Annual Variability in Seed Production by Woody Plants and the Masting Concept: Reassessment of Principles and Relationship to Pollination and Seed Dispersal

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ABSTRACT: By analyzing 296 published and unpublished data sets describing annual variation in seed output by 144 species of woody plants, this article addresses the following questions. Do plant species naturally fall into distinct groups corresponding to masting and nonmasting habits? Do plant populations generally exhibit significant bimodality in annual seed output? Are there significant relationships between annual variability in seed production and pollination and seed dispersal modes, as predicted from economy of scale considerations? We failed to identify distinct groups of species with contrasting levels of annual variability in seed output but did find evidence that most polycarpic woody plants seem to adhere to alternating supra-annual schedules consisting of either high or low reproduction years. Seed production was weakly more variable among wind-pollinated taxa than animal-pollinated ones. Plants dispersed by mutualistic frugivores were less variable than those dispersed by either inanimate means or animals that predominantly behave as seed predators. We conclude that there are no objective reasons to perpetuate the concept of mast fruiting in the ecological literature as a shorthand to designate a distinct biological phenomenon. Associations between supra-annual variability in seed output and pollination and seed dispersal methods suggest the existence of important reproductive correlates that demand further investigation.

Keywords: crop size, mast fruiting, pollination, seed dispersal, seed production.

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The number of seeds produced by populations of polycarpic plants often fluctuates considerably from year to year. This variation may have strong effects not only on the recruitment of the plant populations themselves (e.g., Schupp 1990; Jones et al. 1994; Crawley and Long 1995; Shibata and Nakashizuka 1995), but also on the populations of many species of animals that have seeds as their major food (e.g., Mattson 1971; Flowerdew and Gardner 1978; Gashwiler 1979; Pucek et al. 1993; Wolff 1996) and on the interactions between plants and their consumers (Janzen 1971; Smith and Balda 1979; Ostfeld et al. 1996). Given these manifold implications, it is not surprising that an abundant literature has built up, nourished by both animal- and plant-oriented ecologists, dealing with patterns of annual variation in seed output, its consequences, and its proximate and ultimate (evolutionary) causes.

Many of these investigations have focused on the phenomenon of "masting," or "mast seeding," and have dealt with species putatively exhibiting this seeding pattern (see Janzen 1971, 1976, 1978; Silvertown 1980; Norton and Kelly 1988; Kelly 1994; for reviews). Masting has been defined as "the synchronous production of seed at long intervals by a population of plants" (Janzen 1976, p. 354), as "[the production of] seed crops synchronously at irregular intervals but with an average periodicity characteristics of the species" (Silvertown 1980, p. 235), or as "synchronously highly variable seed production among years by a population of plants" (Kelly 1994, p. 465). The masting concept has traditionally been invoked under the implicit assumption that it applies to one characteristic, well-defined pattern of annual variability in seed production, whose unique features (synchronicity, high variability, periodicity) distinguish it from the patterns of variability exhibited by the rest (i.e., nonmasting) of polycarpic plants. Rather surprisingly, this key assumption—that is, that masting actually represents a distinct, qualitatively different pattern of annual variability in seed production that deserves a separate name in its own right—has gone essentially untested un-

til recently (Kelly 1994). This has been so, at least in part, for the following two reasons. First, published quantitative, long-term comparative data on seed production by "nonmasting" plants are scarce and thus have never been reviewed. And second, the critical elements of the masting concept, such as bimodality in seed production, synchronicity, or high variability, have only rarely been objectively assessed using quantitative methods (shifting in resource allocation between reproduction and vegetative growth, although considered by Kelly 1994 as a further element essential to the masting concept, was never included as such in any of the "classical" definitions of the term). Only in recent years, Kelly and associates (Norton and Kelly 1988; Webb and Kelly 1993; Kelly 1994; Kelly and Sullivan 1997) have reviewed and reassessed some of the hypotheses and concepts associated with mast seeding. These studies have concluded that mechanisms related to economy of scale (i.e., larger reproductive efforts are more efficient in terms of successful pollination or seed production and survival; Janzen 1978; Norton and Kelly 1988) seem to have favored the evolution of occasional large efforts rather than regular smaller ones. Nevertheless, when quantitative seed production data from a taxonomically diverse array of species are examined critically, difficulties arise when attempting to objectively classify species as either masting or nonmasting and, among masting species, to define mast versus nonmast years and to establish intermast intervals. Species apparently fall along broad continua of interannual variability in seed production, with no indication of multimodality (Kelly 1994). These findings cast reasonable doubts on the usefulness and ecological significance of the masting concept and prompt for critical reexamination of patterns of annual variability in seed production using data from as many species as possible.

Questions and Predictions

By analyzing a large sample of published and unpublished data on annual seed production by a taxonomically and ecologically diverse array of polycarpic woody plants, we will specifically address in this article the following three questions. First, do polycarpic plants tend naturally to fall into two distinct groups characterized by high and low annual variabilities in seed production roughly corresponding, respectively, to masting and nonmasting species? Second, do plant populations tend to exhibit significant bimodality in annual seed output or, in other words, does annual variability in seed production tend to reflect the occurrence of distinct high and low seed production years, rather than random fluctuations around an average value? Third, are there significant relationships between annual variability in seed production and pollination and seed dispersal modes, as

would be predicted if economy of scale considerations were the major determinants of mast seeding (predictions 1–3 below)?

In contrast to wind-pollinated plants, for which massive and synchronous flowering may be reproductively advantageous, animal-pollinated plants may satiate their animal pollinators when flower numbers exceed some threshold (Ims 1990a; Sork 1993; Kelly 1994). According to this view, masting should have evolved more often (i.e., variability in seed production should be greater) among wind- than among animal-pollinated plants (prediction 1). An analogous reasoning applies to seed dispersal methods (Kelly 1994). The reproductive advantages derived from satiation, or "swamping" (Ims 1990a), of seed predators have been often considered as a major selective pressure favoring the evolution of masting (Janzen 1971, 1978; Silvertown 1980; Sork 1993; Kelly 1994). Nevertheless, saturating crops may not only satiate seed predators but also, in the case of some animal-dispersed plants, seed dispersal agents as well (Herrera 1995; and references therein). We therefore suggest that, depending on a species' seed dispersal method (abiotic vs. biotic and, among the latter, mutualistic vs. nonmutualistic), a trade-off may arise between the advantages of satiating predators and the disadvantages of simultaneously satiating dispersers, leading to dispersal dependence of variability in seed production. According to this hypothesis, seed production of plants that have their seeds actively dispersed by (potentially satiable) animals should be less variable than that of those dispersed mainly by (insatiable) inanimate means (e.g., wind, water, gravity; prediction 2). Among plants with seeds dispersed by animals, those depending on prevailingly mutualistic counterparts (e.g., those with fleshy fruits, dispersed by frugivorous vertebrates) should be less variable than those depending for dispersal on animals that are predominantly seed predators and that only incidentally behave as seed dispersers (e.g., plants dispersed by scatter-hoarding vertebrates; prediction 3).

Methods

The Data Sample

We screened the botanical, ecological, and, to a lesser extent due to accessibility limitations, forestry primary literature for quantitative data on annual variation in seed or fruit abundance ("seed output" hereafter). Only polycarpic woody plants were considered because inclusion of the few data available for perennial herbs would have inflated disproportionately the ecological and life-history heterogeneity represented in the sample. Studies reporting annual variation in seed output were strongly biased in favor of abiotically dispersed, dry-fruited, com-

mercially valuable tree species. To compensate for the scarcity of reports for fleshy-fruited plants dispersed by frugivorous vertebrates, we had to rely extensively on our own and others' unpublished information for these species. To be included in the sample, a time series of seed output for a given plant species at a specific location (an individual "data set" hereafter) should include data for at least 4 yr from the same locality and should all have been obtained from the same plants or plots using identical sampling procedures. Only investigations using truly quantitative evaluation methods (i.e., based on actual counts of fruits or seeds in explicitly defined sampling units such as branches, individuals, or fall traps) were considered. Studies reporting seed output in the form of semiquantitative or indirect indexes were not considered.

We compiled a sample of 296 data sets from 144 different species that fulfilled all the above requirements (see appendix). In order to test predictions 1–3 mentioned above, species in the sample were classed into pollination and seed dispersal categories. Species were classified as either predominantly wind pollinated (168 data sets from 75 species) or animal pollinated (128 data sets from 69 species). Three categories were recognized for dispersal. The first was "endozoochorous" (108 data sets from 57 species)—species producing berries, drupes, or analogous structures with seeds dispersed by frugivorous vertebrates that ingest fruits and discard seeds undamaged. The second category was "dyszoochorous" (sensu van der Pijl 1982; 87 data sets from 44 species)—plants generally producing dry fruits or functionally analogous structures (nuts, legumes, cones), which are dispersed by animals that feed on the seeds themselves and destroy many or most of them. In our sample, most plants in this category are dispersed by scatter-hoarding birds and mammals and only a few by ungulate mammals. The third category is "nonzoochorous" (101 data sets from 43 species)—species that usually accomplish dispersal without the concourse of animals, such as those dispersed by wind, water, or gravity. Assignment of species to pollination and seed dispersal categories was based on relevant life-history information found in the original or related investigations, in general treatises on pollination (Proctor and Yeo 1973; Faegri and van der Pijl 1979), seed dispersal (Ridley 1930; van der Pijl 1982), or on our own unpublished observations.

The sample was dominated by medium- and short-term data series and was affected by some biases that must be explicitly acknowledged. On average, data sets consisted of data for only 7.6 ± 4.8 yr (mean ± 1 SD; this notation will be used throughout this article unless otherwise stated). The vast majority of them (82.8%)

consisted of ≤ 10 yr of data (41.9% were ≤ 5 yr), and only nine data sets (3.0%) had data for ≥ 20 yr (seven of these are from New Zealand). Duration of time series was not independent of either pollination or seed dispersal categories. Series of seed output of wind-pollinated species (8.7 ± 5.4 yr, $N = 168$) were significantly longer ($\chi^2 = 29.7$, df $= 1$, $P \ll .001$; Kruskal-Wallis ANOVA) than those of animal-pollinated ones (6.2 ± 3.3 yr, $N = 128$). Furthermore, duration of series increased significantly from endozoochorous (6.4 ± 4.3 yr, $N = 108$) through dyszoochorous (7.9 ± 3.5 yr, $N = 87$) to nonzoochorous (8.8 ± 5.9 yr, $N = 101$; $\chi^2 = 28.2$, df $= 2$, $P \ll .001$; Kruskal-Wallis ANOVA). The sample also exhibited considerable taxonomical biases. Two out of 31 plant families represented in the sample (Pinaceae, Fagaceae) accounted collectively for 40.9% of data sets and 31.3% of species. Species from only two plant genera contributed 28% of data sets (*Quercus*, 15.2%; *Pinus*, 12.8%).

Assessing Variability

The vast majority of studies included in the sample reported values for fruit or seed "abundance," which represents an unknown fraction of actual fruit or seed "production." Data based, for example, on counts of fruits borne on branches or collected by seed fall traps presumably reflect standing crops more closely than actual production. We would expect the fraction of actual production accounted for by abundance data to differ among investigations (depending, e.g., on field methods, species-specific patterns of fruit shedding, and extent of fruit removal by animals) but not among years for the same study system, provided the same sampling methods were consistently applied. For this reason, we considered justified an evaluation of annual variability in fruit or seed production indirectly by assessing variability in estimates of abundance, as done also by previous authors (e.g., Silvertown 1980; Webb and Kelly 1993; Kelly 1994).

For each data set, variability in seed output was evaluated using the coefficient of variation of yearly values (CV $=$ SD/mean; throughout this article, CVs are reported as $100 \times$ SD/mean). The CV is an acceptable index of proportional variability that is independent of the mean (McArdle and Gaston 1995). Furthermore, previous reviews of variability in seed or fruit abundance have also used the CV of seed output among years as a measure of variability (Silvertown 1980; Webb and Kelly 1993; Kelly 1994). Using the same measure here will provide an opportunity for taking advantage of previously published data.

Coefficient of variation values were obtained from published sources using one of the three following proce-

dures (mentioned in decreasing order of frequency of occurrence in our data sets). Whenever possible, CVs were computed from raw numerical data presented in tabular form in the original publications. When the data were presented graphically, digital images of graphs were obtained with a scanner and numerical values then extracted from these images with a computer. Finally, in the few studies in which the original seed output values could not be reliably extracted from the publication by any of these methods, CVs were computed from original data furnished by the authors upon request. We recomputed from the original sources as many CVs as possible of those presented by Silvertown (1980, app. 1), which may explain some discrepancies between his and our figures. Coefficient of variation values from his study for which we did not have access to the original publications were incorporated to our data sample without modification.

Statistical Analyses

Answering the first and second questions addressed in this article require testing frequency distributions for multimodality. This was done using a modification of the bootstrap procedure described by Efron and Tibshirani (1993, pp. 227–233). Bootstrap samples were drawn from the data and the optimal kernel density distribution that minimized the approximate mean integrated square error was estimated for each generated sample (SAS Institute 1995). The number of modes was then determined for each of these bootstrapped distributions, and empirical P values determined from the relative frequencies of density distributions with different number of modes. These P values were then used to test the null hypothesis that the density distribution had a single mode against the alternative hypothesis that it had ≥ 2 modes.

The short duration of most time series in our sample unfortunately precluded rigorous statistical tests of multimodality of annual seed production at the within-species level, as required by the second question. This limitation was circumvented in part by conducting an assessment of multimodality on the whole species sample. Annual seed output data in each individual data set with the raw data available were first log transformed and then standardized to mean 0 and standard deviation unity. A composite frequency distribution was then obtained by combining data from all data sets into a single frequency distribution. If annual seed output of most or all species in the sample tended to fluctuate randomly around a species-specific mean value, then we would expect (because of the central limit theorem) this composite frequency distribution not to depart significantly from a zero-mean normal distribution. Alternatively, a bi-

modal composite distribution would be expected if within-species bimodality in seed output prevailed in the sample.

Appropriate statistical testing of predictions 1–3 requires accounting satisfactorily for the biases inherent to the data sample, particularly the taxonomical effects and the relationship detected between length of time series and pollination and dispersal categories. To this end, we concurrently applied methods based on phylogenetically independent contrasts (PICs; Burt 1989) and mixed-model ANOVA that incorporated taxonomy-dependent, nested covariance structures. Phylogenetically independent contrasts were obtained using the phylogenetic arrangement proposed by Chase et al. (1993). Pairs of taxa in the sample (either families or genera) were chosen that differed in pollination or seed dispersal mode, such that each pair would constitute an independent contrast of variability in annual seed output (mean CV), averaged over all the species included in each subclade (for similar approaches, see Jordano 1995; Grubb and Metcalfe 1996; Saverimuttu and Westoby 1996; Swanborough and Westoby 1996). Randomization tests for paired comparisons (Manly 1991) were used in conjunction with PICs to assess the significance of between-clade differences in mean CV value, to test the null hypothesis that average between-clade difference in mean CV was 0.

A mixed general linear model was fitted to the data using procedure MIXED in the SAS package (release 6.12; SAS Institute 1996*a*, 1996*b*). The coefficient of variation of annual seed output (CV) was the dependent variable in the model, and pollination method and the seed dispersal category were included as fixed effects. The MIXED procedure implements a generalization of the standard linear model, the generalization being that the data are permitted to exhibit correlation and non-constant variability (although they are still assumed to be normally distributed). It thus allows modeling not only the means (fixed effects, similar to those in the standard linear model), but also their variances and covariances. This feature is particularly useful in the present case, where the data cannot properly be treated as statistically independent units and some covariance structure is expected to occur. Due to biological similarities, correlations will most likely exist between measurements of variability in seed output conducted, for instance, on species of the same genus. To account for these possible taxonomical correlates of CV, the taxonomical affiliation of each data set was incorporated into the mixed linear model as four hierarchically nested, random effects, namely, class (angiosperms vs. gymnosperms), family, genus, and species. It must also be noted here that a further advantage of including taxonomic affiliation as random effects in the model is that inferences drawn from

the analysis apply to an entire population of taxonomic levels, rather than to the particular taxonomical groups represented in the sample (Bennington and Thayne 1994). This is an important consideration in view of the unequal and biased representation of taxonomical categories in the data sample.

For a variety of ecological parameters, estimates of annual variability often increase with the number of years included in the calculation (Pimm and Redfearn 1988; Ariño and Pimm 1995; Halley 1996). To test for this possibility and to account statistically for the potential influence on results of the unequal duration of studies on species with different pollination or seed dispersal modes, the number of years on which each data set was based was also included in the model as a further random effect.

The mixed linear model was fitted using the method of restricted maximum likelihood (see SAS Institute 1996*a*, 1996*b* for details). Overall significance of fixed effects and the a priori contrasts involved in predictions 2 and 3 were tested using Type III Wald χ^2 tests. The statistical significance of random effects was tested by applying Wald Z tests to their estimated covariance parameters (SAS Institute 1996*a*). Model-corrected least squares means and standard errors of CV for different pollination and seed dispersal categories were obtained using the LSMEANS statement in procedure MIXED.

Results

Question 1: A Continuum of Variability Levels

Mean CV of seed output for the whole sample of data sets considered ($N = 296$) is 115.2 ± 49.8 (range = 12.0–233.4). The frequency distribution of CVs for individual data sets departs only marginally from normality ($D = 0.050$, $P = .073$; Kolmogorov test) and has a single mode (fig. 1*A*). Nevertheless, as species differ broadly in the number of independent data sets represented in the sample (range = 1–13 data sets per species), the distribution of the CVs of all data sets pooled may provide a distorted or biased picture of the actual patterns of "interspecific" variation. To examine this possibility, a mean CV was computed for each species. The frequency distribution of these species means ($N = 144$) departs also marginally from normality ($D = 0.070$, $P = .084$; Kolmogorov test) and has a weakly bimodal appearance, with modes at or around the intervals 60–80 and 120–140 (fig. 1*B*). This suggests that two distinct groups of species might be represented in the sample differing in degree of annual variability in seed output. We tested the null hypothesis that the estimated density function for the data in figure 1*B* had a single mode (H_0), against the alternative that it had two or more modes (H_1), using the bootstrap procedure described above in "Statistical Anal-
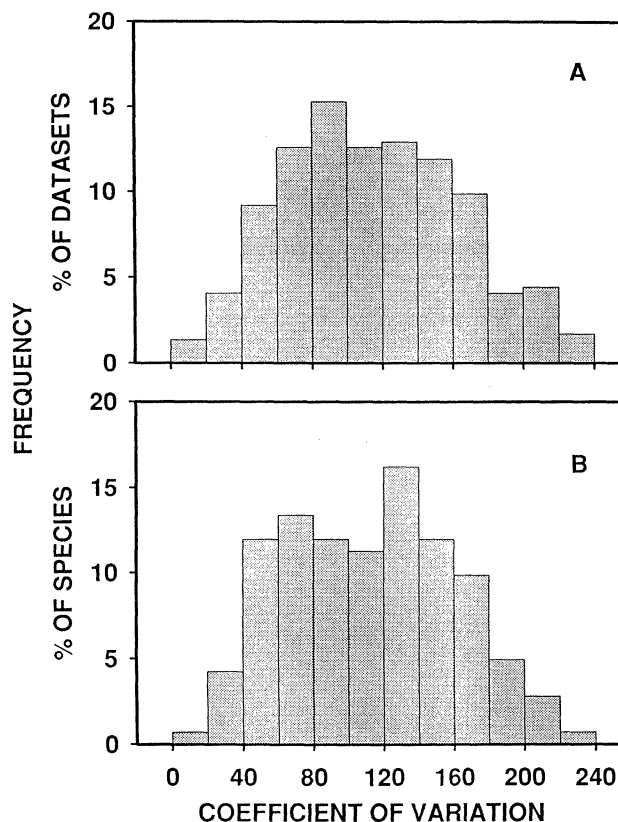

Figure 1: Frequency distributions of the coefficient of variation (CV) of annual seed output for individual data sets (*A*, $N = 296$) and species (*B*, $N = 144$) considered in this study. Species means used to construct graph *B* were obtained by averaging CV values from individual data sets (see text for further details).

yses." Using 250 bootstrap repetitions, the null hypothesis H_0 of a density distribution with a single mode could not be rejected ($P = .29$).

Question 2: Bimodality of Seed Production

The composite frequency distribution of standardized, within-species annual seed output data (all species combined) is shown in figure 2. The observed distribution departs significantly from normality ($D = 0.073$, $P < .01$; Kolmogorov test), and also differs significantly from a normal distribution with mean 0 and standard deviation unity ($D = 0.057$, $P < .001$; Kolmogorov test). The distribution has two distinct modes, with relatively low (−1.0 to −0.6) and relatively high (0.4–1.0) standardized seed output values overrepresented, and values around the expected mean (−0.6 to 0.2) underrepresented. The null hypothesis that the observed frequency distribution had a single mode was rejected ($P < .002$, 500 bootstrap repetitions). In conclusion, therefore, there is evidence
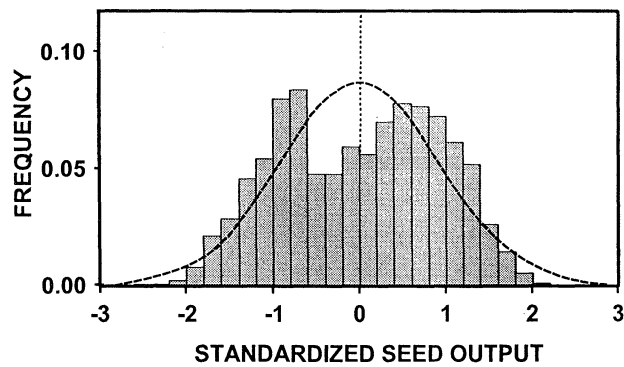
Figure 2: Composite frequency distribution of standardized ($\overline{X} = 0$, SD $= 1$), within-species annual seed output data (*bars*), and the expected normal curve if, within most or all species, annual seed output tended to fluctuate around a mean value. In each data set, annual seed production data were log-transformed prior to standardization.

that, in most plant species considered here, annual seed output does not fluctuate around an average value but rather exhibits a marked trend toward bimodality, with prevalence of either high or low reproduction years and a scarcity of intermediate ones. Similar results were obtained when separate frequency distributions of standardized values were obtained for the different pollination and seed dispersal modes (results not shown).

Question 3: Test of Predictions

Annual variability in seed output depended significantly on taxonomic affiliation at the genus and species levels but not at the class and family levels (table 1). All covariance attributable to these random effects occurred at the two lowermost taxonomic levels. There was no sig-

Table 2: Mean coefficient of variation of annual seed output for species differing in seed dispersal methods

Seed dispersal method	Model-adjusted mean CV $\pm$ SE
Endozoochorous	82.57 $\pm$ 7.58[a]
Dyszoochorous	119.76 $\pm$ 12.88[b]
Nonzoochorous	117.50 $\pm$ 9.97[b]

Note: Values shown are least-squares, model-adjusted means obtained after accounting for other effects incorporated into a mixed-model ANOVA (see text). Means sharing the same superscript do not differ significantly (tested using planned contrasts in ANOVA).

nificant variance component in CV attributable to the effect of variation among data sets in the number of years of data entering into the computation of CV (table 1).

After accounting for the random effects incorporated in the model (table 1), there was no significant effect of pollination type (prediction 1; $\chi^2 = 1.29$, df $= 1$, 151, $P = .26$), and a significant effect of seed dispersal method ($\chi^2 = 9.22$, df $= 2$, 151, $P = .010$), on the CV of seed output among years. The contrast between the CV of animal (endozoochorous plus dyszoochorous combined) and abiotic dispersal categories (prediction 2) was not statistically significant ($\chi^2 = 0.75$, df $= 1$, 151, $P = .39$), while those between endozoochorous and either dyszoochorous (prediction 3; $\chi^2 = 6.85$, df $= 1$, 151, $P = .009$) or other methods (dyszoochorous plus nonzoochorous combined; $\chi^2 = 9.18$, df $= 1$, 151, $P = .003$) were both significant. Differences between dispersal categories in mean annual variability are summarized in table 2. Endozoochorous taxa have distinctly lower annual variabilities in seed output than either dyszoochorous or

Table 1: Covariance parameter estimates for the random effects in a mixed linear model having the coefficient of annual variation of seed output (CV) as the dependent variable and pollination (wind or animal pollination) and seed dispersal (endozoochorous, dyszoochorous, or nonzoochorous) categories as fixed effects

Covariance parameter*	Estimate	SE	Wald Z	P
Years	2.526	4.039	.63	.53
Class	.000	$\cdots$	$\cdots$	$\cdots$
Family (class)	.000	$\cdots$	$\cdots$	$\cdots$
Genus (family and class)	767.912	289.933	2.65	.008
Species (genus, family, and class)	507.123	181.260	2.80	.005
Residual	1,047.002	117.368	8.92	$\ll$.0001

Note: Model fitted to the 296 data sets in the sample using SAS procedure MIXED and restricted maximum likelihood estimation method. See "Statistical Analyses" in the "Methods" section for justification of the approach and further details.

* "Years" = number of years of data included in the computation of CV. Random taxonomical effects were specified in the model as a series of hierarchically nested effects, namely, "class" (gymnosperms vs. angiosperms), "family nested within class," "genus nested within family and class," and "species nested within genus, family, and class."

nonzoochorous ones, while the two latter categories have similar average variabilities.

The robustness of the preceding results was evaluated by fitting the same mixed model after excluding all *Quercus* and *Pinus* data sets. Results remained essentially unchanged, but the elimination of the data from these two numerically dominant genera in the sample resulted in improved statistical significance for the effects of both seed dispersal type ($\chi^2 = 16.56$, df $= 2$, 100, $P < .001$) and pollination mode ($\chi^2 = 3.87$, df $= 1$, 100, $P = .052$). After omitting the data for *Quercus* and *Pinus,* the effect of pollination mode thus became nearly significant, with wind-pollinated taxa exhibiting larger average CV values (model-adjusted mean $\pm$ SE $= 127.16 \pm 10.18$) than animal-pollinated ones (105.01 ± 8.27), as predicted by prediction 1.

The phylogenetic relationship among the taxa represented in the sample that were used in the analyses of phylogenetically independent contrasts is depicted in figure 3. In most cases, contrasts were estimated using averages across species within families. A total of seven contrasts were available for comparing the two pollination modes (wind vs. animal pollination; fig. 3*A*), and 11 contrasts were used for the comparison of endozoochorous versus nonzoochorous plus dyszoochorous seed dispersal categories (fig. 3*B*). Likewise, 11 contrasts were available for the comparison of animal-dispersed (endozoochorous plus dyszoochorous) versus nonzoochorous clades (not illustrated in fig. 3*B*). Three of the seed dispersal contrasts were among genera within families: *Fraxinus* (nonzoochorous) versus *Olea* and *Phillyrea* (endozoochorous) within the Oleaceae (*contrast 1,* fig. 3*B*), *Liriodendron* (nonzoochorous) versus *Magnolia* (endozoochorous) within the Magnoliaceae (*contrast 11,* fig. 3*B*), and *Thuja* and *Libocedrus* (nonzoochorous) versus *Juniperus* (endozoochorous) within the Cupressaceae (*contrast 8,* fig. 3*B*).

Results of PIC analyses are similar to those from the mixed-model ANOVA. For pollination type, there was a trend for abiotically pollinated clades to exhibit higher mean CV than paired, biotically pollinated ones (five out of seven contrasts), but the difference was marginally nonsignificant (randomization test for paired comparisons, $P = .084$, $N = 2,500$ repetitions). The contrast between mean CV values of zoochorous (endozoochorous plus dyszoochorous combined) and nonzoochorous clades was not significant ($P = .137$, $N = 2,500$ repetitions; mean CV of nonzoochorous clades exceeded that of paired zoochorous ones in seven out of 11 comparisons). The contrast between endozoochorous and dyszoochorous plus nonzoochorous clades combined, however, was significant (randomization test for paired comparisons, $P = .026$, $N = 2,500$ repetitions). In eight

out of 11 instances, mean CV values for endozoochorous clades were lower than those for paired dyszoochorous plus nonzoochorous ones (fig. 4).

Discussion

Sampling Biases and Their Implications

Current knowledge of medium- and long-term seeding patterns of natural populations of woody plants is not only very imperfect, but also much more seriously biased than we had anticipated before compiling the literature data for this study. To date, the majority of published studies comprising data for ≥ 4 yr have been conducted on an ecologically, taxonomically, and geographically very restricted subset of woody plants, namely, dry-fruited, economically important (as sources of timber or wildlife food) species from north temperate or boreal habitats. Quantitative information on southern hemisphere or herbaceous perennial plants is remarkably sparse. Data available are also biased against fleshy fruited, endozoochorous plants, which contrasts with their prevalence in many forests and scrublands around the world (e.g., Howe and Smallwood 1982; Webb and Kelly 1993; Herrera 1995). Nearly two-thirds (63%) of the 108 data sets in the endozoochorous category considered in this study came from unpublished sources (see appendix). Concerning habitat type, long-term studies of seeding patterns of tropical trees and shrubs continue to be as rare in the literature as they were 20 yr ago when Janzen (1978) stressed their ecological significance and called for increased attention to their study. From a taxonomic viewpoint, data sets from the families Fagaceae and Pinaceae predominate in our sample and would almost certainly have predominated even further had we had opportunities to scan the forestry literature more thoroughly. Fagaceae and Pinaceae account altogether for 40.9% of our data sets, which contrasts sharply with the tiny 1.6% they contribute to the combined total of world species of all families occurring in our sample (estimated using family species richnesses in Mabberley 1997).

In view of the important biases that affect the primary literature on seeding patterns of woody plants, we emphasize that conclusions and generalizations drawn from such an imperfect sampling of nature should be interpreted with caution. Our finding of significant taxonomical effects on annual variability levels of seed output effectively indicate that conclusions may change depending on the taxonomic composition of the species sample under consideration. Future analyses based on data from an ecologically, taxonomically, and geographically more balanced sample of species may thus call for some reconsideration of the results reported here. In this respect, we note that exclusion of the numerous data sets from *Pinus*
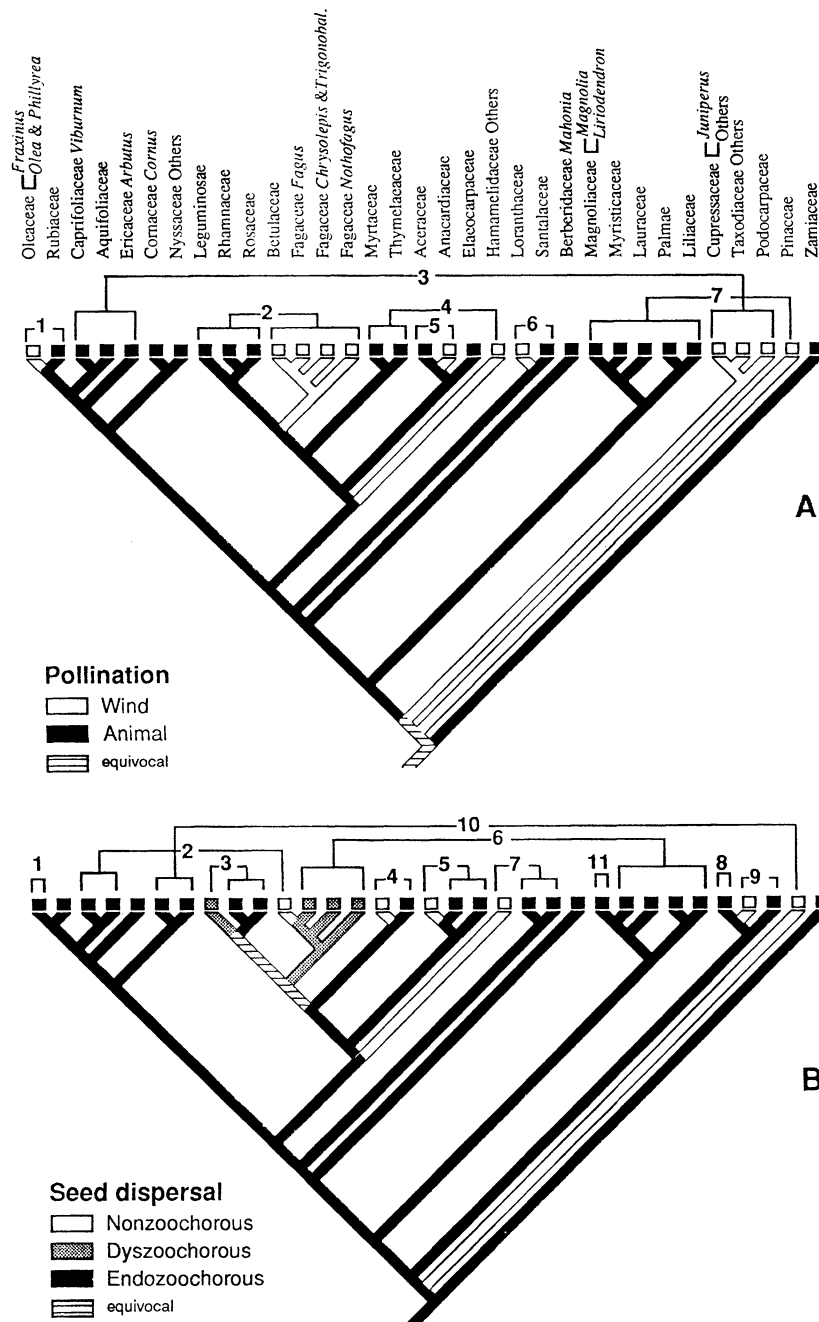
Figure 3: Phylogenetic relationships among the families included in the data sample, based on Chase et al.'s (1993) rbcL phylogeny, and paired contrasts used in the comparison of pollination (A) and seed dispersal modes (B). Character states for pollination and seed dispersal mode are mapped on the tree using different shading styles, and subclades used in the paired comparisons of mean variability in annual seed output (CV) values are labeled with numbers. To avoid graph cluttering, only contrasts involving the comparisons of clades of endozoochorous versus dyszoochorous plus nonzoochorous combined are illustrated for seed dispersal mode.
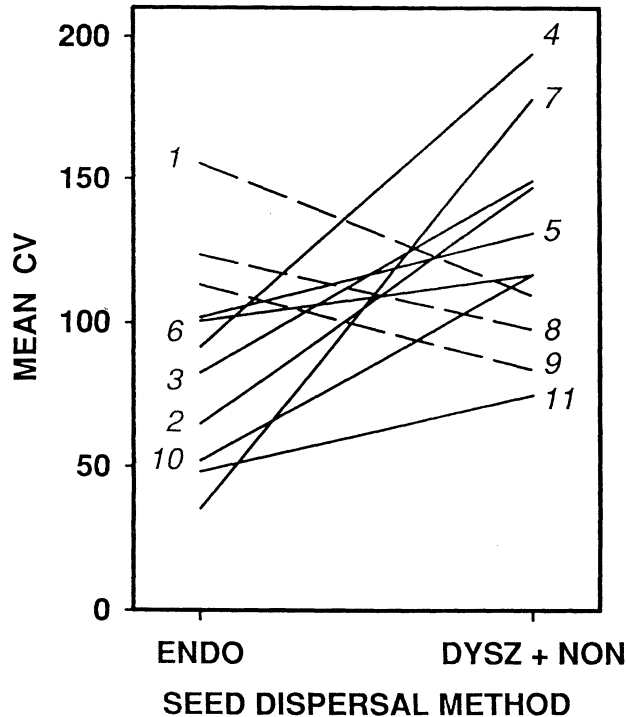
Figure 4: Relationship between average coefficient of variation (CV) of annual seed output and seed dispersal mode (*endo* = endozoochorous, *dysz* = dyszoochorous, *non* = nonzoochorous) for the clades used in the phylogenetically independent contrasts (PIC) for seed dispersal mode. Contrasts involved are illustrated in figure 3B. Each PIC pair is connected by a line, and numerals refer to the PIC codes in figure 3. Contrasts where mean CV values for endozoochorous clades were higher than those for paired dyszoochorous or nonzoochorous ones are shown as dashed lines.

and *Quercus* species from the analysis brought about a considerable improvement in the statistical significance of the effects of pollination and dispersal mode on CV of seed output. After the exclusion, the effect of pollination mode became marginally significant and prediction 1 thus gained some support. It seems paradoxical that the information from precisely the two most extensively investigated plant genera with regard to variability in seed production may hinder rather than facilitate the detection of interspecific patterns.

The Elements of the Masting Concept

To be meaningful, the masting concept logically requires that a "nonmasting" concept exist for reference and comparison. This implies multimodality of the frequency distribution of CV of seed output, with species tending to cluster into two or more distinct, objectively distinguishable groups characterized by different levels of annual variability in seed output. The present study has shown that CV values (either as species means or as val-

ues for individual data sets) fall along a broad continuum and exhibit a unimodal distribution that does not depart significantly from normality. This finding corroborates the earlier results of Kelly (1994) based on a smaller sample, and shows, on a quantitative basis, that there is no empirical support for any division of woody plants into distinct groups differing in mean levels of supra-annual variability in seed output, as tacitly implied by the masting concept.

Supra-annual reproductive synchrony of locally or regionally coexisting conspecifics has been generally associated with the masting concept and considered an essential element in most definitions (Janzen 1976; Silvertown 1980; Kelly 1994). It is thus remarkable that, despite this important role, most investigations have focused on patterns of annual variation in seed production at the plant population level, while patterns of supra-annual variability in fruiting at the individual plant level, which are essential to address the issue of synchrony, have been only rarely examined (but see Janzen 1978, 1989; Vander Kloet and Cabilio 1984; Crawley and Long 1995). Of particular biological interest would be to know whether woody plants actually fall into distinct groups characterized by differing levels of individual synchrony (i.e., multimodality of synchrony levels) and whether some predictable relationship exists across species between synchrony and variability levels. Unfortunately, these aspects cannot be properly addressed using the population-level CV figures examined here (see Herrera 1998*b* for discussion). No relationship between individual synchrony and variability in seed output in a small set of species was found in the earlier article (Herrera 1998*b*).

Supra-annual intraspecific bimodality in seed production, that is, the existence of distinct high- and low-reproduction years, is a further essential, yet elusive element of the masting concept that has resisted attempts at objective, quantitative assessments (Kelly 1994). A rigorous analysis of this aspect would require separately testing time series of seed production for as many individual species as possible. Unfortunately, such ideal analysis will be impossible until really long time series of seed production become available. In the meantime, our indirect analytical approach has proven useful at least to suggest some general trends. Results indicate that, within species, large oscillations of seed output between high- and low-production years are significantly more frequent than small fluctuations around a mean value. This suggests that supra-annual bimodality in seed output is not a phenomenon limited to a relatively restricted group of (putative masting) species but is probably the rule among polycarpic woody plants. The ultimate and proximate causes that may be proposed to explain this phenomenon are largely the same and involve the same biological mechanisms that have accumulated over the years in the

ecological literature to explain masting and will not be reviewed here. Among these, hypotheses related to economies of scale seem to account, in one way or another, for most observed patterns of supra-annual variability in seed output (Kelly 1994), and results of this study corroborate that interpretation.

Variability in Seed Output and Economies of Scale

This study has revealed significant relationships between dispersal and, to a lesser degree, pollination method, and level of annual variability in seed output. Our findings are consistent with Kelly's (1994) view that factors related to economies of scale, operating in relation to pollination, dispersal, and escape from predators, are probably the major ecological and evolutionary determinants of supra-annual patterns of seed output in polycarpic plants (see also Janzen 1978; Ims 1990*a*).

When all data sets were considered, no significant relationship was found between interannual variability in seed output and pollination method (prediction 1). After exclusion of data from *Pinus* and *Quercus*, however, the effect of pollination method became nearly significant, with wind-pollinated taxa being, as predicted, more variable than animal-pollinated ones. This ambiguous result probably reflects inconsistencies among plant genera or species in the relative magnitude of the advantages and disadvantages derived from production of large floral displays and lends support to Kelly's (1994) contention that no general prediction can probably be made about the expected effects of masting on animal pollinators. Consequences of annual variations in flower production on pollinator-induced variations in fruit production have been explored too infrequently (but see, e.g., Elmqvist et al. 1988; Copland and Whelan 1989; Vaughton 1991; Holm 1994) for assessing the frequency of occurrence of satiation of animal pollinators. Indirect evidence, however, suggests that satiation may frequently occur. Fruit set is pollen limited in many animal-pollinated plants (review in Burd 1994), which means that often there may be more flowers available than can be visited and pollinated by local pollinator populations.

Prediction 2, that seed output should be less variable for animal-dispersed plants (endozoochorous plus dyszoochorous combined) than for those dispersed by inanimate means, was not supported by results. The reason was that nonzoochorous and dyszoochorous plants were statistically indistinguishable and that both groups were significantly more variable in seed production than the endozoochorous one. This suggests that it is not the participation of animals in seed dispersal in itself that makes endozoochorous plants that different with regard to annual variability in seed output, but rather the kind of relationship they maintain with their dispersal agents and

the immediate advantages derived (or disadvantages avoided) from making fruit abundance to match mutualists' demands as closely as possible. For dyszoochorous plants, in contrast, dispersal agents are probably equivalent to seed predators in their numerical and feeding responses to annual variations in crop size.

Our results have verified prediction 3 that seed production should be less variable among plants dispersed by mutualistic frugivores than among those that rely for dispersal on animals that predominantly behave as seed predators. This result is consistent with the economy of scale interpretation that, among endozoochorous plants, the detrimental reproductive consequences of satiation of dispersers will operate against the evolution of large interannual fluctuations in crop sizes. That fruit removal rates by frugivores (and thus seed dispersal rates) depend on intraspecific or seasonal variations in crop sizes has been well documented (e.g., Davidar and Morton 1986; Murray 1987; Obeso 1989; Laska and Stiles 1994), but dispersal consequences of annual variation in crop size have been examined by few studies. These investigations, however, have effectively shown that frugivore populations become swamped, and seed dispersal success of plants tends to decline beyond certain fruit abundance threshold (Jordano 1987; Herrera et al. 1994; Herrera 1998*a;* and references therein). A 12-yr study of fruits and frugivores has shown that seed disperser populations did not respond numerically to increases in the abundance of their fruit resources and that the abundance of fruits and frugivores were decoupled (Herrera 1998*a*). If future studies confirm the generality of these results, then the lack of a numerical response of frugivore populations to annual variations in fruit supply would frequently lead to satiation during periods of fruit superabundance.

Prediction 3 implicitly assumes that the advantages derived to endozoochorous plants from satiating seed predators are comparatively minor in comparison with the disadvantages derived from saturating mutualists. This will happen, for instance, if endozoochorous plants generally suffer smaller losses to seed or fruit predators than plants having other seed dispersal methods. There is some support for this assumption (Herrera 1987), but claims about its generality are premature. In fact, endozoochorous plants are not free from the attack of fruit and seed predators, and these may destroy a large fraction of the crops of some species (e.g., Courtney and Manzur 1985; Herrera 1986; Jordano 1987; Englund 1993; Sperens 1997). Supra-annual variability of seed output in endozoochorous plants thus is most likely subject to conflicting pressures: increasing variability in seed output may enhance reproductive output through escape from seed predators but simultaneously decrease seed dispersal success as a consequence of occasional satiation of mutualistic dispersal agents. This will impose a trade-

off on plants whose resolution will depend, in each case, on the relative magnitudes of the detrimental reproductive consequences derived from seed predation and dispersal failure. According to this hypothesis, it may be predicted that endozoochorous species having specialized (e.g., monophagous) flower, fruit, or seed predators should tend to favor avoidance of seed predators over avoidance of dispersal failure (no opportunity is left for dispersal if flowers or developing fruits are destroyed before maturation) and thus exhibit proportionally greater annual variability in seed output. Two of the three PICs in figure 4 that are contrary to prediction 3 (PICs 1 and 8) because of higher interannual variability of endozoochorous species relative to dyszoochorous plus nonzoochorous ones clearly support this prediction. The fleshy fruited clades involved in these contrasts all have specific flower (*Phillyrea* spp.; Herrera et al. 1994; Traveset 1994), fruit (*Olea europaea;* Jordano 1987), or seed (*Juniperus* spp.; Roques et al. 1984) predators that often inflict heavy reproductive losses.

Conclusion

There seems to be no compelling reason to perpetuate the concept of "mast fruiting" in the ecological literature as a shorthand to designate a distinct, well-defined, genuinely interesting biological phenomenon. None of the findings of this article that support this view, namely, the absence of distinct groups of species regarding annual variability and the evidence suggesting that most polycarpic woody plants seem to adhere to alternating supra-annual schedules involving either high- or low-reproduction years, is essentially new. Neither do our results differ in any important way from those highlighted by Kelly (1994) on the basis of a smaller data sample. Moreover, tests of predictions conducted here also provide clear support for the economies of scale hypothesis originally proposed to explain the masting phenomenon (Janzen 1978; Norton and Kelly 1988; Kelly 1994). Why, then, our seemingly radical view? To reconcile observed facts with the assumptions underlying the conventional notion of mast fruiting, Kelly (1994) opted for a broad extension of the concept by proposing a series of subcategories ranging from strict through normal to putative masting. By virtue of this extended classification, virtually any conceivable supra-annual fruiting schedule involving some degree of variability may be shoehorned into the mast-fruiting concept. Rather than adopting this all-encompassing view, our proposal here is that the use of the term should simply be discontinued and that the study of supra-annual fruiting patterns of plants should be best approached using objective quantitative parameters rather than ambiguous and potentially misleading verbal labels. Dissecting population-level CV values (such as those considered in this study) into its temporal, spatial, and individual components of variability as well as devising quantitative indices to measure interindividual reproductive synchrony across years are some possible avenues for this much-needed quantitative research (Herrera 1998b).

Improved knowledge of patterns of supra-annual variation in seed output is critical to our understanding of, among other, plant life-history evolution, vegetation dynamics, and plant-animal interactions. Results of this study, by demonstrating for the first time significant associations between supra-annual variability in seed output and pollination and seed dispersal methods, suggest the existence of important reproductive correlates that demand further investigation. Furthermore, quantification and analysis of reproductive synchrony in plants deserve consideration in their own right (Ims 1990a, 1990b). Dismissal of the masting concept should not induce any decline of interest on the study of reproductive variability in plants, but rather pave the road for a change of attitude toward broadening the focus of studies on reproductive variability and lessening the prevailing emphasis on the most extreme cases. Investigations on within-season temporal patterns of reproduction in plants have contributed in important ways to our knowledge of the ecology and evolution of plant reproduction (e.g., Augspurger 1981; Rathcke and Lacey 1985; Kochmer and Handel 1986; Gómez 1993), and similarly valuable results are to be expected from studies focusing on supra-annual patterns.

Table A1: The data sample used in this study

Species	CV (years of data)	Reference
Abies concolor (W, N)	201.0 (14), 201.0 (6)	Fowells and Schubert (1956), pp. 1–48*
Abies grandis (W, N)	151.7 (26)	Eis et al. (1965)
Abies pinsapo (W, N)	119.1 (4), 120.6 (4), 136.6 (4)	M. Arista, unpublished data
Acacia adsurgens (A, D)	146.5 (9)	Davies (1976)
Acacia albida (A, D)	59.5 (8)	Dunham (1990)
Acacia aneura (A, D)	165.9 (9), 179.7 (9), 186.7 (8), 172.4 (7)	Davies (1976)
Acacia craspedocarpa (A, D)	207.0 (8)	Davies (1976)
Acacia cuthbertsonii (A, D)	150.0 (9)	Davies (1976)
Acacia sclerosperma (A, D)	94.8 (9), 135.5 (9)	Davies (1976)
Acacia sp. (A, D)	223.5 (9)	Davies (1976)
Acacia tetragonophylla (A, E)	147.9 (9), 187.0 (9)	Davies (1976)
Acacia victoriae (A, D)	199.9 (9), 110.9 (9)	Davies (1976)
Acer mono (A, N)	135.3 (5)	Tanaka (1995)
Acer palmatum (A, N)	152.9 (5)	Tanaka (1995)
Acer platanoides (A, N)	145.6 (19)	Pucek et al. (1993)
Acer rubrum (A, N)	124.8 (4)	Jones et al. (1994); R. H. Jones, personal communication
Acer rufinerve (A, N)	87.5 (4)	Tanaka (1995)
Acer saccharum (A, N)	140.0 (8)	Curtis (1959)*
Amelanchier ovalis (A, E)	139.5 (4)	P. Jordano, unpublished data
Arbutus unedo (A, E)	89.3 (12)	Herrera (1998a)
Astrocaryum mexicanum (A, E)	22.8 (12), 31.0 (10)	Martínez-Ramos et al. (1988)
Ateleia herbert-smithii (A, N)	58.1 (7)	Janzen (1989)
Berberis hispanica (A, E)	99.0 (4), 142.7 (4) 84.9 (4)	P. Jordano, unpublished data
Betula nigra (W, N)	168.8 (4)	Jones et al. (1994); R. H. Jones, personal communication
Betula pubescens (W, N)	67.0 (5)	Sarvas (1954)*
Betula verrucosa (W, N)	42.0 (6)	Sarvas (1954)*
Carpinus betulus (W, N)	179.0 (19)	Pucek et al. (1993)
Carpinus caroliniana (W, N)	125.7 (4)	Jones et al. (1994); R. H. Jones, personal communication
Carpinus cordata (W, N)	171.7 (5)	Shibata and Nakashizuka (1995)
Carpinus japonica (W, N)	217.9 (5)	Shibata and Nakashizuka (1995)
Carpinus laxiflora (W, N)	189.6 (5)	Shibata and Nakashizuka (1995)
Carpinus tschonoskii (W, N)	161.3 (5)	Shibata and Nakashizuka (1995)
Cassia desolata (A, D)	201.9 (9), 172.2 (9), 174.6 (8)	Davies (1976)
Cassia helmsii (A, D)	233.4 (9), 149.2 (9), 199.4 (9), 225.0 (8)	Davies (1976)
Cornus drummondii (A, E)	75.3 (4), 17.4 (4)	Willson and Whelan (1993), personal communication
Cornus sanguinea (A, E)	51.0 (5)	Guitián et al. (1996)
Crataegus monogyna (A, E)	60.8 (4), 88.5 (4)	J. Guitián, unpublished data
	140.3 (4), 99.4 (4)	P. Jordano, unpublished data
Dacrycarpus dacrydioides (W, E)	169.0 (7)	Kelly (1994), personal communication
Dacrydium cupressinum (W, E)	139.0 (33), 112.0 (11), 103.0 (7)	Kelly (1994), personal communication
Daphne gnidium (A, E)	103.6 (12)	Herrera (1998a)
Daphne laureola (A, E)	81.5 (4), 80.6 (4), 76.9 (4)	P. Jordano, unpublished data
Elaeocarpus dentatus (A, E)	76.0 (28)	Kelly (1994), personal communication
	65.4 (8), 85.7 (8)	Cowan and Waddington 1990
Encephalartos altensteinii (A, D)	144.3 (4), 123.1 (4), 136.0 (4), 180.9 (4)	Donaldson (1993)
Encephalartos caffer (A, D)	166.4 (4)	Donaldson (1993)
Encephalartos friderici-guilielmi (A, D)	111.4 (4), 101.6 (4)	Donaldson (1993)
Encephalartos horridus (A, D)	127.3 (4)	Donaldson (1993)
Encephalartos lehmannii (A, D)	127.7 (4), 141.4 (4)	Donaldson (1993)

Species	CV (years of data)	Reference
Encephalartos longifolius (A, D)	181.5 (4), 88.8 (4)	Donaldson (1993)
Encephalartos trispinosus (A, D)	200.0 (4)	Donaldson (1993)
Encephalartos villosus (A, D)	133.6 (4), 171.7 (4)	Donaldson (1993)
Eucalyptus regnans (A, N)	206.0 (5), 202.7 (5), 173.2 (5)	Ashton (1975)
Fagus grandifolia (W, D)	123.8 (10)	Gysel (1971)
Fagus sylvatica (W, D)	159.4 (9)	Nielsen (1977)
Faramea occidentalis (A, E)	69.8 (4)	Schupp (1990)
Fraxinus excelsior (W, N)	229.2 (11)	Flowerdew and Gardner (1978)
	69.9 (11)	Tapper (1996)
	50.2 (6), 88.2 (6)	Tapper (1992)
Hymenaea courbaril (A, D)	97.2 (8), 112.7 (6), 84.8 (5), 167.0 (4)	Janzen (1978)
Ilex aquifolium (A, E)	81.7 (4)	J. R. Obeso, unpublished data
Ilex sp. (A, E)	40.7 (4)	Jones et al. (1994); R. H. Jones, personal communication
Juniperus communis (W, E)	126.5 (5), 97.7 (5), 141.8 (4)	Jordano (1993)
Juniperus oxycedrus (W, E)	152.5 (12)	Herrera (1998a)
	71.5 (5)	A. Traveset, unpublished data
Juniperus phoenicea (W, E)	108.4 (5)	A. Traveset, unpublished data
	166.6 (5), 134.8 (5)	Jordano (1993)
	145.2 (4), 164.0 (4)	P. Jordano, unpublished data
Juniperus sabina (W, E)	139.7 (5)	Jordano (1993)
	89.0 (4), 117.9 (4)	P. Jordano, unpublished data
Larix occidentalis (W, N)	168.0 (6)	Shearer (1960)*
Libocedrus decurrens (W, N)	84.0 (5)	Fowells and Schubert (1956), pp. 1–48*
Liquidambar styraciflua (W, N)	178.0 (4)	Jones et al. (1994); R. H. Jones, personal communication
Liriodendron tulipifera (A, N)	75.0 (4)	Jones et al. (1994); R. H. Jones, personal communication
Lonicera arborea (A, E)	62.4 (4), 113.5 (4), 36.9 (4)	P. Jordano, unpublished data
Lonicera splendida (A, E)	37.6 (4)	P. Jordano, unpublished data
Magnolia virginiana (A, E)	48.2 (4)	Jones et al. (1994); R. H. Jones, personal communication
Nothofagus fusca (W, N)	148.0 (16)	Kelly (1994), personal communication
Nothofagus menziesii (W, N)	163.0 (24), 128.0 (19)	Kelly (1994), personal communication
Nothofagus solandri (W, N)	171.0 (30), 177.0 (29), 151.0 (24), 212.0 (24)	Kelly (1994), personal communication
Nyssa aquatica (A, E)	65.0 (6)	Kelly (1994), personal communication
Nyssa sylvatica (A, E)	45.3 (4)	Jones et al. (1994); R. H. Jones, personal communication
Olea europaea (W, E)	219.7 (5)	A. Traveset, unpublished data
	157.8 (4)	J. Alcántara and P. Rey, unpublished data
Osyris quadripartita (A, E)	50.1 (4)	Herrera (1988)
Persea borbonia (A, E)	174.1 (4)	Jones et al. (1994); R. H. Jones, personal communication
Phillyrea angustifolia (W, E)	125.4 (5)	A. Traveset, unpublished data
Phillyrea latifolia (W, E)	210.8 (12)	Herrera (1998a)
	93.5 (5)	A. Traveset, unpublished data
Picea abies (W, N)	119.6 (9), 96.2 (9), 96.8 (9), 109.5 (9), 102.7 (9)	Hagner (1965)
	162.0 (9), 122.0 (9), 174.0 (9), 127.0 (8), 214.0 (8), 173.0 (8), 153.0 (8), 142.0 (6)	Sarvas (1968)*
Picea glauca (W, N)	124.8 (5)	Zasada et al. (1978)
	137.0 (10)	Kelly (1994), personal communication

588

Species	CV (years of data)	Reference
Pinus banksiana (W, N)	102.0 (5)	Kraft (1968)*
Pinus contorta (W, N)	71.0 (15), 94.0 (10)	Dahms and Barrett (1975), pp. 1–13*
Pinus edulis (W, D)	69.5 (10)	Forcella (1981)
Pinus lambertiana (W, N)	168.0 (13), 168.0 (6)	Fowells and Schubert (1956), pp. 1–48*
Pinus monticola (W, N)	94.0 (6)	Barnes et al. (1962), pp. 1–7*
Pinus palustris (W, N)	82.0 (10)	McLemore (1975), pp. 1–10*
Pinus ponderosa (W, N)	128.0 (12)	Dahms and Barrett (1975), pp. 1–13*
	93.0 (10)	Schubert (1970)†
	138.0 (8)	Shearer and Schmidt (1971)*
	153.0 (7)	Daubenmire (1960)
	132.2 (6)	Linhart and Mitton (1985)
	144.0 (6)	Larson and Schubert (1970), pp. 1–15*
	102.0 (5)	Fowells and Schubert (1956), pp. 1–48*
	118.1 (4), 181.8 (4), 89.6 (4), 78.2 (4)	Linhart (1988)
	84.1 (15)	Lester (1967)
Pinus resinosa (W, N)	82.4 (6), 67.3 (6), 66.9 (6), 71.3 (6), 90.4 (6), 92.4 (5), 61.3 (5), 95.9 (5)	Mattson (1971)
Pinus sylvestris (W, N)	58.7 (9), 56.7 (9), 63.6 (9), 41.7 (9), 57.5 (9)	Hagner (1965)
Pinus taeda (W, N)	92.0 (13)	Pomeroy and Korstian (1949)*
	59.0 (10)	Lotti (1956), pp. 1–2*
	78.0 (7), 66.4 (7), 78.0 (5)	Wenger (1957)
Pistacia lentiscus (W, E)	117.2 (12)	Herrera (1998*a*)
	59.0 (5)	A. Traveset, unpublished data
Pistacia terebinthus (W, E)	198.0 (12)	Herrera (1998*a*)
Podocarpus totara (W, E)	111.0 (7)	Kelly (1994), personal communication
Prumnopitys ferruginea (W, E)	38.0 (7)	Kelly (1994), personal communication
Prumnopitys taxifolia (W, E)	129.0 (7)	Kelly (1994), personal communication
Prunus mahaleb (A, E)	62.1 (8), 64.7 (4), 63.6 (4), 12.0 (4)	P. Jordano, unpublished data
	26.5 (4)	J. Guitián, unpublished data
Prunus prostrata (A, E)	27.4 (4)	P. Jordano, unpublished data
Pseudotsuga menziesii (W, N)	150.6 (27)	Eis et al. (1965)
	146.3 (8)	El-Kassaby and Barclay (1992)
	141.3 (6)	Gashwiler (1970)
	157.8 (6)	Gashwiler (1979)
	128.8 (6)	Hedlin (1964)
Quercus agrifolia (W, D)	118.8 (12)	Koenig et al. (1994)
Quercus alba (W, D)	146.2 (12)	Beck (1977)
	115.9 (8)	Sork et al. (1993)
	101.3 (7), 125.6 (7)	Downs and McQuilkin (1944)
	54.9 (6)	Christisen (1955)
	74.3 (5)	Goodrum et al. (1971)
	109.2 (4)	Farmer (1981)
	112.4 (4)	Feret et al. (1982)
Quercus borealis (W, D)	195.0 (7), 102.7 (7)	Downs and McQuilkin (1944)
Quercus cinerea (W, D)	51.9 (6)	Goodrum et al. (1971)
Quercus coccinea (W, D)	142.3 (12)	Beck (1977)
	104.5 (7), 164.2 (7)	Downs and McQuilkin (1944)
	212.2 (5)	Christisen (1955)
Quercus chapmanii (W, D)	98.1 (14)	DeGange et al. (1989)
Quercus chysolepis (W, D)	123.0 (12)	Koenig et al. (1994)
Quercus douglasii (W, D)	161.8 (12)	Koenig et al. (1994)
Quercus falcata (W, D)	132.9 (18)	Goodrum et al. (1971)

Table A1 (*Continued*)

Species	CV (years of data)	Reference
Quercus geminata (W, D)	74.8 (14)	DeGange et al. (1989)
Quercus ilex (W, D)	58.4 (5), 82.7 (5), 79.5 (5)	D. Siscart and J. Retana, unpublished data
Quercus inopina (W, D)	78.1 (14)	DeGange et al. (1989)
Quercus kelloggii (W, D)	157.4 (12)	Koenig et al. (1994)
Quercus lobata (W, D)	147.8 (12)	Koenig et al. (1994)
	101.4 (5)	Griffin (1976)
Quercus marilandica (W, D)	107.1 (18)	Goodrum et al. (1971)
	73.5 (6)	Christisen (1955)
Quercus montana (W, D)	153.7 (7), 90.4 (7)	Downs and McQuilkin (1944)
Quercus nigra (W, D)	61.7 (6)	Goodrum et al. (1971)
Quercus prinus (W, D)	224.4 (12)	Beck (1977)
	57.2 (4)	Goodrum et al. (1971)
Quercus robur (W, D)	81.0 (15)	Crawley and Long (1995)
Quercus rubra (W, D)	152.7 (12)	Beck (1977)
	123.9 (8)	Sork et al. (1993)
Quercus stellata (W, D)	100.0 (18)	Goodrum et al. (1971)
	21.9 (6)	Christisen (1955)
Quercus velutina (W, D)	98.7 (12)	Beck (1977)
	92.7 (8)	Sork et al. (1993)
	90.9 (7), 85.9 (7)	Downs and McQuilkin (1944)
	97.4 (6)	Christisen (1955)
Rhamnus legionensis (A, E)	74.0 (6)	P. Guitián and J. Guitián, unpublished data
Rhamnus myrtifolius (A, E)	74.4 (4)	P. Jordano, unpublished data
Rhamnus saxatilis (A, E)	33.4 (4), 123.8 (4), 110.4 (4)	P. Jordano, unpublished data
Rhopalostylis sapida (A, E)	48.0 (7), 64.0 (5)	Kelly (1994), personal communication
Rhus radicans (W, E)	45.5 (4)	Jones et al. (1994); R. H. Jones, personal communication
Rosa canina (A, E)	51.4 (12)	Herrera (1998a)
	28.6 (4), 19.7 (4), 30.3 (4)	P. Jordano, unpublished data
Rosa sicula (A, E)	30.0 (4)	P. Jordano, unpublished data
Rosa sp. (A, E)	76.6 (4)	J. Guitián, unpublished data
Rubia peregrina (A, E)	115.9 (12)	Herrera (1998a)
	137.1 (5)	A. Traveset, unpublished data
Rubus chamaemorus (A, E)	148.0 (6), 112.9 (6), 46.6 (6), 59.0 (6)	Ågren (1988)
Rubus sp. (A, E)	178.4 (4)	J. Guitián, unpublished data
Rubus ulmifolius (A, E)	106.6 (12)	Herrera (1998a)
Smilax aspera (A, E)	186.8 (12)	Herrera (1998a)
Sorbus aria (A, E)	40.4 (4)	P. Jordano, unpublished data
Sorbus aucuparia (A, E)	115.5 (8), 144.9 (4)	J. Guitián, unpublished data
	145.4 (7), 132.0 (7), 85.2 (7), 110.4 (7), 213.5 (7), 132.2 (6), 132.9 (5), 151.1 (5)	U. Sperens, unpublished data
Taxodium distichium (W, N)	84.0 (6)	Kelly (1994), personal communication
Thuja plicata (W, N)	111.8 (6)	Gashwiler (1970)
Tsuga heterophylla (W, N)	98.6 (6), 118.4 (6)	Gashwiler (1970)
Vaccinium corymbosum (A, E)	54.4 (4)	Vander Kloet and Cabilio (1984)
Vaccinium myrtillus (A, E)	73.8 (6)	Laine (1978)
Viburnum tinus (A, E)	93.0 (12)	Herrera (1998a)
Virola surinamensis (A, E)	58.6 (5)	Howe (1986)
Viscum album (W, E)	19.9 (4)	P. Jordano, unpublished data

Note: The pair of letters in parentheses following species names denote, respectively, pollination (W = wind pollinated, A = animal pollinated) and seed dispersal (D = dyszoochorous, E = endozoochorous, N = nonzoochorous) categories. CV = 100 × coefficient of variation of seed output among years. Years of data = number of years on which the computation of CV is based.

* As cited in Silvertown (1980).

† As cited in Silvertown (1980), full reference not available.

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