

No seed size–number trade-off in European beech: climate governs investment per seed

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81 **Key words**

82 | *Fagus sylvatica* | mast seeding | size–number trade-off | reproductive allocation | climatic gradients | nitrogen
83 limitation | seed provisioning |

84

85 Abstract

- 86 • Mast seeding trees can vary seed output by orders of magnitude among years, but it remains unclear whether
87 high seed production reduces per-seed investment, as predicted by fixed-budget allocation models.
- 88 • We quantified individual seed production with seed mass in European beech across 2,792 trees and 123
89 populations spanning the species' range and quantified seed protein and lipid content in 35 populations.
- 90 • Seed mass increased with seed production, with seeds from high-seeding years being 14% heavier than those
91 from low-seeding years, providing no evidence for a seed size–number trade-off and instead supporting
92 variable reproductive allocation. In contrast, protein content decreased by 31% with increasing seed
93 production, whereas lipid content increased (by 14%), indicating that nitrogen becomes constraining at high
94 reproductive output while carbon-based provisioning is maintained. Climate further structured provisioning:
95 seed mass and protein content were the lowest at climatic range margins, being 28% and 32% lower,
96 respectively, than at the center of the climatic range.
- 97 • European beech can increase seed output without reducing per-seed biomass, but that nitrogen limitation and
98 climatic constraints may strengthen regeneration bottlenecks at both trailing and leading margins, especially
99 as climate warming intensifies.

100 Introduction

101 The existence of trade-offs is a fundamental feature of ecological strategies (Stearns, 1989). Given finite resources,
102 organisms must allocate them among growth, storage, and reproduction, and even within these domains, resources
103 may be divided differentially (Genet *et al.*, 2009; Thomas, 2011; Hartmann *et al.*, 2020; Cope *et al.*, 2021). For
104 plants, one important allocation problem lies in the balance between producing many small seeds or fewer large
105 ones, the seed size–number trade-off (Smith & Fretwell, 1974; Muller-Landau, 2010). Life-history theory predicts
106 that for a given reproductive effort, producing larger seeds necessarily reduces their number, generating a negative
107 relationship between seed number and seed mass, as described by Smith-Fretwell model (Smith & Fretwell, 1974).
108 Across species the trade-off is clearly observed, and small-seeded species clearly produce more seeds (Leishman
109 & Leishman, 2001; Henery & Westoby, 2001; Muller-Landau *et al.*, 2008; Qiu *et al.*, 2022). Within species,
110 however, empirical results are mixed (Guo *et al.*, 2010). This question is particularly relevant for mast-seeding
111 trees, where seed output can vary by orders of magnitude among years (Bogdziewicz *et al.*, 2025), and the ecological
112 consequences of such fluctuations depend not only on seed number but also on how seed size is maintained or
113 altered across years. For example, a 30% decrease in seed mass in high-seeding years in the subtropical *Castanopsis*
114 *fargesii* translated into a fivefold decrease in germination rate, canceling the benefits of masting such as reduced
115 seed predation (Huang *et al.*, 2021).

116 Mast-seeding species pose an interesting case for the seed number–seed size trade-off because their reproductive
117 effort varies enormously among years. For example, a single European beech (*Fagus sylvatica*) or white spruce
118 (*Picea glauca*) individual may produce 250,000+ seeds in a high-seeding year, while a tussock of *Chionochloa*
119 can produce >15,000 flowers, yet in failure years reproductive investment approaches zero (Hacket-Pain *et al.*,
120 2022; Bogdziewicz *et al.*, 2025). This fluctuation is interpreted as interannually variable reproductive allocation
121 (Bogdziewicz *et al.*, 2024), with high-seeding years involving a larger fraction of resources devoted to reproduction,
122 often at the expense of stored reserves, growth, or defense (Han *et al.*, 2011; Redmond *et al.*, 2019; Gonzalez *et al.*,
123 2023; Hacket-Pain *et al.*, 2025). If reproductive allocation indeed varies strongly across years, then increases in
124 seed number do not need to come at the expense of seed size. Under the allocation theory, when the resource
125 budget is limited, seed number is expected to fluctuate, whereas seed size is constrained by stabilizing selection on
126 offspring survival (Smith & Fretwell, 1974; Sadras, 2007).

127 Importantly, in mast-seeding trees, initiation of reproductive allocation starts long before the optimal conditions
128 for seed development are known. Floral initiation typically occurs in the year preceding seed maturation (Journé
129 *et al.*, 2025; Hirsch *et al.*, 2025), and thus before the resource pool available for seed filling is realized. As a
130 result, even when reproductive allocation increases in mast years, subsequent environmental constraints during
131 seed development may limit the extent to which all initiated seeds can be fully provisioned (Espelta *et al.*, 2008;
132 Pearse *et al.*, 2015). Under such circumstances, rather than aborting excess reproductive structures, trees may
133 respond by reducing per-seed investment, allowing a larger fraction of initiated seeds to mature at smaller size.
134 Indeed, while empirical tests in mast-seeding plants remain scarce, available evidence is partially consistent with
135 this expectation. Seed mass declined with increasing seed production in *Pinus armandii* (Wang & Ives, 2017),
136 *Castanopsis fargesii* (Huang *et al.*, 2021), and in high-crop individuals of *Quercus ilex* (Bonal *et al.*, 2007). In
137 contrast, seed size did not decline with larger crops in *Quercus lobata* (Koenig *et al.*, 2009a). Taken together,
138 the available evidence suggests that increases in seed number can coincide with reduced per-seed investment,
139 potentially diminishing the ecological benefits typically attributed to mast seeding.

140 Beyond variation in seed mass, the orders-of-magnitude variation in seed number characteristic of mast
141 seeding may also alter the storage compounds (e.g. protein and lipid content) of individual seeds. Increased
142 plant biomass production is often associated with reduced concentrations of macro- and micronutrients (Kaspari
143 & Welte, 2024). In mast-seeding trees, however, resource-budget models suggest that sufficient accumulation of
144 reserves crucial for reproduction, particularly nitrogen, is required to initiate mass-flowering years (Miyazaki *et al.*,
145 2014; Sala *et al.*, 2012; Han & Kabeya, 2017). Such storage could buffer seed nutrient composition against large
146 increases in reproductive output, maintaining protein content even when the biomass of produced seeds increases
147 sharply. However, as for seed mass, this buffering is contingent on the temporal decoupling between reproductive
148 commitment and seed development. Because flower initiation precedes seed maturation by a year (Journé *et al.*,
149 2025; Hirsch *et al.*, 2025), plants may commit to more seeds than can be fully provisioned if conditions during seed
150 development are unfavorable, resulting in reduced per-seed investment. Which components of seed provisioning

151 are reduced under such conditions depends on which resources constrain seed development. In contrast to nitrogen-
152 rich compounds such as proteins, lipid provisioning is less likely to be constrained, particularly if seed mass is
153 maintained, as carbon supply is largely branch-autonomous and carbon limitation of reproduction is unlikely in
154 temperate trees (Hoch, 2005; Han & Kabeya, 2017).

155 Beyond resource constraints associated with variable seed number, the environment in which seeds develop
156 also shapes how much a tree invests per seed. The Smith–Fretwell model implies that environmental conditions
157 can shift the optimal seed size, leading to adaptive differentiation among populations (Smith & Fretwell, 1974).
158 For example, *Prunus virginiana* shows habitat-specific optima: plants in riparian sites produced many smaller
159 seeds, where frugivore-mediated dispersal favored high seed number, whereas on dry slopes plants produced fewer
160 but larger seeds, where seedling establishment was the limiting stage (Parciak, 2002). In contrast, broad-scale
161 geographic patterns in seed mass are more often interpreted as responses to environmental constraints than as local
162 adaptation. Across and within species, seed mass commonly declines toward colder climates, most frequently along
163 latitudinal gradients (Moles *et al.*, 2007; Liu *et al.*, 2013; Frenne *et al.*, 2013). Because latitude covaries strongly
164 with temperature, this pattern is generally attributed to thermal limitation. In a meta-analysis, De Frenne *et al.*
165 (2013) showed that intraspecific seed mass increases with temperature, consistent with longer growing seasons,
166 prolonged seed development, and reduced frost risk. In long-lived mast seeding trees, these climatic effects on seed
167 mass have rarely been evaluated together with variation in seed number, despite the potential for large fluctuations
168 in fecundity to directly influence per-seed investment.

169 Here, we test whether European beech expresses a seed size–number trade-off, and how seed provisioning
170 varies across climatic gradients. We quantified seed production and seed mass in 123 populations across the
171 species’ range and assessed protein and lipid composition in 35 of these populations. If high-seeding years reflect
172 increased reproductive allocation rather than reallocation within a fixed resource budget, seed mass should be
173 maintained even as seed output increases. Conversely, declines in seed mass in high-seeding years would indicate
174 short-term constraints on per-seed provisioning, consistent with temporal decoupling between floral initiation and
175 seed development. Such declines are expected to carry fitness costs, as heavier European beech seeds germinate
176 more successfully and produce larger seedlings (Pawłowski *et al.*, 2024). Across climatic gradients, we expected
177 seed mass, protein, and lipid content to reflect constraints on seed development, with heavier, better-provisioned
178 seeds in regions with longer growing seasons and favorable thermal conditions, and reduced mass and nutrient
179 concentrations toward climatic margins of the species’ range, where growing seasons are shorter, temperatures are
180 suboptimal, or heat and drought limit seed filling. With respect to protein and lipid content, we predicted contrasting
181 responses of proteins and lipids. Protein content was expected to be maintained, or to decline in high-seeding
182 years and toward climatic margins if nitrogen storage fails to buffer reproductive investment. In contrast, lipid
183 concentrations were expected to show little variation with either seed number or climate, given that reproduction
184 in temperate trees is unlikely to be carbon-limited.

185 **Methods**

186 **Study species** European beech is an economically and ecologically important forest-forming tree, distributed
187 from the mountains of the Mediterranean to southern Scandinavia and eastwards to Poland and the Carpathians
188 (Packham *et al.*, 2012). It is a wind-pollinated, masting species. Masting benefits European beech by enhancing
189 pollination efficiency and reducing seed predation (Nilsson & Wästljung, 1987; Bogdziewicz *et al.*, 2020). Mast
190 years are also characterized by a shift in allocation from radial growth towards reproduction (Hacket-Pain *et al.*,
191 2025). Seeds are dispersed mainly by scatter-hoarding animals such as rodents and jays (Zwolak *et al.*, 2016;
192 Wróbel *et al.*, 2022). Storage materials of beech seeds include mainly fat and proteins, constituting up to 40 and
193 20% of dry weight, respectively (Prasad & Gülz, 1989; Kalemba *et al.*, 2019). Seeds lack long-term dormancy,
194 germinate the following spring, and seed size and provisioning are crucial for seedling survival under shade and
195 drought stress, with larger seeds translating into more vigorous seedlings (Pawłowski *et al.*, 2024). Among seed
196 storage materials, proteins, the main nitrogen source are crucial for early seedling establishment (Kalemba *et al.*,
197 2019). Embryonic axes completely deplete proteins while elongating to a length of 15 mm, and seedlings with 20
198 mm and longer embryonic axes deplete proteins from cotyledon (Kalemba *et al.*, 2019).

199 **Seed production and mass data** We sampled seeds in 2023 and 2024, from 2,792 individual co-dominant
200 to dominant trees, at 123 sites spanning the natural distribution of European beech across Europe (Fig. 1). At 30
201 of these sites, no viable seeds were recorded during the study, resulting in a final sample of 1,906 trees at 93 sites.
202 Most sites included 20–30 dominant or co-dominant trees, while two plots, one in Poland and another two in the
203 UK, contributed larger samples of 100 trees each. For each tree, we measured diameter breast height (DBH) and
204 assigned a shading class on a five-level ordinal scale (1 = fully shaded, 5 = fully exposed) to describe canopy light
205 exposure (Clark *et al.*, 2021).

206 Seeds were collected from the forest floor beneath the crown of each tree shortly after seedfall using a
207 standardized 3.5-minute search (Foest *et al.*, 2025). The ground below each tree was searched for seeds for 3.5
208 min and seeds were later classified as sound, empty with formed pericarps (not pollinated), or damaged by *Cydia*
209 sp. moth. Only filled (pollinated) seeds that were not infested/predated were retained for analysis presented in
210 this study. All viable seeds from each tree were weighed individually to the nearest 0.001 g after air-drying at
211 room temperature for four weeks. We chose air-drying rather than oven-drying in order to preserve samples for
212 subsequent analyses of proteins and lipids. To verify that this approach did not bias seed mass estimates, we
213 oven-dried a subset of seeds for 24 hours at 80 °C and compared mass before and after drying. Seed mass decreased
214 by 7% on average after oven-drying, and this percentage loss was consistent across sites and years (SD of the %
215 decline = 0.0055).



Figure 1: Map of the 123 study sites where European beech seed production was measured in 2023–2024. Each point represents one study site (N trees = 2,792). The darker gray area indicates the natural distribution of European beech. The climate space covered by our sample is shown in Fig. S1.

216 **Climate data and growing season metrics** Daily weather data for each site were obtained from the
 217 corresponding 0.1° grid cell of the E-OBS dataset (Cornes *et al.*, 2018). To determine growing season length, we
 218 first averaged daily minimum temperature across all years from 1950 to 2024 to obtain long-term daily means for
 219 each site (Körner & Basler, 2010). The start and end of the growing season were then defined as the first and
 220 last day of the year when long-term daily means exceed 5 °C and growing-season length was calculated as the
 221 number of days between them (Körner & Hiltbrunner, 2018; Körner, 2021). The 5 °C threshold is based on Körner
 222 (2021) and follows from the cessation of cambial activity below 5 °C (Cabon *et al.*, 2020). Within the site-specific
 223 growing season length, we calculated mean-growing season temperature and mean-growing season precipitation
 224 for our observation period using weather data from 1950 to 2024. We used long-term climate data to characterize
 225 site-level climatic conditions rather than interannual variation during the sampling years.

226 **Seed nutrient content** Protein and lipid content were determined for 4830 seeds collected in 2023 from a
 227 subset of randomly selected 35 sites, where at least 10 viable seeds were available for protein and lipid content
 228 analyses.

229 Ten whole seeds per tree (N = 483) were extracted from the pericarp and seed coat and ground in liquid
 230 nitrogen. Samples of 100 mg were used for protein determination, and samples of 200 mg were used for lipid
 231 determination.

232 To extract proteins, samples were extracted in 0.5 mL of 60 mM Tris–HCl buffer (pH 6.8) containing 10% (v/v)
 233 glycerol and 2% (w/v) SDS, following the protocol of Stone and Gifford (Stone & Gifford, 1997). The homogenate
 234 was centrifuged at 18,000 × g for 20 min. Protein content was determined using the 2-D Quant Kit, with bovine

235 serum albumin used as a standard.

236 Lipids were extracted using chloroform:methanol [2:1 (v/v)] supplemented with 0.05% butylated hydroxy-
237 toluene (BHT), according to Freeman *et al.* 1966. The homogenate was mixed with an aqueous phase containing
238 1 M potassium chloride and left overnight at 4 °C to allow phase separation. The lower phase (chloroform containing
239 lipids) was collected, dried by vacuum distillation, and the resulting oil was weighed.

240 **Analysis** To examine the relationship between individual seed mass, seed production, and climate, we fitted
241 a generalized linear mixed model (GLMM) with seed mass as the response variable, while tree ID nested with
242 site ID were included as random intercepts. This allowed the seed size–number relationship to be estimated
243 from within-tree variation across years, accounting for differences in resource acquisition among individuals (van
244 Noordwijk & de Jong, 1986; Pease & Bull, 1988; Reznick *et al.*, 2000). The model was fitted with a Gamma error
245 distribution and a log link, as seed mass is a continuous, positive variable. Fixed effects included annual, tree-level
246 seed production, shading class, DBH and climatic predictors, i.e., the long-term averages of growing season length,
247 mean growing-season temperature, and mean-growing season precipitation. In addition, we included interaction
248 terms between growing season length and growing season climate (temperature and precipitation). All predictors
249 were standardized to a zero mean and unit variance prior to analysis to facilitate comparison of effect sizes.

250 To analyze variation in seed protein and lipid content, we fitted two additional GLMMs with seed protein
251 content or seed lipid content (both expressed as percentage of dry mass) as response variables. The fixed-effects
252 structure was the same as in the seed-mass model. Because protein and lipid content data were available for a single
253 year only, year was not included as a random effect. These models were fitted using a Beta error distribution with
254 a logit link.

255 Collinearity among predictors was assessed using variance inflation factors (VIF) calculated with the *car*
256 package, and all predictors showed low collinearity ($VIF < 1.6$) (Fox *et al.*, 2024). Mean growing season precipitation
257 and its interaction with growing-season length had no significant effect in the models, and were excluded from
258 further analyses. All analyses were conducted in R version 4.2.3 (R Core Team, 2023), and the models were fitted
259 using the *glmmTMB* package version 1.1.7 (Brooks *et al.*, 2017).

260 **Results**

261 **Seed number relationship with seed mass, protein, and lipid content**

262 Seed mass varied substantially across the 52,861 seeds measured from 1,906 trees, ranging from 0.012 g to 0.709
263 g. Seed production per tree had a positive relationship with seed mass (Table 1, Fig. 2). The estimated seed mass
264 for low seed production (10 seeds per tree⁻¹ yr⁻¹, based on a standardized 3.5-minute ground collection) was 0.23
265 g, while it increased to 0.26 g (~14%) for high seed production (200 seeds per tree⁻¹ yr⁻¹ per ground collection).
266 Lipid content also increased with higher seed production. For instance, the estimated lipid content for low seed

267 production (10 seeds tree⁻¹ yr⁻¹) was 34.8% and it increased to 39.7% (i.e. by 14%) for high seed production (200
 268 seeds tree⁻¹ yr⁻¹). In contrast, the protein content declined with increasing seed production (Table 1, Fig. 2). For
 269 example, the estimated proportion of protein in seed dry mass for low seed production (10 seeds tree⁻¹ yr⁻¹) was
 270 0.24, while it decreased to 0.16 (by ~31%) for high seed production (200 seeds tree⁻¹ yr⁻¹). Tree size (DBH) and
 271 shading class had a weak, but significant negative effect on lipid content, but not on seed mass or protein content.
 272 For example, the estimated lipid content for small trees (32 cm DBH) was 38.4%, decreasing by 4.9% to 33.5% in
 273 large trees (75 cm DBH) (Table 1). Tree size categories correspond to the 10th and 90th percentiles of the observed
 274 diameter at breast height (DBH) distribution (Fig. S2).

Table 1: Models summary. Predictors were z-standardized prior to the analysis. Generalized linear mixed models were fitted with a log link (Gamma for seed mass; Beta for protein and lipid content). Significant effects ($p < 0.05$) are shown in bold. GS stands for growing season. Coefficients are shown on the link scale; standard errors in parentheses. Models included tree-ID nested within site-ID random intercepts. $N_{\text{tree}} = 1,906$, $N_{\text{site}} = 93$.

Predictor	Model A: Seed mass		Model B: Protein %		Model C: Lipid %	
	Estimate (SE)	p	Estimate (SE)	p	Estimate (SE)	p
Intercept	-1.413 (0.019)	< 0.001	1.285 (0.038)	< 0.001	-0.562 (0.032)	< 0.001
Seed number	0.036 (0.003)	< 0.001	-0.052 (0.019)	0.007	0.079 (0.029)	0.006
Shading class	0.001 (0.004)	0.803	0.011 (0.015)	0.498	-0.049 (0.022)	0.027
DBH	0.003 (0.004)	0.549	-0.005 (0.018)	0.785	-0.060 (0.026)	0.021
Temperature (GS)	-0.018 (0.021)	0.405	-0.119 (0.0469)	0.011	-0.034 (0.040)	0.402
Growing season length	0.027 (0.023)	0.239	0.010 (0.049)	0.839	-0.005 (0.042)	0.905
Precipitation (GS)	-0.012 (0.015)	0.438	0.044 (0.031)	0.147	0.021 (0.029)	0.460
Temp (GS) × GS length	-0.025 (0.011)	0.026	-0.104 (0.0323)	< 0.001	-0.026 (0.028)	0.368

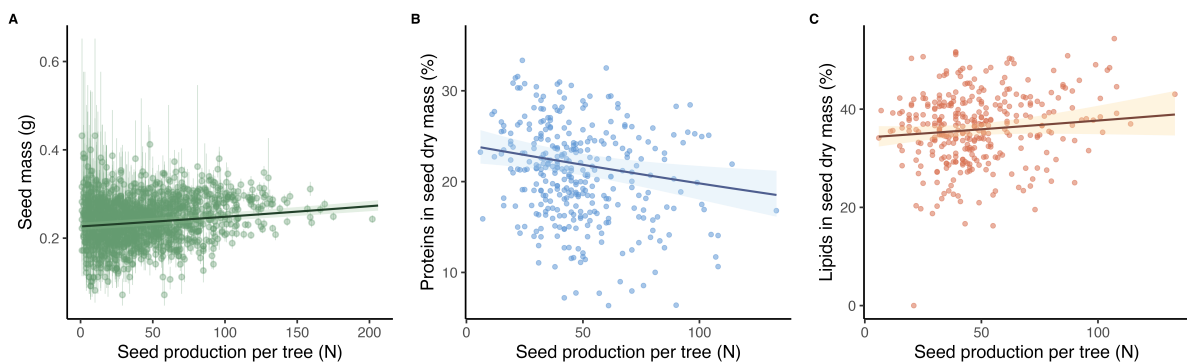


Figure 2: Seed mass and lipid content increase, while protein content decreases with increasing seed production. (A) Relationship between seed production per tree and individual seed mass. Seed production represents the number of seeds collected per tree during a standardized 3.5-minute ground search (Foest *et al.*, 2025). (B) Relationship between annual seed production per tree and seed protein content. (C) Relationship between annual seed production per tree and seed lipid content. Points represent tree-level mean seed mass with 95% confidence intervals (A) or tree-level measurements of protein and lipid content (B, C), and solid lines show the generalized linear mixed-model predictions with 95% confidence intervals. Models included tree ID and site ID as random intercepts (seed mass: $N_{\text{tree}} = 1,906$, $N_{\text{site}} = 93$; protein and lipid content: $N_{\text{tree}} = 419$, $N_{\text{site}} = 35$).

275 **Climate relationship with seed mass, protein, and lipid content**

276 Growing season length and mean annual temperature jointly influenced seed mass (Table 1). In consequence, seed
277 mass was estimated to be lowest (~0.18-0.20 g) at the sampled climatic range margins, i.e., sites characterized by
278 short growing seasons (less than 150 days) and low growing season temperatures (less than 14 °C), as well as at
279 sites with very long growing seasons (above 210 days) and high temperatures (above 17 °C) (Fig. 3A). Seed mass
280 peaked (~0.25 g) at sites characterized by intermediate conditions, i.e., either long growing seasons (180-210 days)
281 and mild temperatures (~14 °C), or shorter growing seasons (150-160 days) and warm temperatures (16–17 °C)
282 (Fig. 3A).

283 These joint climatic effects translated into a clear spatial structure across the European range (Fig. 4). Predicted
284 seed mass was high (~0.24 g) across large parts of western and central Europe, with particularly high values (~0.26
285 g) in the British Isles and along Atlantic-influenced regions of western Europe, where mild temperatures coincide
286 with extended but not extreme growing seasons. In contrast, lower seed mass (~0.20-0.22 g) was predicted
287 toward northern (Scandinavia) and high-elevation margins characterized by short and cool growing seasons, as
288 well as toward southern and southeastern margins (Balkans) where very long growing seasons coincide with high
289 temperatures.

290 Growing season length and growing season temperature jointly influenced protein proportion in seed dry
291 mass (Table 1). Protein proportion was highest (~0.24-0.25 %) at sites characterized by long growing seasons
292 (180-210 days) and intermediate growing season temperatures (approximately 13-14 °C) (Fig. 3B). In contrast,
293 protein proportion declined toward warmer conditions, reaching lowest values (~0.17-0.18) at sites with high
294 growing season temperatures (above 16-17 °C) and long growing season length (Fig. 3B). Generally, the effects of
295 temperature and growing seasons length on protein content of seeds largely mirrored the effects of climate on seed
296 mass.

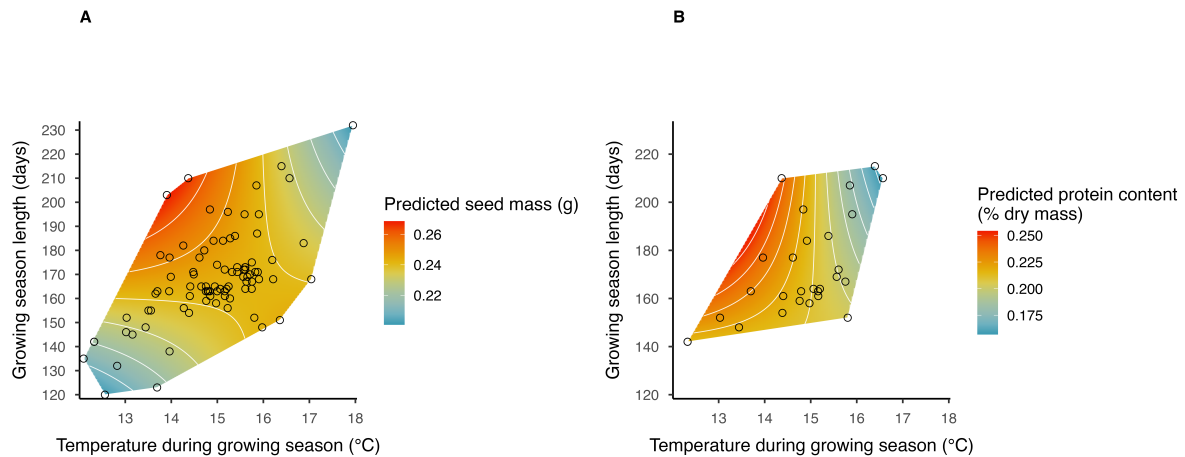


Figure 3: Seed mass peaks under intermediate growing-season conditions, whereas seed protein proportion decreases toward warmer and longer growing seasons. The color surface represents model-estimated A) seed mass, and B) % protein in seed dry mass, with warmer colors indicating higher values. Black circles show observed site-level combinations of mean growing-season temperature and growing-season length, which define the convex hull of the data. Note that the axes range in panel B were adjusted to match that in panel A, as the range of values in panel B was narrower; the climate conditions represent the long-term norms, not annual variation.

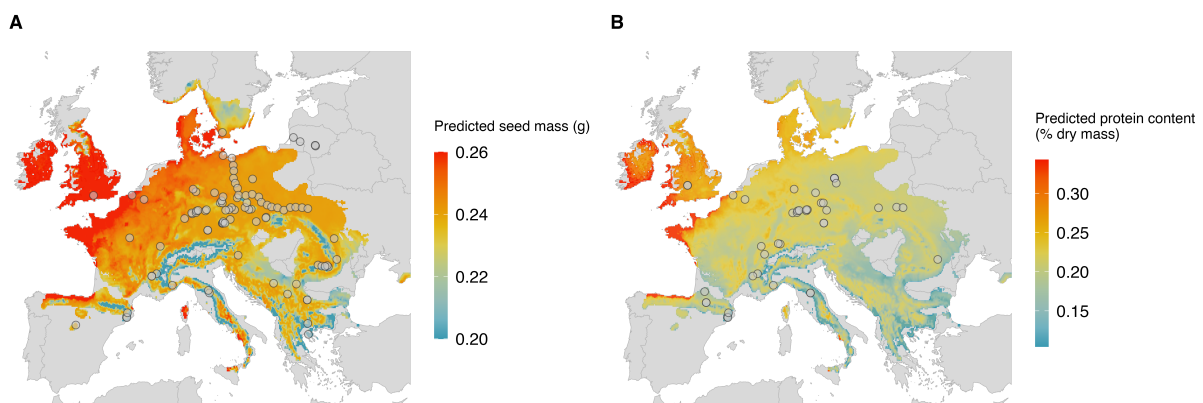


Figure 4: Seed mass and seed protein content peak in Atlantic and Atlantic-temperate regions of western Europe. Predicted individual seed mass (g) (panel A) and % protein in seed dry mass (panel B) values are shown across the European distribution of European beech based on the fitted GLMM. Predictions were generated for each grid cell within the beech distribution using site-level mean growing-season temperature and mean growing-season length. Other co-variates were held constant at their reference values, with total seed production and DBH fixed at its median value across sites and shading class fixed at its most frequent level. Study sites at which seeds mass (panel A, N = 93 sites) and protein content (B, N = 35 sites) were measured are shown as gray points. Color scale indicates predicted seed mass or protein content, with warmer colors representing higher values.

297 Discussion

298 Our results show that European beech can increase seed output without reducing seed mass, while revealing nitrogen
299 availability and climate as key constraints on seed provisioning. Contrary to predictions of fixed-budget allocation
300 models (Smith & Fretwell, 1974), individual seed mass increased with higher seed output, indicating that high-
301 seeding years involve an increase in reproductive allocation rather than redistribution within a constant resource pool
302 allocated to reproduction. This provides rare, range-wide empirical support for a long-standing assumption that
303 has been difficult to quantify in long-lived trees (Kelly, 1994; Bogdziewicz *et al.*, 2025). In contrast to seed mass,
304 increased seed production was associated with reduced protein content but higher lipid concentrations, implying
305 that carbon supply for seed filling is not limiting, whereas nitrogen becomes constraining at high reproductive
306 output. This is consistent with the view that nitrogen is a key resource limiting reproduction in temperate trees
307 (Pearse *et al.*, 2016; Abe *et al.*, 2016; Han & Kabeya, 2017). Finally, seed mass and protein content declined
308 toward the climatic margins of the species' range, a pattern with asymmetric demographic consequences: reduced
309 provisioning is expected to exacerbate regeneration failure at the trailing edge while constraining establishment and
310 spread at the leading edge.

311 Our results demonstrate that European beech does not exhibit a seed size–number trade-off. Allocation models
312 predict that, under a fixed reproductive budget, increasing seed number must come at the cost of reduced seed
313 size (Smith & Fretwell, 1974). Instead, we observed a positive association between seed output and seed mass,
314 consistent with a scenario in which reproductive allocation increases in high-seeding years. Similar patterns have
315 been reported in other mast-fruited trees, including *Quercus lobata*, where seed size was also maintained across
316 large variation in crop size (Koenig *et al.*, 2009a). In contrast, declining seed mass with increasing seed production
317 has been documented in several other masting species (e.g. Bonal *et al.*, 2007; Wang & Ives, 2017; Huang *et al.*,
318 2021), indicating that mast seeding does not universally relax size–number trade-offs. This heterogeneity suggests
319 that species differ in the extent to which reproductive investment can be increased during high-seeding years.
320 Although the small number of available studies precludes generalization, plausible drivers include differences in
321 nutrient storage capacity, particularly nitrogen (Miyazaki *et al.*, 2014; Han *et al.*, 2025), the degree of temporal
322 decoupling between floral initiation and seed development (Hirsch *et al.*, 2025), and life-history strategies governing
323 abortion versus provisioning of initiated seeds (Pearse *et al.*, 2016). In addition, masting species differ in how
324 flexibly resources can be diverted away from other functions, such as growth or defense, during high-reproductive
325 years (Barczyk *et al.*, 2025; Hirsch *et al.*, 2026). Comparative analyses across masting species will be required
326 to determine which of these mechanisms explains why some species maintain seed size under high reproductive
327 output while others do not.

328 While variable reproductive allocation explains why seed mass is maintained in high-seeding years, our results
329 also show spatial structuring of seed provisioning across the species' climatic range. Seed mass and protein content
330 increased with growing-season temperature and growing-season length, but only up to intermediate values of both,
331 resulting in a climatic optimum characterized by moderately warm summers and long growing seasons. This is

332 consistent with intraspecific syntheses showing larger seeds in warmer environments, where longer seasons and
333 reduced frost risk allow more complete seed filling (Frenne *et al.*, 2013), but it also indicates that high temperatures
334 constrain provisioning. Similar responses have been reported in temperate and Mediterranean oaks, including *Q.*
335 *robur*, *Q. ilex* and *Q. macrocarpa*, in which seed mass increases toward warmer regions (Koenig *et al.*, 2009b;
336 Bogdziewicz *et al.*, 2019; Moreira *et al.*, 2021). Variation in seed size of this magnitude (30% in our study across
337 climates) can have substantial fitness consequences: experimental and comparative studies show that a 5-11%
338 difference in seed mass is associated with 0.5-2% increase in germination success, establishment, or early survival,
339 particularly under stressful conditions (Gómez, 2004). Importantly, seeds produced at climatic margins in our
340 study were both smaller and poorer in protein, a combination that is likely to further reduce germination capacity
341 and early seedling performance, as nitrogen content directly constrains enzymatic activity during germination and
342 early growth (Milberg & Lamont, 1997; Leishman & Leishman, 2001; Muffler *et al.*, 2021; Pawłowski *et al.*, 2024).
343 Beyond direct effects on provisioning, seed size also mediates biotic interactions (Lichti *et al.*, 2017; Wróbel *et al.*,
344 2022). Smaller seeds are less likely to be cached and buried by small mammals (Lichti *et al.*, 2017), a process
345 that enhances germination and seedling establishment (Zwolak *et al.*, 2016). Thus, the climate-driven reductions
346 in seed mass and nitrogen content could potentially lower effective dispersal and establishment at range margins,
347 possibly tightening regeneration bottlenecks. Whether such variation translates into demographic constraints at the
348 trailing edge or limits northward advance remains to be tested experimentally, as other factors such as competition,
349 local adaptation, and biotic interactions also vary across the range.

350 Protein content declined as seed output increased, whereas lipid content and seed mass increased. This pattern
351 supports the view that carbon rarely limits seed filling in temperate trees, whereas nitrogen can (Hoch, 2005;
352 Pearse *et al.*, 2016; Han & Kabeya, 2017). Experimental source–sink manipulations show that fruiting branchlets
353 in temperate trees can sustain fruit development without importing carbon from the rest of the tree, consistent with
354 branch-level carbon autonomy (Hoch, 2005). Stable carbon supply during reproduction is further supported by
355 isotope and seasonal non-structural carbohydrates evidence, indicating that fruit production in masting broadleaves
356 does not rely on mobilizing stored carbon reserves (Hoch *et al.*, 2013). By contrast, multiple studies point to stronger
357 constraints on mineral nutrients: in a masting pine, large crop production caused measurable depletion of stored
358 N and P, demonstrating that reproduction can deplete nutrient pools over timescales longer than the seed-filling
359 season (Sala *et al.*, 2012). In *Fagus crenata*, masting is linked to large N investment into reproductive organs and
360 to N-limitation for subsequent reproductive commitment, such as reduced N status of winter buds and constraints
361 on flower primordia formation (Han *et al.*, 2008; Miyazaki *et al.*, 2014; Abe *et al.*, 2016). Experimental fruit
362 removal in *Quercus ilex* similarly prevented seasonal depletion of leaf N, while starch dynamics did not indicate
363 carbohydrate depletion in fruiting trees, again separating nutrient limitation from carbon limitation (Roncé *et al.*,
364 2020, 2023). In this context, our observation that protein (N-rich) provisioning declines with high fecundity, while
365 lipid provisioning (largely carbon-based) is maintained, is consistent with a scenario in which beech can sustain
366 carbon supply for seed biomass and lipid deposition, but progressively dilutes N allocation per seed as reproductive

367 demand increases.

368 Several aspects of our study design should be considered when interpreting these results. Our inference is based
369 on extensive spatial replication rather than long time series: seed production and seed mass were measured over two
370 years, and seed nutrient composition in a single year. While this limits direct inference about temporal dynamics
371 within individual populations, the broad geographic coverage encompassed the full range of interannual variation in
372 seed production documented in a 45-year beech monitoring study using comparable count methods (Bogdziewicz
373 *et al.*, 2020; Hackett-Pain *et al.*, 2025). This indicates that the variation required to detect seed size–number
374 relationships and provisioning patterns was captured at the species level. Furthermore, spatial variation in seed
375 protein content may also reflect long-term differences in nitrogen availability across Europe. Atmospheric nitrogen
376 deposition is highly heterogeneous, with consistently higher inputs in Western and parts of Central Europe than in
377 Northern and Eastern regions, broadly overlapping with the geographic patterns of seed mass and protein content
378 observed here (Sanczuk *et al.*, 2024). Although seed filling in European beech is primarily governed by internal
379 nitrogen storage and remobilization and is largely decoupled from short-term soil nitrogen dynamics (Han & Kabeya,
380 2017), sustained nitrogen inputs may influence the size of internal nitrogen pools over longer timescales. Testing
381 this hypothesis would require integrating spatially explicit nitrogen deposition data with multi-year measurements
382 of seed provisioning. Moreover, while our spatial coverage spanned most of the European range of beech, some
383 regions were underrepresented, including the southernmost parts of the species' range in southern Italy and Sicily,
384 where climatic stress may be strongest. These limitations highlight the need for multi-year studies combining seed
385 production, provisioning, and experimental assessments of seedling performance to fully resolve the demographic
386 consequences of variation in seed mass and nutrient composition across space and time. Finally, the interpretation
387 of geographic variation in seed provisioning as direct evidence for range-limiting processes requires caution. Within
388 a site, seed mass is positively associated with germination success and seedling performance (Muffler *et al.*, 2021;
389 Pawłowski *et al.*, 2024). Among sites, however, seed size covaries with multiple environmental factors, making
390 it difficult to infer fitness consequences from spatial patterns alone. Thus, while our results reveal geographic
391 variation in seed provisioning, the demographic consequences of this variation remain to be tested directly.

392 In summary, our study indicate that the large interannual variation in seed production in European beech is
393 accommodated through changes in reproductive allocation rather than through a trade-off between seed number
394 and seed mass. By increasing seed mass at high seed output, beech departs from predictions of fixed-budget
395 allocation models, while declining protein content reveals nitrogen, rather than carbon, as the principal constraint
396 on seed provisioning. Importantly, the absence of a seed size–number trade-off implies that the ecological benefits
397 of masting in beech are not reduced by diminished per-seed biomass, but post-germination growth can be reduced
398 by lower protein provisioning. Germination trials with diverse seed provenances across a range of seed production
399 investment are thus an important next research step. The decline in seed mass and nitrogen content toward climatic
400 margins identifies a pathway through which climate can constrain regeneration at climatic range edges, as well as
401 migration in response to climate change.

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Author Contributions Statement

MB, AHP, KK, PJ, and JSz designed the study. KK, PJ, UE, JSz, and EMK conducted the analysis. KK and MB co-wrote the first draft of the manuscript. All other authors contributed to data collection. All authors contributed to the interpretation of the analysis, revised the draft, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data Availability Statement

The data and code supporting this study are available in Figshare (<https://doi.org/10.6084/m9.figshare.31331731>).

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602 **Supporting Information**

603 **Authors:** Kondrat et al.

604

605 **No seed size–number trade-off in European beech: climate governs investment per seed**

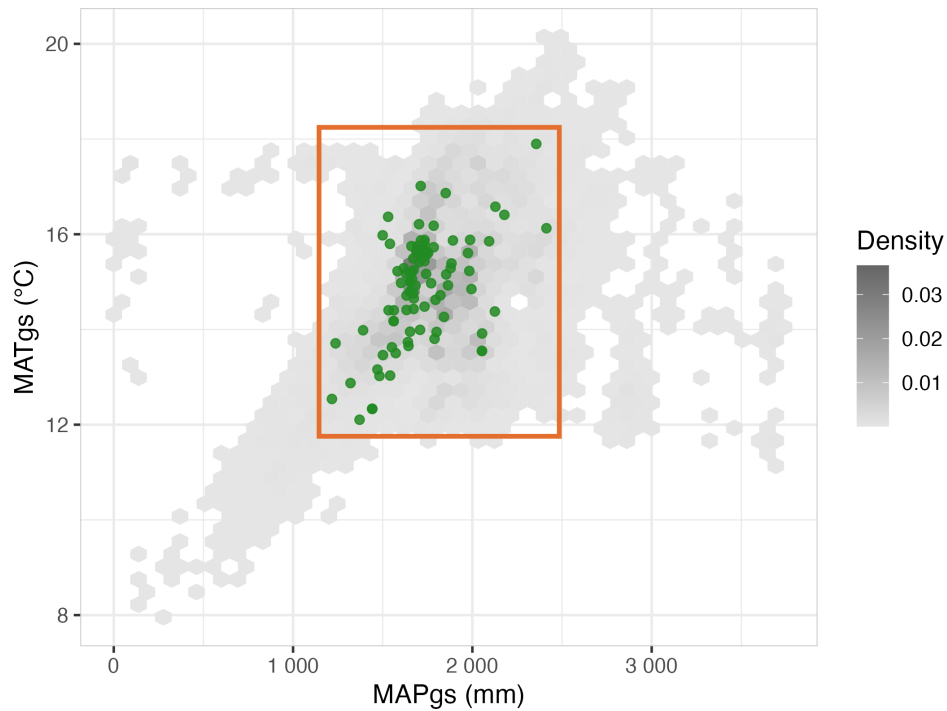


Figure S1: Climate coverage of sampled sites within the European beech climatic distribution. Each green point represents one population and the orange rectangle denotes the climatic envelope spanned by the sampled sites. Grey hexagons show the density of grid cells across the European beech range derived from E-OBS climate data, plotted as mean growing-season temperature (MATgs) against mean growing-season precipitation (MAPgs).

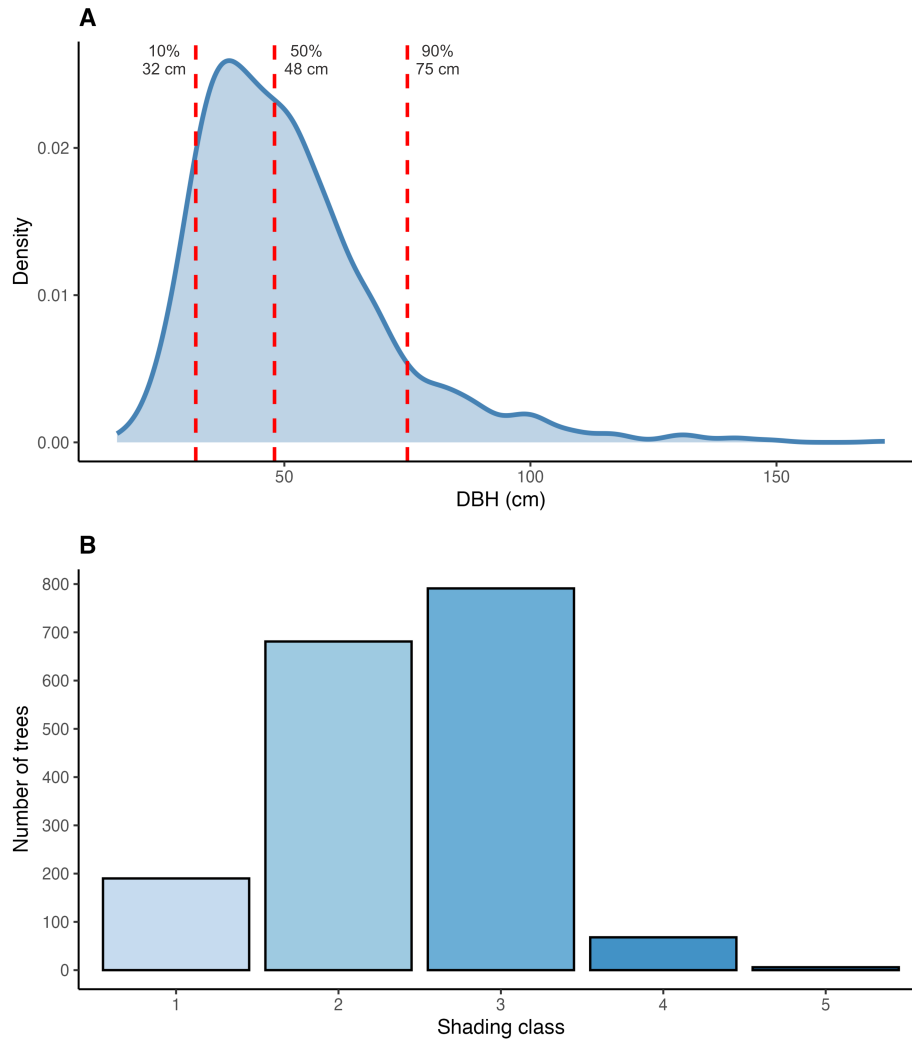


Figure S2: Distribution of tree size and shading conditions across the study dataset (A) Density distribution of diameter at breast height (DBH) for all sampled trees. Dashed vertical lines indicate the 10th, 50th (median), and 90th percentiles. (B) Frequency distribution of trees across shading classes.