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Review

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Mechanisms of mast seeding: resources, weather, cues, and selection

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Contents

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Summary

Mast seeding is a widespread and widely studied phenomenon. However, the physiological mechanisms that mediate masting events and link them to weather and plant resources are still debated. Here, we explore how masting is affected by plant resource budgets, fruit maturation success, and hormonal coordination of cues including weather and resources. There is little empirical support for the commonly stated hypothesis that plants store carbohydrates over several years to expend in a high-seed year. Plants can switch carbohydrates away from growth in high-seed years, and seed crops are more probably limited by nitrogen or phosphorus. Resources are clearly involved in the proximate mechanisms driving masting, but resource budget (RB) models cannot create masting in the absence of selection because some underlying selective benefit is required to set the level of a 'full' seed crop at greater than the annual resource increment. Economies of scale (EOSs) provide the ultimate factor selecting for masting, but EOSs probably always interact with resources, which modify the relationship between weather cues and reproduction. Thus, RB and EOS models are not alternative explanations for masting – both are required. Experiments manipulating processes that affect mast seeding will help clarify the physiological mechanisms that underlie mast seeding.

I. Introduction

Mast seeding, also known as masting, mass flowering, masting behaviour or mast fruiting, is synchronous and highly variable seed production among years by a population of perennial plants (Ims, 1990; Kelly, 1994; Kelly *et al.*, 2008). Masting is widespread in long-lived species throughout the plant kingdom, particularly in woody and wind-pollinated species (Herrera *et al.*, 1998), and has profound consequences for animal populations that depend, either directly or indirectly, on mast seed or fruit crops. These include populations of ground-nesting birds (McShea, 2000; Schmidt & Ostfeld, 2003; Schmidt *et al.*, 2008), insect herbivores (Elkinton *et al.*, 1996), and Lyme-disease-carrying ticks (Jones *et al.*, 1998), all of which fluctuate in conjunction with the abundance of seeds or fruits in their environments. These and other results involving interactions between animal populations and variable seed production provide support for adaptive, functional explanations of masting such as predator satiation (Janzen, 1971; Silvertown, 1980) and enhanced dispersal (Jansen *et al.*, 2004; Fletcher *et al.*, 2010). However, the role that resources play in modifying, or driving, the mechanisms of mast seeding remains complex. A recent review focused primarily on the role of resources in proximate (mechanistic) causes of masting (Crone & Rapp, 2014); here we update and broaden that review to consider other proposed models for mast seeding.

Numerous studies have suggested that masting relies on a combination of weather cues and internal plant resource dynamics (Sork *et al.*, 1993; Kelly & Sork, 2002; Rees *et al.*, 2002). Both weather and resources may affect seed production at three stages: flower production, pollination success, and seed maturation (Fig. 1). The main physiological processes that can account for these mechanistic links are resource dynamics, pollination, and hormonal regulation. Understanding these mechanisms has proved complex, but is important for several reasons.

First, in order to predict how masting may be affected by climate change, we need to understand how weather operates to determine seed set (Crone & Rapp, 2014). Second, we need to know the mechanisms driving masting in order to manipulate the pattern of seed set of plants where desirable, such as in 'masting' nut crops (Rosenstock *et al.*, 2011; Smith & Samach, 2013) or where a seed crop is critical to the survival of a species, such as the breeding of the threatened kakapo parrot *Strigops habroptilus* (Harper *et al.*, 2006). Third, in order to understand the evolution of masting, it is important to know whether masting is an emergent ecological phenomenon that requires little specialized physiology, or whether it relies on a selectively favoured mechanistic apparatus. Mast seeding imposes inescapable costs on plants, principally that of delayed reproduction (Ims, 1990). Therefore, plants should only exhibit mast seeding when either there is some compensating ecological benefit (Norton & Kelly, 1988) or external constraints limit the number of years in which plants are physically able to make large seed crops.

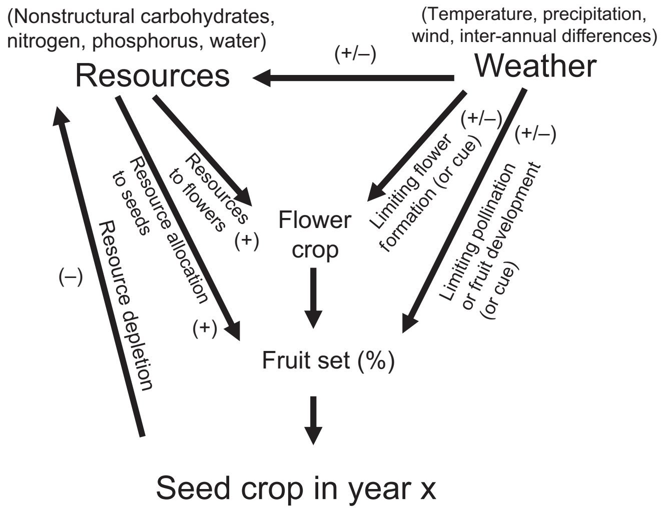

Fig. 1 A conceptual diagram linking weather and internal plant resources to masting via flower induction, pollination, and fruit maturation.

Masting is about variability among years, and thus is concerned with variance in seed production, not its long-term mean. Resources will have a large effect on the long-term mean investment in reproduction, in conjunction with life-history strategies that determine the fraction of available resources devoted to reproduction (the 'reproductive allocation'). Here, however, we focus on ways in which resources and other factors affect variability in flower or seed crops across years.

Our primary goal is to clarify hypotheses for masting, taking care to separate proximate factors (resource constraints and weather cues) from ultimate factors (evolutionary benefits). The impacts of resources on proximate factors were recently reviewed (Crone & Rapp, 2014) but ultimate and proximate factors interact, so that understanding masting requires both to be considered. We then review the mechanistic links between weather, resources, and seed set in masting species, focusing on ways that our knowledge of these links can be improved. We divide mechanisms into those involving plant resources, pollination, and the perception of cues by plants, and summarize evidence for these mechanisms from both natural and managed plant populations. We conclude with a discussion of evolutionary perspectives of the mechanisms of masting and how the two avenues for examining masting behaviour used by a majority of current studies – the 'resource budget' and 'economy of scale' (EOS) models – provide complementary approaches for understanding this important phenomenon.

II. Ultimate and proximate hypotheses for masting behaviour

The broad categories of hypotheses for masting behaviour are summarized in Table 1. There is considerable confusion in the literature concerning these hypotheses, at least partly as a consequence of mixing ultimate and proximate levels of analysis (Sherman, 1998). Those at the ultimate level of explanation are concerned with the functional, adaptive advantages of masting. These ultimate-level explanations of masting describe the selection pressures that have shaped proximate-level mechanisms allowing masting to occur.

By contrast, proximate-level hypotheses focus on the mechanisms producing masting behaviour, which do not necessarily require ultimate-level benefits. Some factors, such as pollination and environmental prediction via fire, can play a role at both the ultimate and proximate levels, further complicating the situation. In this section, we outline ultimate-level and proximate-level models and review how resources are expected to affect them.

1. Ultimate-level hypotheses

The hypothesized ultimate-level (adaptive) benefits of masting all involve some EOS. The key feature of EOS models is that

Table 1 Levels of analysis and direct effects of hypotheses for mast seeding

Level of analysis	Ultimate	Proximate	
Hypothesis	Provides economy of scale?	Increases synchrony?	Increases individual variability CV_i?
Predator satiation	Yes	No	No
Pollination efficiency	Yes	Yes	No[a]
Environmental prediction	Yes	Yes	Yes
Weather cues	No	Yes	Yes[b]
Resource budget model	No	No	Yes

Proximate effects listed are only those unavoidably created directly by the hypothesis; effects caused by an indirect mechanism under selection from the hypothesis are not included.

[a] Pollination efficiency could increase individual variability (CV_i) if it causes seed crops to fail in some years.

[b] Size of CV_i resulting from weather cues depends on which cue and the degree of plant sensitivity to it (Kelly *et al.*, 2013).

individual plants that produce most of their flowers or seeds in years when other plants are also flowering or seeding heavily have lower costs per surviving offspring (Norton & Kelly, 1988; Kelly, 1994) and so are selectively favoured. EOSs require both high individual variability (CV_i) and high among-individual synchrony (S) to produce benefits (Koenig *et al.*, 2003), but the EOS itself may not produce these directly (Table 1).

Although a wide range of possible EOSs have been suggested, three have found the most empirical support (Table 2a). The first and most commonly invoked is predator satiation, which occurs when seed predators consume a lower proportion of larger seed crops (Janzen, 1971). In a related variant, dispersal efficiency creates an EOS when seed dispersers are attracted to a large fruit crop and thereby increase dispersal-related fitness benefits. This is most likely in scatter-hoarding species that form large numbers of small hoards and are thus not limited by storage sites (Vander Wall, 2010). As the disperser is also a major consumer of seeds, dispersal is successful largely to the extent that predator satiation prevents the scatter-hoarder from consuming all the seeds (Jansen *et al.*, 2004).

The second is pollination efficiency, whereby the per cent seed set is higher in high-flowering years, an EOS observed most commonly in self-incompatible, wind-pollinated species (Kelly *et al.*, 2001). The third is the environmental prediction hypothesis, found primarily in fire-prone landscapes where plants that make large seed crops immediately after fire have higher seedling survival. This is most often seen in herbaceous plants, because woody plants can more efficiently exploit post-fire regeneration opportunities by releasing seeds from serotinous fire-protected woody fruits (Kelly, 1994).

2. Proximate-level hypotheses

Proximate hypotheses (Table 2b) vary both in terms of whether they are adaptive or not and in the strength of their links to plant resources, as discussed in the next section. With respect to selection, several of the proximate hypotheses, such as Moran effects (Koenig, 2002) on pollination or resources, can be viewed as environmental constraints with which plants have to cope. To the extent that this is the case, such environmental factors serve as a 'veto' on reproduction (Fig. 2d), and are not necessarily adaptive; that is, there is no inherent cost of delayed reproduction, because the plants make seeds in every year in which conditions make it possible to do so.

In contrast, some weather cues may have large effects on flowering because selection has favoured plants that all respond to the cue in the same way, resulting in high synchrony and individual variability (Kelly *et al.*, 2013). In this case, weather provides information that the plant perceives and uses to coordinate its seed crop rather than as a physical process directly impeding the process of seed production. The level of variability (the plant's CV_i) depends on what the weather cue is, how much it varies, and the biological sensitivity of the plant to that physical variation.

Note that pollination can be important both at a proximate level (pollination Moran effects driven, for example, by geographically synchronous weather washing pollen out of the air column) and at the ultimate level as an EOS (pollination efficiency/pollen coupling driven by density-dependent pollination success) (Table 2). Environmental prediction via fire is also important at both proximate and ultimate levels, but this EOS is not commonly observed so is less likely to cause confusion. In any case, it is not always possible to target a factor as playing a role solely in the ultimate or proximate spheres.

III. The role of plant resources in masting

1. Clarifying the potential role of resources

There are at least four different mechanisms of seed production in which resources play a role. Illustrated graphically in Fig. 2, these are: (a) 'resource matching', in which a constant fraction of a variable annual resource increment is devoted to seeding; (b) 'switching', in which a variable fraction of a relatively constant annual increment is devoted to reproduction; (c) 'storage', in which resources are stored up over several years and then expended in a high-seed year; and (d) 'veto', in which a variable fraction of a relatively constant annual resource increment is kept from being devoted to reproduction by some mechanism (the veto) that limits investment in seed production. With these alternatives in mind, four implicit assumptions about resource use often made in the literature are worth discussing in detail.

First, resources are clearly required to make seeds, which contain carbohydrates, nitrogen (N) and phosphorus (P). However, this does not mean that resources are necessarily limiting to seed set, even in a high-seed year. The amount of resources devoted to seeding is an evolutionary tradeoff against how much is required for other processes, including maintenance, growth, and defence (Fig. 2b), as well as how much is stored in a particular year (Fig. 2c). The effect of resources on masting patterns is more complicated than simply demonstrating that large seed crops require a substantial input of resources.

Second, the intuitively appealing idea that plants must 'save up' resources over several years to then expend in a high-seed year (Fig. 2c) is not the only means by which a mast event could occur. High-seed events could also result from resource matching (Fig. 2a) or from 'switching' (Fig. 2b), both of which are based on

Table 2 Detailed effects of factors affecting mast seeding at ultimate and proximate levels, including whether each hypothesis requires the two essential components of mast seeding, high individual plant variability (CV_i) and synchrony among plants (S)

(a) Ultimate (evolutionary) level of explanation

Type	Hypothesis	Comments
Adaptive hypotheses (economies of scale): *individuals that produce more flowers or seeds in years when other plants are also flowering or seeding heavily have lower costs per surviving offspring*	Predator satiation	Seed predators consume a lower proportion of larger seed crops. Includes *dispersal efficiency*: seed dispersers successfully disperse a larger proportion of a large seed crop, usually by satiation of scatter-hoarding seed predators. Has no direct effect on CV_i or S
	Pollination efficiency (pollen coupling)	Higher cross-pollination in high-flowering years. Particularly relevant in self-incompatible wind-pollinated species and when pollination efficiency at mean flowering effort is low. Increases S
	Environmental prediction	In fire-prone landscapes, plants that seed immediately after fire into the low-competition, high-nutrient seed bed have more surviving offspring. Produces high CV_i and high S

(b) Proximate (mechanistic) level of explanation

Type	Hypothesis	Comments
Environmental constraints: *external factors or plant resources limit seed set in some years but not others, resulting in variable seed set*	Resource matching	Inter-annual variation in some limiting resource determines observed variation in seed set as a side effect of environmental variability. CV_i varies directly with level of environmental variation. Synchrony is not required, but may result from spatial consistency of weather (a *resource-accumulation Moran effect***)**. Supported by finding a positive correlation between growth and reproduction within individuals among years. Opposed by finding greater variation in seed set than in the environment, which implies selection for higher CV_i
	Resource budget	Plants produce a high-flower crop only once resources accumulate above a threshold, and are then expended on setting seed. Produces high CV_i, but needs an additional factor for synchrony, typically *pollination efficiency*
	Pollination failure (pollination Moran effect)	Spatially synchronous inter-annual environmental variation in factors that cause pollination failure (independent of flower crop size) drives variation in seed set. Produces synchrony; may increase CV_i depending on extent and frequency of failure
	Pollination efficiency (pollen coupling)	Low pollination efficiency at times of low population-level flowering (density-dependent) synchronizes seeding events among individuals. Increases synchrony. May increase CV_i if pollination fails in some years
Weather cues: *conspecifics all respond to the same shared environmental cues as signals for high flower production*	Weather cues	Seeding varies in response to some weather cue, which increases S. CV_i depends on frequency of the cue that is used and sensitivity of the plant to it. Selection for the use of a particular cue must arise from an EOS favouring increased CV_i and synchrony. An example is *differential temperature* (ΔT), where a large difference in temperature between consecutive years is a cue for high seed set

current-season resource allocation. How and when resources are acquired to support large seed crops is a key empirical question.

Importantly, if resources are stored by plants, it may be through an active (selected) strategy (Fig. 2c) or more passively, as in cases of an environmental veto (Fig. 2d). In the latter case, the plant allocation to fruit ripening in some years is unable to be spent, for example because pollination failure restricts the number of fruits that can be ripened. Such unspent resources could be carried forward, until a year of high pollination success combined with a large resource pool allows a large fruit crop to be ripened. The pattern of seed set in *Quercus lobata* in California is consistent with such a scenario (Koenig *et al.*, 2015; Pesendorfer *et al.*, 2016), as is seed set in *Astragalus scaphoides*, a North American forb (Crone *et al.*, 2005; Crone & Lesica, 2006).

Third, variation in seed crops over years does not necessarily indicate the existence of underlying cyclic behaviour driven by resource production and use. If plants have large seed crops every second or third year, the resulting pattern could easily be interpreted as a semi-regular 2-yr or 3-yr resource-driven 'cycle'. However, the alternative null hypothesis is that high-seed crops are driven by the stochastic occurrence of external cues and/or variation in resource accumulation. Indeed, cyclicity may even be produced by weather cues *per se*, as suggested by El Niño-driven seed production in southeast Asian Dipterocarps (Ashton *et al.*, 1988).

Fourth, mast-seeding plants often exhibit lagged autocorrelation; that is, a tendency for low-seed years to follow high-seed years and vice versa (Sork *et al.*, 1993; Koenig *et al.*, 1994). Together with weather correlates, lagged autocorrelations sometimes explain a high proportion of the variance in the seed set of masting species (Rees *et al.*, 2002; Kelly *et al.*, 2013; Pearse *et al.*, 2014). This can be interpreted as: (1) a consequence of internal resource depletion making heavy reproduction impossible the year after a large seed crop; (2) an indication that the plants are following a weather cue which alternates up and down by chance or which by definition cannot remain high for several years in a row (e.g. the 'differential temperature' model of Kelly *et al.* (2013), discussed in the next section); or (3) tautological, given that variation across years necessarily results in the rare high years often being followed by low

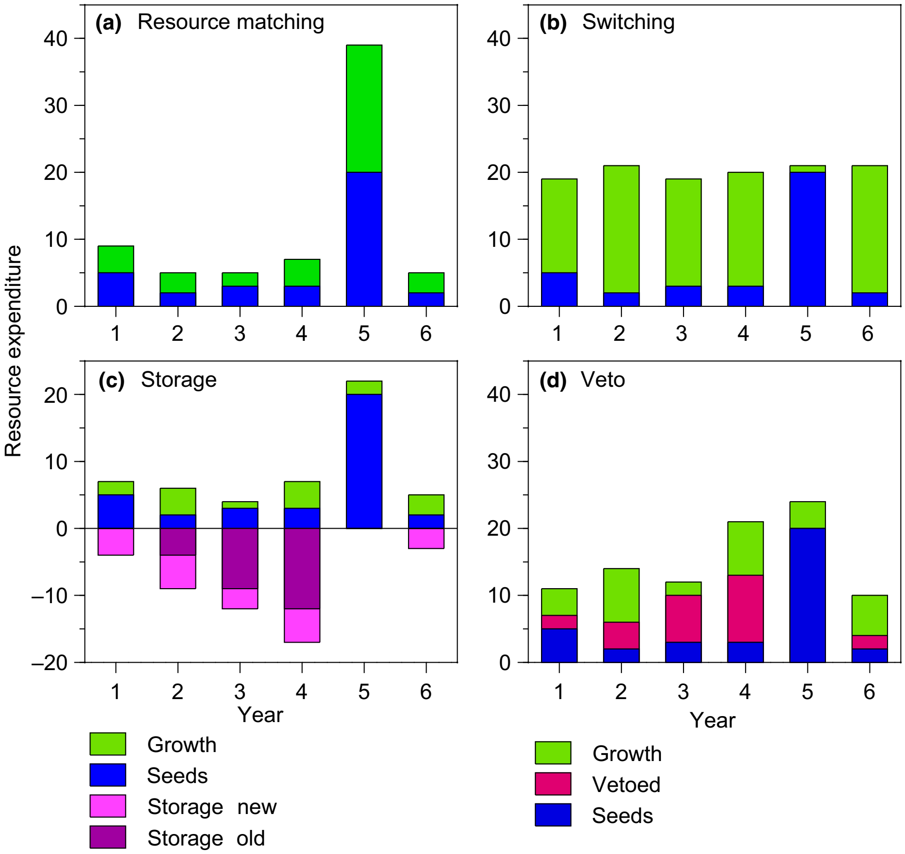

Fig. 2 Hypothetical ways that resources (in arbitrary units) can be devoted to mast seeding. The seed crop series (blue) is identical in all panels, with a moderate level of inter-year population variability (CV_p) of 1.20. (a) Resource matching: a constant fraction (here about half) of a variable annual resource increment is devoted to seeding; the rest is devoted to growth and maintenance. Note that resource accumulation has to have a similar among-years CV to seedfall, as a constant fraction is devoted to reproduction. (b) Switching: a variable fraction of a relatively constant annual increment is devoted to reproduction; the size of the seed crop in any year is determined by the proportion 'switched' towards reproduction. (c) Storage: resources are actively stored up over several years (shown below the line, both carried forward (dark pink) and newly added to storage (pale pink)) then expended in a high-seed year. (d) Veto: the plant allocates resources to reproduction, but in some years a veto cue such as pollination failure reducing seed set limits investment in seeds. The resources that cannot be turned into seeds (maroon) are added to the following year's reproductive allocation. A large seed crop occurs when a large accumulated resource pool coincides with a small veto, but each year the plant is setting the maximum possible number of seeds. In (a) and (b) the large seed crop is created with current-season resources, in (c) mainly with actively stored resources, and in (d) mainly with passively stored resources.

years and vice versa. The first explanation implies that resources control masting, whereas the others are largely or wholly independent of resource levels. Thus, the existence of lagged autocorrelations is not decisive in determining how resources influence the dynamics of mast seeding.

2. Resources and weather

Weather is centrally involved in masting, as indicated by the strong correlations between weather and masting found in most species. Any potential effects of resources vary with the selective factors determining CV_i and S. Of the three main EOSs, environmental prediction via fire automatically produces high CV_i and high S as a result of fire frequency, pollination efficiency produces high S but has limited effects on CV_i, and predator satiation does not directly affect either CV_i or S (Table 1). Where an EOS does not directly produce high S and CV_i, it must select for the plant to respond to a weather cue as a proximate driver in order for masting to occur (Table 2). The details of the cue, and exactly how sensitive the plants are to variation in the cue, determine the resulting levels of CV_i and S (Kelly *et al.*, 2013).

There is no *a priori* requirement for the weather cues that increase S and CV_i to be correlated with good growing conditions and higher resource acquisition rates. The only absolute requirement is that the cue be spatially synchronous over wide areas so all plants can respond similarly (Norton & Kelly, 1988), a criterion met by both temperature and to a lesser extent rainfall (Koenig, 2002). Consistent with this, masting can be triggered by factors that reduce plant resources such as fire (Kelly, 1994) and drought (Wright *et al.*, 1999), by factors that affect resources very little such as brief cool spells (Ashton *et al.*, 1988), or by factors apparently unrelated to resources (Tapper, 1996). In the latter case, the problem of how the plants translate their sensitivity to the cue into a seed crop of a particular size – that is, the physiological mechanism linking weather to seed production without affecting resources in some way – is difficult to envision (Pearse *et al.*, 2014). However, the ideal weather cue minimizes the cost of storage by correlating with increased resources (Norton & Kelly, 1988; Kelly *et al.*, 2013), and thus, in practice, observed weather cues are likely to positively affect resource acquisition in some way.

The most likely role of resources under a weather cue model is to act as a veto on large seed crops occurring consecutively. There are, however, at least two caveats to this scenario. First, if masting is created by switching (Fig. 2b), then resources *per se* are not necessarily limiting and plants could seed heavily in consecutive years by repeatedly diverting resources from growth and maintenance. Second, masting plants might rarely show resource vetos because they may be synchronized by weather cues which rarely trigger masting in consecutive years. This is the case for the differential temperature (ΔT) model proposed by Kelly *et al.* (2013) that involves the difference in temperature between two consecutive years, and thus by definition cannot be very high two years in a row.

A second way in which resources may play a role when weather cues are driving masting is by influencing the sensitivity of plants to the cues (Fig. 3). Evidence for this comes from experimental work demonstrating an effect of fertilizer addition on the slope of the relationship between weather and seed production in *Nothofagus solandri* (Fig. 3a; Smaill *et al.*, 2011), and an apparent effect of resource addition on the intercept of the relationship between weather and seed production in *Chionochloa pallens* (Fig. 3b; Hay *et al.*, 2008; D. Kelly *et al.*, unpublished data). In both cases, however, the increases with resource addition were small relative to weather-driven variation among years (in *C. pallens*, *c.* 10-fold and > 1000-fold, respectively).

3. Resource matching: a hypothesis for masting with little support

The literature on resource matching provides a good example of the potential confusion that can arise from mixing levels of analysis. As originally described by Büsgen & Münch (1929), the resource matching hypothesis proposed that high-seed years occur when more resources are available. It is thus tempting to take *any* relationship between resources and masting as support for the resource matching hypothesis, but to do so is confusing correlation with causation. A relationship between resources and seed crop size is expected no matter what drives masting, and thus demonstrating that resources correlate with seed production has no discriminatory power.

A more explicit version of the resource matching hypothesis is that the fraction of resources devoted to reproduction is constant, in which case variation in seed crops tracks variation in resource accumulation from year to year (Kelly & Sork, 2002; Fig. 2a). This is the nonadaptive, null hypothesis for mast seeding, as no EOS is implied to be selecting for the observed variability in annual seed production.

Resource matching would be supported by a positive correlation between growth and reproduction within individuals among years, but this has almost never been shown (Kelly & Sork, 2002). Instead, negative correlations are more common (Monks & Kelly, 2006; Barringer *et al.*, 2013), contrary to the predictions of resource matching. Also, resource matching has been shown to be unlikely in many systems as a consequence of greater variation in seed set than in the environment, a finding that implies selection for enhanced inter-annual variability (Koenig & Knops, 2000).

4. Resource budget models: stored resources and thresholds for seed set

A second hypothesis that depends on resources is the resource budget (RB) model (Table 2b), which proposes that resource allocation within a plant drives CV_i (Isagi *et al.*, 1997; Rees *et al.*, 2002). This model has been thoroughly and recently reviewed by Crone & Rapp (2014); here we briefly summarize the more cogent points, and discuss several assumptions. Mechanistically, the RB model suggests that a plant cannot accumulate the necessary resources to produce a 'full' seed crop in any given year, and therefore has to draw on resources that have accumulated over multiple years. In those years when the resource budget has not reached the threshold necessary for a full crop, the plant does not invest, or invests very little, in reproduction.

The RB model depends on a number of assumptions. First and most fundamental is that plants cannot just produce a smaller annual seed crop equal to the level of annual resource acquisition. The RB model therefore implicitly requires that some other factor, such as pollination efficiency (Kelly *et al.*, 2001) or high accessory costs of reproduction (Kelly, 1994), sets the size of a full crop at a

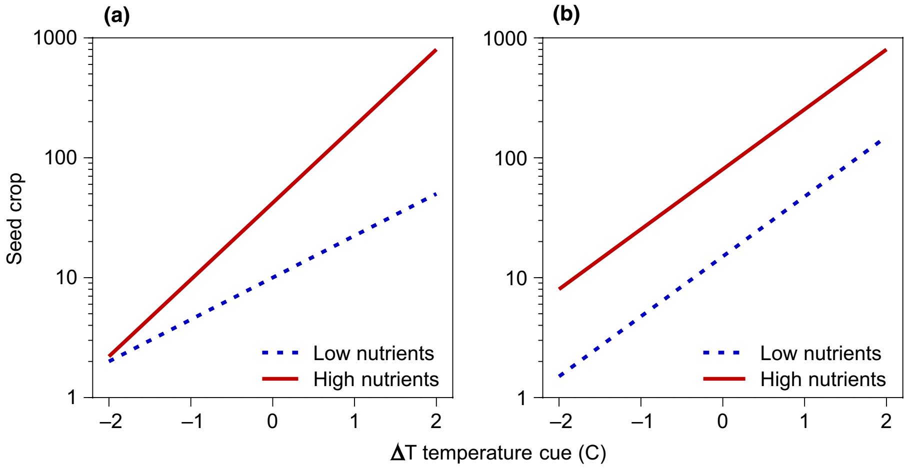

Fig. 3 Hypothesized ways that individual plant resources (e.g. nutrient concentrations) can modify the relationship between weather cue (in this example the temperature (ΔT) cue) and flowering (arbitrary units). (a) Plants with higher nutrients have a steeper slope to the relationship, indicating higher sensitivity to the weather cue (higher mean flowering and higher CV_i). (b) Plants with higher nutrients have a higher intercept (higher mean but same CV_i). In both cases, synchrony is maintained with the rest of the population but higher-nutrient plants produce more flowers for a given temperature cue.

higher level than the plant can continuously sustain. Alternatively, the full crop may be selected to be larger than the annual mean by predator satiation so that fruiting becomes intermittent (Janzen, 1974). As pollination efficiency, high accessory costs, and predator satiation are all EOSs (Table 2), RB dynamics are unlikely to evolve without a selective advantage of masting.

Second, the RB model requires resource storage (Isagi *et al.*, 1997; Fig. 2c), and thus the model is potentially falsified by finding that mast seed crops are generated using current-season resources (Ichie *et al.*, 2013). A modified RB model which assumes switching (Fig. 2b) rather than storage (Fig. 2c), however, would probably behave in a dynamically similar way, so it is possible that this caveat can be overcome by an appropriate modification of the original hypothesis.

Third, internal resource dynamics can produce a high CV_i but cannot create high *S* among individuals, as each individual plant could produce high- and low-seed crops on its own schedule (Satake & Iwasa, 2000). Instead, synchronization has to come from other factors such as pollination efficiency (often referred to as pollen coupling in RB models) or environmental drivers (which exhibit high spatial synchrony as a result of the Moran effect; Koenig, 2002), with the former more commonly invoked (Satake & Iwasa, 2000; Venner *et al.*, 2016).

The combination of such synchronizing factors with RB models (Table 2b) can produce population-wide patterns of masting similar to those observed in nature (Satake & Iwasa, 2000, 2002b; Pesendorfer *et al.*, 2016), especially when pollination efficiency follows a logistic response (Venner *et al.*, 2016). However, although the population-wide pattern produced by these models is realistic, the plant-level pattern usually is not, because it assumes that individual plants do not reproduce in years when their resources fail to exceed some threshold. As a result, most plants in most years should have zero reproduction, which is not generally the case (Monks & Kelly, 2006, Kelly *et al.*, 2013), although it has been found in *Chionochloa pallens* (Rees *et al.*, 2002).

RB models have been well explored theoretically, and the necessary mechanisms (resource depletion and pollen coupling) are common in plants. However, in very few species has the model been fully tested empirically, so the extent to which the RB model applies to real-world examples of masting is still uncertain (Crone & Rapp, 2014). Recent work, however, has begun to provide more concrete evidence for the role of resource limitation and the RB model in some systems (Sala *et al.*, 2012; Rapp *et al.*, 2013; Funk *et al.*, 2016; Pesendorfer *et al.*, 2016).

IV. Which resources limit seed set?

For a resource to drive masting behaviour according to the RB model, it must be utilized and depleted during seed production, initially stored and used in years subsequent to its acquisition, and translocated from the tissues where it is accumulated to shoots that set seed (Isagi *et al.*, 1997; Hoch, 2005; Ichie & Nakagawa, 2013). It is currently unclear what resources fulfill these conditions and affect masting behaviour. It is also unclear where critical resources are stored and for how long. Finally, resource limitation in low-seed years could inhibit any or all stages of flower and seed development, and we know little about which stage or stages are most affected by such factors or how they differ among taxa.

1. What is stored?

Three general types of resources are potentially important to masting behaviour: carbon (C), nutrients, and water.

Carbon Nonstructural carbohydrates (NSCs), which represent C limitation, are the best studied class of resource compounds implicated in masting dynamics (Miyazaki, 2013). Our literature review revealed three cases of NSCs being depleted following masting and no examples lacking NSC depletion following a mast event (Table 3). There is, however, mixed support for transport of NSCs in different systems. In the temperate tree *Styrax obassia*, ^{13}C was transported from neighbouring tissue to reproductive shoots, but only when the neighbouring shoots were not reproductive themselves (Miyazaki *et al.*, 2007). By contrast, girdling experiments that limit the import of NSCs from neighbouring tissues have indicated that a series of masting tree species produce an equivalent seed set with or without the ability to translocate NSCs (Hoch, 2005; Hoch & Keel, 2006). For example, in the Dipterocarp tree *Dryobalanops aromatica*, girdling experiments found that fruit set was maintained via local photosynthate, but flowering was strongly affected by phloem disruption, suggesting that transport, possibly of hormones rather than resources, is an important component of flowering but not fruit maturation (Ichie *et al.*, 2005).

Surprisingly, there is little evidence in masting species for NSCs being stored for multiple years for use in flower, fruit, or seed production (Table 3). By observing the fate of pulsed C isotopes in trees, two studies have estimated the turnover rate of stored carbohydrates to be less than or equivalent to the length of a single season in 13 temperate tree species (Hoch *et al.*, 2013; Ichie & Nakagawa, 2013). Moreover, the retention time of stored carbohydrates was not related to variation among species in variability of seed crops.

NSCs are presumably a common currency of C stores in cases where the C is not currently invested in photosynthetic structures which pay a return on their investment, for example in deciduous plants over winter. For plants actively fixing C, however, NSC storage may not account for the effect of initial C investment on the overall C budget. For example, by investing NSCs in leaves as opposed to storage, plants may gain ‘interest’ on their initial C allocation investment. Whenever excess C is devoted to interest-generating leaves rather than non-interest-generating (and more predation-prone) carbohydrate storage, it would imply that masting follows a switching model (Fig. 2b) rather than a storage model (Fig. 2c), at least for C.

Nutrients N, P and potassium (K), are transported plant-wide, being acquired through the roots but used in above-ground tissues. In contrast to C (Körner, 2003; Wiley & Helliker, 2012), there is strong evidence for nutrient limitation in the growth and reproduction of plants. We found two studies suggesting that N pools are depleted after a high-seed year and two studies that observed a depletion of P after a high-seed year (Table 3).

Table 3 Summary of studies presenting support and nonsupport for the role of specific resources in masting

	Depleted after fruiting	Translocated from nonreproductive tissue		Stored over multiple years
Resource	Yes	Yes	No	No
Nonstructural carbohydrates	Crone *et al.* (2009) Marquis *et al.* (1997) Miyazaki *et al.* (2002)	Miyazaki *et al.* (2007)	Hasegawa *et al.* (2003) Hoch & Keel (2006) Hoch (2005)	Hoch *et al.* (2013) Ichie *et al.* (2013)
Nitrogen	Sala *et al.* (2011) Han *et al.* (2008) Ichie & Nakagawa (2013)	Sala *et al.* (2011)	Ichie & Nakagawa (2013)	
Phosphorus	Sala *et al.* (2011) Ichie & Nakagawa (2013)	Sala *et al.* (2011) Ichie & Nakagawa (2013)		

In whitebark pine (*Pinus albicaulis*), concentrations of N and P were initially depleted in tissues near seeds in a high-seed year but were depleted throughout the entire tree over time, suggesting translocation of these nutrients from nonreproductive to reproductive tissues (Sala *et al.*, 2012). In *Dryobalanops aromatica*, N and K concentrations were not depleted, although over half of the total stored P was used during the masting event (Ichie & Nakagawa, 2013). In *Fagus crenata*, N addition increased the expression of genes involved in floral transition, and high concentrations of N correlated with high flower set in the following year (Miyazaki *et al.*, 2014). As noted earlier (see section III, subsection 2, 'Resources and weather'), nutrient addition increased seeding in *Nothofagus solandri* and *Chionochloa pallens*. We know of no studies that have determined the residence time of stored nutrients consumed in a mast event.

Water The rapid dynamics of water usage in most plants and the spatial heterogeneity in water abundance, which reduces synchrony in the water status within a population, make it an unlikely candidate to drive the internal resource dynamics causing interannual variation in seed set. However, water limitation and drought stress very probably interact with the acquisition and storage of other resources.

In three oak species (genus *Quercus*), for example, there is a stronger negative correlation between past and current reproduction in drought-limited individuals (Barringer *et al.*, 2013), suggesting that water affects either the acquisition or storage potential of some limiting resource. Similarly, in a masting *Nothofagus* species, drought years correspond to lower foliar N and a concomitant decrease in seed production, suggesting that water limitation decreases N availability or mobilization which then affects seed production (Smaill *et al.*, 2011). Water availability is also a correlative link between seed set and environmental conditions in some systems (Koenig *et al.*, 1996; Crone & Lesica, 2006; Pérez-Ramos *et al.*, 2010; Smaill *et al.*, 2011), and water-reduction experiments indicate that drought increases early seed abortion in *Quercus ilex* (Pérez-Ramos *et al.*, 2010).

2. Where are resources stored, and for how long?

Mobile resources may be stored in various tissues, either passively (proportional to the overabundance of the resource at the time of acquisition) or actively (stored even when that resource could be used immediately for other purposes). There is considerable controversy as to whether C resources are actively or passively stored, a debate that revolves around the overall degree of C limitation (Körner, 2003; Wiley & Helliker, 2012).

Mobile C resources such as NSCs are located throughout masting plants (Bazot *et al.*, 2013), but those resources used for reproduction are often local to the reproducing shoot (Miyazaki *et al.*, 2002; Hoch, 2005) and are quickly turned over by other processes such as leaf-set (Hoch *et al.*, 2013; Ichie *et al.*, 2013). Because C-based resources have such a short residence time, it is unlikely that C limitation directly causes the tradeoff between current and future reproduction in most systems, except perhaps via more complex feedbacks through changes in leaf investment. In contrast, sugars and carbohydrates act as mobile signals throughout plants, where they can affect long-term resource allocation through interactions with the hormones abscisic acid and ethylene (Koch, 1996; Cheng *et al.*, 2002; Leon & Sheen, 2003). Thus, depleted carbohydrates or sugars could potentially affect seed set in subsequent years without themselves being stored during that period.

By contrast, N is transported by perennial plants throughout the season and is thought to be stored across seasons. N is initially taken up by roots and transported to above-ground tissue and, in deciduous plants, it is resorbed from senescent leaves and stored in stem and root tissues (Vogt *et al.*, 1996; Palacio *et al.*, 2007; Millard & Grelet, 2010). In sessile oak (*Quercus petraea*), a deciduous masting species, N is stored over winter as the amino acids arginine and asparagine in coarse roots and twigs (Bazot *et al.*, 2013).

P is stored in organic or inorganic forms, and similarly exhibits seasonal patterns of transport (Schachtman *et al.*, 1998). Similar to C resources, nutrient stores are sensed by plants, so nutrient abundance may have cascading effects on development via hormonal regulation (Rubio *et al.*, 2009).

3. General or species-specific patterns linking resources to masting?

If different masting species deplete and translocate different resources for reproduction, is there a common mechanism that links resource use to masting behaviour? There is currently evidence for either C or nutrient limitation in several systems (Miyazaki *et al.*, 2007; Crone *et al.*, 2009; Sala *et al.*, 2012; Ichie & Nakagawa, 2013). One potential link between nutrient limitation and C limitation is that each may be perceived by the plant and translated into hormonal signals (Leon & Sheen, 2003; Rubio *et al.*, 2009).

Progress in this field will be made by following the depletion, storage, and later use of resources. In particular, following the organ-specific allocation of N and P over high- and low-seed years or in individuals with experimentally reduced seed crops could bolster the emerging evidence for the general role of these resources in masting behaviour (Sala *et al.*, 2012; Ichie & Nakagawa, 2013). As masting, a population-wide phenomenon, is predicated on responses by whole organisms, experiments that reduce seed set and follow nutrients throughout entire plants rather than individual branches would be particularly valuable.

V. Pollination, fruit development, and masting

From the standpoint of efficiency, perennial plants should allocate resources only to flowers that will develop into seeds. To the extent that this is true, a limiting resource budget should reduce the number of flowers produced in the subsequent year. However, plants commonly produce flowers that do not mature into fruits, and this can occur because of either pollen limitation of flowers or flower abortion.

Pollination success (or, equivalently, avoiding pollen limitation) is both a potential selective benefit of masting and a proximate driver of variable seed crops (Table 2). This dual role of pollination as both a potential ultimate and proximate driver of masting can cause confusion, which we resolve here by detailing the developmental process from a flower to a seed. Pollination is an especially appealing factor potentially governing masting dynamics because it is a population-wide event that could drive inter-annual synchrony in seed set between individuals (Satake & Iwasa, 2000, 2002a). Theoretically, these population-wide dynamics could scale up to synchronize large geographical regions, although this has not been empirically demonstrated.

The production of a mast seed crop can be the product of either high flower success – that is, a high proportion of flowers maturing into seeds ('fruit maturation masting') – or high initial flower production ('flower masting') (Table 4). In cases of flower masting, pollination success may be a consequence of the abundance of pollen in high-flowering years. As such, pollination efficiency is a likely evolutionary advantage (EOS) of flower masting (Table 2). Typically in these cases the size of the flower crop will be determined by an environmental cue or internal resource, and flowers that are produced in high-flowering years will have high success at both pollination and maturation into fruit. By contrast, pollination failure as a result of factors unrelated to the size of the flower crop (such as inclement weather) is a potential driver of fruit set in cases of fruit maturation masting and may drive masting behaviour even in the absence of any selective advantage to doing so.

The effects of wind pollination, as opposed to animal pollination, have been explored primarily because the former is disproportionately common among masting species (Herrera *et al.*, 1998) and because wind pollination does not require an intermediate vector (the pollinator) whose populations may fluctuate independently of flower abundance or which may be satiated in years of large flower crops (Kelly & Sork, 2002). Nevertheless, animal pollination is important in many masting species, including Dipterocarps and *Astragalus scaphoides*, in which pollination has been implicated as an important component of masting. Also, to the extent that pollinators are insensitive to inter-annual variation in masting flower abundance (generalist pollinators which can rely on alternate floral resources in low-flowering years, or short-generation-time species which can increase during a mast event), the pollination efficiency hypothesis (Table 2) may be important in animal- as well as wind-pollinated systems.

1. Pollination Moran effects versus pollination efficiency

There are two important ways in which pollination success can affect population-wide masting patterns (Table 5). First, pollination success could be driven by external factors such as climatic conditions, a density-independent process we refer to as a *pollination Moran effect* (Table 2b). When a pollination Moran effect is in play, each individual in the population experiences a similar climate, and thus pollination success driven by particular weather patterns could create population- or even region-wide fluctuations in seed set as a result of the generally large spatial synchrony in weather patterns (Koenig & Knops, 1998, 2013; Koenig, 2002; Lyles *et al.*, 2009). This process is independent of any selection for variable seed crops.

Second, pollination success could be driven by a *pollination efficiency* (or *pollen coupling*) economy of scale, the dependence of fertilization success on pollen from other individuals, as is generally the case in primarily outcrossing species. In contrast to the pollination Moran effect, the pollination efficiency hypothesis

Table 4 Summary of studies presenting data on whether fewer flowers are produced or more are aborted in low-seeding years

Fewer flowers	Flowers aborted	Both fewer flowers and flowers aborted
Campbell (1981) (*Aciphylla aurea*; *Celmisia viscosa*)	Kelly *et al.* (2001) (*Nothofagus* (three spp.))	Pearse *et al.* (2015) (*Quercus lobata*)
Crone & Lesica (2006) (*Astragalus scaphoides*)	Montesinos *et al.* (2012) (*Juniperus thurifera*)	Pérez-Ramos *et al.* (2010) (*Quercus ilex*)
Kelly *et al.* (2013) (*Celmisia lyallii*; *Phormium* (two spp.))	Norton & Kelly (1988) (*Dacrydium cupressinum*)	Shibata *et al.* (2002) (*Carpinus japonica; Castanea crenata; Fagus crenata; Quercus crispula; Quercus serrata*)
Kelly *et al.* (2000) (*Chionochloa* (11 spp.))	Shibata *et al.* (2002) (*Fagus japonica; Ostrya japonica*)	Sork *et al.* (1993) (*Quercus alba*)
Kon *et al.* (2005) (*Fagus crenata*)		
Shibata *et al.* (2002) (*Carpinus* (three spp.))		

Table 5 Studies presenting data testing predictions of two hypotheses where pollination success mediates masting behaviour; studies present data supporting the predictions except for the cases indicated by '*NO*'

	Pollen coupling (pollination efficiency) hypothesis				
			Pollination Moran effect		
Pollination type	More pollen (or ♂ flower) production in high-seed years	Coupled investment in ♂ and ♀ flowers	Pollen limitation	Greater pollen limitation in low-seed years	Correlation between pollen availability and weather
Not animal pollinated	Montesinos *et al.* (2012) Mooney *et al.* (2011)	Montesinos *et al.* (2012) Mooney *et al.* (2011)	Koenig *et al.* (2012) Lazaro *et al.* (2006) Pearse *et al.* (2015) Rapp *et al.* (2013)		Koenig *et al.* (2015)
Animal pollinated	Crone *et al.* (2009)		Crone & Lesica (2006) *NO*: Brookes & Jesson (2007) *NO*: Pias and Guitian (2006) *NO*: Tamura & Hiura (1998)	Crone & Lesica (2006) *NO*: Pias & Guitian (2006)	

No studies have tested whether there is a high cost of ♂ reproduction, which is a prediction of pollen coupling.

assumes that fruit set is density dependent (Satake & Iwasa, 2000). Pollination efficiency predicts that, in low-seed years, most individuals do not have a large flower crop, while individuals that do flower will suffer low pollination success, as pollen is not readily available from other members of the population. As such, pollination efficiency can explain the high synchrony in seed set among individuals (Table 2). Indeed, in theoretical models of masting, pollination efficiency is necessary to synchronize masting behaviour in the absence of selection for weather cues (Satake & Iwasa, 2000, Satake & Iwasa, 2002b).

For pollination efficiency to be important, several assumptions must be met. First, there must be greater pollen production and availability in high-seed than in low-seed years. Therefore, for dioecious and monoecious plants where male and female flowers are produced independently, there must be a correlation between male and female investment in high-seed years (Norton & Kelly, 1988). Both the pollination Moran effect and pollination efficiency imply that, in years with low seed set, at least some individuals in a population are pollen limited. This is particularly true for the pollination Moran effect, in which pollen limitation, rather than resources, can be the sole driver of low seed set in some years (Table 2).

2. Evidence for pollen limitation in masting species

Given the central role of pollen limitation in both the pollination Moran effect and pollination efficiency, there are surprisingly few studies experimentally demonstrating pollen limitation in masting species (Table 5). There are, however, numerous studies that provide correlative evidence of pollen limitation by showing a positive relationship between the number of male flowers in a given year and the per cent flower maturation (Nilsson & Wästljung, 1987; Norton & Kelly, 1988; Kelly *et al.*, 2001; Rapp *et al.*, 2013). Such evidence, however, cannot distinguish between pollen limitation and flower abortion, as discussed in the next section.

Two sets of studies implicating pollen limitation in masting are worth mentioning. In *Astragalus scaphoides*, a North American forb, pollen supplementation increased seed set only in low-seed years (Crone & Lesica, 2006), a pattern consistent with either the pollination Moran effect or pollination efficiency. In the same system, investment in flowering was less in years following a high-seed year, consistent with resource depletion. *Astragalus scaphoides* is, however, insect pollinated and relatively short-lived compared with most masting trees, so the relevance of this important study to the question of pollen limitation in more standard masting systems, which are disproportionately wind-pollinated and overwhelmingly long-lived, is unclear (Herrera *et al.*, 1998; Koenig & Ashley, 2003).

Correlative and experimental evidence for pollen limitation has also been found in *Q. lobata*, a wind-pollinated Mediterranean oak. In this system, individuals that flower at the phenological extremes of the flowering season (either late or early) set fewer acorns than those that flower at the population peak when pollen is probably most abundant (Koenig *et al.*, 2012). Also, pollen supplementation in this species increased acorn set, but not in every year (Pearse *et al.*, 2015).

Other attempts to demonstrate pollen limitation in masting species by pollen addition have thus far been less successful. In *Aciphylla squarrosa*, a dioecious, insect-pollinated, long-lived masting herb, pollen supplementation did not increase seed set under natural conditions, but did in conjunction with experimental removal of 80% of flowers (Brookes & Jesson, 2007), although pollen limitation may occur in other populations (Young, 2006). Pollen supplementation did not increase seed set in *Sorbus aucuparia*, an insect-pollinated tree (Pias & Guitian, 2006). Similarly, pollen supplementation failed to produce greater seed set in *Styrax obassia*, a wind-pollinated temperate tree, although pollination experiments in this study were only carried out during a high-seed year when pollen limitation might not be expected (Tamura & Hiura, 1998).

3. Flower abortion does not equal pollen limitation

Pollen limitation is often thought to be the mechanism governing a mismatch between female flower abundance and seed set (Houle, 1999; Kon *et al.*, 2005; Lazaro *et al.*, 2006), but there are other processes that may drive this relationship. One alternative is that flowers abort despite being pollinated, allowing plants to allocate their limited resources to other, nonreproductive processes, or to favour higher quality embryos such as outcrossed over selfed seeds (Becerra & Lloyd, 1992). Resource allocation away from pollinated flowers is thought to be common, particularly when seasonal weather is unpredictable and creates conditions such as drought that are inimical to fruit maturation (Burd, 1995, 1998; Knight *et al.*, 2006). Such resource allocation can result in high rates of flower abortion even in the presence of abundant pollen, as seen in the *Q. lobata* pollen supplementation experiment discussed above (Pearse *et al.*, 2015).

A second alternative is that fertilized flowers may be depredated or damaged by diseases, insects, or weather. Examples include a loss of female flowers in masting oaks during hail events and late frosts, and the failure of fruit crops over large areas caused by pathogen epidemics and insect outbreaks (Cecich & Sullivan, 1999; Augspurger, 2009).

4. Links between pollination and weather

The pollination Moran effect is a potential mechanistic link driving the correlation between weather patterns and seed set. While there is little direct evidence to suggest that weather drives pollination success in masting species, several lines of circumstantial evidence are consistent with this hypothesis. In systems where seed set is linked to inter-annual variation in weather, those weather patterns that are strong correlates of seed set often occur at the time of pollen release, although there appears to be substantial variation in this trend (Koenig & Knops, 2014). For example, high seed set in several North American oak species correlates with high temperatures in the spring months when pollination occurs (Sork *et al.*, 1993; Koenig *et al.*, 1996), and comparative studies suggest that the weather factors correlating with seed production in different species of oaks exhibit similarities related to their life history – particularly the number of years they require to mature acorns – and phylogeny (Pérez-Ramos *et al.*, 2015; Koenig *et al.*, 2016).

Mechanistically, weather could inhibit pollination in a variety of ways. First, certain weather patterns could directly inhibit the transport of pollen by either removing it from the air, in the case of wind pollination (D'Amato *et al.*, 2007; Pérez-Ramos *et al.*, 2010), or inhibiting the flight of pollinators, in the case of animal pollination (Corbet *et al.*, 1993). Although adverse weather such as a heavy rainstorm during pollen release could greatly reduce wind pollination success in some years, Sarvas (1962) found such effects to be surprisingly small in a long-term study of *Pinus sylvestris* which included direct counts of windblown pollen. Weather could also affect flowering synchrony within a given year, which in turn could influence pollination efficiency (Koenig *et al.*, 2015). For example, *Q. lobata* trees flowering at the same time as other conspecifics have higher seed set than trees flowering early or late in the season (Koenig *et al.*, 2012; Pesendorfer *et al.*, 2016). Between years, this pattern is also present: in years of cold springs, flowering is less synchronized and such years are also those with low seed set (Koenig *et al.*, 2015).

VI. Hormonal control of seed set and masting

Hormonal control of seed set plays a particularly important role in hypotheses that view masting as an adaptive response to internal or external cues, as opposed to being externally driven. In these scenarios, a signal-transduction apparatus must exist that conveys information from the cue and results in a particular investment in flower or seed set. Indeed, because cues for reproduction or growth may also be factors that limit reproduction, distinguishing cues from proximate drivers will necessarily involve understanding how signals are transduced. For example, drought may act as an environmental cue, but could also have a direct effect on resource acquisition.

The process of mast seeding almost certainly involves the redistribution of resources from various plant tissues, the induction and completion of floral and seed development, and, at least in some cases, a concomitant decrease in vegetative growth. All of these processes are governed by hormonal regulation in plants, whether they mast or not. It is less clear what role hormones play in mast seeding beyond their general role in flower and seed set.

1. Hormonal control of seed set in nonmasting plants

Floral induction responds to numerous external and internal stimuli, including resource status, temperature, water, day length, herbivory, disease, and ontogeny (Bernier & Périlleux, 2005; Turnbull, 2011). Flowering and fruit ripening are known to be under strong hormonal control in *Arabidopsis* and *Sinapis,* model systems in which the physiology of flowering has been closely studied (Coen & Meyerowitz, 1991; Bernier & Périlleux, 2005; Turnbull, 2011; Blumel *et al.*, 2015). A sprawling signalling cascade that includes long-distance signals, short-distance signals, and the integration of branching crosstalk pathways modulates the switch in an *Arabidopsis* meristem to produce a flower (Bernier & Périlleux, 2005).

Current studies are rapidly determining which aspects of flowering pathways are conserved across plant species and which aspects are taxon-specific. Of particular interest are the long-distance (systemic) signals that coordinate flowering and fruit set with various external and internal cues perceived elsewhere in the plant (Turnbull, 2011; Blumel *et al.*, 2015). Fig. 4 highlights the location of origin and the putative roles of major plant hormones and mobile signals important to flowering and fruit development. These signals are prime targets for understanding the mechanistic basis of masting (Kobayashi & Shimizu, 2013).

2. Hormonal control of seed set in masting plants

While there has been substantial effort to categorize the signals that mediate flowering and seed set in model plants (Table 6), there is only limited evidence to suggest which signals are important for masting (Turnbull *et al.*, 2012; Miyazaki *et al.*, 2014). Woody plants and other perennial species often delay reproduction during a developmental phase that may last years or decades, a phenomenon not represented in annual model plant systems (Bohlenius *et al.*, 2006).

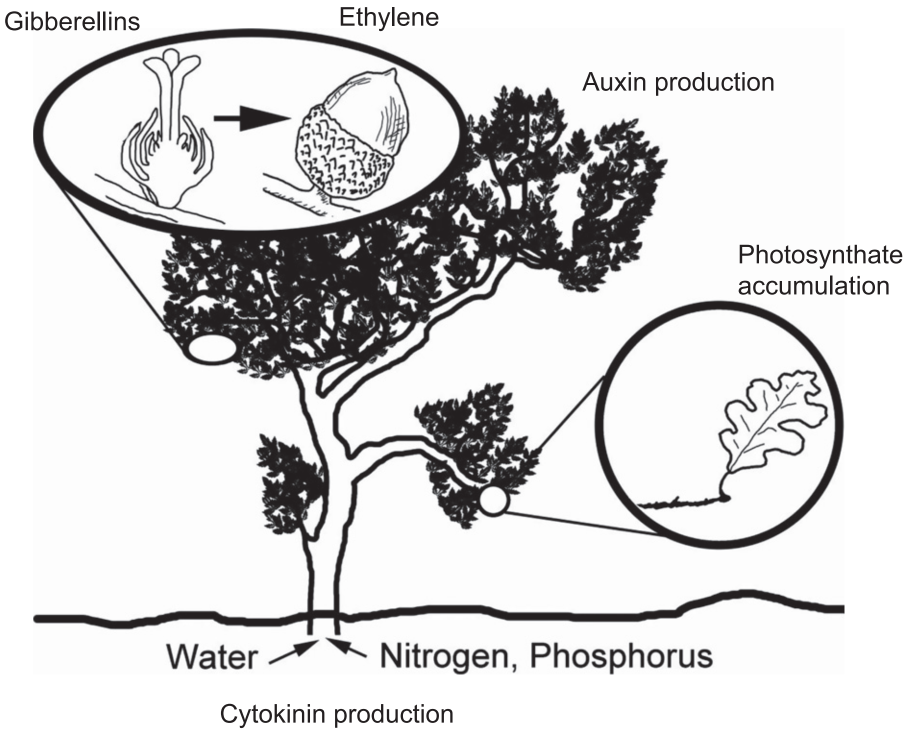

Fig. 4 A schematic showing the origin of resources and mobile signals that may influence flowering or fruit maturation in masting plants.

Table 6 The potential role of mobile signalling molecules in flower and seed set in masting plants

Signalling molecule	Putative role in flowering and seed set
Gibberellins (GAs)	Promote floral induction in *Arabidopsis*. Increase flowering in masting *Chionochloa.* Role in flower induction may be species-specific. Produced in leaves
Abscisic acid (ABA)	Is affected by carbohydrate concentrations, and implicated in resource allocation during reproduction
Ethylene (ETH)	Induces organ abortion, including flower and fruit abortion. A volatile signal produced and consumed endogenously within the fruit and flower
Cytokinins	Promote floral induction in *Sinapis.* Root-derived signal that is transported throughout aboveground plant tissue. May interact with other signals, such as TSF ('Twin Sister of FT')
FT and TSF proteins	Induce flowering in various plants. Lack of FT ('Flowering locus T') represses flowering in immature *Populus* trees. Produced in leaves and transported through phloem
Sugars	Act as mobile signals *per se* and also interact with other mobile signals such as FT and GA. Are in constant flux with metabolic demands and source–sink dynamics

Recently the flowering locus T protein (FT), in conjunction with the FT/Constans (CO) regulatory group, has been shown to be a potential mobile signal that suppresses reproduction during early development in *Populus* trees (Bohlenius *et al.*, 2006). Intraspecific variation in this signal also appears to be responsible for latitudinal differences in the seasonality of flowering and growth cessation, making this pathway a candidate for explaining variation in masting. The *FT* allele also appears to regulate flower set in *Fagus crenata*, a masting tree, where higher levels of N elicit a greater expression of *FT*, which ultimately results in a greater flower crop (Miyazaki *et al.*, 2014).

Gibberellins (GAs), a class of plant hormones, have been implicated as long-distance (systemic) signals associated with high seed set (Turnbull, 2011). The exogenous application of two gibberellins (GA_3 and GA_4) to snow tussocks (*Chionochloa pallens* and *Chionchloa rubra*), New Zealand masting grasses, caused an increase in flowering and concomitant decrease in survival in some, but not all, years (Turnbull *et al.*, 2012). Moreover, gibberellin addition appeared to interact with cues such as drought that naturally correlate with high flowering. The effect of GA addition on flowering suggests that GAs are involved in the regulation of flower production in this species, and future studies that follow endogenous GA concentrations through high- and low-seed years could indicate whether GAs are involved in the mast seeding observed in this genus.

In the above examples, hormones were found to regulate the production of flowers, but in other masting species, variation in seed set appears to be mediated by flower or immature fruit abortion as opposed to variation in flower numbers (Table 4). Less is known about the mechanisms underlying fruit abortion, but the volatile plant hormone ethylene is typically implicated as a proximal signal mediating organ abortion in plants (Bleecker & Kende, 2000). As such, ethylene may be involved in fruit abortion in masting species in cases where pollen limitation cannot account for low fruit to flower ratios.

In determining whether aspects of these signalling pathways influence masting behaviour, two lines of evidence will be particularly useful. First, as masting is a whole-plant phenomenon, it would be useful to know which long-distance internal signals mediate inter-annual variation in seed set. Second, we need to understand individual plant variability in masting within plant populations and to what extent masting is related to genetic and phenotypic differences among individuals (rather than microsite favourability, resource acquisition and recent flowering history; Rees *et al.*, 2002). The molecular tools required to ask questions such as these are currently being developed, and thus we expect studies exploring the long-distance signals that mediate masting and the genetic alleles underlying variation in masting among individuals to be areas of active future research.

VII. Evolutionary perspectives on masting behaviour

By understanding how a complex trait such as masting works, it is possible to better infer the evolutionary processes that have shaped that trait (West-Eberhardt, 2003). Numerous studies have explored how adaptive hypotheses such as predator satiation, pollination efficiency, and seed dispersal might provide fitness benefits to plants with synchronous and variable seed set. Other key aspects of masting as an evolvable trait have yet to be elucidated, however.

1. Heritability of masting

For selection to act upon a trait, that trait must be heritable. Heritability of variable seed production has not been demonstrated, in part because of logistical difficulties. Most masting organisms are long-lived and take decades to reach reproductive maturity, and then more years are required to quantify inter-annual variability in seed set (CV_i). Consequently, assessing heritability based on parental regression or known siblings is a challenge, as the offspring of known parents must be reared in a common environment for decades.

Although masting is a population-level phenomenon, many aspects of masting, such as CV_i, are measured at the individual level (Koenig *et al.*, 2003). In order to do this, individual reproduction could be compared to population means. For example, synchrony of an individual could be considered the correlation between its inter-annual seed set and the mean population seed set (Buonaccorsi *et al.*, 2003). Qualitative accounts indicate that there is substantial individual variation in each of these masting attributes (Koenig *et al.*, 2003). Thus, heritability of masting should be testable with the appropriate data on seed production by individuals of known genetic relatedness. Such data already exist to some degree (El-Kassaby & Barclay, 1992), but have not been used to assess the heritability of masting *per se*.

2. Phylogenetic signal of masting

Mast seeding is taxonomically widespread, but there is little quantitative evidence as to whether masting behaviour is a phylogenetically conserved trait or whether masting is easily lost and gained within lineages. In a meta-analysis of interannual variation in seed set, the coefficient of variation in seed set was partially explained by both generic and species affiliations (Herrera *et al.*, 1998), but that could be explained by phylogenetic conservatism in features that favour masting rather than conservatism in masting *per se*.

With an increasing number of data sets of seed set in perennial plants and better resolution of plant phylogenies, phylogenetic comparative methods are likely to play a greater role in our understanding of masting. For example, one large mechanistic difference among masting species is whether years of high seed set are driven by greater floral initiation or less flower abortion (Table 4). In most examples within the genus *Quercus* (oaks), the majority of variation in seed set is related to floral abortion (Sork *et al.*, 1993; Pérez-Ramos *et al.*, 2010; Pearse *et al.*, 2015), whereas in the same family variation in *Fagus* is related to floral initiation (Table 4). Comparative analyses indicate similarities in how masting by different species responds to weather that correspond, at least to some extent, to their phylogeny and life history (Koenig *et al.*, 2016). However, most masting examples in Dipterocarps, *Nothofagus* spp. and *Chionochloa* spp. appear to involve differences in floral initiation (Ashton *et al.*, 1988; Kelly *et al.*, 2000, 2001), and summer temperature appears to be a consistent predictor of masting by phylogenetically disparate plants in New Zealand (Schauber *et al.*, 2002; Kelly *et al.*, 2013).

3. Quantitative genetics of masting

The standing variation in masting behaviour could be used to illuminate the mechanisms that underlie masting. Techniques such as quantitative trait locus (QTL) analysis or genetic correlations could be used to identify alleles associated with variable and synchronous seed set. QTL analysis has already begun moving in this direction in alternate bearing crop plants, whose fruit production may have some similarity to that of natural populations of masting plants (Smith & Samach, 2013). In apple (*Malus domestica*), for example, alternate (or biennial) bearing was strongly associated with four genomic regions that contain genes known to modulate floral hormones and shoot growth (Guitton *et al.*, 2012). While alternate bearing, which tends to lack any correlation with weather and exhibits a periodic rather than an irregular pattern of reproduction, lacks some of the properties typical of masting, it is nonetheless likely that similar genes may be involved in the repression of seed set in masting plants in years following a large seed set.

VIII. Unifying resource budget and economy of scale models of masting

We began this review by saying that ultimate-level EOS models and proximate-level RB models have been two largely separate strands of study on mast-seeding plants. Our consideration of how resources are involved, however, indicates that neither of these two strands can stand alone.

RB models cannot create masting in a purely mechanistic, nonselective way for two reasons. First, RB models assume that plants cannot just produce a small flowering effort every year, and therefore resources must be saved up until a threshold greater than the annual gain in resources is reached. The existence of that threshold requires some economy of scale, such as a need to satiate predators or saturate the air with pollen. Second, RB models generate individual variability (CV_i) but need a synchronizing cue, which is most commonly assumed to be pollen coupling (a pollination EOS). If the synchronizing factor is weather instead of pollen coupling (as, for example, in Rees *et al.*, 2002), selection through the plant becoming hypersensitive to the cue in order to increase the CV_i may still be involved (Kelly *et al.*, 2013). Hence the internal dynamics in RB models are driven largely by resource levels, but the population-level response would not resemble masting without two contributions from selectively favoured factors.

In contrast, EOS models have sometimes assumed that variable seed crops (CV_i) could be driven entirely by weather cues without any requirement for resources to limit reproduction (Crone & Rapp, 2014). This is essentially the opposite of the RB mechanism, which proposes that CV_i is driven entirely by resources.

In practice, resources are involved in most EOS models. First, while cues could in principle be any weather variable, they seem to more often involve high flowering following weather variables which are positively associated with resource acquisition. Second, resources always represent a final veto on the size of seed crops, even if this ceiling is rarely reached. Third, recent studies have shown that resources play a role in determining the shape of the relationship between weather cues and flowering levels for individual plants, even under models that seem least likely to require resource inputs such as the differential temperature hypothesis of Kelly *et al.* (2013).

Several recent papers illustrate this complementarity of EOS and RB models. Venner *et al.*'s (2016) modified theoretical RB model using pollen coupling effectively created very strong density dependence of seed set, which we argue is an economy of scale, as only flowering efforts over a rather sharp pollen density threshold resulted in efficient seed set. As a result, their plants have a pollination EOS that has particularly strong effects because of the steepness of the logistic link used in their model. They reported the 'unexpected' result that population-level masting was most likely in the models when pollination was inefficient, but this is precisely the expected outcome if we note that the largest wind-pollination selective benefits to mast seeding come when plants are at low density or reproductive allocation is low (Kelly *et al.*, 2001). Thus, their RB model favours masting because the inefficient pollination provides an EOS as well as synchrony.

Recent studies of oaks also demonstrate the complementarity of RB and EOS models. In *Q. lobata*, long-term study has found that an RB model modified to deal with individual variation among trees combined with a pollen limitation EOS was able to explain masting patterns (Pesendorfer *et al.*, 2016). Although the precise mechanism by which pollen limitation occurs is not known for sure, the 'phenological synchrony' hypothesis of Koenig *et al.* (2015) proposed that colder temperatures during the pollination period in spring result in greater microclimate variability, greater phenological variability, and hence reduced synchrony among trees in pollen release and successful fertilization. Trees that released (and caught) pollen more asynchronously with the rest of the population had lower pollination success and lower acorn crops (Koenig *et al.*, 2012). Hence, in this modified RB model, higher spring temperatures – a weather cue – were associated with larger acorn crops because of their effect on the strength of pollination efficiency – an EOS – both within and between years.

We consider it likely that both resources and EOS are involved in most, if not all, cases of mast seeding. The search of RB modellers for a purely mechanistic nonadaptive driver of mast seeding appears unlikely to succeed. Similarly, the idea that selection under an EOS could result in masting that is largely independent of resources appears to be rarely borne out in practice.

IX. Conclusions

Masting is an emergent ecological phenomenon that may be accomplished via several mechanistic pathways varying in the relative importance of resources, weather cues, and fitness benefits. At least in theory, masting could be driven almost entirely by resource availability, or entirely by environmental cues independent of plant resources. In practice, however, both resources and environmental cues are required for masting to occur. Exactly what resources and cues are involved, however, is poorly understood in most systems.

Pollination is a key ecological interaction that not only provides a functional (selective) advantage to masting but also synchronizes masting populations either by pollination efficiency or by pollination Moran effects. More work is needed to establish inter-annual differences in pollen limitation and its role in masting behaviour.

The hormonal control of masting is only beginning to be explored. This avenue of research is particularly exciting, however, as it could identify the cues that synchronize masting plants. Moreover, hormonal control may prove to be the most universal aspect of masting among different species. Across taxa, for example, there is little commonality in the plant phenotypic responses to herbivore damage, but jasmonic acid appears to be a highly conserved hormonal signal mediating those responses (Thaler *et al.*, 2012). Whereas the role of resources and developmental processes may differ between systems in masting species, it is nonetheless clearly worth exploring the underlying apparatus that coordinates this important ecological process.

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