

12 Projecting the Success of Plant Population Restoration with Viability Analysis

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12.1 Introduction

Conserving viable populations of plant species requires that they have high probabilities of long-term persistence within natural habitats, such as a chance of extinction in 100 years of less than 5 % (Menges 1991, 1998; Brown 1994; Pavlik 1994; Chap. 1, this Vol.). For endangered and threatened species that have been severely reduced in range and whose habitats have been fragmented, important species conservation strategies may include augmenting existing populations or restoring new viable populations (Bowles and Whelan 1994; Chap. 2, this Vol.). Restoration objectives may include increasing population numbers to reduce extinction probability, deterministic manipulations to develop a staged cohort structure, or more complex restoration of a desired genetic structure to allow outcrossing or increase effective population size (DeMauro 1993, 1994; Bowles et al. 1993, 1998; Pavlik 1994; Knapp and Dyer 1998; Chap. 2, this Vol.). These efforts may require translocation of propagules from existing (in situ) populations, or from ex situ botanic gardens or seed storage facilities (Falk et al. 1996; Guerrant and Pavlik 1998; Chap. 2, this Vol.).

Population viability analysis (PVA) can provide a critical foundation for plant restoration, as it models demographic projections used to evaluate the probability of population persistence and links plant life history with restoration strategies. It is unknown how well artificially created populations will meet demographic modeling requirements (e.g., due to artificial cohort transitions) and few, if any, PVAs have been applied to restorations. To guide application of PVA to restored populations and to illustrate potential difficulties, we examine effects of planting different life stages, model initial population sizes needed to achieve population viability, and compare demographic characteristics between natural and restored populations. We develop and compare plant population restoration viability analysis (PRVA) case studies of two plant species listed in the USA for which federal recovery planning calls for

population restoration: *Cirsium pitcheri*, a short-lived semelparous herb, and *Asclepias meadii*, a long-lived iteroparous herb.

12.1.1 Developing PVA for Plants

Analysis of stage-structured transition matrix models of population growth based on demographic monitoring is the basic tool in plant PVA; it is commonly used to determine a finite rate of population growth (λ) and to project change in size and extinction risk of naturally occurring plant populations (e.g., Menges 1990, 1991, 1998, 2000; Fiedler et al. 1998; Chap. 6, this Vol.). This application is attractive for restorations that otherwise would have unknown potential for persistence. Small populations exposed to relatively high amounts of environmental stochasticity are more vulnerable to extinction because increased fluctuations in population growth rate can more frequently lead to years in which the population falls below a demographic extinction threshold (Gilpin and Soulé 1986; Goodman 1987; Chap. 2, this Vol.). Thus, for plants living in variable environments, modeling that incorporates environmental stochasticity provides a more realistic PVA than traditional deterministic approaches, but requires more data (Shaffer 1987; Lande 1993; Mangel and Tier 1994; Beissinger and Westphal 1998; Menges 2000; Chaps. 6, 11, this Vol.). Such applications may be useful for small restorations under variable environmental conditions with habitats of uncertain suitability, but may be limited by lack of information about specific environmental variability. Use of variance to mean ratios (V/M) as a measure of the relative amount of environmental stochasticity that populations are experiencing provides a solution, at least in part, to this problem (Menges 1998). Stochastic modeling can also be partitioned among different management treatments (e.g., experimental burning) to allow more useful comparative projections (Beissinger and Westphal 1998; Menges 2000; Kaye et al. 2001; Chaps. 6, 11, this Vol.). The effects of the three components of stochasticity (environmental, demographic, and genetic) can operate simultaneously on demographic variability but cannot be separated without experimental manipulations.

Elasticity analysis of contributions of different life stages to population growth can help guide management application and differentiate among approaches used for plants with different life history strategies (Crouse et al. 1987; Crowder et al. 1994; Doak et al. 1994; Heppell et al. 1994; Silvertown et al. 1996; Chap. 6, this Vol.). However, elasticities for some species may not follow expected models (e.g. *Calochortus*, Fiedler et al. 1998), and could focus management on inappropriate life stages of declining populations (Beissinger and Westphal 1998; Menges 1998, 2000; Chap. 9. this Vol.) or restorations. For this reason, modeling of multiple populations helps interpret elasticities.

12.1.2 PRVA Applications

Although PVA has been used to assess more than 100 naturally occurring plant populations, including many endangered and threatened plants (Fiedler 1987; Menges 2000; Chap. 1, this Vol.), its application in restoration ecology is in its infancy. Rarely have restorations been demographically modeled or placed in an experimental or theoretical framework, and no formal PRVAs using integrated modeling have been reported for North American endangered or threatened plant species (Pavlik 1994, 1996; Guerrant and Pavlik 1998).

Non-integrated approaches to PVA can provide information and a framework for restoration by developing short-term and long-term restoration objectives (Pavlik 1994, 1996). Short-term objectives for restored populations may include completion of life cycle, obtaining a particular life stage distribution, attaining a stable or positive growth rate, reaching a desired level of genetic diversity, having a seed/ovule ratio greater than one, increasing population area, achieving normal seed bank density, or utilizing native pollinators. Long-term restoration goals are the same as PVA goals: attaining and maintaining minimum viable population (MVP) size as defined by a 95 % probability of survival after 100 years, as well as re-establishment of MVP size following perturbation (Pavlik 1996). In highly stochastic environments, comparatively larger initial population sizes are required to offset the increased risk of extinction.

Non-integrated demographic analyses (Pavlik 1994) have been used to examine cohort survivorship of restorations of the herbaceous perennials *Pediocactus knowltonii* (Olwell et al. 1990; Cully 1996) and *Isotria medeoloides* (Brumback and Fyler 1996) and the pine *Pinus torreyana* (Ledig 1996). Experimental treatments were used to assess effects of competition and burning on reintroduction of the shrub *Conradina glabra* (Gordon 1996), and herbs *Amsinckia grandiflora* (Pavlik et al. 1993; Pavlik 1994), *Asclepias meadii* (Bowles et al. 1998), and *Stephanomeria malheurensis* (Guerrant and Pavlik 1998). Performances of different seed sources were compared in a *Cirsium pitcheri* restoration (Bowles et al. 1993; Bowles and McBride 1996). For *Amsinckia grandiflora*, demographic monitoring was used in three phases of reintroduction, including an experimental phase to assess the response of the species to grass competition and to compare the performance of different propagule sources; a population enhancement phase using information from the first phase; and a third phase to evaluate the population's self sustainability in the absence of management, as well as its level of genetic diversity (Pavlik 1994; Guerrant and Pavlik 1998). These nonintegrated studies provide valuable but limited information about restorations and do not allow projection of MVP needed to assess whether long-term goals will be reached.

12.1.3 Theoretical Framework

Few theoretical models have been applied to plant population restoration. To examine the effect of size/stage class on founding success, Guerrant (1996) used published natural transition matrices to model extinction rates for three perennial plants with differing life histories: the woody iteroparous *Astrocarum mexicanum*, the semelparous herb *Dipsacus sylvestris*, and the iteroparous herb *Calochortus pulchellus*. In these projections, all three species exhibited a decrease in extinction risk and accelerated population growth with initial establishment of larger or older plants relative to beginning with seedling establishment. Thus, Guerrant (1996) concluded that populations founded with seeds had a significantly higher extinction risk than those founded by larger life stages, and provided a testable theoretical basis for founding population restorations. Guerrant and Fiedler (2003) also modeled the “demographic cost” of reintroduction using studies of seven species with a range of life histories. They projected that substantial losses of individuals would be reduced by outplanting larger individuals, which reduces extinction probability. Therefore, in this chapter we investigate how planting different life stages affects the demographic cost of restoration and the initial population size needed to achieve population viability. Because so little is known about the viability of plant restorations, we compare demographic characteristics of a restored population against a viable natural population as a benchmark of success.

12.2 PRVA Case Studies

To address plant PRVA issues concerning MVP, initial planting size, life stage used for outplanting, and comparison with natural populations, we use case studies of two species in the USA with contrasting life history strategies that result in different restoration applications and PRVA outcomes (Table 12.1). Both species are classified by the federal authorities as threatened and have been the focus of long-term restoration projects coupled with demographic monitoring. Pitcher’s thistle (*Cirsium pitcheri* [Torrey ex Eaton] T. and G.) is a short-lived monocarpic herb endemic to sand dunes of the western Great Lakes, where it colonizes successional habitats and requires frequent cohort replacement to maintain populations (McEachern et al. 1994). Mead’s milkweed (*Asclepias meadii*) is a long-lived iteroparous herb of late-successional midwestern tallgrass prairie and glades (Bowles et al. 1998). Natural reproduction is infrequent in this species, and adult longevity is apparently a large component of population maintenance. Absence of complete life stage transition data prevented a complete PVA for this species, but we present preliminary analysis of population viability.

Table 12.1. Different habitats and biological characteristics result in contrasting restoration strategies for *Cirsium pitcheri* and *Asclepias meadii*

Species	<i>Cirsium pitcheri</i>	<i>Asclepias meadii</i>
Habitat	Early- successional shoreline dunes of the western Great Lakes	Late-successional prairies and glades of the Midwest
Life history	Short-lived monocarpic perennial with frequent cohort replacement	Long-lived perennial with infrequent cohort establishment
Genetic diversity	Comparatively low genetic diversity within and among populations	High genetic diversity within populations, low genetic differentiation among populations
Breeding system	Self compatible with mixed mating	Obligate outcrossing with different genotypes required for reproduction
Restoration strategies	Establish natural stage structure through repeated outplanting, manage for growth and reproduction	Establish adult cohort, maximize genetic diversity, manage for adult persistence, flowering and seed production

12.3 Pitcher's Thistle

12.3.1 Species Background

Pitcher's thistle (*Cirsium pitcheri*) is a threatened (Harrison 1988) species endemic to the western Great Lakes shoreline, and is extirpated from Illinois. *Cirsium pitcheri* inhabits shoreline sand dunes and beaches, where wind-generated disturbance processes maintain open sand and successional vegetation that allow successful seedling establishment (McEachern 1992). This semelparous species has no capacity for vegetative spread; plants reach a threshold size and flower after 3–8 years, disperse seeds, and then die (Loveless 1984). *Cirsium pitcheri* has a mixed mating system, with 35–88 % outcrossing through insect pollination, which produces higher seed set than with self-pollination (Keddy and Keddy 1984; Loveless 1984). Population structures of *Cirsium pitcheri* are temporally variable, depending upon cohort demographic histories and successional stages of vegetation, and this species may depend upon metapopulation processes for long-term persistence (McEachern et al. 1994). Although seed dormancy occurs in *Cirsium pitcheri* (Chen and Maun 1998), Rowland and Maun (2001) found little evidence for a seed bank in two Canadian populations. We observed consumption of flower heads of this

species by eastern white tailed deer, as well as seed by small mammals, and assume that both could substantially reduce seedling numbers. Exclusion of insect seed predators from seed heads may increase fecundity (Louda 1994).

In accordance with recovery planning and to test whether *Cirsium pitcheri* could be successfully restored, a population restoration began in former habitat at Illinois Beach State Park in 1991 (Bowles et al. 1993; McEachern et al. 1994; Bowles and McBride 1996; Pavlovic et al. 2003). The park is located along the west shoreline of Lake Michigan 70 km north of Chicago. It occupies a 1.5-km wide sand deposit with low dunes (up to 3 m), which extends for over 20 km. Secondary dunes were found to replicate appropriate habitat for this species and appeared to be free from problems of shoreline erosion and recreational impacts (Bowles et al. 1993). Two localities separated by <1 km were used to establish population units first south, and then north of the Dead River, which drains into Lake Michigan.

Cirsium pitcheri restoration propagules were grown from seeds collected from natural Indiana, southern Wisconsin, and southern Michigan thistle populations. Thistle cohorts were propagated for one season, over-wintered, and then translocated to the restoration site. Over 100 plants were established in the south unit by 1993, and the first two plants flowered in 1994. Naturally recruited seedlings from flowering plants are now replacing these artificial cohorts, and the first of these naturally recruited plants flowered in 1998.

Plant morphology, performance, and genetics differed between Indiana and Wisconsin seed sources when planted at Illinois Beach. Indiana plants had larger cotyledons and greater growth and survivorship than Wisconsin plants (Bowles et al. 1993; Bowles and McBride 1996). Random amplified polymorphic DNA analysis (RAPDs) also separated these seed sources (K. Havens, unpublished data). In addition, differences in population structure occurred north and south of the Dead River. The younger population north of the river had significantly lower relative abundance of flowering, large juvenile, and seedling plants, while plants south of the Dead River had lower mortality and lower abundance of small juveniles. In addition, naturally recruited plants had not yet flowered north of the Dead River. These differences suggest a greater rate of population growth south of the Dead River. The lack of representation by all demographic stages prevented us from developing an integrated PVA for the restoration north of the Dead River.

12.3.2 Restoration Viability Analysis

Our PRVA assessed the viability of the Illinois Beach restoration by comparing its population size to the MVP size required to achieve an extinction probability (P_e) of <5 % and by determining whether average, as well as annual, life stage transition matrices represented a growing ($\lambda > 1$) or stable ($\lambda = 1$) population. In addition, we determined the initial number of outplantings required

to reach $P_e < 5\%$ and how planting seeds vs. juveniles influences the initial numbers needed. We also determined whether demographic characteristics of the restoration were comparable to a natural population.

12.3.2.1 Demographic Modeling

Demographic monitoring data from 1994 through 2000 was used to develop a matrix model for the Illinois Beach State Park population restored south of the Dead River (Appendix 12.1; see Chap. 6, this Vol., for details on matrix modeling approaches). The matrix model was used to evaluate which stages to manipulate in order to increase the population growth rate, to evaluate the effect of environmental stochasticity on the MVP, and to simulate the effects of population size and initial transplant stage on the probability of extinction and MVP. Elasticities and λ for each matrix were determined using RAMAS/Stage (Ferson 1994). Popproj2 (Menges 1998) was used to calculate P_e using 1,000 runs for 100 years with a quasi-extinction population size of 1. Popproj2 introduces environmental stochasticity into the simulations by randomly choosing among transition matrices.

We analyzed five life stages for *Cirsium pitcheri* including seed, seedling, small juvenile, large juvenile and flowering plants, which may arise either from artificial transplant cohorts or as naturally recruited seedlings from flowering transplanted plants or their descendents (Fig. 12.1). Because greenhouse-grown transplants and naturally recruited individuals have different transition frequencies (Appendix 12.1), and transplants that flower earlier have fewer seed heads (Fig. 12.2), the restoration transition matrices incorporate transplants and naturally recruited individuals into the matrix separately (Fig. 12.1). Large juveniles differ from small juveniles by having attained a threshold flowering size measured by root crown size and a leaf area index. For *Cirsium pitcheri* plants that survived to the flowering stage, individuals remained in the small juvenile stage for 2 years (2.0 ± 1.0 SD, range 1–6), were a large juvenile for only 1 year (1.0 ± 0.7 SD, range 0–2), flowered in their fourth year (4.1 ± 1.1 SD, range 2–7), and died. The transition from sown seed to seedling (G_{s1}) was estimated by dividing the number of seedlings observed by the number of seeds produced the previous year. The number of seeds per flowering plant was estimated by multiplying the number of flower heads for a given year by the average number of seeds per flower head. We assumed that the restoration population, like natural populations (Rowland and Maun 2001), had no seed bank.

Although transplanting began in 1991 and naturally recruited plants began to appear in 1995, we could only develop complete matrices for 1998→1999 and 1999→2000 transitions because too few individuals occurred in each stage for previous years. In order to develop an average matrix, transition frequencies were calculated from transition numbers summed over the years

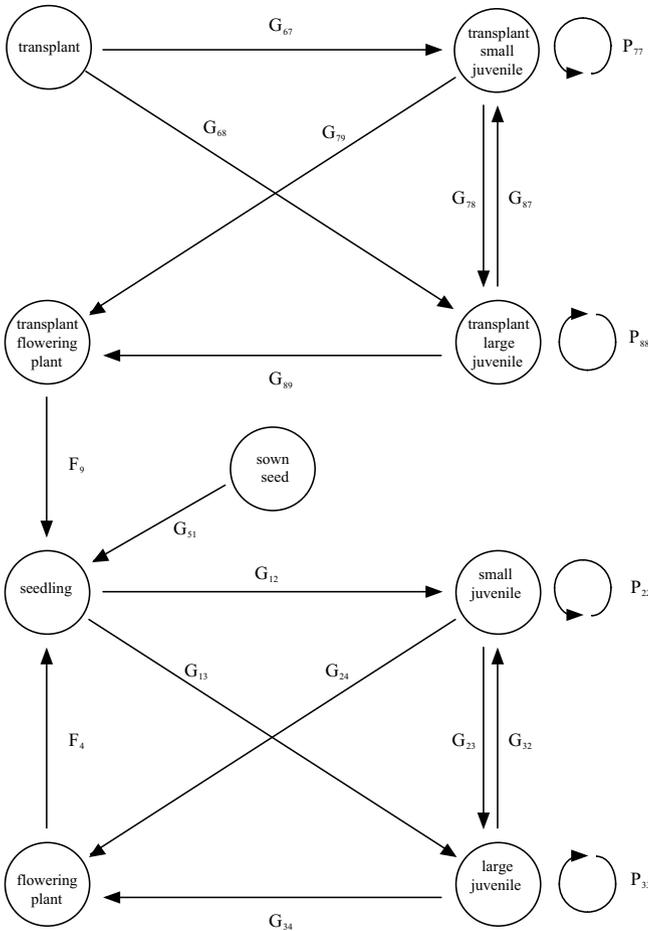


Fig. 12.1. Generalized stage-based population dynamics model for Pitcher's thistle (*Cirsium pitcheri*). Circles Stages, arrows possible transitions between stages. Transition labels indicate growth (G) from one stage to the next, the probability (P) of remaining in that stage and fecundity (F)

Reproductive output in *Cirsium pitcheri* as a function of flowering time since planting and seedling origin

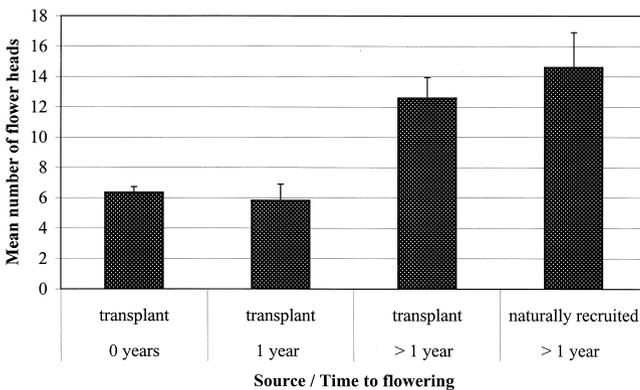


Fig. 12.2. Reproductive output is highest for flowering plants produced from naturally recruited seedlings or from transplants that require >1 year to flower ($F=14.176$, $p<0.0001$)

1991–2000. Thus the simulations for the Illinois Beach restoration included the three matrices in Appendix 12.1.

To determine whether the restored Illinois Beach population was demographically similar to a natural population, the demography of the restored Illinois Beach population was compared with that of a natural population at West Beach, Indiana Dune National Lakeshore (McEachern 1992; McEachern et al. 1994). The sample used for West Beach demographic monitoring included approximately 23% of a population of about 1,900 plants. Appendix 12.2 includes projection matrices of transition frequencies for the natural *Cirsium pitcheri* population at Indiana Dunes West Beach from 1988 to 1993.

Annual transitions were generally similar but variable for both the Illinois Beach restoration and natural West Beach population. A small percentage of seedlings at Illinois Beach became large juveniles the next year but not at the

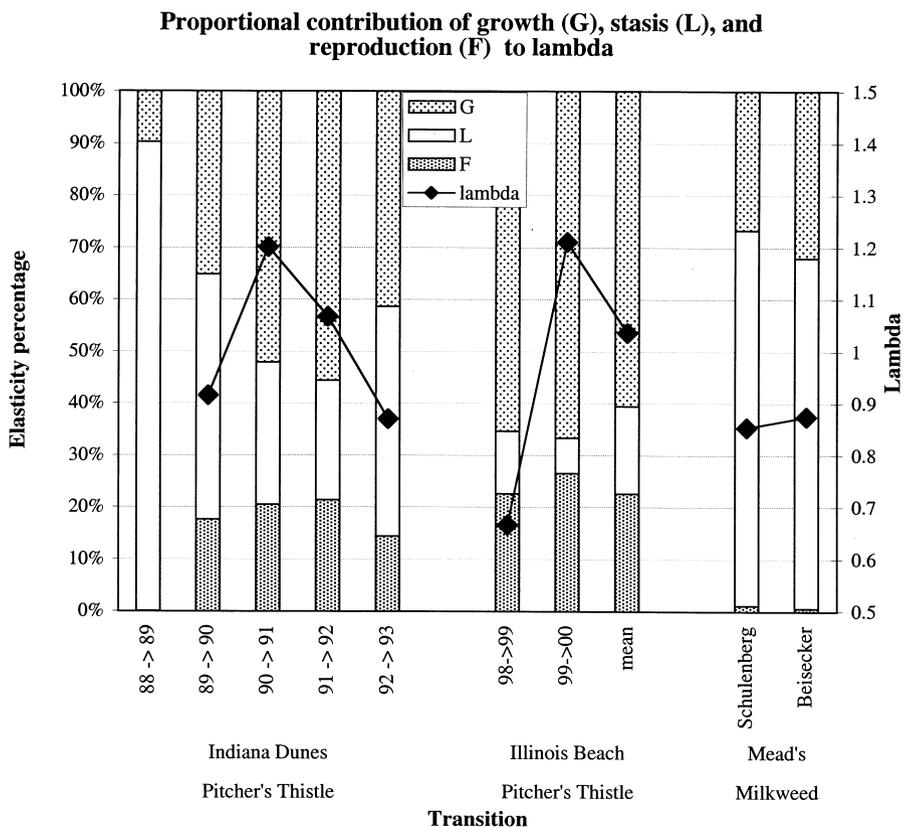


Fig. 12.3. Proportional contribution of growth (G), stasis (L) and reproduction (F) to λ for *Cirsium pitcheri* natural (Indiana Dunes) and restoration (Illinois Beach) populations, and *Asclepias meadii* restoration populations

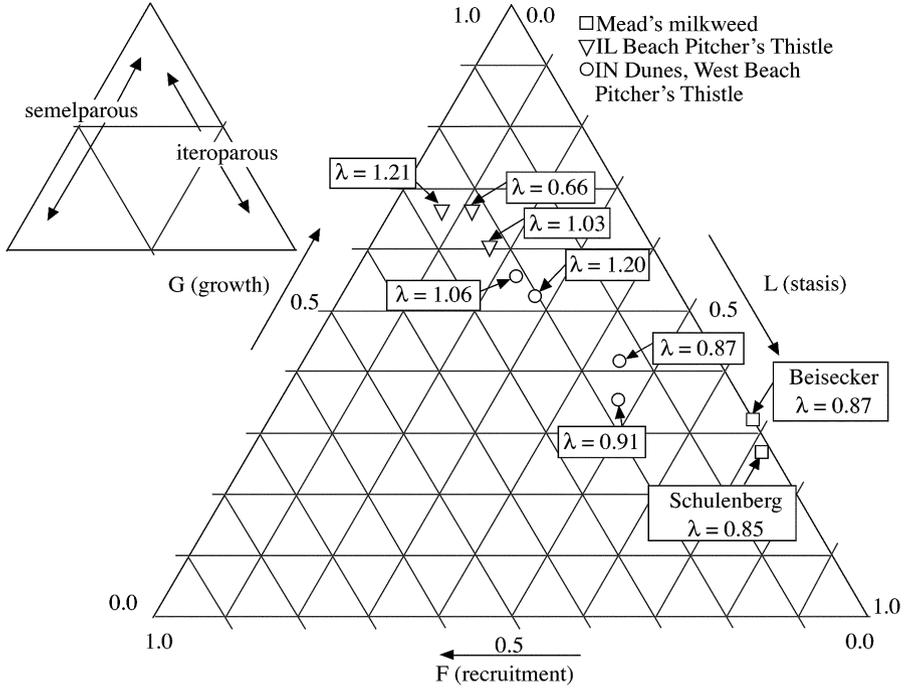


Fig. 12.4. Ordination of growth (*G*), stasis (*L*) and reproduction (*F*) elasticities for *Cirsium pitcheri* restoration (Illinois Beach, triangles) and natural (Indiana Dunes, circles) populations, and *Asclepias meadii* restoration populations (squares)

Indiana Dunes population. Some large juveniles at Indiana Dunes shrank to small juveniles the next year but not at Illinois Beach.

There were variations in λ from year to year in both the restoration and natural *Cirsium pitcheri* populations (Fig. 12.3). Restoration population growth rates ranged from 0.66 to 1.21, with $\lambda=1.03$ for the average matrix (Figs. 12.3, 12.4). These are similar to the values of λ calculated for the natural Indiana Dunes population, which ranged from 0.87 to 1.21 (Figs. 12.3, 12.4). One Indiana Dunes matrix representing the transitions from 1988 to 1989 had a $\lambda=0$ because no seedlings survived (Appendix 12.2) apparently because 1988 had the lowest rainfall record in 50 years.

12.3.2.2 Elasticity Analysis

Following Silvertown et al. (1996), ordination of elasticities was used to evaluate the effect that changes to groups of stage transitions have on λ (see Chaps. 6, 11, this Vol., for an in-depth discussion of elasticities). We grouped elasticities into the *G* region representing the combined effects of changes to

Table 12.3. a *Cirsium pitcheri* variance-to-mean ratios for Illinois Beach State Park restoration population; median (all elements)=0.1695, median (recruited only)=0.2069. **b** Variance-to-mean ratios for Indiana Dunes National Lakeshore West Beach population; median=0.1044. *R* Naturally recruited individuals, *T* transplanted individuals

		State (t) →					Transplants			
		Naturally recruited					Sown seed	T "seedling"	T small juvenile	T large juvenile
<i>a</i> Illinois Beach restored population										
Fate (t+1)	R seedling	0.3795	0.3493	R large juvenile	0.4939	0.0029				
	R small juvenile	0.1687	0.2081	0.0313						1.4161
	R large juvenile		0.0474	0.2057						
	R flowering									
Sown seed										
	T "seedling"					0.1661				
	T small juvenile					1.0728		0.1181	0.1376	
	T large juvenile							0.1086	0.1703	
	T flowering							0.0510	0.2063	
Median (all elements) = 0.1695										
Median (recruited only) = 0.2069										
<i>b</i> Indiana Dunes natural population										
Fate (t+1)	Seedling									
	Small juvenile	0.4393	Small juvenile		Flowering					
	Large juvenile		0.0266	Large juvenile	6.4924					
	Flowering		0.1852	0.0564						
	Median = 0.1044		0.1349	0.0740						
			0.0665	0.0665						

growth on λ , the *L* region representing the combined effects of changes to stasis and retrogression on λ , and the *F* region representing the combined effects of changes to recruitment on λ (Table 12.2).

Although most *Cirsium pitcheri* G/L/F elasticity ratios occur in the semelparous region (Fig. 12.4), several were positioned toward the region where Silvertown et al. (1996) tended to find iteroparous herbs. For *Cirsium pitcheri*, λ tends to increase with increasing *F* in both the natural Indiana Dunes and restored Illinois Beach populations (Figs. 12.3, 12.4). When Silvertown et al. (1996) ordinated 16 populations of *Cirsium vulgare* (semelparous) and 15 *Pedicularis furbishiae* populations (iteroparous), λ also increased with increasing contribution of *F*. They interpreted this to mean that the best management strategy would focus on increasing recruitment. This suggests we should be able to increase *Cirsium pitcheri* λ by increasing recruitment, which makes sense for a semelparous perennial because increasing longevity only (i.e. without growth) does not increase recruitment as it does in iteroparous plants (Silvertown et al. 1996). However, managing for both survivorship and growth may also increase fecundity.

12.3.2.3 Variance/Mean Ratios

High levels of environmental stochasticity are expected for *Cirsium pitcheri* because it inhabits a highly dynamic habitat. The median Illinois Beach *V/M* was 0.17 for all matrix elements (0.03–0.38 for recruited non-fecundity elements and 0.49 for recruited fecundity) and the West Beach *V/M* median was 0.10 (0.03–0.44 for non-fecundity elements and 6.49 for fecundity) (Table 12.3).

The variance-to-mean ratio for the *Cirsium pitcheri* restoration (0.17) was higher than for the natural population (0.10) and both corresponded to very strong environmental stochasticity. In comparison, only one of eleven species

Table 12.2. Generalized matrix for *Cirsium pitcheri*, grouping elasticities into growth (*G*), stasis (*L*) and reproduction (*F*) regions

	State (year t)→			
Fate (year t+1)	Seedling	Small juvenile (crown <1 cm)	Large juvenile (crown >1 cm)	Flowering
Seedling		F=fecundity, recruitment		
Small juvenile		L=stasis		Shrinking
Large juvenile	G=growth			
Flowering				

analyzed by Menges (1998) had a median V/M greater than 0.17. Although seven of these species had populations with V/M greater than 0.10, all but one species had at least one population with median V/M below 0.10. The high variation, especially in non-fecundity elements, requires a relatively high MVP size to reduce extinction probability.

The effect of environmental stochasticity on MVP decreases as λ increases (Menges 1998). Populations with $\lambda < 1$ were sensitive to $V/M < 0.0025$, while populations with $\lambda \approx 1$ were sensitive to $V/M > 0.005$ and populations with $\lambda > 1.15$ were sensitive to $V/M > 0.14$. Three of the five transition matrices for the natural *Cirsium pitcheri* population had $\lambda < 1$ and average $\lambda = 0.96$, indicating that this population, as well as the restoration (average $\lambda = 1.03$), are very sensitive to environmental stochasticity.

12.3.2.4 Minimum Viable Population Estimates

We used the matrix model to simulate the effects of population size on P_e and MVP. Extinction probability varied as a function of initial simulated population size for both populations of *Cirsium pitcheri* (Fig. 12.5). The minimum

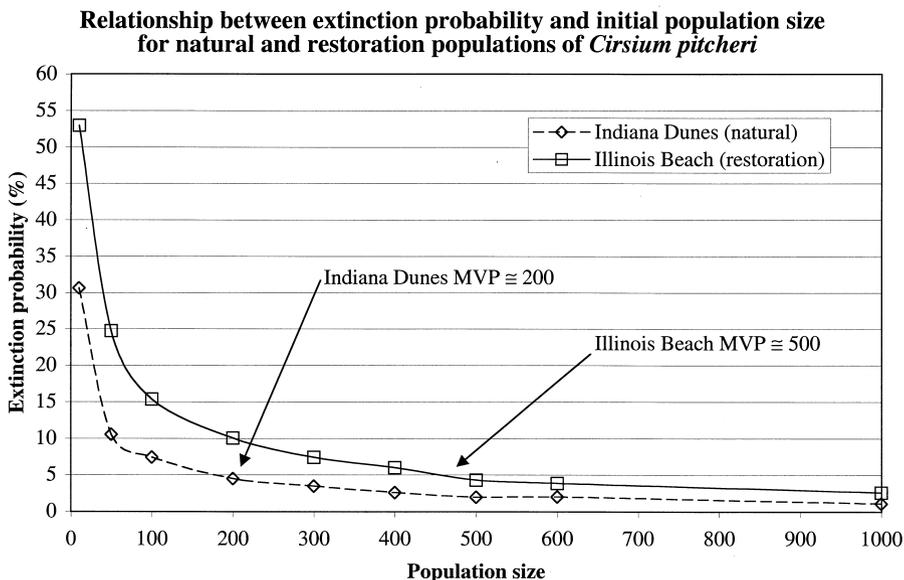


Fig. 12.5. Extinction probabilities are lower for the Indiana Dunes population than for Illinois Beach restoration of *Cirsium pitcheri*. Three empirically derived transitions (Appendix 12.1) from the Illinois Beach State Park restoration were alternatively chosen with equal probability each year of each simulation. For the five Indiana Dunes matrices (Appendix 12.2), the drought transition matrix, 1988-→1989, had a probability of 0.132 and $p = 0.217$ for all other matrices

Table 12.4. Minimum viable population (MVP) size projections (at $P_e=5\%$) is greater for the Illinois Beach State Park restoration of *Cirsium pitcheri* than for the Indiana Dunes West Beach natural population. Observed stage distribution and population size are smaller than MVP for the Illinois Beach restoration

Stages	Observed stage distribution		Projected MVP and distribution ($P_e \leq 5\%$)	
	Indiana Dunes West Beach average	Illinois Beach 2000	Indiana Dunes West Beach	Illinois Beach
Seedlings	222 (50%)	58 (60%)	100	250
Small juveniles	141 (32%)	13 (14%)	60	150
Large juveniles	34 (8%)	11 (11%)	20	50
Flowering plants	43 (10%)	14 (15%)	20	50
Total	440	96	200	500

population size needed for the restored population to be viable for *Cirsium pitcheri*, as indicated by $P_e < 5\%$, was ~ 500 for the Illinois Beach State Park restoration, and ~ 200 for the Indiana Dunes West Beach natural population (Table 12.4).

Simulation methods used to estimate MVP size differed for the restoration and natural population. Each of the three Illinois Beach matrices had an equal probability (0.333) of being chosen in the simulation. The Indiana Dunes drought transition matrix, 1988 \rightarrow 1989, had a probability of 0.132, based on the proportion of years the Palmer drought severity index was equal to or lower than the index value that occurred in the drought year of 1988 (e.g., Karl and Knight 1985). For all other Indiana Dunes matrices $p=0.217$. As the frequency of the drought year matrix increases in the simulation, extinction probability increases exponentially. For example, estimated MVP size for the Indiana Dunes population was approximately 10,000 when drought year matrix frequency was equal to all other matrix frequencies ($p=0.20$) compared to MVP size ~ 200 for our simulation (Table 12.4). The difference between these two MVPs reflects the increased year-to-year population size variability as a result of stochastic events, such as drought (see discussion in Chap. 11, this Vol.).

Estimation of MVP agrees with V/M . Since the natural Indiana Dunes population has a lower V/M than the Illinois Beach restoration, it is not surprising that the MVP for Indiana Dunes (200) is lower than for Illinois Beach (500) (Fig. 12.5).

We suspect that the Illinois Beach MVP is higher than Indiana Dunes MVP because the 1998 \rightarrow 1999 transition matrix, for which $\lambda=0.66$, has a high frequency in the Illinois Beach simulation. We had no rationale for reducing the frequency of the 1998 \rightarrow 1999 matrix in the simulation as we did for the Indiana

Dunes drought matrix because both 1998 and 1999 had Palmer drought severity indices that indicated normal rainfall. We expect estimated restoration MVPs to become more similar to the natural population as monitoring continues and the number of transition matrices in the simulation increases.

Because the restoration population size of 96 is below the estimated MVP, more than 400 transplants are required to increase population numbers to a viable level (Table 12.4). Matrix models for the Illinois Beach State Park restoration of *Cirsium pitcheri* were used to compare the effects of initial transplant number and seed number on P_e . Approximately 1,600 seedlings would need to be planted to establish a viable population compared to approximately 250,000 seeds, illustrating the increased demographic cost (Guerrant and Fiedler 2002) of planting seeds (Fig. 12.6). Using seeds to establish a population of *Cirsium pitcheri* is inefficient because high seed mortality in the restoration results in frequencies for transition from seed to seedling ranging from 0.0032 to 0.0086 (see sown seed transitions, Appendix 12.1).

The number of transplants used to create a viable restoration at Illinois Beach (Fig. 12.6) differs from the MVP for the Illinois Beach restoration (Table 12.4). This is because in the transplant simulation all individuals entering the restoration were in the same transplant “seedling” stage and needed to mature through the larger transplant stages before seed production began

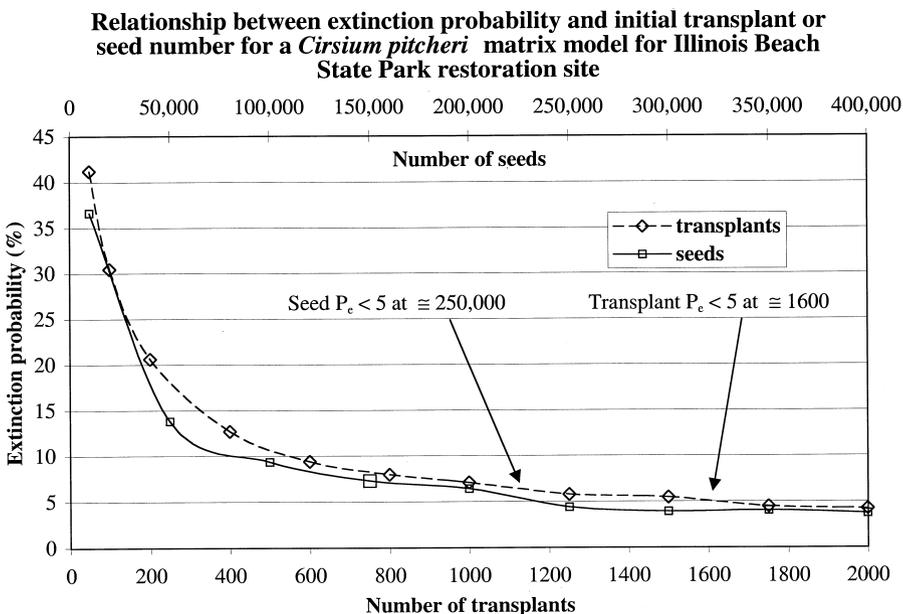


Fig. 12.6. Extinction probability decreases with increasing initial transplant and seed number for a *Cirsium pitcheri* matrix model for Illinois Beach State Park restoration site. Empirically derived transition matrices were alternatively chosen with equal probability each year of each simulation

and naturally recruited individuals were present. In the MVP simulation, individuals in the simulation were all naturally recruited and were divided among the stages in a ratio approximating the natural stage distribution (5:3:1:1, see Table 12.4). The later stages have greater reproductive value than transplant seedlings and the number of plants needed for $P_e < 5\%$ is smaller when divided among all naturally recruited stages compared to transplant “seedlings”.

As with Guerrant’s (1996) simulations, the minimum number of transplants required to establish a viable restoration population of *Cirsium pitcheri*, as well as the extinction risk at the same initial transplant number, were greater for seed compared to non-seed transplants (Fig. 12.6). However, caution must be used when generalizing transplant performance from matrices based on natural populations, since we observed that transplants flower earlier and have lower fecundity (Fig. 12.2) and different transition frequencies (Appendix 12.1) than naturally recruited plants. Our data for *Cirsium pitcheri* suggest that projections based on naturally recruited seedlings would actually have a lower extinction probability than transplants.

12.4 Mead’s Milkweed

12.4.1 Species Background

Mead’s milkweed (*Asclepias meadii*), an iteroparous herb of late-successional tallgrass prairies of the midwestern USA, is classified by federal authorities as a threatened species because of conversion of its habitat to agriculture (Harrison 1988; Betz 1989). As with many other milkweeds, this genetically diverse species expresses late-acting self-incompatibility and has high sensitivity to inbreeding depression and low rates of reproduction (Betz 1989; Betz et al. 1994; Wyatt and Broyles 1994; Bowles et al. 1998; Tecic et al. 1998; Kettle et al. 2000). Large clones may develop by rhizomes when sexual reproduction is prevented (Hayworth et al. 2002). Genets of this species are apparently very long-lived, although ramet numbers vary annually (Betz 1989), and individual plants have persisted for up to 30 years. Most populations in the western part of its range occur in haymeadows, where mowing removes seed pods and promotes clonal spread, and fragmented eastern populations apparently comprise single or few clones that persist vegetatively (Bowles et al. 1998; Tecic et al. 1998; Hayworth et al. 2002).

Recovery planning for *Asclepias meadii* includes restoration of viable populations in the eastern part of its range, which will require large numbers of different genotypes to facilitate outcrossing (Tecic et al. 1998; Hayworth et al. 2002). To help achieve this goal, a genetically diverse ex situ garden population of this species was developed from multiple seed sources, and serves as a

propagule source for restoration (Bowles et al. 1998, 2001). Since 1991, nine restorations have been initiated in Illinois and adjacent Indiana, in which plantings of seeds and 1-year old juveniles have been repeated over time to simulate recruitment (Bowles et al. 1998, 2001). This work has allowed comparison of different establishment methods, as well as in situ vs. ex situ growth rates and environmental and management effects on demographic processes. We analyze viability of restored populations at the Schulenberg Prairie of the Morton Arboretum, DuPage County, Illinois, and the Biesecker Prairie Nature Preserve, Lake County, Indiana.

Field establishment of *Asclepias meadii* is constrained by abiotic factors (Fig. 12.7). Dormant-season prescribed burns enhance seedling establishment and growth, especially in years with greater than average rainfall, while planted juveniles show a greater response to fire during years of normal rainfall (Bowles et al. 1998). There is little evidence for a seed bank, as <1% of field-planted seeds have germinated the second year after planting. Seedling establishment rates in the field are much lower than greenhouse germination, and establishing cohorts by transplanting greenhouse propagated juveniles is therefore more efficient than planting of seeds. Nevertheless, there is little difference in survivorship once plants become established either by planting of seeds or juveniles (Bowles et al. 2001). Cohort mortality has been high over

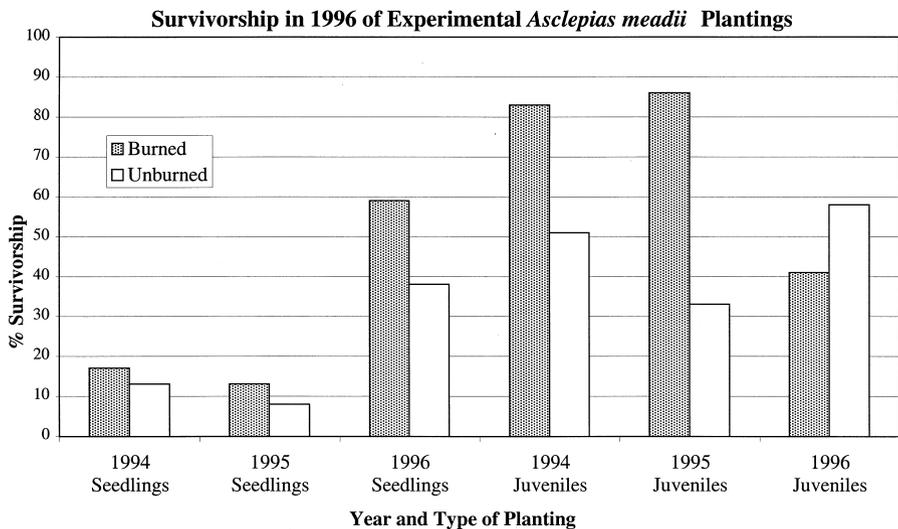


Fig. 12.7. Planted seedling and juvenile Mead's milkweeds respond differently to burning and rainfall. Greater than normal rainfall and higher seedling survivorship ($P=0.001$) occurred in 1996, and seedling survivorship was higher ($P=0.057$) in burned habitat in 1996. Juvenile survivorship was higher in burned habitat in 1994 ($P<0.001$) and in 1995 ($P=0.013$). (Data from Bowles et al. 1998, with permission of the Annals of the Missouri Botanical Garden)

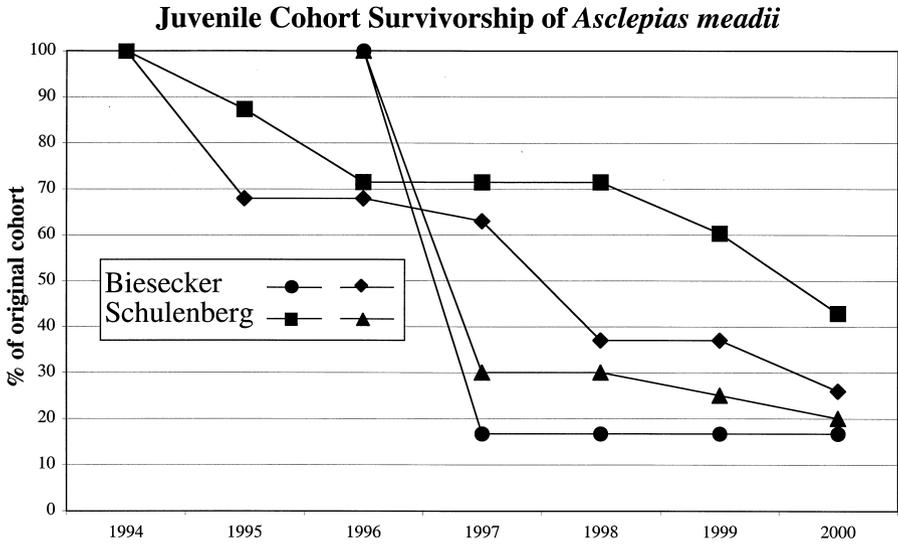


Fig. 12.8. Cohort survivorship of spring-planted 1-year-old Mead’s milkweeds

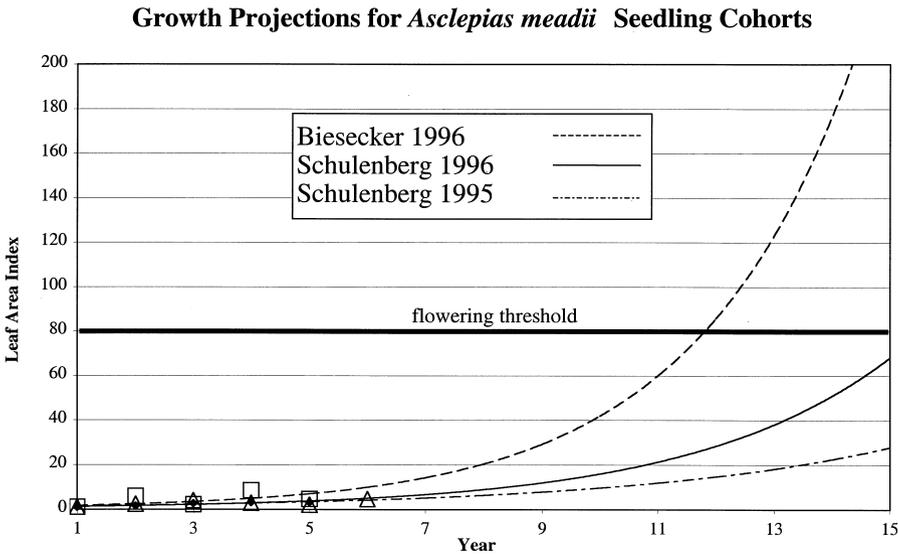


Fig. 12.9. Exponential growth projections of Mead’s milkweed seedling cohorts predict 12 years or more to attain flowering threshold

the first winter after spring planting, and survivorship has then declined to about 20–40% (Fig. 12.8). Despite similar survivorship, plants established as juveniles have greater growth than seedlings and have attained flowering size thresholds after as few as 2 years. Seedling growth is suppressed by competition (Bowles et al. 1998), and 12 or more years may be required for seedlings to reach reproductive size in the field (Bowles et al. 2001; Fig. 12.9). Reproduction may be further constrained by other factors, as natural seed production has occurred only once after five consecutive years of flowering at the Schulenberg restoration. This may have been due to lack of successful crossing between compatible genotypes, or because plants were too small to develop fruits. Dormancy has occurred among plants established from seed or planted juveniles, as well as in cultivated plants.

12.4.2 Restoration Viability Analysis

Projections of population growth and size required to achieve a 95% probability of persistence over time are not currently possible for the Mead's milkweed restorations because of missing data. Except for a single event of seed production, all transitions have been the result of artificial planting, and natural transitions are therefore not yet available. Likewise, despite extensive monitoring of several natural populations (Betz 1989; Kettle et al. 2000), data are also unavailable on complete stage transitions because of the great longevity and low fecundity of this species. As a result, no complete demographic data were available from a natural population with which to compare the stage distribution of the restoration. Also, because natural recruitment has not been observed in the restoration populations, reliable matrix models are not available with which to estimate a MVP.

12.4.2.1 Demographic Modeling

To develop transition frequencies for the restored Schulenberg and Biesecker populations, we used six stages, including seedlings, three juvenile size classes, dormant plants, and flowering plants (Fig. 12.10). The juvenile life stages are size classes based on leaf-area indices, with the smallest including juveniles that retain the linear leaves characteristic of seedlings (Bowles et al. 1998). All juveniles or flowering plants may revert to the smallest stage, or to dormancy. Seedling transitions were based on planted seeds, because naturally recruited seedlings have not been observed, while planted juveniles were entered into the transitions at their appropriate size class. Transition frequencies for the restored populations (Appendix 12.3) were calculated using cumulative annual transitions from 1995 to 2000. At Schulenberg, flowering

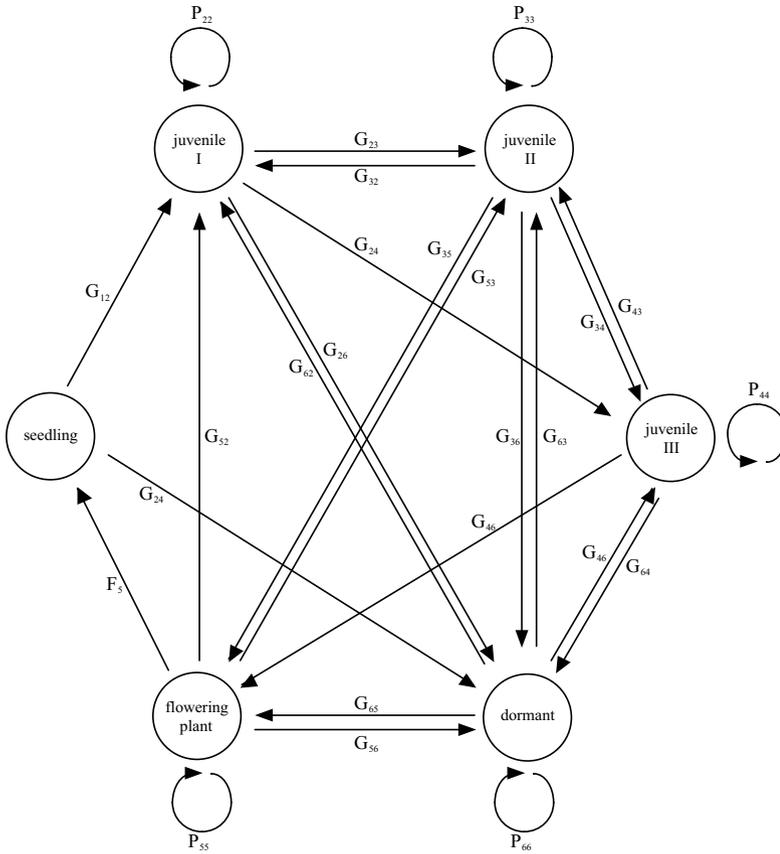


Fig. 12.10. Generalized stage-based population dynamics model for Mead's milkweed (*Asclepias meadii*). Circles Stages, arrows possible transitions between stages. Transition labels indicate growth (G) from one stage to the next, the probability (P) of remaining in that stage and fecundity (F)

occurred in all 5 years, but successful seed production occurred only in 2000, and $\lambda=0.85$. To compensate for lack of seed production at Biesecker, the fecundity transition frequency (F_{51}) was calculated using seed production from Schulenberg. This change in the transition frequency matrix for Biesecker had a relatively small effect on λ ($\lambda_{(F_{51}=0)}=0.869$, $\lambda_{(F_{51}=0.4424)}=0.874$).

Modeling was also hampered by the slow growth and low fecundity of this species. Although our reproduction transitions based on artificial seedling establishment could reflect expected survivorship under natural environmental conditions, it is unknown how well our seed planting technique replicated the natural process of seed dispersal and germination.

12.4.2.2 Variance/Mean Ratios

The V/M ratios for Schulenberg matrix elements ranged from 0.01–0.76 for non-fecundity elements, with 0.33 for fecundity and a median value of 0.10. For Biesecker, V/M ratios ranged from 0.006–0.65 for non-fecundity elements, with 25.81 for fecundity and a median value of 0.18 (Table 12.5). The high fecundity V/M ratio occurred for Biesecker because this site had much lower flowering frequency than Schulenberg, even though seed production was considered identical to Schulenberg.

The comparatively high median V/M ratios for the Schulenberg and Biesecker populations (Table 12.5) may indicate strong environmental stochasticity (Menges 1998), possibly due to effects of fire and rainfall on survivorship and growth of this species (Bowles et al. 1998). Also, because $\lambda < 1$ for both restorations, they appear to be vulnerable to environmental stochasticity (Menges 1998). However, variability in growth and survivorship in restorations may have a genetic origin if ex situ propagation promotes establishment of juvenile plants that might not have survived germination or seedling stages under more stressful natural conditions. Therefore, our λ values of < 1 for could reflect loss of less fit individuals, while survivorship and growth of more fit plants could lead to eventual population stability. Management to maintain these plants, and restoration to increase numbers of differ-

Table 12.5. Variance-to-mean ratios for Mead’s milkweed (*Asclepias meadii*): Schulenberg and Biesecker restorations

	Seedling	Juvenile-I	Juvenile-II	Juvenile-III	Flowering	Dormant
<hr/>						
Schulenberg	State (t)→					
Fate (t+1)						
Seedling					0.3311	
Juvenile-I	0.0154	0.1377	0.0159			0.1931
Juvenile-II		0.0884	0.0269	0.12	0.6917	0.0512
Juvenile-III			0.0266	0.45		0.0216
Flowering				0.1	0.1771	0.0773
Dormant	0.0581	0.7638	0.0941	0.1438		0.1166
Median = 0.1000						
<hr/>						
Biesecker	State (t)→					
Fate (t+1)						
Seedling					25.807	
Juvenile-I	0.0954	0.0383	0.106			0.1276
Juvenile-II		0.0733	0.131	0.3556	0.6	0.1647
Juvenile-III			0.6488	0.2		0.0361
Flowering				2.4	0.6	0.0059
Dormant	0.2125	0.1165	0.2263	0.4533		0.1801
Median = 0.1801						

ent genotypes that can contribute to successful outcrossing and seed production, are important objectives.

12.4.2.3 Elasticities

Elasticities for growth (G), stasis (L) and reproduction (F) categories ordinated in positions expected for late-successional plants, primarily trees and shrubs (Fig. 12.4). Elasticity values were highest for stasis, slightly lower for growth, and lowest for fecundity (Figs. 12.3, 12.4). The ordination also corresponded to findings of Fiedler et al. (1998), that for species of *Calochortus*, which are also iteroparous herbs, most $G/L/F$ ratios positioned toward the lower right of the triangle. Although Fiedler considered this problematic given the more central ordination of iteroparous herbs found by Silvertown et al. (1996), it corresponds to a successional sequence. The ordination positions for *Asclepias meadii* and *Calochortus* may be appropriate for long-lived herbaceous plants, as well as for trees and shrubs as proposed by Silvertown et al. (1996), fitting a late successional position proposed based on Grimes triangle (Silvertown et al. 1992).

Some management applications can be suggested based on ordination position. The similar ordinations of Schulenberg and Biesecker indicate that stasis and growth had much stronger effects on λ than fecundity (Fig. 12.4). This suggests that restoration management should focus on growth and stasis rather than increasing reproduction, which seems applicable because of the time required for flowering, the expected longevity, and the apparently low fecundity of this species. Continuing to introduce plants will have little to do with increasing λ until large numbers of plants can attain threshold sizes for reproduction and then overcome further constraints on seed production. However, continued introductions of additional genotypes would result in larger populations that will have greater reproductive potential, and, presumably, less vulnerability to environmental stochasticity. These population characteristics could veil long-term population change for late-successional iteroparous herbs, such as *Calochortus* (Fiedler et al. 1998) and *Asclepias meadii* (Kettle et al. 2000), and many years of monitoring may be required before realistic PVA projections can be attained for such species (Bowles et al. 2001).

Caution in interpreting $G/L/F$ ratios is advised, however, because L , G and F change when the number of stages change and the effects of stasis, growth and reproduction are not clearly separated among L , G and F (Caswell 2001). A greater number of restoration transition years and natural populations will help illuminate the usefulness of $G/L/F$ ratio ordination to conservation biology. Despite these potential problems with $G/L/F$ ratio ordination, the process of developing the ordination is valuable because it encourages careful thought about the life history of *Asclepias meadii* and implications to management decisions.

12.5 Conclusions

12.5.1 Application of PRVA

Although it remains difficult to project how well PRVA can be applied to endangered plant restorations, our analyses provide some potentially useful conclusions about projecting plant restoration viability.

Encouragingly, our data show that demographic life stage transitions can be used to project population growth rates of restored populations and to identify relative contributions of different life stages to population growth. This may allow projecting the numbers of transplants or seeds needed to achieve population growth – an important objective in population restoration. The most meaningful interpretation of PRVA modeling requires transitions for all life stages, comparative data from multiple natural populations as well as from replicated restorations, and an understanding of how environmental stochasticity (such as drought for *Cirsium pitcheri* or rainfall for *Asclepias meadii*) may affect viability.

Our comparisons indicate that PRVA will be most useful for short-lived species (see discussion of difficulties of PVA with long-lived species in Chap. 9, this Vol.). For example, because of its short life span and rapid cohort development, *Cirsium pitcheri* transplants provided transitions for each stage within 5 years, and demographic data from a natural population strengthened interpretation of elasticities. The Illinois Beach State Park restoration of *Cirsium pitcheri* south of the Dead River has successfully reached short-term goals of completion of its life cycle, a natural stage distribution, overall stable λ , and variation in λ comparable to a natural population. Although natural recruitment is taking place, population expansion into available habitat does not yet appear to be occurring. The long-term goal of reaching MVP size has not occurred, and we do not know whether the population can recover from environmental or demographic stochasticity. However, the 1998→1999 transition matrix had a very low λ , and λ the following year was relatively high, suggesting that the restoration has sufficient size to recover.

As with natural populations (Fiedler et al. 1998), PRVA of long-lived species with low reproductive rates appears problematic without long-term data sets. For *Asclepias meadii*, slow growth and low fecundity limited our interpretation of elasticities and population growth and prevented estimation of a MVP. Further difficulty in interpretation arose because stages were missing and matrices were composites of 6 years of monitoring data rather than separate matrices for each pair of years. Finally, we had no data from natural populations of *Asclepias meadii* with which to compare demographic characteristics. Nevertheless, interpretation of *Asclepias meadii* elasticities supported a logical management need to increase growth. Because Mead's milkweed requires many years to reach maturity, and because natural recruitment has

not occurred in the restoration, reliable matrix models are not available with which to estimate MVP let alone determine whether the restorations have reached short-term or long-term goals. In addition, we do not have a viable natural population with which to compare the stage distribution of the restoration. On the positive side, after initial transplant mortality, survivorship is high. In addition, the single event of seed production indicates that genetic diversity may be sufficient to overcome self-incompatibility in a restoration, which has apparently prevented seed production in many eastern populations (Tecic et al. 1998; Hayworth et al. 2002).

A theoretical basis for plant restoration remains largely undeveloped and our results with *Cirsium pitcheri* suggest that restoration may not match models based on natural populations. For example, although Guerrant's (1996) model indicated that larger initial propagule sizes would reduce extinction probability and demographic cost of restoration plantings, he used published transition data from natural populations assuming similar transition rates (Guerrant and Fiedler 2002). Transitions from natural populations may differ from those initiated by artificial planting. For *Asclepias meadii*, although larger propagules will accelerate time to flowering, seedlings established from seed may result in similar survivorship to transplanted juveniles and will not increase the probability of extinction. Although outplanting larger *Cirsium pitcheri* plants could increase transplant success, naturally recruited flowering plants may have greater fecundity (Fig. 12.2). Thus, projections of λ using transplant-derived transitions could be comparatively low, although earlier flowering of transplants could counter this effect if it increases recruitment over time. Outplanting of propagated plants also may allow establishment of less fit plants that might not have survived natural environmental rigors in the seedling stage and might have lower fecundity. Nevertheless, based on extinction risk analysis, transplanting greenhouse propagated plants that require more than one year to reach flowering threshold is more efficient than planting seeds, thereby reducing the "demographic cost" of reintroduction (Guerrant and Fiedler, 2002). Reintroduction using adults may be more efficient than for juveniles in animals as well (Sarrazin and Legendre 2000). Repeated smaller outplantings to represent natural cohort replacement may also spread over time an otherwise large drain on seeds or propagules provided from ex situ or wild collections.

12.5.2 Differences Between PVA of Restorations vs. Natural Populations

Applications of PVA to restored populations differ in a number of important ways from PVA of natural populations (Table 12.6). Initially, many restored populations are nonviable, or below "quasi-extinction" levels. Here, PRVA can be viewed as projecting how experimental planting and management treatments contribute toward population growth to achieve a viability threshold,

Table 12.6. How PVA factors may differ between natural and restored populations

Factor	Natural population	Restoration
Population viability	Maintain viability by managing to sustain $\lambda > 1$ or to prevent $\lambda < 1$	Manage to increase $\lambda > 1$ and reach viability
Demographic stochasticity	Minor importance in large population	Major importance in small population
Genetic stochasticity	Minor importance in large population	Major importance in small population
Increasing population growth ($\lambda > 1$)	More likely to indicate viability for large population	Small restoration may be non-viable due to stochastic effects
Matrix model stages	Based only on natural recruitment	Natural recruitment and transplants are separate elements
Life stage transitions	May be easily obtainable in natural populations	May be difficult to obtain in non-functional restorations
Monitoring cycle required to produce a transition matrix of naturally recruited individuals	Two or more years if all stages are present	Continue until all stages are present from natural reproduction, which may require many years (e.g., 8 for <i>Cirsium pitcheri</i>)
Incorporation of multiple years into matrix model	Separate matrices for each pair of years monitored	Composite matrices for initial restoration years
Elasticity analysis	More likely to identify important life stage	May emphasize or de-emphasize incorrect life stages if non-functional
Elasticities and λ	Affected by natural birth and death	Manipulated by out-planting

while PVA of many natural populations can be most often viewed as determining how to prevent growth trends from falling below thresholds of viability. Small restored populations with increasing growth may remain highly vulnerable to environmental stochasticity, as well as genetic and demographic stochasticity, which usually are less important in larger populations (Lande 1988; Menges 1991). For example, small numbers of flowering plants may not attract pollinators, or may enforce selfing or inbreeding among related plants (Chaps. 2, 3, 10, this Vol.).

If transition frequencies differ between transplants and naturally recruited individuals, matrix models for restorations will require more complex matri-

ces which have separate elements for stages derived from natural recruitment and transplants.

All transition stages are more likely to be present in natural populations than in restorations, especially for early restoration years. As a result, important variables, such as fecundity, may be difficult to obtain or may differ from natural populations. Also, developing a transition matrix for a natural population may require only 2 years of demographic monitoring if all stages are present each year. Many more years of monitoring will be necessary for restorations in which transplants must complete their life cycle before naturally occurring cohorts can be established and develop all stages. For *Cirsium pitcheri*, all stages were present in the restoration 5 years after transplanting began. *Asclepias meadii* had not completed its life cycle 7 years after initial seed planting and translocation efforts. In addition, since transplant transition frequencies may differ from those of naturally recruited individuals, reliable transition matrices cannot be constructed for a restoration until all stages are present among naturally recruited individuals. For *Cirsium pitcheri*, a transition matrix for naturally recruited individuals was first constructed only after the eighth year of restoration. Another consequence of missing stages at the beginning of restoration for both *Cirsium pitcheri* and *Asclepias meadii* was the necessity to construct composite matrices rather than using separate matrices for each pair of years as can be done for natural populations.

In restorations, as well as in stressed natural populations, elasticities could de-emphasize important but poorly functioning life history stages, leading to improper management conclusions unless compared with natural populations. Demographic characteristics, such as elasticities and λ are affected by birth and death in natural populations in contrast to restorations in which these characteristics may be more strongly affected by the number of transplants introduced.

These differences between restorations and natural populations suggest that traditional PVA approaches may be difficult for restored populations. For example, small short-term data sets may be most interpretable using non-integrated approaches, and experimental approaches will be critical, especially if data are missing for mean vital rates (Pavlik 1994). A greater emphasis could also be placed on absolute growth rate and cohort depletion rates, as opposed to modeling extinction probabilities. Comparisons with natural populations may be important for developing and interpreting models, especially elasticities. We recommend use of both integrated and nonintegrated methods to evaluate plant restoration viability. If both methods agree the validity of conclusions is increased, if they do not agree it suggests that there may be problems with the one or both methods of analysis.

12.5.3 Future Directions

PVAs for natural populations have usually ignored genetic and demographic stochasticity because these factors are considered important only when population size is small, originally suggested as less than 50 (for demographic stochasticity and inbreeding depression) or 500 (for genetic stochasticity) individuals (Franklin 1980; Frankel and Soulé 1981; Shaffer 1981; Lande 1988, 1993; Chap. 11, this Vol.). However, because population restorations may initially be small, demographic and genetic stochasticity could significantly impact their initial stages and may need to be incorporated into PVAs of small populations. As yet, little information is available on interactions between these factors in extinction of small populations (Lande 1988; Beissinger and Westphal 1998).

Genetic applications to restoration often face a tradeoff between maintaining local genetic adaptation, which commonly occurs in plant species, vs. avoiding inbreeding and maximizing genetic diversity and adaptive evolutionary potential (Huenneke 1991; Knapp and Dyer 1998; Barrett and Kohn 1991; Fenster and Galloway 2000). Measures of genetic variation and how it is allocated within and among natural populations, such as the G_{ST} statistic, can help guide species restoration (Hamrick et al. 1991; Weller 1994; Pavlik 1996; Steinberg and Jordon 1998). For example, Pavlik et al. (1993) compared levels of genetic variability between natural and restored populations of *Amsinckia grandiflora*. Genetic applications are strengthened when linked with plant breeding systems, especially effects of self-incompatibility and inbreeding depression. DeMauro (1993, 1994) used multiple genotypes to maximize genetic diversity and reproductive potential in restored populations of the self-incompatible *Hymenoxys acaulis* var. *glabra*. Likewise, Bowles (Bowles et al. 1998, 2001) maximized numbers of genotypes within restorations of *Asclepias meadii*, a species apparently highly susceptible to inbreeding depression.

Metapopulation and spatially explicit models may be more appropriate for plants, but they have not yet received much application (Menges 2000; Chaps. 6, 11, this Vol.). For example, *Cirsium pitcheri* may depend upon metapopulation processes for long-term persistence (McEachern et al. 1994). Metapopulation level analysis of the number, spatial patterns, and dispersal of populations needed for a high probability of persistence (Morris et al. 1999) may be most realistic for this species. There will also be a need for understanding how demographic-genetic linkage could enhance viability among small isolated restorations, and how carrying capacity of small habitat remnants affects species restoration potential. For example, pollen transfer among small populations could increase effective population sizes of self-incompatible species such *Asclepias meadii*, and would help avoid high density packing of individuals that could lead to increased herbivory or attack by pathogens, with cascading effects on population viability (Bowles et al. 1998; Chaps. 10, 3, this Vol.).

Applying PRVA modeling to help understand whether recovery targets are being met by achieving minimum numbers of viable populations could become an important application for agencies charged with listing and delisting endangered species (Bowles and Bell 1999). Coupling this work with experimental procedures (Menges 2000; Kaye et al 2001) would be useful for learning how management treatments, such as prescribed burning, can help accelerate growth of restored populations. However, Coulson et al. (2001) warned that PVA projections will be problematic without good data and unless distributions of vital rates between individuals and years can be predictable over time, a tall order given the impact of humans on environmental change and stress in small habitat remnants.

Acknowledgements. We thank Kay Havens, Pati Vitt, and Susanne Masi at the Chicago Botanic Garden for collaboration on *Cirsium pitcheri* restoration, Jenny McBride and Bob Betz for assistance on restoration of *Cirsium pitcheri* and *Asclepias meadii*, Eric Menges and Pedro Quintana-Ascencio for assistance with analyses, and Ed Guerrant for sharing unpublished information. We also thank the University of Wisconsin Press and Annals of the Missouri Botanical Garden for permission to use data and figures, and the Shawnee National Forest, Illinois Endangered Species Protection Board, US Fish and Wildlife Service, Illinois Department Of Natural Resources, Morton Arboretum and Indiana Division of Nature Preserves for funding and permission to conduct research. Finally, we thank Christy Brigham and Mark Schwartz for the opportunity to participate in this volume.

Appendix 12.1. Stage-based projection matrices of transition frequencies for a restored *Cirsium pitchei* population at Illinois Beach State Park. *R* Naturally recruited individuals, *T* transplanted individuals. The average matrix represents 1991 through 2000

	Naturally recruited				Transplants				
	R seedling	R small juvenile	R large juvenile	R flowering	Sown seed	T "seedling"	T small juvenile	T large juvenile	T flowering
State (1999)→									
Fate (2000)	0	0	0	3.2060	0.0086	0	0	0	5.1588
R seedling	0.5556	0.0000	0	0	0	0	0	0	0
R small juvenile	0.3333	0.8000	0.2500	0	0	0	0	0	0
R large juvenile	0	0.0000	0.6250	0	0	0	0	0	0
R flowering	0	0	0	0	0	0	0	0	0
Sown seed	0	0	0	0	0	0	0	0	0
T "seedling"	0	0	0	0	0	0	0	0	0
T small juvenile	0	0	0	0	0	0.5556	0.7273	0.0000	0
T large juvenile	0	0	0	0	0	0.3333	0.0000	0.1000	0
T flowering	0	0	0	0	0	0	0.0909	0.8000	0
State (1998)→									
Fate (1999)	0	0	0	1.8659	0.0032	0	0	0	1.4268
R seedling	0.1333	0.2308	0	0	0	0	0	0	0
R small juvenile	0.0000	0.4615	0.0000	0	0	0	0	0	0
R large juvenile	0	0.0769	1.0000	0	0	0	0	0	0
R flowering	0	0	0	0	0	0	0	0	0
Sown seed	0	0	0	0	0	0	0	0	0
T "seedling"	0	0	0	0	0	0	0	0	0
T small juvenile	0	0	0	0	0	0.1333	0.2692	0.3333	0
T large juvenile	0	0	0	0	0	0.0000	0.3846	0.0000	0
T flowering	0	0	0	0	0	0	0.0769	0.6667	0

Appendix 12.1. (Continued)

Fate (t+1)	Naturally recruited				Transplants				
	R seedling	R small juvenile	R large juvenile	R flowering	Sown seed	T "seedling"	T small juvenile	T large juvenile	T flowering
Average state (t) →									
R seedling	0	0	0	2.7593	0.0052	0	0	0	2.1600
R small juvenile	0.5366	0.3929	0	0	0	0	0	0	0
R large juvenile	0.0732	0.3929	0.2222	0	0	0	0	0	0
R flowering	0	0.0714	0.6667	0	0	0	0	0	0
Sown seed	0	0	0	0	0	0	0	0	0
T "seedling"	0	0	0	0	0	0	0	0	0
T small juvenile	0	0	0	0	0	0.4545	0.5878	0.0959	0
T large juvenile	0	0	0	0	0	0.0136	0.2041	0.2740	0
T flowering	0	0	0	0	0	0	0.0449	0.5479	0

Appendix 12.2. Stage-based projection matrices of transition frequencies for a naturally occurring *Cirsium pitcheri* population at Indiana Dunes West Beach

	Seedling	Small juvenile	Large juvenile	Flowering
State (1992)→				
Fate (1993)				
Seedling	0.0000	0.0000	0.0000	2.2000
Small juvenile	0.2786	0.6364	0.0000	0.0000
Large juvenile	0.0000	0.2121	0.2500	0.0000
Flowering	0.0000	0.0303	0.7500	0.0000
State (1991)→				
Fate (1992)				
Seedling	0.0000	0.0000	0.0000	12.7273
Small juvenile	0.4545	0.5217	0.1111	0.0000
Large juvenile	0.0000	0.1304	0.1111	0.0000
Flowering	0.0000	0.0435	0.4444	0.0000
State (1990)→				
Fate (1991)				
Seedling	0.0000	0.0000	0.0000	4.0000
Small juvenile	0.7857	0.6250	0.1053	0.0000
Large juvenile	0.0000	0.2500	0.2632	0.0000
Flowering	0.0000	0.1250	0.4737	0.0000
State (1989)→				
Fate (1990)				
Seedling	0.0000	0.0000	0.0000	0.9333
Small juvenile	1.0000	0.6667	0.2051	0.0000
Large juvenile	0.0000	0.0000	0.2821	0.0000
Flowering	0.0000	0.2222	0.4359	0.0000
State (1988)→				
Fate (1989)				
Seedling	0.0000	0.0000	0.0000	0.1818
Small juvenile	0.0000	0.3684	0.0408	0.0000
Large juvenile	0.0000	0.5789	0.5714	0.0000
Flowering	0.0000	0.0000	0.3061	0.0000

Appendix 12.3. Stage-based projection matrices of transition frequencies for two restored Mead's milkweed (*Asclepias meadii*) populations

	Seedling	Juvenile-I	Juvenile-II	Juvenile-III	Flowering	Dormant
Schulenberg Prairie						
Fate (t+1)	State (t)→					
Seedling	0	0	0	0	0.3575	0
Juvenile-I	0.7451	0.5484	0.12	0	0.0667	0.4272
Juvenile-II	0	0.0753	0.5133	0.2778	0.3333	0.1845
Juvenile-III	0	0.0054	0.0467	0.1111	0	0.0583
Flowering	0	0	0.0333	0.0556	0.2667	0.068
Dormant	0.0588	0.0588	0.2473	0.4444	0.1333	0.2621
Biesecker Prairie						
Fate (t+1)	State (t)→					
Seedling	0	0	0	0	0.4424	0
Juvenile-I	0.3088	0.4406	0.1667	0	0	0.5167
Juvenile-II	0	0.104	0.3667	0.25	0.3333	0.175
Juvenile-III	0	0	0.0667	0.1667	0	0.0333
Flowering	0	0	0	0.0833	0.3333	0.0083
Dormant	0.6176	0.2178	0.3444	0.4167	0	0.2417

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