# The interaction of resources and weather cues enables optimization of reproductive delay in masting plants

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# Abstract

Interannual variability of seed production, known as masting, has far-reaching ecological impacts including effects on forest regeneration and the population dynamics of seed consumers. It is important to understand the mechanisms driving masting patterns to help predict how plant populations and ecosystem dynamics may change into the future, and for short-term forecasting of seed production to aid management decisions. We used long-term observations of individual flowering effort in snow tussocks (*Chionochloa pallens*) and European beech (*Fagus sylvatica*) to test how endogenous resource levels and weather variation interact in driving masting in these species. In both species, there was an interaction between the weather cue and plant resources. If resource levels were high, even weak temperature cues triggered relatively high reproductive effort, and depleted resources suppressed reproduction even in the presence of strong cues. Thus, resource dynamics played dual roles of both suppressant and prompter of reproduction, allowing plants to fine-tune the length of intervals between large-seeding years regardless of variable cue frequency. The strong interaction between resource storage and weather cues has immediate application in mast forecasting models increasingly important for global afforestation efforts. Moreover, the important role of resource storage in the plant response to weather cues will dictate the masting responses to climate change.

*keywords:* | flowering | mast seeding | seed production | reproduction | resource budgets |

**Declaration of interests**
No competing interests to declare.

# Introduction

Synchronous and highly variable reproduction among years by a population of perennial plants, called mast seeding or masting, characterizes the reproduction of numerous plant species (Qiu *et al.*, 2023; Journé *et al.*, 2023). Resulting boom and bust dynamics have widespread consequences for food webs, nutrient cycling, plant and fungi community dynamics, and nature management (Ostfeld & Keesing, 2000; Clark *et al.*, 2019; Pearse *et al.*, 2021; Michaud *et al.*, 2024). It is therefore important to understand the mechanisms driving masting patterns to help predict how plant populations and ecosystem dynamics may change into the future (Hacket-Pain & Bogdziewicz, 2021), as well as for short-term forecasting of seed production to aid management decisions (Elliott & Kemp, 2016; Journé *et al.*, 2023). Both these goals are urgent: accumulating evidence indicates that masting patterns can be altered by climate change with severe consequences for seed supply (Hacket-Pain & Bogdziewicz, 2021), but the response hinges on the proximate mechanisms involved (Shibata *et al.*, 2020; LaMontagne *et al.*, 2021; Bogdziewicz *et al.*, 2024). At the same time, ambitious afforestation plans widely planned across countries (Steffen *et al.*, 2015; Richardson *et al.*, 2023) increase seed demand and require mast forecasting tools to aid efficient seed collection (Pearse *et al.*, 2021; Fargione *et al.*, 2021). Yet, while major evolutionary drivers of masting are relatively well-explored (Bogdziewicz *et al.*, 2024), the proximate drivers of mast seeding, imperative for climate change biology and forecasting, are less well crystallized. Multiple drivers play a role, including weather cues, internal resource dynamics, and underlying environmental variation (Norton & Kelly, 1988; Crone & Rapp, 2014; Pearse *et al.*, 2016; Pesendorfer *et al.*, 2021). It remains unclear how these various mechanisms apply across species and how they interact (Bogdziewicz *et al.*, 2024).

In the absence of selection for higher interannual masting variation, weather variation sets the base level of variation in seed production (resource matching) (Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2024). Two major mechanisms can increase masting variation above that generated by resource matching; weather cues and internal resource budgets (Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2024). Selection for high interannual variation in seed production can make plants hypersensitive to weather variation (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2020b). The relationship between seeding and weather is often exponential, with heavy reproduction resulting from high values of the weather cue (Kelly *et al.*, 2013; Fernández-Martínez *et al.*, 2017; Schermer *et al.*, 2020; Smith *et al.*, 2021). Moreover, seed production requires substantial nutrient investment, which led to the formulation of resource budget models (Satake & Iwasa, 2000; Crone *et al.*, 2009). Briefly, these models assume that there is a resource threshold for reproduction so that reproduction is only initiated when sufficient internal resources accumulate. Resources are depleted by seed production, and the time required to replenish depleted resources amplifies the interannual variation in seed production (Crone & Rapp, 2014; Han & Kabeya, 2017). Finally, resource status and cues may be integrated if flowering induction by the weather cue is dependent on the resource state of the plant (Smaill *et al.*, 2011; Monks *et al.*, 2016).

Intense discussion over recent decades has led to the formulation of the general model of masting that unified these various drivers, suggesting that each mechanism is potentially involved in creating masting, but with varying importance across species (Bogdziewicz *et al.*, 2024). For example, the model predicts that in extreme cases, masting can be driven almost solely by weather cues, but whether that is indeed the case needs to be tested (Bogdziewicz *et al.*, 2024). Clarifying these different drivers is imperative for a more accurate prediction of masting both in the long and short term. For example, where cues are dominant, the increased cueing frequency associated with climate warming will lead to more frequent reproduction, but if resource levels are also important then the mast years may also be smaller in magnitude (i.e. dampened interannual variation) (Bogdziewicz, 2022).

A major example of a weather cue hypothesized to generate masting without the need to invoke resource dynamics is the ΔT, i.e. the temperature difference between the two previous summers (see Glossary) (Kelly *et al.*, 2013). The ΔT model gave a good fit to observational seeding data, but was criticized as a proxy that captures the interaction between resource state and environmental drivers (Pearse *et al.*, 2014; Monks *et al.*, 2016). Specifically, the low temperature in T2 (two years before seedfall) may veto reproduction (lack of cue), resulting in resource accumulation. Subsequent hot T1 summer (strong cue) combines with accrued resources and triggers large flowering. Indeed, a model including an interaction between T1 and T2 (T1 x T2) provided a better fit to the data than the ΔT in four *Chionochloa* species, supporting that hypothesis (Monks *et al.*, 2016). Nonetheless, the issue is far from settled. Several studies compared the ΔT fit to reproductive data with models that included ΔT decomposed to various combinations of T1, T2, and lagged reproductive effort, with some finding support for ΔT (Holland & James, 2014; Kon & Saito, 2015; LaMontagne *et al.*, 2021), but others failing to find support (Moreira *et al.*, 2015; Monks *et al.*, 2016). However, the majority of studies were inconclusive. Only one replaced T2 with an estimate of resource state (Monks *et al.*, 2016). Yet, as that study replaced the T2 cue with resource state, the T2 cue was no longer included (Monks *et al.*, 2016). Several studies used lagged (previous year) seed production as a resource depletion proxy (Pearse *et al.*, 2014; Holland & James, 2014; Bisi *et al.*, 2016). Yet, that is an imperfect proxy as it only includes the preceding year's resource investment in seed production, foregoing information on reproductive investment in years before that. Moreover, most of these studies were conducted at the population level which includes noise created by imperfect synchronization of seed production between individuals (Koenig *et al.*, 2003; Abe *et al.*, 2016). Testing whether the flowering production depends on the resource state requires supplementing (not replacing) the T2 cue with an estimate of individual plant resource state.

**Glossary**

- **Weather cue** - weather conditions, such as warm summer, that trigger reproduction, typically by promoting heavy flowering.
- **T0, T1, T2 cues** - weather cues occurring in the same year as seedfall (T0), or lagged by one year (T1) or two years (T2) before seedfall. In the current study, the T1 and T2 cues are summer temperatures (January - February for snow tussocks, and June-July for European beech).
- **ΔT cue** - a weather cue based on a difference (Δ) in weather (temperature T) from one growing season to the next, here temperature difference between the two previous summers (ΔT = T1 - T2).
- **Resource state** - here, reconstructed stored resources from individual-level seed/flower production data, following the Rees *et al.* (2002) method. In short, energy reserves are estimated as residuals of the linear relationship between cumulative seed production and cumulative time (or weather conditions during the growing season).

Using stored resources together with the T2 weather cue is important to test whether the T1+T2 model involves mechanisms unrelated to the resource state. Molecular mechanisms behind weather cues likely include gene regulatory networks that integrate various signals, such as temperature and photoperiod, allowing flowering to occur only when cues are received (Satake & Kelly, 2021). For example, in European beech (*Fagus sylvatica*), high temperatures after the summer solstice (when the day length peaks) trigger flowering (Journé *et al.*, 2024). Crucially, both T1 and T2 summer temperature effects on seed production are seen only after the summer solstice, suggesting environmental signal integration, not resource-related effects in summer T2 (Journé *et al.*, 2024). In another example, drought and subsequent cold temperatures initiate a molecular regulation that triggers flowering in *Shorea*, and drought does not feed into the model via its effect on resource accumulation (Yeoh *et al.*, 2017). Finally, despite the ΔT being initially criticized for lack of possible underlying mechanism, later studies introduced an epigenetic summer memory model (Samarth *et al.*, 2020). The T2 summer temperature initiates the activation of the floral integrator genes such as FT and SOC1. Then, elevated summer T1 temperature is required to activate these genes sufficiently to allow the plant to fully commit to the reproductive transition (Samarth *et al.*, 2020, 2021).

The flowering gene expressions modulated by environmental signals may also be regulated by resource availability. For example in *Fagus crenata* the interannual variation flowering is associated with off-and-on cycles of expression in major flowering genes, with the expression of genes depending on nitrogen supply (Miyazaki *et al.*, 2014). Thus, our current understanding of mechanisms triggering reproduction requires the T1xT2 (or ΔT) model to be supplemented with the resource state of the plant to incorporate the full suite of possible drivers. Such comprehensive testing has not been done so far.

Here, we used 35-year-long flowering observations in 81 alpine snow tussock plants (*Chinochloa pallens*) and 16-year-long seed production observations in 32 European beech (*Fagus sylvatica*) trees to test the drivers of masting in these species. In *C. pallens*, the ΔT provided better fit over the T1+T2 model (Kelly *et al.*, 2013), but with data from a different site T1xT2 was later found to fit even better (Monks *et al.*, 2016). Transplant experiments showed that high T1 temperatures indeed trigger reproduction through activation of molecular flowering pathways (Samarth *et al.*, 2022). The role of low temperatures in T2 summer is unclear, as it may represent either a veto that allows resource accumulation (Monks *et al.*, 2016), or molecular priming that modulates the plant response to summer T1 temperatures (Kelly *et al.*, 2013; Samarth *et al.*, 2020). In *F. sylvatica*, the ΔT consistently scored lower compared to the T1 + T2 and T1 x T2 models, although very few studies are available (Bogdziewicz *et al.*, 2017b, 2020c; Szymkowiak *et al.*, 2024). The effects of summer T2 temperatures on seeding in European beech were long believed to represent resource priming (Piovesan & Adams, 2005; Drobyshev *et al.*, 2014; Vacchiano *et al.*, 2017), but the fact that correlations between seeding and temperature appear only after the summer solstice questions that interpretation (Journé *et al.*, 2024).

We constructed models to specifically test these various mechanisms (summarized in Table 1). By reconstructing the energy budgets of individuals, we tested whether the T2 effects are just a proxy for plant resource state or not. By including the ΔT in the models together with estimated resource reserves, we test whether ΔT is indeed largely independent from the resource

**Table 1:** Summary of predictors we tested and associated hypothetical mechanisms. T1 and T2 are temperature cues (mean summer temperatures one and two years before reproduction, respectively); ΔT is a differential-temperature cue (= T1 - T2), and R is individual plant resource levels (estimated from individual-level annual flower and seed production records, see Glossary).

| **Predictor** | **Hypothetical mechanism** |
|---|---|
| T1 | High temperatures promote heavy flowering through enhancing flowering genes expression |
| T2 | Environmental signal: low temperatures promote heavy flowering through activation of the floral integrator genes that are later activated by T1 cues. Alternatively, surrogate for past seed production: negative summer temperatures decrease seed production in T1, enhancing seed production in T0 |
| T1 x T2 | The response to T1 temperature is amplified by low T2 temperature. Specific values of each year's temperatures interact, with a higher slope of T1 effect for lower T2 temperatures. |
| ΔT | Plants measure the relative change in temperature between T2 and T1, with absolute values of T1 and T2 being unimportant |
| T1 + R or ΔT + R | Resource state acts as a veto, i.e. suppresses reproduction when depleted, even in the presence of cues. |
| T1 x R or ΔT x R | In addition to the resource state acting as veto when resources are depleted, the resource state acts as an amplifier plant response to the cue, if reserves are high. |

state of the plant, as previously hypothesized (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2024). Finally, by including the interaction between an individual's resource state and weather cues, we tested whether accumulated resources modify plant responses to the weather cue.

# Materials and Methods

**Study species** Snow tussocks (*Chionochloa pallens*, Poaceae) and European beech (*Fagus sylvatica*, Fagaceae) are well-studied masting species (masting time series in Fig. S1). *Chionochloa pallens* (midribbed snow tussock, hereafter abbreviated to just snow tussock) is a long-lived grass, up to 1.5 m tall, growing in the alpine zone in New Zealand. European beech (Fagaceae) is a pan-European deciduous forest tree of high economic importance and ecological (Leuschner & Ellenberg, 2017; Chakraborty *et al.*, 2024). Masting in both species reduces seed predation rates, and in beech increases pollination efficiency (Kelly & Sullivan, 1997; Kelly *et al.*, 2001; Bogdziewicz *et al.*, 2020c). In both species, temperature cues (T1, T2, and/or ΔT) and resource reserves are considered masting drivers (Piovesan & Adams, 2005; Kelly *et al.*, 2013; Monks *et al.*, 2016; Vacchiano *et al.*, 2017), but a comprehensive test of a full suite of drivers has not been attempted.

**Flowering and seed production monitoring** In snow tussocks, we monitored flowering in permanent transects at 1070 m, Mount Hutt, Canterbury, New Zealand annually between 1990 and 2024. Three transects, each 20 m long, were marked with steel pegs, and all tussocks that touched the line were mapped (n = 81). Each February, the number of inflorescences (flower stalks, abbreviated to flowers) were counted on each mapped plant (Rees *et al.*, 2002; Kelly *et al.*, 2013). During this interval, no plants died. The flower counts were censuses.

In European beech (*Fagus sylvatica*), we sampled seed production at 15 sites spaced across England annually between 1980 and 2023 (44 years) (Bogdziewicz *et al.*, 2023). The ground below each tree was searched for seeds for 7 minutes, and all seeds found were counted. In this study, we used the data on 32 individuals for which full records were available (no gaps) from 1990 to 2005. Continuous records are required to estimate the energy budgets (see Methods: Reconstructing stored resources). After 2006, the interannual variation and synchrony of seed production in these populations declined due to warming (Bogdziewicz *et al.*, 2020c). That included the disrupted relationship between the weather cues and masting; more frequent cue occurrence appears to deplete the energy budgets of trees, resulting in weaker responses to cues (Bogdziewicz *et al.*, 2021). To exclude that confounding factor, we have used only the 16 years of the data (1990-2005), which resulted in 32 trees spaced across 12 sites.

**Reconstructing stored resources** To reconstruct a plant's stored resources from flowering and seed production data, we followed the approach developed by Rees *et al.* (2002). In short, this analysis involves first fitting a linear model of cumulative reproduction (summed flower or seed count) vs cumulative years (as a surrogate of resource acquisition over time) for each species. We used generalized linear mixed models (GLMMs) implemented via the 'lme4' package (Bates *et al.*, 2015) with plant ID (in tussocks) or plant ID and site ID (in European beech) as random intercepts and year as a random slope. The random effect structure allowed fitting a unique intercept for each plant which estimates stored resources of a plant at the beginning of the monitoring period (Rees *et al.*, 2002), while random slope allowed heterogeneous resource acquisition of individuals over time (Crone *et al.*, 2005). Residuals for each plant of these two models (one for each species) are an estimate of the stored resources of that individual in each year (Rees *et al.*, 2002; Crone *et al.*, 2005). We have also constructed an alternative version, in which stored resources are estimated from accumulated mean growing season temperature instead of accumulated time, but that provided qualitatively the same results (Table S1). Thus, simpler models are discussed in the main text. Note that the approach we used here for the reconstruction of resource reserves makes no assumption about the limiting resource, i.e. whether that is carbon, nitrogen, or another limiting resource (Han & Kabeya, 2017).

**Hypothesis testing** We constructed two sets of models for each species in which annual, plant-level flowering (snow tussocks) or seed production (European beech) was included as a response. All models included plant ID (both species), and site ID (European beech) as random intercepts. We used the Tweedie error family and logit link and for this purpose, we scaled the response values to fall between 0 and 1 at the series level. Each set then included various combinations of predictors including past summer temperatures (T1 and T2 weather cues, or ΔT = [T1-T2]), plant stored resources (estimated resources plant *i* has in year *t*), and interactions. The interactions were between T1 and T2, between T1 and stored resources, or between ΔT and stored resources. We have not fitted models with all possible predictor combinations; rather, we have fitted ones relevant to the hypothesized mechanisms involved. Models were ranked using the standard AIC criteria (Burnham *et al.*, 2011).

# Results

In snow tussocks, the best-fitting model included the interaction term between reconstructed stored resources and summer T1 temperature (Table 2). Moreover, the top model also included the T1 x T2 interaction. Thus, the effect of the T1 cue on reproductive effort is modified both by resource storage and the T2 cue (Table 2). The support for such a complicated model was strong in snow tussocks (AIC weight = 0.96). In European beech, the top model also includes the interaction between resources and summer T1 temperature, but the importance of the T1xT2 interaction is equivocal, with the less complicated model (T1 x Resources + T2) being similarly supported (ΔAIC = 0.57; Table 2). Importantly, despite the direct inclusion of stored resources, summer T2 temperature was retained in the top model for both species, suggesting T2 temperatures do not only affect masting indirectly via resource dynamics (Table 2).

In both species, high reproductive effort required both strong weather cues and large resource storage to align (Fig. 1, 2, Table 3). The interaction between weather cues and stored resources was strong; if resources were depleted, even very hot summer T1 led to only minor reproductive effort (Fig. 2). For example, in snow tussocks, estimated individual-level reproductive effort in response to a 14 °C T1 cue was ~10 flowers if resources were depleted, but was 17-fold larger if resource levels were high (Fig. 2). In contrast, if reserves were large, heavy reproduction could be initiated even if the cue was relatively weak. For example, in European beech, individual-level seed production in response to a 21 °C T1 cue was ~110 for the average level of resource storage, but reached almost 300 if storage was high (Fig. 2). Even a relatively cold T1 (e.g. 19 °C) resulted in relatively good seed production of ~100 seeds if storage levels were high (Fig. 2). Finally, the T1 x T2 negative interaction in snow tussocks resulted in heavy reproduction occurring only when a hot summer occurred after a cold one (Table 3, Fig. 3). The modulating effect of the T2 cue on the T1 cue was similar to that of resource storage; if T2 summer was hot, even high T1 temperatures did not trigger heavy reproduction (Fig. 3).

**Table 2:** Model selection tables. Each model includes individual-level annual flowering (*C. pallens*) or seed production (*F. sylvatica*) as a response, plant ID (both species) and site ID (European beech) as random intercept, Tweedie error distribution, and logit link. T1 and T2 are summer temperatures (June and July in *F. sylvatica* and January and February in *C. pallens*), where numbers indicate lags: 1 for the previous year, and 2 for summer two years before flowering. Resources are reconstructed deviations from the equilibrium energy budget (see Methods).

| Model | AIC | ΔAIC | weight |
|---|---|---|---|
| ***Chionochloa pallens*** | | | |
| T1 × Resources + T1 × T2 | 1052.8 | 0.0 | 0.996 |
| T1 × T2 + Resources | 1065.3 | 12.5 | 0.002 |
| T1 × Resources + T2 | 1065.5 | 12.7 | 0.002 |
| ΔT × Resources | 1078.4 | 25.6 | <0.001 |
| ΔT + Resources | 1100.0 | 47.2 | <0.001 |
| T1 + Resources + T2 | 1101.7 | 48.9 | <0.001 |
| T1 × T2 | 1133.0 | 80.2 | <0.001 |
| T1 + T2 | 1225.4 | 172.6 | <0.001 |
| ΔT | 1231.8 | 179.0 | <0.001 |
| T1 × Resources | 1523.0 | 470.2 | <0.001 |
| T1 + Resources | 1604.2 | 551.4 | <0.001 |
| ***Fagus sylvatica*** | | | |
| T1 × Resources + T2 | 391.8 | 0.0 | 0.57 |
| T1 × Resources + T1 × T2 | 392.4 | 0.6 | 0.43 |
| ΔT × Resources | 406.1 | 14.3 | <0.001 |
| ΔT + Resources | 411.8 | 20.0 | <0.001 |
| T1 × T2 + Resources | 413.0 | 21.2 | <0.001 |
| T1 + Resources + T2 | 413.8 | 22.0 | <0.001 |
| T1 × Resources | 451.1 | 59.3 | <0.001 |
| T1 + Resources | 477.8 | 86.0 | <0.001 |
| T1 × T2 | 530.9 | 139.1 | <0.001 |
| T1 + T2 | 531.8 | 140.0 | <0.001 |
| ΔT | 533.5 | 141.7 | <0.001 |

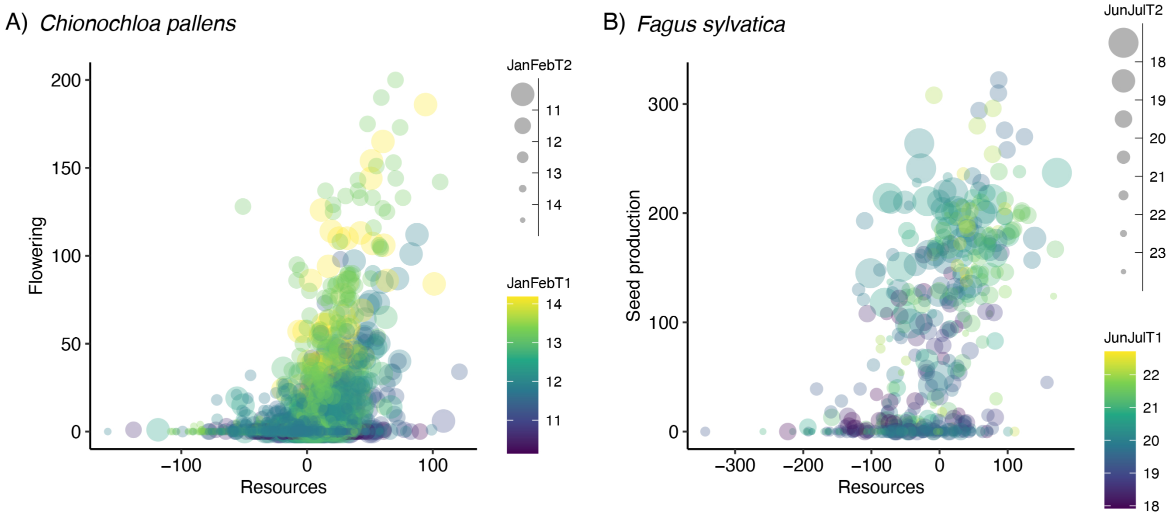

**Figure 1: Relationships between the reconstructed resource reserves and annual variation in flowering effort in *Chionochloa pallens* and seed production in *Fagus sylvatica*.** Each point is an annual flowering effort (or seed production) of an individual plant, mapped along the gradient of the reconstructed annual deviations from the equilibrium energy budget (Rees *et al.*, 2002). Point sizes and colors are scaled according to the mean summer temperatures two years and one year before flowering.

**Table 3:** Summary of the best-fitting generalized linear mixed model testing the effects of previous summer temperatures and energy reserves on annual variation in reproductive output in *Chionochloa pallens* and *Fagus sylvatica*. The models included individual-level annual flowering (*C. pallens*) or seed production (*F. sylvatica*) as a response and were fitted with Tweedie error distribution and logit link. T1 and T2 are mean summer temperatures a year or two years before flowering, respectively. Resources are reconstructed deviations from the equilibrium energy budget (see Methods).

| Effect | $\beta$ | SE | Z | p |
|---|---:|---:|---:|---:|
| ***Chionochloa pallens*** | | | | |
| Intercept | -53.94 | 13.993 | -3.86 | 0.001 |
| T1 | 5.64 | 1.196 | 4.72 | <0.001 |
| T2 | 2.94 | 1.175 | 2.51 | 0.012 |
| Resources | -0.10 | 0.032 | -3.27 | 0.001 |
| T1 × Resources | 0.01 | 0.003 | 3.88 | <0.001 |
| T1 × T2 | -0.36 | 0.099 | -3.62 | <0.001 |
| ***Fagus sylvatica*** | | | | |
| Intercept | -11.91 | 3.804 | -3.13 | 0.002 |
| T1 | 0.98 | 0.106 | 9.19 | <0.001 |
| T2 | -0.77 | 0.104 | -7.41 | <0.001 |
| Resources | -0.12 | 0.029 | -4.14 | <0.001 |
| T1 × Resources | 0.01 | 0.001 | 4.80 | <0.001 |

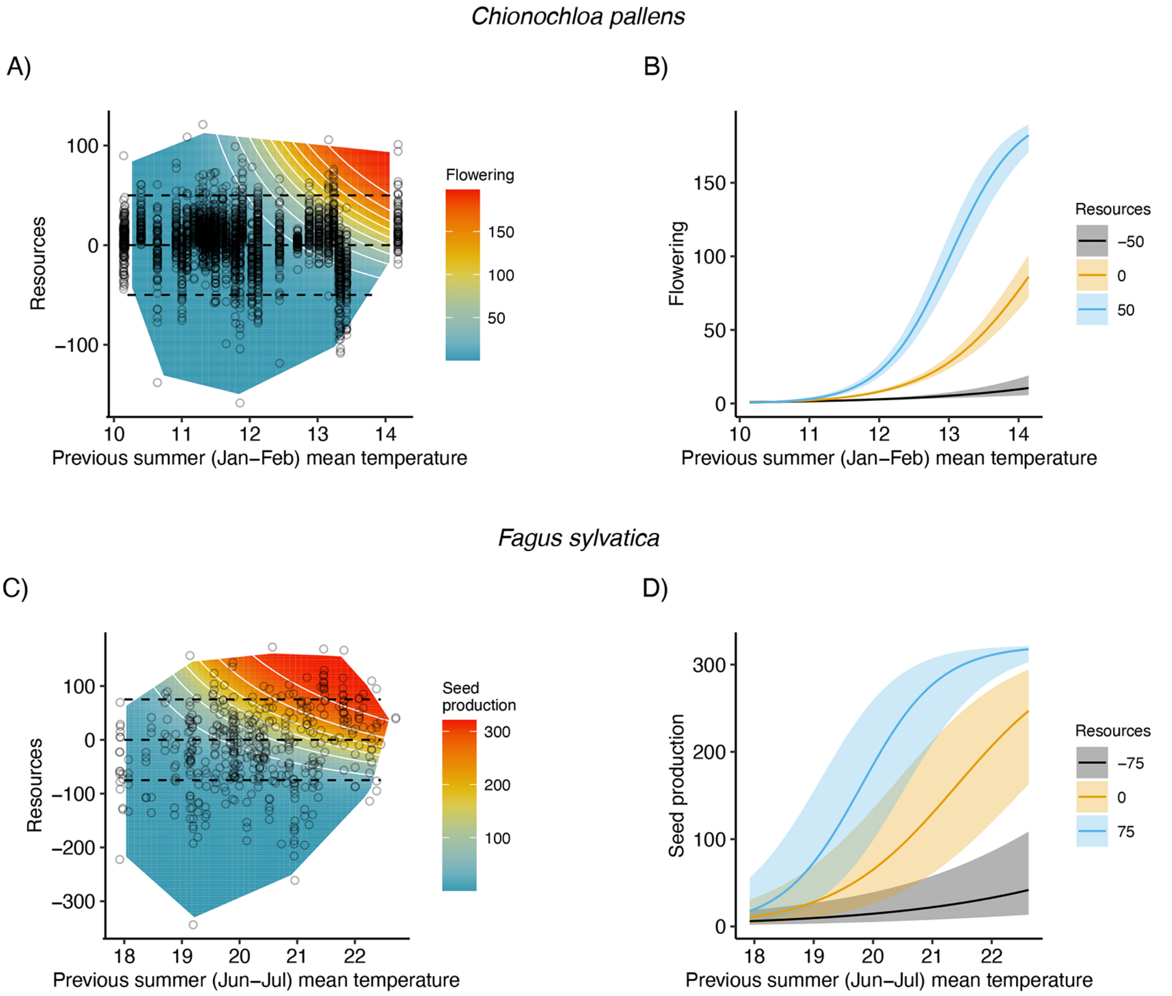

**Figure 2: Previous summer temperatures and reconstructed stored resources interact to determine annual variation in flowering effort in *Chionochloa pallens* and seed production in *Fagus sylvatica*.** A) and C) Surface plots show estimated individual-level flowering (*C. pallens*) or seed production (*F. sylvatica*) effort across combinations of previous summer (January-February in case of *C. pallens* and June-July in case of *F. sylvatica*) mean daily temperature (°C) and the reconstructed deviations from the equilibrium resource budget, with the convex hulls (parameter space across which predictions are computed) defined by observations (black circles). Points show individual-level annual flowering or seed production. Black horizontal dashed lines at A) and indicate the transects plotted in C), i.e., the conditional relationship between flowering or seed production effort and summer temperature for selected levels of reconstructed resource budgets. Prediction lines and associated 95% CI at B) and D) are sections through surfaces highlighted by transects at A) and C). Estimates are derived from GLMM with Tweede distribution and logit link that included plant ID as a random intercept. The best fitting models plotted (AIC selection Table 2) included also the negative effects of summer temperature two years before flowering or seed production (model summary Table 3).

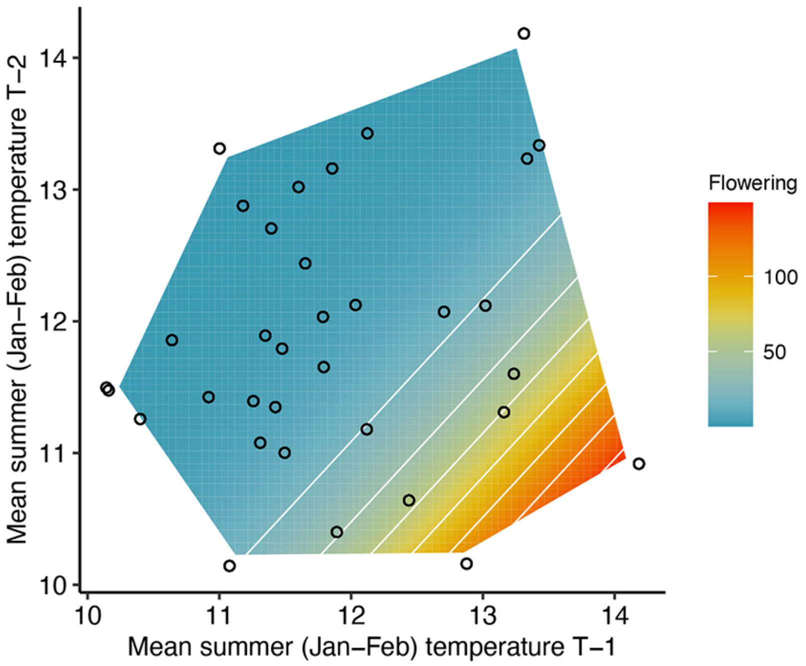

**Figure 3:** Previous summer temperatures interact to determine annual variation in flowering effort in *Chionochloa pallens*. Surface plot show estimated individual-level flowering effort across combinations of previous summer (January-February) mean temperature one and two years before flowering. The convex hull (parameter space across which predictions are computed) is defined by observations (black circles). Note that the apparently small number of points is the result of overplotting, as all individuals in each year fall into the same area defined by past years' temperatures.

# Discussion

Our study was inspired by the recently formulated general model of masting, which suggests that environmental cues could drive masting without the need to invoke resource dynamics (Bogdziewicz *et al.*, 2024). We examined two species where strong weather cues indicated that resource effects might be relatively minor compared to the influence of these cues (Kelly *et al.*, 2013; Vacchiano *et al.*, 2017; Journé *et al.*, 2024). Contrary to this assumption and predictions of the general model, our findings reveal that resource storage enables both species to fine-tune their reproductive schedules, balancing the benefits and costs of masting. This fine-tuning allows plants to optimize their reproductive timing, delaying reproduction when necessary but avoiding excessively long intervals between mast events.

Our findings highlight a dual function of resource storage in its interaction with weather cues (T1) at both low and high resource levels. At low resources, depleted reserves act as a 'veto' on reproduction (Isagi *et al.*, 1997; Crone *et al.*, 2009; Schermer *et al.*, 2020), not as a complete block but as a significant reduction that can suppress reproduction even in the presence of strong cues. This strong effect disproves earlier predictions that a temperature-difference (ΔT) cue would render the resource veto rare and statistically hard to detect (Kelly *et al.*, 2013). The constraint on consecutive heavy reproduction due to resource depletion has important ecological consequences: it prevents large seeding events from aligning with booms in seed consumer populations after mast years, thus maintaining the starvation-satiation cycle that enhances reproductive efficiency (Zwolak *et al.*, 2022). At high resource levels, the T1 x resource interaction has previously undocumented effects. As time since the last major flowering increases and the plant's resource balance becomes more positive, the weather cue needed to trigger heavy reproduction decreases. This beneficially affects reproduction timing by reducing the gap between large events, even when the ideal weather cue is delayed (Waller, 1979; Kelly, 1994; Bogdziewicz *et al.*, 2024). These dual interactive effects enable plants to fine-tune their reproductive schedules: they are less sensitive to cues shortly after a big event but become more sensitive over time. This maintains a more constant long-term reproductive effort, preventing it from being overly influenced by unusual weather patterns, and helps plants balance the benefits and costs of masting—delaying reproduction without waiting too long.

Our findings suggest that the temperature two years prior to flowering (T2) is not merely a surrogate for resource availability but functions as a signal integrated into flowering regulatory networks via molecular pathways. Previous studies have questioned whether T2 primarily reflects resource availability due to its significant effects on seed crop sizes (Monks *et al.*, 2016; Vacchiano *et al.*, 2017). However, our models retained both estimated resource storage and the T2 cue, indicating that T2 operates independently of resource levels. We interpret these results as evidence that temperatures in T1 and T2 are integral components of flowering regulatory networks, likely incorporating multiple signals such as photoperiod (Journé *et al.*, 2024) and nutrient availability (Miyazaki *et al.*, 2014).

The strong role of resource storage in modulating the plant response to weather cues has important implications for masting forecasting. The statistical models used previously have not incorporated interactions, and their major shortcoming was poor performance in accurately predicting seed production in the largest mast years (Journé *et al.*, 2023). In light of the results reported here that is unsurprising, as the coefficient for the T1 cues in these models is averaged across resource conditions. The plant response could be orders of magnitude stronger in years when strong cues and large resource reserves align. We thus suggest that integrating interactions between surrogates of resource levels and weather cues may greatly improve the forecasting models' performance.

The interaction between resource storage and weather cues has significant implications for the climate change biology of mast seeding. Our findings reveal that the fine-tuning mechanism by which plants adjust their reproductive schedules is asymmetrical. At low cue frequency and high resource balance, plants can amplify their flowering response even to weaker cues, producing large seed crops. This allows masting to persist effectively under conditions with infrequent cues, such as in colder climates. In contrast, at high cue frequency, plants will be less able to adjust. Frequent cues lead to repeated depletion of stored resources, and the interaction suppresses flowering due to low resources. However, as soon as plants accumulate some resources, another cue occurs, prompting plants to flower. This results in more frequent reproduction but smaller seed crops, a phenomenon observed as masting breakdown in European beech (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024). Importantly, environmental changes not only increase cue frequency but may also impact resource dynamics through factors such as nitrogen and phosphorus deposition and $CO_2$ fertilization (LaDeau & Clark, 2006; Bogdziewicz *et al.*, 2017a; McClory *et al.*, 2024). The net effect depends on whether resource availability can keep pace with the increased cue frequency. If resources do not increase sufficiently, we predict more frequent but smaller seed crops. Conversely, if resources can match the higher cue frequency, plants may produce frequent and still large crops.

Finally, we highlight the challenges in identifying weather cues driving masting. Distinguishing between absolute and relative temperature cues is crucial; a ΔT (year-to-year temperature difference) cue would render masting largely insensitive to gradual climate warming because increases in mean temperature have little effect on interannual variations (Kelly *et al.*, 2013). Observational data have inconsistently supported absolute versus relative temperature cues, even within the same species. In our study, absolute temperatures (T1 and T2) were better predictors of masting in snow tussocks and European beech than ΔT. Previous studies have variously identified absolute T1, T1 and T2, ΔT, or T1×T2 as significant drivers (Kelly *et al.*, 2008, 2013; Monks *et al.*, 2016; Bogdziewicz *et al.*, 2020c). These discrepancies may result from differences in study sites, data durations, or models used. There is a trade-off between testing too many climate variables—risking spurious correlations—and too few, potentially missing complex drivers. Moreover, modeling studies have shown that ΔT models can fit data well even when the true drivers are absolute temperatures combined with resource availability (Monks *et al.*, 2016), highlighting limitations of observational data (Kelly *et al.*, 2013).

To unambiguously identify masting cues, we propose genetic studies and experimental manipulations. Genetic analyses can detect subtle weather events triggering reproduction (Satake *et al.*, 2021, 2022a), and technological advances are reducing the required effort and cost (Satake & Kelly, 2021). Experimental manipulations, such as altering fertilizer levels, water stress, pollination, or temperature, can also provide insights (Crone & Rapp, 2014; Bogdziewicz *et al.*, 2020a), though they are challenging to implement at large scales. Alternatively, observational studies during climate warming can serve as 'natural experiments' to distinguish between cues. In North American conifers, masting remained unaffected by long-term warming, suggesting ΔT is the cue (LaMontagne *et al.*, 2021). In contrast, European beech experienced 'masting breakdown' under warming conditions, consistent with absolute temperature cues driving masting (Bogdziewicz *et al.*, 2020c; Foest *et al.*, 2024). This led to increased seed predation and decreased pollination efficiency, resulting in an up to 80% decline in viable seed output (Bogdziewicz *et al.*, 2023). However, natural experiments may involve modest temperature changes; for example, LaMontagne *et al.* (2021) reported a low warming rate (0.09°C per decade). An analysis across 50 European beech seed production series indicated that changes in variability are related to the rate of temperature change, suggesting slow warming may not significantly impact masting (Foest *et al.*, 2024).

In conclusion, our study demonstrates that masting in snow tussocks and European beech is driven by the interactive effects of resource storage and summer temperatures. This indicates that resource storage is a key driver of masting, providing selective advantages by allowing high resource levels to act as a trigger for flowering. Understanding these interactions could improve the predictive accuracy of masting forecasting tools (Journé *et al.*, 2023) and explain the reduced cue sensitivity observed with warming in European beech (Bogdziewicz *et al.*, 2021; Foest *et al.*, 2024). Determining whether plants respond to relative (ΔT) or absolute (T1 and T2) temperature cues is essential for understanding how climate change will affect perennial reproduction. We stress that our study is observational, and experiments are needed to draw definitive conclusions about the specific weather cues driving mast crops. Experimental approaches, such as artificial warming or transplanting plants to different climates, are needed. Future research should focus on pinpointing the molecular mechanisms that integrate T1 and T2 cues (Satake & Kelly, 2021; Satake *et al.*, 2022b; Journé *et al.*, 2024), clarifying the role of relative versus absolute temperature variations (Kelly *et al.*, 2013; LaMontagne *et al.*, 2021), and determining how environmental fertilization and increasing cue frequency will influence reproductive patterns in perennial plants.

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**Author Contributions Statement**

DK, MB, JSz, AHP designed the study, DK and AHP collected and curated the data, JSz ran the analysis, all authors contributed to the data interpretation, MB and DK drafted the manuscript, and all authors revised and approved the text.

**Data availability statement**

The data supporting the results will be archived at OSF upon acceptance of the paper.

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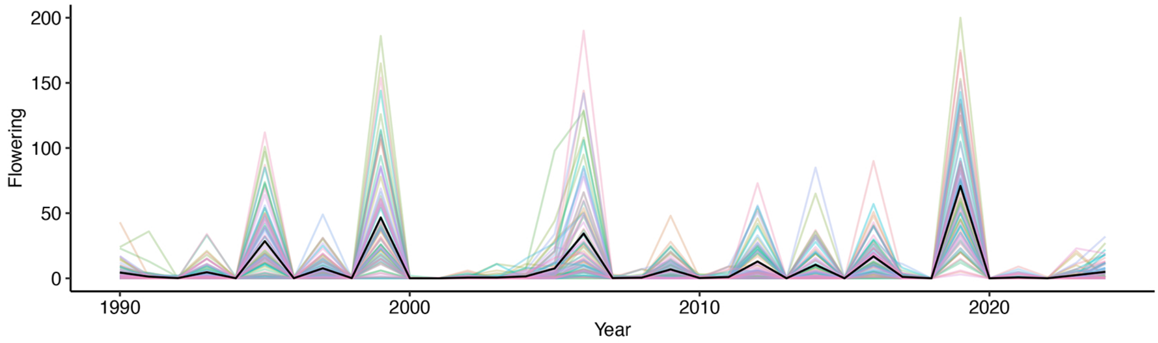
# Supporting Information

Kelly et al. The interaction of resources and weather cues enables optimization of reproductive delay in masting plants

A) *Chionochloa pallens*



B) *Fagus sylvatica*

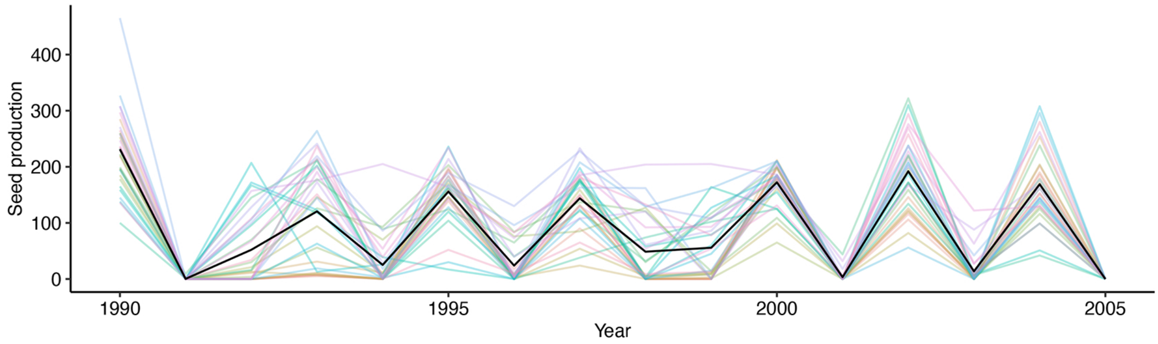


**Figure S1:** Temporal patterns of flowering effort in snow tussocks (*Chionochloa pallens*) and seed production in European beech (*Fagus sylvatica*). Each color line represents an individual plant (N = 81 in tussocks, and N = 32 in beech), while the solid black lines show annual mean flowering or seed production effort across all monitored plants.

**Table S1:** Model selection tables. Each model includes individual-level annual flowering (*C. pallens*) or seed production (*F. sylvatica*) as a response, plantID (both species) and site (European beech) as random intercept, current growing-season mean temperature T_GS (representing current-year favourability for resource gain: Nov-March for *C. pallens* and Apr-Aug for *F. sylvatica*),Tweedie error distribution, and logit link. T1 and T2 are summer temperature (June and July in *F. sylvatica* and January and February in *C. pallens*), where numbers indicate lags: 1 for the previous year, and 2 for summer two years before flowering. Resources are reconstructed deviations from the equilibrium energy budget, here estimated based on cumulative temperature during growing season as a surrogate of resource acquisition over time (see Methods). Each model included mean temperatures in the growing season in the year seed production occurs, i.e. November - March in snow tussocks and April - August in European beech.

| Model | AIC | ΔAIC | weight |
|---|---|---|---|
| ***Chionochloa pallens*** | | | |
| T1 × Resources + T1 × T2 | 1043.8 | 0.0 | 0.998 |
| T1 × Resources + T2 | 1057.5 | 13.7 | 0.001 |
| T1 × T2 + Resources | 1058.0 | 14.2 | <0.001 |
| ΔT × Resources | 1069.1 | 25.3 | <0.001 |
| ΔT + Resources | 1091.8 | 48.0 | <0.001 |
| T1 + Resources + T2 | 1093.6 | 49.8 | <0.001 |
| T1 × T2 | 1133.0 | 89.2 | <0.001 |
| T1 + T2 | 1225.4 | 181.6 | <0.001 |
| ΔT | 1231.8 | 188.0 | <0.001 |
| T1 × Resources | 1533.1 | 489.3 | <0.001 |
| T1 + Resources | 1610.2 | 566.4 | <0.001 |
| ***Fagus sylvatica*** | | | |
| T1 × Resources + T2 | 390.0 | 0.0 | 0.55 |
| T1 × Resources + T1 × T2 | 390.4 | 0.4 | 0.45 |
| ΔT × Resources | 404.4 | 14.4 | <0.001 |
| ΔT + Resources | 409.8 | 19.9 | <0.001 |
| T1 × T2 + Resources | 410.4 | 20.4 | <0.001 |
| T1 + Resources + T2 | 411.8 | 21.8 | <0.001 |
| T1 × Resources | 452.6 | 62.6 | <0.001 |
| T1 + Resources | 479.8 | 89.8 | <0.001 |
| T1 × T2 | 530.9 | 141.0 | <0.001 |
| T1 + T2 | 531.8 | 141.8 | <0.001 |
| ΔT | 533.5 | 143.5 | <0.001 |

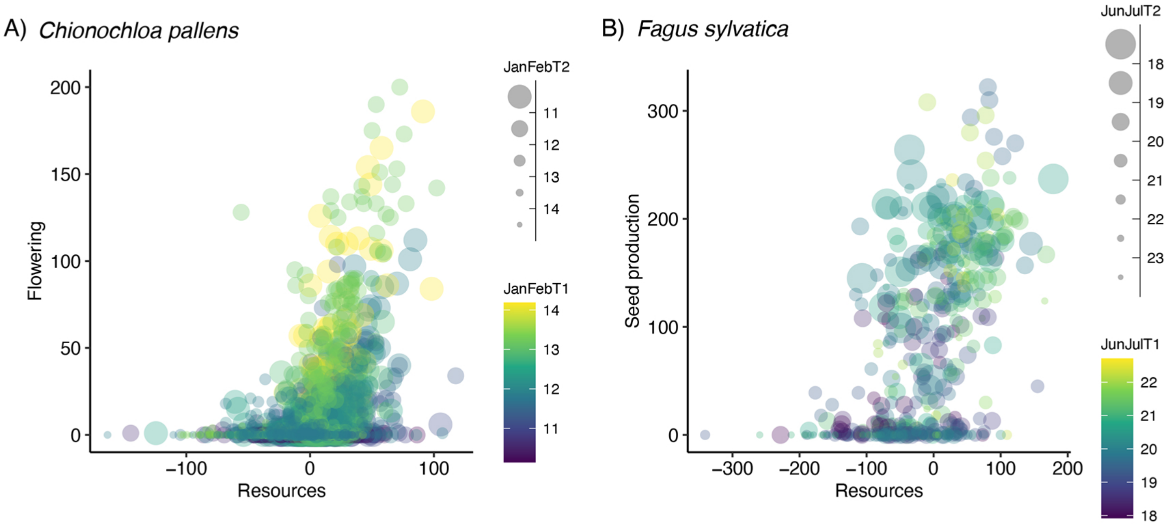


**Figure S2: Relationships between the reconstructed energy reserves and annual variation in flowering effort in *Chionochloa pallens* and seed production in *Fagus sylvatica*.** Each point is the annual flowering effort (or seed production) of an individual plant, mapped along the gradient of the reconstructed annual deviations from the equilibrium energy budget, here estimated based on cumulative temperature during the growing season as a surrogate of resource acquisition over time. Point sizes and colors are scaled according to the mean summer temperatures two years and one year prior to flowering.