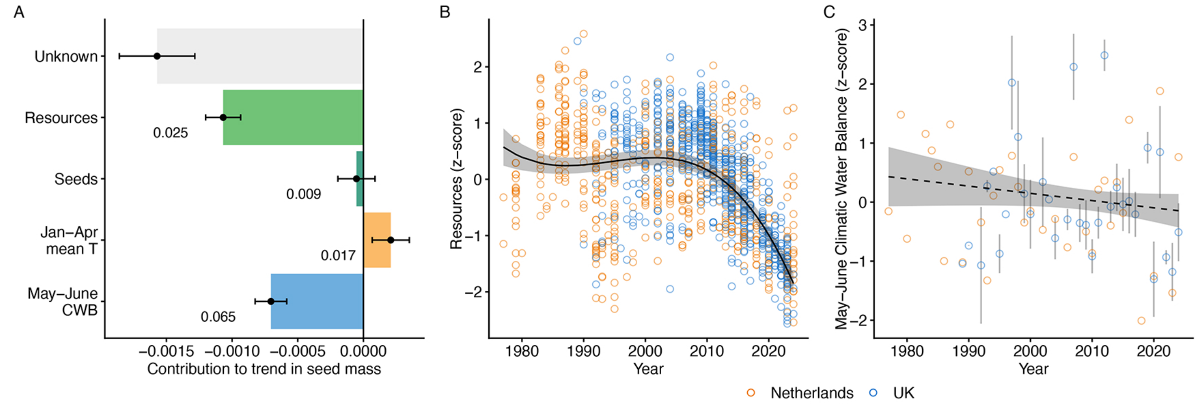

Figure 2: Seed mass decline in beech is associated with shifts in resource dynamics and increasing aridity. A) The analysis, based on 7 sites and 103 trees (1976-2024), indicated that the decline in reconstructed stored resources is the main contributor to the observed decrease in European beech seed mass, with an additional important effect via increasing drought (climatic water balance, CWB). The difference between the modeled contributions and the observed trend was considered an unknown contribution to the temporal variation of annual seed mass. The numbers alongside the bars show the sensitivity of seed mass to predictor changes (see Methods: Trend attribution, note that predictors are z-transformed). Error bars for associated contributions indicate SE. See Methods for information about the methodology used to calculate the contributions. Temporal trends of B) reconstructed resource levels C) summer (May-June) climatic water balance (CWB), with prediction line derived from GLMMs (Table S2). Points at B) show annual-tree level measurements, while at C) site level means and associated SD. Resources are estimated from measured individual- level seed production, following the Rees *et al.* (2002) method, see text

Discussion

Seed mass in European beech declined non-linearly by 13% over the study period, with the decrease emerging in the mid-2000s, and was attributed primarily to reduced estimated resource availability for reproduction, with an additional negative contribution from increasing summer drought. The dominant role of reconstructed resources suggests that the decline in seed mass is a direct response to progressing aridity, as well as an indirect consequence of altered reproductive dynamics under climate warming. In the UK, the same shift in reproductive dynamics has already been linked to reduced secondary growth, indicating that repeated reproduction can deplete the resources available for other functions (Hacket-Pain *et al.*, 2025). Consistent with this timing, other key processes—declines in interannual variation in seed production (Bogdziewicz *et al.*, 2020; Jantzen *et al.*, 2026) and in growth (Hacket-Pain *et al.*, 2025)—also showed non-linear changes emerging in the mid-2000s. Our findings suggest that seed provisioning is affected in the same way: as recovery intervals shorten, the resource pool available for seed filling declines, resulting in progressively lighter seeds.

Our results indicate that climate warming can affect tree performance indirectly by altering how resources are allocated among demographic functions. In European beech, warmer summers have increased the frequency of the temperature cues that trigger flowering, shifting reproduction from highly variable and synchronized towards a more regular seed production (Bogdziewicz *et al.*, 2020; Foest *et al.*, 2024; Jantzen *et al.*, 2026). This has direct consequences for reproductive efficiency: pollination efficiency decreases, and pre-dispersal seed predation increases, so viable seed production declined even if total seed output did not (Bogdziewicz *et al.*, 2023; Foest *et al.*, 2025b; Jantzen *et al.*, 2026). What is more, these effects of increasing summer temperature on reproduction are accompanied by indirect ones. By shortening the recovery intervals between reproductive events, warming alters the temporal distribution of reproductive allocation, depletes stored resources, and has been linked to a 28% decline in radial growth (Hacket-Pain *et al.*, 2025). Our results imply that seed mass declines through the same general pathway. Thus, climate warming appears to be reorganizing resource allocation in beech in ways that reduce not only reproductive efficiency, but also tree growth and offspring provisioning (i.e., seed size), creating cascading and interlinked demographic effects that would be missed if reproduction, growth, and seed traits were considered in isolation (Lauder *et al.*, 2019; Macias & Redmond, 2025).

Lighter seeds are likely to reduce regeneration performance. In beech, seed mass positively affects germination, and heavier seeds are associated with larger seedlings (Muffler *et al.*, 2021; Pawłowski *et al.*, 2024). More generally, the effects of intraspecific variation in seed mass on seedling performance are well documented in trees, and available evidence suggests that the advantages of larger seeds are often strongest under stressful conditions. In Scots pine (*Pinus sylvestris*), larger seeds increased emergence and initial shoot growth, with these differences stronger under more stressful soil conditions (Castro, 1999). In white oaks (*Quercus robur*, *Q. petraea*, *Q. pubescens*), seedlings from heavier acorns were taller, heavier-seeded individuals more often became the dominant competitor, and competition reduced the height of inferior competitors by 40% (Landergott *et al.*, 2012). Larger seeds also maintained higher seedling biomass after damage, indicating that seed reserves can buffer early performance under stress (Bartlow *et al.*, 2018). Seed mass may additionally influence animal-mediated dispersal. Scatter-hoarding rodents generally prefer larger, higher-energy seeds, which they cache more often and disperse farther or to safer sites (Lichti *et al.*, 2017). In mixed seed communities, a decline in beech seed mass could place beech at a relative disadvantage relative to larger-seeded heterospecifics. Declining seed mass and increasingly frequent drought are likely to reinforce one another during recruitment, because the benefits of larger seeds tend to be greatest under stress (Castro, 1999; Landergott *et al.*, 2012), whereas beech seedlings are themselves drought-sensitive and show reduced growth and lower establishment under drought (Gebauer *et al.*, 2020; Robson *et al.*, 2009).

Year-to-year variation in seed mass indicates that offspring provisioning in beech is shaped by drought during seed filling and by the state of internal resources. Seeds were, on average, 15% lighter in dry than in wet years, and they were similarly smaller when reconstructed resource levels were low. By contrast, seed mass was unrelated to seed production in the focal year, suggesting that reduced seed mass does not arise from a seed size-number trade-off. Instead, the effect of resource levels agrees with the assertion that mast-seeding plants accumulate resources to support large reproductive events, which then deplete reserves and constrain reproduction in subsequent years (Satake & Iwasa, 2000; Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2025). This interpretation is reinforced by a recent range-wide study in European beech showing that seed mass is not reduced at high seed production, but that seed protein content declines in high-seeding years, implying that nitrogen rather than carbon becomes limiting as reproductive demand increases (Kondrat *et al.*, 2025). Although we lack retrospective measurements of seed nutrient composition, this result suggests an additional consequence of disrupted resource dynamics: repeated reproduction may progressively deplete nitrogen availability more strongly than carbon-based seed biomass.

The negative effect of drought has similarly important consequences for regeneration. In dry years, recruitment may be constrained both directly, because water limitation suppresses germination and seedling performance (Gebauer *et al.*, 2020; Robson *et al.*, 2009), and indirectly, because smaller seeds generally produce seedlings that are less buffered against drought stress (Castro, 1999; Pawłowski *et al.*, 2024). Future work should test whether seed nutrient composition has changed over time, and quantify the consequences of smaller seeds under drier recruitment conditions. This is especially important now that viable seed production is declining (Bogdziewicz *et al.*, 2023; Jantzen *et al.*, 2026), while disturbance rates, and thus the need for regeneration, are increasing (Seidl & Turner, 2022; Grünig *et al.*, 2026).

One limitation of our study is that we infer changes in internal resource status indirectly, rather than from direct measurements of carbon, nitrogen, or other nutrients in tree tissues. Such data would be invaluable for identifying which resources decline through time and for testing whether warming alters carbon and nutrient pools differently, but it is unsurprising that they are unavailable in monitoring programs initiated in the 1970s or 1980s. Our analysis is also restricted to European beech, because this is one of the few species for which long-term individual-level records of both seed production and seed mass exist. Extending similar analyses to other masting species will be important, because climate warming is altering reproductive dynamics more broadly, but not always in the same direction (Hacket-Pain & Bogdziewicz, 2021). For example, warming-associated changes in weather cues have increased the frequency of reproduction in some species, such as water oak (*Quercus crispula*) (Shibata *et al.*, 2020), whereas in others, such as tawa (*Beilschmiedia tawa*), warming lowered cueing frequency and resulted in long-term reproductive failure (Yukich-Clendon *et al.*, 2023). This suggests that climate change may have contrasting effects on seeding frequency, resource dynamics, and other vital functions across species (Macias & Redmond, 2025). By contrast, the negative effect of dry years on seed mass may prove more general, given the widespread effects of drought on photosynthesis and plant carbon balance (Chuste *et al.*, 2020; Hartmann *et al.*, 2020; Trugman & Anderegg, 2025). Testing whether drought consistently reduces seed mass across species will be especially important, because warming appears to be reducing fecundity more broadly (Foest *et al.*, 2026), and a parallel decline in offspring provisioning would further constrain regeneration.

Seed mass is a fitness-related trait that has important effects on recruitment. Using two long-term datasets from European beech, we show that seed mass has declined over recent decades, and that this decline is explained primarily by reduced reconstructed resource availability, with an additional contribution from drought during seed filling. Climate warming can affect tree performance through shifts in resource dynamics that alter investment in each offspring, in addition to its direct effects on growth, mortality, and fecundity. Because seed mass influences dispersal, early seedling growth, and seedling survival (Clark *et al.*, 2007; Lichti *et al.*, 2017; Pawłowski *et al.*, 2024), a sustained decline in seed mass is likely to scale up to reduced regeneration, especially as viable seed production declines and disturbance rates increase (Bogdziewicz *et al.*, 2023; Foest *et al.*, 2026; Grünig *et al.*, 2026). At the same time, concurrent changes in seed mass and masting dynamics may have complex consequences for seed consumers: smaller seeds reduce energetic rewards, while more frequent but less synchronous seed production can increase the prevalence of empty seeds, potentially leading to food shortages for species that rely on beechnuts, particularly if alternative resources are limited.

Acknowledgements

We thank Maria Bogdańska for consultation on desing of the figures. 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. The study was conceived at a workshop funded by the School of Environmental Sciences, University of Liverpool, and co-organised by Samantha Patrick to whom we are grateful. We thank the generations of researchers who have maintained the English Beech Mast Survey, especially Peter Thomas, Jonathan Lageard, J.R. Packham and G.M. Hilton and Rachel Gaulton. We further thank J.H. van Balen for setting up the Dutch study and the board of the National Park De Hoge Veluwe for letting us conduct the field work. CCJ was funded by the Dutch Research Council (NWO) with file number OCENW.M.22.426 of the research programme NWO Open Competition Domain Science.

Author Contributions Statement

All authors designed the study. CCJ, MEV, AHP, LN, and JF collected and curated the data, CCJ and JS analyzed the data, MB led the writing of the manuscript, and all authors revised the paper.

Declaration of interests

No competing interests to declare.

Data availability statement

The data and code supporting the results are archived in the Open Science Framework and are available at: `https://osf.io/psxje/overview?view_only=27923d63e2f440f0b2d52a4805eba222` .

References

Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J. *et al.* (2017). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications 2017 8:1*, 8, 1–9.

Baraloto, C., Forget, P.M. & Goldberg, D.E. (2005). Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, 93, 1156–1166.

Bartlow, A.W., Agosta, S.J., Curtis, R., Yi, X. & Steele, M.A. (2018). Acorn size and tolerance to seed predators: the multiple roles of acorns as food for seed predators, fruit for dispersal and fuel for growth. *Integrative Zoology*, 13, 251–266.

Bogdziewicz, M., Espelta, J.M. & Bonal, R. (2019). Tolerance to seed predation mediated by seed size increases at lower latitudes in a mediterranean oak. *Annals of Botany*, 123, 707–714.

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., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E. *et al.* (2024). Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology & Evolution*, 39, 851–862.

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. (2020). 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*, 56, 119–144.

Bogdziewicz, M., Steele, M.A., Marino, S. & Crone, E.E. (2018). Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytologist*, 219, 98–108.

Castro, J. (1999). Seed mass versus seedling performance in scots pine: a maternally dependent trait. *New Phytologist*, 144, 153–161.

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, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. (2007). Are plant populations seed limited? a critique and meta-analysis of seed addition experiments. *American Naturalist*, 170, 128–142.

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.

Crone, E.E., Polansky, L. & Lesica, P. (2005). Empirical models of pollen limitation, resource acquisition, and mast seeding by a bee-pollinated wildflower. *American Naturalist*, 166, 396–408.

Dri, G., Bogdziewicz, M., Hunter, M., Witham, J. & Mortelliti, A. (2025). Coupled effects of forest growth and climate change on small mammal abundance and body weight: Results of a 39-year field study. *Journal of Animal Ecology*, 94, 2118–2129.

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

Dylewski, L., Ortega, Y.K., Bogdziewicz, M. & Pearson, D.E. (2020). Seed size predicts global effects of small mammal seed predation on plant recruitment. *Ecology Letters*, 23, 1024–1033.

Fernández-Martínez, M., Sardans, J., Chevallier, F., Ciais, P., Obersteiner, M., Vicca, S. *et al.* (2019). Global trends in carbon sinks and their relationships with co2 and temperature. *Nature Climate Change*, 9, 73–79.

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.

Foest, J.J., Bogdziewicz, M., Caignard, T., Hadad, M., Thomas, P.A. & Hacket-Pain, A. (2025a). Comparing two ground-based seed count methods and their effect on masting metrics. *Forest Ecology and Management*, 581, 122551.

Foest, J.J., Szymkowiak, J., Dyderski, M.K., Jastrzębowski, S., Fuchs, H., Ratajczak, E. *et al.* (2025b). No refuge at the edge for european beech as climate warming disproportionately reduces masting at colder margins. *Ecology Letters*, 28, e70284.

Foest, J.J., Szymkowiak, J., Dyderski, M.K., Kelly, D., Kunstler, G., Jastrzębowski, S. *et al.* (2026). Forest fecundity declines as climate shifts. *Nature Climate Change*. In press.

Frenne, P.D., Graae, B.J., Rodríguez-Sánchez, F., Kolb, A., Chabrerie, O., Decocq, G. *et al.* (2013). Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, 101, 784–795.

Gao, C., Liu, F., Miao, Y., Li, J., Liu, Z. & Cui, K. (2023). Variation in seed number/mass trade-off for pinus yunnanensis along a natural climate gradient in the mountains of southwest china. *Plant Ecology*, 224, 203–219.

Gebauer, R., Plichta, R., Urban, J., Volarík, D. & Hájíčková, M. (2020). The resistance and resilience of european beech seedlings to drought stress during the period of leaf development. *Tree Physiology*, 40, 1147–1164.

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.

Grünig, M., Rammer, W., Senf, C., Albrich, K., André, F., Augustynczik, A.L.D. *et al.* (2026). Climate change will increase forest disturbances in europe throughout the 21st century. *Science*, 391, eadx6329.

Hacket-Pain, A. & Bogdziewicz, M. (2021). Climate change and plant reproduction: trends and drivers of mast seeding change. *Philosophical Transactions of the Royal Society B*, 376, 20200379.

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., Friend, A.D., Lageard, J.G. & Thomas, P.A. (2015). The influence of masting phenomenon on growth-climate relationships in trees: Explaining the influence of previous summers' climate on ring width. *Tree Physiology*, 35, 319–330.

Han, Q. & Kabeya, D. (2017). Recent developments in understanding mast seeding in relation to dynamics of carbon and nitrogen resources in temperate trees. *Ecological Research 2017 32:6*, 32, 771–778.

Han, Q., Kabeya, D. & Hoch, G. (2011). Leaf traits, shoot growth and seed production in mature *Fagus sylvatica* trees after 8 years of CO2 enrichment. *Annals of Botany*, 107, 1405–1411.

Han, Q., Kabeya, D. & Inagaki, Y. (2020). Reproduction affects partitioning between new organs of a pulse of ^{15}n applied during seed ripening in Fagus crenata. *New Forests*, 51, 739–752.

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.

Hoch, G. (2005). Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees.

Huang, L., Jin, C., Zhou, L., Song, K., Qian, S., Lin, D. *et al.* (2021). Benefit versus cost trade-offs of masting across seed-to-seedling transition for a dominant subtropical forest species. *Journal of Ecology*, 109, 3087–3098.

Jantzen, C., Burant, J., Gamelon, M., Bakker, E.L. & Visser, M.E. (2026). Masting breakdown in european beech reduces fitness benefits of masting, partly explained by climate change. Preprint.

Jantzen, C. & Visser, M.E. (2026). Long-term annual seed production data of individual european beech (fagus sylvatica) trees in the netherlands. *preprint*.

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*, 246, 1975–1985.

Kidson, R. & Westoby, M. (2000). Seed mass and seedling dimensions in relation to seedling establishment. *Oecologia*, 125, 11–17.

Koenig, W.D., Knops, J.M.H. & Carmen, W.J. (2009). Acorn mass variation in valley oak (quercus lobata): environmental influences and consequences for seedling establishment. *Canadian Journal of Forest Research*, 39, 597–605.

Kondrat, K., Jerzyńska, P., Eichert, U., Szymkowiak, J., Hacket-Pain, A., Adamič, T. *et al.* (2025). No seed size–number trade-off in european beech: climate governs investment per seed. *Ecology Letters*.

Landergott, U., Gugerli, F., Hoebee, S.E., Finkeldey, R. & Holderegger, R. (2012). Effects of seed mass on seedling height and competition in european white oaks. *Flora*, 207, 721–725.

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.

Lenzo, L.J., Forister, M.L., Olwell, P. & Leger, E.A. (2025). Climate change, weather, and geography shape seed mass variation and decline across western north america. *Global Change Biology*, 31, e70416.

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

Lichti, N.I., Steele, M.A. & Swihart, R.K. (2017). Seed fate and decision-making processes in scatter-hoarding rodents. *Biological Reviews*, 92, 474–504.

Macias, D.S. & Redmond, M.D. (2025). Climate-warming alters resource allocation in unpredictable ways. *Trends in Ecology & Evolution*, 40, 428–430.

Mittelman, P., Appleby, S.M. & Balkenhol, N. (2024). Forest composition shapes seed-rodent interactions in a gradient of broadleaves and conifers. *Journal of Applied Ecology*, 61, 1944–1954.

Muffler, L., Schmeddes, J., Weigel, R., Barbeta, A., Beil, I., Bolte, A. *et al.* (2021). High plasticity in germination and establishment success in the dominant forest tree fagus sylvatica across europe. *Global Ecology and Biogeography*, 30, 1583–1596.

Muller-Landau, H.C. (2010). The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 4242–4247.

Muñoz, A., Bonal, R. & Espelta, J.M. (2014). Acorn - weevil interactions in a mixed-oak forest: Outcomes for larval growth and plant recruitment. *Forest Ecology and Management*, 322, 98–105.

Nilsson, S.G. & Wastljung, U. (1987). Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology*, 68, 260–265.

Nussbaumer, A., Gessler, A., Benham, S., de Cinti, B., Etzold, S., Ingerslev, M. *et al.* (2021). Contrasting resource dynamics in mast years for european beech and oak—a continental scale analysis. *Frontiers in Forests and Global Change*, 4, 89.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15, 232–237.

Packham, J.R., Thomas, P.A., Lageard, J.G. & Hilton, G.M. (2008). The english beech masting survey 1980–2007: Variation in the fruiting of the common beech (fagus sylvatica l.) and its effects on woodland ecosystems. *Arboricultural Journal*, 31, 189–214.

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, 1355328.

Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Pesendorfer, M.B., Bogdziewicz, M., Oberklammer, I., Nopp-Mayr, U., Szwagrzyk, J. & Gratzer, G. (2024). Positive spatial and temporal density-dependence drive early reproductive economy-of-scale effects of masting in a european old-growth forest community. *Journal of Ecology*, 112, 1872–1884.

Qiu, T., Andrus, R., Aravena, M.C., Ascoli, D., Bergeron, Y., Berretti, R. *et al.* (2022). Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery. *Nature Communications*, 13, 1–12.

Rees, M., Kelly, D. & Bjørnstad, O.N. (2002). Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist*, 160, 44–59.

Reich, P.B., Oleksyn, J. & Tjoelker, M.G. (1994). Seed mass effects on germination and growth of diverse european scots pine populations. *Canadian Journal of Forest Research*, 24, 306–320.

Robson, T.M., Rodríguez-Calcerrada, J., Sánchez-Gómez, D. & Aranda, I. (2009). Summer drought impedes beech seedling performance more in a sub-mediterranean forest understory than in small gaps. *Tree Physiology*, 29, 249–259.

Roncé, I.L., Dardevet, E., Venner, S., Schönbeck, L., Gessler, A., Chuine, I. *et al.* (2023). Reproduction alternation in trees: testing the resource depletion hypothesis using experimental fruit removal in quercus ilex. *Tree Physiology*, 43, 952–964.

Roncé, I.L., 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.

Sala, A., Hopping, K., McIntire, E.J., Delzon, S. & Crone, E.E. (2012). Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*, 196, 189–199.

Satake, A. & Iwasa, Y. (2000). Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology*, 203, 63–84.

Seidl, R. & Turner, M.G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences*, 119, e2202190119. Publisher: Proceedings of the National Academy of Sciences.

Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. (2020). Decadal changes in masting behaviour of oak trees with rising temperature. *Journal of Ecology*, 108, 1088–1100.

Smith, C.C. & Fretwell, S.D. (1974). The optimal balance between size and number of offspring. *American Naturalist*, 108, 499–506.

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.

Turnbull, L.A., Rees, M. & Crawley, M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, 87, 899–912.

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.

Vázquez-Ramírez, J. & Venn, S.E. (2025). Climate change may alter seed and seedling traits and shift germination and mortality patterns in alpine environments. *Annals of Botany*, 136, 651–667.

WALCK, J.L., HIDAYATI, S.N., DIXON, K.W., THOMPSON, K. & POSCHLOD, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, 17, 2145–2161.

Wang, B. & Ives, A.R. (2017). Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. *Oecologia*, 183, 751–762.

Ward, R.E., Zhang-Zheng, H., Abernethy, K., Adu-Bredu, S., Arroyo, L., Bailey, A. *et al.* (2025). Forest age rivals climate to explain reproductive allocation patterns in forest ecosystems globally. *Ecology Letters*, 28, e70191.

Yukich-Clendon, O.M.M., Carpenter, J.K., Kelly, D., Timoti, P., Burns, B.R., Boswijk, G. *et al.* (2023). Global change explains reduced seeding in a widespread new zealand tree: indigenous tūhoe knowledge informs mechanistic analysis. *Frontiers in Forests and Global Change*, 6, 1172326.

Zi, H., Jing, X., Liu, A., Fan, X., Chen, S.C., Wang, H. *et al.* (2023). Simulated climate warming decreases fruit number but increases seed mass. *Global Change Biology*, 29, 841–855.

Zwolak, R., Bogdziewicz, M., Wróbel, A. & Crone, E. (2016). Advantages of masting in european beech: timing of granivore satiation and benefits of seed caching support the predator dispersal hypothesis. *Oecologia*, 180, 749–758.

Supporting Information

Climate warming reduces seed mass in European beech through altered resource dynamics and drought

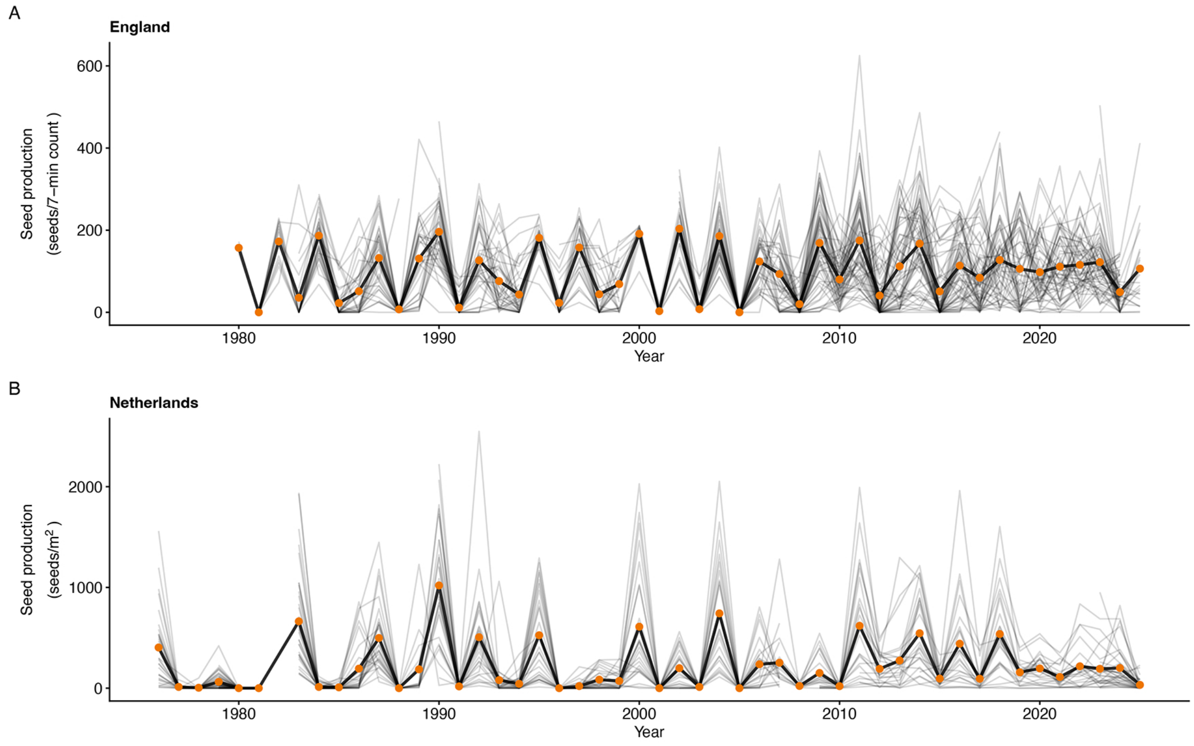

Figure S1: Seed production patterns of European beech in England (A) and Netherlands (B). Each line shows individual tree seed production (England: 85 trees, 6 sites; Netherlands: 74 trees, 1 site), while black thick lines show the country-level means (orange points).

Table S1: Models summary. Results of Generalized Mixed Models testing for the effects of summer (May-June) climatic water balance (Model I) or vapour pressure deficit (Model II), mean January-April temperature, seed production, and reconstructed resource levels on seed mass in European beech. The models were fitted with a Gamma error distribution (log link) and included tree ID (N = 103) and site ID (N = 7) as random intercepts.

Model term	**Slope**	**SE**	z	**P**
Model I				
Intercept	-1.373	0.062	-22.17	<0.001
May-June CWB	0.028	0.007	3.73	<0.001
Country (UK)	-0.199	0.068	-2.92	0.003
Seed production	0.006	0.008	0.79	0.428
January-April mean temperature	0.007	0.007	0.97	0.335
Resources	0.020	0.008	2.64	0.008
Model II				
Intercept	-1.375	0.063	-21.69	<0.001
May-June VPD	-0.024	0.008	-3.24	0.001
Country (UK)	-0.199	0.069	-2.85	0.004
Seed production	0.007	0.008	0.97	0.334
January-April mean temperature	0.011	0.007	1.54	0.124
Resources	0.019	0.008	2.48	0.013

Table S2: Temporal trends in predictors used in temporal contribution analysis. Each row shows a separate model with the year effect on the focal predictor. We used GLMMs, with site ID (all models) or additionally tree ID (resources and seeds model) as random intercepts. The models used a Gaussian error distribution and an identity link.

Predictor	**Slope**	**SE**	**z**	**P**
May-June CWB	-0.011	0.007	-1.49	0.136
Jan-Apr mean T	0.013	0.007	1.84	0.066
Resources	-0.043	0.002	-18.42	<0.001
Seeds	-0.006	0.002	-2.56	0.010