EVALUATING THE WIND POLLINATION BENEFITS OF MAST SEEDING

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Abstract. We developed a conceptual model for evaluating the benefits of wind pollination to mast-flowering species. The benefit that a plant population gains from mast flowering via increased wind pollination efficiency was predicted from how far pollination efficiency at mean seed crop size falls below the maximum. Species were most likely to benefit from mast seeding if mean reproductive effort in the field gave an intermediate level of pollination efficiency, regardless of the cost of unpollinated female structures. To quantify the benefits of different degrees of mast flowering, a simulation model was used to alter the seed production coefficient of variation (CV) and to calculate its effects on weighted mean pollination efficiency. The model was applied to seven real data sets for five species with pollination benefits from mastng that ranged from relatively small (Chionochloa pallens), to moderate (Dacrydium cupressinum, Betula alleghaniensis), to large (Nothofagus solandri, N. menziesii).

Many studies have reported higher seed production coefficients of variation at higher altitudes and latitudes within a species. Our model showed that higher coefficients of variation are favored by reduced mean seed output per plant at higher altitudes. Data for N. solandri at three altitudes in one site showed much higher pollination benefits from mastng at higher altitudes. Reduced plant density (e.g., through fragmentation), which also lowers mean flowering effort per unit area, resulted in large increases in mastng benefits in N. solandri, but only small increases in C. pallens. These contrasting results were primarily due to differences between the two species in mean reproductive effort vs. wind pollination efficiency, rather than to differences in the effects of fragmentation and altitude.

The relative effects of masting on pollination, insect seed predation, and bird seed predation were modeled in B. alleghaniensis. Masting produced a small economy of scale from insect predator satiation, but an almost equivalent diseconomy of scale resulted from increased levels of bird seed predation. Efficiency of wind pollination improved moderately with increasing CV, providing some overall benefits from mastng in this species. Accordingly, we propose that mastng can be favored by either one dominant economy of scale (such as wind pollination efficiency in N. solandri or predator satiation in C. pallens), or a balance among several factors (such as pollination, predator satiation, and predator attraction in B. alleghaniensis). We predict that, in the absence of any selective benefits or disadvantages of mastng, plants would be expected to have coefficients of variation in the range 0.85–1.35.

Key words: economies of scale; fragmentation; mast flowering; mast seeding; modeling; New Zealand; predator satiation; seed set; selective advantage; wind pollination.

INTRODUCTION

Mast seeding (synchronous, highly variable seed production among years by a population of plants; Kelly 1994) is characteristic of many species worldwide, including temperate forest trees (Silvertown 1980, Nilsson and Wästljung 1987, Norton and Kelly 1988, Allen and Platt 1990, Sork et al. 1993, Koenig et al. 1994, Koenig and Knops 1998), tropical trees (Janzen 1971, Foster 1977, Ashton et al. 1988), and temperate herbs (Campbell 1981, Brockie 1986, Kelly et al. 1992, Kelly and Sullivan 1997). The evolution of mast seeding is puzzling because it imposes a number of clear selective disadvantages, including lost opportunities for reproduction (Waller 1979, 1993) and more severe density-dependent mortality among seedlings produced in mast years (Hett 1971). To counter these inescapable disadvantages, some benefits from mast seeding must exist, otherwise masting would be selectively disadvantageous. Such benefits must provide economies of scale, i.e., greater reproductive efficiency at high reproductive effort (Norton and Kelly 1988).

Numerous, non-mutually exclusive hypotheses have been advanced as possible evolutionary advantages of mast seeding. Kelly (1994) identified eight, of which the two best supported empirically are predator satiation (Silvertown 1980, Nilsson and Wästljung 1987, Kelly and Sullivan 1997) and wind pollination (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990). A recent survey of 296 data sets showed that wind-pollinated species were significantly more vari-
able in seed output than animal-pollinated species (Herrera et al. 1998). The principal potential wind pollination benefit of masting is higher fertilization and seed set during years of heavy flowering, due to a pollination economy of scale (Nilsson and Wästljung 1987, Norton and Kelly 1988, Allen and Platt 1990, Smith et al. 1990, Sork 1993, Kelly 1994). It should be noted that masting occurs in both angiosperms and gymnosperms; for simplicity, we apply the general term "flowering" to both.

In an important paper, Smith et al. (1990), made predictions about which characteristics should favor mast seeding in wind-pollinated species. They proposed that wind pollination benefits from mast seeding are likely to occur only in taxa with "expensive flowers" that invest the majority of female effort regardless of fertilization success (Smith et al. 1990:157, assumption 6), either because flowering structures are large, or because unfertilized flowers still develop into inviable seeds. They suggested that members of Typhaceae, Poaceae, Cyperaceae, and Juncaceae (which produce large inflorescences with extensive structural support) and Pinaceae, Taxodiaceae, some Cupressaceae, Salicaceae, and Betulaceae (which group many ovules together in strobili) are likely candidates for pollination benefits from masting. Smith et al. (1990) also state that pollination benefits of masting may be "completely eliminate[d]" in species in which the female parent commits resources to fruit only after fertilization of an inexpensive flower, as in certain nut-bearing trees in the families Fagaceae, Juglandaceae, and, to a lesser extent, Ulmaceae (Smith et al. 1990: 162), and in the genera Acer and Fraxinus. (Note that expensive flowers could favor mast seeding in animal-pollinated, as well as wind-pollinated, plant species. This paper concentrates only on wind pollination.)

This postulated link between expensive flowers and mast seeding has been widely quoted in the literature since its publication in 1990 (Sork 1993, Kelly 1994, Koenig et al. 1994, Tapper 1996, Kelly and Sullivan 1997). However, the model of Smith et al. (1990) has not always successfully predicted the occurrence of mast seeding in the field. Koenig et al. (1994:108) noted that "the success of the wind pollination hypothesis [in various Californian Quercus spp., Fagaceae] is surprising given that oaks commit most of the energy to female growth only after pollination, thereby apparently eliminating the potential advantages of synchronous investment in male and female reproduction." Other papers that do not fit the theory of Smith et al. (1990) include those showing large benefits from pollination in Fagus (Nilsson and Wästljung 1987), and little benefits from pollination in Chionochloa (Poaceae; Kelly and Sullivan 1997). Masting has also been documented in Acer (Graber and Leak 1992) and Fraxinus (Tapper 1996), which have inexpensive flowers.

Here, we propose an alternative model for predicting which plant species will gain wind pollination benefits from mast seeding. We suggest that pollination effi-

The Conceptual Model

To evaluate the importance of wind pollination in mast-seeding species, we propose a conceptual model that predicts in which species mast flowering improves wind pollination efficiency. In wind-pollinated species, there is a curvilinear relationship between flowering effort (pollen crop, or as a proxy, general seeding effort) and pollination efficiency (the percentage of ovules that are pollinated), as shown in Fig. 1. Each plant species will have characteristic values for the asymptote, threshold, and maximum slope, but with this same general shape.

The shape of the pollination efficiency curve shows that very low pollen densities are associated with low seed set (Fig. 1). Seed set increases as pollen densities increase, but benefits diminish with each increment of pollen density. Eventually, seed set reaches an asymptote, where additional pollen density has no effect at all. The position of the asymptote for each species is presumably determined by resource availability or other nonpollination factors. This type of relationship has
been shown in a number of species, although measured in different ways. In some studies, the pollen crop has been measured directly (e.g., Sarvas 1955, 1962, Allison 1990, Smith et al. 1990, Dahl and Strandheide 1996), whereas in others, seeding effort is assumed to correlate with pollen production (Nilsson and Wästljung 1987, Norton and Kelly 1988). Pollination efficiency is sometimes measured by counting female flowers and seeds (Sork 1993), but more often by classifying collected seeds into viable and nonviable, or filled and hollow. There is evidence in some wind-pollinated species that incomplete pollination is primarily responsible for empty seeds, and thus for variation in percentage of seed set: Betula spp. (Sarvas 1955), Pinus silvestris (Sarvas 1962), Dacrydium cupressinum (McEwen 1983), Fagus sylvatica (Nilsson and Wästljung 1987), and Taxus canadensis (Allison 1990). Our model is applicable to all mast-flowering species in which pollination efficiency is measurable, regardless of whether the majority of investment in female reproductive structures occurs pre- or postfertilization (c.f. Smith et al. 1990).

Most authors assume that the pollination efficiency curve does not eventually decline from the high asymptote. Theoretically, it is possible that superabundant pollen could negatively affect seed set, lowering the curve. A review by Young and Young (1992) shows that a minority of studies have reported lower seed set at superabundant pollen loads, but nearly all of these cases were attributed to either hand-pollination effects (e.g., damage to the stigma during hand pollination) or interactions with animal pollinators. We do not know of any data showing lower seed set with superabundant pollen in wind-pollinated species, so this possibility is not considered further here.

Our conceptual model states that the probable wind pollination benefit that a plant population gains from mast flowering is determined by how far pollination efficiency at mean seed crop size falls below the asymptote for pollination efficiency in that species (Fig. 1). Although the degree of benefit is a continuum, for clarity, we identify three broad regions (Fig. 1). For species with a high mean seed crop size relative to their own asymptote (zone C), plants enjoy maximum pollination efficiency even in an average year, and masting cannot improve pollination further. When mean seed crop size falls on the steep part of the curve (B), then increasing the variation in seed crops between years partitions seeds into high seed years (which enjoy higher pollination efficiency and are responsible for most of the seeds) and low seed years (which have worse pollination efficiency than a mean year, but only for a small fraction of the total seed production). The weighted mean pollination efficiency of an individual plant in synchrony with the population therefore rises with increasing among-year variation in seed crop, because a larger fraction of all its seeds are produced in high seed crop, high-efficiency years. In cases in which mean seed crop size is low on the curve (A), even extreme levels of mast seeding are insufficient to lift pollen densities in the high flowering years into the range where adequate pollination ensues. Mast seeding may increase mean pollination levels by a small absolute amount, but overall pollination will still be very poor. Hence, we predict that the largest benefits from wind pollination will be found in mast-seeding species in which the mean seed crop size is on the steepest part of the curve (zone B). Species falling into zone A would be experiencing near-total pollination failure; such cases should be rare and we know of no real examples. Hence, we will concentrate on zones B and C.

Because the key to this relationship is the position of the mean relative to the asymptote, any factor that alters either the mean flowering effort or the position of the equation will alter the relative benefits from masting. The position of the equation (i.e., the value of the asymptote and the pollen density at which it is reached) is largely determined by relatively invariant factors, such as the efficiency of female reproductive structures at catching airborne pollen, and by the level of compatibility of selfed pollen. In contrast, mean reproductive effort per unit area is much more variable. It decreases in many species with increasing altitude.
(because of reduced mean flowering effort per plant) and with reduced plant densities, often caused by anthropogenic disturbance such as fragmentation (lower plant densities result in lower pollen intensities per unit area) (Allen and Platt 1990, McKone 1990, Smith et al. 1988, 1990, Burrows and Allen 1991, Kelly and Sullivan 1997). In both cases, our conceptual model predicts that the pollination benefits from mast seeding would increase when the plant falls in zone B and the mean flowering effort per unit area is reduced. This prediction is consistent with the finding that mast seeding is more pronounced with higher altitudes, both within and between species (Webb and Kelly 1993).

The rest of this paper is devoted to testing our conceptual model against long-term field data sets for five species.

**METHODS**

Total annual seed production data over several years (number of flowers or seeds per unit area) were obtained for populations of *Chionochloa pallens* over 10 years (Kelly and Sullivan 1997); *Dacrydium cupressinum*, Podocarpaceae, over 33 years (Norton and Kelly 1988); *Betula alleghaniensis*, Betulaceae, over 11 years (Graber and Leak 1992); *Nothofagus menziesii*, Fagaceae, over 18 years (Burrows and Allen 1991), and *N. solandri* at three nearby altitudes within one site (1340 m, 24 years; 1190 m, 30 years; and 1050 m, 24 years; updated from Allen and Platt 1990). The *Betula* data are from New Hampshire, eastern United States; the others are from the South Island, New Zealand. The equation for each data set relating the size of the seed crop to the percentage of viable seed was obtained from the papers, except for *D. cupressinum* for which we calculated it from the original data ($y = -14.08 + 12.13 \ln(x)$; $R^2 = 0.574$; $F = 18.9$; df $= 1,16$; $P = 0.0007$). In addition, equations relating total annual seedfall (number of seeds per hectare) to levels of insect and bird predation (percentage not preyed upon) were given for *B. alleghaniensis* by Graber and Leak (1992).

Our classification “nonviable seed” refers to unexpanded ovaries and excludes seed that has been preyed upon. It is assumed in the study species that unexpanded ovaries, and thus nonviable seed, result from pollination or fertilization failure (McEwen 1983, Kelly and Sullivan 1997, McKone et al. 1997) rather than from other factors, such as selective abortion of embryos.

Variation in seed production was quantified with the population seedfall coefficient of variation (CV, i.e., the standard deviation divided by the mean), as recommended by Kelly (1994). Methods of analysis, summarized here, follow those of Kelly and Sullivan (1997). To examine the effect of different degrees of masting (i.e., different coefficients of variation) from that observed in the field, various hypothetical data sets were constructed based on modifications of the field data. The real data were used to guide the relative sequence of high and low seeding years, because temporal variation in these data was presumably determined by the plants’ responses to various environmental factors (Kelly and Sullivan 1997).

The mean was kept constant in all of the data sets (except when modeling fragmentation), so that overall reproductive allocation was invariant. To vary the CV while maintaining the mean and relative temporal pattern, first the required standard deviation was calculated, for any desired CV. For example, to produce a hypothetical data set with a CV of 0.5, the standard deviation was set at half of the field mean value (which was retained invariant in all data sets). Then each real data set was standardized (i.e., converted to mean = 0 and standard deviation = 1). The standardized data set was multiplied by the required standard deviation and was added to the original mean to produce a hypothetical data set with the desired CV, but exactly the same mean, temporal sequence of high and low years, and relative magnitudes among years as the real data (see Kelly and Sullivan 1997: Table 1). When a hypothetical CV was increased above a plant’s actual CV, some low years decreased in the model to negative total numbers of seeds. These were set to zero, and an appropriate constant was then subtracted from all nonzero seedfall values to keep the overall mean reproductive effort the same as in the real data.

Each hypothetical data set was combined with the pollination efficiency equation from that site to predict levels of unfilled seed for each year, which were each then summed to give a weighted mean for all seeds over the whole interval. The effect of various coefficients of variation on weighted mean wind pollination efficiency was calculated as the relative increase in viable seed production at each CV (i.e., absolute increase in viable seed at each higher CV, divided by the pollination rate at CV = 0, which represents constant seed production).

Allen and Platt’s (1990) three adjacent altitudinal data sets of *N. solandri* at Craigieburn Forest were used to determine altitudinal effects on the relationship between wind pollination efficiency and masting intensity. The relative improvements in viable seed benefits of masting were compared among different altitudes. Plants at each altitude had a different equation for pollination efficiency vs. seed crop size, and also had a different mean seed crop per unit area. To test the relative importance of the equations and the means in determining the sensitivity of pollination efficiency to CV, different combinations of equation and mean were used (e.g., the data set from 1340 m used with the mean from 1340, but the equation from 1190 m, and so on).

The *C. pallens*, *N. solandri* (1190 m), and *D. cupressinum* data sets were used to analyze change in the modeled relationship between masting and wind pollination efficiency that might result from reduced plant density due to anthropogenic modification such as graz-
crop size, relative to the asymptote, was relatively high in *Dacrydium cupressinum* (57% at the mean, cf. an asymptote of ~80%; Fig. 2a) and *Betula alleghaniensis* (31% cf. 52%), and very high in *Chionochloa pallens* (77% cf. 83%; see Kelly and Sullivan 1997; Fig. 1b). All four *Nothofagus* spp. data sets had much lower relative pollination at mean efforts (e.g., in *N. solandri* at 1340 m, 18% at the mean cf. 65% maximum; Fig. 2b). Accordingly, the study population of *C. pallens* falls in zone C of the conceptual model, *D. cupressinum* and *B. alleghaniensis* fall in zone B2, and *Nothofagus* spp. fall in zone B1.

In the simulation model, as the seed production cv of each data set was altered, the relative pollination benefits also changed, but to varying degrees in each species (Fig. 3). Modeled increases in pollination efficiency with increasing levels of masting (toward cv = 2) were minimal in *C. pallens*, moderate in *B. alleghaniensis* and *D. cupressinum*, and very large in *N. solandri*. Pollination efficiency in *N. menziesii* increased only up to its field cv of 1.40, and then leveled off. This discontinuity occurred because the *N. menziesii* raw data were more bimodal than the other data sets, with the six highest seed crops being of similar size. As a result, attempts in the simulation model to force coefficients of variation greater than the field value did not result in continuing concentration of flowering into a few high years, and

![Graph](https://via.placeholder.com/150)

**Fig. 2.** Wind pollination efficiency as a function of total seed crop size (no. seeds/m²) in species with (a) high efficiency in a mean year (*Dacrydium cupressinum*), and (b) low efficiency in a mean year (*Nothofagus solandri* at 1340 m a.s.l.).

![Graph](https://via.placeholder.com/150)

**Fig. 3.** Effect of increasing levels of mast seeding (coefficient of variation of seed output) on relative pollination benefits (percentage increase in viable seed over cv = 0) in five plant species. In each case, the predicted pollination level at constant seed output is set as the baseline, and the percentage increase in viable seed with greater coefficients of variation is shown. Data for *Nothofagus solandri* are presented from three different altitudes (numerals indicate meters a.s.l.) at Craigieburn Forest, New Zealand. The other species are *Nothofagus menziesii*, *Dacrydium cupressinum*, *Betula alleghaniensis*, and *Chionochloa pallens*.

The relative effects of masting on pollination, invertebrate seed predation, and vertebrate seed predation were estimated in *B. alleghaniensis* using the equations given in Graber and Leak (1992), inserted into the Kelly and Sullivan (1997) model just described.

**RESULTS**

Actual pollination efficiency varied widely among the five species. Pollination efficiency at mean seed

![Graph](https://via.placeholder.com/150)
Fig. 4. Effects of lowered flowering effort per unit area (such as could occur with reduced plant density after fragmentation) on pollination efficiency in three wind-pollinated mast-seeding plants. The weighted mean seed viability (note the log scale) was modeled under various levels of flowering variability (CV, coefficient of variation of flowering effort). For each species, the model was run with the mean flowering effort from the field (large symbols), mean effort reduced to 50% (medium-sized symbols), and mean effort reduced to 10% (small symbols). The species were Chionochloa pallens, Dacrydium cupressinum, and Nothofagus solandri (at 1190 m a.s.l.).

pollination efficiency gains tapered off. Apart from this exception for N. menziesii above CV = 1.50, the largest calculated benefits from masting were for species in zone B1, as predicted by the conceptual model.

The altitudinal sequence for N. solandri showed that the greatest relative benefits from masting came at the higher altitude sites. Pollination benefits began to tail off at the lower site (1050 m) above CV = 1.5 (Fig. 3), and at the middle site (1190 m) above CV = 1.75, but continued to increase beyond CV = 2.25 at the highest site (1340 m). Modeling with various combinations of means and equations from the different altitudes showed that this was largely because the highest site had the lowest mean seed output (1059 seeds m^{-2}, with 1808 seeds/m² at 1190 m and 1856 seeds/m² at 1050 m), so extreme levels of masting were less likely to saturate pollination in the highest seed years. This suggests that within-species altitudinal effects on the pollination benefits of mast seeding can be predicted by the conceptual model in a way similar to between species effects. If the species is within zone B, and higher altitude sites have lower mean seed outputs, those sites will be lower down the curve and, hence, will benefit more from high coefficients of variation.

In general, simulating the effects of fragmentation by lowering mean flowering effort per unit area resulted in lower absolute levels of pollination in all three species (Fig. 4). Fragmentation also augmented the rate of increase of pollination benefits gained with higher levels of masting (shown by the slope of the lines on the log y-axis in Fig. 4). This effect was small in C. pallens and moderate in D. cupressinum. In N. solandri, benefits of masting were more sensitive to CV at both 50% and 10% mean seedfall compared to the unfragmented mean seedfall. For example, increasing the CV from 1.0 to 1.5 increased sound seed by 33% in the original data set, but by 49% at 10% mean seedfall.

In B. alleghaniensis, we examined the relative effects of wind pollination and seed predation by insects and birds. Pollination efficiency increased from 77.0% at CV = 0 to 81.8% at the field CV of 1.15 (Fig. 5). Seed escape from insect predation increased slightly from 76.5% at CV = 0 to 81.0% at CV = 1.15, and, with almost exact inverse symmetry, seed escape from bird predation decreased slightly from 88.3% at CV = 0 to 83.6% at CV = 1.15. At CV = 2, the net improvement in survival of viable seed (14.8% of all ovules) was completely due to the improvement in wind pollination efficiency.

**DISCUSSION**

**Individual selection vs. population benefits**

Our models are based on population-level means for seed production, seed set, and seed predation rates. In

![Fig. 5. The effects of degree of masting (CV, coefficient of variation of seed output) on reproductive efficiency in Betula alleghaniensis, resulting from changes in percentage of flowers that are wind pollinated, percentage of seeds that escape being eaten by insect predators, and percentage of seeds that escape being eaten by birds.](image-url)
some of the species, the population mean seed set is much higher in high seed years than in low seed years. However, although this shows a clear advantage to the population from mast seeding, it does not necessarily show that selection at the individual level will favor masting. It is possible that individual plants with the highest coefficients of variation and the greatest synchrony with their congeners might not benefit as much as individual plants that are more constant or out of step. Clearly, studies at the individual plant level would be most illuminating, as recommended by Kelly (1994) and Herrera (1998). However, we consider that the population benefits shown here are likely to translate into individual selective pressures. Firstly, we know of no published cases in which the individual benefits differ from the population-level benefits; this would require differential responses within each mast year according to the previous flowering schedule of each plant. Secondly, at the extreme levels of masting shown by Chionochloa and Nothofagus, most plants do not reproduce at all in most years, whereas in years of high seed production, most reproductively capable plants flower heavily. This reduces the potential for less synchronized plants to experience larger benefits than the population mean would indicate. Nevertheless, in this paper we only show improvements in population-level seed set, and cannot prove that this provides individual selective benefits.

**Predicting the wind pollination benefits of masting**

Our conceptual model predicts that masting will benefit all species where mean seed production results in low pollination efficiency relative to the asymptote for pollination efficiency. Smith et al. (1990) predicted that masting would benefit species only when females have a large investment in unfertilized structures. The data in this paper are consistent with the predictions of Smith et al. (1990) for Dacrydium cupressinum (Podocarpaceae) and Betula alleghaniensis (Betulaceae), but not for Chionochloa pallens and Nothofagus spp. Our conceptual model successfully predicted that Nothofagus spp. would gain the largest pollination benefits from masting, and that Chionochloa pallens would gain very small pollination benefits. In C. pallens, the mean flowering effort (which falls in zone C of the conceptual model) is high enough for efficient pollination every year in the absence of masting (Kelly and Sullivan 1997). This conclusion is in agreement with the results of a manipulative experiment in Chionochloa (Tisch and Kelly 1998). In contrast, mean seed production in N. solandri and N. menziesii falls on the steep part of the pollination efficiency curve (zone B1 of the conceptual model), corresponding to a relatively low level of pollination efficiency. The steepness of the curve near the mean implies that masting in Nothofagus spp. results in greatly improved overall seed crop viability. The coefficients of variation in Nothofagus spp. (up to 2.12 for N. solandri at 1340 m) are among the highest for any species anywhere in the world (Webb and Kelly 1993) and the selective benefit of such extreme masting in this genus has, until now, been unknown. *D. cupressinum* and *B. alleghaniensis* are intermediate between *C. pallens* and Nothofagus spp: they gain moderate pollination benefits from masting, consistent with predictions of the conceptual model. As we will discuss masting in these species may also be affected by factors other than wind pollination efficiency (such as predation or frugivore attraction).

Increases in pollination efficiency do not continue indefinitely with ever greater levels of masting. *N. menziesii* pollination efficiency increased very little beyond the species’ field level of masting (CV = 1.4). This outcome was due to the unusual bimodal pattern of total seedfall in the 18 year data set, a special case of the pattern shown by all species, whereby the benefits of increasing masting eventually flatten off. Once most seeds are concentrated into mast years that are large enough for efficient pollination, little additional benefit ensues from greater masting intensity. This pattern is exhibited by *C. pallens* at all CV levels, and it begins to show in *N. solandri* at 1050 m a.s.l. at coefficients of variation above 1.50.

It is also noteworthy that reduced plant densities (such as through fragmentation) can move plants from zone C into zone B, or from zone B to zone A. The simulations showed that reducing plant densities by 90% increased the benefits of masting in Nothofagus as the species moved lower down in zone B. Wardle (1984) commented that isolated trees of Nothofagus spp. had very low percentages of viable seed even in high seed years. The most isolated trees experience such low levels of outcross pollen, even in mast years, that the populations fall into zone C of the conceptual model, and pollination failure is the result.

Our model is essentially complementary to that of Smith et al. (1990), in that they concentrated on the cost of failure of a single female structure, whereas we concentrate on factors affecting the fraction of structures that fail; the overall cost to the plant will be the product of both of these factors. However, plants with means falling in zones A and C of our model cannot affect their pollination efficiency by masting, so there can be no selective pressure on them to increase their reproductive variability, regardless of the cost of unfertilized structures. Additionally, other processes not included in the model of Smith et al. (1990) may be influencing the selective outcome (e.g., predation in C. pallens; Kelly and Sullivan 1997).

Alternatively, some wind-pollinated species with expensive flowers may employ strategies other than masting to decrease losses due to pollination failure. Self-compatibility, by which a plant’s own pollen can fertilize its ovules, effectively shifts the equation to the left in Fig. 1, rather than the position of the mean to the right. Even in low flowering years, local levels of self-pollen will still be high; hence, the species is likely
to have its mean reproductive effort in zone C of our model. Pollination economies of scale that favor mast- ing, such as those described by Smith et al. (1990), are therefore less likely to be important in self-compatible species (Smith and Balda 1979, Nilsson and Wästljung 1987). C. pallens, for example, may achieve a high level of pollination efficiency at low flowering intensities through self-pollination (McKone et al. 1997), which may account for the minimal increases in pol- lination efficiency with masting observed in this species. In contrast, Nothofagus species, which gained large pollination benefits from masting, are thought to be self-stereile (Wardle 1984). Flower density-dependent pollination and seed set relationships have also been observed in several self-incompatible, masting species of the family Fagaceae, and it is thought that cross-pollination may have been an important factor in the evolution of masting in these species (Smith and Balda 1979, Nilsson and Wästljung 1987). However, mast- ing will increase the local density of outcross pol- len relative to self-pollen in high flowering years (Sork 1993). If cross-pollinated offspring are fitter than self-pollinated offspring, as seems likely for most out-cross- ing species and as has been suggested in Chionochloa (McKone et al. 1997), mast ing may provide benefits through higher seed quality rather than seed quantity (Tisch and Kelly 1998). In other words, masting may reduce inbreeding depression.

In summary, we have shown that the primary deter- minants of whether wind pollination economies of scale provide benefits from masting are the shape of the pol- lination efficiency graph (affected by factors like pollen self-compatibility), and the position of the mean re- productive effort per unit area on that graph (affected by plant density and site productivity). The cost of un- fertilized female flowers is a secondary influence operating in species that fall in zone B of our conceptual model.

Comparing pollination and other factors favoring masting

The study population of B. alleghaniensis presently appears to benefit from masting via a net increase in the potentially germinable seed crop (Graber and Leak 1992). Our simulations show that this increase results from the trade-off of three factors: a small economy of scale resulting from insect seed predator satiation, an almost equivalent diseconomy of scale resulting from bird seed predator attraction, and a moderate increase in pollination efficiency. The diseconomy of scale from bird seed predators may have been even larger, before the extinction, early in this century, of the Passenger Pigeon, which apparently traveled long distances in eastern North America to feed on the seed crops of mast-seeding trees (Bucher 1992).

Nilsson and Wästljung (1987) found that a similar trade-off operates in Fagus sylvatica: during large seed crop years, reproductive efficiency reflects a pollination economy of scale, which leads to large, viable seed crops and the eventual escape from predators of a signifi- cant proportion of the seeds. They also found a sim- ilar balance of predation: a relatively constant popu- lation of Cydia fagiglandana, a moth seed predator, is satiated, whereas bird seed predators increase in num- ber and impact with large seed crops. A variable seed crop is commonly more effective in reducing seed pre- dation by insects than by vertebrates (Nilsson and Wäst- ljung 1987), as birds are highly mobile relative to many insect seed predators, and have the ability to scan large areas during food searching. Trees producing seeds in mast years should thus suffer higher losses to generalist, density-dependent foragers (Hett 1971, Augspurger 1981, Kelly 1994). The beneficial trade- offs between the effects of masting on vertebrate and invertebrate predation found in both F. sylvatica and B. alleghaniensis contrast with the single large benefit of mast ing via predator satiation experienced in C. pal- lens, which suffers heavy predation by specialist in- vertebrates, but has few extant vertebrate seed pred- ators (McKone et al. 1998).

As in B. alleghaniensis, pollination benefits with masting are moderate in D. cupressinum. In this species, frugivore attraction may provide an important economy of scale that acts in synergy with wind pol- lination to favor masting (Norton and Kelly 1988). Just as bird seed predators are attracted to large crops in B. alleghaniensis and F. sylvatica, masting may serve to attract generalist seed dispersers or pollinators to large reproductive efforts (Janzen 1971, Givnish 1980, Sork 1993, Kelly 1994, Koenig et al. 1994). Conversely, the negative effect of extreme fluctuation in plant repro- duction on the stability of specialist populations of pol- linators may help to explain why wind-pollinated spe- cies are more variable than animal-pollinated species (Smith et al. 1990, Herrera et al. 1998). Such predic- tions of satiation of specialist pollinators and seed pred- ators are dependent upon a functional response (Lms 1990a, b), and do not apply, for example, to species that are able to reproduce rapidly in response to fluctu- rating resources (e.g., thrips pollinating mast-seeding Dipterocarpaceae; Ashton et al. 1988).

The relative importance of wind pollination in fa- voring the observed field cv can be predicted to some extent by plotting the expected benefits from masting against the actual field cv (Fig. 6). Species along the diagonal from bottom left to top right (e.g., N. solandri) have a level of variation in the field congruent with the expected benefits that wind pollination would provide. For these species, there is no indication that other fac- tors are required to explain the observed field cv. Spe- cies at the top left (e.g., C. pallens) have much higher coefficients of variation than wind pollination would predict, and we predict these species must have some other benefit (predator satiation, in the case of C. pal- lens). Species at the lower right have a lower cv than wind pollination alone would predict. We predict that
such species must show some opposing diseconomy of scale (such as attracting a rapacious generalist vertebrate seed predator), which means that overall, masting is not selectively advantageous. Alternatively, such species may have suffered recent changes to their environment that have altered the benefits of masting (such as reduced plant density from human impacts), but this has not yet had time to exert much selective pressure on the CV. Where there is no selective benefit to a species from mast seeding, there still will be variation in flowering because of weather and other environmental variation (the $V_{env}$ of Kelly 1994), but until now, we have had no way of knowing how large a CV would result. Extrapolating from Fig. 6, we can tentatively predict that species with no selective benefits of any kind from masting should have coefficients of variation approximately in the range 0.85–1.35; that any species with a CV higher than 1.35 has probably had some selective pressure to show mast seeding; and that any species with a CV lower than about 0.85 may have experienced selection for constant seed production (Kelly 1994). Overall, the conditions under which plant populations are likely to benefit from mast seeding are increasingly clear. The most likely plants to have high coefficients of variation are those that are wind pollinated, self-sterile, and have low pollination efficiency at mean reproductive efforts; or those that suffer

![Fig. 6. The predicted benefits of wind pollination (percentage increase in viable seed) from masting with a CV of 2.0, vs. the actual field level of masting (CV), for the data sets analyzed in this paper. Cases at the top left are more variable than expected, and those at the bottom right are less variable than expected, given the nature of their pollination. This suggests the involvement of other factors (such as predator satiation in *C. pallasii*). Excluding *C. pallasii*, the cases fall in a band (regression line $\pm 2\text{ se}$ of the intercept is shown: $F_{1,4} = 16.97, n = 6, P = 0.015, y = 1.109 + 0.0052 x$), where the field CV appears to be consistent with the size of the pollination benefits from masting.](image)

seed predation from a specialist, immobile invertebrate seed predator. In addition, highly variable wind-pollinated species may have expensive unfertilized female structures. Most other plants, especially those with generalist mobile seed predators or specialist animal pollinators or dispersers, should show less variable seed output among years.

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