15

Population Viability Analysis for Plants: Understanding the Demographic Consequences of Seed Banks for Population Health

Daniel F. Doak, Diane Thomson, and Erik S. Jules

ABSTRACT

Many plants share life-history traits that greatly complicate estimation and use of demographic data for viability assessment: large and long-lived seed banks and relatively large temporal variation in demographic rates. Seed banks are especially vexing because they are governed by demographic rates that can be extremely difficult to quantify, especially over the short time periods typically available for conservation planning. Furthermore, if seed banks are demographically important, census and demographic information for adult populations alone may yield misleading information about population viability. Following a survey of how past studies have dealt with these problems, we use simulation models to explore the implications of imperfect seed bank data for conservation planning. Our results emphasize how poor or misleading data on seed banks and demographic variability can alter estimates of extinction times and population growth rates for plants, and how these problems vary with plant life history. Most worrisome is the need for good estimates of environmental variance to qualitatively assess how seed banks will influence population viability analysis results. Finally, we discuss reasonable ways to construct population viability analyses for plants, given the sparse and possibly misleading data usually available.

INTRODUCTION

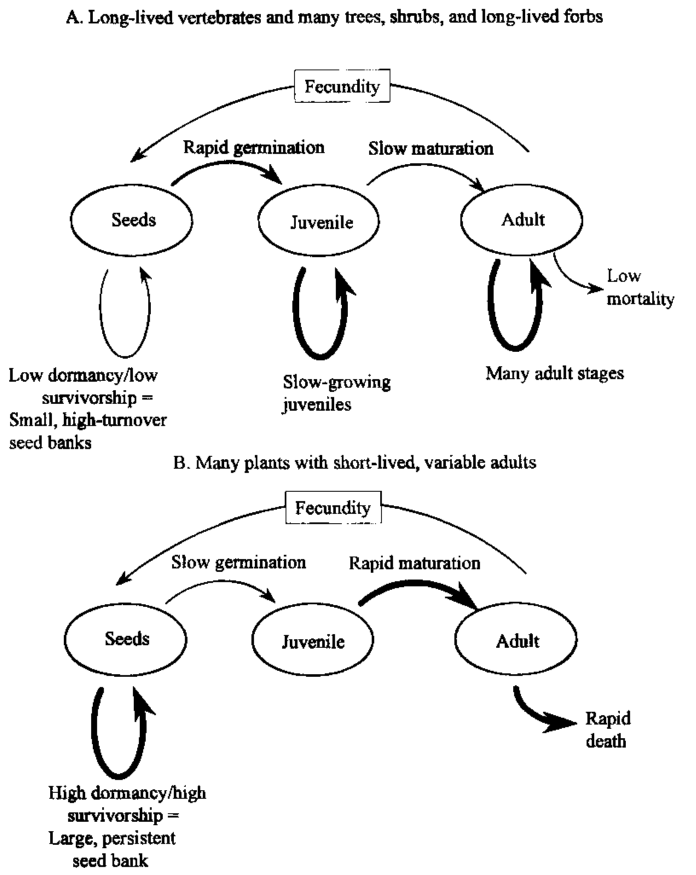
Since the inception of population viability analysis (PVA), both its practice and underlying research on extinction processes largely have focused on animal (mostly vertebrate) species, rather than plants, fungi, water molds, or other major taxonomic groups. This emphasis resulted in part from simple anthropocentrism and in part from the unique legal protections enjoyed by vertebrates in many countries. Perhaps as importantly, much more demographic information is available for many rare vertebrates than exists for endangered species of other taxa. While the basic theory underlying PVAs is not taxon- or life-history-specific, ecologists typically use demographic data to tie general ideas of stochastic growth and extinction to particular populations. In this chapter, we explain the difficulties of obtaining and using adequate demographic data to conduct PVAs for many plants and explore the consequences and possible solutions to these problems.

For many plants, PVAs are not hard to do. Some herbs, and many trees and shrubs, have life histories very similar to those of the vertebrates for which the most informative PVAs are conducted. For example, the life history of the Madagascar triangle palm (*Neodypsis decaryi*; Ratsirarson et al. 1996) is essentially identical to that of a loggerhead sea turtle (*Caretta caretta*; fig. 15.1A); both have high and variable mortality during the ephemeral "newborn" stage, a prolonged juvenile phase with slow growth and increasing annual survival, and finally, a long-lived, high-survival adult period. In this case, there is no sense in which the plant is any more difficult to study than the animal, and many ways in which it is easier (e.g., most life-history stages don't move).

However, this life history is at one extreme of a continuum for plants. Other species follow a very different pattern that is less easy to study. The crucial features of these life histories are relatively stable, long-lived, dormant, or resting stages (seeds, cysts, etc.), often coupled with shorter-lived and less environmentally buffered adult stages. In addition to short-lived plants, this life-history pattern is common among many freshwater invertebrates, some marine algae, and other taxa (Hairston et al. 1996; fig. 15.1B). The importance for PVAs of the seed or cyst banks found in these groups can be thought of in two ways. First, from the most practical viewpoint, these cryptic, often buried, parts of the life cycle are hard to study and their demographic rates difficult to quantify. Second, long-lived resting stages serve to decouple the two life-cycle roles most important for population viability: reproduction and buffering against environmental variation. In most vertebrate life histories, adults are more physiologically and behaviorally buffered against the vicissitudes of their biotic and abiotic environments than other life-history stages; they also constitute the part of the life cycle that directly contributes to population growth. In contrast, for many plants these two functions are performed by very different parts of the life cycle. Dormant seeds in particular do not reproduce, but may be the crucial stage in buffering populations against environmental variability.

Our goals in this chapter are to briefly describe life histories featuring

We thank Alison Graff, Caroline Christian, and Ingrid Parker for very helpful discussion that led to many of the ideas presented. Steven Beissinger and Dale McCullough provided helpful editorial comments. Partial support for this work came from the following NSF awards: DEB-9806722 (to Doak and Jules), DEB9424566 (to Doak) and DEB-9902269 (to Thomson and Doak).


A. Long-lived vertebrates and many trees, shrubs, and long-lived forbs

B. Many plants with short-lived, variable adults

Fig. 15.1 Extremes of plant life-history strategies. *A,* Many plants show life histories qualitatively identical to those of many vertebrates, with long-lived, environmentally buffered adults, weak and catastrophe-prone offspring, and slow maturation. *B,* At the other extreme, many "short-lived" plants exhibit long-lived, highly buffered, and high-dormancy seeds. After breaking dormancy, the resulting juveniles quickly mature to become reproductive adults. This life history is shared by many freshwater invertebrates, fungi, and other species.

seed banks, explore the problems that they generate for PVA, and suggest some possible approaches to overcoming these difficulties in the analysis and management of rare plant species.

SEED DORMANCY AND SEED BANKS

Seed dormancy is an inactive state characterized by reduced respiration and the suspension of embryonic growth. This dormant stage can arise in two general ways: innate (intrinsic) dormancy and enforced (extrinsic) dormancy. In seeds with innate dormancy, factors such as immaturity of the embryo, impermeability of the seed coat, chemical inhibition, or the lack of required environmental cues prevent germination upon release from the parent plant (Rees 1997). Enforced dormancy operates independently of innate dormancy, arising when requirements for germination are not present (e.g., light or water; reviewed in Baskin and Baskin 1998). When seed longevity is high relative to seed production by adults, a substantial "bank" of living seeds may form in the soil. For species with such life histories, successful PVAs depend on the recognition that seeds are individuals in the population, just as are aboveground, photosynthetic plants, and that their demography is important for an understanding of population viability.

Dormant seeds can play an essential role in population growth and persistence, both by virtue of their sheer abundance and because seeds are often less subject to environmental variation than are aboveground individuals. For some species, the seed bank may contain most of a population. Epling et al. (1960) estimated that seeds made up 94 to 97% of the population of the Mojave Desert annual *Linanthus parryae* (15 to 30 seeds for every aboveground plant) and that ungerminated seeds remained viable for up to seven to ten years. Populations of annuals with sporadic reproductive failures provide the most dramatic examples of environmental buffering by seed banks. For example, a population of the winter annual *Sedum pulchellum* in north-central Kentucky that suffered complete mortality of aboveground plants prior to seed production during a drought year subsequently recovered entirely from seed bank recruitment (Baskin and Baskin 1980; see also McCue and Holtsford 1998). Adults of many perennial plants may also experience extreme variation in demographic performance through time (Steenbergh and Lowe 1977, 1983; Burgman and Lamont 1992). For some of these species, too, a seed bank may be crucial for population persistence if seeds are less subject to environmental variation than are aboveground members of the population.

Available evidence suggests that seeds of many plant species can remain viable in the soil for extremely long periods of time (Baskin and

Baskin 1998). For example, *Trifolium trichocalyx*, an endangered fire-dependent annual endemic to Monterey pine forests of California, recruited from a seed bank where it had not been observed for 86 years (U.S. Fish and Wildlife Service 1998). Extreme examples of long-term seed storage include radiocarbon-dated seeds of sacred lotus (*Nelumbo nucifera*) collected from a dry lake bed in China germinating after 1,288 ± 271 years (Shen-Miller et al. 1995) and viable seeds of *Lupinus arcticus* found in frozen silt with the skull of a collared lemming (*Dicrostonyx groenlandicus*) that had been extinct from the area for 10,000 years (Porsild et al. 1967). The frequency of such extreme seed longevities is unknown. However, these cases suggest that dormant seeds can be extraordinarily long-lived, and that understanding the survival and germination rates governing the demography of such seeds may be very difficult.

Experimental data on seed longevity in seminatural conditions are available for over 500 species from at least 33 different studies (reviewed in Baskin and Baskin 1998). Seed survivorship is generally inferred by measuring seedling emergence. This approach misses two important components of survivorship: germination without seedling establishment and seed mortality (Rees and Long 1993). Furthermore, while most of these studies examined buried seeds in natural conditions, many used greenhouse trials to determine germination rates. This almost certainly overestimates germination rates of naturally buried seeds, where enforced dormancy (e.g., by lack of light) frequently inhibits germination. Nonetheless, these studies reveal much about the size and temporal variation of seed banks. Figure 15.2 shows germination rates of known numbers of seeds over a five-year period. The negative exponential germination curve shown by two of the species is typical of many plants and is frequently assumed to describe seed survivorship over long time periods (Rees and Long 1993). However, the wide variety of other emergence patterns (fig. 15.2) suggests that such inferences are dubious. Rees and Long (1993) reanalyzed data collected by H. A. Roberts and colleagues for 145 plant species and concluded that a negative exponential pattern should not generally be assumed to predict seed bank decay.

Two basic messages emerge from this brief review of seed biology. First, understanding seed banks is essential for constructing PVAs of many plant species. While seed banks are often considered separately from the aboveground population, both their numbers and capacity to buffer populations make seeds crucial individuals to account for in plant populations. Second, as for other life-history stages, the demographic behavior of seeds can be summarized with a few conceptually simple, but probably age-dependent, demographic rates. In general, to describe seed demography one must estimate three sets of parameters: age-dependent germination rates of seeds, age-dependent survival rates of nongerminating seeds, and production of new seeds by reproductive plants (fig. 15.1). With this simple framework for incorporating seed banks into PVAs, we next look for precedents in the study of seed bank demography.

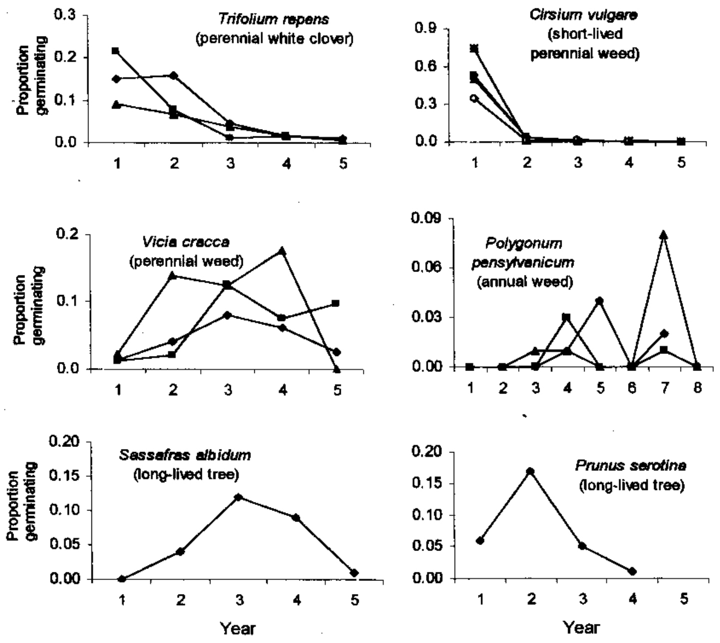


Fig. 15.2 Experimentally determined seed germination rates with increasing seed ages. Germination curves for *Cirsium vulgare* and *Trifolium repens* show classic negative exponential declines in emergence, indicating roughly constant seed germination and survivorship rates. In contrast, data for four other species show evidence of prolonged dormancy and/or variable survivorship. Different lines for each species correspond to different cohorts. Data from Roberts and Boddrell (1985), Toole and Brown (1946), Wendel (1977), and Roberts and Chancellor (1979).

HOW HAVE SEED BANKS BEEN INCORPORATED IN PVAs AND OTHER DEMOGRAPHIC STUDIES?

Given that seed banks can be large, long-lived, complex, and difficult to quantify, how have plant demographers typically incorporated seeds into their analyses? We surveyed 70 demographic studies of herbaceous plants and relatively short-lived shrubs, for both rare and nonrare taxa, to assess how they addressed seed banks. Our sample included 34 studies of herbaceous plants compiled by Silvertown et al. (1993) and an additional 36 located through literature searches. Of the 70 total studies, 22 addressed at least one rare species (a list of these studies is available from the authors).

We first determined which studies provided information on seed dormancy of the focal species. If the study mentioned dormancy, we then assessed whether data were available or were collected on the seed bank. Of the 70 studies, 25 did not mention seed banks (fig. 15.3A). Six of the studies stated, or cited evidence, that seed banks were unlikely to be important for the focal species. However, the majority of studies that mentioned seed banks also collected some form of data on dormancy; in only five cases were seed banks mentioned as potentially important and not studied.

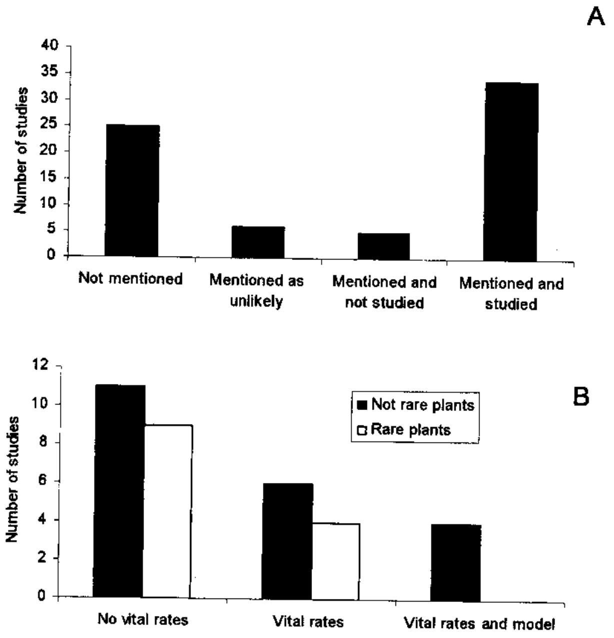


Fig. 15.3 Treatment of seed demography in 70 demographic studies of rare and common plants. *A*, While many studies do not mention the existence of a persistent seed bank, most that do mention it report some data collected to quantify seed demography. *B*, Of the 34 studies involving study of seed banks, the majority did not estimate seed vital rates and, thus, would not allow inclusion of dormant seeds in a demographic analysis.

We next categorized the 34 papers with information on seed banks by the type of data gathered and how the data were incorporated into demographic analyses. Some data on the seed bank, but not age-specific germination or survival rates, were collected in 20 studies (fig. 15.3B). Ten studies measured at least some age-specific vital rates for seeds, under either field or lab conditions. Finally, four studies both measured age-specific rates and incorporated them into some form of population modeling. The first category included studies that carried out viability or germination trials with seeds collected from soil cores but not with seeds of known age, in addition to several cases in which few data were available on dormancy but some form of seed bank was still included in a population model. Although the proportion of studies falling into each category was similar for both rare and nonrare species (fig. 15.3B), it is notable that we were unable to locate any studies for rare plants that both measured seed vital rates and incorporated them into a quantitative population model.

Thus, while seed banks have clearly received a fair amount of attention in demographic studies of both rare and nonrare plants, data adequate for carefully assessing the effects of dormancy on population persistence are rarely available, even for common and well-studied species. This is not surprising, considering how difficult and time consuming it can be to collect such data (e.g., Kalisz 1991). Indeed, plant demographers usually have to make various assumptions about seed survival and germination to include seed banks in their analyses at all (e.g., Gross et al. 1998).

GENERALIZATIONS TO COMPENSATE FOR IGNORANCE

Given the lack of empirical data on seed bank demography, what can we do to address dormancy in PVAs of rare and poorly studied species? An alternative to intensive, long-term studies of seed bank dynamics for individual rare species is to rely on general patterns of variation in seed survivorship and germination among habitats and life-history strategies. Such generalities, if robust, could be used to predict the existence or absence of a substantial seed bank and perhaps even something about its governing vital rates. A considerable body of theory has sought to predict optimal seed dormancy rates as functions of adult life span, habitat variation, and other factors (reviewed by Rees 1997). This theoretical work has largely been concerned with understanding the evolutionary trade-offs between the costs of seed dormancy, which result from the negative effects of delayed reproduction on deterministic population growth, and the benefits of increased buffering from environmental variation (e.g., Ellner 1985a,b, 1997). Dormancy can be understood as a mechanism of escape from unfavorable conditions in time, just as dispersal represents escape in space (Levin et al. 1984). A crucial point to reemphasize here, and one that will assume added importance later, is that increased dormancy (i.e., decreased germination rate) has a direct, immediate cost for individuals and for population growth: a nongerminating seed is delaying reproduction and increasing the possibility of death before ever reproducing. As a result, theory predicts that the strength of selection for dormancy in a particular plant population should vary depending on the need for buffering imposed by the habitat and the degree of investment in other life-history traits, such as long adult life span and long-distance dispersal, that are also mechanisms for persisting in variable environments.

Theoretical predictions about optimal dormancy rates are broadly intuitive. Greater dormancy should be favored as environmental variability increases (Ellner 1985a,b); one of the earliest and simplest evolutionary models of dormancy predicts that the optimal germination rate should decline linearly with the probability of complete reproductive failure in any given year (Cohen 1966). Similarly, sibling-sibling competition among germinating seeds or strong inhibition of seedlings by established vegetation can also select for higher dormancy (Ellner 1986). At the same time, good dispersers should rely less on dormancy than species with seeds that are not well adapted for dispersal (Levin et al. 1984). Both dormancy and dispersal ability, however, may also be affected by trade-offs with adult life span and seed size and shape (Venable and Brown 1988). Thus, long-lived adults buffer against the effects of poor years, obviating the need for dormant stages. Large seeds are less likely to be buried at soil depths conducive to long-term dormancy than small seeds. They are also generally better provisioned, and thus able to establish more successfully under a range of environmental conditions. Small-seeded species are therefore more likely to evolve strong dormancy. At the same time, small seeds are also more likely to disperse well, potentially reducing selection for dormancy.

While the basic predictions of theoretical models are relatively straightforward, it is not easy to untangle this set of potential trade-offs and arrive at simple rules for predicting when seed banks should be important. In fact, providing strong empirical support for these predictions has proved extremely difficult. Thompson et al. (1998) found that mean seed longevity in northwest Europe, measured on a qualitative scale, correlated with habitat type; species occurring in presumably less

variable environments, such as woodlands,
age than those from more disturbed hab
and Venable (1995) showed a weak but si
between variability in reproductive succes
average germination rate for a group of de
species more subject to environmental va
mancy. Similarly, Rees (1993) found a w
tween adult longevity and seed longevity.
(1998) showed that average burial depth co
ite measure of seed size and shape, and t
but significant predictor of longevity.

While these correlations generally supp
they explain only small amounts of the var
are generally significant only when multip
for, such as seed weight (Pake and Venable
eny (Rees 1993). In some cases, the data
prediction about dormancy, such as long-te
success, may be no faster or easier to coll
seeds. Finally, and perhaps most critically
available to test these predictions are bot
toward agricultural weeds. Of the 33 stu
(1998, table 7.5) cite as measuring seed lon
only 11 were ten or more years in duratio
results from 14 of these studies, including
ten years or more. For many of the 179 spec
seed longevity equaled, and almost certa
the study, making it difficult to resolve ac
between species. Worst of all from the pers
only 25 of the species included in these
15.4B).

DOES LACK OF KNOWLEDGE REALLY

The preceding review emphasizes the lack
for most plant species and the lack of pow
allow us to predict seed bank importance f
of the environment or aboveground life
information, how should one proceed in
species? A more specific and useful set of q
important are seed bank dynamics in deter
extinction rates? If seed banks are sometin
the ways in which ignoring them will chan
which life histories are these omissions

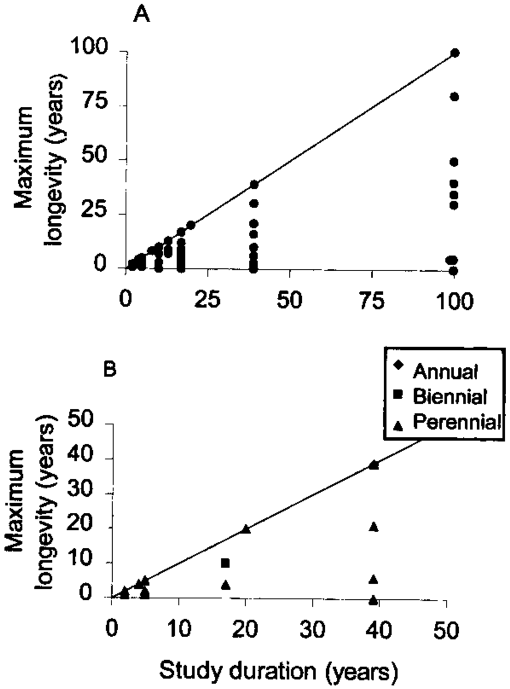


Fig. 15.4 Estimates of seed longevity for 179 species (references compiled in Baskin and Baskin 1998). We report maximum measured longevity as a function of study duration. *A*, Results for all species. *B*, Results for the 25 nonweedy species included in this sample.

simulation models, we next explore each of these issues. Although the results do not provide clear-cut answers, they do suggest how to approach such problems for species of concern.

We developed a stochastic matrix model to simulate a range of plant life histories in variable environments. The model is parameterized with the means and standard deviations (SD) of each demographic rate. Except for fecundity, each demographic rate was drawn from a beta distribution (bounded by zero and one) in each year of a simulation. To create reasonable, bounded distributions for seed production (i.e., no negative numbers and no infinitely large values), we again drew values from a beta distribution and rescaled the values to reflect the desired mean, SD, and maximum. Variations in all vital rates were correlated with a single environmental driving variable, *E*, that fluctuated randomly. In some simulations we also included first-order autocorrelations in environmental variation (i.e., positive correlations in the state of the environment from year to year).

To make these simulations more realistic, as well as sensitive to seed bank effects, we started with small population sizes (ten adult plants), enforced a crude but realistic form of density-dependence by establishing a cap on total adult population size (100 individuals), and allowed simulations to run for 100 years. In different simulations we systematically varied mean seed germination and survivorship rates. When varying the means of these probabilities, we also rescaled SDs to keep variation proportional to means (Doak et al. 1994; Link and Hahn 1996). We also varied the SD of adult survivorships, altering these values from the estimated rate to the maximum possible value (Evans et al. 1996). To summarize simulation results, we use three common measures of population health: probabilities of extinction over set time horizons, times to extinction, and population growth rates.

To parameterize the model, we needed sets of demographic information including data on seed banks and estimates of both the mean and variation in each demographic rate. We found only a handful of studies with estimates of the demographic rates of both adults and seeds under field conditions, particularly for nonweedy taxa. We constructed matrices based on published data for two of these species, each with high seed dormancy but with otherwise contrasting life-history strategies: *Collinsia verna*, a winter annual that occurs in floodplain forests of the eastern United States (Kalisz 1991), and *Calathea ovadensis*, a short-lived perennial herb found in tropical rain forests (Horvitz and Schemske 1995; see tables 15.1 and 15.2). The *Collinsia* data set consisted of demographic rates measured in two different years, while four years of data were available for *Calathea*. In both cases, spatial variabil-

Table 15.1 Mean Matrices for Simulated *Collinsia* and *Calathea* Life Histories

$$\begin{array}{l} & \text{Seed} & \text{Plant} \\ \textbf{Seed} & \left[\begin{array}{c} (1-g_0)s_s \\ g_0 s_s \end{array}\right. & \left.\begin{array}{c} s_{ad}f(1-g_n) \\ s_{ad}f g_n \end{array}\right] \\ \textbf{Plant} & & \end{array}$$

Parameter	Symbol	Mean	Standard Deviation
Fecundity	f	19.18	11.77
Survival from germination to reproduction	s_{ad}	0.226	0.0157
Germination rate of newly produced seed	g_n	0.282	0.1407
Germination rate of seeds in the seed bank	g_o	0.07	0.071
Seed survival	s_s	0.115	0.0778

Notes: *Collinsia* demography is based on table 2 in Kalisz (1991), for transect 3 only, assuming a census immediately following germination. We assumed that the same survivorship rate applied to both germinating and nongerminating seeds.

Table 15.2 Mean Matrix and Demographic Rates for Simulated *Collinsia* and *Calathea ovadensis* Life History

$$\begin{array}{l|ccc} & \text{Seed} & \text{Seedling} & \text{Plant} \\ \hline \text{Seed} & s_s(1-g) & 0 & s_a f \\ \text{Seedling} & s_s g(1-gr_1) & s_j(1-gr_2) & s_a sr \\ \text{Plant} & s_s gr_1 g & s_j gr_2 & s_a(1-sr) \end{array}$$

Rate Description	Symbol	Mean	Standard Deviation	Correlation
Fecundity	f	9.052	4.622	−0.044
Adult survival	s_a	0.831	0.064	0.802
Juvenile survival	s_j	0.096	0.019	−0.997
Growth from juveniles to adults	gr_2	0.809	0.166	−0.475
Shrinking from adult to juvenile	sr	0.005	0.010	0.333
Growth from seed to plant	gr_1	0.034	0.047	−0.983
Germination of seeds	g	0.284	0.237	−0.955
Seed survival	s_s	0.599	0.00	1

Notes: Calathea demography is based on Horvitz and Schemske (1995), for plot 2 only. We collapsed all adult size classes into a single category (plants), then decomposed the transition probabilities into the underlying demographic rates based on a post-breeding census (i.e., the plant to seed transition was the product of adult survivorship and fecundity; transitions out of the seed class incorporated both seed survivorship and germination rates). We assumed that the same survivorship rate applied to both germinating and nongerminating seeds.

ity in demographic rates was also measured, but to simplify the analysis, we used data from a single plot for which the mean deterministic matrix yielded a positive growth rate. While a number of excellent demographic analyses have been published on both of these species, the modeling methods and especially the goals of our models are quite different from that of these previous analyses (Kalisz 1991, 1997; Kalisz and McPeek 1992, 1993).

With the data available for most plant species, there are two broad classes of mistakes that one might make about seed demography: misestimation of seed survivorship patterns and misestimation of seed germination patterns. In either case, errors range from identifying the existence of any seed bank to specifics of age-dependent survivorship or growth. While both survivorship and germination rates are likely to be misunderstood together, we addressed these problems one at a time. Furthermore, we did not address the issue of incorrect age-dependence in either seed survivorship or germination (Kalisz 1997). Rather we concentrate on the more egregious problems of incorrectly estimating average germination or survivorship rates and their interplay with inaccurate knowledge of adult survival variation.

Misunderstanding of Seed Survivorship Rates

Underestimation of seed survivorship will obviously lead to pessimistic PVA results, while overestimation will give rosier pictures of population health. For the *Collinsia* model, these results were quite striking, with rapid decreases in the number of simulations suffering extinction, some increases in extinction times, and steady increases in population growth with increasing seed survival (fig. 15.5A). Note that, even when mean growth is positive, the combination of environmental variation and a cap on population growth rate can lead to extinction probabilities that are quite high (Lande 1993). One peculiarity in interpreting time to extinction (T_{ex}) results should be noted: the decline in T_{ex} at higher seed survival rates is a consequence of fewer populations suffering extinction. In this situation most extinctions happen rapidly, leading to lower T_{ex} values (Lande and Orzack 1988; Kalisz and McPeek 1993). The estimated seed survival, 0.115, is low enough that all populations would be expected to become extinct over 100 years. Marginally higher seed survival rates would result in substantially longer persistence times for many populations, while more than doubling this rate would be necessary to afford a substantially higher probability of continued persistence. These results parallel those of Kalisz and McPeek (1992, 1993) and Kalisz (1997), who modeled somewhat different manipulations of seed demography.

At high seed survivorship rates, the *Calathea* models showed a more modest influence of seed survival on population health (fig. 15.5B). At lower values, however, very small errors in survivorship estimation can lead to dramatically different predictions about population safety. Indeed, the estimated seed survival rate of 0.599 is just above the value needed to ensure essentially no chance of extinction, while slightly lower values predict substantial risk. Thus, small errors in seed survivorship estimation would lead to significant misunderstandings about population health and, most practically, the need for active management intervention.

Overall, these results show that the consequences of misestimated seed survival can be quite severe for an understanding of population health. Seemingly paradoxically, the perennial *Calathea* life history, which certainly relies less on seed banks for environmental buffering than does *Collinsia*, shows the potential for poorer predictions in the absence of accurate seed survival data. This sharp influence on *Calathea* persistence probably results from the need for a minimum seed survivorship simply to achieve positive long-run population growth; greater stochastic variation, and hence more important buffering effects at all seed survivals, leads to the more graded response of *Collinsia*.

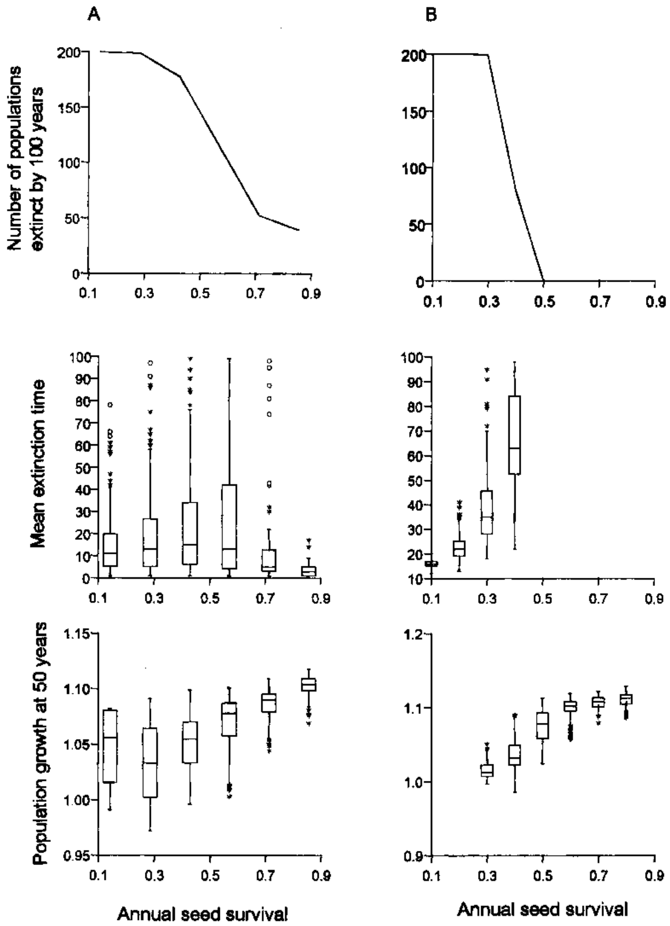


Fig. 15.5 Results of changing annual seed survivorship on simulated plant populations using data (tables 15.1 and 15.2) for *Collinsia verna* (*column A*) and *Calathea ovadensis* (*column B*). Three metrics of population health are shown: number of populations becoming extinct before 100 years (*top panels*), time to extinction for those becoming extinct (*middle panels*), and population growth from year 0 to year 50, $(N_{50}/N_0)^{1/50}$ (*bottom panels*). Results for time to extinction and population growth are shown as *boxplots*. The box is bounded by the 25th and 75th quartiles and is divided at the median, while the *lines* indicate the most extreme values within 1.5 times the interquartile range from the top and bottom of each box (see Sokal and Rohlf 1995 for further information). Results are from 200 simulations for each species for each seed survival level.

The Problem of Estimating Temporal Variation in Demography

While these results seem clear-cut, an added wrinkle should also be considered before moving on to germination rates. As we noted in reviewing the literature on seed dormancy, the major advantage of seed banks is in buffering populations against environmental variation. Thus, correctly analyzing seed bank effects and our ignorance of their dynamics will depend on estimates of variability in other parts of the life cycle, especially the reproductive adults that are most important for deterministic population growth (Caswell 1989; Rees 1994). This dependence forces us to confront two problems. First, we often have no estimates of variance for any life-history stage. Second, when we do have such estimates, they are likely to be biased low after correction for sampling variance (Beissinger and Westphal 1998; Kendell 1998), since they are essentially always based on short series of data. This limitation means that most data sets are unlikely to contain the occasional extremely good or extremely bad years that will drive most variation in vital rates. This problem has, to our knowledge, not been rigorously investigated, but it is closely parallel to the problems of estimating variation in census data (Redfearn and Pimm 1988; McArdle et al. 1990).

Given this likely bias, a sensible precaution is to rerun our sets of simulations with increased levels of temporal variation in other demographic rates, especially adult survivorship (Rees 1994). We manipulated variation in this rate from the observed value up to 90% of the maximum possible for both the *Collinsia* and *Calathea* matrices. For both models, adding variance substantially increased extinction risk (fig. 15.6A and B) and shifted the range of seed survivorship values to which population health was most sensitive. For *Collinsia* this shift means that, if we have underestimated adult variation, there is little concern about error in seed survival estimates, since they will have little influence on population persistence. For *Calathea* exactly the opposite was true; added variation moved the range of high sensitivity into that of estimated seed survival. Additionally, the intuition that increasing environmental variation will lead to more gradual effects of changing seed survival explains the smoother responses of *Calathea* persistence to differences in seed survival with increasing adult variation (fig. 15.6B).

Overall, the results from these simulations suggest that conclusions about the effects of seed survivorship on population health need to be predicated on an understanding of variability in other life stages. However, misestimation of adult variability will not fundamentally change the influence on PVA results of mistakes in estimating seed survival.

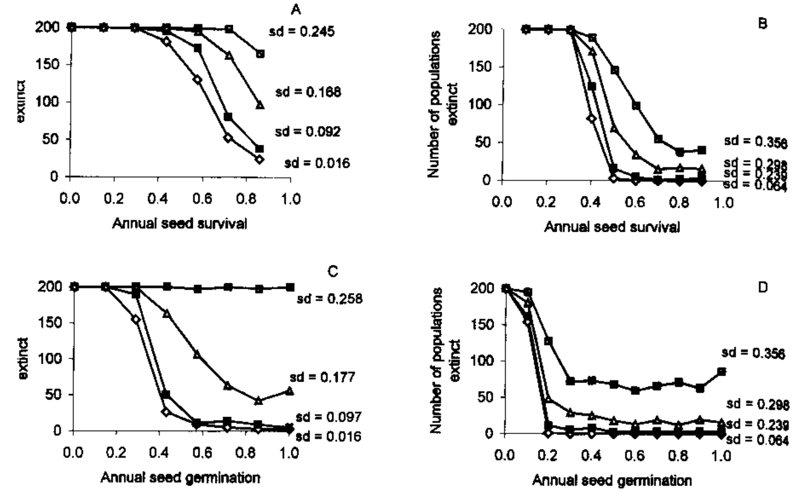


Fig. 15.6 Increasing variation in adult survival alters sensitivity of extinction to seed survival or germination rates. The four lines in each figure are for the estimated and three higher standard deviations of adult survival (sd_{ad}). Results are for *A, Collinsia verna* demography varying across seed survival rates; *B, Calathea ovadensis* demography varying across seed survival rates; *C, Collinsia verna* demography varying across seed germination rates; *D, Calathea ovadensis* demography varying across seed germination rates. See tables 15.1 and 15.2 for empirically estimated values of seed survival and germination.

The Complexity of Misunderstanding Seed Germination

While misunderstanding seed survivorship will influence our estimate of population performance, in some ways the more fundamental rate governing seed banks is germination. As the literature on evolution of dormancy emphasizes, patterns of seed germination should reflect a balance between undelayed reproduction and the safety provided by not simultaneously germinating into a possibly hostile world. Thus, unlike with seed survivorship, our ignorance of germination rates puts us in a potentially odd situation: it is not clear whether overestimating germination rates will yield overly optimistic or overly pessimistic PVA predictions, since some *intermediate* germination rate should be best. Furthermore, this intermediate rate should depend crucially on temporal variation in other parts of the life cycle. Poor estimates of variability in a species' demography will substantially alter estimates of which germination rates are best, or how incorrect estimates of germination may bias our understanding of population health.

To investigate these problems, we performed a series of simulations parallel to those described for seed survivorship, in which we varied both germination rates and the temporal variation in adult survivorship. Using the estimated variation in adult survivorship of *Collinsia* (low SD = 0.016; fig. 15.6), there is no evidence that maintenance of a seed bank is advantageous. Complete, immediate germination of all seeds results in the best population performance, with essentially no probability of extinction over 100 years. A reduction in germination percentage comes at a cost to the probability of extinction, and yields inconsistent gains in the time to extinction for simulations going extinct. However, this simple pattern applies only to simulations using the low estimated variation in adult survival. Increasing variation in adult survival results in poorer population performance for all germination rates but also changes in the optimal germination rate. In particular, for the three highest adult variances examined (SD = 0.258, 0.339, and 0.42), intermediate germination rates were optimal; almost every simulation ended in extinction, but intermediate germination yielded longer times to extinction than did extremely high germination rates (results not shown). These results parallel those of Kalisz and McPeek (1993), who also simulated extreme variation in environments. Thus, we do find evidence for the importance of seed banks, but only if real environmental variation is considerably higher than estimated variation. Most worrisome, understanding whether a mistaken or simplified view of germination biology is optimistic or pessimistic is entirely dependent on knowing the variation affecting adults. Thus, this situation is considerably more complex than that for seed survival, for which higher survival is clearly better.

For *Calathea* simulations, we found no clear advantages for seed banks, even with extremely high adult variation (fig. 15.6). While time to extinction declined with increasing germination rates, these declines were concordant with declines in the number of trials becoming extinct, and there was no intermediate optimum germination rate that minimized extinction probability while maximizing extinction times. For a PVA practitioner, these results are welcome. They suggest that, for all values of adult survival variation, there is a wide range of germination rates over which no perceivable differences in population performance occur. Therefore, mistakes in the estimation of germination rates will not be very important.

Nonetheless, we were puzzled by these results, and tinkered more with the model in an effort to find conditions truly favoring intermediate germination rates. The most obvious target to modify was the estimated correlation structure between demographic rates, which depends on only four years of data and which included rather unlikely, strongly negative correlations. These negative correlations, especially those between adult and juvenile survivorship, helped to buffer the aboveground population against environmental variation, even in the absence of a seed bank. Thus, we ran more simulations with a new correlation structure that resulted in maximum fluctuations in aboveground demography (all correlations equal to 0.9 or -0.9). We also ran a set of simulations in which we added strong autocorrelation in environments ($r = 0.9$) to this modified correlation structure. Results from both these sets of simulations showed that it is nearly impossible to develop a scenario for which it is advantageous to have less than total seed germination.

Our modeling exercise suggests that it is only sometimes possible to find conditions in which population viability is maximized by germination rates that favor a persistent seed bank, and considerable model tuning is often required to achieve these results. Life-history theory shows the clear advantages of seed dormancy, and high dormancy is well documented in many plants. Therefore, it seems odd that we have had such a difficult time illustrating its importance for population health. At least three different factors may account for this apparent contradiction: (1) Estimates of temporal variation in demographic rates, especially adult performance, are typically far too low. (2) Optimal seed dormancy for individual fitness will typically be much higher than that for population persistence. Unless a species consists of many small and extinction-prone subpopulations with strong demic selection, we would expect individual selection to favor higher dormancy than will be best for population performance. This difference will be reinforced by sibling competition (Ellner 1986), but may be altered by dispersal-dormancy trade-offs and metapopulation structure (Cohen and Levin 1987; Kalisz 1997). (3) Germination rates in the field are constrained by enforced dormancy. Because seeds can sense when germination is hopeless, as it often is, germination rates in nature are likely to be much lower than would naïvely seem "optimal" for either population growth or individual fitness. Seeds of many species are able to use quite accurate cues to determine the chances for successful germination and growth, creating correlations between germination and environmental variation that favor lower germination rates (Baskin and Baskin 1998).

While all of these explanations may be important, too few data exist to rigorously assess their ability to explain the mismatch of estimated optimal seed demography and field-estimated demographic rates. Their importance for PVA is simply that estimation of the optimal dormancy rates for population viability is likely to give little guidance on actual seed bank demography.

PVAs FOR REAL PLANTS

While seeds and seed banks are a crucial part of the life cycle and population structure of many plants, few PVAs can call upon high-quality data to understand the demography of seed banks. Thus, we are usually left to make a series of assumptions about how seed demography works and to proceed in the face of ignorance and uncertainty. As many of the chapters in this volume emphasize, most PVAs are conducted with considerable gaps in knowledge, and all must deal with parameter uncertainty (Taylor et al., chap. 12 in this volume; Wade, chap. 11 in this volume). However, we argue that plant seed banks present a particularly troublesome problem that is qualitatively different from those faced in constructing PVAs for most other species. Even without data on some process or complication, a good demographer or good field ecologist can usually make an accurate guess as to whether excluding it from an analysis will be pessimistic or optimistic. Indeed, the majority of biological complications that are frequently excluded from PVAs are known to decrease predictions of population health. Environmental stochasticity, senescence, population ceilings, inbreeding depression, dispersal losses, and mate finding are all left out of many PVAs, with the clear understanding that adding them will only make for more pessimistic results. While leaving out these biological realities obviously can result in less accurate model predictions, there is considerable power in knowing at least the qualitative effects of these omissions (positive or negative), especially when explaining a PVA's results to politicians, judges, or students.

The problem created by seed banks is that they are governed by several parameters that are difficult to understand, and it is not clear how simplified treatments of seed bank processes will influence the qualitative results of PVAs. In particular, underestimation of variation in aboveground performance could make omission of seed dormancy seem optimistic, when in fact it is pessimistic, given an accurate understanding of environmental variability. The conclusions of many PVAs largely revolve around sensitivity calculations of deterministic matrix models (e.g., Crooks et al. 1998; Mills et al. 1999; Mills and Lindberg, chap. 16 in this volume). For species with seed banks, such analyses are likely be mildly to wildly misleading. As we have sought to emphasize throughout this chapter, an understanding of the demography—and hence management—of plants with substantial seed banks is inextricably tied to an understanding of environmental variability. Since variability is just as poorly estimated as seed demography for most species, the plant PVA practitioner is left in an unenviable situation.

So how should one analyze population viability and management for threatened plants? We advocate two general approaches. First, for the majority of plants that require protection and analysis, little or no quantitative demographic data exist. In this situation, beginning to develop a PVA is tantamount to the collection and guesstimation of data for the species. Thus, the question is how to guess about the importance of seed banks and, by extension, how important it is to study them at all. While the work we have reviewed here should caution against broad generalities regarding seed banks, there is a logical classification that may help to prioritize situations in which understanding of seed banks will be critical for population viability (table 15.3). In general, species with shorter and more variable aboveground life spans are most likely to rely on seed banks for population persistence. In addition, the importance of seed banks to population persistence is likely to diminish with increasing population size. Thus, estimation of seed demography is especially crucial in planning reintroduction efforts or the management of critically small populations. In fact, careful monitoring of reintroduction programs may provide some of the best opportunities to collect data on seed dormancy. In these situations, data collection should, if at all possible, quantify seed demography *in nature*, rather than in greenhouse flats or petri dishes. In situ data are considerably more difficult to obtain, but seed behavior in artificial conditions is of very limited value in understanding population viability.

Table 15.3 The Relative Importance of Understanding Seed Demography in Order to Confidently Conduct a PVA for Different Plant Life Histories

	Adult Longevity				
Environmental Variation in Adult Performance	Annual	Biennial	Short-Lived Forbs and Shrubs	Medium-Lived Trees and Shrubs	Very Long Lived Forbs, Trees, and Shrubs
Extremely high	VI: *Trifolium trichocalyx**	VI			
High	VI: *Astragalus tener* var. *titi**	VI: *Erysimum teretifolium**	VI: *Mimetes hottentoticus**		
Moderate	VI: *Chorizanthe pungens* var. *hartwegiania**	MI	MI: *Oenothera deltoides* ssp. *howellii**	NI: *Cupressus goveniana* ssp. *goveniana**	
Low	MI: *Koenigia islandica*	MI	NI: *Epilobium latifolium*	NI: *Coryphanthus robbinsorum**	NI: *Welwitschia mirabilis*, *Silene acaulis*

Notes: VI = very important to understand seed demography and seed bank dynamics to safely reach management conclusions; *MI* = moderately important; *NI* = probably not important. Example species are provided for most of these categories. Asterisks indicate rare or endangered species.

The second approach should be taken in situations when one has some estimates of most demographic rates, but weak information on seed demography or variability of other rates. In this case, we suggest following the route taken in our simulation results: use models that include various assumptions about how seed germination and survivorship operates, in combination with a wide range of assumptions about temporal variation. While one can use a Bayesian framework to incorporate uncertainty (Taylor et al., chap. 12 in this volume; Wade, chap. 11 in this volume), simulating a suite of alternative models that are biologically reasonable may be as or more useful (Burnham and Anderson 1998). It is crucial to take known biases into account (e.g., chronic underestimation of temporal variation) and to explore a wide range of situations. Depending on the life history of the species in question, this type of exploratory modeling is likely to suggest which rates are crucial to estimate, which are not as important, and how robust different management recommendations are likely to be. While we have not emphasized the role of plant PVAs in evaluating management recommendations, it should be clear that analysis of many dangerous and expensive management issues can depend crucially on understanding seed demography (e.g., when to burn or stop the burning of a piece of chaparral or fynbos).

In reviewing PVA concerns for plants, we have emphasized the life-history feature that is most problematic for most species—seed banks. In doing so, we have tried to avoid the easy route of simply reiterating that "more data are needed." Perhaps the most useful lesson from our review and simulations is that too little attention has been given to the interacting problems posed by seed demography and poor data on temporal variability, even though most studies of plants have honestly tried to deal with seed banks. This pattern is part of a larger trend in PVAs. As use of generalized software packages for viability analysis becomes more common, there is a danger that PVA practitioners will stop thinking carefully about the natural history of their species and how different modeling frameworks include or exclude different facets of biology. Especially for plants, different life-history attributes shift the importance of deterministic versus stochastic forces for population viability, as well as the ability to successfully gather the information needed to construct good PVA models. Continuing attention to biological detail is probably as important to the development of useful, credible PVAs as are advances in the general theory of population extinction. While mathematicians are developing new and better ways to conduct PVAs, empirical biologists should constantly critique these tools and use them to flexibly incorporate the idiosyncratic aspects of natural history important to yielding relevant, useful predictions for real species in particular contexts.

LITERATURE CITED

Baskin, C. C., and J. M. Baskin. 1998. *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego, California.

Baskin, J. M., and C. C. Baskin. 1980. The role of seed reserves in the persistence of a local population of *Sedum pulchrellum*: a direct field observation. *Bulletin of the Torrey Botanical Club* 107:429–430.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.

Bekker, R. M., J. P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschold, K. Thompson, and J. H. Wilhelms. 1998. Seed size, shape, and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* 12:834–842.

Burgman, M. A., and B. B. Lamont. 1992. A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic, and genetic effects. *Journal of Applied Ecology* 29:719–727.

Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York.

Caswell, H. 1989. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12:119–129.

Cohen, D., and S. A. Levin. 1987. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. Pages 110–122 in E. Teramoto and M. Yamaguti, editors, *Mathematical topics in population biology, morphogenesis, and neurosciences*, proceedings of an international symposium, Kyoto, November 10–15, 1985. Springer-Verlag, Berlin, Germany.

Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. *Conservation Biology* 12:889–895.

Doak, D. F., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* 4:446–460.

Ellner, S. 1985a. ESS germination strategies in a randomly varying environment: 1, logistic-type models. *Theoretical Population Biology* 28:50–79.

———. 1985b. ESS germination strategies in a randomly varying environment: 2, reciprocal yield-law models. *Theoretical Population Biology* 28:80–116.

———. 1986. Germination dimorphisms and parent-offspring conflict in seed germination. *Journal of Theoretical Biology* 123:173–185.

———. 1997. You bet your life: life-history strategies in fluctuating environments. Pages 3–24 in H. G. Othmer, F. R. Adler, M. A. Lewis, and J. C. Dallon, editors, *Case studies in mathematical modeling: ecology, physiology, and cell biology*. Prentice Hall, Upper Saddle River, New Jersey.

Epling, C., H. Lewis, and F. M. Ball. 1960. The breeding group and seed storage: a study in population dynamics. *Evolution* 14:238–255.

Evans, M., N. Hastings, and B. Peacock. 1996. *Statistical distributions*. 2d edition. John Wiley and Sons, New York, New York.

Gross, K., J. R. Lockwood III, C. C. Frost, and W. F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biology* 12:1291–1301.

Hairston, N. G., Jr., S. Ellner, and C. M. Kearns. 1996. Overlapping generations: the storage effect and the maintenance of biotic diversity. Pages 109–145 in O. E. Rhodes Jr., R. K. Chesser, and M. H. Smith, editors, *Population dynamics in ecological space and time*. University of Chicago Press, Chicago, Illinois.

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65:155–192.

Kalisz, S. 1991. Population dynamics of an age-structured annual: 1, life table analyses of the seed bank and plant cohorts. *Ecology* 72:575–585.

———. 1997. Fragmentation and the role of seed banks in promoting persistence in isolated populations of *Collinsia verna*. Pages 286–312 in M. W. Schwartz, editor, *Conservation in highly fragmented landscapes*. Chapman and Hall, New York, New York.

Kalisz, S., and M. A. McPeek. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* 73:1082–1093.

———. 1993. Extinction dynamics, population growth, and seed banks. *Oecologia* 95:314–320.

Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications* 8:184–193.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.

Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy of Sciences* (USA) 85:7418–7421.

Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* 26:165–191.

Link, W. A., and D. C. Hahn. 1996. Empirical Bayes estimation of proportions with application to cowbird parasitism rates. *Ecology* 77:2528–2537.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: patterns, problems, and artifacts. *Journal of Animal Ecology* 59:439–454.

McCue, K. A., and T. P. Holtsford. 1998. Seed bank influences on genetic diversity in the rare annual *Clarkia sprinvillensis* (Onagraceae). *American Journal of Botany* 85:30–36.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. The reliability of conservation actions based upon elasticities of matrix models. *Conservation Biology* 13:815–829.

Pake, C., and L. Venable. 1995. Is coexistence of Sonoran Desert annuals mediated by temporal variability in reproductive success? *Ecology* 76:246–261.

Porsild, A. E., C. R. Harrington, and G. A. Mulligan. 1967. *Lupinus arcticus* Wats. grown from seeds of Pleistocene age. *Science* 158:113–114.

Ratsirarson, J., J. A. Silander Jr., and A. F. Richard. 1996. Conservation and management of a threatened Madagascar palm species, *Neodypsis decaryi* Jumelle. *Conservation Biology* 10:40–52.

Redfearn, A., and S. L. Pimm. 1988. Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs* 58:39–55.

Rees, M. 1993. Trade-offs among dispersal strategies in British plants. *Nature* 366: 150–152.

———. 1994. Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* 144:43–64.

———. 1997. Seed dormancy. Pages 214–238 in M. J. Crawley, editor, *Plant ecology*, 2d edition. Blackwell Scientific, Oxford, United Kingdom.

Rees, M., and M. J. Long. 1993. The analysis and interpretation of seedling recruitment curves. *American Naturalist* 141:233–262.

Roberts, H. A., and J. E. Boddrell. 1985. Seed survival and seasonal pattern of seedling emergence in some Leguminosae. *Annals of Applied Biology* 106:125–132.

Roberts, H. A., and R. J. Chancellor. 1979. Periodicity of seedling emergence and achene survival in some species of *Carduus, Cirsium*, and *Onopordum*. *Journal of Applied Ecology* 16:641–647.

Shen-Miller, J., M. B. Mudgett, J. W. Schopf, S. Clarke, and R. Berger. 1995. Exceptional seed longevity and robust growth: ancient sacred lotus from China. *American Journal of Botany* 82:1367–1380.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81:465–476.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. 3d edition. W. H. Freeman, New York, New York.

Steenbergh, W. F., and C. H. Lowe. 1977. *Ecology of the saguaro: 2, reproduction, germination, and establishment, growth, and survival of the young plant.* National Park Service Scientific Monograph no. 8. U.S. Department of the Interior, National Park Service, Washington, D.C.

———. 1983. *Ecology of the saguaro: 3, growth and demography.* National Park Service Scientific Monograph no. 17. U.S. Department of the Interior, National Park Service, Washington, D.C.

Thompson, K., J. P. Bakker, R. M. Bekker, and J. G. Hodgson. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* 86:163–169.

Toole, E. H., and E. Brown. 1946. Final results of the Duvel buried seed experiment. *Journal of Agricultural Research* 72:201–210.

U.S. Fish and Wildlife Service. 1998. Endangered and threatened wildlife and plants; final rule listing five plants from Monterey County, CA, as endangered or threatened. *Federal Register* 63:43100–43115.

Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131:360–384.

Wendel, G. W. 1977. Longevity of black cherry, wild grape, and sassafras seed in the forest floor. Forest Service Research Paper NE-375. U.S. Department of Agriculture, Washington, D.C.