

1 Title: From theory to experiments for testing the proximate mechanisms of ~~in~~ mast seeding: an
2 agenda for an experimental ecology
3 Running title: From theory to experiment in masting
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35 **Abstract**

36 Highly variable and synchronised production of seeds by plant populations, known as -is called
37 masting, and is implicated in many important ecological processes, but how it arises remains
38 poorly understood. The lack of experimental studies prevents underlying mechanisms from
39 being explicitly tested, and thereby precludes meaningful predictions on the consequences of
40 changing environments for plant reproductive patterns and global vegetation dynamics. Here we
41 review the most relevant hypothetical-proximate drivers of masting and outline a research
42 agenda that takes the biology of masting from a largely observational field of ecology to one
43 rooted in mechanistic understanding. We divide the experimental framework into three main
44 processes: resource dynamics, pollen limitation, and genetic and hormonal regulation, and
45 illustrate how specific predictions about proximate mechanisms can be tested, highlighting the
46 few successful experiments as examples. We envision that the experiments we outline will
47 deliver new insights into how and why masting patterns might respond to a changing
48 environment.

49
50 Key words: experimental framework, mast seeding, masting, plant reproduction, research
51 agenda

52
53 **Introduction**

54 Masting, or mast seeding, the highly variable and synchronized seed production by plant
55 populations (Kelly 1994; Crone & Rapp 2014), is a widespread reproductive strategy in
56 perennial plants (Kelly & Sork 2002; Tanentzap & Monks 2018). The resulting resource pulses
57 have cascading effects on plant and animal population dynamics, macronutrient cycling, and
58 disease risk in humans (Ostfeld & Keesing 2000; Bogdziewicz *et al.* 2016; Vacchiano *et al.*
59 2018). From the evolutionary perspective, masting results in so-called economies of scale,
60 ie-that is, individual plants that reproduce when other plants are also flowering or seeding have
61 lower costs per surviving offspring (Kelly 1994). The two most supported economies of scale
62 include predator satiation, where large seeds crops enhance seed and seedling survival, and
63 increased pollination efficiency in high-flowering years (Kelly & Sork 2002; Pearse *et al.* 2016).
64 On a proximate level, Masting-masting emerges at the population level by combining two
65 processes: annual variability in seed production and synchronization among individuals (Herrera
66 1998; Koenig *et al.* 2003). Several hypotheses have been proposed to explain the proximate
67 drivers of masting, but it remains unclear to what extent these are valid or how they are
68 conserved among or even within species (Kelly *et al.* 2013; Crone & Rapp 2014; Pearse *et al.*

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69 2014; Monks *et al.* 2016). Observational studies of masting patterns amassed over the past 50
70 years have led to considerable theoretical advances, yet there have been few experimental
71 tests of those theories (Crone *et al.* 2009; Smaill *et al.* 2011; Pearse *et al.* 2015).

72 Global ~~observations-meta-analysis~~ of plant reproductive patterns show that seed
73 production has declined and become more variable over the last 100 years (Pearse *et al.* 2017).
74 Yet, we have little idea what has driven this change. Prior studies have predicted that masting
75 intensity will increase, decrease, or remain unchanged in response to climate change (Kelly *et al.*
76 *al.* 2013; Koenig *et al.* 2015; Monks *et al.* 2016; Bogdziewicz *et al.* 2017b). This uncertainty may
77 partly arise from the fundamentally different mechanisms that appear to underlie masting in
78 closely related taxa ([Table 1](#)) (Koenig *et al.* 2016; Pearse *et al.* 2016; Bogdziewicz *et al.* 2017c).
79 Experiments are now needed both to understand the mechanisms underlying masting, and to
80 better predict the consequences of a changing climate for plant reproductive patterns and global
81 vegetation dynamics.

82 Our aim here is to outline a research agenda that takes the biology of masting from a
83 largely observational field of ecology to one rooted in mechanistic understanding. This
84 understanding can be incorporated into global vegetation models to improve their accuracy and
85 realism in terms of seed production but also growth tradeoffs, seed dispersal, establishment,
86 migration, cascading trophic interactions, and ecosystem resilience to disturbances or climate
87 change (Vacchiano *et al.* 2018; Clark *et al.* 2019). We outline explicit predictions of prevalent
88 hypotheses explaining intermittent and synchronised reproduction at the population level and
89 describe what experiments would be necessary to test them. We do not try to repeat previous
90 reviews of masting theory (Crone & Rapp 2014; Pearse *et al.* 2016; Allen *et al.* 2018; Vacchiano
91 *et al.* 2018). Rather, we illustrate how specific predictions about the proximate mechanisms
92 involved in masting can be tested and highlight successful experiments as examples.

93

94 **Hypotheses, Predictions, and Experimental Tests**

95 We divide our discussion into the three main processes underpinning mast seeding:
96 resource dynamics, pollen limitation, and genetic and hormonal regulation (Fig. 1).

97 Environmental variation has been traditionally recognized as a masting driver, but ~~it appears to~~
98 ~~be involved its effect is~~ largely, if not exclusively, through ~~its effects on~~ these processes. Thus,
99 the discussion of environmental variation as a masting driver is incorporated into the three
100 aforementioned sections.

101

102 **I. Resource dynamics**

103 **1a. Theoretical predictions**

104 The internal resource dynamics of individual plants are potentially responsible for annual
105 variation in individual seed production in at least three ways (Fig. 2) (Pearse *et al.* 2016). The
106 first two hypotheses predict that resources are allocated for either reproduction or growth within
107 each year, whereas the third hypothesis predicts that resources are carried over between years.
108 First, the resource matching hypothesis predicts that a fixed fraction of resources is allocated to
109 reproduction each year. Annual variation in seed production is thus a consequence of annual
110 variation in resource acquisition. Resource matching is essentially a “null” hypothesis for mast
111 seeding, wherein annual variability in seed production entails no adaptive framework beyond
112 using what resources are available each year for reproduction.

113 There are at least two adaptive alternatives to resource matching. One is the resource
114 switching hypothesis, which predicts that a variable fraction of current-year resource acquisition
115 is allocated to seed production (Monks & Kelly 2006; Hackett-Pain *et al.* 2018). Years with more
116 available resources see greater investment in reproduction, whereas years with fewer available
117 resources result in more investment in plant growth and less reproduction. Thus, the ratio
118 between vegetative to reproductive allocation should vary with resource switching but remain
119 constant under resource matching.

120 Finally, the resource storage hypothesis predicts that plants accumulate resources over
121 several years, eventually investing them in a large “mast crop” (Isagi *et al.* 1997; Satake &
122 Iwasa 2000). Storage can be active if plants store resources until a certain resource threshold is
123 reached, or passive if environmental constraints limit seed production in some years, forcing
124 plants to save resources for reproduction in subsequent years (Pesendorfer *et al.* 2016;
125 Bogdziewicz *et al.* 2018). ~~This third hypothesis differs from the first two in that it predicts that~~
126 ~~resources are carried over between seasons rather than allocated into reproduction or growth~~
127 ~~within the same year.~~

128

129 **1b. Experimental tests**

130 The most obvious way to test how resources are involved in seed production is to
131 supplement different macronutrients - nitrogen, phosphorous, carbon - at different seed
132 developmental phases. Ideally, this experiment would be replicated across different species,
133 and flower initiation, anthesis, and seed maturation would be monitored, as these would differ
134 to differentiate between “flowering masting” and “fruit maturation” species in which annual
135 variability in seeding is primarily driven by differences in flower production and fruit abortion,

Commentato [WDK1]: I think the “replicated across different species” is unnecessary, first because it’s obvious and second because it’s completely unrealistic for any one person or experiment to undertake

136 respectively (Pearse *et al.* 2016). Under resource matching, the addition of resources should
137 increase both current growth and reproduction, whereas resource switching predicts
138 disproportionate investment in current reproduction. In contrast, the addition of resources
139 beneath a threshold required to induce flowering would increase seed production only in later
140 years if resource storage were important. In the absence of *a priori* knowledge about this
141 threshold, resources would need to be added at different levels.

142 Resource addition experiments have thus far yielded variable results. A likely
143 explanation for this variability is the potential for different macronutrients to be limiting in
144 different species and both the differing time scales and phenological stages at which resources
145 matter (Miyazaki *et al.* 2014; Pulido *et al.* 2014; Bogdziewicz *et al.* 2017a; Minor & Kobe 2017;
146 Brooke *et al.* 2019). Such differences highlight the desirability of [performing such](#) fully-factorial
147 experiments [being conducted](#) on a variety of masting species over multiple years.

148 An excellent example of a resource addition experiment is that of Smaill *et al.* (2011),
149 who investigated the effect of N fertilizer in *Nothofagus solandri* stands. They found that
150 fertilization increased seed production, but only in some years. This variability was attributed to
151 different responses to weather depending on the treatment. Seed production in unfertilized
152 stands was primarily linked to rainfall the year before dispersal (higher rainfall leading to greater
153 N mineralization and uptake), while in fertilized stands where N limitation was removed, seed
154 production was affected mainly by temperature during flower primordia development. Analogous
155 results were obtained by Miyazaki *et al.* (2014), who combined N fertilization with monitoring of
156 flowering gene expression levels in *Fagus crenata* and found that N addition stimulated flower
157 transition and mass flowering in consecutive years. These studies demonstrate the key role and
158 interaction of resources and environmental variation in driving masting, but they do not explicitly
159 test the resource-related hypotheses outlined above.

160 A second experimental approach is to prevent seed maturation, typically the most
161 resource-demanding phase, by harvesting seeds before they ripen or applying ethylene
162 inhibitors designed to reduce or eliminate flowering (Bukovac *et al.* 2006). This treatment should
163 result in larger seed production in the next year only under the resource storage hypothesis, but
164 would not differentiate resource matching from switching. ~~More comprehensive results~~ [Results](#)
165 [that are more comprehensive](#) are likely to be generated by experiments that not only prevent
166 seed maturation but, conversely, encourage plants to produce more seeds. [This can be](#)
167 [achieved](#) with agricultural sprays that inhibit biosynthesis of ethylene, thereby forcing plants to

168 retain flowers that are otherwise likely to be aborted. This approach could prove particularly
169 powerful combined with tracking analyses of potentially key macronutrients.

170 Thus far the most influential experiment conducted along these lines has been that of
171 Crone *et al.* (2009) studying the wildflower *Astragalus scaphoides*. These authors removed
172 flowers from some plants for one year and from others for three consecutive years to
173 desynchronize flowering. The experiment demonstrated that seed production in this species
174 depletes stored carbohydrates and limits subsequent flowering. Asynchronously flowering plants
175 failed to produce seeds due to density-dependent pollen limitation, but they did not deplete
176 carbohydrate stores and were able to flower in following years and resynchronize with the rest
177 of the population, supporting the resource storage hypothesis.

178 Another set of experiments useful to understand the impact of resource dynamics on the
179 reproductive patterns of masting plants are those that simulate environmental conditions
180 projected by global environmental change models, like warming, CO₂ enrichment, or rainfall
181 exclusion (LaDeau & Clark 2001; Chung et al. 2013; Pérez-Ramos et al. 2013; Bykova et al.
182 2018). The effects of warming or CO₂ enrichment on reproduction in masting plants will depend
183 on the exact way in which resource dynamics influence masting in the first place. In the case of
184 water limitation experiments, drought interacts with the acquisition and storage of other
185 resources (Pearse et al. 2016), but may also serve as the environmental cue that
186 synchronizing reproduction within the population (Espelta et al. 2008, see also section IIIa). In
187 the latter is true case, reproduction of masting species that use using water shortage as cue
188 should be more affected by the water limitation as selection favors would favour plants that are
189 just frail enough to be damaged by these sensitive to drought in order to foster synchrony
190 weather events, because this provides synchrony (Bogdziewicz et al. 2019).

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Commentato [WDK2]: I think this is what you mean (?)

191 Potential complications in experimental tests of resource dynamics, and in all masting
192 experiments more generally, may arise if species take multiple years to develop their seeds
193 (Knops *et al.* 2007). Furthermore, resources added to plants or carried forward to the next year
194 may not be immediately invested into seeds due to poor weather conditions, such as frost or a
195 lack of weather cues required to initiate flowering (Rees *et al.* 2002; Abe *et al.* 2016; Monks *et*
196 *al.* 2016; Bogdziewicz *et al.* 2018). Thus, cohorts of control and experimental plants must be
197 observed for several years so that differences in environmental conditions can be considered.

198

199 II. Pollen limitation

200 Ila. Theoretical predictions

201 Even if endogenous resource dynamics induce the observed annual variability at the
202 individual level, plants require a synchronizing factor to produce population-wide mast seeding.
203 Recent work supports the hypothesis that pollen limitation — up until recently a factor whose
204 role in masting was unclear (Koenig & Ashley 2003), particularly in wind pollinated species
205 (Koenig *et al.* 2012; Pearse *et al.* 2015) — can be that synchronizing factor.

206 Pollen limitation may drive synchronization of seed production in several, mutually non-
207 exclusive, ways (Fig. 3). The first is density-dependent pollen coupling, which predicts that
208 annual variation in density of flowering plants drives pollen limitation in self-incompatible plants
209 (Satake & Iwasa 2000; Kelly *et al.* 2001; Venner *et al.* 2016). In combination with the resource
210 storage hypothesis, pollen coupling predicts that if a plant flowers out of synchrony with its
211 neighbors, it will not receive pollen, will fail to fertilize flowers, will not deplete resources, and will
212 thus flower again in subsequent seasons until other plants in the population flower. When this
213 last step finally happens, flowers will be pollinated and mature into fruits, which will deplete
214 resources and synchronize the endogenous resource dynamics of the individual with the rest of
215 the population.

216 Pollen coupling focuses on among-year variation in flowering synchrony and potentially
217 confers a functional benefit to masting as one of several “economies of scale” along with, most
218 obviously, predator satiation (Pearse *et al.* 2016). At the within-year level, the main mechanism
219 by which pollen limitation is likely to be expressed is phenological synchrony (Koenig *et al.*
220 2015). Plants that flower in synchrony with a higher number of other individuals experience less
221 pollen limitation. In contrast, low flowering synchrony decreases pollen availability and increases
222 pollination failure. The strength of phenological synchrony is in turn driven by weather. Such
223 population-wide pollination outcomes may interact with either resource storage or resource
224 switching to produce mast years when large resource pools coincide with high pollination
225 success (Koenig *et al.* 2015; Pesendorfer *et al.* 2016; Bogdziewicz *et al.* 2017b).

226 There are at least two mechanisms through which weather variability can affect
227 phenological synchrony. The microclimatic hypothesis, proposed originally as a part of the
228 phenological synchrony hypothesis (Koenig *et al.* 2015), predicts that flowering is more
229 asynchronous when microclimatic conditions are more heterogeneous, conditions that translate
230 into greater variability in flowering time. As an example, trees in valleys and at lower elevations
231 are likely to flower later because cold air descends at night, thereby magnifying the microhabitat
232 variation when average temperatures are cooler. Conversely, a relatively homogeneous
233 microclimate in warm years results in synchronous flowering and pollen production and
234 presumably higher pollination success.

235 An alternative proposed here is the photoperiod sensitivity hypothesis, whereby
236 flowering synchrony can be driven by an interaction between daylength and temperature. In cold
237 years, days are already long when spring warming occurs, reducing the effect of a plant's
238 daylength sensitivity on its flowering time (Fu *et al.* 2019). In warm years, the days are still short
239 when spring warming occurs, preventing day-length sensitive plants from flushing and flowering.
240 Thus, in warm years, leaf-out and flowering advance in day length-insensitive individuals, but
241 not in day length-sensitive individuals. Although we know of no explicit tests of this hypothesis,
242 experiments have already confirmed large intraspecific variation in day-length sensitivity
243 within populations in of some species (Zohner *et al.* 2018). Consequently, this response may
244 increase the population-level variability of flowering synchrony under short day conditions (warm
245 years, early spring) and increase synchrony of flowering in late springs (cold years, late spring).

246 Another hypothesis relating weather and pollen limitation posits that warm, dry
247 temperatures during the pollination period increases~~affects~~ pollination efficiency through
248 providing good conditions for pollen release and aerial diffusion (Schermer *et al.* 2019). Thus,
249 this aerial diffusion hypothesis predicts that warm temperatures and dry conditions should
250 decrease pollen limitation through enhancing aerial pollen abundance and dispersal. Pollen
251 limitation may also be a consequence of unfavorable weather events like rainfall washing out
252 pollen from the air column (García-Mozo *et al.* 2007). As in the case of phenological synchrony,
253 such population-wide pollination outcomes may interact with resource dynamics to produce
254 mast years (Schermer *et al.* 2019).

255

256 **IIb. Experimental tests**

257 Pollen limitation can be tested by pollen addition experiments. Additions conducted
258 along a density gradient of flowering plants either in time (in high- and low-flowering years) or in
259 space would test the strength of pollen coupling, which predicts that the positive effect of pollen
260 addition on seed set should be negatively related to the density of flowering plants. The
261 phenological synchrony hypothesis can be examined by combining pollen additions with
262 monitoring of flowering times, the prediction being that the effect of pollen addition should be
263 stronger in individuals whose phenology is less synchronized with other plants in the population.

264 There have been few attempts to manipulate pollen levels experimentally, at least in the
265 wind-pollinated species that disproportionately exhibit mastings. In the case of phenological
266 synchrony, no experimental test was thus far has been conducted. Similarly, pollen coupling has
267 been tested only in one system. Crone & Lesica (2006) added pollen to flowers of mast-seeding
268 *A. scaphoides* and found increased seed set in years when a low proportion of the population

Commentato [WDK3]: Aren't there lots of such studies in insect-pollinated species? That's my impression (guess), anyway.

269 flowered, but no effect in years when the density of flowering plants was high. This result
270 confirmed the density-dependence of pollination success in this insect-pollinated species.
271 Pearse *et al.* (2015) also added pollen to wind-pollinated California valley oak (*Quercus lobata*),
272 but without explicitly exploring whether pollination success was determined by pollen coupling or
273 phenological synchrony. They found increased seed set in one of two years, suggesting that
274 interannual variability in pollen limitation synchronizes seed set consistent with models of mast
275 seeding. Their study also demonstrated that most female flowers were aborted due to factors
276 other than a lack of pollination, leaving considerable remaining uncertainty about the proximate
277 mechanisms involved in masting in this species.

278 A complication of pollen addition experiments is that fruit maturation can be limited by a
279 scarcity of both pollen and resources. Thus, when resources are limiting, supplementing pollen
280 will not result in greater flower-to-fruit transitions. Future experimental attempts should try to
281 discriminate these two factors by crossing pollen addition experiments with resource monitoring
282 or supplementation.

283 Weather can further complicate experimental tests of pollen limitation, by influencing
284 flowering. Manipulating among-plant variation in microclimatic conditions by applying different
285 levels of shading and/or warming can help determine whether microclimatic heterogeneity or the
286 interactive effects of photoperiod and temperature drive flowering synchrony. For example,
287 warm temperatures under short-day conditions should desynchronize flowering under the
288 photoperiod sensitivity hypothesis, while daylength should be unimportant under the
289 microclimatic hypothesis. Similar setups can be used to test whether higher air temperature
290 around a plant enhances aerial pollen concentrations. No experimental tests of weather
291 variation on pollen limitation have thus far been conducted.

292

293 **III. Genes and hormones**

294 **IIIa. Theoretical predictions**

295 To the extent that masting is driven by resources and pollen, plants must have
296 mechanisms to sense their environment and control investment in reproduction as a function of
297 that environment. These mechanisms map onto genetic and hormonal apparatuses that control
298 seed set and are central to understanding the basis of masting (Pearse *et al.* 2016; Satake *et al.*
299 2019). Changes in gene expression and resultant changes in hormone secretion can
300 consequently produce both annual variability and synchrony of seed production.

301 Most theory concerning the role of gene expression and associated hormonal secretion
302 in controlling masting has been developed around their interaction with the environment (Pearse

303 *et al.* 2016). If gene regulatory networks integrate multiple signals such as temperature,
304 nutrients, and photoperiod, flowering and fruiting may happen only when all these different
305 signals are received. If these different signals are integrated in an additive manner, a single very
306 strong signal may be sufficient to activate genes for floral transition (Mangan & Alon 2003; Kalir
307 *et al.* 2005). In other words, if hormones and the genes that control them are hypersensitive to
308 an environmental signal, masting can be at least partially independent of resource- and pollen-
309 based mechanisms. The best developed example of this idea is the weather cueing hypothesis
310 (Fig. 4), which predicts that large seasonal deviations from mean weather values trigger
311 changes in flowering gene expression and associated hormone synthesis responsible for
312 initiating bud formation, flower induction, or flower abortion (Kelly *et al.* 2013; Monks *et al.* 2016;
313 Ascoli *et al.* 2017; Vacchiano *et al.* 2017). ~~Plants should all respond to the cue in the same way,~~
314 ~~#Assuming that~~ regulatory networks are strongly conserved within populations, plants should all
315 respond to the cue in the same way, resulting in high synchrony and ~~individual-among-years~~
316 variability in reproduction. There is no requirement for the weather cues to be correlated with
317 higher resource acquisition rates, and the only absolute requirement is that the cue be spatially
318 synchronous over wide areas so all plants can respond similarly (Kelly 1994). The specific link
319 between weather signal and seeding can be thus species- and possibly even population-specific
320 (Bogdziewicz *et al.* 2019). Nonetheless, the general prediction is that the cue should trigger
321 hormone synthesis and affect flowering in a similar way across individuals within populations.

322 Related to that problem is the untested assumption that the investment in, and timing of,
323 seed production by individual masting trees is under genetic control that selection can act upon
324 (Pearse *et al.* 2016, Koenig *et al.* 2017). First, for selection to act upon ~~any one component of~~
325 masting behavior (synchrony ~~and~~ variability of seed production), the ~~masting~~ trait must be
326 heritable (Pearse *et al.* 2016). The evidence for ~~that~~ this is limited – only one study has explored
327 the topic in a masting species, finding ~~and found~~ important genetic effects on the variability of
328 seed production in *Quercus robur* (Caignard *et al.* 2019). Assessing heritability based on
329 parental regression or known siblings is logistically challenging, as it requires long-term data on
330 seed production by individual plants of known genetic relatedness, or the rearing of ~~the~~ offspring
331 of known parents ~~must be reared~~ in a common environment for decades (Caignard *et al.* 2019).
332 The other method requires long-term data on seed production by individual plants of known
333 genetic relatedness. The substantial individual variation of masting traits among individuals
334 (Koenig *et al.* 2003, Crone *et al.* 2011) allows testing for correlations between relatedness of
335 individuals and masting traits, —but this has ~~not been done yet~~ to be attempted.

336

337 **IIIb. Experimental tests**

338 Experimental tests of the weather cueing hypothesis require manipulating weather
339 variability to simulate cues identified by previous correlational studies. For instance, if flowering
340 appears to be related to relatively warmer years, an experiment could warm plants to trigger
341 masting events. As an example, Kon & Noda (2007) tested the effect of night-time temperatures
342 on flower bud initiation in *Fagus crenata* by heating fruit-bearing branches at different times of
343 flower development. They found that warm temperatures during sensitive development periods
344 vetoed flower initiation and hypothesized that this was because of temperature-related
345 gibberellin secretion.

346 Measuring gene expression levels or hormonal levels in vegetative versus reproductive
347 plant organs before, during, and after applying the cue will help unravel the mechanisms
348 through which plants perceive cues. As a successful example, field transcriptome analysis using
349 the mass flowering [species-tree](#) *Shorea beccariana* showed that expression levels of drought-
350 responsive and sucrose-induced genes increased significantly prior to anthesis (Kobayashi *et al.*
351 *et al.* 2013). Yeoh *et al.* (2017) applied a molecular phenology approach (Kudoh 2016) to tropical
352 trees in *Shorea* to identify proximate environmental cues for community-level masting. The
353 activation of flowering genes was observed twice over four years, and was always followed by
354 anthesis. This result was consistent with the occurrence of interacting drought and cool
355 temperature signals (Chen *et al.* 2018). A fully-factorial design in which pollen and
356 macronutrients are added *ad libitum* will further test whether, or to what extent, weather acts as
357 a distinct mechanism from pollen limitation and resource dynamics.

358 An alternative experiment would be to manipulate directly the hormonal cues presumed
359 to be involved in masting without altering resource or pollen availability. One such study
360 exogenously applied two gibberellins (GA3 and GA4) to snow tussocks (*Chionochloa pallens*
361 and *C. rubra*), which increased flowering in some, but not all, years (Turnbull *et al.* 2012).
362 Gibberellin addition appeared to interact with temperature cues correlating with increased
363 flowering. This finding suggested that temperature-regulated endogenous gibberellin
364 biosynthesis is a causal factor in mast flowering events. In oaks, preliminary studies suggest
365 that manipulating ethylene signaling is critical to explain rates of flower abortion (Pearse *et al.*
366 unpublished). Because differential flower abortion is the primary cause of interannual variation
367 in oak seed crops (Espelta *et al.* 2008; Pérez-Ramos *et al.* 2010; Pearse *et al.* 2015), ethylene
368 appears to be a strong candidate as a hormonal driver of masting in this taxon.

369 Examining the molecular basis of environmental cues, such as weather, and testing
370 whether it is resource-dependent would be a valuable area of future experimentation. A

371 groundbreaking study employing gene expression profiling techniques was that of Miyazaki *et*
372 *al.* (2014), who monitored expression levels of key flowering-time genes, *FLOWERING LOCUS*
373 *T (FT)*, *LEAFY (LFY)* and *APETALA1 (AP1)* for five years in *Fagus crenata*. *FT* moves from
374 leaves to shoot meristems where it acts to induce flower, while *LFY* and *AP1* have been
375 identified as necessary for the determination of the floral meristem identity in *A. thaliana*
376 (Mandel & Yanofsky 1995). The expression levels of these flowering genes showed clear
377 between-year fluctuations in *Fagus crenata* that were associated with a variable flowering and
378 fruiting pattern. Crucially, nitrogen fertilization experiments identified N as a key regulator for the
379 floral transition in this species (Miyazaki *et al.* 2014), showing how resource dynamics maps
380 onto a genetic apparatus that controls seed set.

381

382 **V) Concluding remarks**

383 Despite the crucial role of mast seeding in plant regeneration and many other ecological
384 processes (Ostfeld & Keesing 2000; Vacchiano *et al.* 2018), our understanding of its behavior is
385 mostly based on observational records from natural conditions. Few experiments have been
386 designed to test the predictions of hypotheses for the proximate causes of masting. For
387 example, some of the best experimental tests of resource- and pollen-based hypotheses have
388 come from the bee-pollinated *AstragalusA. scaphoides* (Crone *et al.* 2009), but the relevance of
389 these findings to more widespread, wind-pollinated masting systems, such as long-lived trees,
390 remains unclear. For weather cueing, experimental tests need to generalise more broadly
391 whether correlations between seeding and weather variation are accompanied by changes in
392 gene expression and associated hormone secretion within a broader regulatory network, or
393 instead reflect mechanisms ~~like~~ such as resource or pollen limitation (Pearse *et al.* 2014).
394 Future progress depends on experiments designed to test these hypotheses. As the relative
395 importance of different mechanisms are likely to vary among species, standardised experiments
396 across diverse life strategies would be highly beneficial.

397 We have summarised potential tests of the mechanisms involved in synchronous and
398 intermittent reproduction (Table 24), thereby outlining a-ways to improve our understanding of
399 mast seeding. We envision that these experiments will deliver new insights into how and why
400 masting patterns might respond to a changing climate and macronutrient cycles. This
401 knowledge can subsequently be incorporated into broader ecosystem-scale models to aid
402 predictions of vegetation dynamics and biogeochemical cycles (Vacchiano *et al.* 2018). For
403 example, current dynamic vegetation models rarely allocate carbon to sexual reproduction, and
404 if so, they assume resource matching (Merganicova *et al.* 2019), which is probably unlikely

405 (Pearse *et al.* 2016). In agricultural systems, this knowledge may help predict the timing of
406 commercially valuable fruit and nut crops, such as apple, citrus, and pistachio (Smith & Samach
407 2013). Finally, a better understanding of the timing of resource pulses associated with masting
408 can help inform wildlife managers of changes in animal populations and the public about
409 potential health risks such as Lyme disease (Ostfeld *et al.* 2006). As masting underpins many
410 ecological processes that are important to human well-being, the experimental roadmap we
411 have developed here should ultimately transform our understanding of [#-this phenomenon](#) for
412 the next generation.

413

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419 final manuscript.

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Commentato [WDK4]: I reordered several references in the way I have always felt was easier for readers: first by number of authors (1, 2, 3+), the last—which are all listed as “Author1 et al.”—in chronological order. Note: there are 2 Bogdziewicz et al. 2019s and 2 Satake et al. 2019s; I have added “a” and “b” below but the actual citations in the text need to be fixed.

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Table 1. Summary of selected observational studies supporting different proximate mechanisms of masting seeding in closely related taxa.

Taxa	Resource dynamics			Pollination dynamics		Genetic and hormonal regulation	
	Matching	Switching	Storage	Pollen coupling	Phenological synchrony		Aerial diffusion
<i>Quercus</i>	- Positive correlation between growth and reproduction in <i>Q. ilex</i> ¹	- Negative correlation between growth and reproduction in <i>Q. lobata</i> , <i>Q. douglasii</i> , <i>Q. agrifolia</i> ²	Resource budget models reproduce masting in <i>Q. petraea</i> , <i>Q. robur</i> ³ , <i>Q. rubra</i> , <i>Q. alba</i> ⁴ , <i>Q. lobata</i> ⁵	Positive correlation between number of pollen-producing neighbors and crop size in <i>Q. douglasii</i> ⁶	Positive correlation between seed production and flowering synchrony in <i>Q. lobata</i> ⁷ , <i>Q. petraea</i> , <i>Q. robur</i> ⁸ , <i>Q. ilex</i> ⁹	Positive correlation between seed production and temperature-related aerial pollen concentration in <i>Q. petraea</i> , <i>Q. robur</i> ³	Not studied
<i>Fagus</i> & <i>Nothofagus</i>	No evidence	- Negative correlation between growth and reproduction in <i>F. sylvatica</i> ¹⁰ , <i>N. truncata</i> ¹¹	Resource budget models reproduce masting in <i>F. crenata</i> ¹²	Positive correlation between tree density pollination efficiency in <i>F. sylvatica</i> ¹³ , <i>F. crenata</i> ¹⁴ , <i>N. solandri</i> , <i>N. menziesii</i> ¹⁵	No evidence	No evidence	Combination of genetic and environmental signals regulate flowering gene expression dynamics in <i>F. crenata</i> ^{16,17}
<i>Chionochloa</i>	Not studied	Not studied	Resource budget models reproduce masting in 5 <i>Chionochloa</i> species ^{18,19}	<i>Chionochloa</i> are self-compatible, thus pollination is not expected to play important role in synchronizing their reproduction ¹⁸		High temperature-induced increases in gibberellin levels promote flowering ¹⁹	

Formattato: Larghezza 27,94 cm, Altezza: 21,59 cm

Commentato [WDK5]: Presumably somewhere we need to clarify that "Q." = *Quercus*, "F." = *Fagus*, and "N." = *Nothofagus*. Also, what are the superscripts referring to? If citations, where are they listed?

667

Formattato: Tipo di carattere: Non Grassetto

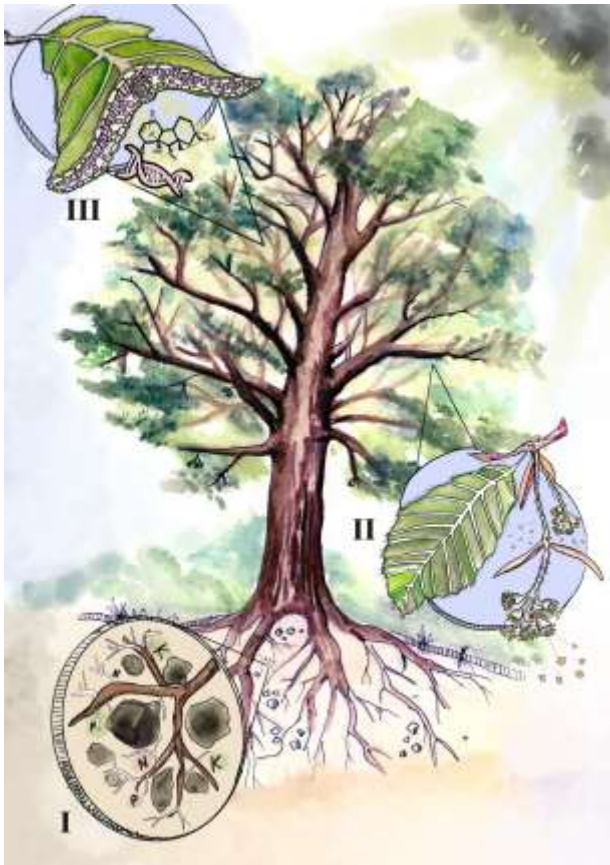
668 **Table 24.** Summary of proximate mechanisms believed to drive mast seeding, the theoretical
 669 predictions derived from the main masting hypotheses, and exemplary experiments.
 670

Mechanism	Hypothesis	Experiment	Prediction	Practical aspects
1) Resource dynamics	Resource matching	Macronutrient addition	Increase in current growth <i>and</i> reproduction	- fully-crossed addition of different macronutrients - monitoring of all seed developmental phases
	Resource switching		Disproportionate increase in current reproduction compared to growth, or vice-versa	- cohorts of plants need to be observed over multiple years due to potential poor weather conditions preventing immediate investment of added resources into seeds
	Resource storage		Increase in seed production only in subsequent years	- environmental control can be in greenhouse and with grafts for larger species such as trees - isotopic labeling can track added nutrients
	Resource storage	Prevent seed development	Increase in seed production in subsequent years	As above, but excluding the addition of macronutrients
2) Pollen limitation	Pollen coupling	Pollen addition	Effect size of pollen addition is negatively correlated with density of conspecific flowers	- pollen addition across populations differing in flowering density or across individuals differently synchronized within the population - requires crossing pollen
	Phenological synchrony		Pollen addition results in larger fruit set in less synchronized individuals, with effect size increasing as	addition with resource monitoring or supplementation as fruit set can be limited by both pollen and available resources

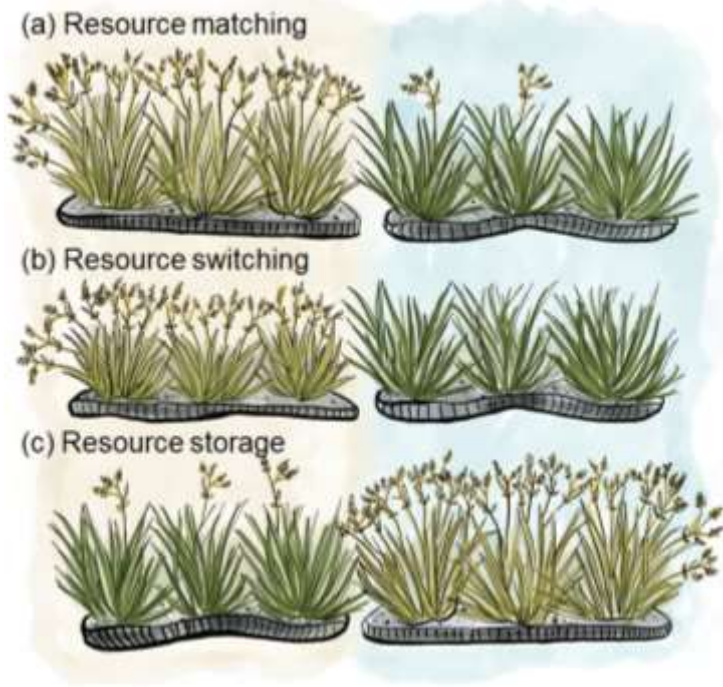
			density of conspecific flowers declines	
	Microclimatic hypothesis (hypothetical driver of annual variation in phenological synchrony)	Manipulating among-plant variability in micro-climate conditions	Larger interindividual heterogeneity in microclimate conditions desynchronizes flowering	- applying different levels of shading or warming throughout the population
	Photoperiod sensitivity hypothesis (hypothetical driver of annual variation in phenological synchrony)	Simulating early and late Springs	Short daylength and high temperatures desynchronize flowering	- simulating early (short days, high temperatures) and late (long days, high temperatures) spring in greenhouse conditions - can use grafts for larger plants
	Aerial diffusion	Manipulating air temperature	Warm air temperature (and low humidity) enhances air pollen concentration	- simulating warm spring temperatures in a random subset of plants
3) Hormones and genes	Weather cueing	Manipulating weather variability	Weather cue results in larger hormone secretion / gene expression and flower / seed production	- manipulation of pre-identified weather signal - requires factorial crossing with resource addition as plant responsiveness to the cue may depend on internal resource state

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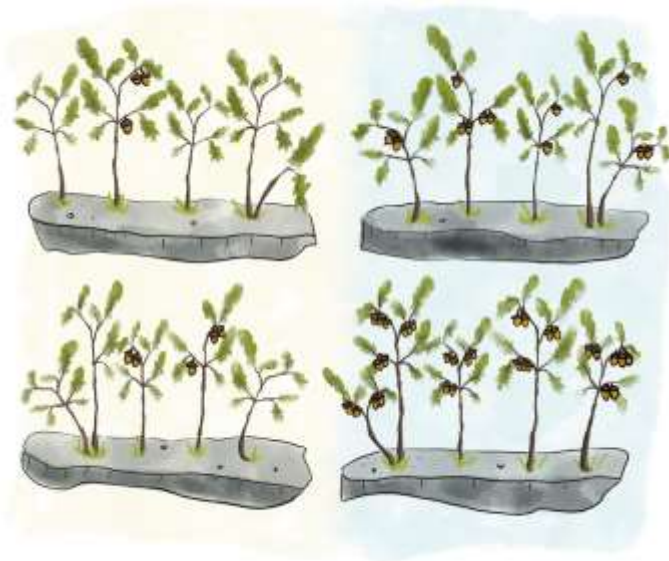
672



673
674 Figure 1. Main processes responsible for driving mast seeding: resource dynamics (I),
675 pollination (II), hormonal and genetic expression (III), all of which are influenced by
676 environmental variation. To produce a mast crop, plants in a population need to initiate many
677 flowers, these flowers need to be pollinated at a high rate, and fertilised flowers need to mature
678 into seeds. The mechanisms responsible for masting determine the success of transition from
679 one seed developmental phase to another and thus population-wide synchrony.
680



681
 682 Figure 2. Graphical representation of resource matching, switching, and storage hypotheses.
 683 Left-hand panel shows plants in environmentally-favourable years, whereas right-
 684 hand panel shows plants in the following and less-favourable years. Resource
 685 matching (a) predicts that environmentally-favorable years should result in both higher growth
 686 and reproduction.



687
688 Figure 3. Graphical representation of pollen coupling and phenological synchrony hypotheses.
689 Left-hand panel shows plants in low-flowering density and environmentally-favourable years,
690 whereas right-hand panel shows plants in high-flowering density but less environmentally-
691 favourable years. Top panels show control plants, while plants in bottom panel receive pollen-
692 addition treatments. Under the pollen-coupling hypothesis, the low density of flowering (left
693 panel) results in pollen limitation. Under the phenological synchrony hypothesis pollen limitation
694 may also happen in years when flowering density is high (right panel) but the within-year
695 synchrony of flowering is low.
696
697



698
699 Figure 4. Graphical representation of weather cueing hypothesis. Left-hand panel shows plants
700 in environmentally-favourable years, whereas right-hand panel shows plants in the following and
701 less-favourable years. Top panel shows control plants, while bottom panel shows plants
702 supplemented with flowering hormones.
703