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Seed banks in plant conservation: Case study of Santa Cruz tarplant restoration

William H. Satterthwaite^{a,*}, Karen D. Holl^b, Grey F. Hayes^{b,1}, Adelia L. Barber^a

^aEcology and Evolutionary Biology, EMS Building University of California, Santa Cruz, CA 95064, USA

^bDepartment of Environmental Studies, University of California, Santa Cruz, CA 95064, USA

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ABSTRACT

Although conservation and restoration practitioners have focused on maximizing above-ground population size and seed set of rare plants, a clear understanding of seed bank dynamics is crucial to managing these species. Santa Cruz tarplant (*Holocarpha macradenia*) is a threatened annual forb restricted to coastal prairie habitats in central California. *Holocarpha* produces disk achenes germinating within a year of production and ray achenes forming a persistent seed bank. We constructed both deterministic and stochastic demographic models for a restored *Holocarpha* population, using demographic rates measured separately for unmanipulated plants and plants growing in plots where vegetation was clipped. The deterministic models indicated that regardless of germination from the seed bank, the population would decline without clipping or similar treatments that enhance survival and reproductive output. Deterministic models showed only a slight positive effect of increased ray seed germination rates on population growth, which would need to be balanced against a potential loss of buffering against environmental variation as the dormant seed bank was reduced. Our stochastic simulations suggested that extinction risk for *Holocarpha* populations would be minimized by intermediate levels of ray seed germination. Thus, managers should focus on improving the performance of aboveground plants before considering actions to stimulate germination, since the former will yield a greater increase in deterministic population growth and not sacrifice any buffering effect of the seed bank. This case study emphasizes the importance of considering dormant seeds and seed banks in designing successful restoration and management strategies for plant species at risk of extinction.

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1. Introduction

Successfully restoring plant species through population introductions requires fostering demographic processes that allow for population growth. Models can be useful in predicting

demography and identifying factors that can promote population growth. Demographic modeling and Population Viability Analyses (PVAs) are widely used to address both deterministic and stochastic threats to natural populations of species of concern (Gilpin and Soule, 1986; Beissinger and Westphal,

* Corresponding author. Present address: Applied Math and Statistics, University of California, Santa Cruz, CA 95064, USA. Tel.: +1 831 459 4942; fax: +1 831 459 5353.

E-mail addresses: satterth@biology.ucsc.edu (W.H. Satterthwaite), kholl@ucsc.edu (K.D. Holl), grey@elkhornslough.org (G.F. Hayes), adelia@biology.ucsc.edu (A.L. Barber).

¹ Present address: Elkhorn Slough National Estuarine Research Reserve, 1700 Elkhorn Road, Watsonville, CA 95076, USA. 0006-3207/\$ - see front matter © 2006 Elsevier Ltd. All rights reserved.

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1998; Brook et al., 2000). Managing reintroduced populations requires many of the same considerations as conserving wild populations, however reintroduction projects to date have rarely incorporated mathematical models and the insight they can provide. In particular, stage-structured matrix models accompanied by sensitivity analyses have proven useful for plant conservation (Silvertown et al., 1996), while simulation models have proven useful in comparing extinction risk across multiple management scenarios (Satterthwaite et al., 2002; Menges et al., 2006).

Persistent seed banks are characteristic of many plant species (Baskin and Baskin, 1998) and are commonly assumed to serve as buffers against environmental variability (Cohen, 1966; Ellner, 1985; Rees and Long, 1992), which should reduce extinction risk (Lande, 1993). However, the incorporation of seed bank dynamics into simulation-based population viability analyses often proves challenging (Menges, 2000), and the actual importance of seed banks in reducing extinction risk is unknown for most species (Doak et al., 2002). Clearly, seed banks allow recovery of annual species following catastrophes (Baskin and Baskin, 1980) and may be important in slowing the deterministic decline of fire-dependent species between episodes of high recruitment (Quintana-Ascencio et al., 2003), but it is unclear how important seed banks are in most environments. For example, Volis et al. (2004) found that a seed bank was important for a desert population of *Hordeum spontaneum* but not for a population growing in a Mediterranean climate.

However, most previous studies have examined how population performance was affected by changes in seed bank survival but did not ask whether populations would do better if all seeds germinated as soon as possible instead of having some fraction delaying germination. The tradeoff between immediate germination and forming a seed bank also needs to be addressed, since dormant seeds may die before germinating and delayed germination leads to increased generation times. Both of these factors can reduce population growth rates, leading to the possibility of deterministic population decline or increased time spent at dangerously small population sizes. Doak et al. (2002) used published data from two forb species to ask whether delayed germination reduced extinction risk for two species. They found that delayed germination never appeared to reduce extinction risk for *Calathea ovoidensis* and could only reduce extinction risk for *Collinsia verna* in more variable environments than their data supported. However analyses using more extensive data sets for *Collinsia* suggest that forming a seed bank is favored at reasonable levels of environmental variability (Kalisz and McPeck, 1993; Kalisz et al., 1997).

Holocarpa macradenia (Asteraceae: Madiinae: Santa Cruz tarplant) is an ideal system in which to develop and compare management recommendations based on sensitivity analyses of managed, unmanaged, and introduced populations. It also provides an opportunity for simulation models testing the importance of seed banks for population persistence. At the same time, theoretical investigations of these questions using data collected from *Holocarpa* populations can address ongoing management debates (CDFG, 1995).

Holocarpa is a tall-statured, late season annual forb endemic to central California grasslands on the west coast of the

United States. It was initially found from Monterey County through Contra Costa County at elevations below 300 m (Hickman, 1993) but is now restricted to nine natural populations in southern Santa Cruz and northern Monterey Counties. In addition, *Holocarpa* has been introduced to several sites in Alameda County and three introductions have been attempted in sites near extant natural populations (Holl and Hayes, 2006). It is listed as Endangered by the state of California Department of Fish and Game and as Threatened by the US Fish and Wildlife Service. As is typical of many Asteraceae, it produces different types of achenes (hereafter referred to as “seeds”) from ray and disk flowers. Disk seeds germinate within a year of release while ray seeds appear unable to germinate within a year of release, but can persist for multiple years in the soil and germinate later (CDFG, 1995). *Holocarpa* retains most of its seeds until the first rains, so losses to post-dispersal seed predators are probably small, and seeds rarely disperse more than 1 m from existing plants, although some ray seeds may disperse over long distances via transport by animals (G. Hayes, unpublished data).

Multiple management strategies have been attempted for *Holocarpa* populations, and it is unclear which are most appropriate. Clipping of aboveground vegetation (both *Holocarpa* and its competitors) increases the establishment of seedlings, survival to adulthood, and flower production for *Holocarpa* plants (Holl and Hayes, 2006). Mowing and grazing appear to have similar effects (CDFG, 1995), although clipping or mowing too late in the season or too low to the ground can kill *Holocarpa* plants before seed production. The proper approach to managing the seed bank is particularly contentious. Germination out of the seed bank can be stimulated most effectively by scraping the soil (Bainbridge, 2003). Mowing and fires can stimulate germination to a lesser extent, although badly timed fires can kill seeds in the seed bank (CDFG, 1995). Many land managers have recommended interventions stimulating germination to boost the size of small populations, while others have raised concerns about the effects of losing the seed bank and its buffering role (CDFG, 1995).

This study was initiated to identify the most promising treatments for encouraging the growth and persistence of introduced populations of *Holocarpa* while also identifying the most pressing needs for further data collection on this species. The model results are likely most applicable for introduced populations in similar habitats, although similar strategies may work well in natural populations with similar vital rates. In addition to informing *Holocarpa* management, this study may provide insight into the management of other Asteraceae with dimorphic achenes. More broadly, it offers a valuable case study on the buffering role of seed banks given empirically estimated vital rates and environmental variation.

2. Methods

2.1. Terminology

Following Cohen (1966), we use the term “germination” to refer to the annual probability of a viable seed attempting to germinate, regardless of whether the embryo survives long enough to emerge as a recognizable seedling. Germination

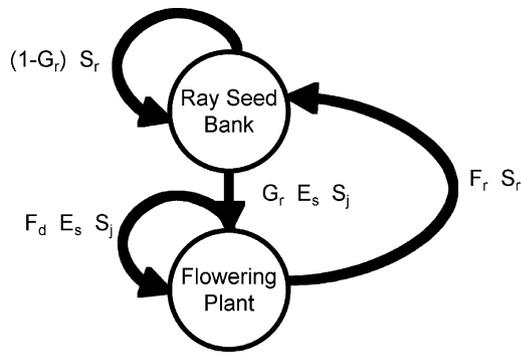


Fig. 1 – Modeled life cycle for *Holocarpa*. Each arrow represents an annual transition, labeled with its component vital rates as defined in Table 1.

can therefore range as high as unity without implying that all seeds produce observable seedlings. Most field estimates of germination rely on counts of recognizable seedlings emerging from a known quantity of seed. Here, the term “emergence” is used to describe the probability that an embryo, having already attempted to germinate, will survive and grow into an observable seedling. Since our data cannot distinguish seeds that never contained embryos from seeds in which embryos died before developing into recognizable seedlings, the emergence term also indirectly incorporates a measure of seed viability.

We use the terms “seed bank” and “delayed germination” but not “dormancy” when referring to *Holocarpa* seeds to avoid confusion among ecological and physiological definitions of dormancy (Thompson et al., 2003; Baskin and Baskin, 2004), however delayed germination in *Holocarpa* ray seeds is analogous to dormancy as commonly defined in ecological modeling papers.

2.2. Model life cycle

Holocarpa's life cycle was modeled as shown in Fig. 1, with vital rates as described in Table 1. The model assumed a census of adult plants at the time of flowering (assumed to be synchronous across the population), just prior to seed release and death of all adult plants. Each plant produced a fixed number of ray and disk seeds. Disk seeds were assumed to always germinate within a year of production and either emerged as juveniles or died at the start of the ensuing grow-

ing season. All ray seeds spent one year in the seed bank (with mortality possible during this first year), after which they had a fixed probability of germinating and possibly emerging, remaining viable in the seed bank, or dying. Seeds that germinated emerged as juveniles and survived to adulthood with fixed probabilities independent of whether they were from ray or disk seeds.

2.3. Vital rate estimation

Vital rates were estimated from a population introduction carried out near Elkhorn Slough in central California (Holl and Hayes, 2006). The site was chosen as appropriate for introduction because it (1) had been actively grazed by cattle, (2) contained a relatively intact coastal prairie community, and (3) had sandy loam soils deeper than 1 m. In addition, it had no previously known *Holocarpa* population and thus likely had no pre-existing seed bank, making it possible to follow population demography through time with the assurance that all recruits originated from the experimental introduction.

Vital rates were estimated separately for control and clipped plots, in which all vegetation (including *Holocarpa*) was clipped to ~5 cm height with a rotary trimmer once a month throughout the growing season (January–June). Crossed with these two treatments were three soil disturbance treatments, but since these treatments did not significantly affect aboveground plant performance (Holl and Hayes, 2006), the data were pooled across the three soil disturbance treatments. The data used were from the most successful of three introduction sites using data from 1999, the one year (out of two) in which plant performance was highest – thus it may be an optimistic estimate of performance of introduced populations in similar habitats.

The probability of successful emergence was determined by counting the number of seedlings recruited from a total of 324 disk seeds planted out in the clipped plots and 108 seeds in the control plots. The survival rate from seedlings to adults was measured for each treatment by marking 225 recruits (the offspring of seedlings transplanted the first year of the experiment) in clipped plots and 75 recruits in control plots and counting the number surviving to flowering. These marked recruits included all recruits within the monitored area that were found during monthly searches carried out in February, March, and April. Seed production was estimated by counting the number of small (<5 mm

Table 1 – Vital rates used in model

Abbreviation	Vital rate	Value – control	Value – clipped
F_d	Disk seeds produced per adult plant	3.4 (0.78)	33 (0.96)
E_s	Germination and emergence success (includes survival of seed from time of seed set to germination, and survival from germination to marking)	0.020	0.15
S_j	Survival of juveniles from marking to flowering	0.04	0.076
F_r	Ray seeds produced per adult plant	9.1 (0.65)	76 (0.91)
S_r	Annual survival of ray seeds in seed bank	Free	Free
G_r	Percent of ray seeds (at least one year old) attempting to germinate each year	Free	Free

Coefficients of variation in the number of seeds produced per individual are reported in parentheses.

diameter), medium (6–10 mm diameter), and large (>10 mm diameter) flower heads on each adult plant in the population one year after the first outplanting and multiplying the number of each type of flower produced by the mean number of ray and disk seeds produced by each sized flower head. Seed production was measured by subsampling 170 small, 357 medium, and 28 large flower heads. The mean and standard deviation in population-wide fecundity were calculated from the estimated seed production of each plant, and coefficients of variation in individual seed production are reported in Table 1.

Greenhouse trials showed that virtually no germination of ray seeds would occur within a year of production, even under ideal germination conditions (Hayes, unpublished data). Long-term data on ray seed survival and germination were unavailable, and could not be readily obtained due to *Holocarpa*'s threatened status and resultant CDFG restrictions. However, it is known that *Holocarpa* seedlings emerged from a pile of soil scraped from a construction site eight years after it last hosted adult *Holocarpa* plants (CDFG, 1995). Seed bank survival may be quite high, since seeds known to be at least 15 years old have successfully germinated (Barber, 2002). Therefore the majority of simulations assumed annual seed bank survival of 0.9 (corresponding to a seed half life of just under eight years), with values as low as 0.8 (implying only 16% of the seed bank would remain after eight years) or as high as 0.95 (implying 66% of the seed bank would remain after eight years) used for some simulations.

The percentage of ray seeds (older than one year) germinating each year was treated as a free variable. Note that the “percent germination” modeled here may be more appropriately called a “percent germination attempt” since it is allowed to range freely from 0 to 1. Ray seeds which attempt to germinate are assumed to have a probability of reaching the seedling stage that is identical to the germination success rate measured for disk seeds, all of which are assumed to attempt germination the first year.

2.4. Comparison to vital rates in a large natural population

No complete demographic analyses have been performed on natural populations of *Holocarpa*. However, data on adult fecundity were collected in 2000 from ten 30 × 30 cm plots established in one of the largest remaining natural populations (Porter), located 0.5 km from the Elkhorn introduction. This was a good year for this population, with the number of aboveground plants approximately doubling from 2000 to 2001 (Table A.1 in Supplementary Data). Seed production per plant was estimated by taking a subsample of one to five seed heads per plant from a subsample of eight to ten plants per plot, chosen by sampling all plants within a small square quadrat that expanded from a corner of the plot until it encompassed at least eight flowering plants. In all, 93 flowering plants were sampled, with plants producing a mean of 177 disk seeds (SD = 96) and 187 ray seeds (SD = 80) each.

2.5. Deterministic model analyses

The *Holocarpa* life cycle and vital rates were used to generate the following Lefkovich matrix model (Caswell, 2001):

$$\begin{bmatrix} B_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} (1 - G_r)S_r & F_r S_r \\ G_r E_s S_j & F_d E_s S_j \end{bmatrix} \times \begin{bmatrix} B_t \\ A_t \end{bmatrix}$$

where B_t denotes the number of ray seeds in the seed bank at time t , A_t denotes the number of adult plants, and vital rates are as defined in Table 1.

Standard matrix analysis techniques (Caswell, 2001) were used to calculate λ , the projected long-term population growth rate, for different combinations of ray seed survival and germination for both control and clipped populations. For ray seed survival and germination fixed at zero, confidence intervals on λ were also calculated for control and clipped populations based on 20000 resamples using a non-parametric bootstrap from the census data (Caswell, 2001). In addition, vital rate elasticity analyses (Morris and Doak, 2002) were used to calculate the proportional change in λ for proportional changes in each vital rate. Since elasticity values were calculated for underlying vital rates rather than entire matrix elements, these elasticity values do not necessarily sum to one and some vital rates may have negative elasticities. Elasticities for germination success and seedling survival were always identical, since any path through the life cycle which includes one must also include the other (Caswell, 2001). Elasticities were also calculated for a composite matrix combining estimated adult seed production from the Porter population with estimates of the remaining vital rates from the clipped population, in order to explore how different patterns in vital rate elasticities might be given a high-end estimate of fecundity.

2.6. Incorporating stochasticity

Simulations incorporating various forms of stochasticity were performed assuming starting populations of 150 juveniles transplanted from a greenhouse facility (similar long-term results were observed for simulations starting with 1500 outplants), which survived to flower the first year with field-measured probabilities of 0.40 (control) or 0.95 (clipped), and no initial seed bank. Survival of each individual outplant, recruit, juvenile, and seed was determined independently, so that all simulations incorporated demographic stochasticity in survival. Demographic stochasticity in reproduction was modeled by drawing the seed production of each plant from a lognormal distribution with mean equal to the population-wide mean seed production for that year and seed type and coefficient of variation (CV) equal to the measured CV in production of that seed type. Each year the total number of ray and disk seeds produced by the entire population was rounded to the nearest integer.

Environmental variation was modeled in four ways for different simulations: (1) the environment remained constant, (2) fecundity of plants varied across years but survival did not, (3) fecundity was constant across years but in some years catastrophes reduced the survival of plants (but not ray seeds) to zero, (4) both fecundity and survival varied across years.

To model continuous variation in fecundity due to variation in the environment, each year the population-wide fecundity was calculated as:

$$F^* = 2Fe^{X_c - \frac{1}{2}\sigma^2}$$

where

- F population-wide fecundity for the year,
- F base fecundity,
- X_{σ} normally distributed random variable with mean = 0 and SD = σ .

so that over time fecundity had an arithmetic mean of F regardless of the variance, with the geometric mean decreasing with increasing variance. In the absence of a seed bank, multiplying the fecundity by a random variable would affect the entire life-cycle loop equally, so that σ^2 would be analogous to the variance in the log of population growth rate commonly used as a measure of variability in growth rates of natural populations (Morris and Doak, 2002).

To model catastrophic variation in survival, each year there was a defined probability of the population-wide juvenile survival rate equaling zero. This precluded reproduction in that year, but did not affect ray seeds persisting in the seed bank. Therefore, a single catastrophe could never cause the extirpation of a population, even if ray seeds older than one year always attempted to germinate, since all ray seeds spend at least one year in the seed bank.

2.7. Quantifying environmental variability

In the absence of long-term vital rate data for the introduced Elkhorn population, long-term census data from 18 extant natural and introduced populations (assembled from CDFG, 1995 and Barber, 2002) were used to estimate realized variation in population growth rate and the probability of catastrophes. For each population (listed in Table A.1 in Supplementary Data), μ (the arithmetic mean of the log growth rate, or conversely the log of the geometric mean λ for the population) and σ^2 (the variance in log growth rate) was calculated using linear regression (Morris and Doak, 2002). This technique allows the use of censuses with data missing for some years. Years in which zero plants were observed were excluded from the analysis of variance in growth rate and treated as breaks in the data (i.e., regression was not used on two censuses straddling a zero). 95% confidence intervals on μ (Dennis et al., 1991) were calculated for each population (Table 2), and in all cases included both positive and negative values, implying populations could be increasing, stable, or decreasing. Serial autocorrelation in growth rates was not modeled because a Durbin-Watson d -test (Draper and Smith, 1981) revealed no significant serial autocorrelation of growth rates for any population.

The estimates of σ^2 observed for these populations may be used to establish rough comparisons for the values of σ^2 used in the models, although direct comparisons are complicated by the presence and unknown behavior of the seed bank. To assess how much variation would be realized in simulated population trajectories depending on the model σ^2 , 20 replicate simulations of 25 years each were run for different values of σ^2 between 0.2 and 2.4 for populations with ray bank percent germinations of 0.3, 0.6, or 0.9. Using the last 10 years of each simulation, variances in log growth rates were calculated using the same methodology as with the census data.

The probability of catastrophes (no above-ground plants surviving to reproduce) was estimated using data from all populations for which there were at least five years with a

Table 2 – Mean log growth rate (μ) with 95% confidence intervals, variance in log growth rate (σ^2), and estimated incidence of catastrophes for each *Holocarpha* population described in Table A.1 of the Supplementary Data

Population	μ	(95% CI)	σ^2	Incidence of catastrophe
Twin Lakes	-0.47	-1.2-0.2	0.66	-
Arana	-0.41	-1.8-1.0	4	1/13
Airport	0.72	-0.44-1.9	0.87	0/6
Porter	0.14	-0.79-1.1	1	0/8
Graham Hill	-0.086	-0.93-0.76	1.6	0/12
Caltrans	0.44	-0.55-1.5	2	1/13
Mezue	0.19	-0.17-0.55	0.39	0/15
Big Belgium	-0.13	-1.2-0.90	4.3	0/19
Big Belgium West	-0.13	-1.2-0.89	3.7	1/19
Upper Belgium	-0.15	-0.98-0.68	2.6	0/19
Nimitz	-1.4	-3.3-0.54	2.3	4/14
Lower Belgium	0.04	-3.2-3.3	9.4	1/8
Lower Harvey	-0.5	-9.6-8.6	1	-
Fowler	0.036	-1.3-1.3	1.5	0/7
Nimitz Way II	-1.4	-3.7-1.0	2.2	-
Nimitz Way III	-1.1	-5.5-3.4	3.2	2/7
Upper Harvey	-0.57	-3.4-2.2	3.1	-
Belgium Fence	-0.61	-3.1-1.9	2.4	2/8

Dashes indicate populations with insufficient data to estimate the incidence of catastrophes.

population size of at least 20 plants. Any census finding no plants following a census where the population size was at least 10 was considered a catastrophe, while any zero following a population below 10 was excluded from the analysis since catastrophic failures in survival could not be distinguished from extinctions resulting from demographic stochasticity in these cases. Catastrophes were modeled as a binomial process with each population treated as an independent set of observations (since catastrophes were not always in the same year across populations), yielding a maximum likelihood estimate of 0.07 probability of catastrophes occurring in any year with 95% confidence interval of 0.04–0.11.

2.8. Comparing extinction risk under different scenarios

In order to compare the relative extinction risk under different scenarios (clipped vs. control, varied survival and germination of the seed bank, various forms of environmental variability; summarized in Table 3), simulations were projected for 50 years. Any simulation that had a five-year running average (arithmetic mean) adult population below five at any point was counted as a quasiextinction, since such small populations could be at high risk from other factors not incorporated in this model, such as the failure of pollinator services. Extinction risk for each scenario was estimated based on the number of quasiextinctions in 10000 replicate runs.

To determine whether an intermediate percent germination reduced extinction risk, multiple scenarios identical in all respects except for ray seed percent germination (varied from 0.1 to 1.0 in steps of 0.05) were run. Except as noted, all of these simulations assumed ray seeds in the seed bank had an annual survival probability of 0.9. Binomial confidence

Table 3 – Key to different scenarios for which extinction risk of introduced populations were estimated, and pointer to figure with the results

Plants clipped?	Type of environmental variation	Seed bank survival	Ray seed germination	Results
No	Varying fecundity only	0.80/0.90/0.95	0.05–1.0	Extinct
No	Catastrophes only	0.80/0.90/0.95	0.05–1.0	Extinct
No	Catastrophes and varying fecundity	0.80/0.90/0.95	0.05–1.0	Extinct
Yes	Varying fecundity only	0.80/0.90/0.95	0.05–1.0	Fig. 4a
Yes	Catastrophes only	0.80/0.90/0.95	0.05–1.0	Fig. 4b
Yes	Catastrophes and varying fecundity	0.80/0.90/0.95	0.05–1.0	Fig. 4c

A result of “extinct” means all combinations of seed bank survival and germination resulted in extinction, so no figure is presented.

intervals (Clopper and Pearson, 1934) were calculated for each extinction risk estimate based on the number of extinctions observed and the total number of trials.

These estimates of extinction risk do not incorporate uncertainty in measured vital rates. Prior experience with data sets based on larger populations and more years suggests that confidence intervals on extinction risks that incorporate parameter uncertainty are likely to include both zero and one in most cases (Ludwig, 1999; Satterthwaite et al., 2002), so the numbers presented here are not intended to quantify precisely the danger faced by *Holocarpha* populations. Rather, they are best used to compare the likely efficacy of different management strategies and the importance of various parts of the life cycle (Beissinger and Westphal, 1998).

3. Results

3.1. Deterministic analyses

For control plots, populations are predicted to decline regardless of ray seed survival or germination ($\lambda < 0.90$ even for 95% ray seed survival). For low ray seed germination, seed bank survival (S_r) has the highest elasticity (Fig. 2a), since persistence of the seed bank is vital to slowing the decline of the population. As ray seeds germinate more quickly, ray seed germination (G_r) has an increasingly negative elasticity, since germinating seeds cannot replace themselves, and depleting the seed bank hastens the decline of the population.

For clipped plots, λ increases with increased ray seed germination and populations are predicted to grow only if there is some germination from the seed bank (95% confidence interval on $\lambda = 0.20$ – 0.61 if there is no contribution from the seed bank). Seed bank survival again has the highest elasticity when ray seed percent germination is low, since persistence of the seed bank slows the decline predicted for populations with only minimal contributions from the seed bank (Fig. 2b). As ray seed germination increases, the performance of aboveground plants, especially juvenile survival, becomes progressively more important to population growth. The elasticity of percent ray seed germination is consistently low but positive, indicating that proportional changes in germination will have smaller effects on population growth rate than changes in the performance of adult plants, although the deterministic growth rate will always increase with increasing ray seed germination. While results shown are for 0.9 survival in the seed bank, changing ray seed survival to 0.8 or 0.95 yielded nearly identical results (data not shown).

When using the much higher estimates of fecundity from the Porter population, λ was estimated to be substantially greater (2.04–2.76 depending on the contribution from ray seeds). While even larger increases in population size for a single year are not unprecedented (Table A.1 in Supplementary Data), it is unlikely that population growth is this rapid every year. Given these very high estimates of fecundity and seedling survival, the elasticities for disk seed production and seedling survival were much higher than the elasticities for ray seed survival or germination (Fig. 2c). This hypothetical population is predicted to grow so fast that the delayed contribution of ray seeds, which remain in the soil for at least one more year than disk seeds, can make only minor contributions to the population growth rate.

3.2. Stochastic analyses

Variances in log growth rates for simulated populations were lower than the input values of σ^2 (Fig. 3), with the difference reduced as the germination of ray seeds increased, reflecting the buffering effect of the seed bank. Thus it may be most appropriate to consider models using input values of σ^2 slightly greater than the values calculated from census data.

Extinction appears inevitable for stochastic model populations using vital rates from control plots, regardless of seed bank survival and germination or the amount and type of environmental variation (data not shown). For clipped plots, any percent germination of 0.2 or greater resulted in persistence in the absence of environmental variability, given annual seed bank survival of 0.9. Continuous variation in fecundity alone created the risk of extinction (Fig. 4a), with increased variance leading to increased extinction risk. Given $\sigma^2 = 0.2$ the probability of extinction was minimized by complete germination from the seed bank and the probability of extinction did not decrease significantly for intermediate germination given $\sigma^2 = 0.4$. For all simulations using higher values of σ^2 , extinction probability was minimized at some intermediate percent germination, although the reduction was never more than 9% of the extinction risk given complete germination. Extinction appeared virtually certain for σ^2 values of 2.4 or above, which is within the range of σ^2 estimates for natural populations.

When environmental variation was modeled as catastrophes alone, an intermediate percent germination always resulted in a significantly reduced probability of extinction (Fig. 4b). The effects on extinction were more pronounced than in the case of variation in fecundity alone, with the

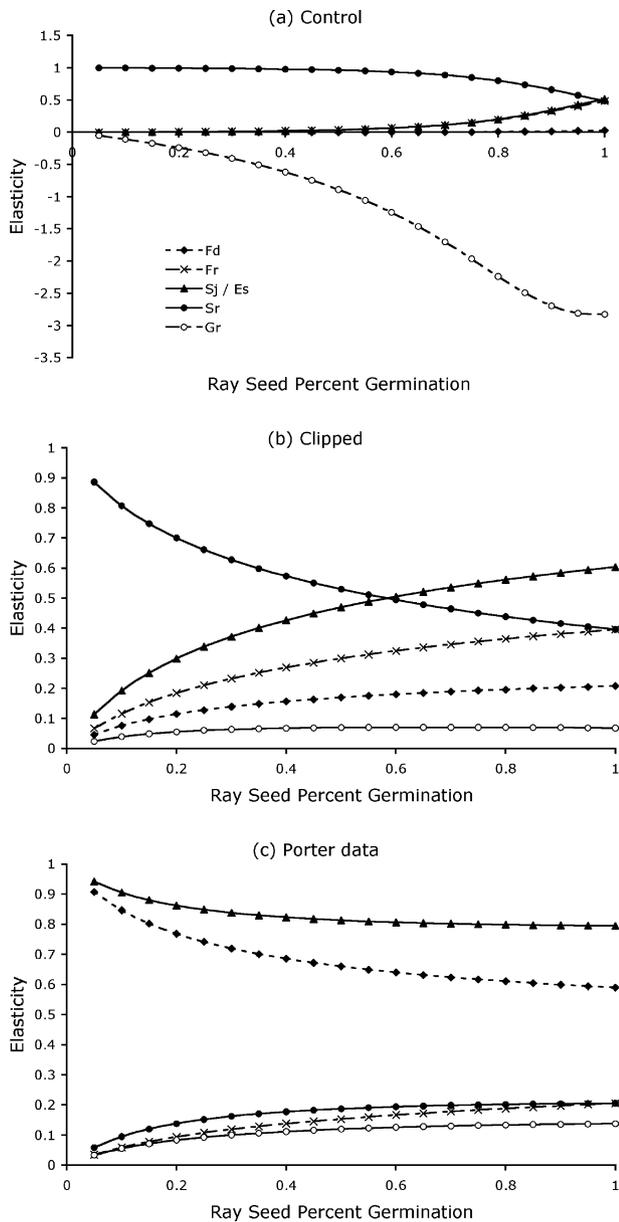


Fig. 2 – Vital rate elasticities in growth rate vary with percent ray seed germination in (a) control and (b) clipped populations. Panel c presents elasticity analyses for clipped populations with ray disk seed production increased to the values observed in the Porter population. Ray seed survival in the seed bank is 0.9, for extinction risk $\sigma^2 = 0.4$ and the annual probability of catastrophes = 0.07. Note that growth rate elasticities for emergence and juvenile survival are identical, since any path through the life cycle that includes one of these transitions must include the other.

extinction risk reduced by as much as 74% of the peak risk when the annual probability of catastrophe was 0.04. For every simulation incorporating variation in both fecundity and catastrophes (Fig. 4c), intermediate percent germination significantly reduced extinction rates, never by more than 9%.

Given a fixed $\sigma^2 = 0.4$ and probability of catastrophe = 0.07, the efficacy of intermediate germination in buffering against

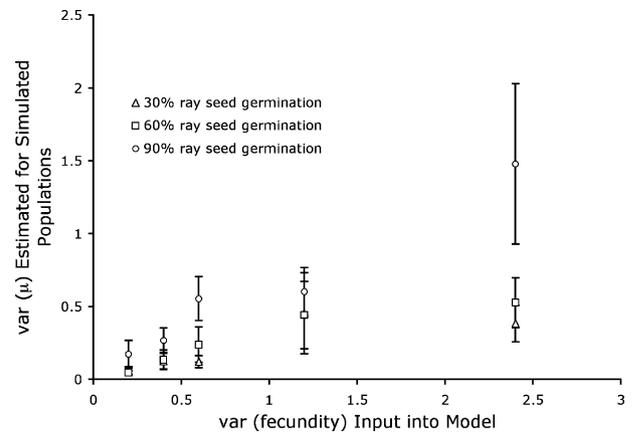


Fig. 3 – Variance in log growth rate of 10-year simulated population trajectories is lower than the value of σ^2 for fecundity input into the model. The difference increases as the proportion of ray seeds germinating each year decreases. $n = 20$, error bars represent $\pm 2SE$.

extinction depended strongly on seed bank survival (Fig. 5). For seed bank survival of 0.95, the optimal percent germination reduced extinction risk by 35%. When seed bank survival was reduced to 0.9, the optimal percent germination yielded only a 9% decrease in extinction risk, while there was no significant reduction in extinction risk given seed bank survival of 0.8.

3.3. Extant populations

In 12 of 18 populations, the best estimate of long-term population growth rate was negative (Table 2). However, in all cases population growth rate was so variable from year to year that 95% confidence intervals on mean growth rate included both positive and negative values for all 18 populations.

4. Discussion

4.1. Fostering population growth in *Holocarpha*

Clearly, clipping or some equivalent ongoing management strategy like mowing or grazing should be employed on the introduced *Holocarpha* populations at Elkhorn, as rapid decline is predicted for the unmanaged control populations regardless of seed bank dynamics. This result concurs with other experiments on both introduced and natural populations (Bainbridge, 2003; Holl and Hayes, 2006). We suggest that clipping or equivalent treatments should also be a high priority for other extant *Holocarpha* populations, since long-term decline cannot be ruled out in any of them. Comparing the performance of clipped and unclipped populations suggests that poor performance of adult plants rather than the lack of an established seed bank was likely the main cause of failure for the unclipped population introductions carried out by Holl and Hayes (2006).

In the absence of management actions enhancing the performance of aboveground plants, treatments to stimulate germination from the seed bank would not be wise

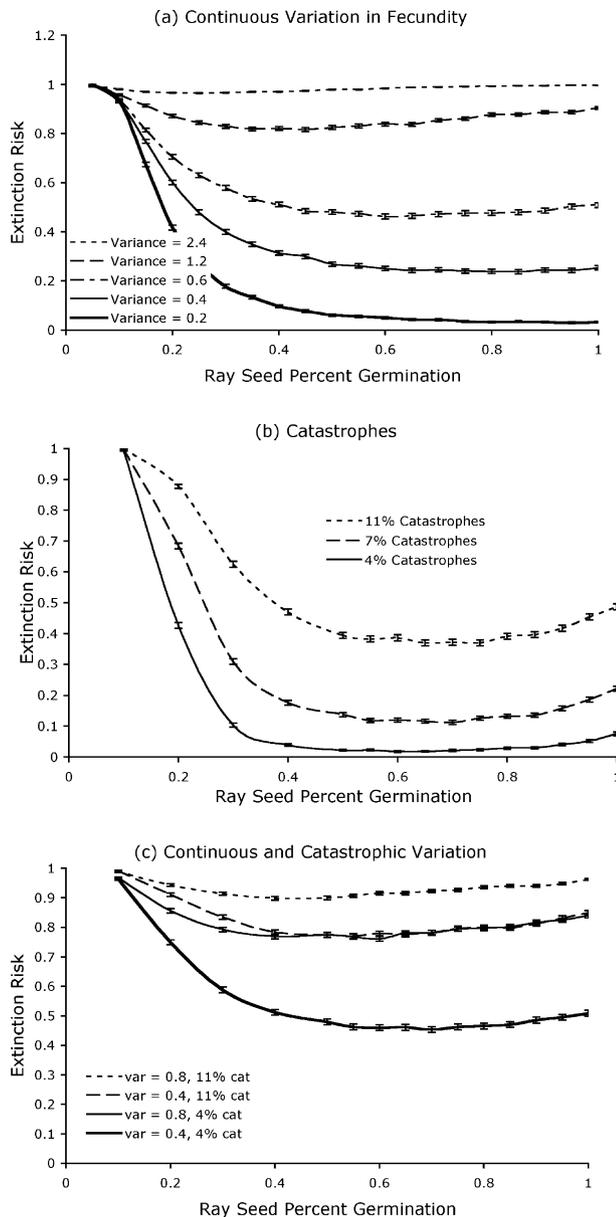


Fig. 4 – An optimal level of delayed germination slightly reduces extinction risk given only continuous variation in the environment (a), while reducing extinction risk more strongly given catastrophic variation in the environment (b) or both continuous and catastrophic variation (c). All simulations assume 0.9 annual survival of ray seeds in the seed bank. Error bars are binomial 95% confidence intervals.

for populations like the Elkhorn introduction. Given fecundities and establishment success as low as those in the control plots, stimulating germination will simply hasten population decline, while also reducing the ability to buffer against environmental variability.

Our results clearly indicate that accurate assessment of the viability of both introduced and natural populations of *Holocarpha* requires good information on seed bank densities and dynamics should be a high priority. Experiments and monitoring efforts to determine seed bank densities and dynamics should be a high priority. Experiments should also be designed to look for age-specific seed

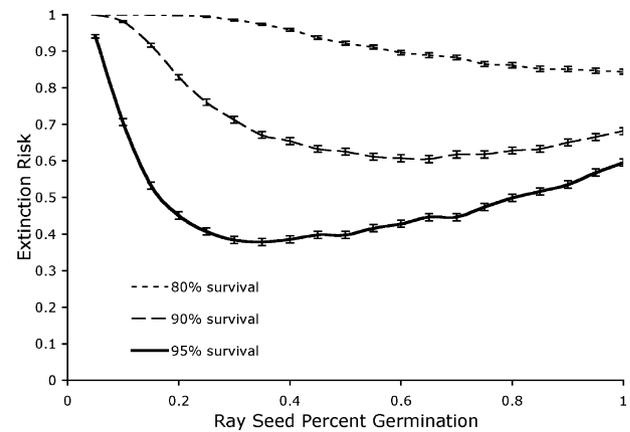


Fig. 5 – Reduced survival of ray seeds in the seed bank increases extinction risk and reduces the advantage of an optimal level of delayed germination. Error bars are binomial 95% confidence intervals.

demography, as the exponential decay model used in this study does not describe the seed biology of all species with seed banks (Baskin and Baskin, 1998).

With clipping, long-term survival of restored populations at Elkhorn seems possible, but only with some contribution from the seed bank. However, elasticity analyses suggest that a proportional change in juvenile survival brings about the biggest boost in population growth rate, and proportional increases in seed production would also enhance population growth more than proportionally increased ray seed germination. It would be worth exploring the effects of additional management options to increase juvenile survival, such as supplemental water or herbivore control (Maze, 2004).

The observation that patterns in the relative elasticities of different life history transitions varied substantially between control, clipped, and hypothetical high fecundity populations highlights the importance of performing elasticity analysis on transition rates using the values expected for managed plots, rather than relying on a single analysis of a population matrix constructed from an unmanaged population (Mills et al., 1999; Satterthwaite et al., 2002; Quintana-Ascencio et al., 2003). This is especially important when management actions are likely to produce large changes in some transition rates, and when these changes cause a previously declining population to increase, as would be hoped for with successful management. This requires that scientists and managers collaborate to set up manipulations in a comparative manner and to collect and analyze data to allow for adaptive management (Holl et al., 2003).

If vital rates are radically different for natural populations, the results of elasticity analyses from these introduced populations may not apply to them. However, even in analyses using the much higher estimates of fecundity from the Porter population, juvenile survival still had the highest elasticity and the elasticity of ray seed germination remained very low even using these greatly boosted estimates of fecundity (Fig. 2c vs. 2b). Most of the natural populations are smaller

than Porter and likely have substantially lower fecundity every year, and thus are more similar to the introduced populations.

4.2. Seed bank in long-term population viability

When environmental variability was modeled as continuous variation in fecundity alone, the accumulation of a seed bank provided a small but significant reduction in the risk of extinction. The advantage accorded by the seed bank increased when models included the possibility of catastrophes, which is likely appropriate for natural populations of *Holocarpha* and other annual species in variable environments. Several populations experienced at least one catastrophe since 1978 (Table 2) and catastrophic extirpations (even without obvious human impact) of plants have been documented in multiple environments (e.g. Baskin and Baskin, 1980; Menges, 1990). This reinforces the point that catastrophes need to be incorporated into PVAs whenever possible (Mangel and Tier, 1993). The need to estimate probabilities of catastrophes highlights the value of long-term census (or even presence–absence) data in addition to detailed studies of individual vital rates.

Clearly, detailed knowledge of seed bank dynamics is critical to evaluating how to manage species with seed banks for conservation, but current monitoring efforts for *Holocarpha* (and indeed almost all endangered plants) focus exclusively on aboveground plants. This study reiterates the need for monitoring programs and assessments of species' critical habitat, to consider the number and locations of seeds in the seed bank as well as aboveground plants (Adams et al., 2005).

If populations have vital rates such that they are predicted to decline rapidly without increased contribution from the seed bank, germination should be stimulated – at least if other vital rates have low elasticities or appear to be at or near their maximum levels already. For most situations, however, we advise caution in stimulating germination from the seed bank. Before taking management actions that could deplete the seed bank, managers need to consider the possibility of catastrophes or extreme environmental variance, even with no direct evidence of such extreme variability in the recent past, as short-term censuses will tend to underestimate the level of environmental variance and the occurrence of rare events (Morris and Doak, 2002). Seed bank longevity may also be a key factor in determining whether to stimulate germination for a species of concern. The capacity of a seed bank to buffer variability is reduced, and the costs of delaying germination are increased, as seed longevity decreases. This would suggest employing strategies to stimulate germination more often for plants with short-lived seed banks, taking care not to completely deplete the seed bank.

4.3. Conclusions – priorities for *Holocarpha* management and research

We recommend that managers of existing *Holocarpha* populations focus on actions that will increase the performance of aboveground plants, rather than taking actions to stimulate germination that may deplete the seed bank and reduce its

capacity to buffer populations against environmental variability. For large populations, clipping or mowing may be the most cost-effective alternatives and have been shown to benefit *Holocarpha*. For small populations, we recommend a similar approach if resources are very limiting, although it would be useful to compare indiscriminate clipping with more targeted efforts to eliminate exotic plant competitors while promoting the growth of *Holocarpha* through targeted watering and herbivore control. Future research into the biology of *Holocarpha* should focus on determining seed bank survival and germination rates and identifying the triggers for ray seed germination in the field. Monitoring efforts would benefit from incorporating estimates of seed bank densities.

Given the limited success of past introductions (Holl and Hayes, 2006; East Bay Regional Parks, unpublished data), the protection and enhancement of existing populations should take priority over further introduction attempts. Introductions should only be attempted if sufficient resources are available for ongoing clipping or other management, and should ideally be designed as experiments that will fill in gaps in our knowledge of the *Holocarpha* life cycle or compare methods of promoting plant growth and seed production.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2006.09.018](https://doi.org/10.1016/j.biocon.2006.09.018).

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