Oecologia (1993) 95:314–320

Oecologia

Extinction dynamics, population growth and seed banks

An example using an age-structured annual

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Received: 22 July 1992 / Accepted: 23 March 1993

Abstract. The goal of this paper is to test theoretical predictions about the effects of seed banks on population dynamics and extinction rates in variable environments using simulations based on data from a natural population of the winter annual *Collinsia verna*. In the simulations, we varied the frequency of demographically good and bad years and the autocorrelation between conditions in consecutive years to examine the impact of seed dormancy on population growth rate, extinction rate and time to extinction. The existence of a seed bank enhanced population growth rates under all environmental regimes except when good years were very frequent, but this enhancement was minimal. In addition, the presence of the seed bank decreased the likelihood of extinctions and increased the time to extinction. The time to extinction was longest when the environmental conditions were most unpredictable.

Key words: Seed banks – Extinction – Temporal variation – *Collinsia verna* – Demography

Persistent seed banks, dormant seeds in the soil which remain viable for more than one season (Thompson and Grime 1979), are a common feature of plant life cycles (Leck et al. 1989) that are favored by natural selection when probabilities of adult survival and reproduction vary temporally (Cohen 1966, 1967). At the population level, the presence of seed banks may enhance population persistence by decreasing the chances of population extinction in "bad" years. However, seed banks may retard population growth rates in "good" years because dormant individuals are delaying reproduction (Lewontin 1965; Mertz 1971). Seed banks can also stabilize population dynamics by damping oscillations in population size to stable equilibria (MacDonald and Watkinson 1981; Pacala 1986). These theoretical treatments of seed bank evolution and population dynamics underscore the necessity of incorporating temporal variation in the design and analysis of demographic studies of seed bank in natural populations.

The traditional tools of demography assume long-term constancy of the environment and therefore long-term stability of vital rates (Cohen 1979; Caswell 1989). However, to address the demographic consequences of seed banks, we need to consider demography in variable environments. A synthetic theory of demography in variable environments is emerging (for reviews see Tuljapurkar 1989; Caswell 1989). In particular, estimators of population growth rates, stable age distributions, and extinction rates for populations with variable vital rates are being developed (Lande and Orzack 1988; Tuljapurkar 1989; Caswell 1989). Cohen (1979) suggests a method for predicting long-term population growth rates using stochastically varying transition matrices. Following Cohen (1979), Bierzychudek (1982) generated transition matrices using field data from two populations of *Arisaema triphyllum* in each of two years and examined the long-term dynamics of each population using simulations that assumed the frequency of conditions represented by each transition matrix to occur with equal frequency and no autocorrelation between the conditions in consecutive years. Unfortunately, few other empirical demographic studies of populations in temporally variable environments have applied these approaches (but see Gotelli 1991).

In this paper we address the role of the seed bank and the effects of temporal variation in environmental quality on the probability of extinction and the population dynamics of the winter annual *Collinsia verna* with data derived from a natural population (Kalisz 1991). Using bootstrapping techniques to analyze the data of Kalisz (1991), Kalisz and McPeek (1992) showed that the population was increasing rapidly in one year ($\lambda_b = 1.80$, 95% confidence interval = 1.72–1.97 where λ_b is the bootstrapped estimate of geometric population growth rate) and was declining rapidly in another ($\lambda_b = 0.41$, 95% confidence interval = 0.37–0.44). Therefore, this population which expresses a seed bank as a part of its life cycle, exists in a demographically variable environment. Here we use the data of Kalisz (1991) to examine the effects of the seed

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bank on the long-term dynamics of the population in a series of environments by varying the frequencies of "good" and "bad" years and the autocorrelation between the conditions in consecutive years. In addition, the demographic consequences of the presence and absence of the seed bank are investigated through its effect on the time to extinction (Cooper 1984; Lande and Orzack 1988) and on the population's age/stage structure

Methods

Collinsia verna (Scrophulariaceae) has a two-stage, age-structured life cycle (Fig. 1). Individuals are "born" when seeds are formed on the adults (not at germination). An individual in the (A) stage is an adult plant, and an individual in the (S) stage is a dormant seed in the seed bank. The letters A and S indicate the stage of the life cycle, and numerical subscripts indicate the age of individuals. For example, S_1 individuals are seeds which persist in the seed bank for one year while A_1 individuals are plants which germinate from seeds produced in the previous season. A_1 individuals are always derived from seeds produced in the previous season. A_2, A_3 and A_4 plants are derived from seeds produced two, three or four seasons ago, respectively. Movement from one stage/age to another along an arrow connecting two stages/ages take place over one year.

An individual in the seed stage (S) has one of three fates: the seed can die, persist in the seed bank (grow older but remain a seed), or emerge and potentially become a fruiting adult. Seeds on an adult plant have one of three fates; they can enter the seed bank (S_1), emerge and survive to become reproductive (A_1), or die. Once an individual has passed from the seed to the adult stage, it is constrained by its annual habit to reproduce and die. Therefore, the age of an individual, whether it is a seed or adult, is determined by its duration in the seed bank. Seeds of *C. verna* can persist for at least three years in the seed bank (Kalisz 1991).

The form of the transition matrix used in the simulations is detailed in Kalisz and McPeek (1992) and has the basic form described by Charlesworth (1980, pp. 8–10) for an annual with a seed bank. Because of the presence of the seed bank, all variables used to calculate elements of the matrix could not be estimated from the same set of individuals. Therefore, data were collected separately on adult and seed stages. The data collection scheme was organized around three 75 m transects in a population at the Raccoon Grove Forest Preserve near Monee, IL USA (for detailed descriptions of the sampling methods, see Kalisz 1991; Kalisz and McPeek 1992). In each of two consecutive years the fates of all seedlings emerging in the study quadrats (Year 1 – $n = 5{,}981$; Year 2 – $n = 5{,}973$) were scored for their survival to fruit set and the number of seeds produced. These data were used to quantify the probability of survival to fruit set and the fecundity of surviving plants during each of the two consecutive years. The survival, persistence and emergence of seeds in the seed bank were estimated along the same transects using experimentally-constructed seed banks (see Kalisz 1991 for a detailed description of the sampling design). From these experimentally-constructed seed banks we estimated the probabilities that (1) seeds germinate without entering the seed bank, (2) seeds enter the seed bank, (3) seeds germinate after spending one year in the seed bank, (4) seeds survive from the first to second year in the seed bank, (5) seeds germinate after spending two years in the seed bank, (6) seeds survive from the second to the third year in the seed bank, and (7) seeds germinate after spending three years in the seed bank (data for 1–5 were collected in each year, only one year's estimate for 6 and 7 were obtained).

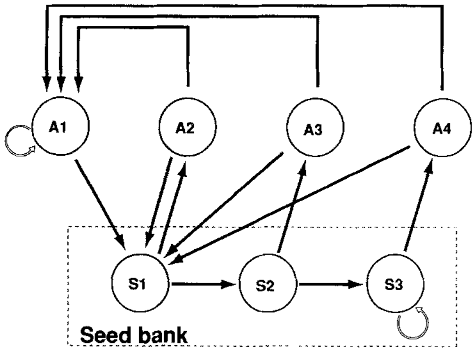

Fig. 1. Life cycle graph for the two stage, four age-class life history of *Collinsia verna*, a winter annual. S_1–S_3 represent seeds from 1 to 3 years old, respectively. A_1–A_4 represent adult plants from 1 to 4 years old, respectively. Arrows connecting two circles indicate the paths of transition between stage/age classes. The time scale for the transitions is 1 year

Based on our previous bootstrapping analyses (Kalisz and McPeek 1992) we categorize Year 1 as a "good" year ($\lambda_b = 1.80$) and Year 2 as a "bad" year ($\lambda_b = 0.41$). We do not claim that these values represent the exact extremes of λ expressed by this population. However, they are typical of the maximum and minimum population growth rates reported in other studies (summarized in Table 8 of Caswell 1986). In addition, these two years represent more than a four-fold difference in λ for the population. Therefore relative to each other, Year 1 is demographically "good" and Year 2 is demographically "bad". Although this population may experience worse and better years, the fact that the λs are similar to others reported in the literature and that we see a quadrupling of population growth rate between the years means they are likely to be near the extremes. As in any similar demographic matrix analysis, the utility of demographic parameters calculated from a set of data lies in the "projection" of population dynamics into the future and not in the precise "prediction" of future population dynamics (Caswell 1989; DeKroon et al. 1986). In essence we ask the question, "If these two years were the extremes, could the seed bank influence the extinction dynamics and population growth under these conditions?"

In the present series of simulations we study the long-term dynamics of *C. verna* populations when both the frequency of good and bad years and the autocorrelation between the conditions in consecutive years are varied. We vary the expected frequency of good years from 0.10 to 0.90, and the autocorrelation between conditions in consecutive years from -0.90 to $+0.90$. (Note that some combinations of highly negative autocorrelations and year-type frequencies are not possible.) For each regime, the autocorrelation between the conditions in consecutive years is specified as follows (Tuljapurkar and Orzack 1980): given that last year was a good year, the probabilities that the present year will be good or bad are p and $1-p$, respectively; given that last year was a bad year, the probabilities that the present year will be good or bad are $1-q$ and q, respectively. The autocorrelation between conditions in consecutive years is $\Phi = p + q - 1$, and once these values are specified, the expected relative frequency of good years is $(1-q)/(1-\Phi)$. The expected relative frequency of bad years is 1 minus the relative frequency of good years.

In the simulations presented we generate "good" or "bad" year transition matrices from these data using bootstrapping techniques (Efron 1982; Caswell 1989; Kalisz and McPeek 1992; McPeek and Kalisz 1993). For each iteration we constructed a bootstrapped data set from the original data for one year. If the iteration was chosen to be a "bad" year, we used the data from the year in which $\lambda_b = 0.41$. If the iteration was chosen to be a "good" year we used the data from the year in which $\lambda_b = 1.80$. To construct a "bootstrapped" data set, individuals are sampled at random with replacement from data sets for that year. We used the same methods described in Kalisz and McPeek (1992) and McPeek and Kalisz (1993) to generate bootstrapped samples for the overall population. The bootstrapped data set is used to calculate the elements of the transition matrix, and this transition matrix is used to project population numbers into the next year. A new bootstrapped sample and matrix is generated for each iteration (year). The condition (good or bad) in subsequent years is chosen according to the specified probability regimes described above.

For each regime of good and bad years and autocorrelations considered, we perform 50 replicate simulations of 250 iterations/replicate (years/replicate). For each iteration, the year type is determined (good or bad). A bootstrapped sample of the original data for that year type is made, and a population transition matrix is constructed from the bootstrapped sample according to the methods of Kalisz and McPeek (1992). This transition matrix is then multiplied by the vector of stage/age abundances resulting from the previous iteration to calculate the new abundances for each stage/age. If the abundance in any stage/age class falls below 0.50 after an iteration, that stage/age class is considered to be extinct.

We record a number of population descriptors during each simulation. To track population growth rate we calculate r according to the formula $r = \ln(N(t)) - \ln(N(t-1))$ for each iteration and calculate the arithmetic mean of r over the 250 iterations to characterize population growth (Tuljapurkar and Orzack 1980; Tuljapurkar 1982). We also record the final number of individuals in each stage/age class and the iteration in which the population (all stage/age classes) goes extinct if applicable. We also calculate the percentage of extinctions in the 50 replicate simulations for each environmental regime. We present results from two series of simulations. The first series examines population demography with the seed bank included in the life cycle. To contrast the population dynamic effects of the seed bank, the second series examines the demography when the seed bank is not included (i.e. no dormancy).

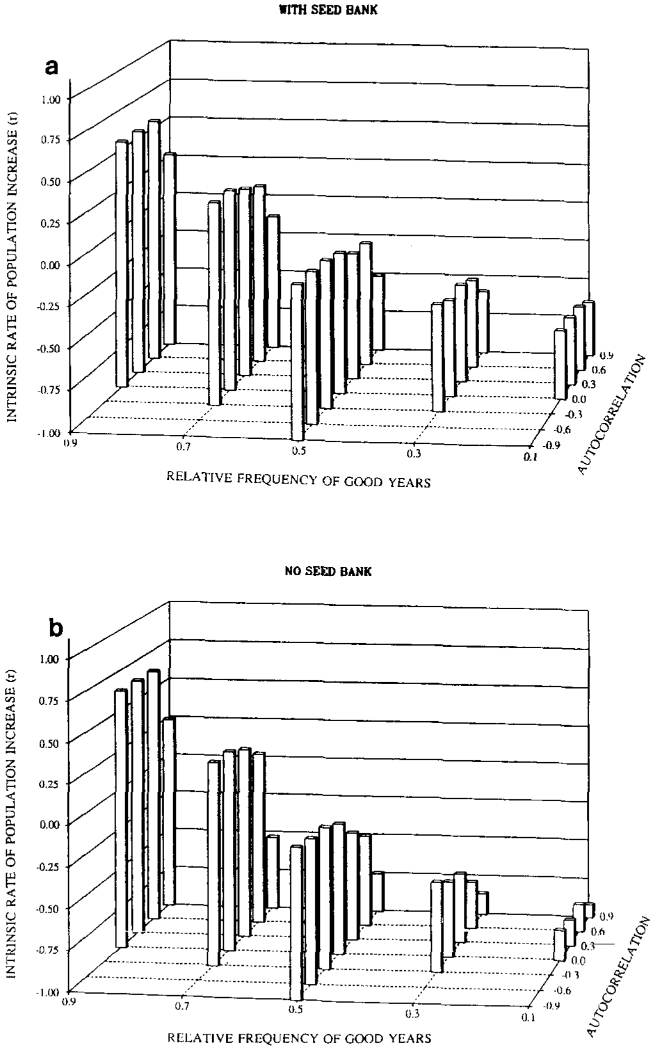

Fig. 2a, b. The average intrinsic rate of increase (*r*) calculated from the change in population size over 250 iterations of each replicate for each combination of autocorrelation between consecutive year types and the frequency of good years. Panel (**a**) gives results when the seed bank is included in the life cycle, and panel (**b**) gives results when the seed bank is deleted from the life cycle. Each bar represents the average of 50 replicates combination

Demographics with a seed bank

We present results from one series of simulations using the above methods applied to the transition matrix that describes the complete life cycle of *C. verna* including the seed bank (Fig. 1: Kalisz and McPeek 1992). We repeated all simulations using several different initial population stage/age abundances (only A_1 adults initially present in abundances of 100–1,000,000, only S_1 seeds initially present in abundances of 100–1,000,000, combinations of A_1 and S_1 individuals over similar abundance ranges), but the qualitative results were not affected by the initial conditions. Therefore, we discuss only results from simulations with 100 A_1 individuals initially present in the population.

Demographics without a seed bank

We also conducted a series of simulations using these methods but omitting the seed bank from the life cycle. With no seed bank, only A_1 individuals are present in the population, and the transition matrix collapses to a single value. This value in each iteration is determined by the product of three parameters from the original data sets: the probability of germination of seeds produced in the previous year, the probability of survival from seedling to reproductive adult, and the number of seeds produced by an adult. However, in our original data set survival and germination probabilities are calculated on the assumption of a third fate for seeds, namely dormancy. To account for the fates of dormant seeds in this analysis, we assume that the seeds that would have entered the dormant pool germinate and survive with the same probabilities as directly developing seeds. Bootstrapped estimates of these parameters in the original good year and bad year data sets are used in these simulations. All other methods are identical to simulations using a transition matrix including a seed bank. Again, initial population size has no effect on the qualitative results of these simulations, and so all results are from simulations with 100 A_1 individuals initially present.

Results

Demographics with a seed bank

Average population growth rate (r) is affected both by the relative frequency of good and bad years and by the autocorrelation between conditions in consecutive years (Fig. 2a). Average growth rate increases with increasing frequency of good years (Fig. 2a). Average growth rate decreases at the highest positive autocorrelation, because more populations go extinct as a result of long runs of bad years (Fig. 2a); the populations that go extinct have large negative r values which decrease the average r value.

For populations that persist, average population size increases with the increasing frequency of good years (Fig. 3a). However, in contrast to the effects on r, population size increases as the autocorrelation values become more positive. Replicates with more positive autocorrelations that do not go extinct are those with long runs of

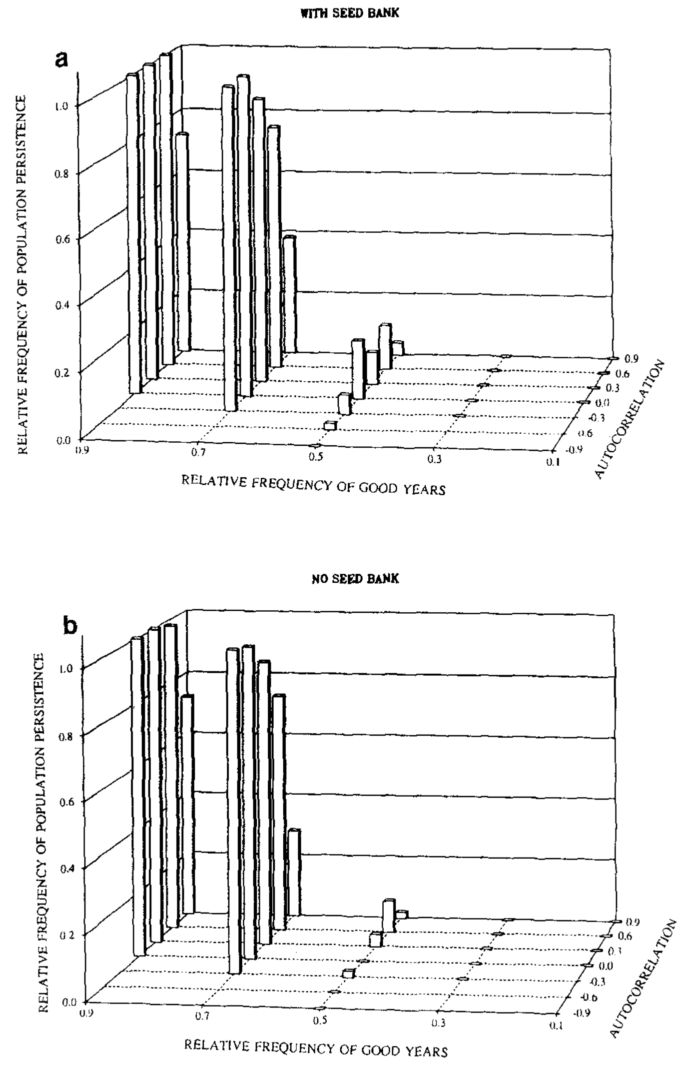

Fig. 3a, b. The relative frequency of populations persisting (not going to extinction) in the 50 replicate population for each combination of autocorrelation between consecutive year types and frequency of good years. Panel (**a**) gives results when the seed bank is included in the life cycle, and panel (**b**) gives results when the seed bank is deleted from the life cycle

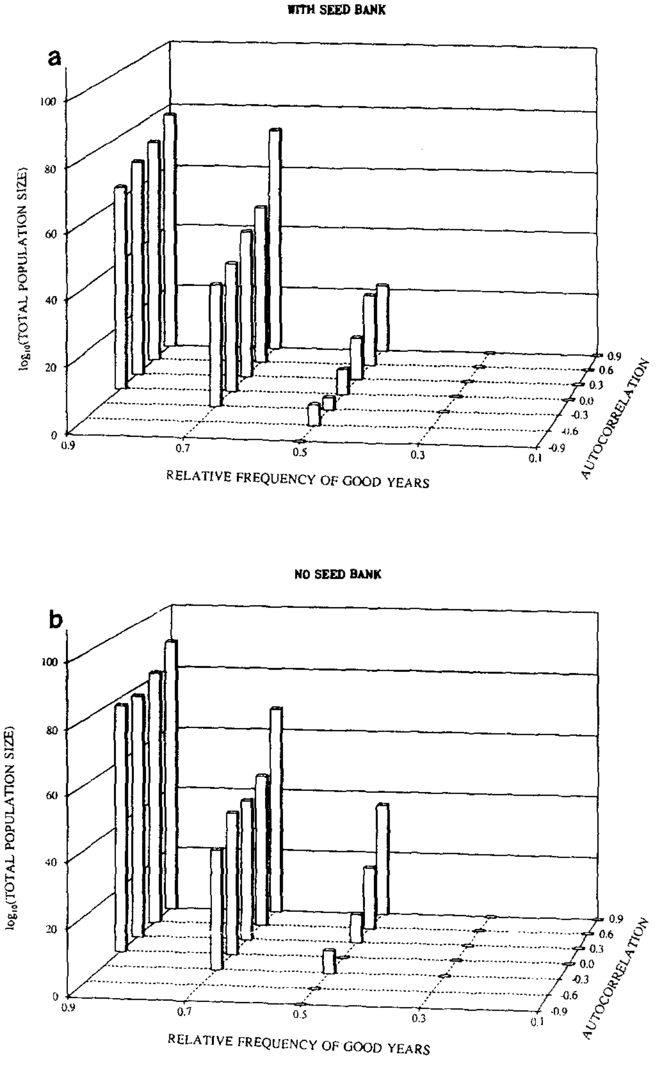

Fig. 4a, b. The $\log_{10}$ (TOTAL POPULATION SIZE) at the end of 250 iterations for each combination of autocorrelation between consecutive year types and the frequency of good years. Populations that went extinct are excluded from the analysis of this variable. Panel (**a**) gives results when the seed bank is included in the life cycle, and panel (**b**) gives results when the seed bank is deleted from the life cycle. Each bar represents the average of 50 replicates for each combination.

good years. When the frequency of good years is ≤ 0.3, no populations persist.

The persistence of populations increases with the increasing frequency of good years (Fig. 4a). Persistence decreases as autocorrelations become more positive, again because longer runs of bad years occur as autocorrelations become more positive which increases the probability of extinction.

An interesting pattern is apparent in the average time to extinction (Fig. 5a). Populations that go extinct persist longest when good and bad years occur with equal frequency. However, under these conditions most populations go extinct. When good and bad years are equally frequent, increasing the autocorrelation causes the populations to go extinct more quickly. When the frequency of good years is < 0.5, all populations are extirpated quickly (less than 20 iterations). This rapid extinction is due to the large negative values of r for these conditions (Fig. 2a). When the frequency of good years is > 0.5 the time to extinction is also short (Fig. 5a). Persistence greatly increases with the frequency of good years > 0.5 (Fig. 4a). Only populations experiencing a run of bad years early in the simulation go extinct, and this accounts for the short time to extinction. Most populations escape extinction by quickly growing to large sizes.

In contrast to the above population parameters, the frequency of good and bad years and autocorrelations have little effect on the age/stage structure of populations. The average frequencies of all seeds range between 75.2%–79% in the final populations across all environmental regimes (for populations that do not go extinct). However, as the frequency of good years decreases, the frequencies of older seeds (S_2, S_3) and older adults (A_2, A_3, A_4) increase.

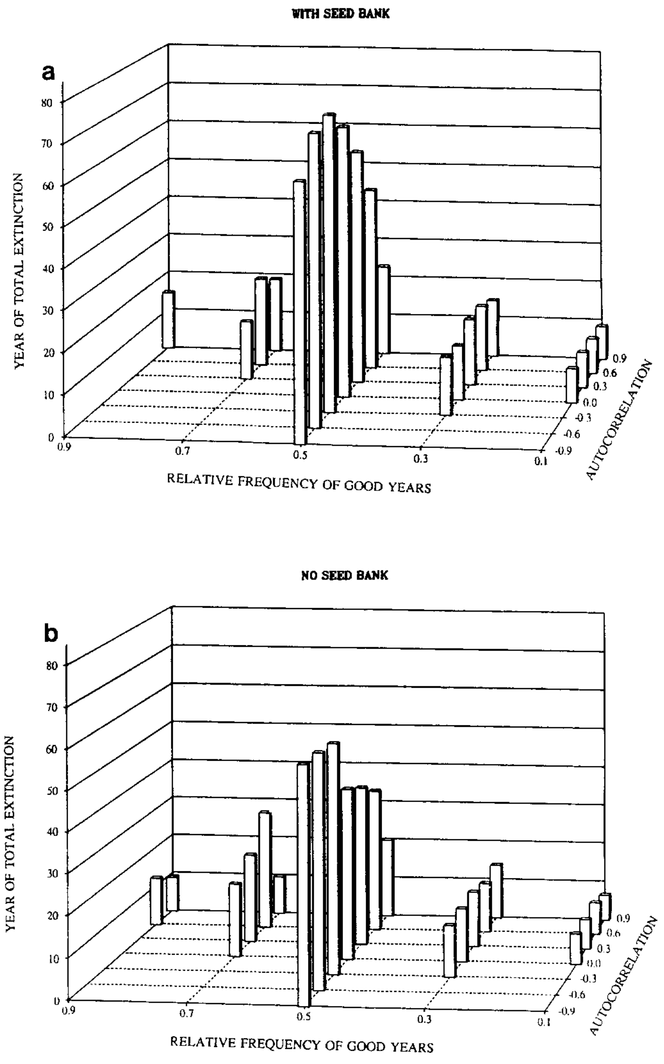

Fig. 5a, b. The average year in which the population went completely extinct for each combination of autocorrelation between consecutive year types and the frequency of good years. Panel (**a**) gives results when the seed bank is included in the life cycle, and panel (**b**) gives results when the seed bank is deleted from the life cycle. Each bar represents the average of 50 replicates for each combination

Table 1. The differences between the average rate of increase (r) with and without the seed bank ($r_{\text{with seed bank}} - r_{\text{without seed bank}}$) for all combinations of frequencies of good/bad year and autocorrelations used in this simulation. The plus and minus signs in parentheses under the differences identify whether the r's are positive or negative

Autocorrelation	Frequency of good years 0.9	0.7	0.5	0.3	0.1
0.9	0.024 (+)	0.395 (−)	0.239 (−)	0.263 (−)	0.263 (−)
0.6	−0.072 (+)	0.038 (+)	0.202 (−)	0.259 (−)	0.227 (−)
0.3	−0.075 (+)	−0.006 (+)	0.115 (−)	0.173 (−)	0.254 (−)
0.0	−0.075 (+)	−0.003 (+)	0.062 (−)	0.122 (−)	0.233 (−)
−0.3	–	−0.010 (+)	0.036 (−)	0.098 (−)	–
−0.6	–	–	0.039 (−)	–	–
−0.9	–	–	0.009 (−)	–	–

Table 2. The differences between the percent of populations persisting for the 250 iterations with and without the seed bank (Persistence with seed bank – Persistence without seed bank) for all combinations of frequencies of good/bad year and autocorrelations used in this simulation

Autocorrelation	Frequency of good years 0.9	0.7	0.5	0.3	0.1
0.9	0	10%	2%	0	0
0.6	2%	2%	4%	0	0
0.3	0	0	0	0	0
0.0	0	2%	18%	0	0
−0.3	–	0	4%	0	–
−0.6	–	–	2%	–	–
−0.9	–	–	0	–	–

Demographics without a seed bank

The qualitative pattern of changes in r with increasing good years and autocorrelation is the same with and without the seed bank (Fig. 2), but there are quantitative effects of deleting the seed bank on r. Deleting the seed bank from the life cycle increases r under a restricted set of conditions, specifically when the populations are growing the fastest (i.e., when the frequency of good years is 0.9 and autocorrelation is ≤ 0.6 and when the frequency of good years is 0.7 and autocorrelation is ≤ 0.3) (Table 1, Fig. 2). However, the differences in r with and without the seed bank under these conditions are minimal (Table 1). Under the majority of conditions, r values with the seed bank are greater than r values without the seed bank, and these differences can be substantial (Table 1). The presence of the seed bank augments population growth rates when r is negative, and this positive effect of the seed bank increases as the frequency of good years increases and the autocorrelation becomes more positive (Table 1). Changes in final population size for those populations that persist with and without the seed bank (Fig. 4) reflect changes in r.

The qualitative pattern of population persistence are similar with and without the seed bank (Fig. 3). When good and bad years are equally frequent, the presence of the seed bank increases the likelihood of population persistence as compared to populations in which the seed bank is absent (Table 2). The presence or absence of the seed bank has little or no effect on persistence when good years occur with a frequency of ≤ 0.3 because all of those populations go extinct or with a frequency of ≥ 0.7 because nearly all of the populations persist (Table 2 and Fig. 4).

In general, the presence of a seed bank delays the time to extinction as compared to populations without seed banks (Table 3, Fig. 5). This effect is largest when the frequency of good years is 0.5 and autocorrelation is near

Table 3. The differences between the average time to extinction for populations with and without the seed bank (Time to Extinctions with seed bank − Time to Extinction without seed bank) for all combinations of frequencies of good/bad year and autocorrelations used in this simulation. *** Mean that no populations with seed banks went extinct but some populations without seed banks did go extinct for that set of conditions. NE means no populations with or without seed banks went extinct

	Frequency of good years				
Autocorrelation	0.9	0.7	0.5	0.3	0.1
0.9	5.64	9.16	2.91	0.48	1.84
0.6	***	−7.58	9.95	3.76	0.66
0.3	NE	−8.6	17.63	1.50	0.60
0.0	NE	***	24.83	0.22	1.10
−0.3	–	NE	16.16	1.62	–
−0.6	–	–	13.70	–	–
−0.9	–	–	4.80	–	–

0.0. (It is unclear why the time to extinction is greater for populations without seed banks (i.e., negative values in Table 3) in two cases when the frequency of good years is 0.7.)

Discussion

Theoretical treatments suggest that the production of some fraction of dormant seeds by individual genotypes will be beneficial during years when survival or reproduction are low by preventing extinction of those genotypes. However, the production of dormant seeds will be demographically costly during years when survival and reproduction are high by preventing those same genotypes from increasing at maximal rates (Cohen 1966, 1967; Venable and Brown 1988). At the population level, this means that populations containing genotypes that produce dormant seeds should be buffered from extinction in bad years, but growing at less than maximal rates in good years (Lewontin 1965; Mertz 1971). We see these population level effects in our simulation results, but they are apparent only under particular environmental conditions. All populations go extinct if the frequency of good years is ≤ 0.3. However, when the frequency of good years is ≥ 0.5, the frequency of extinctions for simulations with the seed bank is always less than or equal to the frequency of extinctions when the seed bank is included (Fig. 3 and Table 2). Also, the average iteration in which populations go extinct is delayed in general when the seed bank is included in the life cycle (Fig. 5 and Table 3).

The likelihood of extinction for a population depends on several factors involving the scale of the environmental variance and the population biology of the species. As shown by the simulations, the frequency and autocorrelation of year types strongly affect the likelihood of persistence, and the ability to forecast the likelihood of extinction or persistence for a population will be influenced by the actual series of good and bad years. Year quality or vital rates for populations of any species are expected to exhibit a continuous distribution, encompassing the range from superlative to extremely poor conditions. Although the two years used in these simulations seem to represent extremes in year quality, we do not know the actual distribution of year types or the true extremes experienced by this population. Such data can only be ascertained through long-term demographic studies (e.g., Woolfenden and Fitzpatrick 1984).

Our simulation results also illustrate the demographic ramifications of a seed bank to population growth. Populations without a seed bank grow faster than those with a seed bank only under limited conditions. When the frequency of good years is high (≥ 0.7) and autocorrelations are not extremely positive (Table 1), the no seed bank populations have a slight advantage. This is the range of environmental conditions in which populations have the highest growth rates (Figs. 1 and 3). Furthermore, in this range of conditions the differences in population growth rates with and without a seed bank are small, with the largest difference in the average geometric growth rate ($\bar{\lambda}$) being -0.134 (i.e., $r_{\text{with seed bank}} - r_{\text{without seed bank}} = -0.075$ in Table 1). Therefore, the "cost" of having a seed bank in terms of population growth rates is relatively small and is only apparent when populations are growing rapidly.

Populations with a seed bank grow faster than those without a seed bank as the frequency of good years decreases and as the autocorrelation becomes more positive (Table 1, Figs. 1 and 3). When good years are infrequent, the presence of the seed bank increases population growth rates in two ways. First, during good years that follow bad years, germination of seeds from the seed bank augments the adult population, and thereby increases offspring production. Second, during bad years the presence of dormant seeds reduces population decline by increasing the chances that some individuals in the seed bank will emerge and reproduce during the next year. Making the autocorrelation more positive causes longer runs of years with similar conditions. Therefore, more positive autocorrelations also can mean longer runs of bad years, and these effects of the seed bank on population growth rates are magnified, because the expected length of runs of bad years exceeds the residence time of seeds in the seed bank.

Ellner (1985a) modelled the evolution of seed dormancy in which the frequency of years with total reproductive failure is allowed to vary. His model predicts that the fraction of seeds germinating directly into adult plants should be $\leq (1 - P_0)$, where P_0 is the frequency of years with total reproductive failure. We can use the fraction of seeds germinating directly to provide an estimate of the frequency of bad years for *C. verna*. Using Ellner's prediction and the fact that on average 67.8% and 43.5% of the *C. verna* seeds produced in one spring survived and emerged in the following autumn in the two years of the study (Kalisz 1991), the frequency of P_0 can be estimated to be between 32% and 57%. Also, in controlled environment studies, 38% of *C. verna* seeds from this population germinated in the first season (S. Kalisz and D.A. Thiede, unpublished data), which gives an estimate of $P_0 = 0.62$. If these estimates of the frequency of extremely bad years and the simulation results are accurate, they suggest a high probability of extinction for this population.

Population size and population structure are also likely to influence the likelihood of extinction. The *C. verna* population examined in this study is very large (ca. 10^6 reproductive individuals, Kalisz 1986) and covers several hectares. Significant spatial variation in demographic conditions are apparent in this population, as well as temporal variation (Kalisz 1986; Kalisz 1991; Kalisz and McPeek 1992). If extinction is very localized (e.g., on the scale of several meters^2) within the large study population, both germination of seeds from the seed bank and/or local seed dispersal from nearby areas could reestablish the *C. verna* population at these local sites.

Dispersal from other populations may also critically affect the dynamics of persistence and extinction. *C. verna* seeds may float and may be carried long distances in streams (F. Swink, pers. comm.). If complete extinction at this site does occur, long distance dispersal of seeds from upstream populations could re-establish or maintain the study population. Given that extinction is a likely outcome of local population dynamics in our simulations for a large range of environmental conditions, seed dormancy and dispersal between populations are probably important in the persistence of *C. verna* populations on both a local and regional scale (cf. Venable and Levin 1985; Venable 1989; Venable and Brown 1988; Levin et al. 1984; Klinkhamer et al. 1987; Harrison and Quinn 1989; Cohen and Levin 1991; McPeek and Holt 1992).

It bears repeating that the interpretation of these projections is dependent on the assumption that the two years represent extremes in year types. If more extreme year types exist, the role of the seed bank may be even more significant. Although the seed bank of the species used in this study is of relative short duration (probably 5–6 years), the seed bank had significant effects on the demographic parameters estimated. For species with longer-lived seeds, these effects can be expected to be even more important. In general, the results of the simulations support the models which implicate the role of the seed bank in increasing the probability of population persistence and increasing population size in a variable environment.

Acknowledgment We would like to thank Hal Caswell, John Fitzpatrick, Eric Menges and Steve Tonsor for useful discussions throughout this study. This research was supported by NSF grants BSR-8713967 and BSR-9006647 to S. Kalisz and NSF Research Training Group grant BSR-9113598. This is contribution number 726 of the W.K. Kellogg Biological Station.

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