

Chapter 15

What is the Effect of Seed Collection on Extinction Risk of Perennial Plants?

Eric S. Menges, Edward O. Guerrant Jr., and Samara Hamzé

Introduction

The ultimate purposes of *ex situ* plant conservation collections are to provide sufficient plant material to establish new populations, reintroduce populations, or augment existing populations. In removing material from natural populations, we also want to minimize their extinction risk. The existence of genetically representative samples stored off-site both reduces the probability of catastrophic loss of the donor population's genetic legacy, and provides the genetic material necessary to reintroduce or augment the population if needed. *Ex situ* methods are thus a means to an end: enhanced medium- to long-term survival of wild populations. However, the act of removing samples for off-site storage increases, however slightly, the short-term risk of extinction. We are left with a basic conflict, which we must resolve to the advantage of endangered species: How can we collect enough material to meet conservation goals, without damaging populations in the process?

The answer to this question depends on the kind of material collected. Seeds are widely considered to be the propagule of choice for *ex situ* conservation collections. Seeds usually can be collected in greater numbers than plant parts or whole plants. For plants with orthodox seeds (i.e. those that can survive frozen dry storage), it is easier and more economical to maintain a greater fraction of the genetic complement of a collection as seeds in a seed bank, than it is to grow plants (Eberhart *et al.* 1991, Frankel *et al.* 1995,). Seeds that can be stored, rather than requiring the growing of plants, help conservationists avoid artificial selection for individuals that do well in a garden setting, possibly reducing adaptation to their native habitats (Frankel *et al.* 1995, Reinartz 1995). In a garden setting, plants may acquire diseases or pests that could be transferred to wild populations after outplanting (Brown and Briggs 1991, Gordon 1994). Finally,

and perhaps most important for the current discussion, removing seeds is thought to be far less damaging to the survival prospects of a sampled population than is removal of other plant parts or entire plants (Frankel *et al.* 1995, Menges 1998). But less damaging does not necessarily mean that there is no meaningful damage. Seed removal may still significantly reduce population growth rate, and increase probabilities of extinction.

Our challenge is to balance the seed collection with harm to the population from which we are collecting. In this chapter, simulate various seed collection scenarios and the resulting population dynamics of various species, using empirically derived data. We address several questions. What is the relative vulnerability to seed harvest of perennial plants across a wide range of life histories? How do intensity and frequency of harvest interact to affect population persistence? How does population size affect a sampled population's response to collection? Is it better to harvest infrequently but heavily, or frequently and lightly?

Demographic models

To explore some of the potential impacts of seed collection on sampled populations, we used empirically derived stage-based transition matrices as a basis for stochastic modeling (Menges 1990, 1998, Guerrant 1998). These models summarize (as demographic parameters) data on the fate of individuals (survival, growth), their fecundity (seed production), and the fate of seeds (germination, entry into persistent seed bank, survival). Individuals are generally divided into classes based on stage or size. Projection matrices, often specific for individual populations or years, can be used to estimate whether populations governed by these demographic parameters are likely to be increasing or decreasing at equilibrium (judged by the finite rate of increase, λ). Because environments are variable, stochastic simulations using varying matrices or matrix elements can explore extinction risks (Menges 2000).

Using stochastic simulations, we examined the impact of intensity and frequency of seed harvests, and the effects of population size on extinction risk in plants. We started with published projection matrices

for species with at least two projection matrices so stochastic approaches could be used. We then simulated various levels and patterns of seed harvest. We examined 22 taxa representing a wide range of perennial life histories (Table 1).

From the literature, we chose species with published projection matrices representing perennial plants with a range of life histories. Almost no studies of annuals are summarized with projection matrices. These might be expected to be particularly sensitive to seed collection, especially if they lacked seed banks. Most of our included species are perennial herbs (n=20 cases) that reproduce iteroparously [repeatedly] (17) (Bierzychudek 1982, 1999, Fiedler 1987, Moloney 1988, Menges 1990, O'Connor 1993, Horvitz and Schemske 1995, Lesica 1995, Nantel *et al.* 1996, Byers and Meagher 1997, Menges and Dolan 1998, Valverde and Silvertown 1998, Guerrant unpubl., Kaye unpubl.). One perennial herb reproduces semelparously [produce seeds once, then dies] (1) (Werner and Caswell 1977), or may do either (2) (Lesica and Shelley 1995). Six of the herb species also spread clonally. We also considered 5 species of nonclonal woody plants: three tree species and two shrubs (Table 1). In total, 22 species (25 cases) were examined.

We only included species represented by two or more separate projection matrices, preferring studies with 3 matrices or more. The different matrices represented two or more pairs of years for one population (preferred) or two or more populations of the species. Only studies with explicit matrices were included to avoid problems with our interpretations of data in other formats. Matrices had to include seeds or seedlings produced as fecundity terms, in order to perform the simulations of seed harvests. For species where a seed stage was incorporated into the matrix, the authors document seed dormancy. Thus, we are confident that the pitfall of artificial dormancy pointed out by Caswell (1989) was avoided. In only one case (Bierzychudek 1982) the matrix included a seed stage where there was no seed dormancy, but correcting this error made little difference in the values of lambda (Bierzychudek 1999) and no difference in extinction probability (this paper). In choosing among multiple matrices for a given species, we avoided those producing very high or very low finite rates of increase (lambda) as seed harvesting effects were overwhelmed by these extreme rates of increase.

Our approach was to apply stochastic matrix modeling using available demographic data summarized in projection matrices, for populations of wild plants. Stochastic modeling was preferred over deterministic approaches as a more realistic depiction of both the demography of wild populations and the process of seed harvesting. It also allowed us to estimate the probability of extinction under various seed harvest scenarios, arguably the most fundamental worry of conservationists. We introduced stochasticity by randomly alternating matrices representing different years, and harvest or no harvest years. If there were no published matrices representing different years for a species, we alternated published matrices from different populations, assuming that this variation was comparable to temporal variation. Alternating matrices rather than varying individual matrix elements preserves correlations among different parts of life histories, for example the tendency for positive correlations among life history parameters (e.g. Horvitz and Schemske 1995, Fieberg and Ellner 2001). Because positive correlations project more variable population trajectories, matrix alternation produces a more conservative risk assessment (Greenlee and Kaye 1997, Menges 2000) while having no data requirements relating to the variance structure of life histories. Complete specification of correlation structure does alter estimates of stochastic population growth (which correlates with extinction risk; Fieberg and Ellner 2001).

Seed harvest scenarios varied the level of harvest in each year harvested, and the probability of harvest in each year, in various combinations. Individual year harvest levels were 10, 50, or 100% of fecundity. Probabilities of harvest were 10, 50, or 90%. We evaluated harvest scenarios with the initial population size of 10, 50, 100, or 500. The product of 3 harvest levels, 3 harvest probabilities, and 4 initial population sizes yielded 36 harvest scenarios. We also examined four no-harvest scenarios, one for each initial population size. In total, there were 40 scenarios for each case.

“No harvest” matrices were simply the published matrices. Initial simulations suggested the most informative cases were matrices with finite rates of increase (λ) not far from one. Extinction probabilities

for cases with high or low values for λ were not affected by seed harvest. Therefore, when there were multiple matrices for a species, we selected those with $0.85 < \lambda < 1.2$.

Differential harvest matrices were produced by reducing each fecundity term (seed production or seedling production) by 10, 50, or 100% (see discussion of assumptions below). For a species with three published matrices, we produced 12 matrices representing three harvest matrices and one “no harvest” matrix for each of the original matrices. We generally based our simulations on a single set of matrices (usually a single population) for each species. However, for *Pedicularis furbishiae*, we simulated seed harvesting on two individual populations as well (resulting in three cases for this species).

Many life history studies and population viability analyses have used λ (the finite rate of increase) to compare years, populations, or treatments (Menges 2000). However, stochastic simulations do not equilibrate to produce a meaningful estimate of λ . In addition, λ does not always adequately predict transient dynamics (Werner and Caswell 1977, Bierzychudek 1999) which may lead to extinctions, even in apparently growing populations. Furthermore, periodic harvesting will prevent an equilibrium from being reached. Transient dynamics, while realistic, are difficult to compare among species.

For these reasons, we used extinction probability (EP) as one measure of extinction risk. Extinction risk may be the major concern of conservationists and is appropriate in the case of periodic seed harvests, which are likely to be a stochastic process. Extinctions of local populations may cause loss of alleles and thus erosion of overall genetic variation. The use of stochastic simulations with multiple matrices allows the direct estimate of EP.

Modeling Protocol

For each analysis, we conducted stochastic simulations using POPPROJ3 (modified from earlier POPPROJ programs [Menges 1998]). This program allows the selection of matrices for each year of the simulation with specified probabilities of selection for each matrix. For example, if the probability of

seed harvest was 10% in any year, there would be a 10% chance of choosing one of the matrices with reduced fertility, representing a seed harvest year. Because each year is independent, there can be runs of several years with harvests or no harvests.

We performed separate analyses for each of the 40 harvest scenarios, for each of the 25 cases. The probabilities of any matrix being selected reflected the designated probability of seed harvest (see above), but otherwise different years or populations were weighted evenly. We began each simulation with one of the specified total population sizes. Initial populations were at stable stage distribution for one of the original matrices (the matrix with the median finite rate of increase or else the finite rate of increase closest to one for cases of two original matrices). Simulations were run 1000 times for 100 years each. The population was considered extinct when its size dropped below one.

Some Assumptions

An implicit assumption of our approach is that seedling recruitment and seed production are correlated in species lacking seed dormancy. This occurs because the matrix elements representing fecundity are actually products of total seed production and the probability of seedling emergence and survival; they represent seedlings added to the population at the time of the annual census. Since seed harvesting may take place before that census, the proportion of seeds removed may not exactly translate to the proportional reduction of fertility as defined by seedlings. For plants with seed banks, fertility is a combination of seedlings produced by last year's seeds and seedlings from dormant seeds, and this assumption is not necessary.

In addition, we assume that the variety of matrices represents the variance structure of population dynamics through time (environmental stochasticity). This is likely to be only approximately true when only a few matrices (years) are used. When only a few years of data are used for population projections, some errors in projection can be expected (Fiedler *et al.* 1998, Bierzychudek 1999). The

projections are also independent of density. If removal of seeds or declines in population size are compensated by (negative) density-dependent effects, then our projections will be too pessimistic.

Finally, our seed harvest scenarios assume several things specifically about the seed harvests themselves. We assume that the seed harvests are scaled to the population's annual seed production. When seed production is higher, this same percentage seed harvest is a greater absolute harvest. Comparing species using relative seed harvests is necessary given a wide range of fecundities among species. Secondly, seed harvests are stochastic, in that in any given year there is a probability of seed harvest. This means that there can be unusual runs of years with relatively frequent or infrequent seed harvests, compared to the mean seed harvest probability. We believe that this is a more realistic scenario than regularly spaced seed harvests. Thirdly, seed harvests are assumed to vary randomly, whereas in many situations there may be particular patterns of seed harvests over time.

RESULTS and DISCUSSION

Response to Harvest: An Example

For many species, increased frequencies and intensities of seed harvests led to increased extinction risks, and smaller populations were most vulnerable. We illustrate the full range of 40 scenarios for the mean projection matrix for *Pedicularis furbishiae*, a non-clonal perennial herb that is narrowly endemic to the banks of the St. John River in northern Maine and adjacent New Brunswick (Menges 1990). Extinction risks are low (< 25%) for infrequent (10% of years), small (10% of seeds) harvests for all population sizes of 50 or more (Figure 1). Frequent (50% or higher), intense (50% or more seeds) harvests threaten populations smaller than 500. Complete, intense harvests threaten even these large populations. Various intermediate combinations of population size, harvest frequency, and harvest intensity produce intermediate extinction risks (Figure 1).

Our modeling scenarios produced 40 scenarios for 25 cases. To organize these results, we first classify species into broad categories of response to harvesting, below.

Classifications of Population Responses

Effects of seed harvests varied widely across species. We distinguish four distinct categories of response (Table 1, Figures 2 and 3). These are: insensitive, extinction-prone, sensitive type I (high initial extinction risk), and sensitive type II (low initial extinction risk). We assumed that a safe harvest caused no more than a 5% increase in EP over baseline EP (no harvest scenario).

Insensitive cases

For 9 cases, termed “insensitive”, seed harvest regardless of intensity level or frequency caused no extinction risk over 100 years ($EP=0$) for populations of 50 or more individuals (Table 1). For 5 of these cases, no harvest effects were evident at any population size. For 3 cases, harvest effects were only seen for very small (10) populations. In one case, harvest effects were evident only at 100% harvest for 90% of years, but for all population sizes. Because these effects are only seen at extremely small population sizes or extremely high harvesting levels, we consider these species “insensitive” to seed harvests. All three tree species simulated were insensitive to seed harvests. Other insensitive species included shrubs and iteroparous herbaceous perennials (Table 1).

Extinction-prone cases

For 4 cases, termed “extinction-prone”, EP was 100% even without seed harvests. These 4 cases were all herbs, including 2 herbs combining seed production and clonal growth. Populations are predicted as heading toward extinction even without seed harvests, due to their demographic rates. In such cases, seed harvests for *ex-situ* conservation could be justified as necessary in a desperate situation. The effects of seed harvests on extinction-prone species may be secondary to fundamental issues of population dynamics, which themselves may be tied to habitat quality.

Sensitive cases

The most interesting cases are those “sensitive cases” in which seed harvests increase extinction risk under certain circumstances. In general, for this group, increasing harvest intensities markedly increases extinction risk (Figure 2).

Two types of sensitive species can be distinguished. For sensitive type I (high initial extinction risk), which occurred in 2 iteroparous herbs with clonal growth (*Danthonia sericea* and *Eupatorium resinosum*), initial extinction risk was fairly high (EP > 40% without seed harvest for initial populations of 500) and it increased with seed harvest (e.g. Figure 3). Sensitive type II cases have initially low extinction risk (EP = 0% without harvest for initial populations of 500) with increased extinction risk with seed harvest frequency and intensity (10 cases, e.g. *Pedicularis furbishiae*, Figure 1; *Fumana procumbens*, Figure 3). All these species are non-clonal and all but one are herbaceous. There is little (< 5%) increased extinction at 10% harvest, 10% of years, for any population size, but variable sensitivity to higher levels of harvests among species. Sensitive cases (extinction risks increased with seed harvests) had alternate matrices with $\lambda > 1$ and $\lambda < 1$.

Variation Within A Species

The population response of a species can vary from one population to another, depending on the demography of each population. For *Pedicularis furbishiae*, a growing population at Hamlin ($1.05 < \lambda < 1.12$) is insensitive to seed harvests, while a declining population at St. Francis ($0.59 < \lambda < 1.08$) is extinction-prone at any seed harvest level. However, the mean *Pedicularis furbishiae* “population” ($0.77 < \lambda < 1.02$) is sensitive to seed harvests (Figure 1).

Effects of Initial Population Size and Seed Harvesting Patterns

Across all four response types, small populations (10) had the highest extinction probabilities. As expected, increasing initial population size resulted in decreased EP. When the effects of initial population size were examined within the most frequent response type, sensitive type II (low initial EP; n=10 cases), we found that harvesting can occur only at the lowest intensity (10%) and with no more than 50% probability of harvest for initial populations of 10 (Table 2). However, as initial population size increases to 50, low-intensity, frequent harvests (i.e. 10%-90%) can occur without increasing extinction risk. Once initial populations have at least 100 individuals, either 10% harvest-90% frequency or 100%

harvest-10% frequency is safe. On average, even populations of 500 cannot sustain more than 50% harvest- 50% frequency or 100% harvest-10% frequency. However, reasonable harvesting levels will not threaten healthy populations of 500 or more.

The nine “insensitive” species, regardless of population sizes, have no probability of extinction in the absence of harvesting. Populations of 10 individuals are only slightly affected by 50% harvest-90% frequency or 100% harvest-50% frequency. For populations of all sizes, the EP rises more than 5% above the baseline EP of zero only at the highest intensity and frequency of harvest (e.g. *Primula vulgaris*, Figure 3).

Effects of Frequent vs. Intense Harvests

For all species combined, frequent low intensity harvests rather than infrequent but high intensity harvests produced relatively lower extinction risk (Figure 2). Similarly, we found that the ten sensitive species type II (with low initial EP) were less affected by frequent harvest than intense harvest.

For individual species, frequent harvests of lower intensity usually produced lower extinction risk (e.g. Figure 5). For example, a comparison of 100/10 vs. 10/90 harvest scenarios (each removing 9-10% of seeds in total) for individual species, for initial population size = 10, shows significantly lower extinction risk for the frequent, low intensity scenario (Wilcoxin signed rank test, $p = 0.009$). Other comparisons of intense vs. frequent harvests at initial population size = 50 sometimes show that frequent harvests produced lower extinction risks. For 100-50 vs. 50-90 (each removing 45-50% of seeds), the differences in extinction risk are significant ($p=0.005$), but for 50-10 vs. 10-50 (each removing 5% of seeds), the difference are not ($p=0.47$).

RECOMMENDATIONS

For most woody species and rapidly-expanding perennial herb populations, short-term seed harvests of any intensity and frequency are unlikely to cause short-term extinctions. Of course, this

conclusion depends upon the quality of data. Since demographic parameters vary widely in such herb populations, short-term studies may not capture the extent of demographic variation. Longer-term changes driven by succession or other environmental change may be important to such species but may not be anticipated by short-term demographic data (e.g. Bierzychudek 1999). In addition, sites supporting growing populations may be insensitive to seed harvest, while unfavorable sites may have vulnerable populations. To the extent that data are only collected in one type of site, extrapolation of results to other types of habitats may be misleading. We did not simulate seed harvest effects on annual plants (there are few studies with projection matrices for annuals). Annuals without persistent seed banks depend on each year's seed production for recruitment and persistence and would be especially sensitive to seed harvests.

Long-lived tree species may appear unaffected by seed harvest in our scenarios, which use 100-year simulations to compare species. However, this result is probably influenced by the demographic inertia created by the long life span of many trees. Tree populations without any seedling recruitment may nevertheless persist for many centuries (and so have little extinction risk apparent in our 100-yr simulations). Removal of seeds by seed harvests could exacerbate long-term declines caused by other recruitment limitations. However, in many trees, fecundity can be huge and recruitment limitations ultimately reflect competition or the disturbance regime (e.g. Platt *et al.* 1988, Alvarez-Buylla 1994).

Even in species sensitive to some levels of seed harvests, there are generally safe seed harvest levels that emerge from modeling based on empirical data. Harvesting 10% of the seeds in 10% of the years typically does not create increased extinction risks. We refer to this as the 10/10 rule, which is a safe seed harvesting level for all the species we investigated.

However, many species are sensitive to higher levels of harvests. For example, harvesting 50% of seeds in 50% of the years is generally an unsafe harvesting level (the 50/50 rule). Only populations larger than 500 can tolerate this level of harvesting without significant extinction risk over 100 years.

Our third seed harvesting rule concerns the frequency and intensity of harvesting, which we shall refer to as “Slow But Sure”. In this study, we contrast 9-10% overall harvest but with divergent harvesting schedules. Less intense harvests (e.g. 10%) that occur more frequently (e.g. 90% of years) produce lower extinction risks than heavier harvests (e.g. 100%) that occur infrequently (10%). This occurs partly because some populations may depend on consistent fecundity to maintain population sizes, especially if they are short-lived and lack a seed bank. Massive seed removal in one year may cause a population crash and subsequently produce higher extinction risk. In addition, massive seed collection in consecutive years, possible in the simulations due to their stochastic nature, increased extinction risk in some species. To the extent that multiple seed collections are not coordinated among workers, this may be a realistic scenario. Smaller populations are most sensitive to concentrated harvests, and they may also experience greater collection pressure because of the lower overall abundance of seeds.

Slow but sure collections, spread out over time, not only produce lower extinction risk, but also may have other benefits that we have not modeled. If seedling recruitment conditions vary widely, having propagules available in favorable years will lower extinction risk. Also, spread-out collections can be integrated with monitoring of wild populations to help assess their viability and the potential effects of seed collection. Finally, seed collections made over a period of years may have advantages in sampling genetic variation that is sporadically available due to the emergence of new genotypes from the seed bank.

Our simulations of collection patterns include random variation, but actual collections may be more systematic or concentrated in time. For example, seed collections of palms for forest garden plantings in Veracruz, Mexico, are heavy but concentrated for a few years and then subsequently lighter and more sporadic (T. Ticktin, personal communication). Although our modeling suggests that concentrated harvests can threaten populations, such harvests for only a few years would be unlikely to have long-term effects on long-lived species. Unfortunately, data sets detailing actual harvesting patterns are uncommon (but see Nantel *et al.* 1996).

Many other questions about harvesting seeds were not addressed in our study. Genetic considerations suggest sampling seeds equitably from many individuals and from a diversity of microhabitats, avoiding oversampling from the largest and most fecund plants (Falk and Holsinger 1991, Holsinger and Gottlieb 1991, Frankel *et al.* 1995). Multiple collections through a fruiting season will sample phenological variation among and within plants, and perhaps different mixtures of selfed and outcrossed progeny. Spreading collections spatially and temporally is consistent with collecting smaller numbers of seeds more frequently to minimize demographic risks (Falk and Holsinger 1991). Isolated plants should not be the focus of collection efforts if these plants produce genetically inferior progeny due to inbreeding depression (Burrows 2000).

This study did not consider the demographic effects of harvesting plants or plant parts (other than seeds) from wild populations. However, demographic considerations give us the basis to make some general comments. First, most plant species' λ are more sensitive to variation in mortality and growth than to fecundity (Menges 1998, Silvertown *et al.* 1996). This sensitivity varies with the life history of the species and the context of the individual population, being highest in woody plants and herbs of shaded and late-successional habitats (Silvertown *et al.* 1996, Oostermeijer 2000). Any harvests of plant parts or whole plants ideally should be monitored to detect any increases in mortality. Increased mortality should be avoided in sensitive species or populations. In such situations, it may not be possible to harvest plants and still avoid elevated extinction risks (Nantel *et al.* 1996).

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Table 1. Characteristics of 25 cases (22 perennial species, herbaceous perennials unless indicated as shrubs or herbs) for which seed harvesting effects were modeled.

Species	#Matrices	Matrices	Range of λ	Citation	Growth Form	Repro	Response
<i>Arabis fecunda</i> – Vipond	3	years	0.73-1.79	Lesica & Shelly 1995	Semelparous + iteroparous	Seed	Sensitive II-low
<i>A. fecunda</i> – Charley's	3	years	0.80-1.15	Lesica & Shelly 1995	Semelparous + iteroparous	Seed	extinction prone
<i>Ardisia escallonioides</i>	2	sites	0.98-1.10	Pascarella & Horvitz 1998	Shrub	Seed	insensitive
<i>Arisaema triphyllum</i>	2	years	0.89-0.93 *	Bierzychudek 1982, 1989	Iteroparous	Seed/clonal	extinction prone
<i>Astragalus scaphoides</i>	4	years	0.83-1.31	Lesica 1995	Iteroparous	Seed	sensitive II-low
<i>Astrocaryum mexicanum</i>	2	sites	0.99-1.02	Piñero <i>et al.</i> 1984	Tree	Seed	insensitive
<i>Calathea ovandensis</i>	4	years	0.90-1.25	Horvitz & Schemske 1995	Iteroparous	Seed	sensitive II-low
<i>Calochortus obispoensis</i>	2	years	0.96-1.03	Fiedler 1987	Iteroparous	Seed	insensitive
<i>Danthonia sericea</i>	4	sites	0.60-1.33	Moloney 1988	Iteroparous	Seed/clonal	sensitive I-high
<i>Dipsacus sylvestris</i>	4	sites	0.53-2.22	Werner & Caswell 1977	Semelparous	Seed	sensitive II-low
<i>Erythronium elegans</i>	5	years	1.00-1.05	Guerrant (unpubl.)	Iteroparous	Seed/clonal	insensitive
<i>Eupatorium perfoliatum</i>	3	sites	0.77-1.09	Byers & Meagher 1997	Iteroparous	Seed/clonal	extinction prone
<i>Eupatorium resinosum</i>	3	sites	0.75-1.17	Byers & Meagher 1997	Iteroparous	Seed/cl	sensitive I-high

						onal	
<i>Fumana procumbens</i>	6	years	0.86-1.09	Bengtsson 1993	Shrub	Seed	sensitive II-low
<i>Heteropogon contortus</i>	4	years	0.90-1.13	O'Connor 1993	Iteroparous	Seed	sensitive II-low
<i>Horkelia congesta</i>	6	years	0.89-1.07	Kaye (pers. comm.)	Iteroparous	Seed	sensitive II-low
<i>Neodypsis decaryi</i>	3	sites	1.06-1.16	Ratsirarson <i>et al.</i> 1996	Tree	Seed	insensitive
<i>Panax quinquefolium</i>	4	sites	0.88-1.18	Nantel <i>et al.</i> 1996	Iteroparous	Seed	sensitive II-low
<i>Pedicularis furbishiae</i> - all	3	years	0.77-1.27	Menges 1990	Iteroparous	Seed	sensitive II-low
<i>P. furbishiae</i> – Hamlin	2	years	1.05-1.12	Menges 1990	Iteroparous	Seed	insensitive
<i>P. furbishiae</i> - St. Francis	3	years	0.58-0.98	Menges 1990	Iteroparous	Seed	extinction prone
<i>Primula vulgaris</i>	2	years	0.95-1.04	Valverde & Silvertown 1998	Iteroparous	Seed/cl onal	insensitive
<i>Silene regia</i>	3	years	1.32-1.42	Menges & Dolan 1998	Iteroparous	Seed	sensitive II-low
<i>Themeda triandra</i>	4	years	0.83-1.33	O'Connor 1993	Iteroparous	Seed	insensitive
<i>Thrinax radiata</i>	2	sites	1.09-1.31	Olmsted & Alvarez- Buyulla 1995	Tree	Seed	insensitive

* Corrected values, as used in Bierzychudek (1999), for Brooktondale population.

Table 2. Mean percent extinction (EP) for sensitive type II species (with a low initial extinction probability). Shaded entries indicate <5% increase of EP over baseline EP.

Figure Captions

Figure 1. Extinction percentages for 4 initial population sizes (10, 50, 100, 500) for various simulated seed harvest scenarios, for *Pedicularis furbishiae* (from 3 mean matrices): a “sensitive type II” case.

Figure 2. Extinction percentages, by sensitivity class, all species combined, for initial population size of 50.

Figure 3. Effects of seed harvest on extinction percentages for four species with initial population size of 10.

- a) [UPPER LEFT] An extinction prone species (*Arisaema triphyllum*).
- b) [LOWER LEFT] A species sensitive to seed harvest with low initial extinction risk – sensitive type II (*Fumana procumbens*).
- c) [UPPER RIGHT] A species sensitive to seed harvest with high initial extinction risk – sensitive type I (*Eupatorium resinosum*).
- d) [LOWER RIGHT] An insensitive species (*Primula vulgaris*).

Figure 4. Effect of initial population size of three species on extinction risk under the 50/50 harvesting scenario. as=*Astragalus scaphoides*, ca=*Calathea ovandensis*, hc=*Horkelia congesta*.

Figure 5. Comparison of 100/10 vs. 10/90 harvest scenarios for ten species, for initial population size = 10. Wilcoxon signed rank test, $p = 0.009$. af=*Arabis fecunda*, as=*Astragalus scaphoides*, ca=*Calathea ovandensis*, ds=*Dipsacus sylvestris*, fp=*Fumana procumbens*, hc=*Horkelia congesta*, hp=*Heteropogon contortus*, pf=*Pedicularis furbishiae*, pq=*Panax quinquefolium*, sr=*Silene regia*

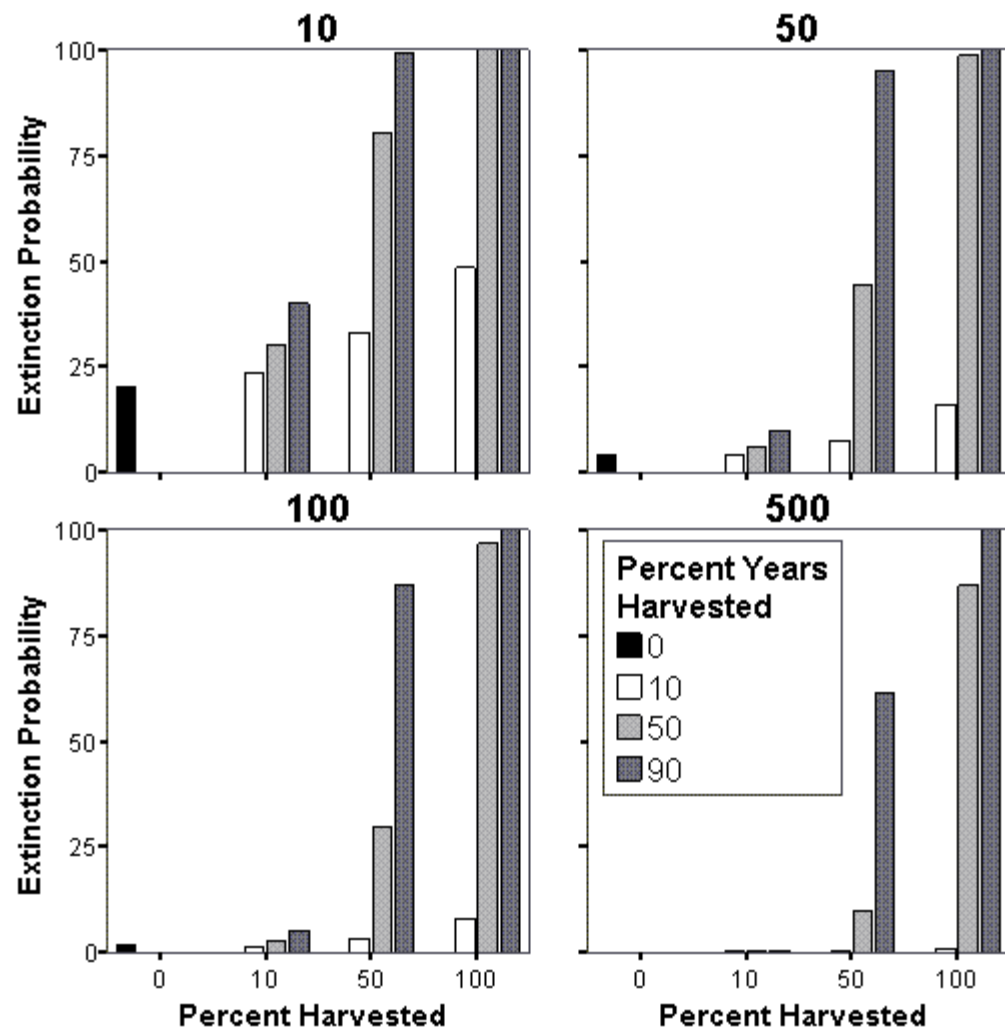


Figure 1.

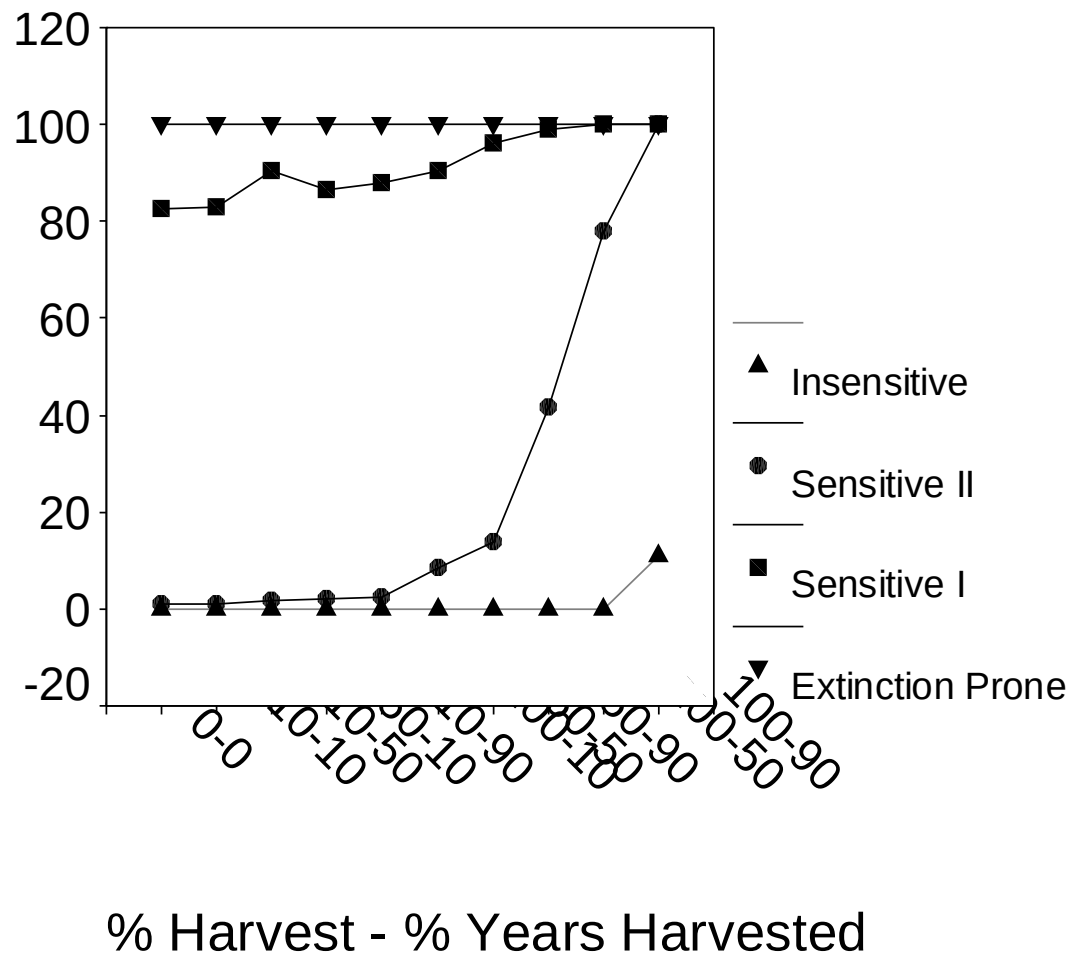


Figure 2.

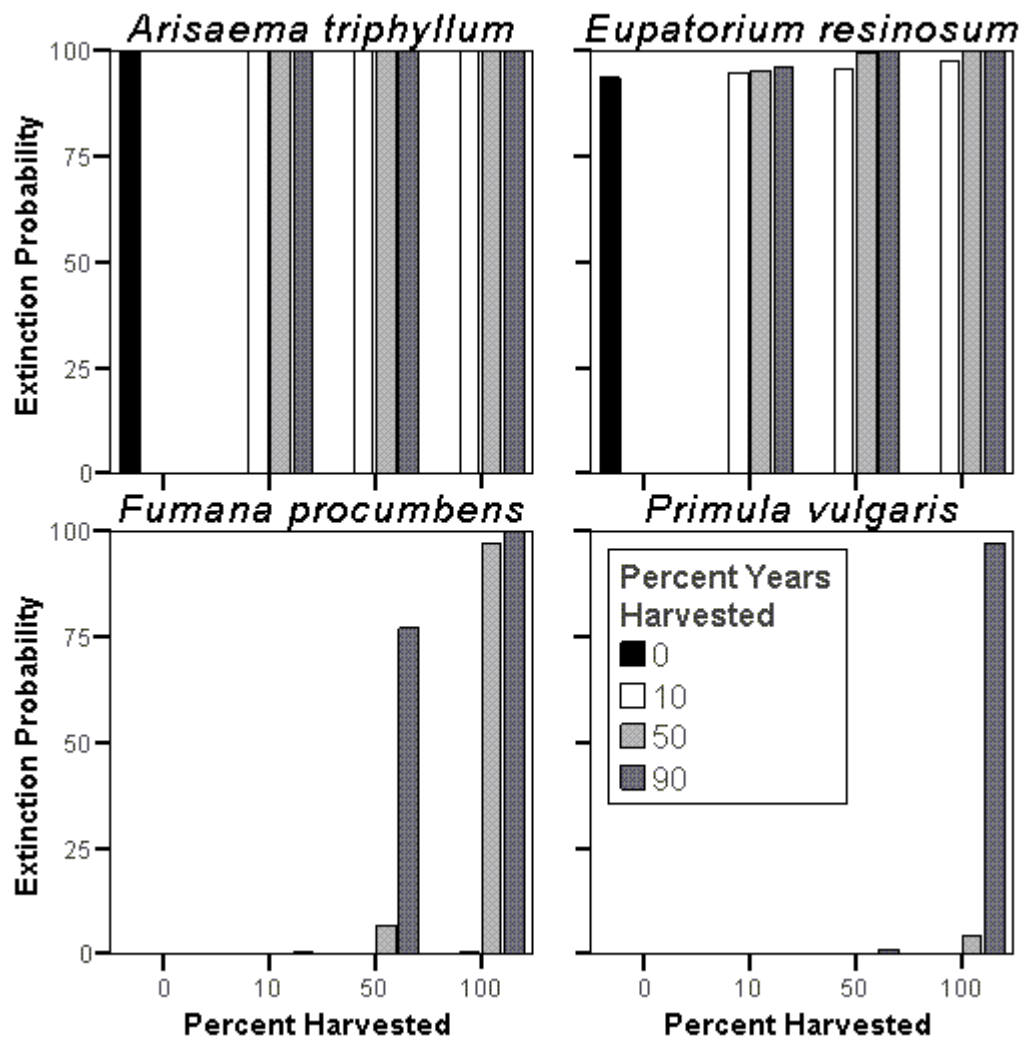


Figure 3.

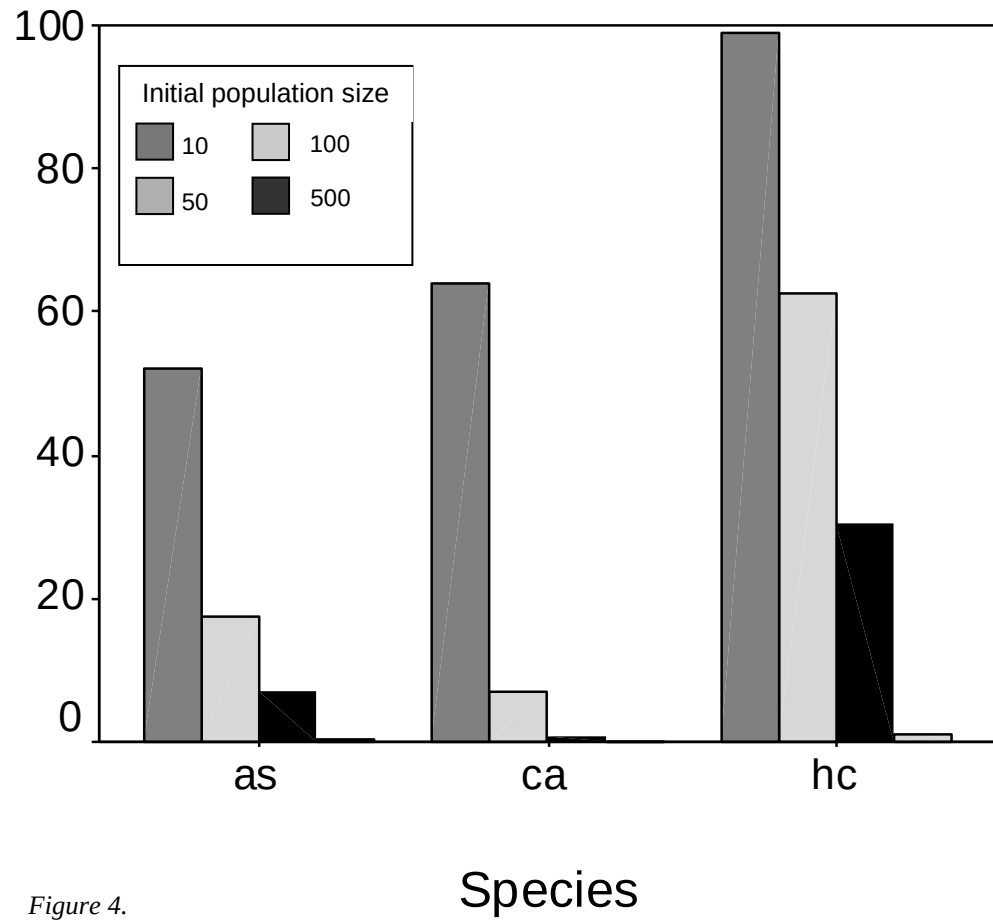


Figure 4.