Modelling the temporal variation in the seed production of North American trees

D.F. Greene and E.A. Johnson

Abstract: Many aspects of temporal variation in tree seed production (e.g., the probability distribution, periodicity, unimodality) are poorly understood. In this paper, we used 32 annual seed production records from 22 species to show that there are no discernible endogenous cycles, and there is a modest (but seldom significant) tendency for a high seed production year to be followed by an unusually low production year. Finally, we found that all of the records conformed to a single lognormal probability distribution, although our ability to discriminate among species, given short and extremely variable records, is admittedly very limited. We used the lognormal to develop the distribution of the sums of local seed production events (summed across 4 years) as an aid in predicting postharvest or postfire tree regeneration success. Our conclusion is that reliable (defined as 90% of the time) adequate stocking at the edge of an area source requires that the species of interest must comprise a very large fraction of the total basal area per area. Indeed, if the species constitutes less than about 50% of the source, neither burns nor even very narrow strip cuts will be reliably stocked.

Résumé: Plusieurs aspects de la variation temporelle de la production semencière des arbres (distribution de probabilité, périodicité, caractère unimodal) sont peu connus. Dans cet article, les auteurs utilisent 32 relevés de production annuelle de semences provenant de 22 espèces afin de démontrer l’absence de cycle endogène décelable et une tendance modeste (rarement significative) pour qu’une année de production abondante suive une année de production anormalement faible. Enfin, les auteurs ont constaté que tous les relevés avaient une distribution de probabilité log-normale unique, bien que la capacité de discriminer entre les espèces soit très limitée, compte tenu de la courte durée et de la forte variabilité des relevés. La distribution log-normale a été utilisée pour calculer la distribution des sommes des productions semencières locales (sommaton sur 4 ans) en vue d’aider à prédire le succès de régénération après coupe ou feu. Les auteurs concluent que l’espèce considérée doit constituer une proportion très importante de la surface terrière totale pour être sûr (90% des cas) d’obtenir une distribution adéquate. En fait, il y a peu de chances d’obtenir une distribution de la régénération dans les brûlis ou même les coupes par bandes très étroites si l’espèce représente moins d’environ 50% de la source.

Introduction

Even where seed sources are ample and distances are small, postdisturbance sexual recruitment in a cut or a natural burn tends to be unreliable for species lacking an aerial seed bank (Greene et al. 1999; Coates et al. 1994; Peters 2002). The two major sources of variation are the variation in juvenile survivorship (especially fluctuations in granivore density and in summer precipitation) and the variation in seed supply. Here, we will focus on this latter factor.

Across an interval of several years most (but not all) tree species appear to produce many more very small crops than they do very large crops, and this has traditionally been referred to as masting. A further commonly observed attribute is spatial synchronicity of crop production schedules among most reproductive adults in a population (“normal masting” according to Kelly 1994) or, more rarely, all of the members (“strict masting” according to Kelly 1994). Nonetheless, there is at present no agreement on a quantification of the term “masting” (e.g., Silvertown 1980; Janzen 1976; Kelly 1994) or on a division between “masting” and “nonmasting” species. In this paper we will avoid using the term.

The main control (but hardly the only one) on the final crop size appears to be weather at the time of reproductive bud differentiation (Owens 1969). In particular, dry, warm weather at the time of differentiation is the main determinant of final crop size (e.g., Eis 1973; Piovesan and Adams 2001; Lester 1967) for both hardwoods and conifers. Nonetheless, this factor typically explains by itself only about 25% of the variance in a long production record (e.g., Eis 1976). Subsequent losses are due to factors such as humidity levels during pollination and preabscission granivory (Owens and Blake 1985). An additional factor is the negative effect of the size of the current crop on the size of the subsequent crop, presumably because of resource depletion (Piovesan and Adams 2001).

Koenig and Knops (2000), using ordinal scale measures (“bumper” crop, medium crop, failure, etc.), have shown that...
individual population seed crop records are not bimodal but continuous. By contrast, Herrera et al. (1998), using interval scale data from individual records for woody plants, argued that records were bimodal: the typical species produced a peak of very small crops but another peak of very large crops. In particular, Herrera et al. (1998) showed that the individual distribution cannot be lognormal (unimodal and right skewed). In this paper, our primary objective is to model the variation in seed production as a lognormal process with random draws on short records. Thus, clearly our intention is to test the conclusion of Herrera et al. (1998). We will examine the fit of a large number of production records to this model and then test for differences among species. In addition, we feel obligated to examine two other issues that could have bearing on the shape of the probability distribution.

The first issue is cycling. Many authors have argued for species-specific, reasonably dependable intervals between “mast” (big) crop years (cf. Young and Young (1992) for a number of examples), but only Sork et al. (1993) have provided statistical evidence. We will show that neither our nor their (three Quercus species) records show evidence of cycling. The second issue involves the common assertion that large-magnitude seed crops are invariably followed by very small seed crops, perhaps because of resource depletion by the maturing large crop at the time of differentiation of the following year bud crop (e.g., Coates et al. 1994; Owens and Blake 1985; Provesan and Adams 2001). A contrary argument would be that small crops are the norm for strongly skewed seed production distributions. That is, a large crop is typically followed by a small crop.

**Methods and model**

**Selection of seed production studies**

Examination of the literature uncovered over 100 studies of seed or cone production by North American tree species. We narrowed this list down to 32 records on 22 species using the following criteria. First, the record length had to be at least 7 consecutive years to minimize the possibility that not a single very large crop had been recorded. (Previous analyses have been less restrictive in their selection, e.g., Herrera et al. (1998) used any record greater than 3 years.) Second, the study (seed trap studies, in particular) could not have more than 50% of the years with zero apparent production. We assumed that such records indicated a total trap area that was too small relative to the basal area per area of the species of interest and thus would spuriously amplify the coefficient of variation of the crop production record. Third, the maximum absolute number of seeds trapped or cones counted in a single year had to be at least 100. So, for example, the 11-year record for Fagus grandifolia Ehrh. of Graber and Leak (1992) could not be used, as the highest total number of seeds that they trapped was eight in a single year. Finally, for consistency, the measure of central tendency in the study had to be the mean annual crop size. Thus, for example, the cone surveys of Franklin et al. (1974) could not be used, as they provided only the median crop sizes.

All of the records in Table 1 are based on populations rather than individuals. Twenty of the records are derived from seed trap studies, seven are population means on ovulate cone counts on individual trees, and five are population means for fruit counts on individual trees of various Quercus species. Almost all of the records represent averages across more than one stand. However, only one of our studies (Alexander et al. 1982) is drawn from a very wide range of elevations (3000–3800 m above sea level).

**Model**

Annual seed production appears to be determined by a sequence of factors each of which reduces the final number of seeds. The life history sequence begins with bud differentiation and ends with seed abscission. Here we use the lognormal distribution as a heuristic model of this multiplicative process. That is, a sequence of stage-specific survivorship values should lead to a record of final crop sizes that are right skewed and can perhaps be tolerably modelled as a lognormal.

The lognormal probability density distribution (Zar 1999) is

\[ f(Q) = \frac{1}{\sqrt{2\pi} \sigma Q} \exp\left\{\frac{1}{2} \left(\frac{\ln Q - \ln \bar{Q}_s}{\sigma}\right)^2\right\} \]

where \( f(Q) \) is the probability of \( Q \) reproductive units per year (multiseeded fruits, ovulate cones, single seeds, etc.), \( \sigma \) is the standard deviation of the logarithm of reproductive units per year, and \( \bar{Q}_s \) is the mean of the logarithms of the reproductive units; \( \bar{Q}_s \) and \( \sigma \) are estimated with the usual maximum likelihood estimation for a Gaussian distribution and are uniform, minimum variance, unbiased estimators. When any record had a value of \( Q = 0 \) for any year, every annual value in that record was increased by the smallest possible value. For example, if a study used 10 seed traps each of 2 m², then the smallest possible annual value would be 1 seed per 20 m² = 0.05.

**Statistical analyses**

In what follows, we will test the null hypothesis that there is no significant difference in the magnitude of the temporal variation among species and thus, \( \sigma \) is a constant. We will assume that \( \sigma = 2.06 \) (a value derived as the midpoint of the nine records in Table 1 that are longer than 20 years). (Note that these longer records tend to be more variable than the shorter records in Table 1. We choose them because they are more likely to reveal any effects of postcrop depression.) Any measure of central tendency in seed crop size (e.g., mean or median) will vary interspecifically because of differences in individual seed mass and will vary intraspecifically because of differences in tree size or (for seed trap studies) density of conspecifics (Greene and Johnson 1994). Consequently, to make species comparable, we standardize by using \( Q/\bar{Q}_s \) where \( \bar{Q}_s \) is the best estimate of the median (i.e., \( \bar{Q}_s \) is the exponential of the mean of the logarithms). Likewise, for graphical presentation, differences in record length (\( N \)) are normalized by ordering the \( i \)th years of a record from the largest (\( i = 1 \)) to smallest (\( i = N \)) crop size and expressed as \( d/N \).

**Detecting cyclic crop production**

To examine the contention of Sork et al. (1993) for statistically discernable cycles among tree species, let us initially adopt their method. They argued that, using the arithmetic values from what is clearly a right-skewed distribution, the
highest positive (and significant) Pearson product moment correlation coefficient at a specified lag (cycle length) indicates the apparent cycle. As in Sork et al. (1993), we will only examine the lags of 2, 3, or 4 years. (One could examine longer lags for the longer records in Table 1, but our main point here is to show the problems with the approach of Sork et al. (1993).) Unlike Sork et al. (1993), however, we will argue that the degrees of freedom should be based on the record length rather than on the product of the total number of trees and the record length (because the production by individual trees is well correlated in time).

One might expect that random draws of $Q$ (seed years) from eq. 1 would, at a significance level of 0.05, give significant positive correlations with lagged $Q$ values 7.5% of the time (because we have three chances) and would do so irrespective of either the lag or $N$. This is not the case. The probability of attaining a significant positive correlation declines with $N$ from 0.272 when $N = 7$ to 0.081 when $N = 33$. Further, the probability of a positive significant correlation is greater at a larger lag ($L$) when $N$ is small, e.g., when $N = 7$, the probability is five times greater for $L = 4$ than for $L = 2$. By $N = 20$, there is little difference in the probability of a significant correlation for any of the three lags. The reason for these results from the random draws is that we are working with right-skewed distributions. Imagine a record with $N = 7$ where there are two large seed production values ($Q$) and the rest are much smaller. If the two largest values happen to be located at position $i = (1, 5)$ or $(2, 6)$ or $(3, 7)$, then we will assuredly obtain a significant positive correlation at $L = 4$. By contrast, at $L = 2$, it becomes more unlikely that the two largest $Q$ values will not be paired on either side by low $Q$ values. This effect of the skewed distribution (i.e., the effect of having violated the underlying Gaussian assumption of the correlation analysis) has virtually disappeared by $N = 20$ when we consider only modest lags.

### Depression of a subsequent crop by a current large crop

Imagine that a large crop depresses the size of the next crop and that the magnitude of the decrease is proportional to the size of the current crop. This strict resource depletion

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Table 1. The 32 data sets used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>$N$</th>
<th>$\sigma_k$</th>
<th>$CV_Q$</th>
<th>Measurement</th>
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<td>2.0</td>
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<td>1</td>
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<tr>
<td></td>
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<td>2.14</td>
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<tr>
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<td>Eis 1973</td>
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<td>2.41</td>
<td>1.65</td>
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<td>Pinus taeda</td>
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<td>Abies grandis</td>
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<td></td>
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<td>1.43</td>
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<tr>
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<td>1.79</td>
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<td>1.10</td>
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<tr>
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<td>1.29</td>
<td>1.14</td>
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<td></td>
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<td>1.89</td>
<td>1.14</td>
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<td>Quercus coccinea</td>
<td>Downs and McQuilken 1944</td>
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<td>1.54</td>
<td>1.20</td>
<td>2</td>
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<td>7</td>
<td>1.61</td>
<td>0.85</td>
<td>2</td>
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<td>Koenig et al. 1994</td>
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<td>1.44</td>
<td>1.43</td>
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<tr>
<td>Quercus douglasii</td>
<td>Koenig et al. 1994</td>
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<td>1.39</td>
<td>1.58</td>
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<td>Quercus kelloggii</td>
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<td>2.19</td>
<td>1.51</td>
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</tbody>
</table>

Note: The first 14 studies are for conifers, while the remaining 18 studies are for hardwoods. $N$ is the record length (years), $\sigma_k$ is the standard deviation of the logarithms of the crop values, $CV_Q$ is the coefficient of variation of the arithmetic crop values, and measurement indicates the way in which the crop size was measured (1 = filled seeds in traps, 2 = filled plus hollow or predated seeds in traps, 3 = ovulate cone counts with binoculars, and 4 = acorn counts estimated with binoculars that include both filled and hollow acorns).
argument, if true, ought to lead to a significant negative correlation (at $L = 1$ as in the preceding analysis) regardless of whether the species has a 2-year or 3-year reproductive schedule. We will examine the effect of a prior crop on a subsequent crop in two ways. First, we will examine the effect of the single biggest crop ($Q_{\text{max}}$) in a record on the next crop. Second, we will calculate Spearman rank correlations at a lag of 1 year for entire records.

Four of the 32 data sets have the largest crop in the final year of the record (three are from Downs and McQuilken (1944) and one from Reukema (1961)). For the remaining 28 data sets, we adopt the null expectation that the year subsequent to the biggest crop ($Q_{\text{max}}$) will be unaffected by the previous reproductive allocation. That is, the year after the biggest crop should have, in terms of the ordered $i$, an expected value of $i = 0.5N + 1$.

**Results and discussion**

**Skew**

All of our 32 records (Table 1) are right-skewed since the arithmetic means are greater than the median. The coefficients of variation $\text{CV}_Q = \sigma/Q$ (where the standard deviation and mean are now derived from the arithmetic values) are between 0.95 and 2.88 with average of 1.37. (Note that if the records could be well expressed by a Poisson distribution, then the $\text{CV}_Q$ values should be near 1.0.) These $\text{CV}_Q$ values, a measure of the temporal variation in crop size, are similar to other middle- and high-latitude values (Koenig and Knops 2000) but tend to be a good deal higher than those reported by Herrera et al. (1998) in their study of trees and shrubs.

Typically, with our seed trap studies, the zero values constitute about 20% of the records, while the studies based on cone counts or *Quercus* fruit counts show a much smaller percentage of zero values. We assume therefore that the great majority of the zero values from the seed trap studies simply represent insufficient total trap area.

**Comparison with the lognormal model**

We tested the hypothesis that none of the observed $\sigma_k$ values in Table 1 were significantly different from the assumed value of 2.06. Only two of the 32 studies (*Pinus resinosa* Ait., which is too low, and *Picea glauca* (Moench) Voss, which is too high) are significantly different ($\chi^2$, $p < 0.05$) (Zar 1999). We might have expected 1 (3%) or 2 (6%) exceptions out of 32 cases if the null hypothesis was correct.

Figures 1a, 1b, and 1c show the observed ordered records for, respectively, $N = 7$ or 8, $N = 10, 11, 12, 15, 20$, years. In this figure, the 95% confidence intervals were generated from eq. 1 with $\sigma_k = 2.06$ and 1000 trials with $N$ random draws of $N = 8, N = 11$, and $N = 24$ (for Figs. 1a, 1b, and 1c, respectively). About 8% of the observed nonzero values lie outside the 95% confidence intervals. There are a number of possibilities for this deviation from the model. First and foremost, of course, there may simply be significant differences among the species (examined below). Second, as we will show later, there is some tendency for a large crop to depress the size of a subsequent crop (note how few observations lie outside the confidence intervals for the larger production years in Fig. 1). Finally, it is the longer records that show a higher proportion of observations outside the confidence intervals and we must remind ourselves that the central tendency (the median crop size) is not static but must be increasing with time as the trees grow (i.e., individual seed production is proportional to individual basal area; Greene and Johnson 1994). Incorporation of these latter two factors (autocorrelation at a lag of 1 year and growth of trees) in a simulation would certainly widen the confidence intervals in Fig. 1.

Some of our studies are for total seeds (hollow as well as filled) in traps or cone–acorn counts (some of the acorns of course may be hollow), while others are for filled seeds only (traps). As it is well known, at least for conifers, that the proportion of filled seeds to total seeds tends to increase with seed number (e.g., Alexander et al. 1982), one wonders what effect this might have on our variability measure. With the six species (Table 1) of MacDonald (1992), Graber and Leak (1992), and Alexander et al. (1982), the net effect of switching from total seed counts to filled seed counts is only a moderate steepening of their original slopes in Fig. 1. There is, on average for these six species, an increase in the $\text{CV}_Q$ of 20%. The largest relative crop sizes are little affected (e.g., the maximum relative seed production ($Q/\bar{Q}$) for MacDonald’s (1992) *Abies grandis* (Doug. ex D. Don) Lindl. would only increase from 36 to 39 as we switch from all seeds (filled plus empty) to filled seeds only, but the smaller crop sizes are dramatically affected as the proportion filled drops from well over 75% for large crops to virtually 0% filled for tiny crops.

Herrera et al. (1998) argued that their records for shrub and tree species were not lognormally distributed; indeed, they tended to be bimodal with a surfeit of very small and very large crop sizes. Here, we imitate their procedure to test their conclusion. First, each record was standardized in a logarithmic form as $(\ln Q - \bar{Q_k})/\sigma_k$ so that now, $\bar{Q_k} = 0$ and $\sigma_k = 1$ for each of the standardized records. (Recall from the Methods and model section that $\bar{Q_k}$ and $\sigma_k$ are the mean and the standard deviation of the logarithms of the $Q$ values within a record.) Then, the records were pooled.

Our pooled standardized records (Fig. 2) were, like those of Herrera et al. (1998), seemingly bimodal. One of our modes (as with them) is clearly negative. That particular outcome, however, is merely a consequence of our treatment of the original arithmetic zero values. Consider our two longest records ($N = 37$ for the *A. grandis* and *Pseudotsuga menziesii* (Mirb.) Franco of Eis 1973), which have 12 or 15 zero values, respectively. As discussed in the Methods and model section, we assigned the zero values the smallest possible nonzero value given the trap area available (i.e., a single seed is captured). But all of the zeroes within a particular record were given that same value. Now, since the zero values are primarily in the long records, and given that there are only a few long records, it should not be surprising that the left side (the negative half) of Fig. 2 looks much less smooth than the right half. In effect, one cell received a surplus of these transformed zero values, while a nearby cell was relatively impoverished.

It is likely that this is the explanation as well for the negative mode seen by Herrera et al. (1998). While they were forced, like us, to deal with zero values, they do not mention in their paper how they did this. In any case, it does not matter, as whatever approach they used (e.g., assigning a value
Fig. 1. (a) Ordered records from Table 1 as a log–log plot with $N = 7$ or 8 years. The axes show $Q/Q_g$ versus $i/N$ where $Q$ is a crop size, $Q_g$ is the geometric mean (exponential of the mean of the logarithms) crop size in a record, $i$ is an ordered year ($i = 1$ is the biggest crop), and $N$ is the record length (years). (We underline that the $x$ axis does not show the actual calendar sequence.) The curves represent the expectation 95% confidence limits generated from 1000 trials with eight random draws ($N = 8$) on a lognormal distribution with $σ_k = 2.06$. Zero values cannot of course be plotted. Individual records are denoted by their binomial acronyms (from Table 1) and the $N$. (b) As for Fig. 1a but for $N = 10, 11, 12$, and the single record with $N = 15$. The confidence interval is based on random draws with $N = 11$. (c) As for Fig. 1a but for $N > 20$. The confidence interval is based on $N = 24$. 
of 1 to all zeroes), they will end with a set of negative values looking much like our result in Fig. 2.

Our second peak in Fig. 2 was exactly where it ought to be if the underlying distribution was lognormal: at around zero for the standardized log values. Indeed, the right half of the histogram (from zero onward) is indistinguishable from a normal distribution (Kolmogorov–Smirnov test, \( p > 0.05 \)). (Note that the logs of a lognormal distribution will be normally distributed.) Thus, we conclude that most or all of our pooled records are drawn from a lognormal, but the fit for the smallest values is poor because of the manner in which we dealt with the large number of arithmetic zero values.

But how can we explain the other finding of Herrera et al. (1998): their second mode is far from zero on a graph such as our Fig. 2; it is decidedly positive. We think the reason is that our mean \( CV_Q \) is much closer to ours.) Most of these shrub species have short records (\( N = 4–6 \)) and are unpublished. One can find no differences in the \( CV_Q \) values of the four Pseudotsuga menziesii values among conspecific records as among the entire set of records in Table 1. The extremes of the \( CV_Q \) values of the four Pseudotsuga menziesii values include about two thirds of the remaining records. In general, then, there appears to be almost as much variation among conspecific records as among the entire set of records in Table 1.

Even a single species in one landscape can show a large range of values among populations for some measure of temporal variation such as \( CV_Q \). Alexander et al. (1982) provided contemporaneous production records (\( N = 10 \)) for 13 stands of *Picea engelmannii* Pary ex Engelm. on varying aspects, slope angles, and elevations in the central Rocky Mountains. The stands are within 70 km of one another. While the stands range in altitude from 3.05 to 3.80 km above sea level, nonetheless there is no significant correlation between altitude and a variation measure such as \( CV_Q \) (\( p > 0.05 \)). Further, the crop production of the 13 stands was highly synchronized (Kendall’s coefficient of concordance, \( p < 0.001 \)). Here, at least, we might expect some uniformity in the 13 records and, indeed, we find that 12 of 13 stands had their biggest crop in the same year (1977) (this was the second biggest year for a single stand). But the range of \( CV_Q \) values among the 13 stands would include about 40% of the values in Table 1.

In summary, we can draw no conclusions about the characteristic differences in the temporal variation (measured as \( CV_Q \)) among species. Whatever differences might exist are presently undetectable, as they are swamped by the tremendous variation within records and even among conspecific records of nearby stands. Likewise, we cannot detect a significant difference at the level of the genus. Inspection of the *Quercus* values in Table 1 indicates that they tend to be less variable than the non-*Quercus* species values. Nonetheless, the 13 *Quercus* species are not significantly less variable than the 19 non-*Quercus* species (Mann–Whitney test using the \( CV_Q \) values in Table 1, \( p > 0.05 \)).

In conclusion, these skewed records for trees appear to be lognormally distributed. We can find no differences in the value of \( CV_Q \) among our tree species. (The shrubs of Herrera et al. (1998), however, are clearly less variable than their trees.) Finally, like Koenig and Knops (2000) but unlike Herrera et al. (1998), we see no evidence for bimodality. In what follows, we will argue that temporal variation in seed production is approximated by a lognormal distribution (eq. 1 with \( k = 2.06 \)) for all species. Assuming a constant \( k \) is, at worst, a relatively minor error given the remarkable variation within and among intra- or interspecific records.

**Cycles**

We argue here that there is no statistically compelling evidence for cycles in any published record. Using the method of Sork et al. (1993) (discussed in detail in our Methods and section), we obtained three significant positive correlations from the studies in Table 1. All three species were from Downs and McQuilken (1944) (\( N = 7 \)): *Quercus rubra L.*, *Quercus velutina* Lam., and *Quercus coccinea* Muenchh.). These three records have their highest seed production in the final year of their records, where they cannot be subsequently paired with a further seed production value. The random draws from the lognormal distribution (wei-

**Fig. 2.** Histogram of the pooled standardized logarithms of the values in the records in Table 1.
ghted by the $N$ values of our observed records in Table 1) indicate that we should have 3.5 significant positive correlations (observed = 3) if there is no real cyclic behavior in any of the records. Further, the lognormal expectation was that 52% of the significant positive correlations should have a lag ($L$) of 4 (observed = 3 of 3) and 30% should be $L = 3$ (observed = 0).

The three Quercus species of Sork et al. (1993) were also studied in the earlier publication of Downs and McQuilken (1944). Sork et al. (1993) concluded that the predictable cycles (highest positive correlation, and with degrees of freedom based on the number of trees and record length; see Methods and moddr) were $L = 2$ for Q. velutina, $L = 3$ for Quercus alba L., and $L = 4$ for Q. rubra. By contrast, applying their method (with the inflated degrees of freedom) to these three species for Downs and McQuilken (1944) shows that the highest positive correlation is achieved at $L = 4$ for all three species (two of these are significant). It is interesting to compare these Quercus results with the generalizations from the secondary forest ecology literature. Young and Young (1992) (formerly Schopmeyer 1974) reported “typical masting intervals” for these three species as 2–3 years (Q. velutina), 3–5 years (Q. rubra), and 4–10 years (Q. alba). Owens and Blake (1985, p. 20) referred to Q. alba as “a consistently good seed producer.” It appears to us that these statements about typical masting intervals, so common in the secondary literature, are misleading generalizations from short records.

We can avoid these problems when using right-skewed data by calculating the Spearman rank correlation coefficient (a nonparametric measure). Using this correlation coefficient, only one of the 32 data sets had a significant positive rank correlation, F. grandifolia (Gysel 1971) ($\alpha < 0.05$ at $L = 2$). As we evaluated 32 data sets for three possible lags at 95% confidence, we expected about two significant (but spurious) positive correlations (observed = 1) even if the records were uncorrelated in time. Note that none of the Quercus records showed significant cycles with this nonparametric test and none of the records with $N > 10$ showed any significant cycles.

As another example from the primary literature of erroneously assuming periodicity within a record, Caron and Powell (1989) argued for a 2-year interval in Picea mariana (Mill.) BSP, but they made no statistical test. A Spearman rank test revealed no significant lag at 2, 3, or 4 years ($p < 0.05$).

To summarize, the method of Sork et al. (1993) (but without inflation of the degrees of freedom) gave results that were indistinguishable from random draws on a noncyclic lognormal record (with $\sigma_s = 2.06$), and the more statistically correct approach (Spearman rank correlation) likewise cannot discern cyclic behavior. Different studies on Quercus species indicate the same result: cycles inferred from short records on the same species differ from one study to another.

We see no support for statistically discernable short cycles in the studies assembled in Table 1. (It is certainly possible that cycles exist at much longer lags.)

Depression of the subsequent crop by a very large crop

Ignoring the four data sets where the largest crop occurred in the final record year (see Methods and model section), 17 of the 28 records had post-$Q_{\text{max}}$ crops with $i/(0.5N + 1) > 1.0$, i.e., they had crops that were smaller than the record median. We expected 14. The lower confidence interval ($\alpha = 0.05$) on the proportion (17/28) included 14. In short, there was a (barely) insignificant tendency for the subsequent year to yield an unexpectedly small crop. Small crops typically follow very large crops because small crops are the norm.

It might be argued that the Pinus species in Table 1 with their 3-year reproductive schedule (i.e., the interval from bud differentiation to seed maturation) should not be mixed with the non-Pinus 2-year schedule species. Of six Pinus records in Table 1, two had their maximum crop in the second to last year. Of the remaining records, two of four show an unexpectedly small crop 2 years after the largest crop. That is, there is no hint that seed maturation of a large crop is seriously impacting bud differentiation in the 3-year Pinus species.

A second way to see the effect of resource depletion is to examine the entire record at a lag of 1. Unlike other authors such as Koenig and Knops (2000), we will only use the nonparametric Spearman rank correlation. For our 32 data sets, 25 showed negative correlations. Of these, only 10 were significantly negative (one-tailed, $p < 0.05$). Perhaps more cogently, of our nine longest records ($N > 20$), only four yielded a significant negative correlation (but none were significantly positive).

In conclusion, there is some tendency for a large crop to depress the size of the subsequent crop (we have a surfeit of negative correlations, and the uncommon significant correlations are never positive), but this effect is not strong. It typically accounts for less than 10% of the explained variance (judging from the values listed in Koenig and Knops 2000) and is therefore much less important than meteorological factors.

Summed seed supply over 4 years

Greene and Johnson (1994) have developed a predictive equation for the mean annual seed production of a tree ($Q$), which can be easily extrapolated to a stand as the mean deposited seed density. One might expect that the summation of the seed production ($Q$) over several years ($T$) would be

$$\sum Q \approx TQ$$

no matter what the probability distribution of $Q$ due to the central limit theorem. Unfortunately, for small-seeded species, the best upland postdisturbance seedbeds (typically mineral soil and humus produced by fire or scarification) do not remain receptive for more than about 4 years (Arlidge 1967; Greene et al. 1999; Zasada et al. 1987; note that all three studies are for Picea), i.e., the $T$ of interest is small. While we might expect that the receptive interval for a good seedbed will vary a great deal from one site to another (primarily as a function of the local rate of leaf litter aggradation), nonetheless, $T$ will typically be so small that we still expect a great deal of variation around the expected sum ($TQ$).

The probability of obtaining a certain sum of seeds over 4 years is intimately connected with the issue of reliability in regeneration management. Now, one might merely multiply the mean annual seed production of a population ($\overline{Q}$) by four times (as above with $T = 4$) to arrive at the mean total

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seed density. Consequently, this approach leads to a prediction that less than 50% of the treated blocks will receive adequate numbers of seeds to produce the tree density required for acceptable good stocking. This is because seed production distributions are, as we have seen, so strongly right-skewed; the mean value is almost eight times larger than the median value, and summing over 4 years is not sufficient to mute the variation.

We show this in Table 2 where the results of a simulation using eq. 1, \( \sigma = 2.06, \) and \( N = 12 \) are depicted. The 12 years from each of 1000 trials were divided into consecutive segments of 4 years each (i.e., \( T = 4 \) and we had 3000 data points). As expected from the central limit theorem, this additive process approaches a normal distribution of sums but is still somewhat right-skewed, with a median of 3.8, not 4.

In addition to the simulation results, Table 2 also shows the cumulative distribution of the seed production for the sum of 4 years for the pooled studies in Table 1. These 109 empirical quadruplets were arbitrarily begun in the first (oldest) year of each record. A record length not evenly divisible by 4 would have a remaining 1–3 years that were simply left out of the analysis. The agreement in Table 2 between expected and observed is very good (Kolmogorov–Smirnov test, \( p > 0.05 \)). Also shown in Table 2 are the observed quadruplets for our most commonly represented species in Ta-ble 1 (Pinus ponderosa (pp), and Pseudotsuga menziesii (pm) records, respectively, in Table 1.)

<table>
<thead>
<tr>
<th>( \sum Q / \overline{Q} )</th>
<th>0.33</th>
<th>0.43</th>
<th>0.50</th>
<th>0.71</th>
<th>1.48</th>
<th>2.29</th>
<th>2.88</th>
<th>3.48</th>
<th>4.17</th>
<th>4.82</th>
<th>5.62</th>
<th>6.45</th>
<th>8.00</th>
<th>8.65</th>
<th>9.1</th>
<th>9.6</th>
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<tr>
<td>cp pred</td>
<td>0.01</td>
<td>0.02</td>
<td>0.03</td>
<td>0.04</td>
<td>0.17</td>
<td>0.30</td>
<td>0.38</td>
<td>0.45</td>
<td>0.56</td>
<td>0.66</td>
<td>0.75</td>
<td>0.82</td>
<td>0.91</td>
<td>0.95</td>
<td>0.96</td>
<td>0.98</td>
</tr>
<tr>
<td>cp obs all</td>
<td>0.01</td>
<td>0.03</td>
<td>0.03</td>
<td>0.06</td>
<td>0.16</td>
<td>0.29</td>
<td>0.38</td>
<td>0.48</td>
<td>0.58</td>
<td>0.64</td>
<td>0.72</td>
<td>0.82</td>
<td>0.94</td>
<td>0.97</td>
<td>0.97</td>
<td>0.98</td>
</tr>
<tr>
<td>cp obs ag</td>
<td>0.04</td>
<td>0.14</td>
<td>0.41</td>
<td>0.55</td>
<td>0.68</td>
<td>0.73</td>
<td>0.81</td>
<td>0.91</td>
<td>0.95</td>
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<tr>
<td>cp obs pp</td>
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<td>0.31</td>
<td>0.61</td>
<td>0.69</td>
<td>0.69</td>
<td>0.85</td>
<td>0.92</td>
<td>1.0</td>
<td></td>
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<td></td>
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<tr>
<td>cp obs pm</td>
<td>0</td>
<td>0.17</td>
<td>0.55</td>
<td>0.61</td>
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<td>0.72</td>
<td>0.78</td>
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</tr>
</tbody>
</table>

Note: The top row of values provides the \( \sum Q / \overline{Q} \) values. In the second row is the predicted (pred) cp for a simulation with 3000 summed quadruplets (see text). The third row shows the 109 observed (obs) summed quadruplets from the pooled records in Table 1 (= “all”). The final three rows show the 22, 18, or 13 summed quadruplets for all of the Abies grandis (ag), Pinus ponderosa (pp), and Pseudotsuga menziesii (pm) records, respectively, in Table 1.

An application with parallel strip cuts

In the following calculations, we will demand reliable seed establishment that compares favorably with contemporary planting operations: 90%. That is, we expect that postharvest sexual recruitment will be successful in 90 of 100 harvest blocks. Assuming that we can sum the seed production of 4 consecutive years (as above), then, from Table 2, we see that this requires that we must have \( \sum Q / \overline{Q} > 1.0 \). That is, we need to find (or create via a prescription) a situation in the harvest block where adequate regeneration can occur with as little as 25% of the expected long-term production over 4 years.

Modifying the model of Greene (2000) as a summation across 4 years, we will model recruitment by small-seeded species (Picea, Betula, Tsuga, etc.) into a set of parallel strip cuts as

\[
F_{Dx} = 1533B_D m^{0.58} S \left( \sum Q / \overline{Q} \right) \exp(-0.015x_{max}/2)
\]

where \( F_{Dx} \) is the seedling density (number per square metre) at distance \( x \) (metres), \( B_D \) is the basal area (square metres) per area (square metres) and is directly proportional to the mean seed production, \( m \) is the seed mass (grams), \( x_{max} \) is the cut width (metres), and \( S \) is the seedbed-mediated juvenile survivorship (strongly varying among seedbeds types but here averaged across all of these types). Note that for simplicity, the mortality due to granivores is assumed to be independent of seedbed type and is implicit in the \( S \) value. Also, again for simplicity, the survivorship is assumed to be constant for 4 years and then it abruptly declines to zero. (In truth, there would of course be a smoother decline as leaf litter aggrades.) Further, note that eq. 2 assumes that about half of the area consists of residual strips and that this halving of the source strength cancels the seed input from an opposite side.

The exponential expression is the dispersal term, and it follows from the argument of Greene and Johnson (1996) that a negative exponential decline is a tolerable statement of the observed dispersal from an extensive area source to distances less than about 200 m (but not beyond). The coefficient (0.015) in the dispersal term requires that the seed density at 200 m from an edge will be 5% of the edge seed density and this rate of decline will be roughly correct for small-seeded conifers with terminal velocities on the order of 0.60.9 m/s (cf. the empirical curves in Greene and Johnson (1996); other coefficients are available for particular larger-seeded species in that reference). We need now to average that dispersal term across a narrow strip cut and this can be done with little underestimation as

\[
\text{exp}(-0.015x_{max}/2)
\]

That is, we merely divide the cut width by 2.

The juvenile survivorship \( S \) of a cohort across the earliest 3 years (for each of the cohort, not the cut) can be estimated (Greene and Johnson 1998) as a function of seed mass (and thus germinant size) and the proportions of seedbeds that are optimal (minimal, thin humus, well-rotted logs, or Sphagnum) or poor (all others). With 17% (an estimate for typical scarification results in clearcuts in Ontario; Fleming et al. 1987) of the area as optimal seedbeds (very unlikely without scarification on an upland site), small-seeded species would have \( S = 0.02 \); with 5% optimal seedbeds (as if only rotted logs and skidding contributed in an upland site), then \( S = 0.007 \). We will use these two extremes for \( S \) in what follows.

Summarizing, the model proposes that the density of postharvest natural regeneration is primarily dependent on seed
production (a function of residual basal area per area), juvenile survivorship (a function of seedbeds), and dispersal (a function of cut width). There is, of course, abundant empirical evidence to support this contention (cf. reviews such as Coates et al. 1994; Greene et al. 1999).

Having established averages across a cut, we can rephrase eq. 2 as an average seedling density ($F_D$). For a small-seeded conifer with 0.0025 g for its seed mass (let us use *Picea glauca* as our example), we have

$$F_D = 990B_D \sum \frac{Q}{Q} \exp(-0.0075x_{\text{max}})$$

for 17% optimal seedbeds or

$$F_D = 347B_D \sum \frac{Q}{Q} \exp(-0.0075x_{\text{max}})$$

for 5% optimal seedbeds.

According to Greene et al. (2000), we require a mean recruitment density ($F_D$) of about 1 seedling/m² for 60% stocking with 4-m² sampling quadrats (the result is not greatly different if we use, for example, Alberta’s 10-m² quadrat but with 80% stocking). Thus, setting eqs. 3a and 3b equal to 1.0, and given that $\sum Q/Q$ needs to be at least 1.0 for 90% reliability (see above), we can solve for the relationship between $B_D$ (source basal area per area) and $x_{\text{max}}$ (cut width) (Fig. 3).

Let us interpret Fig. 3 in relation to a forest that had (all species lumped) a basal area (square metres) per area (square metres) of 0.003 (i.e., 30 m²/ha). With 17% optimal seedbeds (eq. 3a), this high reliability requires that the target species must have at least one third of the basal area (with $x_{\text{max}} = 0$). For a cut width of 50 m (typical of strip cuts; Greene 2000), the target species requires about half of the basal area. For a monoculture (i.e., all 30 m²/ha), the cut width cannot exceed 145 m. Obviously, one cannot obtain adequately stocking of strip cuts with locally rare species.

With only 5% optimal seedbeds (eq. 3b), the situation is of course much worse. Given that strip cuts are seldom scarified, this example is more interesting than the previous one. At a cut width of 0 m, the target species must comprise 96% of the basal area. The maximum width permitted for reliable regeneration for a monoculture would be a mere 5 m. It is therefore not surprising that almost no single species has ever been reliably regenerated with a strip cut prescription. The only exception to this generalization is *Picea mariana* in lowland sites. This is because (i) the proportion of optimal seedbeds can be quite high due to *Sphagnum* (Groot and Adams 1994), (ii) the receptivity of the *Sphagnum* is not limited to a short period, and (iii) this species often approaches a monoculture in lowlands. The other situation where unscarified strip cuts are reliably stocked is in the eastern hardwood forest where virtually all of the species are, presently, considered commercially valuable and there is a large supplement to the regeneration provided by asexual recruitment from stumps (Greene 2000).

The role of seed production variation in this constrained recruitment success is clear from inspection of eq. 3a or 3b. Pretend that seed production was invariant and the species always produced the same mean number of seeds. That is, now, $\sum Q/Q = 4.0$. The maximum cut width for a monoculture (30 m²/ha) with 5% optimal seedbeds would now be 190 m rather than 5 m. Thus, even the summing across 4 years has not sufficiently subdued the pernicious effect of temporal variation in crop production.

**An application with wildfire**

We can apply the approach used above for small-seeded species to wildfires if we can estimate the proportion of optimal seedbeds. To the best of our knowledge, the only studies to date that attempt to determine this value for an entire burn are those of Lutz (1956) and Noel (2001). For this latter study, the proportion of optimal seedbeds (in this case, surviving *Sphagnum*, mineral soil, and thin burnt humus) was about 15% in a 12 000 ha late-spring fire. This is similar to the 17% value used in Fig. 3, and thus, we will simply use eq. 3a.

As before (Fig. 3), reliable stocking out to a distance of 50 m from a nominal burn edge or large residual stand would require that the species in question control about 15 m²/ha ($B_D = 0.0015$). This result is in rough agreement with studies by Stewart et al. (1998) (about 50% of a residual stand) and other papers summarized in Greene and Johnson (2000). We point out, however, that this result is for the first few years after fire. The subsequent availability of rotten boles a few decades after the fire coupled with the attainment of reproductive status by the initial postfire cohorts increases the stocking potential beyond 50 m (Galipeau et al. 1997).

The main conclusion is that small-seeded conifers lacking aerial seed banks (i.e., all northern conifers except *Picea mariana*, *Pinus contorta* Doug., ex Loud., and *Pinus banksiana* Lamb.) will adequately colonize only a small portion of a large burn. A primary constraint, as with strip cuts, is the tremendous variation in seed production.

**Caveats**

Note that we have not included the temporal variation (due to granivores, herbivores, and drought) in juvenile age-specific survivorship in this assessment. Especially, there is
evidence that granivores concentrate on the most locally abundant seeds. While in a subsequent paper, we will show that the magnitude of this survivorship-related variation is, at least in the boreal forest, not nearly as great as the variation in crop production, nonetheless, it is not trivial. This can be seen in studies where repeated sowings lead to coefficients of variation for juvenile survivorship much lower than seen in Table 1 (e.g., Zasada et al. 1987; Fleming and Mossa 1995; Charron and Greene 2002). Clearly, as the period of inviability (T) becomes shorter (e.g., more rapid leaf abscission due to fast growth of dense asexual Populus), the relative contribution of the survivorship stage to unreliability is increased.

Conclusions

The distribution of tree seed production years is strongly right-skewed, we find no evidence for bimodality, and the distribution can be modelled as a lognormal function. With the assumed parameter value \( \sigma_k = 2.06 \), the largest value in 10 years would be about four times the annual mean, and the median value would be about eight times less than the mean. That is, the skewness of the record is so strong that the mean seed year is itself a noteworthy event.

We have no evidence that the tree species examined here differ from one another in their temporal variation of crop sizes. There is too much variation within and among con-specific production records for us to detect interspecific differences, if they existed. Nonetheless, as we showed, the assumption of a universal \( \sigma_k \) value permits us to develop the very useful distribution of summed crop production values across the receptive time interval of a mineral soil or humus seedbed. The three conifer species with the largest number of records conformed reasonably to that expected distribution.

The reader is reminded of the limited data set; it is weighted heavily toward oaks and conifers of commercial importance. We have few species with multiple records. Qualitative assessments by the present authors lead us to think that many species that produce seeds in the late spring (e.g., several species of Populus, Ulmus, and Acer) are much less variable in their crop production than those shown in Table 1.

We concluded that reliable natural regeneration by seed after disturbance is limited to a short distance from the edge of an area source unless the species of interest is a virtual monoculture and there is a relatively high proportion of optimal seedbeds. Species lacking aerial seed banks, advance regeneration, or a strong capacity for asexual regeneration cannot recruit well beyond a few tens of metres from the edge of a harvest block or burn. This conclusion is of course hardly new; it has been shown repeatedly by empirical studies. Our main contribution here has been to sketch quantitatively (eq. 2) the relative roles played in this constraint by temporal variation in seed production, source strength (basal area per area), dispersal, and the quality of the seedbeds.

As for cycles in seed production, we found no statistically significant effect. If the magnitude of the eventual crop is primarily determined by weather at the time of bud differentiation and by weather at the time of pollination, then a lack of cycles is precisely what one would expect given that this weather does not exhibit cyclic behavior (Robinson and Henderson-Sellers 1999).

Finally, there is clearly a tendency for a crop in the year after a major crop to be smaller than expected, but the effect is weak. That is, the contribution of resource depletion to the variation in crop sizes appears to be very limited relative to weather cues and, perhaps, to other factors such as pollination success or preabscission predation.

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