

Importance of the seed bank for population viability and population monitoring in a threatened wetland herb

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Received 14 July 2004

Abstract

Although demographic models have become increasingly important tools in plant conservation, few models have considered the implications of seed banks for population persistence. Based on a 15-year study of the threatened herb, *Helenium virginicum*, we created a stage-class transition matrix to model the population dynamics of the plant. Our goal was to determine the role of the seed bank in population persistence and in the design of monitoring programs for the plant. Using data from marked plants, a long-term study of seed viability, and a seed bank census, we created a deterministic model and three stochastic models. The stochastic models were a model in which yearly correlations among parameters were retained, a model in which parameters were uncorrelated, and a model in which parameters were derived from log-normal distribution. We also constructed a fourth model in which we assumed a minimum seed lifetime consistent with the seed viability data. Both elasticity and perturbation analysis suggested that seed survival within the seed bank had by far the largest effects on the population growth rate (λ), with 47–64% of the change in λ being controlled by seed survival. Correlations among life history parameters had little effect on λ in the original models, but substantially reduced λ (from 0.97 to 0.86) when seed survival was limited. Given the importance of the seed bank and the high yearly variability in adult plant density, we used simulations to compare power to detect declines with seed bank samples versus censuses of adult plants. The power of adult plant censuses was extremely low (13–22%). The power of seed bank censuses was substantially higher (48–59%), but was limited by large pulses of recruitment to the seed bank in good years. Power was only moderately reduced when seeds were sampled every two or four years instead of yearly (from 59% to 48%). Together, our results suggest that seed survival is crucial to persistence of *Helenium* populations and that future empirical studies should focus on understanding the factors that affect seed survival. In addition, managers should consider seed bank censuses rather than above-ground plants when designing monitoring programs for plants in variable environments where above-ground plants vary greatly from year to year.

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Keywords: Population viability analysis; Seed bank; Elasticity; Plants; Threatened species; Population monitoring

1. Introduction

Demographic models are increasingly important tools in the conservation of plants. They are useful for assessing extinction risk, identifying which life stages are most important to population growth, guiding future data collection, and modeling effects of manage-

ment plans on a population (Boyce, 1992; Menges, 2000; Doak et al., 2002). However, available data may limit the effectiveness of demographic models. For example, models can provide inaccurate assessments if they fail to include important life stages such as seed banks (Doak et al., 2002).

Seed banks have only recently begun to be incorporated in demographic models of plant populations. This is probably because seed bank data (e.g. seed survival and germination rates) are often more difficult to collect

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than data for adult plants. In addition, seed banks are highly variable in composition, lifetime, and functional significance. Thompson and Grime (1979) classified seed banks into four types, distinguishing between transient and persistent seed banks. They defined transient seed banks as having no viable seeds persisting for over one year, and persistent seed banks as those with viable seeds persisting for extended periods of time. The potential contributions of transient and persistent seed banks to the long-term survival and viability of populations have been considered in theoretical studies (Cohen, 1966, 1967). These studies suggest that the development of a persistent seed bank is advantageous to long-term persistence of plant populations in highly variable environments. More transient seed banks should evolve when the environment is more stable and there is a high probability of successful reproduction and germination (Cohen, 1966). Thus, seed banks should be an important life stage when modeling the persistence of plant populations for conservation purposes.

Several demographic models have incorporated seed banks, but these have been transient seed banks (Type I/II – Thompson and Grime, 1979), or persistent seed banks in which most seeds germinate soon after release (Type III – Thompson and Grime, 1979). While Type III seed banks are considered persistent, these seed banks function much like a transient Type I seed bank (Kalisz and McPeck, 1992; Groenendael et al., 1994; Pfab and Witkowski, 2000; Silva et al., 2000; Raimondo and Donaldson, 2003; Menges and Quintana-Ascencio, 2004). The demography of transient and persistent seed banks may vary greatly, and thus their roles in population persistence and growth are likely to be different as well. Demographic models of populations with Type IV persistent seed banks (Thompson and Grime, 1979), in which most of the seeds remain in the seed bank, could help increase our understanding of the role of seed banks in population persistence.

Helenium virginicum is a Federally Threatened wetland-herb, narrowly endemic and disjunct between Virginia and Missouri, USA (Simurda and Knox, 2000). It inhabits sinkhole ponds that are seasonally inundated (Knox et al., 1995). *H. virginicum* has a highly variable above-ground plant population and a persistent seed bank (Knox, 1997). We used 15 years of demographic data from one sinkhole pond to create a stage class matrix model (Caswell, 2001) for *H. virginicum*. We also incorporated data from a six-year seed viability experiment and a seed bank census.

Using these data we created four initial models to investigate the effects of stochasticity on population growth. These were a deterministic model and stochastic models that had correlated parameters drawn from actual data, uncorrelated parameters drawn from actual data, or parameters drawn from a log-normal distribution fit to the data. We conducted an elasticity analysis

for the deterministic model and perturbation analysis on the uncorrelated stochastic model to determine the relative importance of the life-history stages to population growth (Caswell, 2001). To investigate how limited seed survival would affect our results, we created a fifth model that limited seed survival to 8 years, the minimum lifespan consistent with the seed viability study.

As population monitoring is necessary to evaluate the status of *H. virginicum*, we also used our model to design a monitoring program for the plant. The above-ground population of *H. virginicum* is highly variable, exhibiting large fluctuations depending on stochastic factors such as hydroperiod (Knox, 1997). Because of fluctuating population size, it may be difficult to detect demographic trends in the population (Gibbs et al., 1998). We hypothesized that the seed bank would be much more stable than above-ground population of *H. virginicum*. Thus, we used our model to determine whether monitoring the seed bank would be more statistically powerful than monitoring above-ground plants. We simulated monitoring above-ground plants and seed bank samples over varying lengths of time and at different frequencies. We then determined power to detect real population declines with each of these strategies.

2. Methods

2.1. Study site and species

Helenium virginicum (Asteraceae) is a perennial herb that is disjunct between the Appalachian highlands and the Ozark plateau and narrowly endemic to 30 sinkhole ponds in west-central Virginia and 30 sinkhole ponds in southeastern Missouri (Knox et al., 1995; Van Alstine, 1996; Simurda and Knox, 2000; P. McKenzie USFWS pers. com.). The narrow endemism of the plant seems to reflect its limitation to rare sites where competition with other species has been reduced by an unusual combination of stressful edaphic and hydrologic conditions (Knox, 1997; Knox et al., 1999) and by a self-incompatible breeding system (Messmore and Knox, 1997). The disjunction may reflect a vicariance event, as many other species of fish, beetles, and angiosperms have sister taxa that are disjunct between these two regions (Simurda and Knox, 2000). The species is listed as Threatened under the U. S. Endangered Species Act (US Fish and Wildlife Service, 1998).

Kennedy Mountain Meadow is a seasonally inundated sinkhole pond about 6 km southeast of Stuarts Draft, VA, USA, at an elevation of 475 m. It is also the type locality for *H. virginicum* (Blake, 1936). The site consists of a shallow circular depression about 1 ha in area and about 65 cm deep, occupied by a sparse vegetation of *Sphagnum* spp., graminoids, and forbs, with several copses of trees growing on hummocks within

the basin. The basin floor is lined with a lens of acid gray clay to a depth of 2 m. This lens lies in a deep matrix of cobble, gravel, and sand that overlies dolomite and limestone bedrock. Erosion of the underlying bedrock has created a shallow depression that accumulates standing water from winter through mid-summer, but is generally dry during the remainder of the year. The basin is surrounded by a mixed hardwood and pine forest (Knox, 1997).

2.2. Quadrat sampling

Using a stratified random method of sampling, one of us (Knox, 1997) established 53 permanent 1 m × 1 m quadrats within the high-water marks of the basin in the summer of 1986. Every year thereafter, during the late fruiting period for *H. virginicum* (September or October), all *H. virginicum* plants growing within each quadrat were mapped, placing plants into one of three stage classes: rosette plants with the longest leaf <2 cm, rosette plants with the longest leaf >2 cm, and bolted (flowering or fruiting) plants. The number of heads per plant was also recorded for bolted plants. These data allowed us to follow the fate of plants from one year to the next.

2.3. Seeds and the seed bank

Seeds of *H. virginicum* are dispersed in late fall and germinate poorly (<5%) until stratified. Tests of the viability of undamaged seeds (Malone, 1967), taken from heads collected from *H. virginicum* plants growing at the site, found 92% of ungerminated seeds to be viable. Using this method, we first removed the achene wall, broke seed coats by scratching with a dissecting needle, and then soaked seeds in the dark in a solution of 0.5 g 2,3,5-triphenyltetrazolium chloride in 200 ml of distilled water for 48 h at room temperature. Seeds with embryos that stained pink when viewed under 20× magnification were judged to be viable. An ongoing long-term study of the viability of seeds, formed in the fall of 1996 that have been buried at the Kennedy Mountain Meadow site since June of 1997, reveals continued high germinability (ca. 80%) after more than seven years (J. Knox, unpubl. data). Seeds do not germinate in the dark or under a standing column of water (Knox, 1997). The mean number of seeds per head was previously determined during a breeding study (Messmore and Knox, 1997) and by counts made on heads collected in the field. In the field, seeds that have dispersed do not germinate until about one year after dispersal (Knox, 1997). In 1991, the seed bank at Kennedy Mountain Meadow was sampled by determining the number of germinable seeds present in 212 soil core samples (each 10 cm deep × 5.5 cm wide) collected just outside each of the four corners of the

53 quadrats at Kennedy Mountain Meadow (Knox, 1997).

2.4. Long-term seed viability study

To investigate seed viability within the seed bank, a long-term field study was begun on 16 September 1996. We collected one head from each of 240 *H. virginicum* plants in a sinkhole pond near Stuarts Draft, VA. The heads were stored outdoors under a roof in a mesh bag. In June 1997 the achenes were separated and sorted to remove those that were damaged. Into each of 130 plastic cylindrical vials (75 × 15 mm), we put 33 achenes in the center of each vial between two plugs of washed quartz sand. Each vial had two 1.5-mm holes drilled near the top and bottom, to permit soil and water transfer between the vials and surrounding sinkhole pond soil, thus exposing the seeds to the chemistry and environmental factors of the natural environment. We buried the vials 8 cm deep with their long axes perpendicular to the ground in washed quartz sand in a standard plastic dishpan (40 × 32 × 17 cm) that had holes drilled to allow free movement of water. Dishpans were buried within Kennedy Mountain Meadow at a site with high *H. virginicum* recruitment. The surface of the sand in the dishpan was at about the same level as the surrounding soil surface, and depths were consistent with the depth of seeds found in the seed bank census. A layer of aluminum window screen was tethered over the top of the dishpan to prevent disturbance of the sand and vials. Several times each year, we removed three vials at random from the dishpan and tested the germinability of achenes in each. These tests were conducted over 15 days at room temperature in a lighted laboratory on 128 g washed quartz sand that had been moistened with 50 ml of distilled water in a 1-L covered plastic container. Over the course of seven years, 17 samples of three vials each have been taken from the field site and been tested for germination and viability.

2.5. Parameter estimation

Helenium virginicum had four stage classes in our models: seeds, small immature plants (basal leaf <2 cm), large immature plants (basal leaf >2 cm), and adult bolting plants. We used data from the seed germination experiment and the 15-year census of marked plants to parameterize our transition model, which was adapted from Doak et al. (2002). Stage transitions for seeds were seed survival (s_s) and germination to small (g_s) and large immature plants (g_l). Seed germination and survival were estimated from the seed burial experiment described above (see Appendix One). Germination from the seed bank could not be separated from germination of new seeds. Thus, we considered a range of scenarios for the proportion of new plants that arose from the

Table 1
Stage class transition matrix model, adapted from Doak et al. (2002)

	seeds	small	large	adults
seeds	$s_s*(1-g_s-g_l)$	0	0	sds
small	s_s*g_s	smsm	0	adsms
large	s_s*g_l	smlr	lrlr	adlr + adlrs
adults	0	0	lrad	adad

g_s and g_l represent germination to small and large stage classes, s_s is survival within the seedbank, sds is seed production by adults, and adsms and adlrs are seeds produced that germinate to small and large plants within the same year. Smsm, smlr, lrlr, adlr, lrad, and adad are transition probabilities from one stage to another.

seed bank vs. new seeds. We called this proportion “ G ” and had it range from 0.1 (10% of new plants from the seed bank) to 0.9 (90% of new plants from the seed bank) in steps of 0.1. In separating seed survival (s_s) from seed germination to small and large plants (g_s and g_l), we follow Doak et al. (2002).

Both small and large immature plants have been observed to transition into adult plants by bolting (smad and lrad) and to remain in the same stage class (smsm and lrlr). Small plants may also transition to large plants (smlr). Only adult plants reproduce, and seeds may either enter the seed bank (sds) or germinate to small or large plants (adsms and adlrs). Following reproduction, adults may remain as adults or transition back to large plants (adlr). Parameter estimates for transitions were based on the 15 years of data on marked *H. virginicum* collected by J.S.K. Further details on parameter estimation are given in Appendix A. From these parameter estimates, we produced a transition matrix (Table 1).

2.6. Model formulation

2.6.1. Deterministic model

We constructed a deterministic model using the equation:

$$X_{T+1} = M * X_T,$$

where X is the population vector and M is the transition matrix (Caswell, 2001). We constructed the transition matrix for the deterministic model using the mean values for all transition probabilities (Table 2). We constructed

Table 2
Stage class transition matrix with mean parameter values

	seeds	small	large	adults
seeds	0.987	0	0	1025
small	0.0012	0.078	0	0.0075
large	0.0006	0.121	0.202	0.1307
adults	0	0	0.147	0.135

Parameter values shown are based on the assumption that half of new plants arise from the seed bank ($G = 0.5$). All parameters were estimated from 15 years of demographic data, except seed production, which was based on data collected in 2000.

this model, and all subsequent models, in Matlab version 6.0 (Mathworks, Inc.). A deterministic λ and elasticity matrix were calculated for each of the nine combinations of parameter values, reflecting different assumptions about the number of new plants arising from the seed bank (i.e. different values for G).

2.6.2. Stochastic models

Because yearly fluctuations are likely to be important in understanding long-term persistence, we constructed three stochastic models from the 15 year dataset. These three models varied in how we incorporated year-to-year fluctuations and correlations among parameters. We first constructed a correlated model. This model assumed that each transition probability is correlated with the other probabilities and drew one entire matrix with replacement from the sample of 15 years. This matrix was then used to project the population the following year. The second model was an uncorrelated model. This model assumed that each transition probability is independent of the others. For each time step we created a transition matrix by randomly drawing each transition probability with replacement from the 15 years of data. For the third model, we assumed that each parameter followed a lognormal distribution (truncated at 0 and 1 for all probabilities), following existing PVA software (Applied Biomathematics, 1990). At each time step we created a transition matrix by drawing each element from a lognormal distribution with mean and variance determined by the data.

We used 1000 replicate runs of 500 years for the uncorrelated, correlated, and lognormal models using each of the 9 possible parameter values. We calculated

the mean and variance in yearly growth rate (λ) for each of the 27 models run.

2.6.3. Limited seed survival model

Because the germination study had only been carried out for 6 years, the long-term dynamics of seed survival are poorly understood. For example, even long-lived seeds usually have a finite lifetime (Baskin and Baskin, 1998). By assuming a constant yearly survival of 0.987 based on the first six years of data (see Appendix A), we may be overestimating the longevity of seeds in the seed bank. Thus we created an additional model that put an upper bound on seed survival consistent with the data available.

Based on the 6-year study of seed germination and an additional year of untabulated data, seed survival must be at least 8 years for most seeds. To create a low-end estimate for seed survival, we assumed survival at a rate of 0.987 for the first seven years followed by death in the eighth year. We then constructed a model with seeds divided into 8 age classes. Each year seeds progressed to the next class with a probability of 0.987, and seeds in the final age class died. We calculated a deterministic λ for this transition matrix, assuming equal germination from seed bank and new seeds (i.e. $G = 0.5$). Use of other values for G had little qualitative affect on our results. We used 1000 replicate runs of 500 years each for all three stochastic models and calculated the means and standard deviation for λ .

2.7. Elasticity and perturbation analysis

We calculated an elasticity matrix for both the original deterministic model and the limited seed survival model (Caswell, 2001). Elasticity analysis determines the relative contribution of each parameter to the population growth rate, adjusted for the magnitude of each parameter. To determine whether the inclusion of stochasticity affected the model's sensitivity, we also con-

ducted a stochastic perturbation analysis to compare with the deterministic elasticity analysis for the original model. Perturbation analysis adjusts each parameter by a similar percentage and evaluates the change in λ associated with each parameter change. For the perturbation analysis we used the uncorrelated model under the assumption that half of the new plants came from the seed bank ($G = 0.5$). Use of other G -values did not substantively change our results. We conducted the perturbation analysis by reducing each parameter independently by 10% and then using 1000 replicate runs of 500 years each to calculate the percent decrease in mean λ associated with each parameter reduction.

2.8. Population monitoring model

A common goal of monitoring plant populations is to detect population trends. Thus, choosing the most statistically powerful method is desirable (Gibbs et al., 1998). Using the uncorrelated stochastic model, we estimated the relative efficacy of sampling the seed bank versus censusing adult plants for monitoring the *H. virginicum* population. We created a simulation in which we simulated monitoring both adult plants and the seed bank for declining populations. Declining populations with mean λ s of 0.95, 0.90, or 0.85 were simulated by selecting the appropriate seed survival rate.

To simulate seed bank censusing, we used the seed bank data and the total volume of the basin to estimate the size of the seed bank as 1,440,000 seeds. The sample data consisted of 212 soil core samples with 0–7 seeds per sample and a total of 88 seeds present. To simulate sampling of the seed bank at different seed bank sizes (Fig. 1), we multiplied the percent decrease in seed bank in the model by 88, giving the expected numerical decrease in the seed samples. We then randomly removed this number of seeds from the 212 actual samples (Fig. 1). This reduced the total number of seeds without changing the distribution of seeds among samples. We

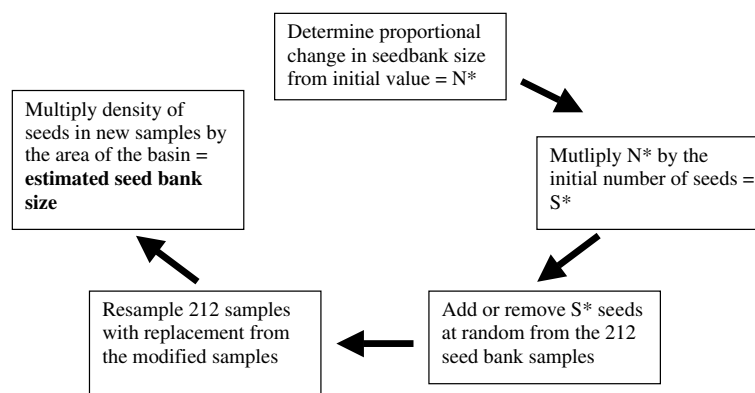


Fig. 1. Flowchart showing the algorithm by which new estimates of seed bank size were created based on changes in "actual" seed bank size in stochastic simulations.

then simulated a resampling of the seed bank by selecting 212 new samples with replacement from the corrected samples. We estimated total seed bank size from this new, bootstrapped seed sample by multiplying the seeds obtained per unit volume by the volume of Kennedy Mountain Meadow (Fig. 1). This sampling algorithm was designed to simulate the error associated with estimating seed bank size from small seed samples. However, we also retained data on the simulated seed bank sizes (i.e. without sampling) to keep track of the effects of seed bank sampling on variability and power. The algorithm assumes that the spatial distribution of seeds does not change with seed bank size, which is consistent with previous data showing no spatial relationship between the location of adult *H. virginicum* plants and seeds in the seed bank (Knox, 1997).

We ran this model using uncorrelated stochasticity, with half of germination from new seeds ($G = 0.5$), and with 1000 replicates each of 8, 12, 20, 32, and 40 years. Thus, we created 1000 replicate time series for adult plants and seeds which simulated the expected variability in both of these stages. For each time series we simulated censusing adult plants and sampling the seed bank for every year, every 2 years, and every 4 years. We then used Spearman's correlation analyses (Sokal and Rohlf, 1995) to determine whether population size (plants or seeds) significantly decreased with time. Statistical power was determined as the number of significant declines divided by 1000, the total number of time series generated. While Spearman's correlation is not the most powerful test for population declines, it is widely used in cases where little is known about underlying population dynamics (e.g. Rieman and Meyers, 1997; Thompson et al., 1997).

3. Results

3.1. λ values

The deterministic λ s for the basic model were above 1, indicating population growth ($\lambda = 1.027$ to 1.219 for $G = 0.1$ to 0.9). λ increased as the proportion of seeds germinating from the seed bank increased. The stochastic growth values for all three models were lower, though still greater than one (Fig. 2). There was not a substantial difference between the mean growth values of the uncorrelated, correlated and lognormal values. The Limited Seed Survival Model had a similar deterministic λ to the other models. However, the Limited Seed Survival Model had substantially lower mean λ values for the three stochastic models: 0.860 for the correlated model, 0.974 for the uncorrelated model, and 0.977 for the lognormal model. Thus, correlations among parameters substantially reduced population

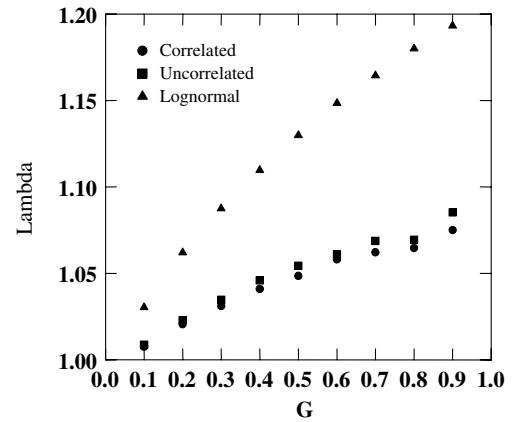


Fig. 2. λ values for the stochastic correlated, uncorrelated, and lognormal models as a function of the proportion of new plants arising from the seed bank ($G = 0.1–0.9$).

growth when seed lifetime was limited, but had little effect when seed lifetime was unlimited.

3.2. Elasticity and perturbation analysis

The elasticity matrix for the deterministic model is shown in Table 3. Seed bank survival contributed the vast majority of the elasticity (64%) followed by adults' seed production (10%) and germination of seeds to small and large immature plants (3% and 7%). The elasticity matrix for the Limited Seed Survival Model is shown in Table 4. Seed bank survival, as a sum of the eight seed bank stages, contributed a lower, but still large component of the elasticity (summed 47%) followed by adult seed production (15%) and germination of seeds to small and large immature plants (5% and 10%). The perturbation analysis yielded very similar results, with seed bank

Table 3
Elasticity matrix for the deterministic stage class matrix model

	seeds	small	large	adults
seeds	0.642	0	0	0.101
small	0.031	0.002	0	0
large	0.070	0.015	0.019	0.002
adults	0	0.016	0.087	0.014

Elasticities are based on parameter values when half of all new plants arise from the seedbank ($G = 0.5$). Values represent the proportional change in the population growth rate with a proportional change in each parameter, and are scaled so that elasticities sum to one.

Table 4
Elasticity matrix for limited seed survival model with parameters based on half of new plants from the seedbank ($G = 0.5$)

	seeds1	seeds2	seeds3	seeds4	seeds5	seeds6	seeds7	seeds8	small	large	adults
seeds1	0	0	0	0	0	0	0	0	0	0	0.1512
seeds2	0.126	0	0	0	0	0	0	0	0	0	0
seeds3	0	0.103	0	0	0	0	0	0	0	0	0
seeds4	0	0	0.082	0	0	0	0	0	0	0	0
seeds5	0	0	0	0.062	0	0	0	0	0	0	0
seeds6	0	0	0	0	0.045	0	0	0	0	0	0
seeds7	0	0	0	0	0	0.029	0	0	0	0	0
seeds8	0	0	0	0	0	0	0.014	0	0	0	0
small	0.008	0.007	0.007	0.006	0.006	0.005	0.005	0.004	0.004	0	0.001
large	0.017	0.016	0.014	0.013	0.012	0.011	0.010	0.009	0.023	0.030	0.004
adults	0	0	0	0	0	0	0	0	0.024	0.131	0.022

“Seeds1” to “seeds8” represent eight year-classes of seeds in which seeds all die in the 8th year.

Table 5
Perturbation matrix for stochastic model with uncorrelated parameters and half of the new plants from the seedbank ($G = 0.5$)

	seeds	small	large	adults
seeds	0.9278	1.0000	1.0000	0.9953
small	0.9975	0.9993	1.0000	0.9995
large	0.9973	0.9990	0.9987	0.9996
adults	1.0000	0.9991	0.9959	0.9995

Values given are the proportional change in λ values when each parameter is lowered by 10% of its initial value. Values closer to one represent parameters that have little affect on λ in stochastic simulations.

survival having by far the largest effect of the mean stochastic λ (Table 5).

3.3. Population monitoring model

Power for detecting declines with adult plants was extremely low (13–22%; Fig. 3). The power estimated for sampling the seed bank was much higher than that expected from sampling plants, though power from seed

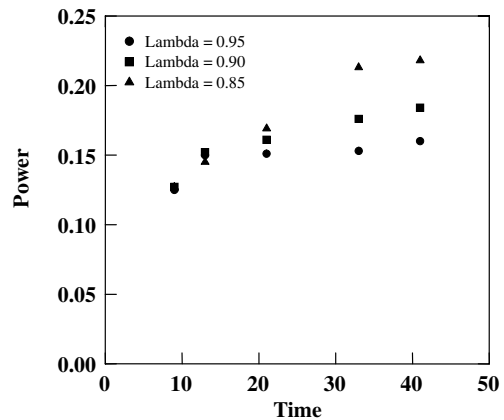


Fig. 3. Statistical power to detect real declines for *Helenium* populations from adult plants based on simulations with the uncorrelated stage class matrix model. Model was run for mean stochastic λ values of 0.95, 0.90, and 0.85.

bank samples still never exceeded 59% (Fig. 4). Power for the “actual” seed bank was somewhat higher than the sampled seed bank for all λ s. The difference was as high as 33% for 8 year samples, but was reduced to only 2% for 40-year samples. This indicates that more extensive seed bank sampling would provide limited increases in power for longer monitoring programs. Power varied inversely with λ in all simulations, though these differences were not large (5% for 8 years and 10% for 40 years).

The power for the sampled seed bank increased as sampling frequency increased (Fig. 5). Sampling every

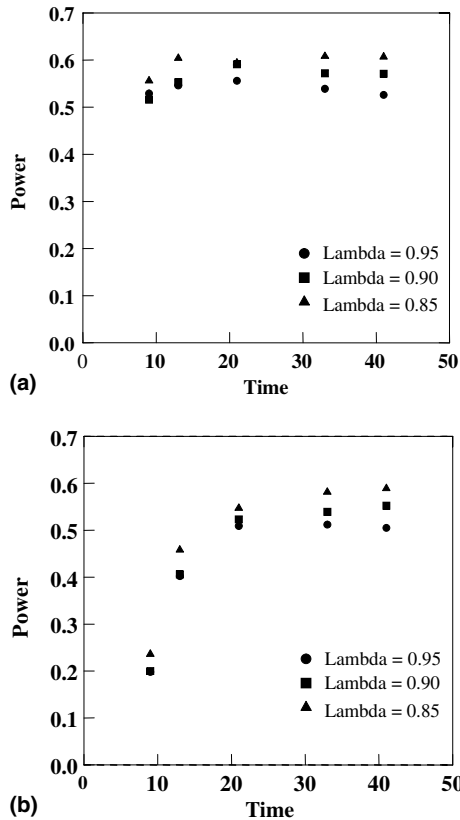


Fig. 4. Statistical power for sampling “actual” seed bank and “simulated” seed samples for the uncorrelated stage class matrix model. (a) Power for the “actual” simulated seed bank in the monitoring model for mean λ values of 0.95, 0.90, and 0.85. (b) Power for seed samples in the monitoring model for mean λ values of 0.95, 0.90, and 0.85.

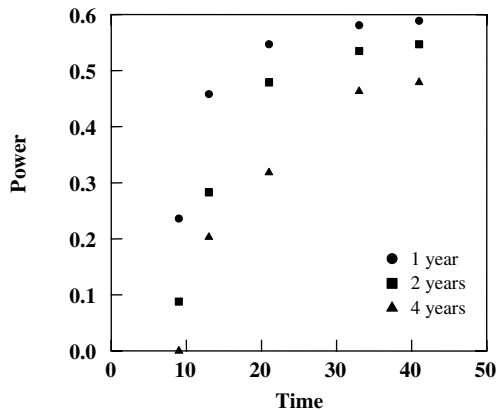


Fig. 5. Statistical power for sampling seed bank in the monitoring model with a mean λ of 0.85. Sampling was compared for surveys every 1, 2, and 4 years.

year yielded much greater power (about 30%) than sampling every 4 years for short sampling periods. The difference in power decreased to only a 10% difference for long sampling durations (>30 years). For 20 year samples, the power to detect declines was 32% for seed

banks sampled every four years vs. 16% for plants sampled yearly. For 40 year samples, the power was 48% for seed banks samples every four years vs. 21% for plants sampled yearly.

4. Discussion

Our results suggest that seed survival in the seed bank is a major contributor to the long-term persistence of *H. virginicum* populations. The elasticity and perturbation analyses show that seed survival is the major contributor to population growth. When seed survival was assumed to be limited, λ values decreased, and correlated stochasticity caused λ to decrease further. This suggests that persistent seed banks buffer a population from environmental stochasticity, and that more conservation efforts should focus on this stage. Our monitoring model also suggests that the seed bank provides a better life stage for population monitoring than do adult plants. Nevertheless, power to detect declines within the seed bank was still somewhat limited by the magnitude of fluctuations in seed bank size.

4.1. Variation in seed survival

The mean λ values for the deterministic and stochastic models with unlimited seed survival were all greater than 1, and stochasticity did not substantially reduce population growth rates. Because *Helenium* numbers do not appear to be increasing at Kennedy Mountain Meadow (Knox, 1997), these high λ values suggest that these models fail to take into consideration some important component of *H. virginicum*'s life history. Because the best estimate of yearly seed survival was a poor fit to the data from the seed survival experiment ($R^2 = 0.26$), we feel this was a likely source of error. In addition, the Limited Seed Survival model had substantially lower mean λ values for all three stochastic models. The results obtained in this model are much more consistent with observed trends in our demographic data (Knox, 1997). This is not to suggest that the Limited Seed Survival model is accurate, only that unlimited seed survival may be missing some aspects of long-term seed dynamics. Further empirical studies of seed survival would be useful in this respect.

Interestingly, the way in which stochasticity was modeled became much more important when seed survival was limited. Correlated stochasticity among parameters had few effects when seed survival was unlimited. However, in the limited seed survival model, correlations among parameters reduced the mean λ from 0.974 in the uncorrelated model to just 0.860 in the correlated model. This demonstrates that longer-lived seeds make correlations among parameters much less important to the overall dynamics of the population. This is

consistent with theory suggesting that a long-lived seed bank may act to buffer a population from environmental stochasticity (Cohen, 1966).

4.2. Elasticity and perturbation analysis

Elasticity analysis indicates that the seed bank contributes substantially to the long-term persistence and viability of the population. *H. virginicum*'s seed bank reflects the characteristics of the Type IV (very long-lived) seed bank categorized by Thompson and Grime (1979). The elasticity matrix calculated for the deterministic model showed that the seed bank was the greatest contributor to λ , contributing 64% compared to the next highest contribution of 10% from reproduction. The elasticity matrix calculated for the limited seed survival model showed similar results, with a combined contribution of all eight seed bank stages of 47%, as compared to the next highest contribution of 15% from reproduction. Thus, even when seed survival was limited, the seed bank remained the main contributor to population growth. The perturbation analysis gave similar results, suggesting that the seed bank remains crucial to population growth in the presence of environmental stochasticity.

Those studies that explicitly incorporate seed bank dynamics for seed banks of Types I–III (transient, present during summer (I) and during winter (II), and persistent with a large number germinating directly after dispersal (III); Thompson and Grime, 1979) have found seed banks to have less influence on λ than what we observed. Elasticity values range from 0.1% to 3.5% in the Type III seed bank of *Collinsia verna* (Kalisz and McPeck, 1992), from 3% to 7.8% for the Types II and III seed bank of *Poa annua* (Groenendaal et al., 1994; Lush, 1988), and from 2.4% to 2.9% for the Type III seed bank of *Espeletia timotensis* and *E. spicata* (Silva et al., 2000). In our study we found elasticities for seed survival of 46–64%, suggesting that in Type IV seed banks, seed survival is the single most important parameter affecting persistence.

While results from studies of plants having transient seed banks show elasticities lower than ours, these studies have obtained similar results regarding the increased importance of the seed bank in the presence of environmental stochasticity (Kalisz and McPeck, 1992; Menges and Quintana-Ascencio, 2004). Kalisz examined seed bank effects in the demography of *C. verna*. Elasticity analysis showed that the elasticity of seed survival in the seed bank increased significantly during a bad year (from 0.1% to 3.5%). Thus, the seed bank was substantially more important when environmental stochasticity had a negative effect on the population. Menges and Quintana-Ascencio (2004) examined the effects of fire in *Eryngium cuneifolium*. For *E. cuneifolium*, the transitions with highest elasticity were survival and germina-

tion in the seed bank. As time since fire disturbance increased, growth rates decreased and the elasticity of seed survival increased from 8% for 3–6 years postfire to 29% for >20 years postfire. In these studies, seed survival had highest elasticity values in years with low λ values. The trends observed in *C. verna* and *E. cuneifolium* of increased elasticity of seed survival in the seed bank with decreased λ are consistent with our results for *H. virginicum*.

Two of the main goals of elasticity analysis are to identify targets for management and needs for future research (Doak et al., 1994; Olmsted and Alvarez-Buylla, 1995; Caswell, 1996; Schemske et al., 1994; Drechsler, 1998; de Kroon et al., 2000). Our elasticity analysis suggests that protecting the seed bank is crucial to the persistence of *H. virginicum* populations. Unfortunately, little is known about the factors that contribute to seed survival. Thus, more information about the environmental factors that affect seed bank survival are badly needed for wetland herbs like *Helenium*.

4.3. Population monitoring

Because numbers of above-ground plants are highly variable, we used our model to determine the statistical power to detect declines from counts of above-ground plants versus samples from the seed bank. Our model revealed that monitoring adult plants had very low power to detect population declines. Power to detect declines ranged from 13% to 22%, depending on the magnitude of the decline and the number of years of the survey. These estimates may even be overly optimistic, since they assumed no sampling error in plant counts. Simulated samples from the seed bank had much higher power, ranging from 51% to 59%. This was still not as high as we expected, and managers may be wary of initiating monitoring programs that have less than a 60% chance of detecting a decline over a 40-year time period. This limited power did not appear to result from sampling error. For the “actual” seed bank in our models, power to detect declines was only moderately higher, ranging from 53% to 61%. Rather, the limited power appeared to be caused by good years in which large pulses of adult plants created a substantial increase in the seed bank (seed bank size during these pulses commonly doubled) and made it difficult to detect a long-term decrease in the seed bank. Power appears to level off with time because longer time series generally give higher power to detect linear changes in population size but are also increasingly likely to contain a large jump in seed bank size. Similarly, the small difference between the different rates of population decline (i.e. mean λ s) results from the fact that ability to detect a decline is mostly determined by the presence or absence of large pulses that are independent of the overall rate of decline.

While sampling the seed bank is a more powerful monitoring method, it can be logistically difficult and time consuming. When choosing a monitoring program it is often necessary to consider trade-offs between effort and statistical power (Gibbs et al., 1998). Thus, we examined power under different durations and sampling frequencies for the seed bank. Our results suggest that sampling the seed bank infrequently, though work-intensive, may still be a better option than sampling above-ground plants. For example, for a 40-year monitoring plan the power from sampling every year, 59%, decreases only to 48% when sampling every four years. Thus, sampling can be done every four years, thereby reducing the intensity of the sampling effort and still yielding much greater power than samples of above-ground plants. For longer-term monitoring programs, seed bank samples can probably be taken even less frequently. Although there are few other studies that examine these issues (see Taylor and Gerrodette, 1993; Philippi et al., 2001), we expect that our results will be relevant to most plants with highly variable above-ground populations but large and long-lived seed banks.

4.4. Study limitations

A common technique in population viability analysis of endangered species is the projection of extinction rates (Mace and Lande, 1991; Boyce, 1992; O'Grady et al., 2004). In our analysis of *H. virginicum* we originally defined the population to be quasi-extinct when less than 10 seeds remained in the seed bank. In our initial models, when seed survival was not limited, the seed bank often decreased but never reached quasi-extinction for time horizons of 100–500 years. For the Limited Seed Survival Model quasi-extinction did occur, but this depended on arbitrary assumptions about seed mortality. Thus, we decided not to include an analysis of extinction rates in our study. In any case, the basic goal of our analysis was not to predict extinction probability for *H. virginicum*, but rather to determine the role of the seed bank in its long-term survival and in successfully monitoring the population.

The greatest limitation of our study was our limited data for seed survival. Although we did have six years of seed survival data from the field, the fit of the data to a constant death rate was quite poor ($R^2 = 0.26$). Additionally, these data were taken from an experiment in which seeds were kept in constant conditions and not allowed to reach the surface of the soil. In nature, seeds may be predated, damaged, or lost permanently to unsuitable soils at greater depths. To overcome this limitation we modeled high end estimates for survival (potentially infinite) and low end estimates (8 years). While the low and high end estimates showed similar trends regarding the relative importance of the seed bank to long-term persistence, both λ and the impor-

tance of correlations among parameters varied considerably. It is worth noting that although our seed survival data are limited, they exceed the amount of data used in previous studies. We hope that our work will motivate studies on this or other species that include more detailed information on seed bank dynamics.

5. Conclusions

Our results consistently suggested that a persistent seed bank buffers *H. virginicum* populations from environmental stochasticity. Because of the critical contributions of the seed bank to the long-term persistence of the population, conservation efforts should concentrate on maintaining the long-term conditions required for survival and germination from the seed bank. This likely includes attention to maintaining the natural hydrology of Kennedy Mountain Meadow and preventing disturbance to *Helenium* sites, even during periods when above-ground plants are not present. Additionally, populations should not be ignored or assumed to be extinct simply because no plants are currently present. Future research efforts should focus on obtaining a better understanding of factors affecting germination and seed survival. In addition, the seed bank may provide a less variable and therefore more statistically powerful stage for population monitoring as compared to adult plants. More attention to seed banks, their role on population persistence, and the conditions necessary for their survival and germination could substantially improve our understanding of threatened plants in variable environments.

Acknowledgments

We thank Laura Galloway and Will Satterthwaite for helpful comments on earlier drafts of the manuscript. Emilio Bruna and Robert Humston provided useful suggestions about modeling seed bank dynamics. We are also grateful to Simon Levy for assistance with Matlab code, and to Jennifer Fallon for help in collecting seed data.

Appendix One. Parameter estimation

Parameters were defined and estimated as follows:
smsm. The proportion of small, immature plants in year t remaining as small immatures in year $t + 1$. This was estimated from the fates of marked plants.
smlr. The proportion of small, immature plants in year t that transitioned to large immature plants in year $t + 1$. This was estimated from the fates of marked plants.

smad. The proportion of small, immature plants in year t transitioning to adult plants in year $t + 1$. This was estimated from the fates of marked plants.

lrlr. The proportion of large, immature plants in year t remained as large immature plants in year $t + 1$. This was estimated from the fates of marked plants.

lrad. The proportion of large, immature plants in year t transitioning to adult plants in year $t + 1$. This was estimated from the fates of marked plants.

adlr. The proportion of adult, bolting plants in year t transitioning to large, immature plants in year $t + 1$. This was estimated from the fates of marked plants.

adad. The proportion of adult, bolting plants in year t remaining as adult, bolting plants in year $t + 1$. This was estimated from the fates of marked plants.

sds. The number of seeds produced per adult bolting plant. This was estimated by counting the viable seeds in twenty heads collected from plants at Kennedy Mountain Meadow in 2003. The average number of heads per individual in year t was multiplied by average number of seeds per head to give seeds per adult bolting plant.

s_s. The proportion of seeds in the seed bank that survive and remain viable seeds in the seed bank. Seed germination studies show that germination occurs in approximately 80% of collected seeds over 6 years (J.S. Knox, unpublished data). In these studies the remaining ungerminated seeds were tested for viability. Of the 38 ungerminated seeds, 35 were still viable (92.1%). After adjusting the fraction germinating to include all seeds that were likely, we fit a negative-exponential to the six years of data to determine the mean survival per year. Based on this approach, seed survival was estimated to be 0.987, though the fit of the model was poor.

g_s, adsms. We could not determine how many of the new immature plants grew from new seeds verses seeds from the seed bank. Thus, we considered a range of possible scenarios for the origin of immature plants. To calculate the transition probabilities of new and old seed germination into immature plants we used the data on number of immature plants observed each year. We calculated germination from seeds in the seed bank, *g_s*, and germination from new seeds, *adsms*, with the following expression (Doak et al., 2002):

$$G * \text{new small}_{t+1} = s_s * g_s * \text{seeds}_t, \quad (1)$$

$$(1 - G) * \text{new small}_{t+1} = \text{adsms} * \text{adults}_t, \quad (2)$$

where G is the proportion of observed immature plants that came from seed bank, $1 - G$ is the proportion of immature plants that came from new seeds, *new small* is the number of small plants that were detected that year for the first time, t indicates the current year, and $t + 1$ indicates the next year. Values for *g_s* and *adsms* were calculated for a range of G from 0.1 to 0.9 in 0.1 increments. Seeds were estimated from the seed bank sample taken in

1994. The number of seeds observed was converted to density and then multiplied by the volume of the basin to arrive at an estimate of 1,440,000 seeds.

g_l, adlrs. We used Eqs. (1) and (2) to calculate germination from the seed bank to large plants (*g_l*) and new seeds germinating to large plants (*adlrs*). Values for *g_l* and *adlrs* were calculated for a range of G from 0.1 to 0.9 in 0.1 increments.

sds_m. The proportion of seeds in the seed bank in year t germinating to small, immature plants in year $t + 1$. We calculated *sds_m* with the equation:

$$\text{sds}_m = s_s * g_s.$$

sdlr. The proportion of seeds in the seed bank in year t germinating to large, immature plants in year $t + 1$. We calculated *sdlr* with the equation:

$$\text{sdlr} = s_s * g_l.$$

sds_d. The number of seeds in the seed bank in year t that remain in the seed bank in year $t + 1$ was then calculated using the equation:

$$\text{sds}_d = s_s * (1 - g_s - g_l).$$

The above equations are modified from Doak et al. (2002).

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