

# The evolutionary ecology of mast seeding

Dave Kelly

**M**ast seeding is the intermittent production of large seed crops by a population of plants. It is also sometimes called mass seeding, mass fruiting, periodic flowering, supra-annual flowering, sporadic seasonal synchrony and so on. Masting is most likely in long-lived plants, which are less affected by the costs of not reproducing in some years<sup>1</sup>. Although trees are the best-known examples, especially in the northern hemisphere<sup>2</sup>, there are also many masting herbaceous plants<sup>3</sup>.

The earliest explanation for masting was the resource-matching hypothesis: that seed output varies because the plant's available resources vary (Klebs 1904, cited in Ref. 4). Interest in the evolutionary implications of masting was renewed when insightful papers by Janzen<sup>5,6</sup> and Silvertown<sup>7</sup> elaborated on earlier ideas<sup>8</sup> that masting served to reduce levels of loss to seed predators. These established predator satiation as the most popular explanation for masting. However, since 1987 the field has become crowded with alternative hypotheses.

## Definitions of masting

Masting is a population phenomenon, so is technically not applicable at the individual level (although single large trees may locally satiate seed predators<sup>9</sup>). Though definitions vary, that of Janzen<sup>6</sup> is typical: 'mast seeding is the synchronous production of seed at long intervals by a population of plants'. This suggests that there are two types of years: seeding (mast) years and non-seeding years. While this concept is clear ('strict masting'; Table 1), most real data sets on plants diverge to some degree ('normal masting'; Table 1). Strict masting and normal masting differ in important ways. The emphasis in the above definition on mast and non-mast years is appropriate for strict masting species, but not for normal masting species (Fig. 1). A more general definition is 'synchronous highly variable seed production among years by a population of plants'. Two elements of this definition have not been defined precisely: how variable between years, and how synchronous between individuals?

If the variation in seed production simply mirrors variation in the environment, and hence the amount of growth plants achieve, there is nothing more to explain in evolutionary terms: climate determines seed output. All plants will be affected by environmental variability, but there may also be selective forces favouring exaggerated or de-emphasized variation in seed output. Explicitly, the amount

**The past seven years have seen a revolution in understanding the causes of mast seeding in perennial plants. Before 1987, the two main theories were resource matching (i.e. plants vary their reproductive output to match variable resources) and predator satiation (i.e. losses to predators are reduced by varying the seed crop). Today, resource matching is restricted to a proximate role, and predator satiation is only one of many theories for the ultimate advantage of masting. Wind pollination, prediction of favourable years for seedling establishment, animal pollination, animal dispersal of fruits, high accessory costs of reproduction and large seed size have all been advanced as possible causes of masting. Of these, wind pollination, predator satiation and environmental prediction are important in a number of species, but the other theories have less support. In future, important advances seem likely from quantifying synchrony within a population, and examining species with very constant reproduction between years.**

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of variation in seed output at the population level ( $V_{\text{seed}}$ ) will depend on environmental variation ( $V_{\text{env}(t)}$ ) as experienced by species  $i$ , on factors which select for greater variation ( $V_{\text{mast}}$ ), and factors favouring more constant reproduction ( $V_{\text{const}}$ ):

$$V_{\text{seed}} = V_{\text{env}(t)} + V_{\text{mast}} - V_{\text{const}}$$

Hence, masting can be formally defined by the presence of  $V_{\text{mast}}$ , which is identified by the presence of 'switching'<sup>10</sup> (diversion of resources away from vegetative growth, such as wood increment, in a high seed year) or 'resource accumulation' (resources accumulated over several years are used in a large reproductive effort, producing significant, endogenous, negative seedfall auto-correlations in polycarpic plants<sup>2</sup> or synchronous death in monocarpic plants).

In the absence of net selection for masting ( $V_{\text{mast}}$ ) or constant reproduction ( $V_{\text{const}}$ ), the default situation will be for  $V_{\text{seed}} = V_{\text{env}(t)}$  in polycarpic plants, and for asynchrony in monocarpic plants. The former is shown

by the tendency for polycarpic species in harsher environments to have higher  $V_{\text{seed}}$ . For example, Webb and Kelly<sup>3</sup> showed higher CVs (coefficient of variation, i.e. standard deviation divided by the mean) of seed output at higher altitudes for 23 cases from New Zealand. However, each species will have different levels of sensitivity to the environment<sup>11</sup> and so  $V_{\text{env}(t)}$  will vary among species in the same environment.

This formal definition via  $V_{\text{mast}}$  allows the delineation of three different types of masting (Table 1): strict masting, normal masting and putative masting. For strict masting, the existence of  $V_{\text{mast}}$  is indisputable because the population reproduces synchronously. Also, the distribution of seed crop size among years is bimodal (i.e. some years no seeds are produced; other years many are produced) while the environment varies continuously. Few species appear to show this type of masting<sup>12</sup>. The plants which most closely approach strict masting are all synchronized monocarps, such as bamboos and the shrub genus *Strobilanthes*; these seed only in a large fatal episode<sup>6,13</sup>. However, where the individuals in a population of monocarps are imperfectly synchronized, then population seed output among years will vary more continuously, approaching normal masting. The relative rarity of strictly synchronized monocarpic plants is presumably a result of the same constraints as on the evolution of periodicity in insects<sup>14</sup>.

Normal masting is shown both by imperfectly synchronized monocarps, and most polycarps. Some (perhaps most)

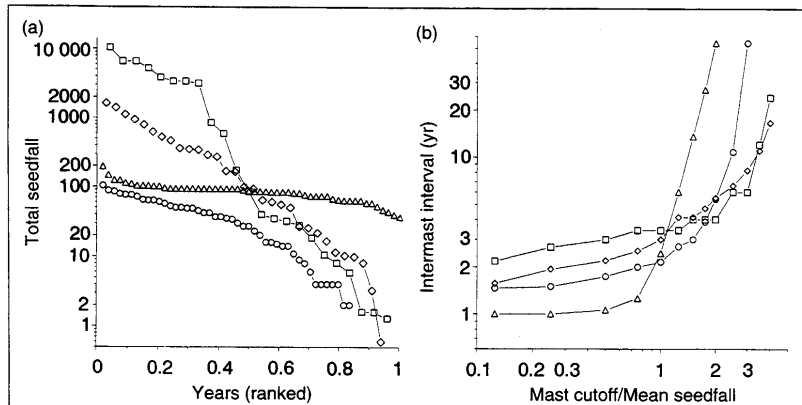
**Table 1. Types of masting and how to recognize them**

Type	Characteristics	Objective mast species?	Objective mast years?	Examples	Comments
Strict mast	Bimodal seed output with no overlap between the tails.	Yes	Yes (if highly synchronized)	Shown only for highly synchronized monocarps e.g. bamboo and <i>Strobilanthes</i> <sup>6</sup> .	Masting species and mast years can be unambiguously identified. Equals 'true mast' of Lalonde and Roitberg <sup>24</sup> . More common in models than in the field.
Normal mast (1) bimodal	Bimodal seed output with overlap between the tails; bimodality is statistically significant.	Yes (soft)	Yes (soft)	<i>Quercus lobata</i> , <i>Q. douglasii</i> , <i>Q. agrifolia</i> , <i>Q. kelloggii</i> <sup>20</sup> .	Statistical identification of mast species and mast years is sample-size dependent and hence 'soft'. Includes polycarps and imperfectly synchronized monocarps.
Normal mast (2) switching	Seed crops vary greatly but are not bimodal. In high seed years, resources are diverted from vegetative growth (e.g. reduced wood increment <sup>10</sup> ) or reserves (e.g. negative autocorrelation in seed crops <sup>21</sup> ).	Yes (soft)	No	<i>Dacrydium cupressinum</i> <sup>10</sup> , <i>Q. alba</i> , <i>Q. rubra</i> , <i>Q. velutina</i> <sup>21</sup> .	Statistical identification of mast species is 'soft'. Mast years cannot be identified since seed output varies continuously (Fig. 1).
Putative mast	Seed crops vary greatly but no evidence for switching (data not available or insufficient).	No	No	Most published papers on mast.	Strictly, ought not to be called mast unless bimodality or switching is shown. However, if $CV > 1.6$ , switching is highly likely to be present (see Fig. 2).

synchronized monocarps show normal mast, due to either poor within-cohort synchrony which may spread a mast 'year' over 6–9 years<sup>6,15</sup>, or the presence in the population of many overlapping cohorts (e.g. some bamboos<sup>6</sup> and *Tachigalia versicolor*<sup>16</sup>). Most published examples of mast derive from polycarpic species like *Fagus*, *Quercus* and *Pinus* species and these seem to display only normal mast (Table 1, Fig. 1): they seed most years, but with some very heavy seed years. With normal mast, the presence of  $V_{mast}$  is confirmed by finding significant bimodality or the presence of switching. In both cases, mast species can be identified, but the categorization is sample-size dependent, and hence 'soft' (probabilistic). Where

bimodality exists (as in imperfectly synchronized monocarps), mast years can be identified but again the categorization is soft. Under switching, mast years cannot be identified because seed output ranges continuously from low to high (Fig. 1a). Generally then, there is no basis in normal mast species for dividing years into mast and non-mast years, as many authors have. Throughout this article I therefore avoid 'mast year' as undefined and discuss seed output quantitatively (i.e. high and low seed years).

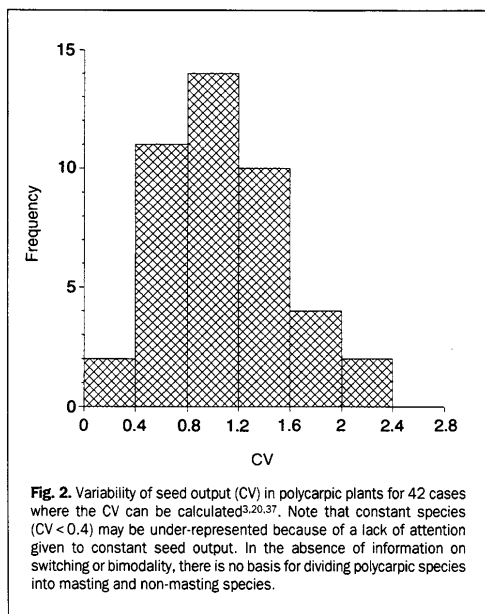
The third type of mast is putative mast, where variation in seed output is demonstrated, but there is no proof that anything more than environmental variation



**Fig. 1.** Examples of variation in seed output from four polycarpic trees. Diamonds: *Dacrydium cupressinum* over 33 yrs at Harihari<sup>10</sup>,  $CV = 1.39$ . Squares: *Nothofagus solandri* var. *cliffortioides*<sup>31</sup>, 24 yrs, Craigieburn 1050 m,  $CV = 1.46$ . Circles: *Picea abies*<sup>37</sup>, 54 yrs, region 5,  $CV = 0.97$ . Triangles: *Pinus sylvatica*<sup>37</sup>, 54 yrs, region 5,  $CV = 0.54$ . (a) Total seedfall among years (log scale, units as in original papers) ranked from highest to lowest year. Seedfall varies continuously from high to low years. *Nothofagus*, with the highest range and the fewest years, seems most nearly stepped, but for no species is there any objective division into mast and non-mast years. (b) Variation in calculated inter-mast interval as a function of the cutoff point for defining a mast year. In the absence of an objective definition of a mast year, there is no way to define the inter-mast interval.

( $V_{env(t)}$ ) is involved. In other words,  $V_{mast}$  may not be present (although putative mast could also serve as a precursor to the evolution of  $V_{mast}$ ; cf. Ref. 14). As might be expected, since  $V_{env(t)}$ ,  $V_{mast}$  and  $V_{const}$  all vary continuously, published data for plant species show a complete range of  $V_{seed}$  from very constant to highly variable (Fig. 2). Both ends of this continuum are of interest, but mast species will occur only at the high end. The more constant end of the continuum is probably as interesting as the masting end, but has received much less attention.

Of these three types, strict mast is rare, and putative mast has no demonstrated evolutionary significance, so much of the rest of this article concentrates on normal mast.



### Measuring masting

The question then arises of how to measure masting. For normal masting the best measure is the CV for seed output among years<sup>7,17</sup>. Other possible indices, such as the standard deviation of log numbers and the Gini coefficient, are either biased<sup>18</sup> or highly correlated with the CV but computationally difficult<sup>19</sup>, respectively.

For species that show strict masting, the length of the 'intermast interval' can be measured and may be relevant to the predator satiation hypothesis<sup>6</sup>. However, for normal masting species the intermast interval is undefined since mast years cannot be identified (Box 1). In these species, time series analysis can quantify the length of possible cycles in seed output<sup>10,17,20</sup>.

### Hypotheses to explain masting

At least eight hypotheses have been developed to explain mast seeding (Table 2), with varying levels of experimental support. Most conform with Norton and Kelly's<sup>10</sup> requirement for 'economies of scale': larger reproductive efforts are more efficient, favouring occasional large efforts rather than regular smaller ones.

#### Wind pollination

This hypothesis has received much recent support in a range of species<sup>9,10,12,20</sup>. Many of the well-known masting species are wind pollinated, both for trees<sup>12</sup> and bamboos<sup>6</sup>. Economies of scale seem most likely in species when the female parent invests significant resources in fruit regardless of whether they are fertilized<sup>12</sup>. The hypothesis is also supported in species which do not do this, such as some<sup>20</sup> (but not all<sup>2,21</sup>) species of *Quercus*.

#### Predator satiation

Predation is 'probably still the most widely known explanation for reproductive synchrony' in both plants and animals<sup>14,22,23</sup>. There is good support for this hypothesis in the literature (Table 2). However, there are several caveats that deserve wider recognition.

First, the hypothesis is usually phrased<sup>7,20,23,24</sup> in terms of starving the predators in low seed years (the numerical response, or changes in predator population size) as well as swamping them in high years (the functional response, or changes in seeds eaten per predator). However, since few plants completely eschew reproduction in some years, the functional response of the predator may be more important than the numerical response<sup>22,25</sup>. For example, in Sweden, *Fagus sylvatica* seed losses m<sup>-2</sup> to the moth *Cydia fagiglandana* were about the same in both the low seed year of 1982 and the high year following<sup>9</sup>. Predation losses were therefore a lower fraction of the larger seed crop, but the moth population showed no numerical response. Silvertown<sup>7</sup> also searched for a numerical response but failed to find evidence for it. If the numerical response is relatively unimportant, then the occurrence of consecutive mast years is not evidence against all forms of predator satiation (cf. Refs 7,10), although it may be evidence that predator satiation would be a weaker selective force.

### Box 1. Intermast interval and endogenous cycles of seed output

A number of authors have used the gap between mast years to measure masting. Janzen<sup>6</sup> presented data on the intermast interval for synchronized monocarpic bamboos, although the 'mast year' was defined as the peak of a flowering event spread over several years. Silvertown<sup>7</sup> said that seed crops in polycarpic trees came at 'irregular intervals but with a periodicity characteristic of the species'. More recently, Sork and Bramble<sup>17</sup> studied intermast intervals in various species of North American oaks.

However, there are several difficulties with using intermast interval for normal-masting species. The most serious stems from the inability to define a mast year objectively (Fig. 1a). If seed output is continuously variable, as is typical, then there is no clear way to define which years are mast years. If the cutoff for a mast seed crop is arbitrarily set lower, there will be more years classified as mast years, and hence a shorter mean intermast interval (Fig. 1b). The more variable the seed output is for a species, the less steeply the intermast interval will vary with the position of the cutoff. Hence, intermast interval in *Dacrydium* varies less with value of the cutoff than for *Pinus*. However, in all these examples an accurate, repeatable value for the intermast interval could not be produced.

Secondly, while calculation of CVs for seed output is progressively less reliable for data sets much <10 years, the length of data set needed for accurate calculation of intermast interval is even longer, since it is based on the mean interval between supra-annual events. For example, if the very long 33-year data set for *Dacrydium*<sup>10</sup> is divided into three segments of 12, 11 and 12 years, and a mast year is as defined by Norton and Kelly<sup>10</sup>, the mean intermast intervals are 2.20, 1.67 and 3.33 years for the three segments. Even a 12-year data set is too short for accurate estimation of intermast interval. Similarly, two 9-year series for *Pinus banksiana* were not enough to clearly identify a putative 4–6 year cycle of seed output<sup>26</sup>. This problem might be circumvented to some extent by recording data for individual trees and using these as replicates<sup>17</sup>.

Time series analysis offers a way to circumvent these problems. Instead of intermast intervals, we should look for endogenous cycles in seed output. This no longer implies that mast years can be identified, but allows the effects of cycle length on predator populations or resource accumulation to be examined. Serial autocorrelation can identify cycles in the data<sup>10,20</sup> and allow comparisons between species<sup>17</sup>. The resolution is limited to integer steps of one year. Spectral analysis is a more powerful way of analysing for cycles<sup>26</sup>, but requires long data sets.

The conclusions are that for normal-masting species (i.e. most species) intermast interval is not a useful concept, but that time series analysis is useful for identifying endogenous rhythms in seed output. A number of reports, such as USDA Forest Service manuals, provide intermast intervals for various tree species (which being polycarpic, probably show normal masting). For many of these, the published intervals appear to be derived from arbitrary divisions of continuously variable seed output into mast and non-mast years (cf. Fig. 1a). Only analyses based on serial autocorrelation or spectral analysis of quantitative data seem likely to withstand critical scrutiny.

**Table 2. Hypotheses which have been suggested as favouring mast seeding, ranked in order of experimental support**

Hypothesis	Definition	Typical tests	Status
Wind pollination	Large flowering efforts increase chances of successful wind pollination <sup>9</sup> .	Higher % fertilization in high flowering years.	Well documented <sup>9,10,12</sup> ; especially likely where resources still allocated even to unpollinated reproductive structures <sup>12</sup> , but also found where this does not occur <sup>20</sup> .
Predator satiation	Large seed crops satiate seed predators, which thus destroy a lower % of crop <sup>5,7</sup> . Decrease in predator populations in low seed years possible but not essential.	Lower % predation in high seed years. Higher % predation in species with higher CV of seed output.	Well supported by many examples <sup>2,7,9,22,38</sup> . However, depends on shape of functional response; masting may increase losses <sup>9,22</sup> .
Environmental prediction	Large reproductive episodes timed to anticipate favourable conditions for reproduction and establishment <sup>12</sup> .	Higher seed or seedling survival from high seed years.	No supporting evidence for climate, and seems unlikely given long lead time between flowering and seedling establishment. Well established where fire is the trigger for high seed years, especially in monocots <sup>26,27</sup> .
Resource matching	Plants vary reproductive effort to match the varying resources available <sup>10</sup> .	Variable seed output achieved without switching resources from vegetative growth or reserves.	Likely to be important in most plants in setting background levels of variation according to variability of environment ( $V_{env}$ ) <sup>3</sup> . Can account for putative masting, but not, alone, for strict or normal masting.
Animal pollination	Large flower displays attract animal pollinator <sup>34</sup> .	Higher % fertilization in high flowering years.	Argued both for <sup>15,34</sup> and against <sup>2</sup> . Could favour constant reproduction <sup>22</sup> , depending on functional response of pollinators <sup>28</sup> .
Animal dispersal	Large fruit displays attract generalist animal disperser <sup>39</sup> or result in wider dispersal by scatterhoarders <sup>12</sup> .	Higher % fruit dispersed or greater dispersal distances in high seed years.	Some evidence in support <sup>29</sup> and against <sup>20,30</sup> . Could favour constant reproduction <sup>22</sup> , depending on functional response of dispersers. Requires strong selection advantage to effective dispersal.
Accessory costs	High accessory costs of reproduction make small reproductive efforts less efficient per seed produced <sup>5</sup> .	Lower accessory costs per seed for large reproductive efforts within a plant.	Does not require synchrony between individuals, hence cannot alone explain masting. May exaggerate variation between high and low years.
Large seed size	Selection for larger seed size increases contrast between high and low seed years (if another factor sets lower limit for efficient reproduction in terms of seed density, not seed biomass) <sup>2</sup> .	More variable seed number among years in related species with larger seeds.	Does not require synchrony between individuals, hence cannot alone explain masting. May exaggerate variation between high and low years. Assumes some other factor sets lower limit in terms of seed numbers per unit area, not seed biomass.

Second, the expected relationship between reproductive synchrony and predation levels depends on the functional response of the predator. A specialist predator may be successfully swamped by a large seed year, while a generalist, highly mobile predator may ignore small seed crops altogether, but cause high losses when the seeds are abundant, especially in spatially heterogeneous environments<sup>5,22,24</sup>.

Therefore, we cannot uncritically assume that variable reproduction might satiate a predator without knowing the functional response of the predator. In some cases, large seed crops may actually worsen predation.

*Environmental prediction*

This hypothesis proposes that the plants can predict which years will be best for seedlings<sup>12</sup>. As initially proposed (for climate), it is without empirical support, and seems unlikely given the unpredictability of the environment and the long lead times between flower initiation and seed germination. It is very well documented in cases of mast flowering triggered by fire, especially in monocots like Australian *Xanthorrhoea* spp.<sup>26</sup>, and explains why tussock grasses like *Chionochloa* species in New Zealand (Fig. 3) flower after fire even though their carbohydrate reserves have declined<sup>27</sup>. After a fire, enhanced nutrient availability and reduced competition are predictably more favourable for seedling establishment. Woody dicots can exploit this opportunity more rapidly by storing seeds in serotinous fruits or cones, but monocots, lacking wood,

cannot protect seeds well from fire and must flower after the fire event.

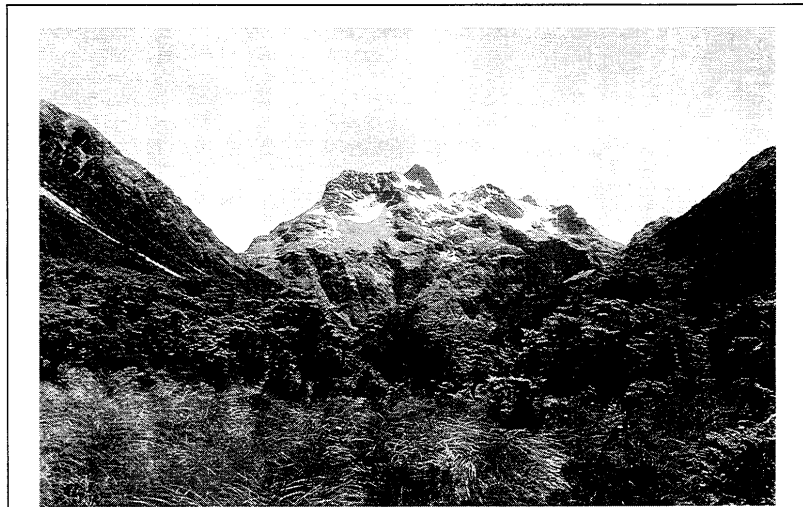
*Resource matching*

There are three resource-related theories relevant to masting: resource limitation, resource accumulation and resource matching. Resource limitation was an early hypothesis for masting: that is, the plants produced a large crop occasionally as they could not produce a large crop every year. This theory is rejected as it fails to explain why plants would not produce a small crop every year<sup>10</sup>. Resource accumulation refers only to the need, if masting is present, for plants to build up reserves before a masting episode. This may be detected by serial autocorrelation<sup>17</sup>.

Resource matching is a hypothesis for the existence of masting which says that seed crops mirror the variable resources available (Table 2). This hypothesis can account for putative masting, but not for strict or normal masting, since it is concerned with  $V_{env(t)}$  rather than  $V_{mast}$ . A weather event, such as a warm summer, is required in normal masting species as a signal to synchronize the population, but masting involves reallocation of resources within the plant, so goes far beyond simple tracking of climate<sup>2,10,20,24</sup>. Also, masting in the aseasonal tropics can be triggered by minor temperature changes which must minimally affect resource levels<sup>28</sup>. Strict masting species apparently respond to internal calendars<sup>6</sup> rather than weather. However, through  $V_{env(t)}$  climate does help set the baseline level of  $V_{seed}$ .

### Animal pollinators

Most authors mention this factor as a likely *disadvantage* to masting, assuming the standard view of animal satiation<sup>2</sup>. However, whether animal pollination is hindered or helped by masting depends on the shape of the functional and numerical responses. If animals are attracted by large floral displays, masting could improve pollination<sup>10,15</sup>. The synchronized monocarp *Frasera speciosa* has enhanced pollination through between-year synchrony<sup>15</sup>. It has been assumed that masting would swamp specific pollinators, but in thrips-pollinated tropical dipterocarps, the pollinators have such short generation times that their numbers increase dramatically during a mast event<sup>28</sup>. No general prediction can be made about the expected effects of masting on animal pollinators.



**Fig. 3.** The most variable masting species from Fig. 2 are from communities in the Southern Alps of New Zealand, shown here. In the foreground at about 800 m altitude is a mixture of *Chionochloa* tussock species, principally *C. rubra*, the most variable species in Fig. 2 is *C. pallens*<sup>28</sup>. In the centre is a forest of *Nothofagus solandri* var. *cliffortioides*<sup>34</sup>, the second most variable species in Fig. 2. In the background is Carrington Peak (2010 m), Waimakariri catchment, South Island, New Zealand. Photo by C.J. Burrows.

### Animal fruit dispersal

Much of the argument above for animal pollinators also applies to this hypothesis. Masting may enhance or reduce dispersal, depending on the responses of the disperser to large seed crops<sup>10</sup>. There is some evidence in support of the hypothesis; Christensen and Whitlam<sup>29</sup> showed better bird dispersal of large seed crops of *Pinus edulis*. In contrast, Koenig *et al.*<sup>20</sup> found no evidence for enhancement of dispersal in five *Quercus* spp. and Herrera *et al.*<sup>30</sup> found none for the tree *Phillyrea latifolia*. This hypothesis seems ripe for more experimental testing.

### Accessory costs of reproduction

This hypothesis proposes that small reproductive efforts are energetically inefficient because of high accessory costs (Table 2). In models examining the selective advantage of masting, Lalonde and Roitberg<sup>24</sup> found that high 'startup costs' of reproduction favoured masting. Their startup costs were a constant fraction of reproductive effort, which does not provide any economy of scale to large efforts in contrast to this hypothesis – if startup costs were a decreasing proportion of large reproductive efforts the advantage ought to be even greater. However, synchrony between individuals in a population is not required. Hence, this hypothesis alone cannot account for masting, but it may serve to emphasize pre-existing masting, by enhancing the difference between high and low seed years.

### Large seed size

Selection for large seed size, like high accessory costs, alone does not explain masting as there is no requirement for synchrony between individuals. If masting already exists, with synchrony maintained by some other factor, larger seed size may enhance masting under certain conditions<sup>2</sup>. If the other factor sets a lower limit for efficient reproduction in terms of seed density rather than seed biomass, and larger seed size is selected for, then the large-seeded

crops cannot reduce seed density to compensate for the greater resources required. In this case, the intervening years must have compensating reductions in seed number to maintain the overall mean level of reproductive allocation, increasing the CV or length of the cycle of seed production (Box 1). There is evidence for a link between seed size and length of the cycle in oaks<sup>2</sup>.

### Proximate and ultimate causes of masting

The final distinction to be drawn is between proximate and ultimate causes of masting<sup>17</sup>. Proximate causes are the immediate factors that affect whether a particular year will be a high seed year, such as weather<sup>31</sup> or the levels of stored reserves in the plants<sup>17,20,21</sup>. Ultimate causes are the evolutionary advantages that can explain why some species are highly variable in seed output, while others at the same site have constant reproduction<sup>3</sup>. Of the above hypotheses, only resource matching cannot be an ultimate cause.

This article concentrates on the ultimate causes. Therefore, studies showing high correlations between seed crops and various weather attributes are useful for predicting future seed crops, but throw little light on the ultimate reason for masting in the species.

Nevertheless, weather retains some interesting roles. Initial variation in seed crops due to environmental variation is necessary to get mast seeding established<sup>7,23,24</sup>. Also, the level of variability in the environment ( $V_{env(t)}$ ) determines the default level of variability against which selection can act to increase ( $V_{mast}$ ) or decrease ( $V_{const}$ ) variability in particular species.

### Conclusions

The evidence lends most support to the first three hypotheses as ultimate causes: wind pollination, predator satiation and environmental prediction. Of these, environmental prediction applies only in specific habitats (fire-prone) and plant groups (herbaceous perennials). Predator

satiation has much support, but the relationships between predator and plant are much more complex than is usually assumed. In contrast, wind pollination is simply interpretable, applicable in many masting species, and frequently found when it has been searched for. Wind pollination must surely dethrone predator satiation from its current position as the assumed default explanation for mast seeding.

The general conclusions of Ims<sup>22</sup> for reproductive synchrony in plants and animals still hold: (1) there may be multiple causes in any particular case; (2) a single cause (such as seed predation, animal pollination, or dispersal) may select for or select against synchronous variable seed production, depending on the details of the relationship; (3) there is a need for more empirical tests of the hypotheses; and (4) the most revealing studies compare the success of highly variable and less-variable species, or in-synchrony versus out-of-synchrony individuals.

**The way ahead: future work**

There are four main areas where we may expect advances in the next few years. First, we need to document the level of synchrony between individuals and how this affects selection<sup>20,21,32</sup>. Most previous work has used totals for groups of plants. This is particularly important in monocarpic species, where each plant uses all its resources in flowering, and the degree of synchrony determines whether the population shows strict masting or normal masting. Such work will help answer the question from the *Definitions* section above ('how synchronous?') and also will show how common strict masting really is. Out-of-synchrony individuals are very important for testing the penalties for falling out of step, to show whether there is a present benefit to synchrony<sup>22</sup>. This work will also address the question of spatial scale: how large an area is needed to encompass the relevant 'population'?

Second, which theories are mutually exclusive? How do we separate the theories when several may apply in the same species, for example, the common case of a plant which is wind pollinated and has seed predators? It was previously thought these two theories might be separated by the requirement under predator satiation, but not wind pollination, to avoid consecutive high years<sup>10,20</sup>. However, since predator satiation does not require a numerical response<sup>9,22</sup>, this test is not decisive. More promising is the distinction between selection for mast *flowering* (e.g. wind pollination) and mast *seeding* (e.g. predator satiation), which act at different seasons<sup>17</sup>.

Third, ecophysiological studies of species could determine the variation in total net photosynthesis over a number of years ( $V_{env(t)}$ ) and examine how this is allocated among growth and reproduction. This would elucidate the degrees of switching resources among sinks within the plant, which must be the basis of exaggerated variation among years for masting species, and constant reproduction in those species with constant seed output among years<sup>10</sup>.

Fourth, why do some species show very constant reproduction, even at sites where other species are masting<sup>3?</sup> What factors ( $V_{const}$ ) are acting to produce very constant reproduction from year to year, such as in the serotinous *Pinus contorta*<sup>33?</sup> Occasional large synchronized flowering episodes should entail various costs compared to constant seed production, such as reduced opportunities for reproduction in low years<sup>1</sup>, or higher seedling densities leading to greater losses to competition, herbivory or pathogens<sup>34</sup>. Perhaps, in species with constant seed output, these costs are more significant. This opposite end of

the seedfall variability spectrum has received very little attention (Fig. 2), but we should be curious when plants can be constant in a varying environment.

Finally, masting needs to be described more numerically. The terminology of strict masting (masting versus non-masting species; mast versus non-mast years) has been widely and inappropriately applied to normal masting species, obscuring interesting patterns in the levels of variation in seed output. Janzen<sup>6</sup> said that Kawamura showed in 1927 that there is a 'distribution of flowering and seeding within a mast crop – a concept largely ignored by all before and after in their documentation of bamboo flowering or seeding'. Let us ensure that it is not ignored in future.

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