

Dissecting components of population-level variation in seed production and the evolution of masting behavior

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Mast-fruiting or masting behavior is the cumulative result of the reproductive patterns of individuals within a population and thus involves components of individual variability, between-individual synchrony, and endogenous cycles of temporal autocorrelation. Extending prior work by Herrera, we explore the interrelationships of these components using data on individual seed production in 59 populations of plants from 24 species spanning a large range of annual variability, from species exhibiting strong masting to others with little annual variability in seed production. Estimates of population and individual variability were not biased by sample size or average overall seed production when based on untransformed seed production values, but these values declined as log-transformed seed production increased. Population variability was more strongly correlated with individual variability ($r = 0.86$) than individual synchrony ($r = 0.73$). These latter two components were also significantly correlated ($r = 0.45$), but randomizations confirm that they need not covary closely. Thus, selection can act separately on inter-annual variability and between-individual synchrony. We illustrate the potential for such fine-tuned selection on seed production patterns by discussing several examples and by demonstrating significant differences in components of population-level variation in seed production among species related to their life-history.

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The intermittent, synchronous production of large seed crops, known as masting or mast seeding (Janzen 1969, 1971, Silvertown 1980, Kelly 1994, Kelly and Sork 2002), is a population phenomenon that results from the cumulative behavior of individual plants. Masting as a reproductive strategy is paradoxical because it requires that plants delay reproduction (Waller 1979) and potentially be subject to more intense density-dependent mortality (Hett 1971). Such a strategy can

evolve if individual plants achieve greater fitness through variable seed production across years than they would through more constant annual production because of an advantage achieved through some “economy of scale” (Norton and Kelly 1988). Three common mechanisms that benefit from economy of scale are predator satiation (Janzen 1969, 1971, 1978), more efficient pollination (Smith et al. 1990), and increased probability of seed dispersal (Norton and Kelly 1988).

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Greater interannual variability at the population level can be achieved when selection favors increased seed production during some years with reduced production during others, increased interannual variability directly, or higher interplant synchrony (Janzen 1969, 1971, 1978). Plants can also vary the strength and length of endogenous cycles in seed production (Sork et al. 1993, Koenig et al. 1994).

The components of masting need not vary in parallel. For example, localized seed predators may select for greater variability or more pronounced endogenous cycles but not increased synchrony if individual trees can satiate the seed predators found in a small area (Janzen 1978). In contrast, regional seed predators or more efficient wind pollination may select for synchrony but not necessarily greater variability. Some seed predators may select for an increase in the intermast interval (Janzen 1969, 1971, 1978), while a specialist seed predator with an extended diapause might select for high variability and the associated low predictability of seed crops (Kelly et al. 2000). Patterns of seed production within a population may reflect selection on any of these elements concomitantly or independently.

Species with different life history characters, pollen vectors, and seed dispersal modes may experience selection for masting differently. For example, Waller (1979) argued that the disadvantage of skipping some years of reproduction is smaller in long-lived plant species. Norton and Kelly (1988) and Smith et al. (1990) suggested that mast flowering is more likely to evolve in wind-pollinated species because increased pollen availability enhances pollination success, while in animal-pollinated species increased flowering may saturate the pollinators. Finally, large seed crops may be less efficient for frugivore-dispersed species if more fruit is available than can be dispersed, but an advantage for predator-dispersed species if sufficient fruit is produced to effect satiation of those predators (Kelly 1994, Herrera et al. 1998, Kelly and Sork 2002). Focusing on population variability, both these latter studies found evidence to support the predictions that wind-pollinated species should show greater interannual variability than animal-pollinated species and that frugivore-dispersed species show less interannual variability than species dispersed by other means.

Recently, Herrera (1998) proposed that discussions of the proximate and ultimate causes of masting should focus on the behavior of individual plants with respect to their variability and synchrony rather than on the more easily obtained population-level estimates of inter-annual variability. Using a sample of 16 plant studies, he found that population variability (CV_p , defined as the coefficient of variation of mean seed production across years) was closely correlated with mean individual variability (\overline{CV}_i , calculated by averaging across individuals the coefficient of variation of

seed production across years for each individual), but only weakly correlated with individual synchrony (as measured by the Kendall rank correlation nonparametric index τ). In his analysis, \overline{CV}_i and τ , the two main components of CV_p , were not correlated. This result lends support to the hypothesis that selection can potentially act independently on individual variability among years and on within-year synchrony in seed production.

This paper has three goals. First we extend Herrera's (1998) analysis of the decomposition of CV_p with several refinements, including a more extensive dataset, a parametric measure of synchrony, and an index of the endogenous cycle (temporal autocorrelation) as an additional component of population-level variability in seed production. The latter was added because prior studies have demonstrated that endogenous cycles can be significant in masting species (Sork et al. 1993, Koenig et al. 1994) and such cycles may be a response to particular selective pressures. Second, we explore the consequences of those relationships for our understanding of masting behavior with three questions: (1) how do the components of masting behavior correlate with each other? (2) does the incorporation of endogenous cycles improve our understanding of masting behavior? and (3) is there evidence that the components of masting may differ among species with different life-history characters? Third, we discuss ways in which plants may be able to optimize their reproductive schedules in the face of two or more contradictory selective pressures by altering different components of masting.

Methods

We obtained individual seed production data from 59 populations of 24 species of plants (see Appendix). We used all available datasets that reported individual plant data and, within these studies, we included all individuals that reproduced at least once during the course of the study. Studies ranged from 4 to 22 years in length ($\bar{X} = 9.8$ years) and involved 5 to 120 individuals ($\bar{X} = 32.5$ individuals). Methods for estimating seed productivity ranged across studies. In order to investigate the potential for selection acting on different components of masting, we compared plant species according to their growth form (herbaceous or woody) and their primary pollen vector (animal or wind/gravity). We were unable to effectively compare species according to their primary seed dispersal vector because of poor representation in our data of species dispersed by mutualistic frugivores.

For each data set, we calculated the mean seed production of the population as measured by the mean of the annual means, and the coefficient of variation of the annual means (CV_p ; here presented as $SD/\text{mean} \times 100$). We estimated mean individual synchrony (\overline{r}_p) as

the mean of all pairwise Pearson correlations between individuals (Buonaccorsi et al. 2001). As an index of an endogenous cycle, we used temporal autocorrelations at 1-yr time lags and partial autocorrelations at 2-yr time lags (controlling for lag 1) calculated for both the population annual totals ($ACF1_p$ and $ACF2_p$) and by averaging values calculated for each individual ($ACF1_i$ and $ACF2_i$). Analyses involving autocorrelations were restricted to datasets with at least six years of data.

Values were also calculated following log-transformation ($\log[X + 1]$) of the individual seed production values; these results are presented when they differed from those using the untransformed data. Measures were summarized for all 59 datasets and for the 24 datasets obtained after averaging results from multiple studies performed on the same species. The majority of datasets (43 datasets of 12 different species) were on oak (*Quercus* spp.), but the remaining studies included a wide diversity of genera and families (see Appendix) from the United States, New Zealand, Spain, and Central America. Oaks were divided into species requiring a single year to mature acorns (1-yr species) and those requiring two years to mature acorns (2-yr species).

All relevant variables did not depart significantly from normality (see below). However, because of widely unequal sample sizes, we used non-parametric tests in the comparisons of the masting characteristics of taxa with different life-history traits. Multiple regressions were used to compare the relative importance of individual variability and synchrony on population variability. Statistical tests were performed using SPSS (1999).

To explore the potential relationships among \overline{CV}_i , \overline{r}_p , and CV_p in combinations beyond those occurring in the 59 datasets, we used randomizations. For each of the 59 datasets, annual seed production values for individual plants were first ordered by size such that synchrony was very high. Values were then randomly reordered by progressively increasing amounts to maintain the identical \overline{CV}_i while decreasing synchrony. Approximately 270 different combinations were calculated for each dataset yielding a total of 16,000 reshuffled datasets from which we calculated CV_p contours resulting from various combinations of \overline{CV}_i and synchrony.

Results

The 59 datasets varied widely in CV_p , \overline{CV}_i , and mean pairwise synchrony (\overline{r}_p); three representative examples are shown in Fig. 1. Distributions of CV_p , \overline{CV}_i , and mean pairwise synchrony (\overline{r}_p) and both population and mean individual autocorrelations were normally distributed (Kolmogorov-Smirnov one-sample tests, all $P > 0.07$; Fig. 2). The major components of masting (CV_p , \overline{CV}_i and \overline{r}_p) were not significantly associated with number of years of data or number of individuals (Table 1), but the log of mean seed production was inversely correlated with CV_p and \overline{CV}_i . There were generally significant positive correlations between the partial lag 2 autocorrelations and both the number of years of data and the number of individuals, while lag 1 autocorrelations were significantly correlated with the number of years included in the datasets (Table 1).

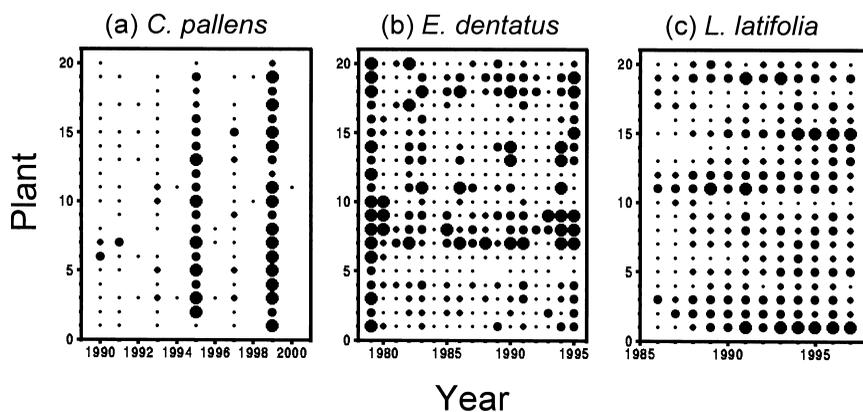


Fig. 1. The effect of \overline{CV}_i and synchrony on CV_p , illustrated by three of the 59 datasets. The size of each dot is proportional to that year's seed crop for each individual plant; a blank means zero seeds. (a) A high CV_p (178) resulting from high \overline{CV}_i (mean 210) and high synchrony (mean pairwise $r = 0.89$), in *Chionochloa pallens*, Mt. Hutt, New Zealand (Kelly et al. 2000). (b) A low CV_p (67) resulting from moderate \overline{CV}_i (122) but low synchrony (0.34), in *Elaeocarpus dentatus*, Orongorongo, New Zealand (Schauber et al. 2002). (c) A very low CV_p (29) resulting from low \overline{CV}_i (52) and moderate synchrony (0.53), in *Lavandula latifolia*, Sierra de Cazorla, Spain (C. M. Herrera, pers. comm.). Each species is represented by 20 plants and the statistics given are based on the plants illustrated.

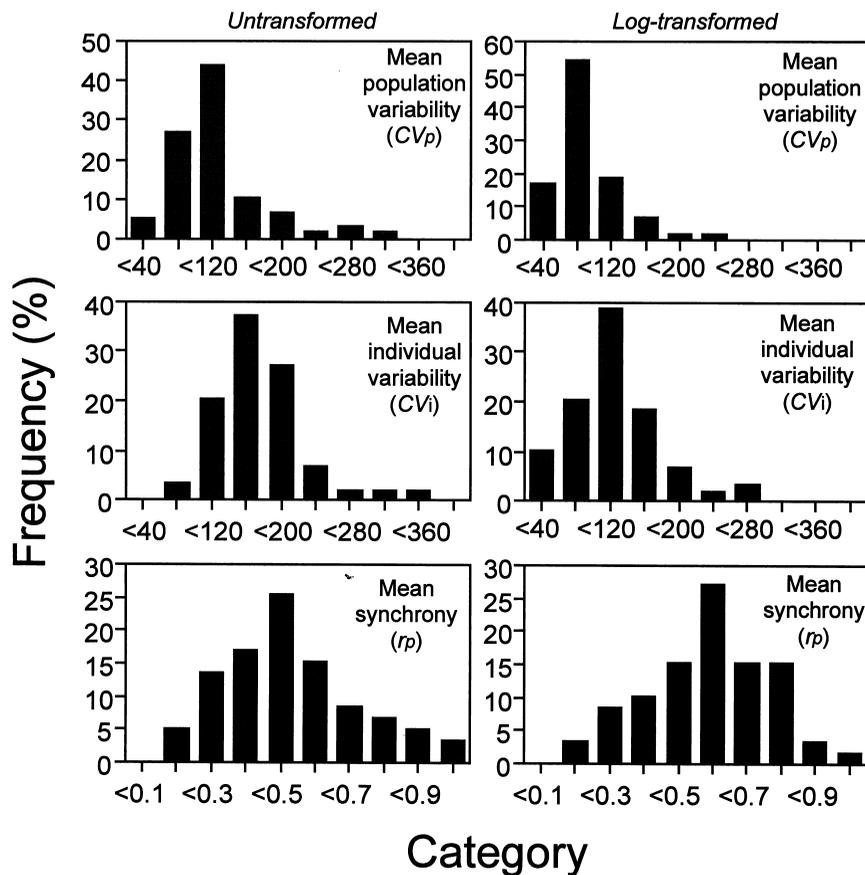


Fig. 2. Frequency distributions of the three primary variables considered here, using both untransformed (left column) and log-transformed (right column) values. None of the variables deviates significantly from normality using Kolmogorov-Smirnov one-sample tests.

Interrelationships between variability and synchrony

Correlations between measures of population variability (\overline{CV}_p), individual variability (\overline{CV}_i), and synchrony (\overline{r}_p) were all significantly positive, usually highly so, in both the complete dataset and the dataset combining multiple samples for the same species (Table 2). In

Table 1. Pearson correlations with sample sizes and overall mean seed production for all datasets. $N = 59$ (sample sizes slightly reduced for autocorrelations). Results using log-transformed data, when different from those using untransformed data, are in parentheses. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	N years	N individuals	Mean seed production
\overline{CV}_p	0.16	0.14	-0.09 (-0.26*)
\overline{CV}_i	0.25	0.17	-0.25 (-0.35**)
\overline{r}_p	0.12	0.00	0.05
$\overline{ACF1}_p$	0.23	0.03	0.14
$\overline{ACF2}_p$	0.29* (0.36**)	0.32* (0.24)	0.09
$\overline{ACF1}_i$	0.27*	0.11	0.13
$\overline{ACF2}_i$	0.48***	0.26 (0.33*)	0.04

general, \overline{CV}_i was more highly correlated with \overline{CV}_p than \overline{r}_p with \overline{CV}_p . In stepwise regressions of \overline{CV}_p on \overline{CV}_i and \overline{r}_p , \overline{CV}_i entered first and was highly significant ($P < 0.001$) in all cases. By itself, \overline{CV}_i explained 74% (all datasets) and 87% (species combined) of the variance (82 to 94% using log-transformed data). The inclusion of \overline{r}_p significantly increased R^2 values in all cases except using the log-transformed data combining species, but its inclusion only increased the proportion of the total variance explained by a few percent.

The relationship between \overline{CV}_p and \overline{CV}_i is positive and linear (Fig. 3), while the interrelationships among \overline{r}_p , \overline{CV}_p and \overline{CV}_i are curvilinear with one outlier (Fig. 4). We investigated the expected relationships among these variables further using randomizations. Results (Fig. 4) support the conclusion from the stepwise regression that \overline{CV}_p is largely dependent on \overline{CV}_i , as they are nearly orthogonal to the x-axis (\overline{CV}_i) over most of the range of the data. Fig. 4 also indicates that a moderate \overline{CV}_p can result from either a high synchrony combined with a relatively low \overline{CV}_i , or lower synchrony combined with relatively high \overline{CV}_i . However, the only way to get a very high \overline{CV}_p is for both \overline{CV}_i and synchrony to be high.

Table 2. Pearson correlations among mean population variability, mean individual variability, and mean synchrony. Values are for the untransformed data; log-transformed values are presented in parentheses when significance values differ. * = $P < 0.05$; *** = $P < 0.001$.

	Mean population variability (CV_p)	Mean individual variability (CV_i)
All datasets (N = 59)		
$\overline{CV_i}$	0.86***	–
r_p	0.73***	0.45*** (0.27*)
Multiple samples for same species combined (N = 24)		
$\overline{CV_i}$	0.94***	–
r_p	0.76***	0.65*** (0.42*)

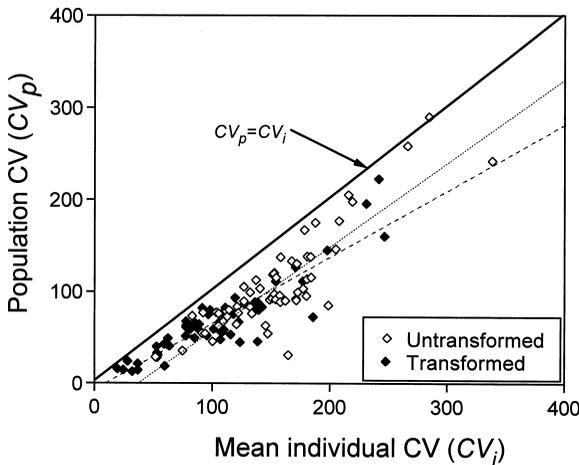


Fig. 3. Relationship between individual ($\overline{CV_i}$) and population (CV_p) variability using data from all 59 individual populations. Regressions are: $CV_p = 0.91 (\overline{CV_i}) - 33.0$, $R^2 = 0.74$ (untransformed; dotted line); $CV_p = 0.72 (\overline{CV_i}) - 6.82$, $R^2 = 0.82$ (log-transformed; dashed line); both $P < 0.001$. Solid line is where $CV_p = CV_i$.

Variability and synchrony vs temporal autocorrelations

Using the untransformed values, correlations between the temporal autocorrelations and the measures of variability and synchrony were generally low and at best marginally significant (Table 3). This indicates that the strength of short-period endogenous cycles is independent of the synchrony and within-plant variability, at least using untransformed data. Using the log-transformed combined dataset, the 1-yr lag correlations were significantly negatively correlated with both CV_p and $\overline{CV_i}$ (Table 3, bottom).

Are different life-history characters associated with different patterns of masting?

Our analyses found several differences between species varying in their life-history traits (Table 4). Using both

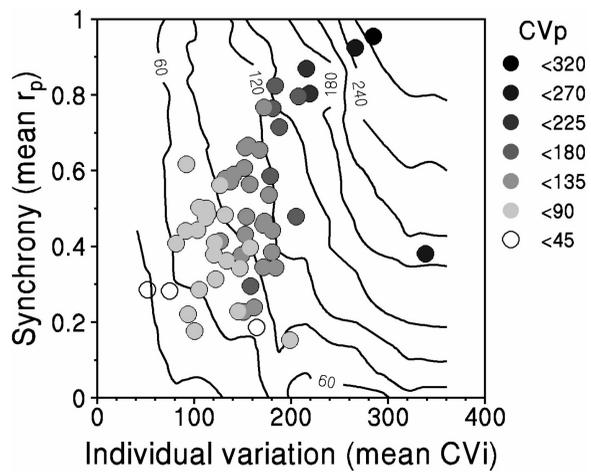


Fig. 4. Interrelationships among $\overline{r_p}$, CV_p and $\overline{CV_i}$ based on randomized permutations. For each of the 59 datasets used in the analyses, annual data for individual plants were reshuffled to vary synchrony from high to low while holding $\overline{CV_i}$ constant, and calculating the resulting CV_p . Plotted are CV_p contours resulting from 270 different combinations of each dataset, giving a total of 16,000 reshuffled datasets. Circles are the actual CV_p values for the 59 datasets.

all populations and combining multiple studies for the same species, $\overline{CV_i}$ was significantly lower among woody compared to herbaceous species. Analyses using the combined data also revealed significantly lower synchrony among animal-pollinated species compared to those pollinated by wind or gravity. Considering oaks by themselves, $\overline{ACF1_i}$ was significantly more negative among species requiring one year to mature acorns compared to those requiring two years to mature acorns.

Discussion

Masting as a distinct phenomenon

Our results support prior studies (Kelly 1994, Herrera et al. 1998, Koenig and Knops 2000) demonstrating that masting and its components are normally distributed, rather than bimodally distributed with a well-defined set of “masting” and “non-masting” populations. Based on this finding, Herrera et al. (1998) proposed abandoning the term “mast-fruiting” altogether. While acknowledging the importance of treating masting quantitatively with objectively defined parameters, we believe it useful to retain the term “masting” to focus attention on a complex, evolutionarily interesting phenomenon and for terminological simplicity. In general, selection for masting presumably has been stronger when variability in annual seed production and inter-individual synchrony is greater.

Table 3. Pearson correlations of measures of variability and synchrony with temporal autocorrelation. Values are for the untransformed data; log-transformed values are presented in parentheses when significance values differ. * = $P < 0.05$; ** = $P < 0.01$.

	Mean population variability (CV_p)	Mean individual variability (CV_i)	Mean pairwise synchrony (r_p)
All datasets (N = 56)			
$ACF1_p$	-0.01	-0.12	0.12
$ACF2_p$	0.20	0.23	0.02
$ACF1_i$	-0.07	-0.16 (-0.29*)	-0.04
$ACF2_i$	0.23	0.34* (0.26)	0.04
Multiple samples for same species combined (N = 23)			
$ACF1_p$	-0.28 (-0.50*)	-0.40 (-0.57**)	-0.10
$ACF2_p$	0.18	0.04	0.05
$ACF1_i$	-0.40 (-0.54**)	-0.49* (-0.57**)	-0.37
$ACF2_i$	0.27	0.06	0.31

Table 4. Results of tests (Mann–Whitney U-test for dichotomous variables; Kruskal–Wallis ANOVA for seed dispersal vector) for differences in the components of masting across life-history characters. For all populations and analyses combining multiple studies of the same species, two variables were tested: growth form (woody vs herbaceous) and pollination vector (animal vs wind/gravity). For oaks, we tested differences according to whether species mature acorns in 1 or 2 years (1-yr vs 2-yr species). Only results yielding a significant effect are listed. Values are means \pm SE (N). Variables untransformed. * = $P < 0.05$; *** = $P < 0.001$.

Test	Category 1	Category 2	z-value
All populations (N = 59 studies)			
CV_i vs growth form (woody [cat 1] vs herbaceous [cat 2])	148.7 \pm 6.6 (54)	201.4 \pm 19.5 (5)	2.4*
Multiple samples for same species combined (N = 24 species)			
CV_i vs growth form (woody [cat 1] vs herbaceous [cat 2])	142.7 \pm 12.8 (20)	192.9 \pm 18.9 (4)	2.0*
r_p vs pollination vector (animal [cat 1] vs wind/gravity [cat 2])	0.39 \pm 0.07 (7)	0.54 \pm 0.13 (17)	2.1*
Oaks only (N = 43 studies)			
$ACF1_i$ vs oak type (1-year [cat 1] vs 2-year [cat 2])	-0.27 \pm 0.02 (26)	-0.12 \pm 0.03 (17)	3.5***

Sample size and productivity biases

Mathematical considerations suggest that sample size and productivity may influence CV_p (J. P. Buonaccorsi, unpubl.). However, our empirical results generally indicate that neither individual nor population CV is likely to be strongly biased by either of these factors, particularly if productivity data are not log-transformed (Table 1). Similarly, correlations between sample size or mean seed production with lag 1 autocorrelations were small and in all but one case non-significant. In contrast, partial lag 2 autocorrelations were significantly correlated with both the number of individuals and number of years of data included in the samples, which suggests that caution must be used in interpreting patterns found in higher-order lag effects, especially when sample sizes or the number of years of data are small.

Relationships among $\overline{CV_i}$, CV_p and synchrony

The relationships between variability and synchrony found here generally support Herrera's (1998) conclusion that mean individual variability correlates strongly with population variability and less so with synchrony

(Table 2), although our larger sample size reveals the latter relationship to be stronger than previously noted. Populations that exhibit high annual population variability in seed production generally do so both because individuals have highly variable interannual seed production and because individuals tend to be more synchronized than individuals in populations with low annual variability.

The components of population-level variation in seed production may nonetheless differ significantly between different categories of species, thus offering insight into the selection pressures acting on various populations. The potential range of such variation was outlined by randomization of the actual datasets. High population variability requires both high individual variability and high individual synchrony, but moderate levels of variability do not require high synchrony. In particular, intermediate levels of CV_p can be generated by quite variable levels of individual synchrony providing that individual variability is moderate to high (Fig. 4).

We found several potential examples of such differences related to life-history characters (Table 4). First, woody plants had lower individual variability ($\overline{CV_i}$) than herbaceous species, suggesting that selection for masting in our sample of herbaceous species has led to

higher individual variability, but not necessarily to higher synchrony. In contrast, synchrony was significantly greater among wind-pollinated compared to animal-pollinated taxa, suggesting that selection related to this character has been stronger on synchrony than individual variability. Species of oaks were not distinguishable on the basis of individual variability or synchrony, but rather by their lag 1 autocorrelations, with species that mature acorns in a single year exhibiting more negative autocorrelations than those requiring two years to mature acorns.

These results are generally compatible with those reported earlier by Herrera et al. (1998) or Kelly and Sork (2002), who looked specifically for relationships between mean population variability (CV_p) and life-history traits. However, our point here is not so much to focus on the selective factors resulting in the observed differences as to emphasize that selection may not be acting identically on different components of masting behavior and that knowledge of more than annual variability may be necessary to fully test predictions. For example, Herrera et al. (1998); see also Kelly and Sork (2002) predicted that masting should be more pronounced in wind-pollinated species, but found only a small difference in CV_p between the two categories. Our results here support their prediction, but suggest that the difference between these two groups may be primarily in greater synchrony among wind-pollinated species rather than higher individual variability. Future studies of the relationships between seed production and life-history characteristics should, whenever possible, assess relative selection pressures on all available components of population-level variation in annual seed production, not just on annual variability.

Life-history and selection on different masting components

The selective or ultimate cause of strong masting is usually an economy of scale in the sense of a reproductive process that is more efficient in larger episodes

(Norton and Kelly 1988). Such economies of scale may usually act on both \overline{CV}_i and \overline{r}_p in concert, but, as we demonstrate here, in some cases they may select separately for increased individual variability or increased synchrony among individuals, and in some cases may even select for endogenous cycles uncorrelated with either \overline{CV}_i or \overline{r}_p . Dissecting masting into its various components allows the elucidation of ways in which individual plants may modify their seed production patterns to maximize their fitness in the face of potentially contradictory selective pressures. Expanding on comments by Janzen (1978), we suggest various scenarios where selection might act differently on the separate components and give examples of plants whose differing seed production patterns fit these cases (Table 5).

The most pronounced masting will result from agents selecting for both high variability (\overline{CV}_i) and high synchrony (\overline{r}_p). Such factors include wind pollination, which may increase the rate of seed set through fewer, larger, synchronized flowering efforts (Nilsson and Wästljung 1987, Norton and Kelly 1988, Houle 1999, Kelly et al. 2001) or increase the rate of outcrossing in self-compatible species (Janzen 1978, Tisch and Kelly 1998). Pronounced masting may also be selected for by predator satiation if it involves a mobile, generalist predator that can move between trees, in which case satiation may be successful only when plants exhibit both high \overline{CV}_i and high \overline{r}_p . This covariance may potentially lead to synchrony in seed production by species complexes within a community and over a large geographic area where they share seed predators, such as appears to be the case for the Dipterocarp forests of Malasia (Curran and Leighton 2000) and the alpine grasslands of New Zealand (Kelly et al. 2000).

Alternatively, if local effects are such that predators are attracted over a wide area to trees with unusually large seed crops and such areas consequently suffer relatively greater predation, then selection may act to decrease population variability in seed production by decreasing individual variability, synchrony, or both. In the case of small, relatively immobile specialist predators that may be satiated by individual trees, selection

Table 5. Possible examples of how various selection pressures may separately affect individual variability and synchrony in the seeding patterns of plants.

\overline{CV}_i	\overline{r}_p	CV_p	Selection pressures	Possible examples	Reference
High	High	High	Pollination efficiency in wind pollinated plants Regional seed predators (requires large scale synchrony)	<i>Nothofagus solandri</i> Dipterocarpaceae	Kelly et al. 2001 Janzen 1974, Curran and Leighton 2000
High	Low	Moderate	Sufficient for localized seed predators Required when localized specialist and mobile generalist predators both occur Animal dispersal in species-rich forests	<i>Cassia grandis</i> <i>Betula alleghaniensis</i> <i>Fagus sylvatica</i>	Janzen 1978 Kelly et al. 2001, Nilsson and Wästljung 1987
Low	High	Moderate	Animal pollination or animal dispersal Architectural constraints	<i>Lavandula latifolia</i> Arecaceae (Palms) <i>Hybanthus</i>	Herrera et al. 1998 Webb and Kelly 1993 Augsburger 1979, 1981
Low	Low	Low	None (synchronized only by weather)		

may act to increase individual variability but not synchrony. Examples may include *Cassia grandis* in Costa Rica and its various insect seed predators (Janzen 1978) and the *Fagus sylvatica*–*Cydia fagiglandana* system in Sweden (Nilsson and Wästljung 1987). Thus, predator satiation may select for or against synchrony depending on the functional response of the predators, or even fail to select for any evolutionary response on the part of plants in the case of small immobile predators (Janzen 1971, 1978, Kelly 1994, Romanach and Levey 2000). The effects of predator satiation will depend on a variety of factors including the size, mobility, abundance, lifespan, and degree of specialization of the predators.

These distinctions between individual variability and synchrony open the possibility for “designer” masting tailored to the particular selective forces facing plant populations. For example, a population with both a small specialist invertebrate predator and a mobile generalist vertebrate predator might maximize fitness by increasing \overline{CV}_i to locally satiate invertebrates while simultaneously reducing synchrony, and thus CV_p , minimizing attractiveness to the vertebrate predator. Possible examples include *Betula alleghaniensis* (Kelly et al. 2001) and many if not most temperate oak species (Sork et al. 1993, Koenig et al. 1994). The ability, at least in theory, to modify different aspects of masting may allow novel solutions to the opposing selective economies and diseconomies of scale that face many plant species (Table 5).

One further element that has not been addressed here is the extent of spatial synchrony in seed production, which may have a strong influence on the behavior of predators and seed dispersers. Moreover, if populations across a region have an underlying synchrony due to spatially synchronous weather effects, selection may act to enhance or decrease synchrony in seed production. Currently, relatively few data are available on geographic synchrony in seed production. Koenig and Knops (1998) demonstrated detectable synchrony on a sub-continental scale in annual seed production by conifers, while Koenig et al. (1999a, b) demonstrated significant differences in spatial synchrony among species of California oaks. Such differences may in some cases reflect the choice of environmental cue used to signal flowering (Norton and Kelly 1988). Additional work, covering many populations over large geographic areas over periods of many years, will be needed before useful generalizations will be possible.

Conclusions

We are far from being able to perform a comprehensive analysis of the ways in which the various components of masting vary among species, much less test the

adaptive significance of different patterns. However, several tentative conclusions can be made. Population variability in seed production is highly correlated with individual variability (\overline{CV}_i) and somewhat less so with individual synchrony (r_p). Therefore, when only population-level values are available, useful inferences may still be possible about the selective factors that may be involved. However, more complete data on individual behavior opens the door for more intricate questions and analyses about the nature of selection on the evolution of masting. In particular, the different components that make up population-level mast seeding allow subtle responses by a plant species to the advantages and disadvantages of large intermittent seed crops. Plants may even be able to reconcile two apparently contradictory selective forces by responding to one through the \overline{CV}_i and the other through synchrony. Exploring such possibilities remains largely a challenge for the future.

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Species	Family	Vegetation type	Pollination vector	Seed dispersal vector ¹	Locality	N years	N individuals	CV _p	CV _i	\bar{r}_p	Source ²
<i>Carya glabra</i>	Juglandaceae	Woody	Wind	Anim: P	Missouri	12	5	175	188	0.71	V. Sork
<i>Celmisia spectabilis</i>	Asteraceae	Herbaceous	Animal	Wind	New Zealand (Hutt 1070)	6	37	138	181	0.77	D. Kelly
<i>Chionochoa macra</i>	Poaceae	Herbaceous	Wind	Wind	New Zealand (Hutt 1070)	11	34	146	205	0.48	Kelly et al. 2000
<i>Chionochoa macra</i>	Poaceae	Herbaceous	Wind	Wind	New Zealand (Hutt 1600)	9	69	258	266	0.92	Kelly et al. 2000
<i>Chionochoa pallens</i>	Poaceae	Herbaceous	Wind	Wind	New Zealand (Hutt 1070)	11	79	177	208	0.80	Kelly et al. 2000
<i>Elaeocarpus dentatus</i>	Elaeocarpaceae	Woody	Animal	Anim: F	New Zealand	22	21	64	121	0.38	P. Cowan
<i>Hymenaea courbaril</i>	Leguminosae	Woody	Animal	Anim: F	Costa Rica, Bagaces	6	15	90	162	0.24	Janzen 1978
<i>Hymenaea courbaril</i>	Leguminosae	Woody	Animal	Anim: F	Costa Rica, Guapote	5	56	85	199	0.15	Janzen 1978
<i>Hymenaea courbaril</i>	Leguminosae	Woody	Animal	Anim: F	Costa Rica, Sendero	4	19	167	178	0.59	Janzen 1978
<i>Lavandula latifolia</i>	Labiatae	Woody	Animal	Gravity	Spain	12	23	29	52	0.29	Herrera 1998
<i>Nothofagus truncata</i>	Fagaceae	Woody	Wind	Wind	New Zealand	22	21	205	216	0.87	P. Cowan
<i>Phillyrea latifolia</i>	Oleaceae	Woody	Wind	Wind	Spain (Agr)	9	53	290	285	0.95	Herrera 1998
<i>Phillyrea latifolia</i>	Oleaceae	Woody	Wind	Wind	Spain (Hoy)	17	41	242	338	0.38	Herrera 1998
<i>Prunus mahaleb</i>	Rosaceae	Woody	Animal	Anim: F	Spain	12	70	70	81	0.41	Herrera 1998
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Hastings)	20	63	91	171	0.34	W. Koenig and J. Knops
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Jasper Ridge)	11	28	96	157	0.56	W. Koenig and J. Knops
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Poza)	11	25	92	154	0.48	W. Koenig and J. Knops
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Santa Rosa Pl.)	7	20	93	151	0.23	W. Koenig and J. Knops
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Sedgwick)	7	20	63	105	0.29	W. Koenig and J. Knops
<i>Quercus agrifolia</i>	Fagaceae	Woody	Wind	Anim: P	California (Switzer's)	7	20	46	100	0.18	W. Koenig and J. Knops
<i>Quercus alba</i>	Fagaceae	Woody	Wind	Anim: P	Minnesota (Cedar Creek)	6	11	84	132	0.48	W. Koenig and J. Knops
<i>Quercus alba</i>	Fagaceae	Woody	Wind	Anim: P	Missouri	12	15	119	152	0.61	V. Sork
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Hastings)	20	21	89	158	0.40	W. Koenig and J. Knops
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Hopland)	7	17	133	168	0.65	W. Koenig and J. Knops
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Palomar)	7	20	76	134	0.36	W. Koenig and J. Knops
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Switzer's)	7	20	80	114	0.49	W. Koenig and J. Knops
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Tower House)	7	19	103	141	0.59	W. Koenig and J. Knops
<i>Quercus chrysolepis</i>	Fagaceae	Woody	Wind	Anim: P	California (Yosemite)	7	20	113	137	0.57	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Dye Creek)	7	21	68	109	0.49	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Hastings)	20	55	103	177	0.54	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Hopland)	7	19	84	121	0.41	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Jasper Ridge)	11	29	95	180	0.38	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Liebre Mtn)	7	20	130	172	0.77	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Poza)	11	25	97	153	0.43	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (San Joaquin)	7	24	119	152	0.66	W. Koenig and J. Knops
<i>Quercus douglasii</i>	Fagaceae	Woody	Wind	Anim: P	California (Sierra Foothills)	7	23	99	132	0.58	W. Koenig and J. Knops
<i>Quercus ellipsoidalis</i>	Fagaceae	Woody	Wind	Anim: P	Minnesota (Cedar Creek)	6	90	36	75	0.28	W. Koenig and J. Knops
<i>Quercus engelmannii</i>	Fagaceae	Woody	Wind	Anim: P	California (Santa Rosa Pl.)	7	19	99	173	0.47	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Hastings)	20	21	114	180	0.44	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Hopland)	7	21	62	145	0.23	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Liebre Mtn)	7	20	77	103	0.44	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Mt. Palomar)	7	20	76	105	0.50	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Tower House)	7	17	198	219	0.80	W. Koenig and J. Knops
<i>Quercus kelloggii</i>	Fagaceae	Woody	Wind	Anim: P	California (Yosemite)	7	22	31	165	0.19	W. Koenig and J. Knops
<i>Quercus lobata</i>	Fagaceae	Woody	Wind	Anim: P	California (Dye Creek)	7	18	138	184	0.82	W. Koenig and J. Knops

Appendix. (Continued)

Species	Family	Vegetation type	Pollination vector	Seed dispersal vector ¹	Locality	N years	N individuals	CV _p	CV _v	\bar{r}_p	Source ²
<i>Quercus lobata</i>	Fagaceae	Woody	Wind	Anim: P	California (Hastings)	20	86	92	171	0.46	W. Koenig and J. Knops
<i>Quercus lobata</i>	Fagaceae	Woody	Wind	Anim: P	California (Jasper Ridge)	11	36	115	184	0.34	W. Koenig and J. Knops
<i>Quercus lobata</i>	Fagaceae	Woody	Wind	Anim: P	California (Pozo)	11	25	90	127	0.56	W. Koenig and J. Knops
<i>Quercus lobata</i>	Fagaceae	Woody	Wind	Anim: P	California (Sedgwick)	7	11	77	122	0.31	W. Koenig and J. Knops
<i>Quercus macrocarpa</i>	Fagaceae	Woody	Wind	Anim: P	California (Tower House)	7	17	91	149	0.38	W. Koenig and J. Knops
<i>Quercus robur</i>	Fagaceae	Woody	Wind	Anim: P	Minnesota (Cedar Creek)	6	90	137	158	0.29	W. Koenig and J. Knops
<i>Quercus rubra</i>	Fagaceae	Woody	Wind	Anim: P	England	12	30	79	112	0.48	Crawley and Long 1995
<i>Quercus rubra</i>	Fagaceae	Woody	Wind	Anim: P	Minnesota (Cedar Creek)	6	20	55	91	0.44	W. Koenig and J. Knops
<i>Quercus rubra</i>	Fagaceae	Woody	Wind	Anim: P	Massachusetts	11	120	115	154	0.68	J. Elkinton and W. Healy
<i>Quercus velutina</i>	Fagaceae	Woody	Wind	Anim: P	Missouri	12	13	105	127	0.41	V. Sork
<i>Vaccinium corymbosum</i>	Ericaceae	Woody	Animal	Anim: F	Missouri	12	18	77	92	0.62	V. Sork
<i>Viola cazortensis</i>	Violaceae	Herbaceous	Animal	Anim: F	Canada	4	49	54	94	0.22	Vander Kloet and Cabilio 1984
					Spain	10	59	54	147	0.34	Herrera 1998

¹ "Anim: F" = dispersal by frugivores; "Anim: P" = dispersal by scatterhoarding predators.

² Unpublished data except when a citation is listed.