Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony

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Abstract

Mast seeding, or masting, is the variable production of flowers, seeds, or fruit across years more or less synchronously by individuals within a population. A critical issue is the extent to which temporal variation in seed production over a collection of individuals can be viewed as arising from a combination of individual variation and synchrony among individuals. Studies of masting typically quantify such variation in terms of the coefficient of variation (CV). In this paper we examine mathematically how the population CV relates to the mean individual CV and synchrony, concluding that the relationship is a complex one which cannot isolate an overall measure of synchrony, and involves additional factors, principally the number of plants sampled and the mean productivity per plant. Our development suggests some simple approximate relationships of population CV to individual variability, synchrony and the number of individuals. These were found to fit quite well when applied to data from 59 studies which included seed production at the individual level.

1. Introduction

Mast seeding, or masting, is the variable and synchronous production of seeds by a population of plants from year to year (Janzen, 1971; Silvertown, 1980). The mechanisms of masting (e.g., Koenig and Knops, 1998) and the adaptive value of masting (Kelly, 1994; Sork, 1993) are of considerable evolutionary interest, both for their own sake and because of the often substantial effects of the pulsed resources produced during a masting event on animal populations (Ostfeld and Keesing, 2000). Two of the most commonly cited benefits of masting include satiation of seed predators (Janzen, 1971; Silvertown, 1980; Kelly and Sullivan, 1997) and increased pollination efficiency (Janzen, 1971; Smith et al.,1990; Kelly et al., 2001).

In general, temporal variation in seed production is expressed as the coefficient of variation (standard deviation/mean, sometimes expressed as a percent) in annual seed production, the idea being that dividing by the mean allows comparison of variation between species that differ in the number of seeds produced per individual as well as comparisons between studies that differ in how seed production was measured (e.g. Silvertown, 1980). The coefficient of variation of the total or mean annual seed crop for the population is denoted CV_p. This quantity is often used as an overall measure of variability in seed production; see for example Herrara et al. (1998).

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Herrera (1998) suggested that CV_p can be divided into two primary components when data exist on seed crops produced by individual plants across years. First is the mean temporal variation of individual plants, denoted $\overline{CV}$, while the second is the synchrony of seed crops among individuals across years. Identifying the contributions to masting is valuable because it allows us to see the extent to which the population variability reflects individual variability and individual synchrony with the population (e.g. DeSteven and Wright, 2002). Species with low synchrony do not qualify as masting species from the perspective of a reproductive strategy regardless of the value of CV_p. Thus, synchrony is a key ingredient of masting (Janzen, 1978). In fact, studies of masting that address evolutionary questions should focus on both variability and synchrony among individuals across years rather than population variability alone. Herrera (1998) argues that, without synchrony, the production of large crops by some individuals in a given year should be accompanied by small crops in other individuals such that CV_p will be small relative to $\overline{CV}$, the mean individual level CV. Alternatively, if there is a high level of synchrony, CV_p should be similar to $\overline{CV}$. Here we use pairwise Pearson correlation coefficients to measure synchrony primarily because it directly enters into the mathematical relationships resulting from decomposing CV_p data. See Buonaccorsi et al. (2001) for a general review of various methods for quantifying and assessing spatial synchrony.

Reasons for synchrony have been explored elsewhere (e.g., Kelly, 1994; Herrera, 1998; Kelly and Sork, 2002) and here we consider the interrelationships among various metrics used to quantify masting, following initial attempts by Herrera (1998). Specifically, we explore the mathematical relationships among empirical measures of CV_p, $\overline{CV}$ and synchrony based on decompositions of data collected over time for many individuals. We show that while individual variability and synchrony contribute to CV_p, as suggested by Herrera (1998), there is no simple way to express the exact relationship among the three. In fact, one cannot obtain an expression involving just CV_p, $\overline{CV}$ and an overall measure of synchrony. We also show that perfect synchrony does not necessarily imply that CV_p equals $\overline{CV}$, as has been claimed, and characterize the relationship between CV_p and $\overline{CV}$ in the absence of synchrony. Finally, we use our expressions to develop approximate relationships relating CV_p to $\overline{CV}$ and an overall measure of synchrony and demonstrate that this provides an effective fit to 59 mast data sets.

Our objective here is to resolve some issues concerning the exact numerical relationship among population variability, individual variability and synchrony based on data. There are other approaches that can be taken to provide additional insight, but are beyond the scope of this paper. One approach, under study, is to formulate a stochastic model which captures dynamics for individual plants, spatial correlation among plants and additional within plant variability, and then examine the relationships among theoretical measures of population CV, individual CVs and synchrony under these models. A second approach is to explore the data empirically (e.g., carrying out various regression analyses) without relying on underlying theoretical models, in order to identify emergent patterns. Extensive investigations of this sort, using different models than the ones presented here, are carried out by Koenig et al. (2003).

2. General relationships among CVs and synchrony

This section examines the mathematical relationship between CV_p, individual variation, and synchrony for a set of data with n plants and T years, where x_{it} is the seed count for plant i in year t. The mean, standard deviation and CV for plant i are denoted by $\bar{x}_i$, s_i and

$$CV_i = s_i/\bar{x}_i,$$

respectively. The mean individual CV is $\overline{CV} = \sum_{i=1}^{n} CV_i/n$. It will also be useful to define the coefficient of variation for plant i relative to the overall mean $\bar{x}$; that is

$$CV_{im} = s_i/\bar{x}.$$

The standard deviation of yearly means is denoted by s_p and the population coefficient of variation by $CV_p = s_p/\bar{x}$. The CV_p is the same if yearly totals, rather than means, are used since s_p and $\bar{x}$ will both change by the same scaling constant.

There are two natural decompositions associated with the data, which are described in detail in Appendix A. The first leads to

$$
\begin{aligned}
CV_p^2 &= \frac{\sum_i s_i^2}{n\bar{x}^2} - \frac{SSI}{n\bar{x}^2(T-1)} \\
&= \frac{\sum_i CV_{im}^2}{n} - \frac{SSI}{n\bar{x}^2(T-1)} \\
&= \frac{\sum_i \bar{x}_i^2 CV_i^2}{n\bar{x}^2} - \frac{SSI}{n\bar{x}^2(T-1)},
\end{aligned}
\tag{1}
$$

where SSI is the sum of squares due to the interaction of plants and years and is related to synchrony, in that $SSI = 0$ under one concept of perfect synchrony (described in more detail later).

The second decomposition leads to

$$CV_p^2 = \frac{\sum_i s_i^2}{n^2 \bar{x}^2} + \frac{\sum_i \sum_{k \neq i} s_{ik}}{n^2 \bar{x}^2}$$

$$= \frac{\sum_i CV_{im}^2}{n^2} + \frac{\sum_i \sum_{k \neq i} r_{ik} s_i s_k}{n^2 \bar{x}^2}$$

$$= \frac{\sum_i \bar{x}_i^2 CV_i^2}{n^2 \bar{x}^2} + \frac{\sum_i \sum_{k \neq i} r_{ik} s_i s_k}{n^2 \bar{x}^2}, \tag{2}$$

where r_{ik} is the Pearson correlation between counts for plants i and k and s_{ik} is the covariance between plants i and k. Correlation has been widely used to measure synchrony and one summary measure of synchrony over the n individuals is the mean correlation $\bar{r} = \sum_i \sum_{k \neq i} r_{ik} / (n(n-1)/2)$ over all pairs of plants.

Unfortunately, as seen from Eqs. (1) and (2), the relationship between CV_p, $\overline{CV}$, and synchrony is not simple, even when the latter is measured as the mean Pearson correlation coefficient. One reason for this stems from the use of individual CV_is, each defined relative to the mean of the individual plants, rather than individual CVs defined relative to the overall population mean (CV_{im}s).

It is only exactly true that *population variation = individual variation + synchrony*, if we think of population variation as CV_p^2, measure individual variation with $\sum_i CV_{im}^2 / n^2$ and measure synchrony with either $\sum_i \sum_{k \neq i} r_{ik} s_i s_k / n^2 \bar{x}^2$ or $-SSI/n\bar{x}^2(T-1)$.

2.1. Perfect synchrony

One, but not the only, definition of perfect synchrony is that plots of counts over time for different individuals are piecewise parallel (see Figs. 1 and 2). Mathematically, this means there are constants $c_2, ..., c_T$ such that $x_{it} = x_{i,t-1} + c_t$ for each i and for $2 \leqslant t \leqslant T$. This means that seed production in all plants changes by the same amount in moving from one year to the next. The interaction term SSI is related to synchrony in that when the data are piecewise parallel, then $SSI = 0$, as noted by Herrera (1998). This does not imply however that CV_p will equal $\overline{CV}$. With piecewise parallelism, the standard deviation in counts over years is the same for each plant and is equal to s_p, the standard deviation in mean counts over years. This leads to

$$CV_p - \overline{CV} = s_p \left[\frac{1}{\bar{x}} - \frac{\sum_i (1/\bar{x}_{i.})}{n} \right] \leqslant 0. \tag{3}$$

The inequality at the end results from the fact that the harmonic mean is less than or equal to the arithmetic mean (Casella and Berger, 1990, p. 183). Hence, CV_p is not equal to $\overline{CV}$ and the difference can be made large or small depending on several factors (see below). If the individual CVs are defined relative to the overall mean, however, then it is true with perfect synchrony of this type, that $CV_p = \sum CV_{im}/n$.

Figs. 1 and 2 illustrate further how factors other than synchrony influence the difference between CV_p and $\overline{CV}$ in masting data. Under conditions of perfect synchrony
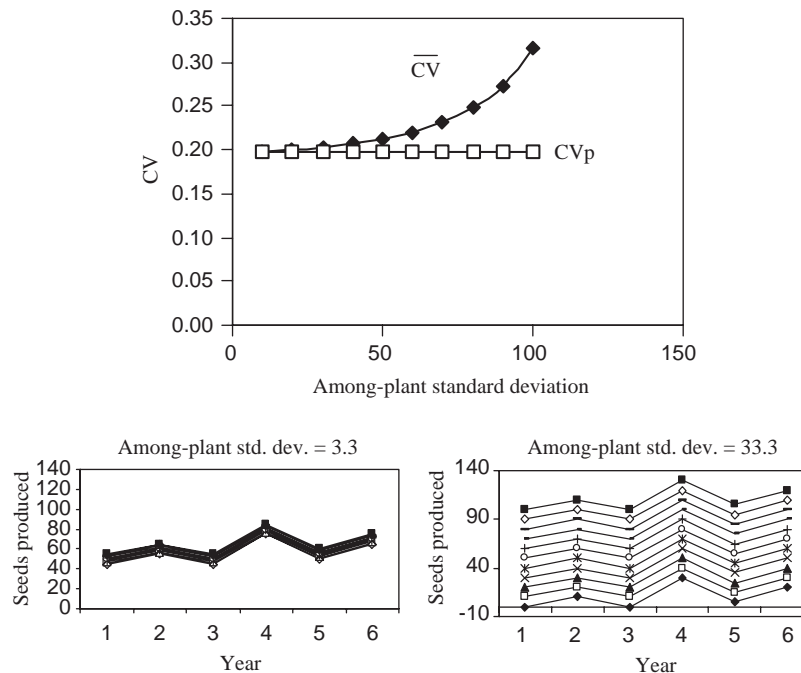

Fig. 1. (A) Plot of CV_p and mean CV_i as a function of within year standard deviation for generated data sets with perfect synchrony. (B) and (C) present two of the data sets.
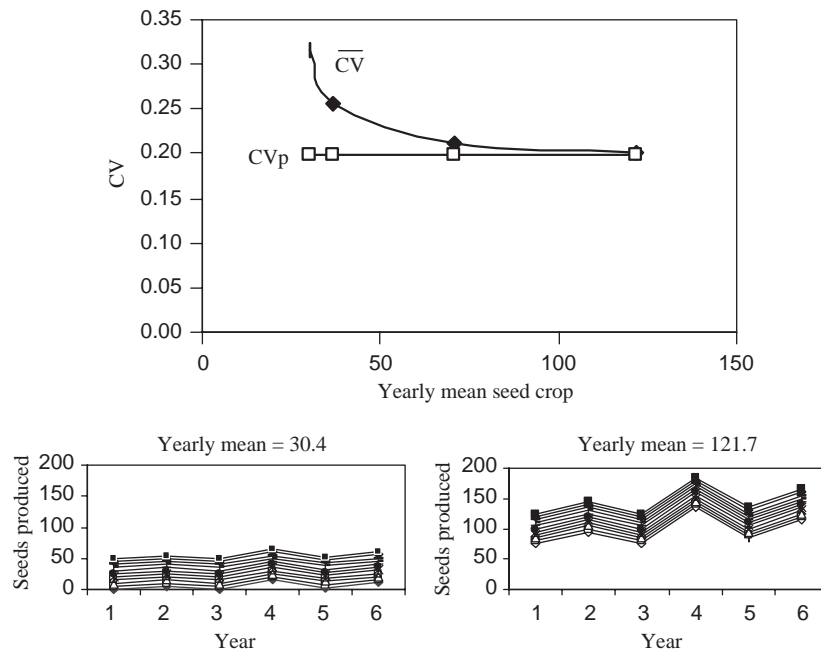
Fig. 2. (A) Plot of CV_p and mean CV_i as a function of yearly mean seed crop for generated data sets with perfect synchrony. (B) and (C) present two of the data sets.

as just defined, with the among-year standard deviation fixed, the difference between CV_p and $\overline{CV}$ will increase with the standard deviation in mast production across individual plants (which reflects the term in brackets in Eq. (3)) as portrayed in Fig. 1. In other words, the larger the discrepancy in crop size between good producers and poor producers, the larger the difference between CV_p and $\overline{CV}$. For Fig. 2, we continue to maintain perfect synchrony, keep the variation among plants and CV_p constant, while allowing the overall mean and among-year variation to change. Again the CV_p remains constant while $\overline{CV}$ decreases as the yearly mean increases. These two figures illustrate that the difference between CV_p and $\overline{CV}$ cannot be interpreted as being just due to synchrony, since there is perfect synchrony throughout.

Perfect synchrony in the sense of piecewise parallelism will imply a mean pairwise correlation coefficient of $\bar{r} = 1.0$. The converse is not true, however; that is $\bar{r} = 1.0$ can occur even without piecewise parallelism.

Another type of perfect synchrony is to have constant relative change; that is $x_{i,t} = c_t x_{i,t-1}$, where as before this is for each i and $2 \leqslant t \leqslant T$. This is equivalent to piecewise parallelism on the $\log(x)$ scale. In this case it can be shown (see Appendix B) that all the pairwise correlations, and hence the mean correlation, equal 1.0, when calculated in terms of either x or $\log(x)$. Further, in terms of the x values, $CV_p = \overline{CV}$, yet $SSI \neq 0$. Meanwhile, for the $\log(x)$ values, there is piecewise parallelism, that is $SSI = 0$ and $\bar{r} = 1.0$, but $CV_p \neq \overline{CV}$ (although $CV_p = \sum CV_{im}/n$). These results point out

further the difficulty with trying to characterize what "perfect synchrony" implies about the relationship between CV_p and $\overline{CV}$.

2.2. No synchrony

In the case of no synchrony, which we take here to be that all pairwise correlations are equal to 0, then from Eq. (2),

$$CV_p^2 = \frac{\sum_i \bar{x}_{i.}^2 CV_i^2}{n^2 \bar{x}^2} = \frac{\sum_i s_i^2}{n^2 \bar{x}^2}. \tag{4}$$

This relationship shows explicitly how even in the absence of synchrony, a change in individual variances can lead to an increase in CV_p. It also shows that other things being equal, CV_p will decrease as the number of individuals in the study increases. This effect of sample size makes sense intuitively because unless the plants are perfectly synchronized, adding more plants will increase the chance that high producers will cancel out low producers in their effect on total crop size. This effect is important because plant level data sets are rare and many of those available have low numbers of individuals (e.g., half of the 16 data sets in Herrera (1998) had less than 30 plants).

2.3. Some approximate relationships

In terms of correlation, Eq. (2) shows that, other things being equal, an increase in correlation between plants will lead to an increase in CV_p, but this result

involves the individual pairwise correlations rather than an overall measure of synchrony for the population. As this expression shows, there is nothing exact that can be stated about the relationship between CV_p, $\bar{CV}$ and $\bar{r}$ = the average pairwise correlation between distinct pairs of plants. We can make, however, make use of Eq. (2) to try and develop some approximate relationships.

Define

$$A = \sum_i CV_{im}^2/n$$

to be the average of the squared individual CVs when defined relative to the overall mean. Writing $s_i = \bar{x}A^{1/2} + e_i$, where $e_i = (s_i - \bar{x}A^{1/2}) = s_i - (\sum_i s_i^2/n)^{1/2}$, then $CV_p^2 = Z + Q$ (exactly) where

$$Z = A\left[\frac{1}{n} + \frac{(n-1)\bar{r}}{2n}\right]$$

and $Q = \sum_i \sum_{k \neq i} r_{ik}[\bar{x}A^{1/2}(e_i + e_k) + e_ie_k]/n^2\bar{x}^2$. Using a linear Taylor series expansion about $Q = 0$ yields

$$CV_p \approx Z^{1/2} + E, \tag{5}$$

where $E = Q/(2Z^{1/2})$. Given the definition of e_i, the quantity Q, and hence the remainder E, will be largely influenced by the "variability" in the individual plant standard deviations. Notice that if all the s_i are the same then each e_i, and hence Q, equals 0. Eq. (5) provides some insight into how CV_p depends on the mean correlation, the within plant variances, the number of plants and the average within plant variability (relative to the overall productivity). In particular, it shows that with a fixed n and amount of within plant variation, then CV_p^2 increases approximately linearly in synchrony.

The mean of the individual CVs, is widely used in summarizing individual variability (see Herrera, 1998),

but does not arise naturally from the decompositions. One can make use of it by treating $A^{1/2}$ as approximately $\bar{CV}$. There are a couple of ways to motivate this approximation; one by using just the first terms of a Taylor series expansion of the CV_{im}^2 around $\bar{CV}$ and another by considering the inequality $(\sum_i (a_i^2))^{1/2} \geqslant n^{-1} \sum_i |a_i|$ (see Casella and Berger, 1990, p. 181) and treating the inequality as an approximation. Using this ad hoc approximation yields

$$CV_p \approx \bar{CV}\left[\frac{1}{n} + \frac{(n-1)\bar{r}}{2n}\right]^{1/2} + E. \tag{6}$$

3. Data fitting

The effectiveness of the above simple, but approximate, expressions, are examined by seeing how well they fit to 59 masting data sets involving 24 species of plants. These data, which are described in detail in Koenig et al. (2003), involve a wide range of values for the number of individuals and the number of time points. Fig. 3 shows a three-dimensional plot of CV_p versus $\bar{r}$ and $\bar{CV}$ for these data. We examine two fits to the data. The first fit, based on Eq. (5), is

$$CV_p = A^{1/2}\left[\frac{1}{n} + \frac{(n-1)\bar{r}}{2n}\right]^{1/2} + 0.1349,$$

where the 0.1349 is the value of E in Eq. (5) which minimized the sum of squared residuals. This fit explained 94.2 percent of the total variation in observed CV_p, with a plot of fitted CV_p versus observed CV_p given in Fig. 4a.

The second fit, based on Eq. (6), is

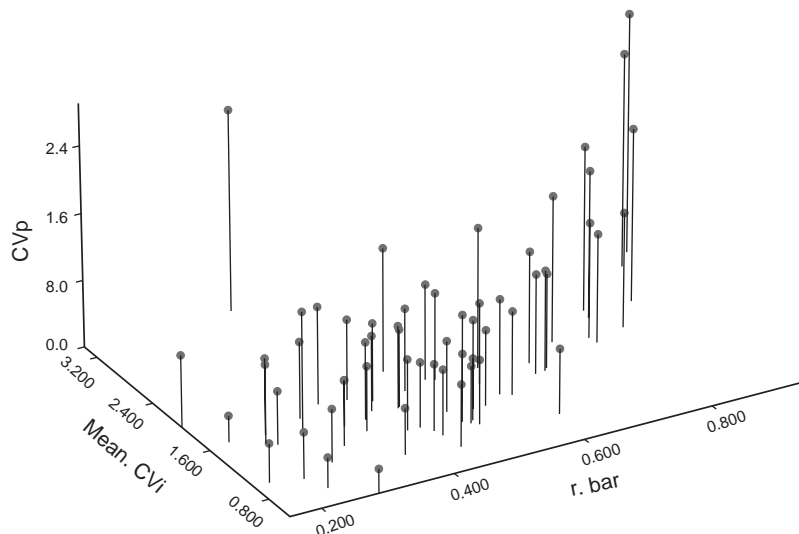$$CV_p = \bar{CV}\left[\frac{1}{n} + \frac{(n-1)\bar{r}}{2n}\right]^{1/2} + 0.2554,$$

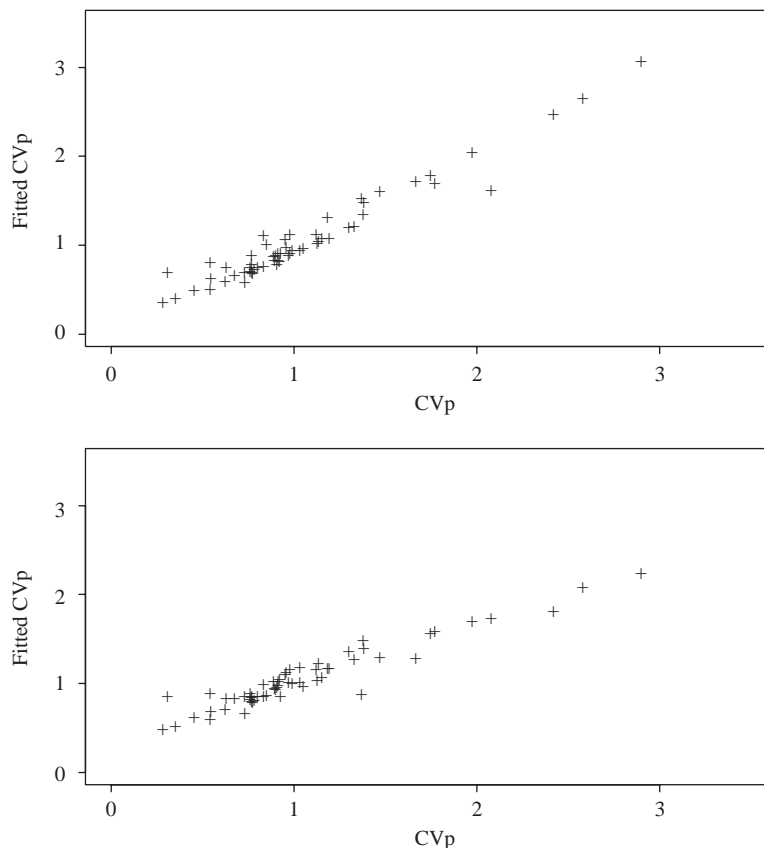Fig. 3. Plot of CV_p versus mean pairwise correlation (rbar) and mean individual CV (meancvi).

Fig. 4. Plot of fitted values for CV_p, from approximations, against actual CV_p, using 59 real datasets. (a) Approximation using mean CV_{im} (Eq. (5)), 94.2 percent of variation in CV_p explained. (b) Approximation using mean CV_i (Eq. (6)), 83.2 percent of variation in CV_p explained.

where again the constant was chosen based on least squares. This fit explained 83.2 percent of the variation in observed CV_p (Fig. 4b).

The quality of these fits, suggest that Eqs. (5) and (6) (and especially the former) provide a useful tool for understanding the contributions of synchrony and individual variation to CV_p.

4. Discussion

Herrera (1998) has argued that, while population CV may provide a useful index of mast seeding, it is an inadequate measure for dissecting out the ecological and evolutionary cause of mast seeding in plants. The approach he suggested was to decompose the population-level temporal variation into two components; within-plant variability and among-plant synchrony. In this paper, we have shown that the population temporal variation, as measured by the coefficient of variation, is a complicated function of a combination of factors, predominantly affected by within-plant variability and synchrony, but also including the number of plants and the overall mean productivity. While it is true

that population CV is related in some manner to mean individual CV and an overall measure of synchrony, we have shown that there is no simple expression for this relationship. The expressions given also lead to the conclusion that:

(1) Perfect synchrony (in the sense of piecewise parallel profiles over time), does not imply that population CV is equal to mean individual CV, as is demonstrated in Eq. (3), unless the individual CVs are defined relative to the overall mean rather than using the individual means. Related to the latter point, it is the CVs defined relative to the overall mean that enter into the decompositions in a natural way. On the other hand, if the profiles over time are piecewise parallel over time in terms of log(seed count) (meaning all plants have the same relative change in seed counts in a year) then population CV does equal mean individual CV, when calculated on the seed values themselves.

(2) The population CV_p may be large even when there is no synchrony among plants, (Eq. (4)), especially when the number of sample plants is low or the mean productivity is low.

(3) With a fixed amount of within-plant variability, CV_p increases as the amount of synchrony increases, with the rate of increase generally depending on the number of individuals, the amount of within plant variability, and the overall mean.

(4) While no simple relationships resulted, Eqs. (5) and (6) provide some simple and useful approximations which account for 83–95 percent of the variation in CV_p in 59 real data sets.

Nothing in this analysis suggests that CV_p is not a useful measure of variation in population-level seed output (cf. Herrera, 1998). The CV_p is clearly affected by mean CV_i and inter-plant synchrony (as also shown empirically by Herrera). However, there are also influences of sample size in terms of number of plants sampled, and productivity per plant.

Acknowledgements

Appendix A. Justification of Eqs. (1) and (2)

Eq. (1) results from the use of analysis of variance decompositions (Neter et al., 1996). Using the standard notation for means over indices, write $\bar{x}_{i.} = \sum_j x_{ij}/T$ for the mean for plant i, $\bar{x}_{.j} = \sum_i x_{ij}/n$ for the mean for year j and $\bar{x}_{..}$ for the grand mean. For notational convenience, the main text uses simply $\bar{x}_i$ and $\bar{x}$ for $\bar{x}_{i.}$ and $\bar{x}_{..}$ respectively. Define $SS_{tot} = \sum_i \sum_j (x_{ij} - \bar{x}_{..})^2$ (total sum of squares), $SST = T \sum_i (\bar{x}_{i.} - \bar{x}_{..})^2$ (among plant sum of squares), $SSW = \sum_i \sum_j (x_{ij} - \bar{x}_{i.})^2$ (within plant sum of squares), $SSY = n \sum_j (\bar{x}_{.j} - \bar{x}_{..})^2 =$ (among year sum of squares) and $SS_I = \sum_i \sum_j (x_{ij} - \bar{x}_{i.} - \bar{x}_{.j} + \bar{x}_{..})^2$ (sum of squares due to interaction between plant and year).

The standard decomposition for the one-way analysis of variance with plants as groups, yields $SS_{tot} = SST + SSW$, while the standard decomposition for a two way analysis of variance with one observation per cell yields $SS_{tot} = SSY + SST + SSI$. Equating these two, $SST + SSY + SSI = SST + SSW$ and so $SSY = SSW - SSI$. Using the earlier defined s_p^2 and s_i^2, we have $s_p^2 = SSY/(n(T-1))$ and $SSW = (T-1)\sum_i s_i^2$. Hence $s_p^2 = (SSW - SSI)/n(T-1) = \sum_i s_i^2/n - SSI/(n(T-1))$. Dividing both sides by $\bar{x}_{..}^2$ leads to Eq. (1).

Eq. (2) results from first expressing $\sum_i \sum_k \sum_j (x_{ij} - \bar{x}_{i.})(x_{kj} - \bar{x}_{k.})$ in two ways; as

$$\sum_j \sum_i (x_{ij} - \bar{x}_{i.}) \sum_k (x_{kj} - \bar{x}_{k.})$$
$$= n^2 \sum_j (\bar{x}_{.j} - \bar{x}_{..})^2$$

and as

$$\sum_i \sum_j (x_{ij} - \bar{x}_{i.})^2 + \sum_i \sum_{k \neq i} \sum_j (x_{ij} - \bar{x}_{i.})(x_{kj} - \bar{x}_{k.})$$
$$= (T-1)\left[\sum_i s_i^2 + \sum_i \sum_{k \neq i} s_{ik}\right].$$

Equating the two,

$$n^2 \sum_j (\bar{x}_{.j} - \bar{x}_{..})^2 = (T-1)\left[\sum_i s_i^2 + \sum_i \sum_{k \neq i} s_{ik}\right].$$

Dividing both sides by $n^2(T-1)\bar{x}_{..}^2$ yields Eq. (2).

Appendix B

Suppose $x_{i,t} = c_t x_{i,t-1}$, for each i and $2 \leqslant t \leqslant T$. Defining $c_1 = 1$, then from successive multiplications $x_{i,t} = q_t x_{i1}$ where $q_t = \prod_{j=1}^t c_j$, with $\prod$ denoting product. Denote the mean and variance of $q_1, ..., q_T$ by $\bar{q}$ and s_q^2, respectively. Now $\bar{x}_i = \sum_{t=1}^T x_{iT}/T = \bar{q}x_{i1}$ and $x_{it} - \bar{x}_i = (q_t - \bar{q})x_{i1}$, which implies that $s_i^2 = \sum_{i=1}^T (x_{it} - \bar{x}_i)^2/(T-1) = x_{i1}^2 s_q^2$ and hence for every i, $CV_i = s_i/\bar{x}_i = s_q/\bar{q}$. The mean in year t is $\bar{x}_{.t} = \sum_i x_{it}/n = q_t \bar{x}_{.1}$, where $\bar{x}_{.1}$ is the mean in year 1. Hence $\bar{x}_{..}$, the grand mean, equals $\bar{q}\bar{x}_{.1}$, $s_p^2 = \bar{x}_{.1}^2 s_q^2$ and so $CV_p = s_q/\bar{q} = \overline{CV}$, since each individual CV_i equals $s_q/\bar{q}$.

The correlation between series i and j is

$$r_{ij} = \frac{\sum_t (x_{it} - \bar{x}_{i.})(x_{jt} - \bar{x}_{j.})/(T-1)}{s_i s_j}$$
$$= \frac{\sum_t (q_t - \bar{q})^2 (x_{i1}x_{j1})/(T-1)}{[s_q^2 x_{i1}^2 s_q^q x_{j1}^2]^{1/2}} = 1.$$

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