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Population-level estimates of interannual variability in seed production: what do they actually tell us?

Carlos M. Herrera, Estación Biológica de Doñana, CSIC, Apartado 1056, E-41080 Sevilla, Spain (herrera@cica.es).

The number of seeds produced by populations of polycarpic plants often varies considerably from one year to another. Such variation in reproductive output has important consequences for the demography and population dynamics of both the plant populations themselves and their consumer organisms (e.g., Gashwiler 1979, Schupp 1990, Pucek et al. 1993, Jones et al. 1994, Crawley and Long 1995, Elkinton et al. 1996, Wolff 1996), which justifies the interest traditionally elicited by the phenomenon among ecologists (Janzen 1976, 1978, Waller 1979, Silvertown 1980, Norton and Kelly 1988, Smith et al. 1990, Lalonde and Roitberg 1992, Kelly 1994). Investigations on the causes and consequences of annual variability in seed production have mainly focused upon highly variable species. Recent reviews, however, have shown that polycarpic plants tend to fall along a broad continuum of variability levels, and that distinct groups of species do not seem to exist (Webb and Kelly 1993, Kelly 1994, Herrera et al. in press). In view of the continuous distribution of species along the gradient of interannual variability in seed output, Herrera et al. (in press) have suggested that verbal labels often used to characterize variability patterns (e.g., "masting" and "non-masting" species) should be abandoned in favor of quantitative assessments, and that the rather crude variability measurements commonly in use should be replaced by more precise and biologically interpretable ones. This note is intended as a contribution in that direction, and its purpose is to call attention to the limitations of some population-level sampling schemes and measurements of variability in seed production. Using data from several plant populations, I will also illustrate some apparently unrecognized difficulties involved in making biological inferences from population-level estimates of variability. As an alternative, I propose two measures of the major components of annual variability which, if used in conjunction, have straightforward biological interpretations.

In comparative studies, interannual variability in seed production has been generally assessed by means of population-level estimates, most often the coefficient of variation (Silvertown 1980, Webb and Kelly 1993, Kelly 1994, Herrera et al. in press). Typically, a single estimate of overall seed production is obtained for the plant population under study for each year, by either summing or averaging seed abundance data obtained from counts conducted on either of a variety of possible sampling units (e.g., branches, seedfall traps, permanent plots, or whole plants). A population-level coefficient of variation is then computed from the mean and standard deviation of these annual figures (CV_P hereafter). While there seems to be no question about the *statistical* appropriateness of CV_P as a scale-independent measurement of variability in seed production at the population level (McArdle and Gaston 1995, Herrera 1998, and references therein), the same cannot be said about its *biological* meaningfulness. What can population-level coefficients of variation tell us about the processes and mechanisms that underlie observed patterns of variability in seed production? Or, in other words, to what extent can biological interpretations and inferences be drawn from examination of CV_P figures alone?

Sampling units and components of variability

The biological interpretability of CV_P will simultaneously depend on the nature of sampling units used to obtain annual seed production figures (particularly on whether sampling units coincide with plant individuals or not), and on the interannual consistency of sampling units (i.e., whether sampling units are permanent or not).

Let us first consider the situation most frequently found in the literature (see below), in which seed counts are performed on sampling units that are different from plant individuals such as, for instance, seedfall traps, quadrats, branches, or other plant parts. When these sampling units are exactly the same during all the years of one study (e.g., permanent plots, marked branches), CV_P will reflect annual variance in seed production of the plants whose crops are being sampled plus an additional spatio-temporal variance component due to the interaction between years and sampling units, i.e., the consequence of asynchronous annual variation of seed abundance across sampling units. When sampling units are not the same every year, as when random samples for seed or fruit counts (e.g., tree branches, non-permanent quadrats) are drawn anew each year, CV_P will reflect among-year variance in seed production by the plants being sampled plus sampling variance. Regardless of whether samples are permanent or not, therefore, CV_P values based on sampling units that do not coincide with plant individuals are bound to be "contaminated" by unknown amounts of spurious temporal and spatial variances that are not strictly attributable to temporal variation in seed production by plants. In addition to this contamination, one further limitation on the interpretability of CV_P values based on sampling units other than whole plant stems precisely from the very nature of sampling units. Although CV_P will reflect annual variance in the crop size of individual plants, it will also depend in complex ways on the spatial location of sampling units in relation to individual plants in the population, the number of different plants that are being sampled, and the proportion of whole seed crops which is sampled by each sampling unit (which will depend, among other, on the relative sizes of plants and sampling units).

Let us now consider the simpler and biologically most straightforward, but also less frequent (see below) case in which sampling units are whole plants. If crop sizes are not determined for the same plants in successive years, CV_P will reflect annual variance in individual crop size (= within-plant temporal variance) plus sampling variance. Alternatively, if the same individuals are monitored every year, then CV_P will reflect within-plant variability plus an additional variance component due to the plant × year interaction, caused by crop sizes of different plants varying in different ways across years. Each of these two components of variability is closely related to a distinct and readily interpretable biological concept, namely mean temporal variability in the crop size of individual plants (an unweighted population mean of within-individual variability) and degree of interindividual synchrony across years, respectively. The greater the interindividual synchrony, the smaller the contribution of the plant × year interaction to CV_P. In a population where all plants were perfectly synchronous in seed production over the years, the variance due to the plant × year interaction would be zero, and CV_P thus identical to the population mean of CV values computed separately for individual plants. At least in theory, therefore, different combinations of mean within-plant variability and interindividual synchrony are possible which may yield exactly the same CV_P value. In other words, two or more plant populations might have identical CV_P for completely different biological reasons. This represents a potential drawback for using CV_P as a descriptor in comparative analyses, particularly when inferences are attempted on the biological mechanisms underlying observed variations in CV_P. This thus prompts the questions: To what extent does individual plant-based CV_P actually reflect supra-annual variability in seed production of individual plants? What are the relative contributions to CV_P of within-plant variability and interindividual synchrony in plant populations?

Dissecting CV_P: Within-plant variability and among-plant synchrony

To answer the preceding questions, I gathered temporal series of seed production by populations of woody plants with data for ≥ 4 years and ≥ 10 individual plants, and for which crop sizes had been determined for exactly the same individuals during all the years of the study. I found few published studies that provided sufficiently detailed crop size data for individual plants in different years, thus I included some unpublished datasets to increase sample size (Table 1). Each raw dataset consisted of a rectangular individual × year matrix, whose elements a_{ij} were the number of seeds or fruits produced by individual i in year j. For each dataset, CV_P was computed as the coefficient of variation of yearly totals of fruit or seed production (T_j), which were obtained by summing for each year the production of all plants in the sample ($T_j = \Sigma_i a_{ij}$). In addition, within-plant coefficients of variation in crop size were computed separately for each plant in the sample (CV_i), and a population mean then obtained ($\overline{CV_i}$). Kendall's coefficient of concordance (W; e.g., Zar 1974) was used to assess the degree of supra-annual synchrony among individuals. As used here, this coefficient measures the overall degree of concordance between individual plants with respect to the temporal pattern of variation of their crop sizes across years (i.e., rankings are obtained within individual plants among years), and ranges between 0 (complete discordance) and 1 (perfect synchrony). As W is based on within-

Table 1. Annual variability in fruit or seed production in a sample of tree and shrub populations with crop size data available for individual plants. "N Plants" and "N Years", number of individuals and study years, respectively. CV_P = Coefficient of variation computed over the yearly combined totals ("population-level" value). $\overline{CV}_i$ = Average of coefficients of variation computed separately for individual plants. W = Kendall's coefficient of concordance among individual plants, used here to measure interindividual synchrony in seed production over years. In each dataset, only data from individuals that produced seeds at least once during the duration of the study were included in computations. Different sets of values for the same species are from different geographical locations.

Species	Habit	N plants	N years	CV_P	$\overline{CV}_i$	W	Reference
Abies pinsapo	Tree	31	4	121.0	158.6	0.653	M. Arista (unpubl.)
		31	4	128.7	160.4	0.630	M. Arista (unpubl.)
Cornus drummondii	Shrub	11	4	75.3	93.5	0.362	Willson and Whelan (1993)
		11	4	18.7	80.4	0.019	Willson and Whelan (1993)
Hymenaea courbaril	Tree	19	4	167.1	178.4	0.398	Janzen (1978)
		56	5	85.2	198.8	0.128	Janzen (1978)
		15	6	112.7	167.7	0.541	Janzen (1978)
*Lavandula latifolia**	Shrub	23	12	28.6	51.9	0.314	C. M. Herrera (unpubl.)
Olea europaea	Tree	40	4	157.8	180.0	0.618	J. Alcántara and P. Rey (unpubl.)
Osyris quadripartita	Shrub	27	4	53.4	75.1	0.485	Herrera (1988)
Phillyrea latifolia	Tree	41	17	242.0	338.4	0.254	C. M. Herrera and P. Jordano (unpubl.)
		54	9	284.8	290.2	0.384	C. M. Herrera and P. Jordano (unpubl.)
Prunus mahaleb	Tree	25	8	62.1	72.0	0.631	P. Jordano (unpubl.)
Quercus robur	Tree	29	12	78.3	113.1	0.482	Crawley and Long (1995)
Vaccinium corymbosum	Shrub	49	4	54.4	93.9	0.216	Vander Kloet and Cabilio (1984)
Viola cazorlensis	Shrub	59	10	54.4	147.2	0.227	C. M. Herrera (unpubl.)

* Data on number of inflorescences produced per year, rather than fruits or seeds, were used. Seed production is known to be closely correlated with number of inflorescences in this species (C. M. Herrera unpubl.).

plant ranks, it is unaffected by differences between plants in average (across years) crop size.

CV_P, $\overline{CV}_i$ and W values are summarized in Table 1 for 16 datasets from 11 species of trees and shrubs. Despite the relatively small number of datasets considered, broad ranges of supra-annual variability (Ranges of CV_P and $\overline{CV}_i = 18.7–284.8$ and $51.9–338.4$, respectively) and synchrony level ($W = 0.019–0.653$) are represented in the sample. To account for variation among datasets in sample sizes (number of plants and years), data points will be weighted by the geometric mean of the number of plants and years in the regression and correlation analyses below.

As predicted, both $\overline{CV}_i$ and W contribute significantly to observed variation in CV_P in the sample considered. A multiple linear regression of CV_P on $\overline{CV}_i$ and W revealed statistically significant, direct effects of the two independent variables ($t = 10.77$, $P \ll 0.001$; and $t = 2.91$, $P = 0.012$ for $\overline{CV}_i$ and W, respectively; standardized regression coefficients = 0.961 and 0.260, respectively). $\overline{CV}_i$ and W accounted altogether for virtually all observed variance in CV_P, as revealed by the large coefficient of determination of the regression ($R^2 = 0.900$). Variation in CV_P, however, largely reflects variation in $\overline{CV}_i$ (partial $R^2 = 0.835$), and only secondarily variation in W (partial $R^2 = 0.065$). The importance of $\overline{CV}_i$ as the major determinant of CV_P is evidenced by the close linear relationship existing between the two variables (Fig. 1).

Individual-based annual variability in fruit production and degree of synchrony among individuals covary independently of each other in the data sample considered here. The highest synchrony levels ($W > 0.6$), for example, occur among both very variable (*Abies pinsapo*, *Olea europaea*) and very constant (*Prunus mahaleb*) species (Table 1). The correlation between $\overline{CV}_i$ and W is not statistically significant ($r = -0.183$, $P = 0.50$), and the distribution of data points over the plane defined by $\overline{CV}_i$ and W did not reveal any obvious aggregation into distinct clusters (figure not shown). There is thus no evidence that plant populations which differ in (individual-based) annual variability in fruit

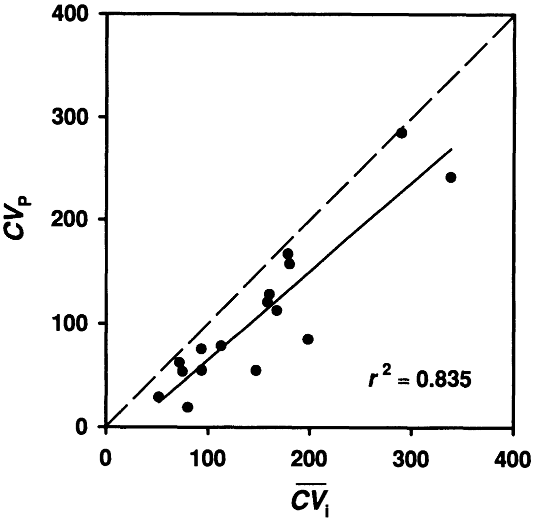

Fig. 1. Relationship between population-level (CV_P) and mean individual ($\overline{CV}_i$) coefficients of variation of annual fruit or seed production in the species sample examined (Table 1). Solid line is the least-squares fitted linear regression for the data. The dashed line represents $CV_P = \overline{CV}_i$, i.e., perfect supra-annual synchrony among individuals (see text).

production differ also predictably in the degree of interindividual synchrony. This may be appreciated in Fig. 1, where vertical distances from data points to the reference line $CV_P = \overline{CV}_i$, reflecting the extent of departure from perfect synchrony, have no obvious dependence on $\overline{CV}_i$.

All the preceding analyses were conducted on the implicit assumption that the 16 data points used are statistically independent. This assumption, however, might be unjustified, as four species (*Abies pinsapo*, *Cornus drummondii*, *Hymenaea courbaril* and *Phillyrea latifolia*) were represented in the sample by more than one temporal series of seed production (Table 1). To test if results were biased in some way by this redundancy, I computed species means for $\overline{CV}_i$, CV_P and W, and then repeated all analyses on this reduced dataset ($N = 11$ species) having single data points per species. None of the conclusions experienced any modification, hence presentation of this re-analysis is omitted.

Discussion

Whenever annual variation in seed production by plant populations has been studied in sufficient detail, it has been found that the proximate biological causes of such variation are that (1) all individuals either do not fruit every year or, even when they do, have fluctuating crop sizes, and (2) not all plants have exactly the same supra-annual rhythm of fruit production (e.g., Piñero and Sarukhán 1982, Clark and Clark 1987, Herrera 1993, Crawley and Long 1995, Tapper 1996). Population-level variability in seed production is thus an individual-based phenomenon, and understanding the proximate and ultimate mechanisms involved requires an adequate recognition of the roles of individual patterns and interindividual synchrony, as explicitly acknowledged by all hypotheses, interpretations and theoretical models addressing population-level variability (Janzen 1978, Silvertown 1980, Kelly 1994, and references therein). Rather paradoxically, however, the bulk of empirical data available on annual variation in seed production by plant populations do not come from individual-centered sampling schemes. Among the 296 long-term seed production datasets for woody plants compiled by Herrera et al. (in press: Appendix), details of the sampling procedure could be ascertained for 226 datasets. Of these, 72.6% were based on sampling units that did not coincide with plant individuals (largely habitat plots, quadrats, and seed fall traps), while only 27.4% used plant individuals as the sampling units. This implies that roughly three quarters of population-level measurements of variability in seed production considered in recent reviews (Kelly 1994, Herrera et al. in press) are to some degree contaminated by extraneous sources of temporal and spatial variability, as noted earlier. Analogous problems of "variance contamination" have also been noted for comparative studies of temporal variability in the size of animal populations (e.g., McArdle et al. 1990, Link and Nichols 1994, Cyr 1997).

When individual plants are the sampling units, population-level measurements of variability in seed production is a compound measurement simultaneously reflecting population synchrony and levels of within-individual variability. In the data sample examined here, however, variation in CV_P almost entirely reflected differences in within-individual variability. The influence of differences in synchrony, albeit statistically significant, was quantitatively negligible. Although the generality of this finding should be corroborated by more extensive analyses, it suggests that CV_P figures from investigations that use individual plants as sampling units are reasonably reliable estimators of within-individual variability.

The finding that within-individual variability and population synchrony were not significantly correlated in the sample examined suggests the need for some reconsideration of current hypotheses on the evolution of highly variable, bimodal supra-annual patterns of seed production. High levels of population synchrony have often been implied from the high levels of supra-annual variability in seed production exhibited by "mast fruiting" species (e.g., Janzen 1976, Kelly 1994), yet degree of synchrony has been only rarely assessed using objective methods (but see, e.g., Vander Kloet and Cabilio 1984, Crawley and Long 1995). This has been due, at least in part, to the fact noted earlier that most studies on long-term patterns of seed production are based on data that simply are not amenable to analyses of interindividual synchrony because of the sampling units used. As a consequence, assessment of individual synchrony has often depended on subjective perceptions rather than on objective measurements. If future studies conducted on a broader array of plant species eventually prove the generality of the results reported here, then both the purported association between synchrony and supra-annual variability, and some life-history theoretical models on the evolution of highly variable seed production schedules that had such relationship as an important feature (e.g., Waller 1979, Ims 1990, Smith et al. 1990, Lalonde and Roitberg 1992), should all have to be revised.

In conclusion, population-level measurements of annual variability in seed production based on sampling units other than individual plants may be useful indices of resource abundance fluctuation as perceived by consumer organisms (e.g., Herrera 1998), but are inappropriate tools for gaining insight on the ultimate and proximate causes of such variability. Whenever sampling units are used that are different from whole plants, CV_P values will unavoidably embody undetermined amounts of spurious variance components that are difficult to interpret biologically even if detailed additional data on the sampling scheme are taken into consideration. Extreme caution should thus be exercised when using this kind of data to make inferences on patterns of within-individual variability in seed production. This can only be properly accomplished by using plants as sampling units, and dissecting population-level variability measurements into its two biologically relevant elements, namely within-plant variability and among-plant synchrony. I have suggested here one simple way of performing this dissection, but other more sophisticated possibilities deserve consideration which could perhaps lead to more powerful comparative analyses (e.g., approaches based on repeated-measures analyses of variance).

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