Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues

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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 to predict how plant populations and ecosystem dynamics may change into the future, and for short-term forecasting of seed production to aid management. We used long-term observations of individual flowering effort in snow tussocks (*Chionochloa pallens*) and seed production in European beech (*Fagus sylvatica*) to test how endogenous resource levels and weather variation interact in driving masting. In both species, there was an interaction between the weather cue and plant resources. If resource reserves 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 reserves and weather cues has immediate application in mast forecasting models increasingly important for global afforestation efforts. Moreover, the important role of resource reserves 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; Yukich-Clendon *et al.*, 2023). 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).

Two major mechanisms can increase masting variation above the baseline generated by weather variation (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 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).

These various drivers of masting have been recently unified by the formulation of the general model of masting, suggesting that each mechanism is potentially involved 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 differential-temperature cue, 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 potentially just 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 in T1 (lack of cue), resulting in resource accumulation. Subsequent hot T1 summer (strong cue) combines with accrued resources and triggers large flowering in year T0. 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 reproduction depends on the resource state requires supplementing (not replacing) the T2 cue with an estimate of each individual plant's 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 reserves** - here, reconstructed stored resources from individual-level seed/flower production data, following the Rees *et al.* (2002) method. In short, resource reserves are estimated as negative of residuals of the linear relationship between cumulative reproductive effort and cumulative time.

Using resource reserves 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 specific 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; Chen *et al.*, 2018). Finally, despite the ΔT being initially criticized for the lack of a known 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).

Resource availability may also regulate the flowering gene expressions modulated by environmental signals. For example in *Fagus crenata* the interannual variation in 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 plant's resource reserves 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 model fitted better than 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; Vacchiano *et al.*, 2017; 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 resource reserves 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 reserves of the plant, as previously hypothesized (Kelly *et al.*, 2013; Bogdziewicz *et al.*, 2024).

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 reserves (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 reserves acts as an amplifier of plant response to the cue, if reserves are high.

Finally, by including the interaction between an individual's resource reserves 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* (mid-ribbed 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 and ecological importance (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; Pesendorfer *et al.*, 2024). 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 from 1990 to 2005. 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 resource reserves To reconstruct a plant's resource reserves from flowering and seed production data, we followed the approach developed by Rees *et al.* (2002). The method allows internal resource dynamics to be estimated from time series of reproductive effort and resource gain without directly measuring a plant's energy stores, and has been used successfully across various woody and herbaceous species (Rees *et al.*, 2002; Crone *et al.*, 2005a; Bogdziewicz *et al.*, 2018, 2019). 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 linear mixed models (LMMs) implemented via the 'lme4' package (Bates *et al.*, 2015) with plant ID as random intercepts and cumulative years as a random slope. The model for European beech included also site ID as a random intercept. The random effect structure allowed fitting a unique intercept for each plant which estimates resource reserves of a plant at the beginning of the monitoring period (Rees *et al.*, 2002), while random slope allowed for different mean rates of reproduction on each plant due to variations in size or heterogeneous resource acquisition of individuals over time (Crone *et al.*, 2005b). The model takes the form:

$$\text{cumulative\_reproduction}_i \sim N\left(\beta_{1j[i]}(\text{cumulative\_year}), \sigma^2\right)$$

$$\beta_{1j} \sim N\left(\mu_{\beta_{1j}}, \sigma^2_{\beta_{1j}}\right), \text{ for plant ID j = 1, . . . ,J}$$

Residuals for each plant from these two models (one for each species) can be used to estimate the resource reserves of that individual in each year. Basically, the regression line represents the long-term mean rate of reproduction for that plant. If the cumulative flowering gets above the regression line, the plant has been reproducing faster than the average (its expenditure is 'in overdraft'), giving a positive residual; whereas after an extended period of low flowering, the cumulative flowering line falls below the regression, suggesting spending has fallen behind the mean and giving a negative residual. To reflect the inverse relationship between expenditure and resource reserves, we take the negative of these residuals, ensuring that positive residuals correspond to lower stored resources (overdraft) and negative residuals to higher stored resources (Rees *et al.*, 2002; Crone *et al.*, 2005b). Temporal dynamics of reconstructed resource reserves are presented in Fig. S1. 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). In fact, because cumulative reproduction is on the Y axis, the units of resource reserves are flower stalks for snow tussocks and seeds for European beech, including exactly the combination of carbon, nitrogen and other resources required for reproduction in that species. The OSF repository that includes the data supporting the paper also includes a a custom R code for the method application.

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 resource reserves (estimated resources plant *i* has in the year before flowering *t-1*), and specific interactions. The interactions were between T1 and T2, between T1 and resource reserves, or between ΔT and resource reserves. 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). Collinearity between predictors was checked with VIF (< 1.3 in all models).

Results

In snow tussocks, the best-fitting model included the interaction term between reconstructed resource reserves and summer T1 temperature (Table 2). 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 reserves and the T2 cue (Table 2). The support for such a complicated model was strong in snow tussocks (AIC weight = 0.99). In European beech, the top model also includes the interaction between resource reserves 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 = 0.48; Table 2). Importantly, despite the direct inclusion of resource reserves, 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, the high reproductive effort required the alignment of both strong weather

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 reserves, abbreviated to R in the Table, are the negative of residuals of cumulative reproduction fitted against cumulative years, see Methods.

Model	AIC	ΔAIC	weight
Chionochloa pallens			
T1 × R + T1 × T2	1052.1	0.0	0.995
T1 × R + T2	1064.0	11.9	0.003
T1 × T2 + R	1064.0	11.9	0.003
ΔT × R	1076.9	24.8	<0.001
ΔT + R	1098.7	46.6	<0.001
T1 + R + T2	1100.2	48.0	<0.001
T1 × T2	1139.0	86.9	<0.001
T1 + T2	1223.7	171.6	<0.001
ΔT	1232.1	180.0	<0.001
T1 × R	1521.1	469.0	<0.001
T1 + R	1603.9	551.8	<0.001
Fagus sylvatica			
T1 × R + T1 × T2	394.8	0.0	0.52
T1 × R + T2	394.9	0.2	0.48
ΔT × R	416.2	21.4	<0.001
T1 × T2 + R	419.9	25.1	<0.001
ΔT + R	420.5	25.7	<0.001
T1 + R + T2	422.3	27.5	<0.001
T1 × R	449.9	55.2	<0.001
T1 + R	479.0	84.3	<0.001
T1 × T2	553.0	158.3	<0.001
T1 + T2	555.0	160.3	<0.001
ΔT	557.0	162.2	<0.001

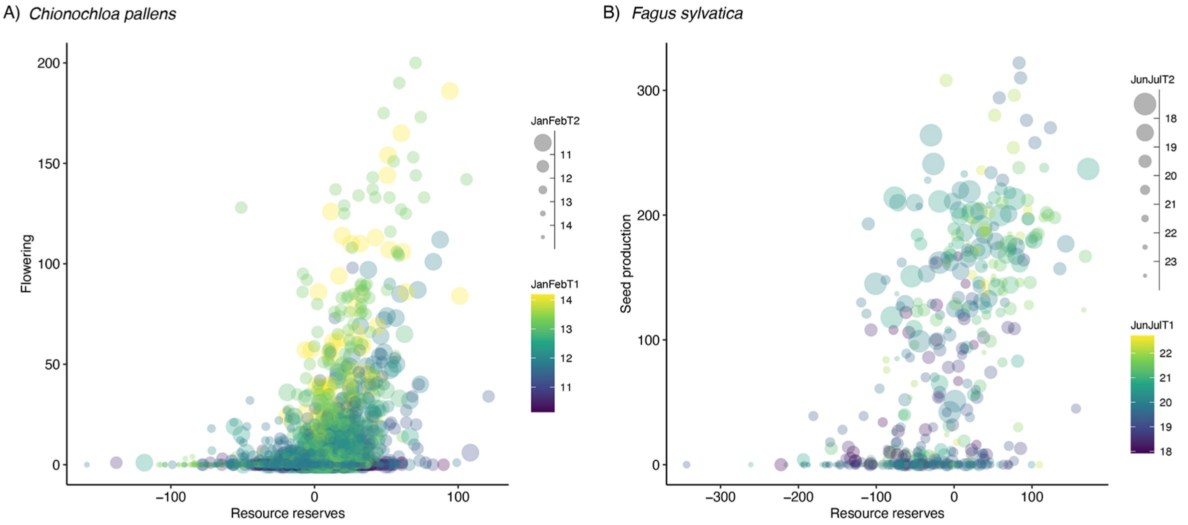

Figure 1: Relationships between the reconstructed resource reserves and annual variation in flowering effort in *Chionochloa pallens* and seed production in *Fagus sylvatica*. Each point is an annual flowering effort (or seed production) of an individual plant, mapped along the gradient of resource reserves (Rees *et al.*, 2002). Resource reserves are expressed as negative residuals of cumulative reproduction fitted against cumulative years, see Methods. Units of resource reserves are flowers in A and seeds in B. Point sizes and colors are scaled according to the mean summer temperatures two years and one year before flowering.

cues and large resource reserves (Fig. 1, 2, Table 3). The interaction between weather cues and resource reserves 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 reserves 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 resource reserves 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 reserves; if T2 summer was hot, even high T1 temperatures did not trigger heavy reproduction (Fig. 3).

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

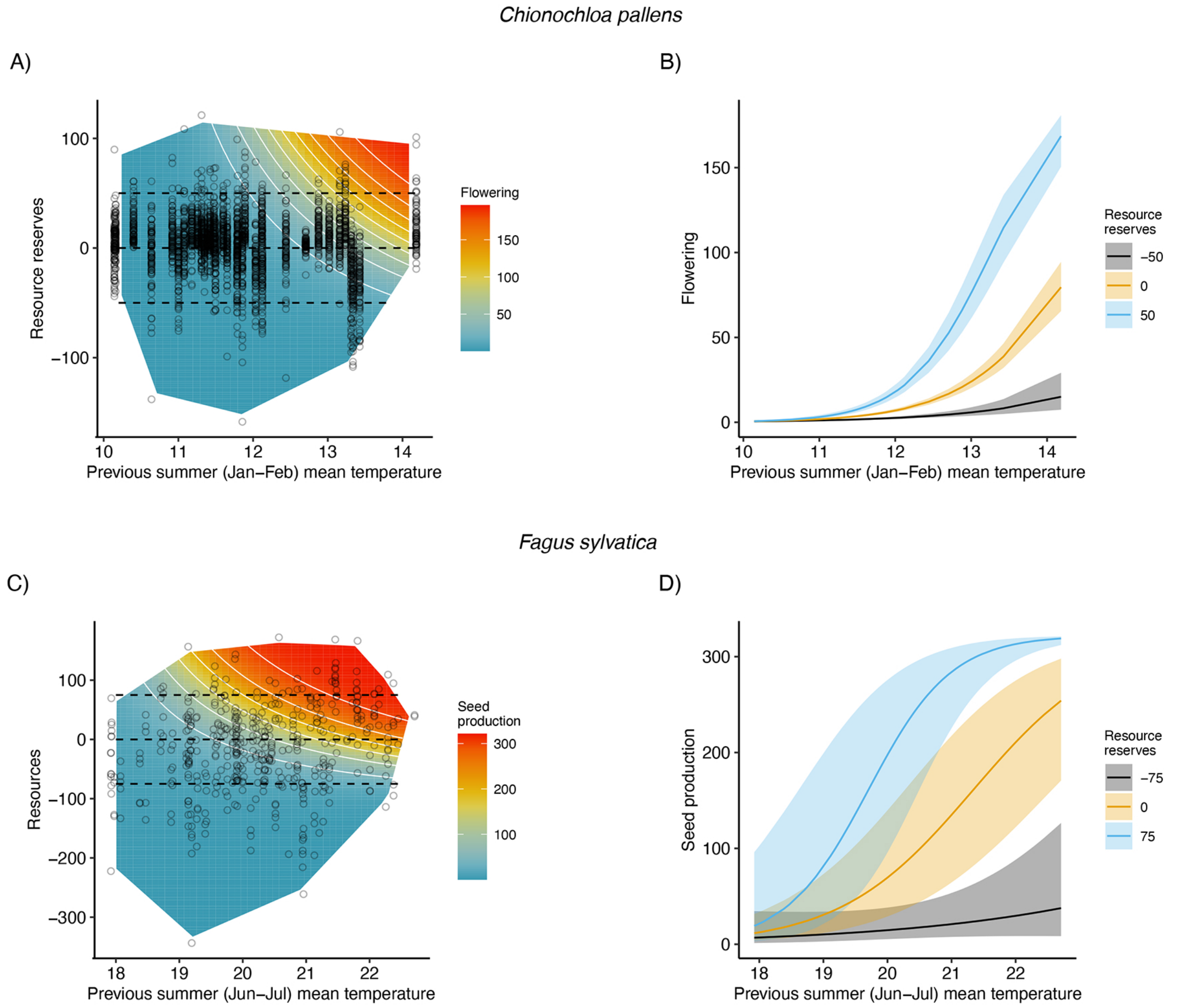

Figure 2: Previous summer temperatures and reconstructed resources reserves interact to determine annual variation in flowering effort in *Chionochloa pallens* and seed production in *Fagus sylvatica*. A) and C) Surface plots show estimated individual-level flowering (*C. pallens*) or seed production (*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 resource reserves, 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 C) indicate the conditional relationships plotted in B) and D), i.e., the relationship between flowering or seed production effort and summer temperature for selected levels of reconstructed resource reserves. Prediction lines and associated 95% CI at B) and D) are sections through surfaces highlighted by transects at A) and C). Resource reserves are expressed as negative residuals of cumulative reproduction fitted against cumulative years, see Methods. Estimates are derived from GLMM with Tweedie 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).

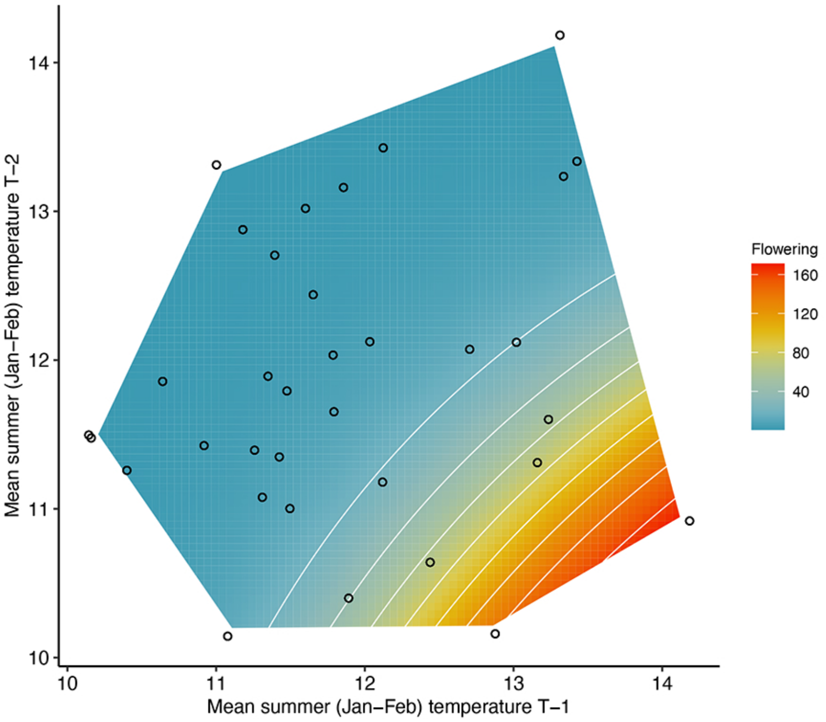

Figure 3: Previous summer temperatures interact to determine annual variation in flowering effort in *Chionochloa pallens*. The surface plot shows estimated individual-level flowering effort across combinations of the previous summer (January-February) mean temperatures one and two years before flowering. 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 (N = 81) fall into the same area defined by past years' temperatures.

Table 3: Summary of the best-fitting generalized linear mixed model testing the effects of previous summer temperatures and resource 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 reserves (R) are reconstructed deviations from the equilibrium energy budget (see Methods).

Effect	β	SE	Z	p
Chionochloa pallens ($R^2 = 0.55$)				
Intercept	-51.90	13.660	-3.80	0.001
T1	5.39	1.156	4.66	<0.001
T2	2.74	1.144	2.39	0.017
R	-0.10	0.031	-3.18	0.001
T1 × R	0.01	0.003	3.81	<0.001
T1 × T2	-0.34	0.097	-3.53	<0.001
Fagus sylvatica ($R^2 = 0.62$)				
Intercept	-5.80	2.638	-2.20	0.028
T1	0.96	0.103	9.33	<0.001
T2	-0.72	0.099	-7.33	<0.001
R	-0.13	0.029	-4.64	<0.001
T1 × R	0.01	0.001	5.34	<0.001

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 reserves also have a strong effect, which 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 reserves in its interaction with weather cues (T1) at both low and high resource levels. At low resource reserves, 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 largely suppress reproduction even in the presence of strong cues. This strong effect runs contrary to 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 reserves, the T1 x resource interaction has been previously hypothesized (Monks *et al.*, 2016; Ascoli *et al.*, 2017), but its effects rarely directly documented. As time increases since the last major flowering episode 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.

While resource reserves clearly play an important role, our findings indicate that temperature two years prior to flowering (T2) acts as a distinct signal integrated into flowering regulatory networks, rather than merely serving as a surrogate for resource reserves. Our models retained both estimated resource reserves and the T2 cue, suggesting that T2 operates independently of resource reserves. 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 reserves 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 those models was averaged across resource conditions. However, 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. Furthermore, our study indicates a practical approach to incorporating resource reserves into forecast models that do not require direct field measurement (Han & Kabeya, 2017), or reliance on climate proxies of resource uptake (Ascoli *et al.*, 2017). Additionally, using the approach proposed by (Rees *et al.*, 2002) does not require assumptions about the resources locally limiting masting. These are often unknown, including in our study systems, but resource reserves are estimated in units of real-world plant reproductive output (flowers or seeds).

The interaction between resource reserves 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 resource reserves, and the interaction suppresses flowering due to low resource reserves. 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 after 2005 (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 (Bogdziewicz *et al.*, 2020a).

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, 2022), 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 (Redmond *et al.*, 2012; Wion *et al.*, 2020; LaMontagne *et al.*, 2021). 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 reserves and summer temperatures. This indicates that resource reserves are a key driver of masting, providing selective advantages by allowing high resource levels to act as a promoter of flowering; a weather cue still provides synchrony, but resource levels modify how big the weather cue has to be. 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.*, 2022; 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 is available at the OSF, together with a custom R code that allows application of the Rees et al. (2002) method: https://osf.io/25vy6/?view$_only = 328a8d6572ba49f38811cd7e2d9735c8$

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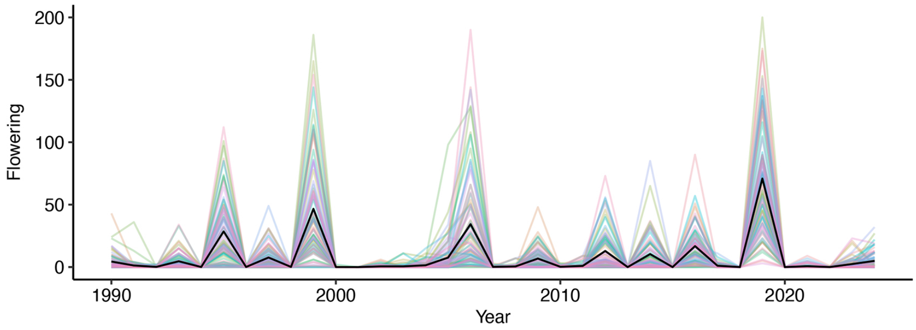
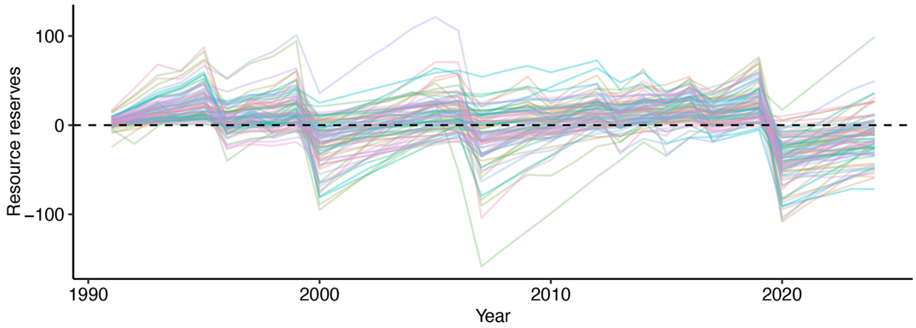
Supporting Information

Kelly et al. Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues.

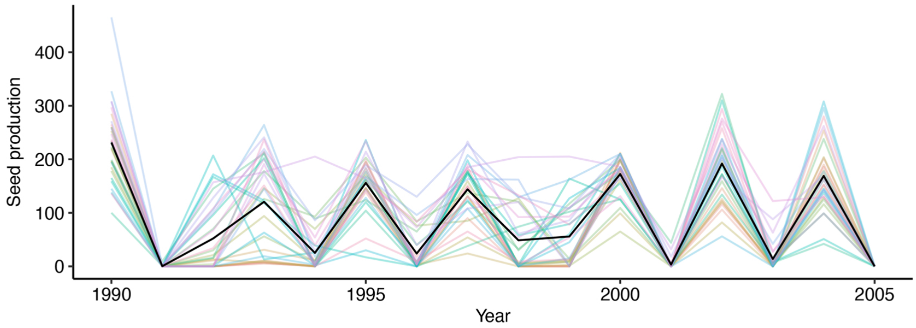
A) *Chionochloa pallens*



B) *Chionochloa pallens*



C) *Fagus sylvatica*



D) *Fagus sylvatica*

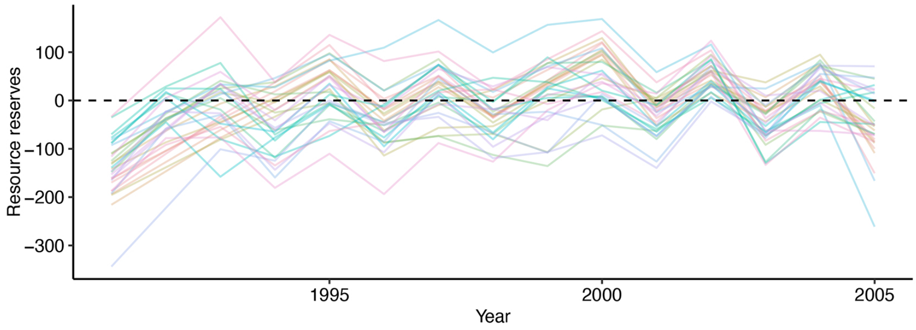


Figure S1: Temporal patterns of A) flowering effort and B) reconstructed resource reserves in snow tussocks (*Chionochloa pallens*), and C) seed production and D) resource reserves in European beech (*Fagus sylvatica*). Note that after large flowering efforts, resource reserves take multiple years to recover. 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. Resource reserves are reconstructed following the Rees *et al.* (2002) method, and are expressed as negative residuals of cumulative reproduction fitted against cumulative years, see Methods.

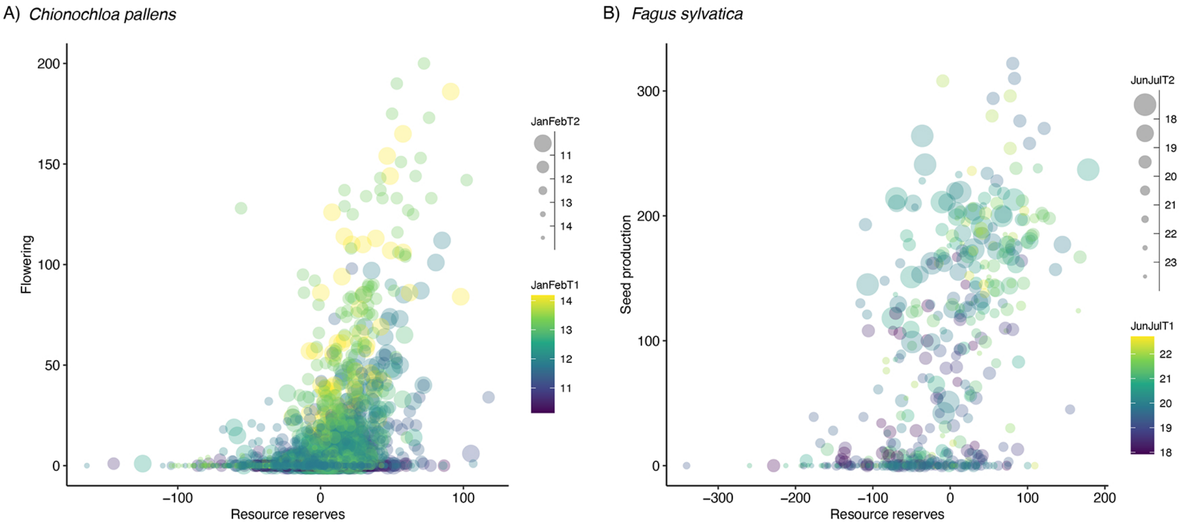


Figure S2: Relationships between the reconstructed energy reserves (estimated using annual resource gain proportional to growing-season temperatures) and annual reproductive effort. Each point is the annual flowering effort (in *Chionochloa pallens*) or seed production (in *Fagus sylvatica*) of an individual plant, plotted against that plant's reconstructed resource reserves (annual deviations from the equilibrium energy budget) at flower initiation. Point sizes and colors are scaled according to the mean summer temperatures two years and one year prior to flowering.