

Expectation, explanation and masting

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ABSTRACT

Masting is the synchronous, episodic production of large seed crops by perennial plant populations. Generally, hypotheses concerning the evolutionary origin and maintenance of masting entail economies of scale, where the benefit of large, synchronous reproductive events accrues by overcoming some environmental constraint, such as pollen limitation or seed predation. Because all perennial plants face some degree of inter-annual environmental variability, assessing the importance of selection via economies of scale requires a clear expectation for the reproductive dynamics of plants adapted to variable environments. Using a dynamic life-history model, I demonstrate that the observed range of reproductive variability and several other aspects of masting should be expected for size-structured populations of plants utilizing optimal allocation strategies in variable environments, even in the absence of economies of scale benefits. Thus, life-history evolution in even modestly variable environments may predispose species to realize reproductive benefits via economies of scale. However, distinguishing the effects of evolved responses to environmental variability from the effects of economies of scale using current criteria is difficult, if not impossible. My results reinforce the dictum that ecologists and evolutionary biologists must carefully consider their expectations before generating and testing explanations for observed phenomena. As variations on an established evolutionary theme, economies of scale undoubtedly provide selective advantages. However, caution should be exercised when inferring that they are the major ecological and evolutionary determinant of reproductive variability of plant populations.

Keywords: optimal life histories, reproductive allocation, seed production, stochastic-dynamic modelling.

INTRODUCTION

Masting, the synchronized, episodic production of large seed crops by perennial plant populations, has important implications both for plant demography and for the dynamics of communities that depend on seeds as a food resource (Janzen, 1971, 1974; Herrera *et al.*, 1994; Kelly, 1994; Jones *et al.*, 1998; Ostfeld and Keesing, 2000; Koenig, 2001; Koenig and Knops, 2001). All hypotheses concerning the evolutionary origin and maintenance of

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masting begin with the assumption that reproductive variability and synchrony are in some sense a remarkable phenomenon requiring an adaptive explanation (Silvertown, 1980; Kelly, 1994; Kelly and Sork, 2002). From this perspective, most evolutionary explanations for masting describe the fitness advantage of reproductive variability and synchrony relative to constant reproductive output (Waller, 1979; Silvertown, 1980; Sork *et al.*, 1993; Kelly, 1994; Herrera *et al.*, 1998). Generally, such ultimate explanations for the origin and maintenance of masting invoke economies of scale, where the benefit of large, synchronous reproductive events accrues via the saturation of some environmental reproductive constraint, such as overcoming the numerical and functional responses of seed predators (Janzen, 1971, 1974; Forcella, 1980; Koenig *et al.*, 1994; Kelly *et al.*, 2000) or ensuring sufficient pollen availability (Nilsson and Wastljung, 1987; Smith *et al.*, 1990; Koenig *et al.*, 1994; Satake and Iwasa, 2000).

Empirically, the identification of masting as an evolved reproductive strategy (i.e. 'normal masting' *sensu* Kelly, 1994) is often confirmed by the presence of either of two phenomena: bimodal seed output or the diversion of resources from vegetative growth or stored reserves to reproduction. Hypothetically, these phenomena demonstrate that reproductive variability is not simply tracking environmental variability, in which case evolutionary explanations for reproductive variability are assumed to be unnecessary (Kelly, 1994). However, these criteria assume that environmental variability can only act as a proximate mechanism for masting (Kelly, 1994).

The *a priori* assignment of environmental variability to a proximate role is implicitly based on the assumption of simple environmental tracking as a baseline response. Here, instead of assuming environmental tracking as a baseline, I ask what patterns of reproductive variability would be expected in the absence of any selection via economies of scale, yet in the presence of environmental variability. Adaptation to inter-annual environmental variation may produce more complicated effects than simple tracking. The potential that evolved adaptations for life in a variable environment may explain the evolutionary basis of masting has not been tested sufficiently (Lalonde and Roitberg, 1992).

This perspective does not assign priority to the effects of environmental variation over economies of scale. Economies of scale imply that individual fitness depends fundamentally on the actions of the other members of the population, and that patterns of reproductive variability and synchrony have evolved to take advantage of this collective benefit. But because all perennial plant populations face some environmental variability, economies of scale should only be invoked as the evolutionary basis of masting when their effects can be reliably distinguished from the effects of environmental variability (Kelly, 1994; Kelly *et al.*, 2001). Thus, to understand the importance of economies of scale in the evolution of reproductive variability, it is critical to understand the expected variability of reproductive output for a population in a variable environment. Here, I simply wish to better delineate these baseline expectations for patterns of population-level reproduction in the face of inter-annual environmental variability.

Empirical components of masting

Masting has two general components: inter-annual variability and synchrony among individuals. Reproductive variability is usually assessed as the population-level coefficient of variation ($CV = \text{standard deviation}/\text{mean}$) of seed production across years. Woody plants exhibit a continuum of coefficients of variation, implying that masting may not exist

as a discrete evolved strategy (Herrera *et al.*, 1998). Recent work suggests that in the absence of selective benefits via economies of scale, coefficients of variation should range between 0.85 and 1.35 (Kelly *et al.*, 2001).

The second component of masting is synchrony among individuals. However, while synchrony among individuals is the basis for most economies of scale arguments, the reproductive output of individual plants has rarely been tracked (Sork *et al.*, 1993; Koenig *et al.*, 1994, 1996; Herrera, 1998). Instead, most studies rely on population-level estimates of seed production drawn, for example, from seedfall traps or branch samples. In the few studies that have recorded individual reproductive output, the population-level coefficient of variation was correlated with the mean individual coefficient of variation of the population (Herrera, 1998). However, the mean individual coefficient of variation was unrelated to the degree of synchrony among reproducing individuals, which makes it difficult to assess the relative influences of variability and synchrony on reproductive success.

As mentioned above, two other empirical patterns are also associated with masting populations: bimodal distributions of reproductive output and the 'switching' of resources from vegetative growth or stored reserves to reproduction. These patterns putatively demonstrate that reproductive output is being actively regulated against the background of more continuous environmental variability. Under limited resources, plant allocation is effectively a 'zero-sum' game (Perrin and Sibly, 1993; Klinkhamer *et al.*, 1997; Iwasa, 2000), and resources devoted to reproduction are, by definition, not allocated to growth, maintenance or storage. Thus, at some level, switching must occur. The question is, then, not *whether* plants allocate, but how their allocation strategy changes in response to their internal state and external environment. Several recent theoretical studies of masting have incorporated allocation from internal reserves as a basic assumption (Isagi *et al.*, 1997; Satake and Iwasa, 2000; Rees *et al.*, 2002) and the model developed here does the same. However, I am aware of no theoretical studies of masting that directly address bimodality of population-level reproductive output.

Despite the fact that masting is a population-level phenomenon, little attention has been paid to the effects of other demographic characteristics, especially population age and size structure, on reproductive variability and synchrony. Perennial plants generally continue to grow after reaching maturity, and thus make reproductive allocation decisions over long periods, sometimes across large changes in size. Because plant size may influence allocation decisions as well as constrain the magnitudes of individual resource uptake, growth and reproductive output, population size-structure may affect both the variability and synchrony of reproduction. Reproductive variability may reflect heterogeneous allocation patterns among plants that differ in size. Alternatively, reproductive synchrony across sizes in a population may imply that allocation decisions are invariant with size once maturity is reached.

In this study, I use a dynamic life-history model to explore the effects of resource allocation and environmental variability on patterns of population reproductive output in the absence of selection via economies of scale. Specifically, I show that the fundamental components of masting (inter-annual variability, inter-individual synchrony and bimodal distributions of reproductive output) can result from life-history evolution in variable environments, without invoking economies of scale. Thus, economies of scale benefits can then be seen as an epiphenomenon of life-history evolution, rather than the ultimate explanation for patterns of reproductive variability and synchrony.

METHODS

A dynamic life-history model

Plants acquire resources necessary for survival, growth and reproduction via photosynthesis and root uptake of soil water and nutrients. The rate of resource acquisition of a plant, its maintenance costs, and its capacities for growth, reproductive output and reserve storage depend critically on its size (Niklas, 1994; Enquist *et al.*, 1998, 1999; Niklas and Enquist, 2001). From an optimality point of view (Iwasa, 2000), natural selection balances a plant's allocation to growth and reproduction over its lifetime to maximize expected fitness (Iwasa and Cohen, 1989; Lalonde and Roitberg, 1992; Perrin and Sibly, 1993; Klinkhamer *et al.*, 1997; Iwasa, 2000). Here I use a dynamic optimization model (Clark and Mangel, 2000) to determine optimal reproductive schedules and to analyse reproductive responses of a size-structured population of trees to variable resource input.

I assume that the net quantity of resources available to a tree each year, $U(t)$, for growth, reproduction and storage is simply resource uptake minus maintenance costs:

$$U(t) = Z a M(t)^{3/4} - b M(t) \quad (1)$$

where $M(t)$ is tree mass at the beginning of its t th growing season, and Z is a stochastic coefficient representing resource availability. Equation (1), which resembles the von Bertalanffy growth equation commonly used in growth models, is based on a recently proposed general model for ontogenetic growth for animals (West *et al.*, 2001) that also appears to work well for plants (B.J. Enquist, personal communication). The first term in the equation ($Z a M^{3/4}$) represents resource uptake as a function of tree mass, and accords well with the scaling of leaf area and root biomass (Enquist *et al.*, 1999; Niklas and Enquist, 2001). Although this allometric relationship was originally derived for interspecific comparisons, it also appears to hold within plant species (M. McCarthy and B.J. Enquist, unpublished data). The second term represents maintenance costs, based on the assumption that, on average, each unit of mass is equally costly.

Under average conditions ($Z = 1$; see below), with all resources allocated to growth, M will show a sigmoidal trajectory in time converging on a maximum size, $M_{\max}$ (West *et al.*, 2001). The values of a and b are related such that as the tree approaches $M_{\max}$, growth slows and $a M^{3/4} - b M$ converges on zero – that is, $M_{\max} = (a/b)^4$ (West *et al.*, 2001). For the purposes of this study, I set $M_{\max} = 100$, and since, based on the scaling of leaf mass and assimilation, $a = 0.3$ (Niklas and Enquist, 2002), $b = 0.0949$. M and U are both measured in arbitrary units of mass.

The environmental coefficient, Z , is assumed to be gamma distributed with mean = 1. A particular value of Z quantifies how many times better or worse the environment is in a given year, compared with the long-term average. The gamma distribution is convenient because it takes only positive values and because it is somewhat left-skewed on a log scale. The latter property is useful because it makes 'bad' years (e.g. $Z = 1/2$) more likely than correspondingly 'good' years (e.g. $Z = 2$), which is an ecologically reasonable assumption. Defining Z in this way allows me to systematically examine the effect of different levels of environmental variability simply by changing the variance of the underlying gamma distribution. In all simulations, I denote environmental variability by its coefficient of variation, CV_Z . Since the mean(Z) = 1 throughout the study, CV_Z is equivalent to the standard deviation of the gamma distribution.

Once a tree has taken up resources and covered its maintenance costs, it must allocate the resources to growth, $G(t)$ (again in arbitrary mass units). However, potential growth is also constrained by tree size. Specifically, I assume that growth capacity corresponds to average environmental conditions, $G_{\max} = aM^{3/4} - bM$. Resource in excess of this constraint, which may be present in years when $Z > 1$, is put into stored reserves, $S(t)$, up to a maximum of $S_{\max} = sM$ (Chapin *et al.*, 1990). Based on empirical measures of maximum non-structural carbohydrate levels in trees (Barbaroux *et al.*, 2003; Hoch *et al.*, 2003), I set $s = 0.1$. When the demands of maintenance and growth cannot be met by the current year's resource uptake, the reserve is depleted to compensate, as far as possible, for the deficit. If reserves are exhausted and deficits remain (i.e. when $Z \ll 1$), growth and reserves are set to zero and the tree is assumed to be 'dormant' throughout that season.

Finally, a plant may allocate some portion of its remaining stored reserves to reproduction. Like uptake, maintenance, growth and storage, reproductive capacity is also size-dependent, with $R_{\max} = rM^{3/4}$. Such a power-law relationship is commonly used in studies of plant life history (Klinkhamer *et al.*, 1992), and the exponent corresponds to empirical observations (both intra- and interspecific) of herbs and trees (Shipley and Dion, 1992; Greene and Johnson, 1994; Niklas and Enquist, 2003). Based on the available data (Klinkhamer *et al.*, 1992; Shipley and Dion, 1992; Greene and Johnson, 1994; Niklas and Enquist, 2003), I set the coefficient $r = 0.03$.

Note that for the capacities $G_{\max}$, $S_{\max}$ and $R_{\max}$, I have dispensed with the (t) notation to avoid clutter, even though these capacities will change through time as a tree grows. Thus, the equations describing plant growth and reproduction (in arbitrary mass units) become

$$G(t) = \min\{U(t) + S(t), G_{\max}\} \quad (2a)$$

$$R(t) = \min\{p\hat{S}(t), R_{\max}\} \quad (2b)$$

where p is the proportion of stored reserves $S(t)$ allocated to reproduction, and $\hat{S}(t)$ represents reserves discounted for any growth and maintenance deficits. The state dynamics of the tree, in terms of its mass and its stored reserve, become:

$$M(t+1) = M(t) + G(t) \quad (3a)$$

$$S(t+1) = S(t) + U(t) - G(t) - R(t) \quad (3b)$$

The problem for the plant is then to optimize values of p , given its mass M , reserves S , age t , maximum lifespan T and the degree of environmental variability CV_Z , to maximize its fitness. Here, I measure fitness as the expected total lifetime reproductive output, which implicitly assumes a stable population near its density-dependent carrying capacity (Charnov, 1993; Clark and Mangel, 2000). I used stochastic dynamic programming to derive optimal allocation strategies (Mangel and Clark, 1988; Lalonde and Roitberg, 1992; Clark and Mangel, 2000) and then examined the resulting reproductive dynamics of populations in which each individual utilized the optimal strategy.

In stochastic dynamic programming, one defines a terminal fitness function, F , for time $t = T$, then uses the method of backwards iteration to choose the action (e.g. the reproductive allocation from stored reserves in our case) that maximizes the expected sum of the immediate plus the future reproductive output (Mangel and Clark, 1988;

Lalonde and Roitberg, 1992; Clark and Mangel, 2000). Thus, working backwards, for $t = T - 1, \dots, 1$:

$$F(M, S, t, T) = \max_p \{E_{Z,D}[R(M, S, p, t, Z) + F(Q(M, S, p, t, Z), t + 1, T)]\} \quad (4)$$

where $Q(\dots)$ is shorthand for updating the state dynamics (M and S) as described by equations (1–3), $E_{Z,D}[\dots]$ indicates the expected value given the probability distribution of Z and an annual probability of death, D , and $\max_p$ denotes maximizing the function with respect to p . I used a maximum lifespan of $T = 300$ years and a constant probability of death of $D = 0.015 \text{ year}^{-1}$. Because the backwards iteration procedure requires discrete values for all variables, I set the possible Z values by doubling from a minimum of $Z = 1/8$ to a maximum of $Z = 8$. The allocation variable, p , ranged from 0 to 1 in 0.1 intervals, and the state variables, M and S , took on 100 evenly spaced values from 1–100 and 0–10, respectively.

The result of the backwards iteration of equation (4) is a ‘choice matrix’, p^* , which contains the optimal values of p for every combination of mass M , reserves S and age t . I compiled choice matrices for a range of resource variability, from $CV_Z = 0.2$ to 0.8. Because Z describes inter-annual variation in resource availability (e.g. as mediated by precipitation or growing degree days), this range represents a very broad spectrum of environmental conditions.

For each level of CV_Z , I then examined the effects of optimal allocation strategies on emergent reproductive dynamics by simulating populations of 500 trees for a period of 6000 years, with the first 1000 years discarded to remove transient behaviour. All trees began with the same initial state, $[M, S] = [1, 1]$, and experienced the same resource availability in each year, with Z being randomly drawn from a gamma distribution of mean = 1 and the appropriate variance. Trees took in and allocated resources according to equations (1–3) and their choice matrix, p^* , based on their state at the start of the year. Each tree also had a probability $D = 0.015$ of dying at the end of each year. Any trees that attained their maximum lifespan ($T = 300$) died at the end of the year. Each dead tree was replaced the next year by one set at the initial state. Thus, the population always contained 500 trees, but the size and age structure could change through time.

The mass, storage and reproductive output were tracked for each tree in the population over the course of the simulation, and population level reproductive output, R_{tot} , was then simply the sum in a given year of all the individual reproductive output values. I used MATLAB and S-plus software for all calculations, simulations and analyses.

Analyses

Inter-annual reproductive variability

I calculated population-level reproductive coefficients of variation (CV_R) over the entire length of each simulation. Most empirical studies are very short compared with the length of my simulations, and the coefficients of variation of a time series may be influenced by the length of the series (Halley, 1996). Thus, to delineate what the expected range of observed variability might be over shorter observation periods, I calculated CV_R values over 200 randomly selected subsamples of each data set and constructed histograms of the resulting distributions of coefficients of variation. The starting point for each subsample was selected at random, and the length of each subsample was drawn, with replacement, from the

distribution of record lengths documented in the empirical literature (Herrera *et al.*, 1998). I compared the simulated distributions to the empirical distribution using a Kolmogorov-Smirnoff goodness-of-fit test. The overall distribution of R_{tot} ($\log_2$ -transformed) was examined to assess the modality of population reproductive output.

Reproductive synchrony and the effects of size structure

To gauge the degree of reproductive synchrony, I used Shannon's evenness index, $E(t)$, to describe the equitability of $R(t)$ across all reproducing individuals in a given year (Lalonde and Roitberg, 1992), where

$$E(t) = - \sum_{i=1}^n \frac{p_i \log(p_i)}{\log(N(t))}$$

where, p_i is the proportion of $R_{\text{tot}}(t)$ contributed by the i th individual and $N(t)$ is the number of reproducing individuals in a given year. $E(t) = 1$ indicates identical values of R for all reproducing individuals, indicating perfect synchrony of reproductive allocation, while values of $E(t) < 1$ indicate increasingly asymmetrical reproductive output among individuals. However, non-reproductive individuals do not figure in the $E(t)$ calculation, so the value of $E(t)$, and thus the degree of observed synchrony, may depend on the number of reproducing individuals, $N(t)$. Therefore, I examined the relationships of both $N(t)$ and $E(t)$ with $R_{\text{tot}}(t)$ to understand the interactions among the number of reproducing individuals, their degree of synchrony, and the total reproductive output of the population.

To quantify the effects of size structure, I assigned population R_{tot} and individual M values to equal width bins, and quantified the proportional contribution made by different size classes to reproductive episodes of different magnitudes. These analyses were also repeated for each level of resource variability.

RESULTS

Life-history variability

Different levels of environmental variability selected life-history strategies that resulted in varied patterns of growth, storage and reproduction (Fig. 1). On average, trees in the least variable environment ($CV_Z = 0.2$) grew more quickly but realized less reproductive output than trees in the more variable environments. Average reproductive output was highest at intermediate values of environmental variability ($CV_Z = 0.4$), and decreased again slightly in the two most variable environments. Trees in the most constant environments also showed reproductive records punctuated by a spike of reproductive output in the last years of life.

Population-level reproductive variability

Figure 2 shows sample time-series of population reproductive output (R_{tot}) from simulations in each of the four environments. In all environments, the patterns were highly variable and characterized by consecutive years of negligible reproductive output punctuated by short (but usually multi-year) reproductive episodes. Interestingly, simulations in the least variable environment produced the most variable, episodic patterns of reproduction. Over

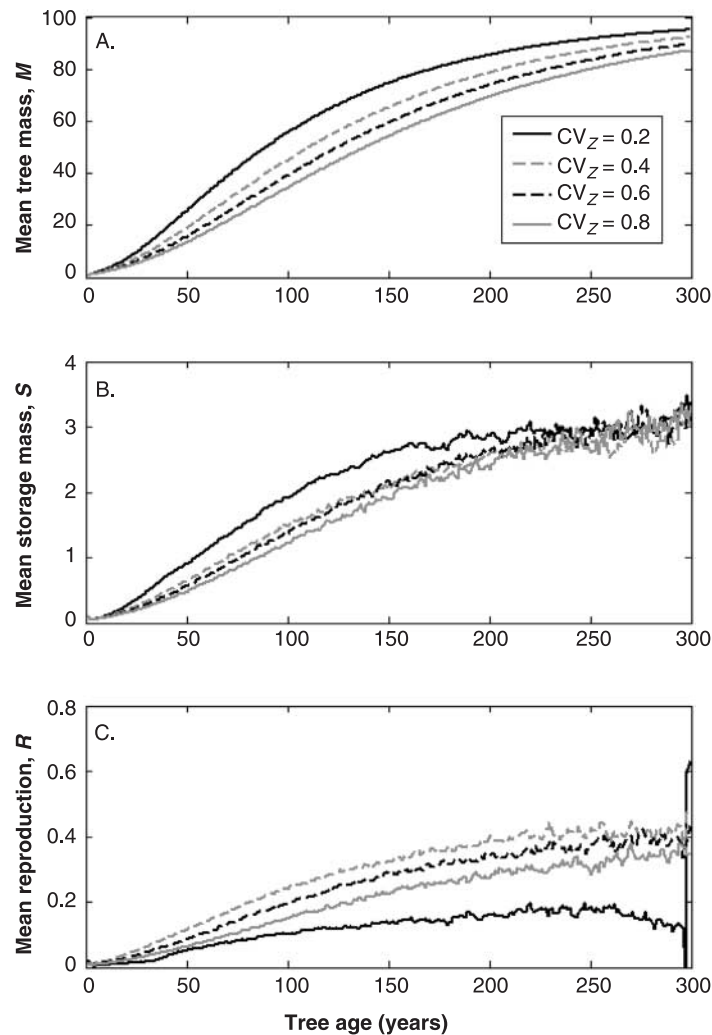


Fig. 1. Mean trajectories of mass (M), stored reserves (S) and reproductive output (R) over tree lifetimes, for all four levels of CV_Z . All in arbitrary mass units. Mean values were compiled for each age from 5000-year simulations of populations of 500 trees.

the course of the entire simulation, population reproductive output was substantially more variable than the environmental fluctuations (i.e. $CV_R > CV_Z$), especially in the least variable environment (Table 1). While ‘good’ years (i.e. those with high Z values) were frequently followed by high reproductive output, this was not always the case. As a result, although R_{tot} was correlated with the value of Z in the previous year, substantial variation in population reproductive output remained unexplained by environmental variation (Table 1). As in the case of individual trees (Fig. 1), an intermediate level of environmental variability ($CV_Z = 0.4$) produced the highest level of mean population reproductive output, as well as the least variable time-series. In all environments, the distributions of reproductive output were highly bimodal (Fig. 3).

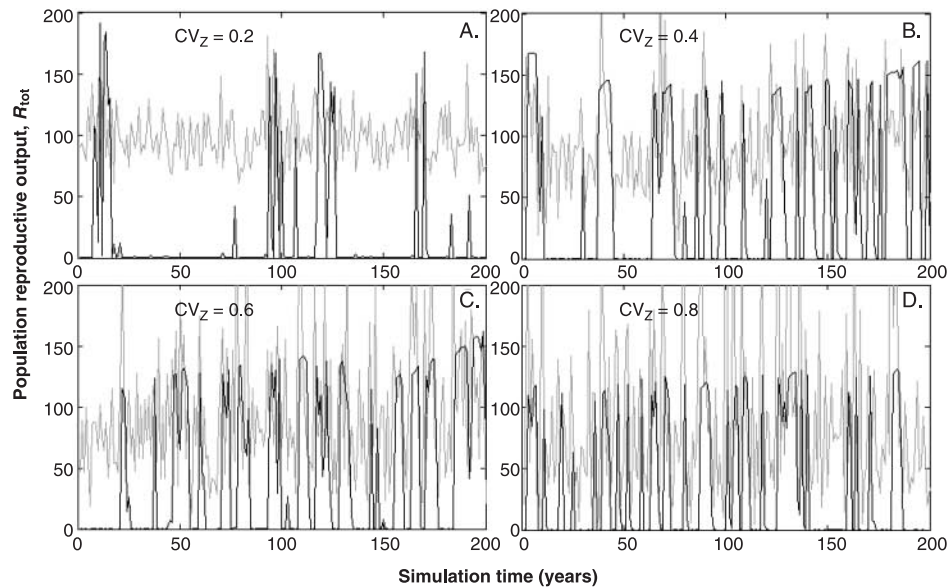


Fig. 2. Sample 200-year time-series of population reproductive (R_{tot} , black line) and environmental coefficient (Z , grey line) for all four levels of environmental variability, CV_Z . For clarity, the environmental coefficient has been rescaled to a mean of 100.

Table 1. Summary for 5000-year simulations of reproductive output for populations of 500 trees facing different levels of environmental variability (CV_Z): mean and maximum population reproductive output (R_{tot}), population reproductive variability (CV_R) both for the entire 5000-year simulation and for the resampled time-series (see text), and correlation between R_{tot} and environmental coefficient, Z , in the current year (lag = 0) and in the previous year (lag = 1)

CV_Z	R_{tot}		CV_R		Correlation (R_{tot} , Z)	
	Mean	Max.	Simulation	Resampled	Lag = 0 year	Lag = 1 year
0.2	28.8	201	2.04	1.45	0.04	0.51
0.4	69.8	190	1.05	1.25	0.30	0.61
0.6	56.3	173	1.15	1.29	0.27	0.64
0.8	43.9	159	1.31	1.50	0.31	0.65

Note: All correlations are significant at the $P < 0.05$ level.

When the R_{tot} time-series were resampled using record lengths drawn from the empirical literature (Herrera *et al.*, 1998), the mean population CV_R values were more similar across environments. Despite a quadrupling of CV_Z , CV_R varied by only 20%, from ~1.25 to 1.50, and showed no trend with changes in CV_Z (Table 1). The CV_R distributions overlap considerably with the empirical distribution (Fig. 4), but tend to display substantially heavier upper tails (i.e. more variable time-series) and a more uniform dispersion than the empirical observations. In all environments, the model distributions were significantly different from the empirical distribution (Kolmogorov-Smirnoff test, range of $KS = 0.15$ – 0.29 , all

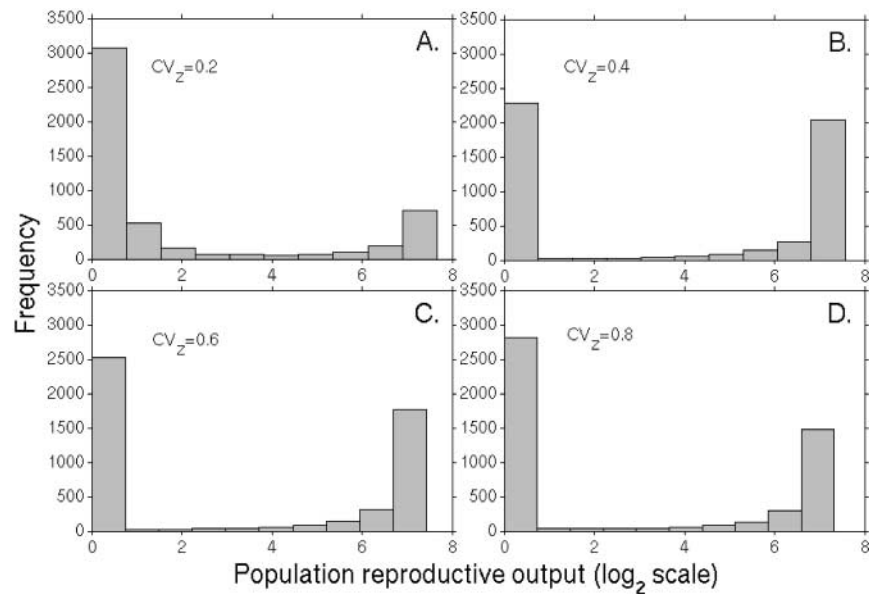


Fig. 3. Distributions of log₂-transformed population reproductive output, in all simulated environments.

$P < 0.05$). Interestingly, for many levels of resource variability, the model produces highly variable reproductive records more frequently than the empirical record, while more constant reproductive records are under-represented in the simulation data.

Reproductive synchrony and size structure

Large reproductive events invariably involved many individuals and high equitability, which implies some degree of reproductive synchrony (Fig. 5). However, substantial reproductive output (> 100) occurred even when less than half of the population was participating. Low equitability only occurred during small reproductive events by a small number of reproducers.

Population size structure was similar across all levels of environmental variability (Fig. 6). However, more constant environments showed an increasing frequency of large individuals, presumably because the trees tended to grow faster (Fig. 1). The partitioning of reproduction among size classes was also similar across the different environments (Fig. 7). The smallest reproductive events were dominated by the smallest individuals, while large reproductive events exhibited fairly even contributions across size classes.

DISCUSSION

The relatively simple life-history model generated the fundamental patterns associated with masting phenomena: high inter-annual variability, synchrony among individuals, and bimodal distributions of population reproductive output. The observed patterns were robust across a wide range of environmental variability. In all environments, large reproductive events were episodic and involved a sizeable fraction of the population reproducing

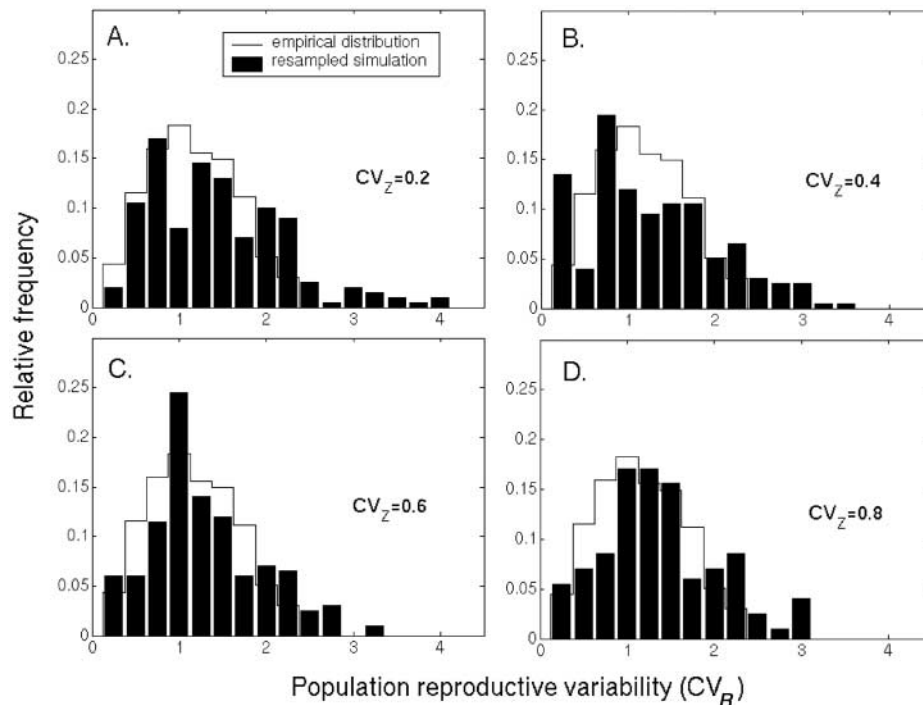


Fig. 4. Distributions of population reproductive variability for all simulations (bars). Two hundred reproductive records were drawn at random from each 5000-year simulation, with the record length drawn from the empirical distribution (see text). The step plot (same in all graphs) is the empirical distribution of reproductive variability from 296 studies of reproduction in woody perennials (Herrera *et al.*, 1998).

synchronously. Together, these results suggest that reproductive variability and synchrony should be expected frequently in populations of polycarpic perennial plants, and that the evolution of individual allocation strategies in response to even modestly variable environments may explain a good deal of the observed population-level variability.

It has recently been proposed that, in the absence of economies of scale benefits, population reproductive coefficients of variation should fall in the range of 0.85–1.35 (Kelly *et al.*, 2001). Coefficients of variation for all of the simulations support the upper end of this prediction (Table 1). However, the resampled distributions of reproductive variability encompassed the entire range of observed variability, and they produced many more variable reproductive records than those recorded in the literature (Fig. 4). If one takes the modelled distributions as a null expectation of reproductive variability, it is difficult to motivate more elaborate evolutionary explanations for reproductive variability in plant populations. Thus, as noted by Kelly (1994), the relative constancy of plant reproduction (or its constrained range of variability) may be an equally remarkable evolutionary phenomenon.

The multi-year runs of high reproductive output observed in the simulation output (Fig. 2) contrast with the empirical observation of negative temporal autocorrelation on short time-scales (Koenig and Knops, 2000). Two factors likely contributed to this pattern.

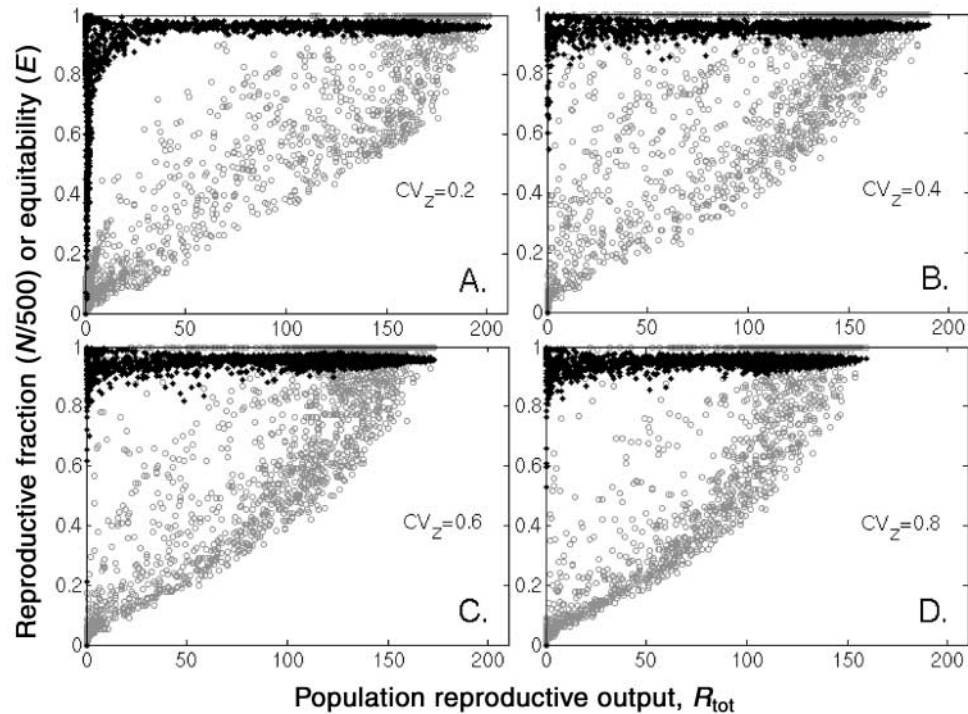


Fig. 5. Relationship between population reproductive output (R_{tot}), the fraction of individuals reproducing (N , grey circles) and the equitability of reproductive output among reproducing individuals (E , black dots), for all levels of environmental variability.

First, at the level of the individual, the reproductive capacity was small relative to the storage capacity, which resulted in significant carry-over of stored reserves even after reproduction. In this regard, more realism could be added to the model by including additional energetic costs reflecting reproductive ‘start-up’ and the remobilization of stored reserves. Second, at the population level, years of high reproduction often involved many but not all individuals (Fig. 5), and runs could result from different subsets of the population reproducing in consecutive years. Thus, due to both sustained reproduction and imperfect synchrony, a given masting ‘event’ can be spread over several years, as observed in so-called ‘normal’ masting species (Kelly, 1994). These results reinforce the conclusion that temporal patterns of allocation and inter-individual synchrony, rather than variability *per se*, are key to understanding masting phenomena (Herrera, 1998).

This study reinforces the difficulty of distinguishing the effects of environmental variability on reproductive variability and synchrony from those of economies of scale (Rees *et al.*, 2002). Increasing the likelihood of pollination or avoiding seed predators via satiation undoubtedly benefits many perennial plants (Silvertown, 1980; Sork *et al.*, 1993; Kelly, 1994; Herrera *et al.*, 1998). However, this study and other theoretical investigations (Lalonde and Roitberg, 1992; Yamauchi, 1996) imply that many of the empirical patterns that are considered the hallmarks of masting (e.g. high values of CV_R , bimodal reproduction in a continuously varying environment) do not require economies of scale

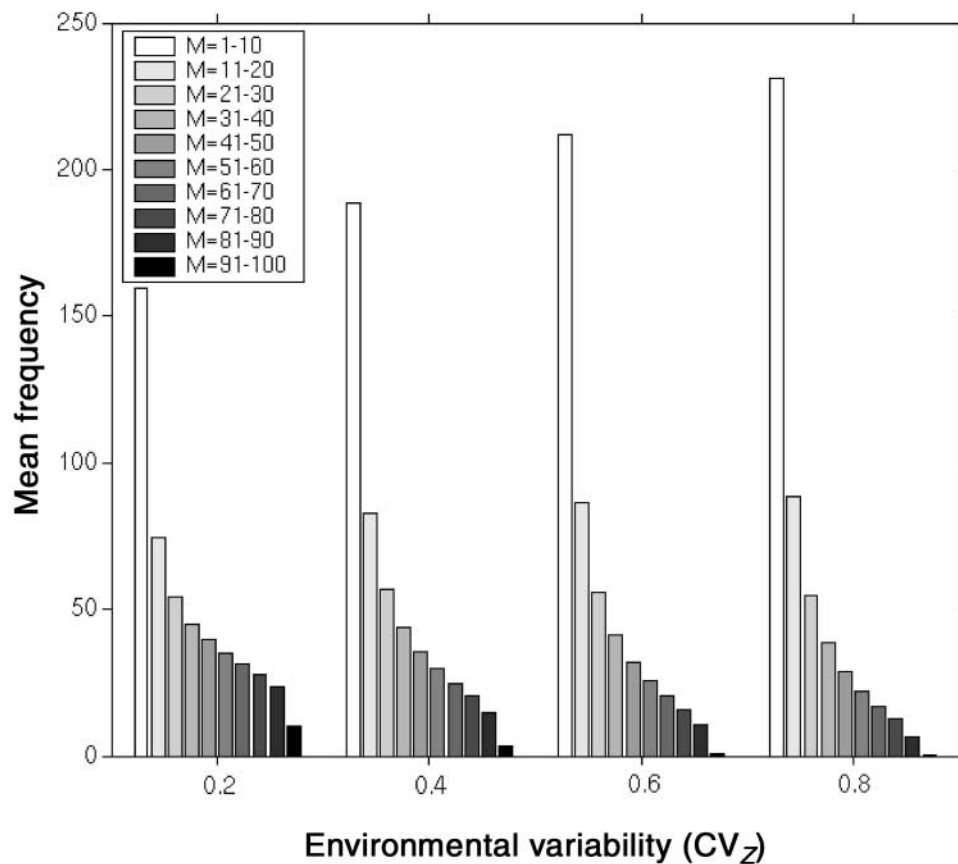


Fig. 6. Mean population size structures over 5000-year simulations for all levels of environmental variability.

dynamics, and may thus be present in plant populations that are not under strong selection for pollination efficiency or predator satiation. Thus, observations generally taken as evidence of economies of scale selection (e.g. increased pollination efficiency or seed survivorship during ‘mast’ years) may arise as epiphenomena of the adaptation of reproductive allocation schedules to life in a variable environment.

Lalonde and Roitberg (1992) found that while seed predators could select for reproductive synchrony, synchronous reproducers could not invade an asynchronous population. They then used a dynamic life-history model to show that optimal allocation strategies could produce reproductive synchrony in a variable environment. Yamauchi (1996), on the other hand, showed how storage could modulate the response of reproductive output to environmental variability, regardless of the specific selective mechanisms. Several studies have highlighted the importance of such storage-dependent strategies in the context of economies of scale in general and pollination efficiency in particular (Isagi *et al.*, 1997; Satake and Iwasa, 2000, 2002a,b; Rees *et al.*, 2002). However, these studies are generally based on populations of mature, non-growing individuals, often in constant environments.

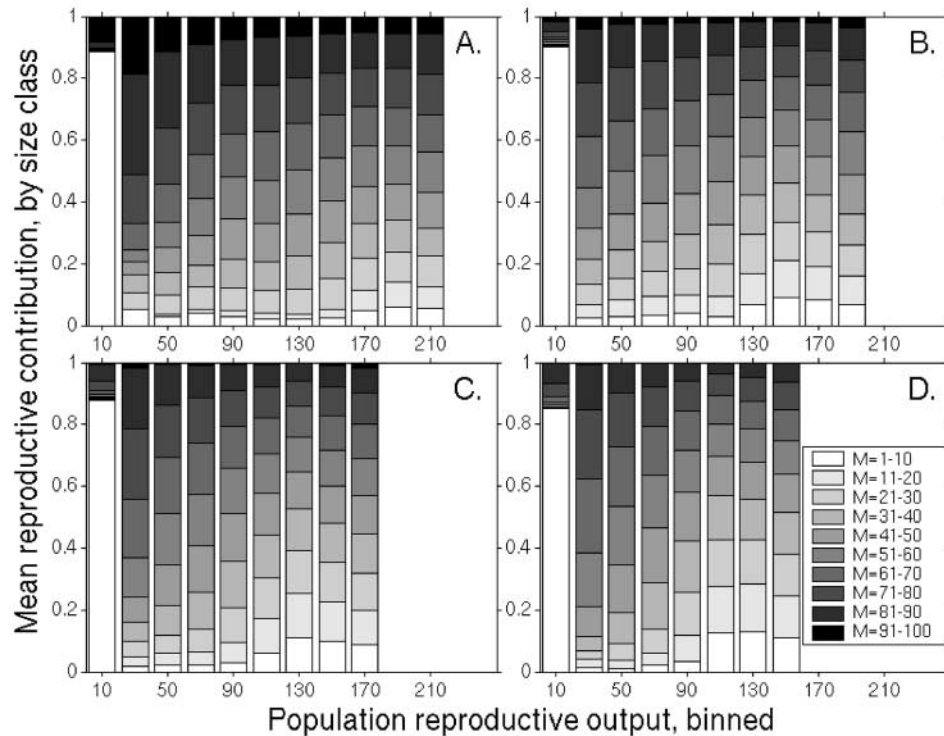


Fig. 7. Mean proportional contribution of individuals in different size classes to reproductive events of different magnitudes, for all levels of environmental variability.

Here, I examined how storage-size dependent strategies evolve in response to environmental variability, when the capacity for both reproduction and storage change with plant size, and when storage serves not only reproduction, but also the demands of maintenance and growth. Under this more complex, but arguably more realistic, set of assumptions, we should expect levels of variability and synchrony comparable to and often exceeding those observed empirically.

The pre-existence of some degree of variability and synchrony may be very important in the evolution of masting, regardless of the selective mechanism (Lalonde and Roitberg, 1992; Yamauchi, 1996; Kelly and Sork, 2002). Thus, even in modestly variable environments, patterns of reproductive variability may predispose plants to take advantage of reproductive economies of scale. However, the fact that storage-mediated reproductive variability and synchrony may itself represent an evolved strategy in response to environmental variability, as demonstrated here, has largely been ignored. Furthermore, because the model generated the most variable reproductive output in the least variable environment (Table 1, Figs. 2 and 4), it is clear that the reproductive output of plant populations in variable environments must be viewed as an evolved response, rather than the simple, proximate mechanism of plants marching in lockstep with their environment. The pronounced variability of reproductive output under modestly variable environmental conditions may have particularly important implications, as some of the

most well-known masting systems occur in tropical environments that are often considered relatively constant (e.g. the Dipterocarp forests of Southeast Asia; Janzen, 1974; Curran and Webb, 2000).

In the model, large reproductive events usually involved many (but not all) individuals (Fig. 3) of varied sizes (Fig. 5), primed by favourable conditions in previous years (Table 1). Because the individual trees were reproducing independently, the observed degree of synchrony can only be attributed to responses to common environmental forcing (Z), known empirically as the 'Moran' effect (Koenig, 2002). However, even though the favourability of the environment was precisely defined in the model by the value of Z in any given year, variation in the environment left much of the variability in reproduction unexplained (maximum correlation coefficients of 0.5–0.65). In real plant populations, environmental favourability is much more difficult to define, and thus correlations between environmental and reproductive fluctuations should be even looser than in the model. Generally, this result suggests that the contingencies of environmental fluctuations, population size structure and dynamics, and individual life histories interact to generate patterns of reproductive variability. More specifically, the changing demands of, and capacities for, uptake, growth, maintenance, storage and reproduction with changing plant size mediate the magnitude of individual reproductive responses to environmental fluctuations.

All else being equal, differences in allocation strategies in response to environmental variability produce differences in growth trajectories and population size structure in the model. However, the simulations lacked many important demographic details, including dispersal, establishment and competition for resources. Thus, understanding how the dynamics of size-structured populations affects patterns of reproductive variability and synchrony remains an important topic for future research.

CONCLUSIONS

The causes and consequences of reproductive variability and synchrony in perennial plants are important and unsolved questions for both ecology and evolutionary biology. For ecology, the episodic production of large seed crops has important ramifications from the population to the ecosystem (Jones *et al.*, 1998; Lima *et al.*, 1999; Ostfeld and Keesing, 2000; Koenig, 2001; Koenig and Knops, 2001). Evolutionarily, masting is a fascinating phenomenon that begs an adaptationist explanation (Waller, 1979; Silvertown, 1980; Sork, 1993; Kelly, 1994; Herrera *et al.*, 1998). However, all explanations must begin with a clear expectation. According to current expectations (e.g. Kelly, 1994; Kelly and Sork, 2002), model output generated here would likely be classified as a 'normal' masting pattern, likely selected by some reproductive economy of scale. Given model assumptions, this result draws into question the criteria currently used to distinguish evolutionarily 'remarkable' reproductive variability from the 'expected background'. It may be that economies of scale should be viewed as selecting for specific environmental cues or temporal patterns of reproduction, rather than for variability *per se*.

The results presented here are cautionary, rather than critical. I have simply documented that the evolution of life histories, even in relatively constant resource environments, will likely generate highly variable and synchronous patterns of reproductive output in perennial plant populations. Because these patterns result from optimal allocation strategies, they should be widespread in perennial plants (Herrera *et al.*, 1998), which should solve the problem of maximizing their fitness in the face of inter-annual

environmental variability. Although reproductive economies of scale undoubtedly provide fitness benefits, caution should be exercised when inferring them as the major ecological and evolutionary determinant of reproductive variability and synchrony in plant populations.

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