

MAST SEEDING IN PERENNIAL PLANTS: Why, How, Where?

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■ **Abstract** For many years biologists have debated whether mast seeding (the synchronous intermittent production of large seed crops in perennial plants) results from weather conditions or is an evolved plant reproductive strategy. In this review, we analyze the evidence for the underlying causes of masting. In the absence of selection for higher or lower variability, plants will vary in tandem with the environment (resource matching). Two selective factors often favor the evolution of masting: increased pollination efficiency in wind-pollinated species, and satiation of seed predators. Other factors select against masting, including animal pollination and frugivore dispersal. A survey of 570 masting datasets shows that wind-pollinated species had higher seed production coefficients of variation (CVs) than biotically pollinated ones. Frugivore-dispersed species had low CVs whereas predator-dispersed plants had high CVs, consistent with gaining benefits from predator satiation rather than dispersal. The global pattern of masting shows highest seed crop variability at mid latitudes and in the Southern Hemisphere, which are similar to the patterns in variability of rainfall. We conclude that masting is often an adaptive reproductive trait overlaid on the direct influence of weather.

INTRODUCTION

A reproductive episode that results in a superabundance of seeds can be a remarkable phenomenon. Anecdotes about entire forests being swamped with seeds, such as Malaysian forests dominated by Dipterocarpaceae (Janzen 1974, Ashton et al. 1988, Curran & Leighton 2000), or an entire area of a bamboo species suddenly coming into flower (Janzen 1976), draw attention. Many years ago, this pattern of reproduction became known as mast seeding, from the German word for fattening livestock on abundant seed crops, and hence years of high abundance are called mast years (Janzen 1971, Silvertown 1980, Kelly 1994). The pulse of resources

through masting can have effects throughout the ecosystem. For example, in the eastern United States masting triggers interacting density fluctuations in rodents, deer, Lyme disease, and gypsy moths (Ostfeld et al. 1996). Such community effects have been recently reviewed elsewhere (Ostfeld & Keesing 2000, Vander Wall 2001), so the focus of this review will be the evolution of masting from the plant's perspective. We ask whether variable seeding is simply a plant's reproductive response to variable weather conditions, or is a reproductive trait that has evolved through natural selection despite the costs of lost opportunities for reproduction (Waller 1979) and probable higher density-dependent seedling mortality in mast years (e.g., Hett 1971).

The most parsimonious hypothesis for variable seed production is variable weather conditions: the resource matching hypothesis (Norton & Kelly 1988, Sork 1993, Kelly 1994, Houle 1999). A recent study by Koenig & Knops (2000) provides evidence both for and against this hypothesis. They found that the scale of autocorrelation in seed production of Northern Hemisphere tree species occurred at the same spatial scale as autocorrelation in rainfall and temperature data, consistent with the underlying effect of climatic factors on masting. However, they also found that seed production has much higher variability than the weather factors, and the temporal patterns of autocorrelation in the climate variables do not match those of seed production. Thus, they concluded that weather alone could not be responsible for masting. In this review, we discuss the role of weather and list criteria for refuting the weather hypothesis as the sole explanation. For many species, selective factors are the ultimate cause of masting, but weather and resources must be involved as proximate causes. One recent advance is the development of new models to explain the mechanism of producing variable, synchronized seed crops. Our discussion will outline these models.

For plants with masting as a reproductive strategy, the question is why has it evolved? Two of the most prominent hypotheses are the pollination efficiency hypothesis, which states that synchronized, occasional flowering increases pollination success in wind-pollinated plants (Nilsson & Wästljung 1987, Norton & Kelly 1988, Smith et al. 1990, Kelly et al. 2001), and the predator satiation hypothesis, which states that large intermittent seed crops reduce losses to seed predators (Janzen 1971, Silvertown 1980). In animal-dispersed plants, masting may be favored or selected against, depending on the response of the disperser to mast crops (Janzen 1969, 1971, 1974, 1978; Silvertown 1980). For all of these hypotheses, the common element is that the selective advantage occurs through an economy of scale (Janzen 1978, Norton & Kelly 1988) whereby large reproductive efforts are more efficient than small ones, so plants reproducing in step with mast years will have higher fitness. In this analysis we will identify the criteria for demonstrating selection and review studies meeting these criteria. Masting has three key elements: variability, synchrony, and periodicity. The population level variation in seed crops (CV_p), as measured by the coefficient of variation ($CV = SD/mean$), results from the interaction of individual variability (CV_i , the average CV of individual plants over time) and synchrony among plants (Janzen

1971, Herrera 1998a). We will consider how economies of scale affect all of these elements.

One little-studied question is the global distribution of masting. Koenig & Knops (2000) reported higher interannual variability in seed production among species (based on CV) at lower latitudes, which suggests that weather conditions associated with latitude may influence the variability of seed production. Herrera et al. (1998) showed that CVs differ among species with different pollination and seed dispersal modes, in a pattern consistent with the selection hypotheses discussed above. However, Herrera et al.'s study did not control for the global distribution of those modes or the underlying variability in weather. One way to examine the evidence for weather versus selection is to study the global patterns of CV taking into account simultaneously the effects of latitude, pollination, and dispersal modes. In this paper, we present just such an analysis.

We have organized our ideas into three main sections. In the first section, we evaluate the roles of weather and the resource-matching hypothesis. Next, we review the evidence for the key selective pressures that might favor the evolution of masting. The third section analyzes patterns of among-year variation from a global perspective. Here we examine the latitudinal trend in variability in a key weather variable (rainfall). We also examine the CVs of 570 seedfall datasets to evaluate the extent to which latitude, pollination mode and dispersal mode can account for global patterns of CV. We conclude our paper by outlining productive areas of future research.

RESOURCES AND WEATHER

Weather and resources are clearly involved in mast seeding, but the exact nature of their involvement is less clear. One alternative is that plants simply respond to variable weather by flowering more in good years. The other alternative is that there are selective advantages to masting (ultimate factors) which modify plant responses to weather and internal resource levels (proximate factors) in order to enhance the interannual variation in seedfall. This section will review data on the links between weather and masting for evidence supporting either the weather or selection arguments. We will then examine cases that involve selective factors to see how weather and resources act as proximate factors.

Resource Matching: Weather Affecting Resources

The resource matching hypothesis states that *in the absence of selection for (or against) masting, seed crops will vary in response to environmental variation* (Kelly 1994).

The resource matching (RM) or weather tracking hypothesis is the oldest hypothesis for mast seeding. It postulated that each plant's available resources vary each year, being higher during favorable conditions, and reproductive effort

mirrors this variation (Büsgen & Münch 1929, Norton & Kelly 1988, Sork 1993, Kelly 1994). Hence, RM should produce a positive correlation between growth and reproduction within years (good years are good for both). Synchrony among plants arises incidentally because they experience similar weather. This nonadaptive hypothesis is the most parsimonious explanation for variability in reproduction.

Support for resource matching comes from various lines of evidence. Adverse weather (e.g., frost or drought) sometimes prevents reproduction, causing synchronization of low years (Sharp & Sprague 1967, Ågren 1988, Allen & Platt 1990, Fenner 1991, Sork et al. 1993, Houle 1999, Selas 2000, Inouye 2000). RM may therefore apply in highly variable environments, where reproduction may be impossible when conditions are bad. A possible example is restricted flowering and growth of perennials in semideserts in frequent dry years (e.g., reproduction in Western Australian shrubs, Davies 1976). Of more interest is how often RM explains high seed years (the core of the RM hypothesis). One good example is *Pinus banksiana* in Quebec, which shows positive correlations within plants across years among reproduction, growth, and good growing conditions (Despland & Houle 1997). Significantly, this species is strongly serotinous and the lifetime seed crop is retained on the tree until fire occurs, making the exact year of seed production irrelevant, so the plant is free to follow resource matching. Other studies claimed as supporting RM (Nienstaedt 1985, Byram et al. 1986, Willson 1986, Oyama 1990, Cremer 1992, Lord 1998) do not directly test it, usually because they compare multi-year averages of growth and reproduction across different plants.

The key evidence that disproves the RM hypothesis is the presence of “switching,” where in successive years plants move resources into, then away from, reproduction (Norton & Kelly 1988). A negative correlation between growth and reproduction (good years for reproduction are bad for growth) demonstrates switching and refutes the RM hypothesis. Such data are common for trees including *Abies*, *Acer*, *Betula*, *Dacrydium*, *Fagus*, *Picea*, *Pinus*, and *Pseudotsuga* (Morris 1951; Holmsgaard 1956, in Silvertown 1980; Eis et al. 1965; Tappeiner 1969; Gross 1972; Harper 1977, p. 654; Norton & Kelly 1988; Fenner 1991; Silvertown & Dodd 1999; Houle 1999; and references therein). Koenig & Knops (1998) in a review of 298 datasets found that negative correlations were widespread in Northern Hemisphere conifers. Negative correlations are also reported for herbaceous plants (e.g., Payton & Mark 1979, Muir 1995, Greer & McCarthy 2000).

Patterns of internal resource allocation in masting plants provide two other tests of RM. First, negative autocorrelation (current reproduction negatively related to previous reproduction) suggests the presence of switching. Negative autocorrelations are widespread (Norton & Kelly 1988; Allen & Platt 1990; Sork 1993; Sork et al. 1993; Sork & Bramble 1993; Koenig et al. 1994; Herrera et al. 1998; Stevenson & Shackel 1998; Koenig & Knops 1998, 2000; Selas 2000). Another test is the existence of bimodality (high and low years) in reproduction, which also suggests switching since environmental conditions are not bimodal (Koenig & Knops 2000). Bimodality is found in many species (Norton & Kelly 1988, Herrera et al. 1998), but not all (Kelly 1994, Koenig & Knops 2000).

Our conclusion is that switching (and hence selection for masting) is much more common than pure resource matching in plants with high interannual variability.

Cues for Masting: Weather as a Signal

Masting requires synchrony among plants, usually reliant on entrainment to a weather cue (Janzen 1971). Weather cues that are correlated with resource abundance offer the advantage of minimizing storage costs (Norton & Kelly 1988, Koenig et al. 1996). Therefore, correlations between high seed crops and years of abundant resources (e.g., Wright & van Schaik 1994, Fenner 1998, Schaubert et al. 2002) do not separate RM from the hypothesis that there has been selection for masting.

Cues are often not associated with increased resources, consistent with selection but not with RM. For example, masting in dipterocarps is triggered by night temperatures dropping 2°C over three nights (Ashton et al. 1988). In *Fraxinus excelsior*, the weather cues for heavy flowering were different from the weather variables associated with greater growth (Tapper 1996). In *Chionochloa pallens*, a simple binary weather cue (January temperatures over 11.5°C) affects flowering more than whole-season growing degree-days (Rees et al. 2002). Flowering may be triggered by drought (van Schaik et al. 1993, Wright et al. 1999) or fire (Payton & Mark 1979, Kelly 1994), both of which decrease resources. Therefore, evidence of the weather signals that trigger masting is universally consistent with selection, but frequently inconsistent with RM.

Resource Models: The Mechanisms of Masting

Ultimately, masting as a reproductive strategy requires some kind of resource allocation mechanism that exaggerates variation among years. The underlying question is, if a plant has a physiological mechanism that alters flowering effort in relation to an environmental signal, why does it do so in just this fashion? Janzen (1971) predicted that in masting species, selection should favor flowering to be hypersensitive to weather variables and to levels of reserves in the plant. Recent work supports this prediction. The first step was developing models for how a plant's internal resource levels influence flowering patterns. Several recent models generate intermittent reproduction by each plant, driven by resource thresholds for reproduction coupled with large expenditure when reproduction occurs (Isagi et al. 1997, Satake & Iwasa 2000). This internal process would lead to strong negative autocorrelations and increase individual variation. The exact level of individual variation depends on how heavily the plant invests in reproduction during years when it does reproduce (the depletion coefficient); with a large depletion coefficient, reserves are exhausted and the plant cannot flower again for some time. Importantly, the model predicts stable flowering provided that the depletion coefficient is below a critical value, otherwise chaotic masting dynamics result (Satake & Iwasa 2000).

A version of this resource threshold model has now been applied to a 12-year dataset for *Chionochloa pallens* in New Zealand (Rees et al. 2002). The population had a high CV_p (1.88) and very high synchrony among plants (mean pairwise $r = 0.77$). Rees et al. showed that RM models fit the data poorly, whereas the resource threshold model fit excellently. The depletion coefficient calculated by the *C. pallens* model was in the region giving chaotic masting dynamics. Moreover, they determined that this value of the depletion coefficient minimizes seed predation by specialist invertebrates. This case illustrates how seed predators can select for a hypersensitive internal mechanism that controls and synchronizes reproduction among individuals.

Thus, the proximate mechanisms that integrate weather cues and resource utilization can produce more variable patterns of reproduction than expected from simple resource matching. Next, we ask why this would be advantageous.

SELECTIVE FORCES AND ECONOMIES OF SCALE

Types of Selective Advantage

An economy of scale (EOS) is required for mast seeding to be selectively advantageous (Janzen 1978, Norton & Kelly 1988). Here we review the three EOS hypotheses with the most experimental testing—wind pollination, predator satiation, and animal dispersal—and comment briefly on the animal pollination hypothesis (that large flower crops attract disproportionately more pollinators). Six other published hypotheses are not reviewed for the following reasons. The outcrossing hypothesis (that mast years facilitate outbreeding: Janzen 1978, Tisch & Kelly 1998) awaits experimental testing. The accessory costs hypothesis (high fixed costs of reproduction favor fewer, larger reproductive episodes: Kelly 1994), and the large seed hypothesis (selection for larger seeds increases the recovery time between seed crops: Sork 1993) do not require synchrony among plants. Three hypotheses apply only in specialized situations: the environmental prediction hypothesis (that plants reproduce heavily in years that will be favorable for seedling establishment: Kelly 1994), the bamboo fire cycle hypothesis (synchronized death of bamboos after masting encourages fire, which prevents trees from out-competing the bamboo: Keeley & Bond 1999), and the predator cleansing hypothesis (the synchronized death of bamboos reduces densities of herbivores feeding on adult leaves: Pearson et al. 1994).

Wind Pollination

The pollination efficiency hypothesis states that *masting should be strongly selected in species that can achieve greater pollination efficiency through synchronized above-average flowering effort*. This efficiency is most likely to be seen in wind pollinated plants because they are at less risk of saturating the pollinators (Janzen 1978, Smith et al. 1990, Sork 1993, Kelly et al. 2001).

To support this hypothesis, one must show that percent fruit set is higher when flower density is higher. This has been frequently shown in wind-pollinated species (Nilsson & Wästljung 1987, Norton & Kelly 1988, Smith et al. 1990, Allen & Platt 1990, Burrows & Allen 1991, Kelly 1994, Shibata et al. 1998, Houle 1999, Kelly et al. 2001), although some species show no effect (Sork 1993, Kelly & Sullivan 1997). The species most likely to gain benefits are those whose pollination success at the long-term average flowering effort is low compared to the maximum achievable with superabundant pollen (Kelly et al. 2001). Pollination is likely to be more sensitive to flowering density in obligate outcrossers (e.g., dioecious or self-incompatible species). The consequences of inefficient pollination should be more severe among species with expensive unpollinated female structures (Smith et al. 1990), so these species should gain more from masting, but empirical tests of this prediction have been equivocal (Kelly et al. 2001).

The pollination efficiency hypothesis depends on the size of the current flowering effort, but the sequence of reproductive efforts among years is irrelevant; for example, having successive mast years would not be disadvantageous (Norton & Kelly 1988). Plants in productive habitats could reach a high enough level of reproductive effort for efficient pollination every year, so they could reproduce constantly and avoid the negative consequences of masting (Hett 1971, Waller 1979, Kelly 1994). Plants in unproductive habitats are unable to reach this level every year, so they accumulate reserves to be expended in occasional large efforts.

Pollination efficiency could apply to animal pollinators if they are attracted to large flowering displays (Kelly 1994). Supporting data are scarce; the insect-pollinated *Acer saccharum* shows higher fruit set in mast years (Curtis 1959, p. 105; Graber & Leak 1992), although its pollen can also be wind-dispersed. In general, animals are more likely to be saturated by large crops, providing diseconomies of scale (Herrera et al. 1998, and see "Global Patterns of Variability in Seed Production," below). We conclude that wind pollination often provides an EOS but animal pollination does not.

Predator Satiation

The predator satiation hypothesis states that *seed predators cause selection for masting when larger seed crops synchronized among individuals experience lower percentage seed predation* (Janzen 1971).

Predator satiation favors masting when variation in seed crops satiates seed predators in high-seed years. Salisbury (1942, p. 2) pointed out that in beech and oaks the only seeds to escape predation were produced in mast years, and that if a species had a constant seed crop its natural enemies could increase in number until all seeds were destroyed every year. Janzen (1971, 1974, 1976, 1978) rekindled interest in mast seeding when he explored predator satiation at length. Predator satiation requires interannual variation in seed crops, but it is unclear whether selection acts directly to favor gaps between mast years by starving predators in

low-seed years, or whether gaps are an inevitable consequence of selection for larger crop size (Janzen 1978, Silvertown 1980).

The simplest evidence for predator satiation is lower seed predation in high-seed years. The ideal data are a long time-series for both seed production and seed predation at a site. Variation in space within a year is sometimes used (e.g., Nilsson & Wästljung 1987) but may not be a good analog for temporal variation. Numerous studies provide evidence of lower predation during mast years, both for insect predators (e.g., McQuilkin & Musbach 1977, DeSteven 1983, Sork 1983, Schupp 1990, Crawley & Long 1995, Sullivan & Kelly 2000, Shibata et al. 1998) and vertebrates (e.g., Boucher 1981, Nilsson 1985, Smith et al. 1990, Crawley & Long 1995, Hart 1995, Wolff 1996, Forget et al. 1999, Vander Wall 2001, Theimer 2001), although some counter-examples exist (Ågren 1988, Hart 1995, Sperens 1997). Ideally, data should record losses separately for different predator species (e.g., Hedlin 1964, McKone et al. 2001). Different seed predators may vary in their responses to masting: Insects may eat less but vertebrates eat more of a large seed crop (Nilsson & Wästljung 1987, Graber & Leak 1992). Different responses can occur even within a guild (e.g., two specialist dipteran predators of *Chionochloa pallens*, McKone et al. 2001).

A thorough analysis for predator satiation requires testing for a numerical response from the predator (reduced predator densities following low seed years), detected by lower seed losses in years following a small seed crop (Silvertown 1980, Kelly & Sullivan 1997). Because predation is often sequence-dependent, two similarly sized flowering efforts could have very different levels of predation if one followed a high seed year and the other followed a low seed year (e.g., Hedlin 1964, McDonald 1992). If the seedfall time series shows simple alternation, then current crop can be a reasonable proxy for the change in crop. It will not be a good proxy where the time series is more complicated, in which case predator satiation may be unrelated to current reproduction but significantly related to the change in reproductive effort (e.g., *Chionochloa pallens*: Kelly & Sullivan 1997). The numerical response should be present in many, though not all, cases of predator satiation. When insect predators have extended diapause (e.g., Hedlin 1964, Kelly et al. 2000), effects from previous years will be more complex.

Selection by predators for or against synchrony is strongly affected by the mobility of the predator (Janzen 1978). If the predator can move easily between plants, selection will favor synchrony among plants at a scale comparable to the predator's mobility. The best large-scale examples involved specialist birds like the passenger pigeon, Carolina parakeet, and the Javanese finch *Serinus estherae* (Janzen 1971, 1976). The mammalian predators of dipterocarp species also select for synchrony on a large scale (Curran & Leighton 2000). In contrast some invertebrates may be satiated at the level of a few trees or even a single tree (e.g., *Cydia fagiglandana*: Nilsson & Wästljung 1987), necessitating very local, or no, synchrony. If the predator is a mobile generalist, it may preferentially forage on an abundant seed crop, causing higher seed losses in mast years (Janzen 1971, Nilsson & Wästljung 1987). Therefore, a plant with several different types of seed predator may experience contradictory selection pressures. For example in *Betula*

allegghaniensis larger seed crops experienced lower percentage losses to insects but higher percentage losses to birds (Graber & Leak 1992). Because of the difference in mobility, these contradictory selection pressures could be resolved; *Betula alleghaniensis* might reduce losses to invertebrates by increasing individual seed crop variability and simultaneously reduce losses to birds by reducing synchrony to reduce the degree of masting (Kelly et al. 2001). However, the dramatic examples of masting clearly require both high interannual variability and high synchrony.

The predator satiation hypothesis is widely studied and widely accepted, perhaps beyond what is warranted by the data. The challenge for future studies is to estimate selective impacts, both by modeling seed survival at the population level, and by using long-term data on individual plants to document the relationship between the selective pressures and individual fitness, while simultaneously estimating the selective impact of multiple seed predators.

Animal Dispersal

The animal dispersal hypothesis states that *masting should be selected against in plants dispersed by frugivores that are saturated with large fruit production, creating diseconomies of scale* (Janzen 1971, Silvertown 1980, Herrera et al. 1998).

The effect of masting on seed dispersal varies among dispersal modes. Abiotic dispersal and dispersal on the outside of animals (ectozoochory) are unaffected by masting, whereas frugivore dispersal (endozoochory) would be negatively affected by masting, and predator dispersal (scatterhoarding or dyszoochory, Janzen 1971) may be affected positively. Dispersal could provide an EOS if large fruit crops attract a generalist frugivore (Bawa 1980, Kelly 1994) or result in wider dispersal by scatterhoarders (Smith et al. 1990). The key evidence supporting this hypothesis would be that in high seed years, either a higher fraction of the seed crop is dispersed, or the mean dispersal distance is greater. However, such evidence is rare (e.g., Christensen & Whitham 1991).

Several studies have shown that dispersal by frugivores is negatively affected by masting (Ballardie & Whelan 1986, Koenig et al. 1994, Herrera et al. 1994, Levey & Benkman 1999). The percentage of fruit crop removed is usually either independent of crop size (Davidar & Morton 1986) or is smaller in large crops due to satiation (Jordano 1987; Herrera et al. 1994, 1998; Herrera 1998b). Therefore frugivore-dispersed plants should be less likely to mast than plants with other kinds of dispersal, just as Silvertown (1980) and Herrera et al. (1998) reported from literature reviews (see also "Global Patterns of Variability in Seed Production," below).

For predator dispersal Vander Wall (2001) claims, with little evidence, that masting enhances dispersal. Dispersal is typically either unaffected or worsened in high seed years. For example, in *Pinus monophylla*, scatterhoarding birds collected 89% of seeds from the canopy in a low seed year but only 43% in a high seed year (Vander Wall 1997). Thus, less dispersal took place in a mast year. Also, seeds may be moved shorter distances in a mast year if animals recache seeds less often when seeds are abundant (Vander Wall & Joyner 1998). Masting benefits

predator-dispersed plants, but wholly by improving the chances of seeds escaping postdispersal predation (Janzen 1971, Vander Wall & Balda 1977, Christensen & Whitham 1991, Herrera et al. 1998, Vander Wall 2001, Theimer 2001), consistent with the predator satiation hypothesis.

Conclusions: Site Productivity and Contrasts with Animals

We have shown that both wind-pollination efficiency and predator satiation often select for masting, and that dispersal by frugivores may sometimes select against it. In this concluding section, we consider the implications of these factors and make two predictions: Masting should be more common in both unproductive habitats and dominant plant species. Secondly, we consider why the equivalent of masting appears to be rarely selected for in animals.

Plants in less productive habitats should show more pronounced masting. Lower productivity increases the time required to recover between high seed crops, whether those seed crops are large to gain wind pollination benefits or to satiate predators. Factors that reduce plant productivity and are associated with more pronounced masting within or among species include altitude (Allen & Platt 1990, Webb & Kelly 1993, Mencuccini et al. 1995, Sullivan & Kelly 2000, Kelly et al. 2001), latitude (Hagner 1965, in Harper 1977), and soil infertility (Janzen 1974). For example, Gysel & Lemmien (1964) measured fruit output of *Elaeagnus angustifolia* and *Lonicera tartarica* in Michigan on normal and impoverished soils. In both cases reproductive output decreased on poorer soils and varied more among years.

Plants that dominate their communities are more likely to show masting (Janzen 1978, Boucher 1981). First, wind pollination tends to be found in dominant rather than sparse species; and second, dominant species are more vulnerable to seed predation, as they cannot escape by having low apparency. Predator satiation is also easier where one species (or group of related species, e.g., the Dipterocarpaceae) dominate the local vegetation, so masting should be especially well-developed in low-diversity communities, e.g., temperate forests (Janzen 1971).

These trends lead to an interesting prediction—that the tropics should have few masting species. Because the tropics are typified by biotic pollination and dispersal (which select against masting, see above), high plant species diversity, high site productivity, and relatively low year-to-year variation in climate, mast seeding should be uncommon there. The spectacular exception of dipterocarp forests may prove the rule (Wright et al. 1999) because these forests are dominated by closely related species that require synchrony and large crops to satiate shared vertebrate seed predators (Janzen 1969).

Finally, we comment briefly on the contrast with animals, within which “masting” is extremely rare. There are a few species of synchronized semelparous insects, most famously six species of cicadas (Heliövaara et al. 1994). Synchronized iteroparity is almost unknown. We know of only two cases where a long-lived iteroparous animal will synchronously breed in some years and refrain in others even given an adequate food supply. Two parrots, the kaka (Wilson et al.

1998), and the kakapo (Clout & Merton 1998) breed only in response to a masting food crop, regardless of supplementary artificial feeding. Other possible cases include the passenger pigeon (Bucher 1992), New Zealand parakeets (Moorhouse 1997), Australian banded stilt (Flannery 1994, p. 89), and New Zealand pigeon (Clout et al. 1995). We conclude that such behavior is so rare in animals yet so common in plants because animals are shorter-lived (increasing the costs of lost reproductive opportunities) and use mobility to solve the problems (finding mates, avoiding predators) that plants respond to by masting. Thus, mast seeding may be one of the “evolutionary consequences of being a plant” (Bradshaw 1972). Massed reproduction in immobile animals such as corals may be analogous to mast seeding.

GLOBAL PATTERNS OF VARIABILITY IN SEED PRODUCTION

One way to evaluate the relative impacts of weather and selection on variability of seed production is to test the two hypotheses simultaneously. Two recent reviews have tested them one at a time. Koenig & Knops (2000) used 443 datasets on reproduction of temperate Northern Hemisphere trees to test predictions of the weather hypothesis. As discussed previously (in the “Introduction,” above) they found that weather influences seedfall CV (seedfall variability decreases at higher latitudes, in parallel with decreases in the CV of rainfall), but that weather could not account fully for the observed patterns. In a separate review of 296 datasets for woody plants, Herrera et al. (1998) compared interannual variability in seedfall against postulated selective factors (pollination efficiency, predator satiation, and seed dispersal), while controlling for phylogenetic constraints. They predicted that wind-pollinated species should have higher CV_{ps} than biotically pollinated species but the differences were not quite significant. For dispersal mode they predicted, and found, that frugivore-dispersed plants had significantly lower CV_{ps} than abiotically and predator-dispersed species. Herrera et al. (1998) conclude that their analysis supports the hypotheses that these factors selected for masting. Here, we integrate the approaches of these two studies to simultaneously test predictions about differences in CV_{ps} across pollination and dispersal modes while controlling for, and estimating, the effect of latitude.

To understand the influence of weather, we will first report a global analysis of the CV of annual precipitation, a key weather factor for plants, using 30 years of data from 19,279 weather stations (downloaded from the Global Historical Climatology Network, <ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/>), which was analyzed with a regression of the CV for rainfall versus latitude, with hemisphere as a class variable. Next, we will examine seed variability data using an Analysis of Covariance (ANCOVA) to evaluate the impact of pollen vector, seed dispersal mode, growth form, and hemisphere as factors, and latitude and length of study as covariates, on the CV of seed production. Our analysis employs 570 studies of ≥ 6 years duration compiled from reviews (Silvertown 1980, Webb & Kelly 1993, Kelly 1994, Herrera et al. 1998, Kelly et al. 2000, Koenig

& Knops 2000, Schaubert et al. 2002) and the primary literature (Appendix A, <http://www.annualreviews.org/MastingAppendix.html>). We particularly sought extra datasets from herbaceous plants and from tropical latitudes. We categorized pollination and dispersal modes in the same way as Herrera et al. (1998).

In our global weather analysis, the CV of rainfall shows a nonlinear association with latitude (Figure 1a) with a peak at about 20–25° and decreasing variability nearer the equator and toward 60° latitude. The regression model had significant first, second, and third order terms (Figure 1a), with a significant effect of hemisphere ($df = 1$ and 19,265; $F = 671.8$, $P < 0.0001$). The mean CV for the Southern Hemisphere (back-transformed CV = 0.303, $n = 7225$) was greater than that of the Northern Hemisphere (CV = 0.248, $n = 12,045$), but both means are small compared to seedfall mean CVs. The conclusion is that the annual variability of a key weather variable, rainfall, changes significantly with latitude. If rainfall affects seed crops, then we predict that CV_p should peak at mid latitudes and be greater in the Southern Hemisphere.

Our analysis of seed production CV_p shows that both latitudinal effects and differences among pollen and seed vectors are significant (Table 1). The analysis supports the hypothesis that climatic factors influence variability in seed production. Latitude had significant first and second order terms (Table 1). The curvilinear relationship between CV_p and latitude is consistent with the precipitation/latitude relationship (Figure 1b), but here the peak is around 45°. Due to an imperfect spread of seedfall data across latitudes, we cannot determine why the latitudinal curves for rainfall and seed production do not concur precisely. Both the precipitation and seedfall data indicate lower variability in the tropics (consistent with the prediction in “Conclusions: Site Productivity, and Contrasts with Animals,” above) but we have very few tropical seedfall datasets. In contrast the prediction from “Conclusions: Site Productivity, and Contrasts with Animals,” above, of higher CV_p at high latitudes is not supported. Similar to the rainfall data, seed production variability for the Southern Hemisphere (back-transformed least squares mean $CV_p = 1.369$, $n = 84$) is greater than that of the Northern Hemisphere ($CV_p = 1.083$, $n = 488$). The estimates of CV_p are almost an order of magnitude greater than precipitation CVs. Thus, one or more factors are causing greater annual variability in seed production than occurs in precipitation.

In addition to the significant effect of latitude the ANCOVA model supports the predictions of the EOS hypotheses. By using the least square mean estimates that remove the effect of the other parameters, we find that CVs differ significantly between pollen vectors and among seed dispersal modes (Table 1) in a pattern consistent with selective economies of scale. Abiotic pollination has a higher mean CV_p than biotic pollination (pollination efficiency hypothesis). Species with seed dispersal by predators had a higher mean CV than species dispersed abiotically or by frugivores, supporting the predator satiation hypothesis. We also found a significant interaction between pollen and seed vector, which is not surprising because selection on pollen mode will affect seeding variability and vice versa. Consistent with the pollination efficiency and seed dispersal

TABLE 1 ANCOVA of factors affecting square root transformed CV of yearly seed production based on 570 datasets from 175 species (For sources of data, see Appendix A, <http://www.annualreviews.org/MastingAppendix.html>)

Source	DF	SS	MS	F Value	Pr > F
A ANCOVA for square root transformed CV of yearly seed production ($R^2 = 0.289$)					
Model	18	9.051	0.502	12.45	<.0001
Pollen vector	1	0.363	0.363	8.99	0.0028
Seed vector	2	0.501	0.251	6.20	0.0022
Pollen \times seed	2	0.410	0.205	5.08	0.0065
Growth form	4	0.657	0.164	4.07	0.0029
Hemisphere	1	0.441	0.441	10.91	0.0010
Pollen \times hemisphere	1	0.089	0.089	2.20	0.1229
Seed \times hemisphere	2	0.708	0.354	8.76	0.0002
Latitude	1	0.414	0.414	10.26	0.0014
Latitude ²	1	0.179	0.179	4.43	0.0359
Latitude \times hemisphere	1	0.259	0.259	6.42	0.0116
Latitude ² \times hemisphere	1	0.096	0.096	2.39	0.1229
Length of study	1	0.654	0.654	16.20	<.0001
Error	551	22.253	0.040		
B Least square means of CV, using back-transformed values of square root transformed CV, by pollination and dispersal mode. Sample sizes are given in parentheses. Overall mean CV = 1.050					
	Abiotic pollination	Biotic pollination	Combined		
Predator-dispersed	1.672 (117)	1.861 (28)	1.765 (145)		
Frugivore-dispersed	1.443 (15)	0.692 (40)	1.034 (55)		
Abiotically dispersed	1.162 (347)	0.741(23)	0.940 (370)		
Combined	1.418 (479)	1.039 (91)			

hypotheses, biotic pollination and frugivore dispersal are associated with the lowest mean CV.

The geographic distribution of pollen and dispersal modes is clearly not random with respect to latitude (Figure 1*b*). Wind-pollinated, predator-dispersed species (filled triangles) are common above 45° latitude while animal-pollinated, frugivore-dispersed species (hollow squares) are common below 45° latitude. However, the ANCOVA model suggests that latitude has an effect even when pollination and dispersal modes are controlled for and vice versa.

We tested the effect of growth form because masting should be favored in long-lived plants, not just in trees (Waller 1979, Silvertown 1980). The mean CV_p s differed significantly among growth forms from a maximum in herbaceous dicotyledons (mean $CV_p = 1.683$, $n = 17$ datasets), through herbaceous monocots (1.403, $n = 20$), trees (1.253, $n = 474$), and shrubs (1.177, $n = 58$), to a minimum in woody monocots (0.700, $n = 3$ palm datasets). The fact that trees do not

have the highest value suggests the need for better study of masting in other kinds of perennials.

Length of study accounted for significant variation in our model (Table 1). Although the average length of study was 11.1 years and we had 86 datasets with at least 15 years of data, the range (6 to 35 years) is considerable. The fact that longer studies had higher CVs of seed production (in contrast to Herrera et al. 1998) suggests either that as number of years increases, the CV becomes larger (the red shift often seen in ecological data; Pimm & Redfearn 1988), or that investigators are more likely to prolong studies of more variable species. Our data support the latter alternative. Datasets that were continued for 20 years or more were already significantly more variable at the 10-year stage (mean CV = 1.53, $n = 39$) than datasets that were terminated after exactly 10 years (mean CV = 1.17, $n = 69$) according to a one-way ANOVA ($F_{1,106} = 14.11$, $P < 0.001$). In contrast, in these longer datasets the mean CVs after 10 years (1.53) did not increase significantly after 15 years (1.52) or after the full duration (mean duration 25.7 years, mean CV = 1.57, $F_{2,114} = 0.14$, NS). These results indicate that plant variability affects study duration rather than study duration affecting the measured variability.

Although we collated many datasets, there are limitations in the spread of data. The 570 datasets spanned 175 species, 74 genera, and 37 families (Table 2) but, as in previous reviews (Herrera et al. 1998, Koenig & Knops 2000), were skewed toward north temperate trees. For example, *Pinus* contributed 135 studies and 14 species, and *Quercus* 58 studies and 23 species (Table 2). Geographically, the datasets span 19 countries, skewed toward the temperate Northern Hemisphere (Figure 1c) with the USA and Finland contributing 50% of all studies.

Finally, we comment briefly on the unavoidable confounding effects in our model. First, we noted earlier that pollen and seed dispersal modes were not distributed randomly with respect to latitude nor are they independent of each other. Statistically our samples should ideally be more balanced across latitude, but the problem is more one of evolution than sampling error. Second, genera and species are very unevenly represented. We decided to include every available dataset despite replication of taxa. When we compared CVs for different sites within a taxon, we found a great deal of variation. In fact, if latitude and local weather conditions as well as pollen/dispersal traits jointly influence CV, then data from separate sites are partially independent and offer additional information. To check that our results were not driven by over-representation of *Pinus*, we ran the ANCOVA excluding this genus ($n = 435$) and the conclusions were identical. Third, we omitted taxonomic status from our final model. If it was included, we lost the latitude effect because different taxa occur in different parts of the world. For this particular analysis, we were more interested in how the CVs vary globally with latitude than in how CVs vary with taxon. Reassuringly, Herrera et al. (1998) found that controlling for phylogeny did not alter the conclusions from their analysis of pollination and dispersal modes.

TABLE 2 Taxa involved in the 570 studies of seed production for 6 or more years (for details of sources see Appendix A)

Family	# studies	Family	# studies	Family	# studies
A List of all 37 families and number of studies per family ranked by frequency of study					
Pinaceae	279	Caprifoliaceae	4	Tiliaceae	2
Fagaceae	95	Arecaceae	3	Bombacaceae	1
Betulaceae	46	Elaeocarpaceae	3	Burseraceae	1
Fabaceae	29	Anacardiaceae	2	Hippocastanaceae	1
Poaceae	20	Cornaceae	2	Labiataeae	1
Cupressaceae	9	Corylaceae	2	Meliaceae	1
Oleaceae	9	Elaeagnaceae	2	Nyssaceae	1
Rosaceae	9	Ericaceae	2	Rubiaceae	1
Agavaceae	8	Eucryphiaceae	2	Smilacaceae	1
Juglandaceae	7	Liliaceae	2	Violaceae	1
Podocarpaceae	7	Monimiaceae	2	Winteraceae	1
Gentianaceae	6	Taxodiaceae	2		
Aceraceae	4	Thymelaeaceae	2		
B List of genera (with family) out of 74 sampled genera with more than 10 studies, ranked by frequency					
Genus (Family)	Number of studies	Genus (Family)	Number of studies		
<i>Pinus</i> (Pinaceae)	135	<i>Chionochloa</i> (Poaceae)	17		
<i>Picea</i> (Pinaceae)	66	<i>Fagus</i> (Fagaceae)	17		
<i>Quercus</i> (Fagaceae)	58	<i>Acacia</i> (Fabaceae)	16		
<i>Abies</i> (Pinaceae)	43	<i>Pseudotsuga</i> (Pinaceae)	12		
<i>Betula</i> (Betulaceae)	35	<i>Tsuga</i> (Pinaceae)	12		
<i>Nothofagus</i> (Fagaceae)	18	<i>Larix</i> (Pinaceae)	11		

Our ANCOVA analysis supports the notion that selection favors the evolution of masting behavior for species with certain pollen and seed attributes. The large values of CV_p relative to the precipitation CVs and the significant effects of pollen and dispersal modes are strong evidence. Ideally, a global analysis would include more data points for tropical, herbaceous, and Southern Hemisphere populations. However, generalizations about the global patterns of CV are now reasonably robust. Our conclusions are consistent with those of Herrera et al. (1998) and Koenig & Knops (2000). We now need studies with a different approach, particularly long-term studies with data for individual plants, to study the selective pressures directly and to see whether they are affecting variability, synchrony, or masting interval. In other words, we need microevolutionary studies, especially from outside the Pinaceae and Fagaceae. It would be helpful to study different species at the same site because they would be experiencing the same weather. In addition, we could benefit from macroevolutionary studies that compare seeding schedules in related species with different pollen or seed dispersal modes. These approaches will answer questions that broad surveys cannot.

FUTURE DIRECTIONS

We highlight eight promising directions for future research. (a) We need more tests of predator satiation that model the selective benefits of masting and test for numerical responses. (b) Physiological work on resource acquisition and depletion will help to quantify the underlying mechanisms of masting. Long-term observational studies on individual plants and manipulative experiments that alter resources would both be worthwhile. (c) We need to study the relationship between site productivity and degree of masting, including more data on tropical plants and plants of arid environments. (d) We should study the selective forces and physiological mechanisms of plants with very constant reproduction. (f) Study of anthropogenic impacts on masting is desirable. For example, global warming may disrupt the temperature cues that synchronize plants, causing masting to fail (McKone et al. 1998), or fragmentation may devalue the benefits of masting (Curran & Leighton 2000, Kelly et al. 2001). (g) We need to model the impact of pulsed resources on animal communities (Ostfeld & Keesing 2000), particularly if global warming may disrupt masting. (h) We need explicit study of the spatial dimension in masting. Studies of local and meso-scale spatial autocorrelation similar to those done with animal populations (Bjørnstad et al. 1999) can clarify the scale of biotic versus abiotic interactions. (i) Time-series analysis of periodicity in masting species (e.g., Bonferroni series) can elucidate both the dynamics of seedfall patterns and interactions with predator population responses if data sets of adequate duration can be assembled.

The history of masting has had several phases. Janzen and others initiated many evolutionary hypotheses over a short period, which were followed by gradual empirical testing of these ideas. Now we are entering an era of mechanistic understanding of the spatial and temporal patterns, the causes, the physiological dynamics, and the cascading consequences of mast seeding.

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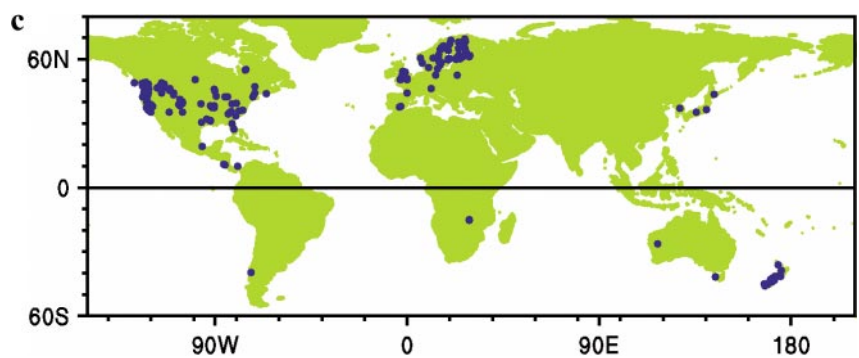
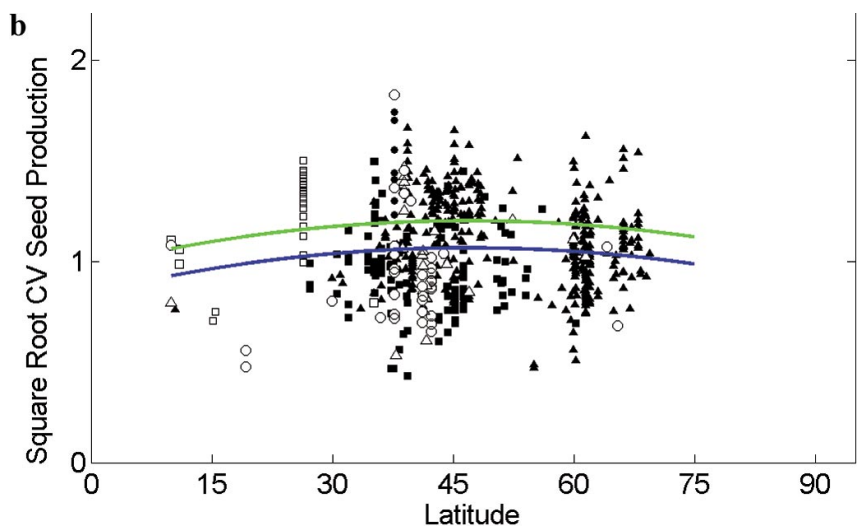
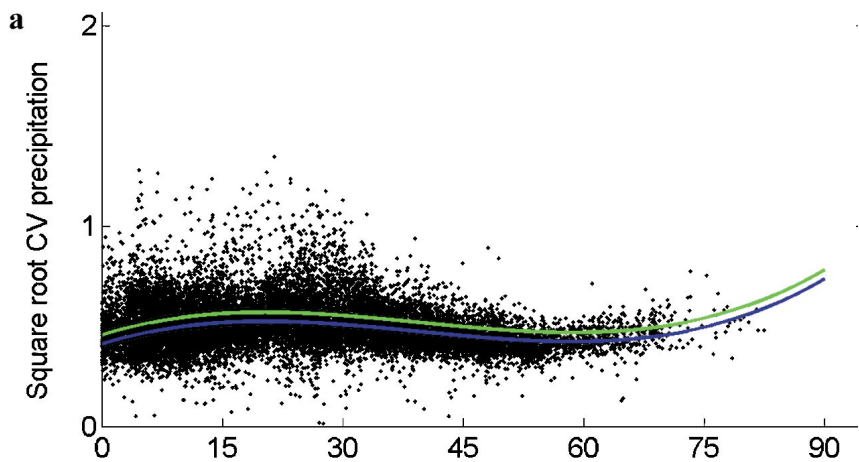
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APPENDIX A: SOURCES OF DATASETS

See <http://www.annualreviews.org/MastingAppendix.html>



See legend on next page

Figure 1 (See figure on previous page) Global patterns of mast seeding. (a) Variability of annual precipitation (CV) from 19,279 weather stations versus absolute latitude (both hemispheres combined). The equation for Northern and Southern hemispheres is: square root $CV_{\text{precipitation}} = \beta_o + 0.0128 (\text{latitude}) - 0.0004 (\text{latitude}^2) + 3.5 \times 10^{-6} (\text{latitude}^3)$ where $\beta_o = 0.4551$ for Southern hemisphere (green line, upper) and 0.4098 for Northern hemisphere (blue line, lower; $R^2 = 11.5\%$, $P < 0.0001$). (b) Seedfall variability (CV_p) in 570 datasets versus latitude. Symbols indicate mode of pollination (open symbols = biotic, filled = abiotic) and dispersal (abiotic = triangle, frugivore = square, predator = circle). The equation for both hemispheres is: square root $CV_p = \beta_o + 0.0095 (\text{latitude}) - 0.0001 (\text{latitude}^2)$ where $\beta_o = 0.9790$ for Southern hemisphere (green line, upper) and $\beta_o = 0.8444$ for Northern hemisphere (blue line, lower). See Table 1 for summary of ANCOVA statistics. (c) Distribution of the 570 seedfall datasets. Note the abundance of data from North America (250 datasets), Europe (216) and Australasia (79), and the dearth of data for Asia (12), Central and South America (11), Africa (2), and the tropics generally.