

## THE EFFECT OF FIRE ON THE POPULATION VIABILITY OF AN ENDANGERED PRAIRIE PLANT

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**Abstract.** We examined the effects of fire on population growth rate and extinction probability of a rare prairie plant. *Lomatium bradshawii* (Apiaceae) is an endangered species of western Oregon and Washington prairies that were frequently burned by Native Americans prior to the late 1800s. Using data from mapped plants in two populations subjected to different fall burning frequencies over a six-year period, we constructed stochastic transition matrix models to evaluate the effects of fire on the viability of the populations. Stochasticity was incorporated into the models through two methods performed by widely used computer programs: randomly shuffling whole annual matrices (using POPPROJ2), or selecting each matrix element from a distribution with observed mean and variance (with RAMAS/stage). Log-linear analysis was used to test for site and treatment effects on transition rates. Unburned plots had stochastic population growth rates ( $\lambda_s$ ) of 0.905–0.927, depending on the site and stochastic method. Burning twice in six years increased  $\lambda_s$  to 0.946–1.091, and three burns yielded  $\lambda_s$  values of 0.996–1.173. The risk of extinction (100 yr, extinction defined as <10 individuals) was very high (97–99%) in the absence of fire for both methods and sites, but with two burns it declined to 57% and 73% for matrix selection and element selection, respectively, at one site, and  $\leq 1\%$  (both methods) at the other. Extinction probability was very low ( $\leq 1\%$ ) for both methods and sites after three burns. Although different methods of incorporating stochasticity gave slightly different quantitative results, they were qualitatively similar. Both site and treatment had significant effects on transition rates in the log-linear analyses. Elasticity analysis suggested that burning decreased the sensitivity of population growth rate to mid-sized plants and increased the importance of seedlings. Fire was an effective tool for maintaining viable populations of this species, although the strength of its effects differed between locations.

**Key words:** elasticity; extinction; fire; matrix model; log-linear analysis; *Lomatium bradshawii*; population viability analysis; stochastic population growth rate.

### INTRODUCTION

Fire is a disturbance that influences plant population dynamics and can change plant community structure (Bond and van Wilgen 1996). Many rare plant species occur in fire-dependent communities (Myers 1989, Johnson and Abrahamson 1990, Campbell et al. 1991, Jacobson et al. 1991, Hardin and White 1992, Carlson et al. 1993, Menges and Kimmich 1996), and fire suppression is the principal threat to 4.1% of the endangered flora in the United States (Schemske et al. 1994). Conversely, some rare species are threatened by burning of their habitat, especially in tropical regions (e.g., Stone and Scott 1985). Therefore, managers can improve conditions for rare plants if they have specific knowledge of

how populations of such species respond to fire (Hessl and Spackman 1995).

The effect of fire on life history processes has been explored for several rare plants. Burning can increase flowering and fruiting (Johnson and Blyth 1988, Hartnett and Richardson 1989, MacRoberts and MacRoberts 1990), seed germination (Borchert 1989, Boyd and Serafini 1992, Jacobs 1993), seedling establishment (Gankin and Major 1964, Barker and Williamson 1988), growth (Barker and Williamson 1988), or combinations of these processes (Menges 1995, Lesica 1999). In some rare plant species, burning has both positive and negative effects, such as increasing seedling recruitment, while killing adults (e.g., Dunwiddie 1990, Menges 1992a). In others, fire has no clear effect on adult survival (Warren et al. 1992) or flowering (McClaren and Sundt 1992). Although prescribed burning is a recommended tool for rare plant conservation in various habitats (Folkerts 1977, Currier 1984, Jacobson et al. 1991, Kaye 1992, Phillips et al. 1992, Hawkes and Menges 1995), decisions to manage habitat with fire should be informed by careful experi-

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mentation, monitoring, and interpretation of results (Owen and Rosentreter 1992).

The overall impact of a disturbance on a population is a summation of its effects on various vital attributes (Noble and Slatyer 1980), and should not be inferred from a response at one or two points in a life cycle. Transition matrix models are appropriate tools for assessing the impact of a management strategy on endangered species, because they synthesize population dynamics at many life history stages (Schemske et al. 1994, Silvertown et al. 1996). They can be used to generate several useful statistics, such as population growth rate, extinction probability, and elasticities. However, only a few matrix-based evaluations of the effect of controlled burning on rare plants have been published to date (but see Manders [1987], Lesica [1997], Menges and Dolan [1998], Gross et al. [1998]). In this paper, we use matrix models to evaluate burning as a management tool for an endangered plant. This approach integrates the influence of fire on plant growth, survival, fecundity, and mortality, so that effects are measured at the level of population dynamics. We focus primarily on stochastic measures of population viability without burning and with two different fire frequencies to test the hypothesis that fire improves conditions for this species. In addition, we compare results derived from two widely used methods of stochastic projection. We use elasticities to evaluate which demographic processes are most important to changes in growth rate caused by fire.

#### *Study system*

*Lomatium bradshawii* (Rose) Math. & Const. (Bradshaw's lomatium, Apiaceae) is listed by the U.S. Fish and Wildlife Service and the Oregon Department of Agriculture as an endangered species (Oregon Natural Heritage Program 1998). It is an herbaceous plant from a perennial taproot, reproducing only by seed. The seeds generally mature in June and passively disperse in July, then germinate by the following April. Its flowers are pollinated by a diverse assemblage of insects, especially solitary bees and flies (Kaye 1992). Most known populations of *L. bradshawii* occur in fragmented habitats in southwestern Washington and the Willamette Valley of western Oregon. Approximately sixteen populations are known, varying in size from <50–25 000 individuals, and <1–40 ha (Parenti et al. 1993). The largest concentration of reported sites is in the southwestern Willamette Valley, west of Eugene, Oregon. A recovery plan for *L. bradshawii* (Parenti et al. 1993) identifies population enhancement as needed for the species' recovery.

*Lomatium bradshawii* occurs in remnants of two types of formerly widespread prairies. Seasonally saturated wetlands in shallow soil over basalt in Marion and Linn counties, Oregon, support a small number of populations (Alverson 1990). Most populations, however, occupy valley-bottom prairie dominated by *Des-*

*champsia cespitosa* (tufted hairgrass) and characterized by deep pluvial clays and a perched water table. The latter habitat type has been described in some detail (e.g., Moir and Mika 1976, Kagan 1980, Alverson 1989, Finley 1994), and typifies the sites included in our study. Both habitat types are part of the prairie-oak savannah ecosystem of western Oregon interior valleys, which was widespread before regional fire suppression and settlement in the mid- to late 1800s (Habeck 1961, Johannessen et al. 1977). Prior to Euro-American settlement, these prairies were maintained by frequent fall fires set by Native Americans to promote food plants, such as camas (*Camassia quamash* and *C. leichtlinii*), and to herd game for improving hunting success (Johannessen et al. 1977). Today, less than 1% of presettlement composition prairies remain, and tools for managing this habitat for native and endangered species are urgently needed (Wilson et al. 1995).

#### METHODS

##### *Study sites, burning treatments, and plots*

We used information from two populations to evaluate the effect of fire on the demography of *Lomatium bradshawii*. Both were within the southwest part of the species' range, in an area west and north of Eugene, Oregon, USA, in valley-bottom prairie habitat that had not burned in several decades. These populations occurred within the Fern Ridge Research Natural Area at two sites: Fisher Butte (44°3' N, 123°15' W) and Rose Prairie (44°5' N, 123°15' W). The land is managed by the Army Corps of Engineers. Two additional populations were included for seed bank evaluation, Buford County Park (43°60' N, 122°56' W), east of Eugene, and the Long Tom Area of Critical Environmental Concern (44°9' N, 123°18' W), which is managed by the Bureau of Land Management. Throughout this report, these sites are referred to as Fisher Butte, Rose Prairie, Buford Park, and Long Tom, respectively.

Three burning treatments were conducted at Fisher Butte and Rose Prairie during 1988–1993 to determine the effects of fire on *Lomatium bradshawii* population dynamics. All burns were conducted in October. These treatments were control (no burning), burned twice in six years (1988 and 1991), and burned three times in six years (1988, 1989, and 1991). The population areas were divided into approximately equal strips, ~4 ha each at Fisher Butte and 2 ha each at Rose Prairie, and randomly assigned one of the three treatments prior to burning (see Pendergrass et al. [1998], Pendergrass et al. [1999] for more details). Burn characteristics at each site, including flame length, height, depth, and heat per unit area were recorded in 1988–1989 and are reported elsewhere (Pendergrass et al. 1998). Permanent monitoring plots were sampled annually in areas exposed to the three treatments. To establish these plots, mature *Lomatium bradshawii* plants (reproductive or large

vegetative) were randomly chosen from throughout the population areas and tagged in 1988. These individuals were numbered, and a subset, 10 at Fisher Butte and six at Rose Prairie, were randomly selected from each treatment type to serve as center points for permanent circular plots (radius, 2 m). All *L. bradshawii* individuals were mapped in each circular plot in May or June of each year (prior to burning) during 1988–1993. Seed production and umbel number were recorded annually for all tagged plants, including those at the center of each circular plot and outside the plots.

#### Transition elements and matrices

Two general approaches, analytical methods and biological classifications, have been used to define categories for stage-based models (Horvitz and Schemske 1995). Analytical methods maximize within-class sample sizes and minimize error of estimates (Vandermeer 1978, Moloney 1986, Fiedler 1987), and biological classifications rely on size, age, gender, reproductive states, development, or some combination of these (e.g., Lefkovitch 1965, Usher 1976, Bierzychudek 1982, Aplet et al. 1994, Maschinski et al. 1997). We used a biological classification that combined plant size and reproductive state to classify each *Lomatium bradshawii* individual into one of six stages: seedling (S), vegetative plant with one or two leaves (V2), vegetative plant with three or more leaves (V3), and reproductive plant with one (R1), two (R2), or three or more (R3) umbels. Reproductive plants were segregated by umbel number, because one-umbel plants rarely produce seed (most of their flowers are male-only), while two-umbel plants produce seeds on the second umbel, and plants with three or more umbels may produce many seeds (T. N. Kaye, unpublished data). Thus differences in the size of reproductive plants affect their sexual function and fecundity rates, a pattern found in several members of the Apiaceae (Schlessman 1978, Lindsey 1982, Lindsey and Bell 1985). We combined vegetative plants with one or two leaves into a single stage, because field observations indicated that plants with one leaf often produced a second leaf later in the year, and therefore leaf number of small plants may be a function of sampling date and/or variation in seasonal phenology, not plant vigor. Seedlings were defined as first year plants, often with cotyledons. All vegetative plants with one leaf were considered seedlings in 1988.

To construct transition matrices, we calculated the proportion of individuals in each stage that remained the same or changed to a different stage from one year to the next. To estimate the number of seedlings produced by individuals in each reproductive stage, we first determined the mean number of seeds produced by each stage (with data recorded for tagged plants) and the number of reproductive individuals within each plot to estimate the number of seeds produced in each plot in year  $t$ . Seedlings observed in year  $t + 1$  were then apportioned among the reproductive stages based

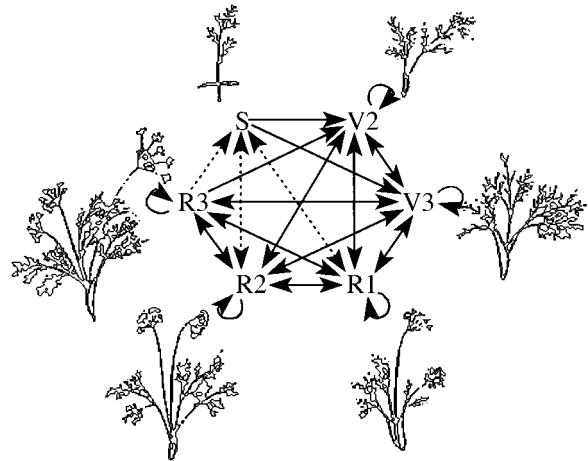


FIG. 1. Conceptual model of the life cycle pathways of *Lomatium bradshawii*. Each arrow represents the possible transitions plants can make from one year to the next. Dashed lines pointing to the seedling stage indicate reproduction. Double-headed arrows indicate regression to a smaller stage or growth to a larger stage. Stages identified in this model are first-year seedling (S), one- or two-leaved vegetative plants (V2), vegetative plants with three or more leaves (V3), and reproductive plants with one (R1), two (R2), or three or more (R3) umbels.

on seed production and density of each stage in year  $t$ . These proportions and fertilities were organized as transition elements in a matrix following standard methods (Lefkovitch 1965, Menges 1986, Caswell 2001) and according to our conceptual model of population dynamics for this species (Fig. 1). Annual transition matrices, hereafter referred to as detailed matrices, were constructed for each of five growing seasons from 1988–1989 to 1992–1993, and for each treatment at Fisher Butte and Rose Prairie. These detailed matrices can be found in Caswell and Kaye (*in press*). A mean matrix for each site and treatment combination was produced from each set of detailed matrices with a corresponding set of variances, one variance (representing environmental stochasticity) for each mean matrix element. Sample sizes for large reproductive plants (R3) were small, because plants in this stage were uncommon in our study populations. In some cases (unburned plots at Rose Prairie in 1989 and 1992, and burned plots at that site in 1991), no R3 plants were observed, making it impossible to estimate transitions for this stage. To resolve this problem, we replaced the R3-column of each of these detailed matrices with the mean values from that stage for the appropriate site and treatment.

We used log-linear analysis to test for treatment and site effects on stage-specific survival and transitions. Count data (Table 1) for each transition were summed across all years. These data formed a four-way transition frequency table with three explanatory variables: treatment ( $T$ , unburned, two burns, or three burns), location ( $L$ , Fisher Butte or Rose Prairie), and initial class

TABLE 1. Four-way transition frequency table used in the log-linear analysis (see Table 2).

Initial state	Fate	Rose Prairie			Fisher Butte		
		No burn	Two burns	Three burns	No burn	Two burns	Three burns
S	V2	42	42	51	15	68	56
S	V3	15	22	24	5	16	8
S	R1	3	1	2	2	5	3
S	R2	0	0	0	0	0	1
S	R3	0	0	1	0	0	0
S	dead	185	86	96	91	411	226
V2	V2	37	58	26	18	44	22
V2	V3	34	50	45	5	23	9
V2	R1	7	12	10	0	4	5
V2	R2	3	3	6	0	4	1
V2	R3	0	0	0	0	1	1
V2	dead	98	76	57	28	83	51
V3	V2	17	22	27	6	9	2
V3	V3	150	72	126	24	27	26
V3	R1	49	38	52	16	26	17
V3	R2	18	26	21	2	23	10
V3	R3	1	1	4	0	0	0
V3	dead	162	135	131	21	64	38
R1	V2	6	5	3	0	6	0
R1	V3	33	18	16	12	9	9
R1	R1	53	28	33	24	20	12
R1	R2	26	33	29	10	21	14
R1	R3	2	3	6	0	1	0
R1	dead	72	47	49	21	37	29
R2	V2	2	3	1	0	2	1
R2	V3	11	9	6	2	12	3
R2	R1	23	23	20	13	15	16
R2	R2	18	33	45	5	40	20
R2	R3	4	7	13	1	4	1
R2	dead	32	54	57	7	38	21
R3	V2	0	0	0	0	1	0
R3	V3	2	0	1	0	1	1
R3	R1	1	1	4	0	2	0
R3	R2	3	5	8	2	4	1
R3	R3	7	17	24	1	3	2
R3	dead	2	10	20	0	4	2

Note: Counts of individuals summed across the five years of the study are shown for each combination of six initial classes, six fates, two locations, and three burning treatments.

(C, stages S–R3). The response variable was individual fate (F, stages V2–R3 and death). A constant 0.5 was added to all cells prior to analysis (as recommended by Fingleton [1984]). In this analysis, the transition frequency table was modeled as a linear function of the logarithm of the cell frequencies (see Silva et al. [1990] for a detailed application of this analysis to demographic data). The presence of an interaction in these hierarchical models implies the presence of all lower-order interactions involving those variables. Tests were performed by determining the reduction in the log-likelihood ratio,  $G^2$ , when a term was added to a model that excluded that term. For example, comparing a null model (CTL, CF for the null hypothesis that the fate of an individual is independent of treatment or location, conditional on its initial state; see Table 2) with a model that includes a location effect (CTL, CFL) can be used to calculate  $\Delta G^2$ , which is compared to a  $\chi^2$  distribution. This comparison tests for a location (L) effect. Degrees of freedom for this test are equal to the

difference in the degrees of freedom in the two models. The effect of a factor is always estimated relative to a specified model, so there may be more than one way to measure the effect of any factor. Two different tests for each factor were, therefore, included in our analyses.

*Stochastic measures of population viability*

We explored two measures of population viability, stochastic population growth rate and extinction probability, using two methods of incorporating environmental variability. Stochastic growth rate ( $\lambda_s$ ) was chosen over the more conventional deterministic growth rate,  $\lambda$ , because it incorporates environmental variability and does not assume a stable (equilibrium) population structure (Tuljapurkar 1990). The sampled *Lomatium bradshawii* populations may not be at equilibrium, especially when burned after several decades without fire. Furthermore,  $\lambda_s$  is always less than  $\lambda$  (Caswell 2001), which makes it a more conservative estimate of population viability. Populations with  $\lambda_s > 1.0$  are projected to grow, while those with  $\lambda_s < 1.0$  are projected to decline.

Environmental stochasticity was modeled in two ways, through element selection (e.g., Maschinski et al. 1997) and matrix selection (e.g., Bierzychudek 1982). Element selection used the average matrices and, at each time step of the simulation, varied each matrix element at random within its observed variance. Element selection allows population trajectories in time to follow an infinite number of pathways bounded only by observed variances, but our use of the method did not account for any intercorrelation of matrix elements. That is, “bad” years for one type of transition were not correlated with “bad” years for others, even though environmental correlation among demographic param-

TABLE 2. Log-linear analysis of the effects of burning treatment and location on stage-specific plant fates.

A) Models				
Model†	df	$G^2$	$P$	
1) CTL, CF (null)	150	252.5	<0.0001	
2) CTL, CFL	120	167.6	0.0027	
3) CTL, CFT	90	131.1	0.0031	
4) CTL, CFL, CFT	60	41.18	0.9698	
5) FCTL	0	0	1.0000	
B) Comparison of effects				
Effect	Comparison	df	$\Delta G^2$	$P$
Location	(1)–(2)	30	84.9	<0.0001
Treatment	(1)–(3)	60	121.4	<0.0001
Location	(3)–(4)	30	89.92	<0.0001
Treatment	(2)–(4)	60	126.42	<0.0001
Location × Treatment interaction	(4)–(5)	60	41.18	0.9698

Note: Relevant comparisons for each test are shown as differences between two models.

† The explanatory variables are initial class (C), treatment (T), and location (L), and the response variable is fate (F).

eters occurs in some species (Horvitz and Schemske 1995, Oostermeijer et al. 1996, Horvitz et al. 1997, Caswell 2000). Matrix selection, on the other hand, preserves the observed correlation structure among transition elements by varying whole matrices, drawn at random from the set of five detailed matrices for each treatment–site combination, at each time step. This limits the number of possible trajectories a simulated population can follow (Burgman et al. 1993). We used RAMAS/stage software (Ferson 1991) to perform element selection simulations and POPPROJ2 (Menges 1986, 1990, 1992b) to implement matrix selection. For both methods, we used an initial population size of 800 plants, distributed in the average observed structure for each treatment and site.

We calculated stochastic lambdas and 95% confidence intervals (following Caswell 2001:396) from simulations using both the element and matrix selection procedures. When the log of population growth is averaged over a very large number of time steps, it converges to a fixed value determined by vital rates and environmental processes (Caswell 2001, Tuljapurkar 1990). For each type of simulation, we ran the models for 2000 time steps to calculate the stochastic growth rate.

To calculate extinction probability, we ran 1000 simulations with 100 one-year time steps. Extinction was defined as falling below 10 individuals. For element selection, distributions were assumed to be normal and truncated to zero and one. If transition rates for a given stage summed to greater than 1.0 (suggesting >100% survival) during element selection, the values were re-scaled to sum to 1.0. In the matrix selection procedure, each detailed matrix had an equal probability at each time step. Extinction probability was calculated from the frequency of extinction events in the simulations. Confidence intervals were based on a normal approximation of a binomial distribution (Steel et al. 1997).

Our use of the transition matrix model assumed that fertility and transition rates are independent of intraspecific plant density. This is an acceptable assumption for populations below a density-dependent threshold (e.g., Shaw 1987), but only while they remain at low densities. Density dependence will eventually limit growth of populations with  $\lambda_s > 1.0$ . Therefore, we tested the effects of imposing a population ceiling on extinction probability and found that there was no effect on extinction probability of limiting population size to twice the initial size. We concluded that omitting density dependence from our models did not substantially alter our results. Demographic stochasticity was also ignored by our models, but it usually contributes much less to extinction probability than environmental stochasticity, except in declining populations with small (e.g., 50 individuals) initial size (Menges 1992b). In addition, these matrix models assume that population growth is a first-order Markov process, in which transition probabilities depend only on a plant's con-

dition in the current year, not on its state in previous years (Lefkovitch 1965).

### *Elasticities*

Elasticities are a proportional measure of the sensitivity of  $\lambda$  to small perturbations in each transition element (de Kroon et al. 1986). One useful property of elasticities is that, for a given matrix, they can be summed for each stage to provide a proportional measure of the importance of each stage for population growth (e.g., Caswell 2001). We calculated elasticities for each of the populations and treatments using weighted mean matrices and a parametric bootstrap process detailed in Caswell and Kaye (*in press*). This bootstrap procedure resamples matrices from a multinomial distribution for transition rates and a Poisson distribution for fertilities to generate 95% confidence intervals.

### *Seed bank analysis*

Our models assume that seeds do not remain in the soil for more than one year without germinating or dying. To test this assumption, we sampled soils from four *Lomatium bradshawii* populations to determine if the species maintains a persistent soil seed bank. Populations examined included Fisher Butte, Rose Prairie, Long Tom, and Buford Park. All soil samples were taken in 1993 after seedling emergence and prior to seed dispersal of the current season. At the first three sites, 20 × 20 cm by 3 cm deep samples were collected adjacent to randomly selected reproductive *L. bradshawii* plants, excluding plants that were included in monitoring plots. At each plant, a random direction and distance ( $\leq 2$  m) were selected for locating the sample. At Buford Park, 20 × 20 cm by 3 cm deep samples were taken at regular intervals along previously established monitoring transects in areas of high *Lomatium bradshawii* density ( $\sim 50$  plants/m<sup>2</sup>). Sample sizes were 15–20 per site.

Soil samples were examined for *Lomatium bradshawii* fruits (single-seeded mericarps) within two days of collection. Each sample was loosened into smaller fragments, then passed through a series of sieves to separate the size fragment appropriate for *L. bradshawii* fruits. The accuracy of this technique was evaluated by placing marked *L. bradshawii* fruits into the first three soil samples to determine if they could be found. All marked fruits were recovered quickly and without confusion. When *L. bradshawii* fruits were encountered, they were evaluated for overall condition and presence of endosperm or embryo. We tested for viability of embryos with tetrazolium chloride (following Moore 1973).

## RESULTS

### *Transition rates*

During 1988–1993, a total of 1151 individual plants were recorded in sample plots at Rose Prairie, and 1273

TABLE 3. Mean transition matrices (left group of matrices) and variances (right group of matrices) for each site, treatment, and year (1988–1993,  $n = 5$ ).

Stage at time $t + 1$	Stage at time $t$											
	Mean, 1988–1993						Variance 1988–1993					
	S	V2	V3	R1	R2	R3	S	V2	V3	R1	R2	R3
Rose Prairie, no burns												
S	0	0	0	0.362	3.462	4.035	0	0	0	0.0311	13.304	6.889
V2	0.068	0.244	0.108	0	0	0	0.0076	0.1079	0.0145	0	0	0
V3	0.094	0.130	0.390	0.228	0.044	0	0.0117	0.0298	0.0380	0.0114	0.0077	0
R1	0.018	0	0.278	0.432	0.584	0	0.0007	0	0.0262	0.0237	0.1112	0
R2	0	0	0.044	0.186	0.272	0.667	0	0	0.0077	0.0111	0.1409	0.2222
R3	0	0	0	0	0.100	0.333	0	0	0	0	0.0400	0.2222
Rose Prairie, two burns (1988 and 1991)												
S	0	0	0	0.764	4.138	10.178	0	0	0	0.3090	7.535	76.093
V2	0.318	0.408	0.108	0.078	0.022	0.125	0.0104	0.0095	0.0042	0.0055	0.0010	0.0469
V3	0.058	0.216	0.246	0.146	0.160	0.083	0.0027	0.0195	0.0290	0.0051	0.0154	0.0204
R1	0.012	0.016	0.254	0.348	0.150	0.100	0.0001	0.0004	0.0071	0.0191	0.0060	0.0300
R2	0	0.014	0.184	0.310	0.524	0.343	0	0.0008	0.0194	0.0267	0.0177	0.0674
R3	0	0.006	0	0.014	0.058	0.350	0	0.0001	0	0.0008	0.0039	0.1675
Rose Prairie, three burns (1988, 1989, and 1991)												
S	0	0	0	0.692	4.800	10.540	0	0	0	0.2813	6.002	27.147
V2	0.336	0.316	0.028	0	0.014	0	0.0203	0.0852	0.0013	0	0.0008	0
V3	0.062	0.184	0.370	0.278	0.080	0.125	0.0029	0.0344	0.0223	0.0269	0.0084	0.0469
R1	0.020	0.156	0.228	0.278	0.240	0	0.0010	0.0329	0.0119	0.0262	0.0555	0
R2	0.012	0.034	0.124	0.342	0.488	0.250	0	0.0046	0.0055	0.0458	0.0469	0.1875
R3	0	0.006	0	0	0.050	0.375	0	0.0001	0	0	0.0100	0.1719
Fisher Butte, no burns												
S	0	0	0	0.322	1.718	5.984	0	0	0	0.1860	2.776	17.573
V2	0.236	0.242	0.054	0.030	0.016	0	0.0245	0.0156	0.0016	0.0014	0.0010	0
V3	0.102	0.220	0.496	0.206	0.140	0.240	0.0057	0.0130	0.0073	0.0058	0.0075	0.1504
R1	0.014	0.056	0.174	0.392	0.342	0.066	0.0002	0.0021	0.0040	0.0147	0.0089	0.0174
R2	0	0.042	0.062	0.180	0.326	0.174	0	0.0031	0.0014	0.0198	0.0304	0.0675
R3	0	0	0.002	0.014	0.048	0.414	0	0	0	0.0004	0.0022	0.1504
Fisher Butte, two burns (1988 and 1991)												
S	0	0	0	0.078	0.892	3.356	0	0	0	0.0045	0.3424	5.390
V2	0.286	0.328	0.106	0.060	0.018	0	0.0165	0.0063	0.0040	0.0013	0.0013	0
V3	0.170	0.262	0.362	0.168	0.090	0	0.0086	0.0145	0.0159	0.0169	0.0026	0
R1	0.006	0.070	0.180	0.278	0.220	0.040	0.0001	0.0032	0.0082	0.0064	0.0176	0.0064
R2	0	0.018	0.120	0.298	0.394	0.146	0	0.0005	0.0051	0.0723	0.0102	0.0325
R3	0	0	0.004	0.022	0.102	0.680	0	0	0.0001	0.0010	0.0135	0.0812
Fisher Butte, three burns (1988, 1989, and 1991)												
S	0	0	0	0.086	0.720	2.538	0	0	0	0.0020	0.2291	4.167
V2	0.334	0.196	0.084	0.046	0.012	0	0.0127	0.0077	0.0049	0.0027	0.0006	0
V3	0.146	0.326	0.496	0.106	0.056	0.028	0.0075	0.0229	0.0347	0.0178	0.0025	0.0031
R1	0.014	0.074	0.166	0.354	0.166	0.060	0.0003	0.0018	0.0027	0.0091	0.0147	0.0064
R2	0	0.050	0.070	0.316	0.458	0.192	0	0.0014	0.0029	0.0308	0.0166	0.0013
R3	0	0	0.018	0.046	0.142	0.632	0	0	0.0003	0.0044	0.0138	0.0279

Notes: Fertilities are found on the top row of each matrix. Probabilities for stasis are along the main diagonals, regression to smaller stages are above the diagonals (excluding the top row), and growth probabilities are below the diagonals in each column. Stages are defined in *Methods: Transition elements and matrices*.

were tracked at Fisher Butte. Many kinds of transitions were observed among the stages of *Lomatium bradshawii*. From one year to the next, plants increased or decreased in size, or remained the same (Table 3). In a single year, some plants grew or shrank two or more stages. For example, at both sites and in all fire treatments, V3 plants grew to R1 or R2 or regressed to V2 stages in one year (Table 3). Some transitions were never or seldom observed, such as plants from S or V2 growing to R2 or R3 stages. The log-linear analyses (Table 2) suggest that fates of individuals in each of the six stages were affected by the burning treatments

( $P < 0.0001$ ) and the locations of the populations ( $P < 0.0001$ ). There was no evidence of an interaction between treatment and location ( $P = 0.9697$ ).

In unburned environments at both sites, the most likely transition for all stages was survival in the same stage-class (matrix diagonals, Table 3) or decline in size. At Rose Prairie, stasis was most likely for V2–R1 plants, while shrinkage to the next smaller stage class was most probable for R2 and R3 reproductive plants. Similarly, at Fisher Butte stasis was most likely for all stages except R2, which most frequently regressed one stage. Plants in burned environments most

often remained the same or grew one stage. For example, plants remained the same size more often than any other transition in both fire treatments at Rose Prairie, except for V3 and R1 plants, which were most likely to grow one stage in the two-burn and three-burn treatments, respectively. Average matrices for the burn treatments at Fisher Butte also showed that stasis was the single most likely transition, except for one-step growth of R1 and V2 plants in the two-burn and three-burn treatments, respectively.

The effect of fire on individual plant fecundity (top row of the matrices, Table 3) was less clear, and appeared to differ between the two sites. Mean matrices for burned environments at Rose Prairie had higher fecundity values in most cases than those for unburned conditions, especially for R3 plants, but plants in the two burn treatments had very similar fecundities. At Fisher Butte, however, fecundity of R2 and R3 plants consistently declined with increasing fire frequency.

#### Population growth rates

Both estimates of stochastic population growth rate increased with burning frequency at Rose Prairie and Fisher Butte, but the magnitude of the fire effect differed from site to site and, to a lesser degree, with the method of calculating  $\lambda_s$ . At Rose Prairie, for example, plant abundance was projected to decline in the absence of fire, but burning twice in six years resulted in growth rates considerably  $>1.0$ . This increase continued in the three-burn treatment, especially for estimates from element selection (Fig. 2), indicating that burned populations were projected to increase in size. Fire also had a positive effect on population growth rate at Fisher Butte, but its effect was less dramatic and a higher burning frequency was required to raise  $\lambda_s$  to 1.0. Population growth rate in the two-burn treatment at Fisher Butte increased over the unburned area, but remained  $<1.0$  (Fig. 2), with three burns in six years required to raise  $\lambda_s$  to 1.0. For either method of calculating  $\lambda_s$ , we rejected the null hypothesis that fire had no effect on  $\lambda_s$  at  $P = 0.028$  (i.e., the probability that we would observe a progressively positive effect of burning in three treatments at two sites if the effects of fire were random was  $[1/6]^2 = 0.028$ ). Both measures of stochastic projection yielded roughly equivalent estimates of  $\lambda_s$ , except for computations for burn treatments at Rose Prairie. Growth rates were higher when calculated by element selection in the two- and three-burn treatments (95% CI, 1.13–1.17 and 1.18–1.20, respectively) than matrix selection (1.03–1.08 and 1.07–1.13, respectively) at that location.

#### Extinction probability

In the absence of fire, both populations were projected to become extinct in nearly all of the 100-yr projections, regardless of our method of modeling environmental stochasticity. At Rose Prairie, burning twice or three times in six years lowered extinction

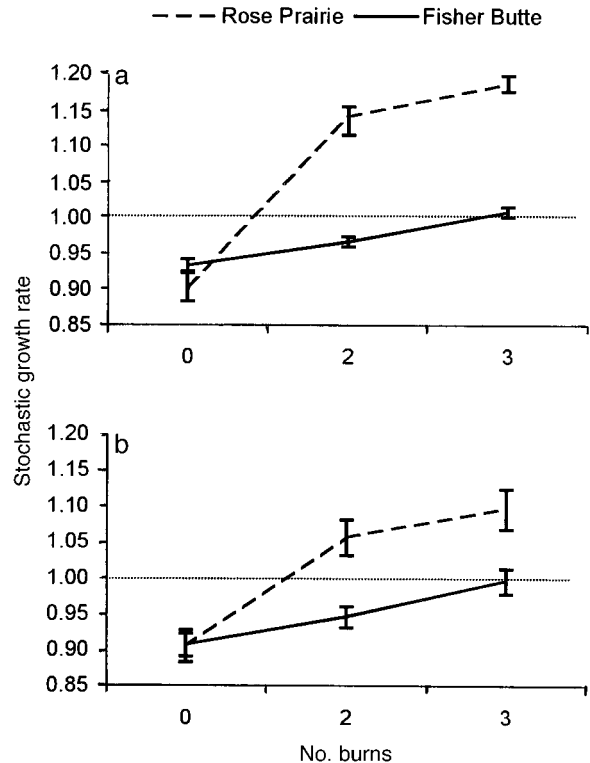


FIG. 2. Stochastic population growth rate ( $\lambda_s$ ) within each site and burning treatment for (a) element selection (calculated with RAMAS/stage), and (b) matrix selection (POP-PROJ2). Each value is a mean of 2000 iterations with 95% confidence intervals.

probability nearly to zero (Fig. 3). Extinction probability at Fisher Butte also declined from near certainty without fire to near zero in prairies burned three times. In the two-burn treatment at Fisher Butte extinction probability was 57% under element selection and 53% by matrix selection (Fig. 3).

#### Elasticities

The effect of fire on elasticities differed between sites. At Rose Prairie, the most important transition in the unburned environment was one-umbel plants staying the same size (elasticity, 0.202), while stasis of two-umbel plants had the greatest effect on  $\lambda_s$  in habitats burned twice and three times (0.141 and 0.120, respectively) (Table 4). Elasticity at Fisher Butte shifted in importance from constancy of three-leaved vegetative plants (0.170) in the unburned treatment to stasis of three-umbel plants in burned areas (0.129 and 0.123). For elasticities summed by stage, most confidence intervals overlapped within a site and treatment combination, but burning appeared to decrease the importance of mid-sized plants and increase the elasticity of small plants (Fig. 4). These effects differed from site to site, however. The elasticity of one-umbel plants, for example, decreased in burned environments at Rose Prairie, while seedlings and small vegetative plants in-

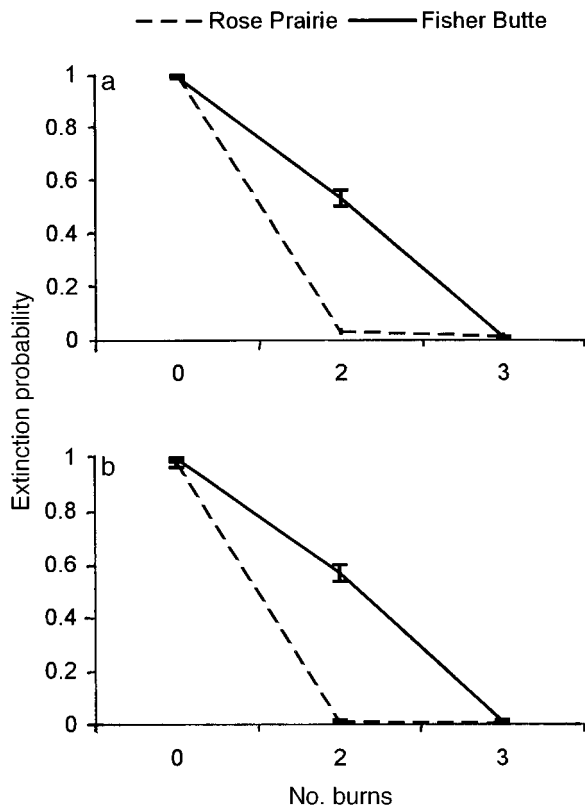


FIG. 3. Extinction probability in burned and unburned stochastic environments calculated through (a) element selection (calculated with RAMAS/stage), and (b) matrix selection (POPPROJ2). All runs were 100-yr simulations iterated 1000 times. Initial population sizes were 800 plants, and extinction was defined as falling below 10 individuals. Vertical lines are 95% confidence intervals.

creased in importance. At Fisher Butte, the elasticity of large vegetative (V3) plants decreased in burned environments, but the impact of seedlings and small vegetatives (V2) on population growth rate was unaffected by fire.

#### Seed bank analysis

No viable seeds were encountered in sieved-soil samples from four *Lomatium bradshawii* populations. Fewer than one fruit per sample was detected at all sites, and no fruits were encountered at Fisher Butte (Table 5). Some fruits were discovered intact, but these either contained no embryo, or the embryo was not viable. The remaining fruits (0–67%) were decayed and/or broken and contained incomplete embryo tissue, if any.

#### DISCUSSION

In the absence of fire, *Lomatium bradshawii* did not maintain populations with projected long-term viability. Unburned populations of *L. bradshawii* at two locations had individual vital rates dominated by stasis and regression to smaller stages. Stochastic projections

estimated growth rates  $< 1.0$  and very high probabilities of extinction (97–100%). Fall burning, in contrast, had several positive effects, despite considerable environmental stochasticity. For example, stasis and growth to larger stage classes dominated vital rates in burned populations, and seedling survival increased relative to unburned plots. Stochastic population growth rates increased, especially in the treatment with highest fire frequency (three burns in six years). Burning twice in six years was sufficient to raise growth rates  $> 1.0$  at Rose Prairie, but not Fisher Butte. At the latter site, stable to positive growth rates were observed only in plots with three burns in six years. Extinction probability declined in burned plots, dropping to near zero at Rose Prairie in both burn treatments. At Fisher Butte, the population burned twice in six years had a 53–57% chance of extinction (depending on our method of modeling environmental stochasticity), whereas the population that was burned three times had almost zero extinction risk in 100-yr simulations.

Regardless of which method was used to incorporate stochasticity, population growth rates consistently increased in burned vs. unburned habitats (Fig. 2), and extinction risk declined in these treatments (Fig. 3), with the estimates of these values becoming nearly identical between methods in most cases. Apparently, any within-population correlation structure between matrix elements that these populations had was insufficient to alter results relative to models that allowed the elements to vary independently. This may not always be the case, and an earlier comparison of the two methods using RAMAS/stage and POPPROJ with data from another rare plant species showed substantial differences in extinction estimates with 25-yr projections (Greenlee and Kaye 1997). Additional comparisons of these techniques and assessments of matrix element correlation are needed to evaluate the widely held concerns of population modelers that such correlation structure is common and affects the results of stochastic matrix model simulations (Caswell 2000, Menges 2000).

The risks of extinction determined here for *Lomatium bradshawii* are comparable to results obtained for other plant species with similar population growth rates and environmental stochasticities. Menges (1992b) applied various levels of environmental stochasticity to published transition matrices for eight plant species, concluding that a “moderate” level of environmental stochasticity (mean-to-variance ratio  $\sim 0.01$ ) was sufficient to limit growth of populations with  $\lambda < 1.05$ , but populations with  $\lambda > 1.12$  were not restrained by even “extreme” levels of stochasticity (ratio  $\approx 0.3$ ). The observed environmental stochasticities for *L. bradshawii* are in the range that Menges considered “moderate” to “strong.” Our estimates of extinction probability were high (53–100%) for populations with  $\lambda < 1.05$ , and low (0–1%) for those with  $\lambda > 1.12$ , as might be expected from Menges’s results, suggesting that

TABLE 4. Elasticities for weighted mean matrices (1988–1993) for each site and burning treatment, where Rose Prairie data are presented in the left group of matrices and Fisher Butte data are presented in the right group of matrices.

Stage at time $t + 1$	Stage at time $t$											
	Rose Prairie						Fisher Butte					
	S	V2	V3	R1	R2	R3	S	V2	V3	R1	R2	R3
No burns												
S	0	0	0	0.013	0.041	0.004	0	0	0	0.015	0.040	0.032
V2	0.015	0.012	0.005	0	0	0	0.043	0.019	0.009	0.004	0.001	0
V3	0.028	0.019	0.108	0.071	0.011	0	0.034	0.039	<b>0.171</b>	0.044	0.016	0.003
R1	0.016	0	0.103	<b>0.202</b>	0.098	0	0.009	0.011	0.078	0.098	0.048	0.002
R2	0	0	0.020	0.134	0.060	0.014	0	0.007	0.043	0.073	0.056	0.010
R3	0	0	0	0	0.018	0.011	0	0	0.005	0.013	0.028	0.051
Total	0.058	0.032	0.236	0.418	0.228	0.029	0.086	0.076	0.306	0.246	0.189	0.097
Two burns (1988 and 1991)												
S	0	0	0	0.016	0.104	0.024	0	0	0	0.004	0.042	0.052
V2	0.083	0.047	0.006	0.005	0.002	0.001	0.051	0.033	0.013	0.004	0.002	0
V3	0.043	0.054	0.041	0.016	0.020	0.001	0.044	0.047	0.068	0.021	0.012	0
R1	0.018	0.013	0.053	0.046	0.033	0.003	0.003	0.017	0.055	0.049	0.046	0.002
R2	0	0.020	0.075	0.077	<b>0.141</b>	0.010	0	0.006	0.051	0.077	0.089	0.015
R3	0	0.009	0	0.006	0.024	0.013	0	0	0.005	0.018	0.047	<b>0.129</b>
Total	0.143	0.142	0.175	0.166	0.323	0.051	0.098	0.103	0.191	0.171	0.238	0.199
Three burns (1988, 1989, and 1991)												
S	0	0	0	0.018	0.106	0.020	0	0	0	0.004	0.034	0.060
V2	0.092	0.044	0.002	0	0.001	0	0.055	0.018	0.013	0.002	0.001	0
V3	0.027	0.036	0.049	0.029	0.007	0.002	0.038	0.044	0.087	0.018	0.007	0.001
R1	0.016	0.032	0.051	0.062	0.061	0.000	0.005	0.015	0.055	0.057	0.034	0.008
R2	0.008	0.010	0.048	0.114	<b>0.120</b>	0.005	0	0.012	0.029	0.067	0.100	0.022
R3	0	0.016	0	0	0.010	0.015	0	0	0.011	0.026	0.055	<b>0.123</b>
Total	0.143	0.139	0.150	0.222	0.305	0.041	0.098	0.089	0.194	0.174	0.230	0.214

Notes: Values for fertility are displayed on top rows. Stasis values are found on the diagonals, growth below the diagonals, and regression above (excluding fertilities). The transition with the highest elasticity is shown in bold for each matrix. Stages are defined in *Methods: Transition elements and matrices*.

lambda and environmental stochasticity interact to control extinction probability in predictable ways (Tuljapurkar and Orzack 1980, Lande and Orzack 1988, Lande 1993).

Density dependence was not incorporated into our models of *Lomatium bradshawii* population dynamics. It is possible that our low estimates of extinction probability for burned populations with positive growth rates were overly optimistic because high densities would eventually reduce plant survival and fecundity, thus limiting population growth. Under this scenario, populations would be kept relatively small and vulnerable to stochastic declines. Our pilot tests with population ceilings, however, suggested that limiting population size did not increase extinction risk. On the other hand, declining populations could experience both positive and negative effects of density dependence. For example, as densities declined, survival could have increased, but fecundity could have either increased due to lowered intraspecific competition or decreased due to Allee effects. Since the relative strengths of these forces are unknown for *L. bradshawii*, their effects on extinction probability are also uncertain. However, our observations of this species suggest that as density declines the gaps created by missing plants are filled by aggressive interspecific competitors, thus lessening benefits of lowered intraspecific density.

Reduced fecundity and progeny fitness at low densities could occur in this species, and this would tend to increase extinction risk over the estimates presented here.

Attempts to validate transition matrix models of plant population dynamics are few and have yielded mixed results. A stochastic model based on random selection between two matrices failed to predict population size 15 yr later (Bierzychudek 1999), but an element selection model from four years of observation estimated population size very well after seven years (Kephart and Paladino 1997). No validations of long-term (e.g., 100-yr) projections from matrix models have been attempted, for obvious reasons. Beissinger and Westphal (1998) suggest that qualitative conclusions should be emphasized over the quantitative results of population viability analyses, and we concur. Without validation and inclusion of population processes like density dependence and demographic stochasticity, the relative predictions of our models, i.e., burning improves population growth rate and lowers extinction risk, should be emphasized over the absolute estimates of these parameters.

#### Elasticities

Fire appeared to shift stage-specific contributions to population growth rate, but these effects differed from

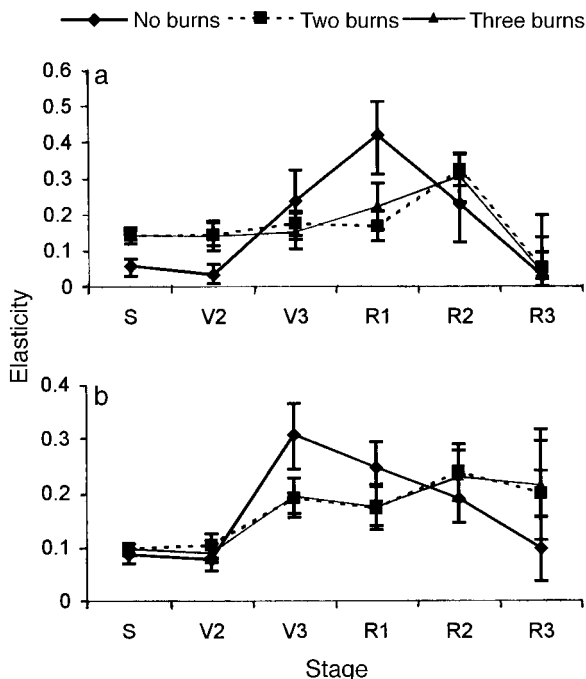


FIG. 4. Stage-summed elasticities for populations in burned and unburned environments at (a) Rose Prairie and (b) Fisher Butte, based on weighted mean matrices from six years of observations. Error bars represent bootstrapped 95% confidence intervals.

site to site. At Rose Prairie, fire appeared to decrease the importance of seedlings and small vegetative plants and increase the contribution of one-umbel reproductive plants (Table 4, Fig. 4). Burning at Fisher Butte, on the other hand, decreased the importance of large vegetative plants. In terms of demographic functions, burning at Rose Prairie increased the importance of fertility and growth, and lowered the elasticities for regression and stasis, but had little effect on these processes at Fisher Butte. The observed site differences in response to burning shown by *Lomatium bradshawii* are not surprising, given the spatial variability in demographic processes observed in many other herbaceous species that have been modeled with transition matrices (e.g., Sarukhan and Gadgil 1974, Bierzychudek 1982, Meagher 1982, de Kroon et al. 1987, van Groenendael and Slim 1988, Menges 1990, Gregg

1991, Horvitz and Schemske 1995, Oostermeijer et al. 1996, Silvertown et al. 1996, Kephart and Paladino 1997). What is noteworthy in this case, however, is that the effect of fire on individual stages and demographic processes differed somewhat among locations, but the trend toward improved population viability did not.

Silvertown et al. (1993) analyzed elasticities from 45 herbaceous species and 21 woody plants, and concluded that these two life history strategies are significantly different in terms of the importance of growth, survival, and fecundity to population growth. The elasticities of *Lomatium bradshawii* for these processes are well within the ranges observed for herbaceous species, and are typical of herbaceous plants of open habitats (Silvertown et al. 1993). In addition, the relative importance of growth and survival may be typical of species with life spans similar to *Lomatium bradshawii*. In a review of five tree species, Caswell (1986) suggested that survival may be most important for long-lived, slow-growing species in general, and Silva et al. (1991) argued that growth might be most important in short-lived, fast-growing species, such as annuals, biennials, and short-lived perennials. Indeed, the relative importance of growth and survival appear to be related to individual longevity (Enright et al. 1995). For *L. bradshawii*, survival and growth had nearly equal elasticities at Fisher Butte, while at Rose Prairie, growth was more important than stasis (but only in burned plots); fire had no consistent effect on these parameters. Therefore, we suggest that for intermediate life spans and growth rates (such as many iteroparous herbs), neither growth nor survival are consistently more significant to population growth. This concurs with the observation of Silvertown et al. (1993) that, on average, elasticities for growth ( $0.439 \pm 0.183$ ) and survival ( $0.398 \pm 0.256$ ) are nearly equal for herbs.

Elasticities identify individual transitions and stages where small errors in transition rate estimates will cause relatively large changes in projected population growth. In some of our matrices, large reproductive (R3) plants had high elasticities, and their transition rates were calculated from observations of relatively few plants (resulting in large bootstrapped confidence intervals for that stage; see Fig. 4). Therefore, larger sample sizes for this stage could lower measurement error and might alter our results.

TABLE 5. Fruits encountered in soil samples from four *Lomatium bradshawii* populations.

Site	N	Mean no. fruits (1 SE)		Intact (%)	Decayed (%)	Viable (%)
		Per sample	Per m <sup>2</sup>			
Fisher Butte	20	0.00 (0.00)	0.00 (0.00)	0	0	0
Rose Prairie	18	0.06 (0.05)	1.50 (1.25)	100	0	0
Long Tom	15	0.13 (0.09)	3.25 (2.25)	100	0	0
Buford Park	20	0.60 (0.22)	15.0 (5.5)	33	67	0

Note: Samples were taken after seedling emergence and before fruit dispersal to detect a persistent soil seed bank.

Elasticities also have important implications for conservation and management, because they identify crucial life history stages where scarce management resources may be targeted for maximum benefit. For example, if fire could not be applied to a particular population because of the risk of burning adjacent property, elasticities from unburned sites suggest that focusing on large vegetative (V3) or small reproductive (R1) plants to improve conditions for those stages (e.g., removing interspecific competitors) would yield a faster growing population than equal improvements to other stages. Recent studies suggest that this type of assessment from a mean transition matrix should be treated with caution, however (Benton and Grant 2000, Heppel et al. 2000). For example, Wisdom et al. (2000) showed that the relative rank of individual elasticities may be unstable when demographic uncertainty, variation, and covariation are incorporated into matrix simulations. Our elasticities are bounded by bootstrapped confidence intervals (Fig. 4), which provide a measure of uncertainty for their estimate, but they do not account for factors like covariation among vital rates.

#### Seed bank

Our data indicate that *Lomatium bradshawii* does not maintain a persistent soil seed bank. Even though some fruits survived at least one year in the soil, the seeds within them were not viable (Table 5). Absence of a soil seed bank may be typical for other *Lomatium* species, as well. For example, 98.5% of all *L. dissectum* seeds distributed in artificial piles were removed by postdispersal seed predators, died of other causes, or germinated within 43 wk of dispersal (Thompson 1985). Similar seed losses were observed for *L. triteratum* in a different component of the same study, and the author concluded that seed survival for longer than one year was unlikely for these species. Although it is possible that larger sample sizes in our study might have detected some viable *L. bradshawii* seeds, our sample strategy maximized the likelihood of detecting seeds by sampling in close proximity to reproductive plants following a year of relatively high seed production (T. N. Kaye, unpublished data). Even if some viable seeds persist longer than one year, they apparently do so in such low numbers as to be of little significance to the population. Therefore, modeling *L. bradshawii* population dynamics without a soil seed bank seems reasonable.

#### Ecological and conservation implications

Prior to Euro-American settlement, Willamette Valley prairies were probably burnt annually in the fall by Kalapuya Indians to promote food plants and game (Boyd 1986, 1999). Very little information is available to document the extent or patchiness of individual past fires, but these burns were apparently very large, covering several hundred hectares (Douglas 1914). Open dry prairies may have burned almost every year, and

wetland prairies and canyons on north slopes were probably exposed to somewhat less frequent blazes. In the absence of fire, native prairies in western Oregon are invaded by shrubs and forest vegetation dominated by *Quercus garryana*, *Pseudotsuga menziesii*, *Pinus ponderosa*, *Abies grandis*, or *Fraxinus latifolia* (Franklin and Dyrness 1988, Streatfield and Frenkel 1997). The historic dependence of prairie habitat on burning suggests that the distribution and evolution of *Lomatium bradshawii* is related, at least in part, to long-term Native American cultural practices, and the decline of this species has been aggravated by habitat loss and fire suppression by postsettlement residents. Therefore, even populations that occur in protected areas, such as wildlife refuges and habitat preserves, are vulnerable unless woody vegetation is controlled and fire or some other management technique is used to enhance population growth. In some cases, more aggressive methods than fire may be required to remove woody vegetation, such as at Long Tom Area of Critical Environmental Concern, where hardwood trees (*Fraxinus latifolia*) shade the herbaceous vegetation and *L. bradshawii* is projected to decline despite frequent burning (Kaye et al. 1994).

Burning may have several effects on prairie communities, any of which could contribute to the positive changes observed for *Lomatium bradshawii*. Burning is widely believed to deliver a pulse of nutrients to soil and plants (Bond and van Wilgen 1996), at least in the first one to two years after a fire (Kucera and Ehrenrich 1962, Old 1969, Ojima et al. 1994). Pendergrass et al. (1998) suggest that burning Willamette Valley prairies consumes thatch and standing biomass, creating bare areas suitable for plant growth and establishment. Voles, which can be significant herbivores of *Lomatium bradshawii* (T. N. Kaye, personal observation; A. Drew, Oregon State University, unpublished data), are negatively affected by prairie fires through short-term reduction in food plants and hiding cover, making them vulnerable to predators (e.g., Vacanti and Geluso 1985). In addition, heat and smoke from burns can stimulate seed germination in many fire-adapted species (Keeley and Fotheringham 1997), although the effect of fire on *L. bradshawii* seeds is unknown. These factors and others, either alone or more likely in combination, may drive the positive effects of fire observed in this study.

The value of controlled burns as a management tool for native vegetation and individual plant species in Willamette Valley prairies has already been described (Pendergrass 1995, Pendergrass et al. 1998, Streatfield and Frenkel 1997, Maret and Wilson 2000). Crown size, umbel number, and seed production of *L. bradshawii* plants increases significantly in areas subjected to fire, compared to plants in unburned areas (Finley and Kauffman 1992, Pendergrass et al. 1999). Our analyses with matrix models drawn from six years of population observations demonstrate that controlled fires

may enhance the population viability of this species, not just individual plant size characteristics.

These results were qualitatively consistent between two locations with similar hydrology and soils, but the applicability of these results to other populations of *Lomatium bradshawii* is unknown, and our models have not been validated for them. Differences in the relative abundance of each stage, plant community composition, past management, seasonal precipitation, soil depth, hydrology, and fire behavior could affect the response of specific populations to controlled burns. Pendergrass et al. (1998) reported that the 1988 burns produced greater heat per unit area and consumed more total biomass at Fisher Butte than Rose Prairie, while the 1989 burns were similar at the two locations, but were more spotty than the year before. Also, although a *Deschampsia cespitosa* community type was widespread at both sites, a *Vaccinium cespitosum* type was present only at Rose Prairie and a *Rosa nutkana*–*Juncus nevadensis* community occurred only at Fisher Butte (Pendergrass 1995). These patterns and other site dissimilarities may account for some of the quantitative differences in fire response between the study populations, such as higher  $\lambda_s$  at Rose Prairie after burns, differences in fecundities and elasticities, and opposite changes in some transition rates between the two sites (e.g., the R2 to R3 transition probability decreased with burning at Rose Prairie, but increased after fires at Fisher Butte [Table 3]). It is likely that other populations of *L. bradshawii* would also exhibit variations in population-level responses due to variation in fire behavior and other site differences.

Fire may not be the only disturbance with positive effects on this species. The presence of populations in areas like Rose Prairie and Fisher Butte, where fires have been suppressed for many years, yet the populations are still extant, suggests that other disturbances may have occurred in these areas to keep the habitat suitable for *Lomatium bradshawii*. Mowing, livestock grazing, floods, and other actions could conceivably benefit the species' population growth and should be explored as alternatives to controlled burning for managing western Oregon prairie remnants, especially in areas with fire-adapted weeds.

#### CONCLUSIONS

Fire and location had significant effects on stage-specific transitions, and stochastic projection models indicated that burning had a positive effect on the population viability of *Lomatium bradshawii*. Transition matrix models derived from field experiments with fire in *L. bradshawii* habitat indicated that populations of this species will decline in the absence of burning, and may grow if burnt two or three times in six years, depending on the location. Furthermore, extinction probability in 100-yr simulations declined from near certainty without fire to very low odds under these burning frequencies. These results contribute to our

ability to manage western Oregon prairies, their constituent species, and *L. bradshawii* in particular. They serve as one of a few available examples of stochastic matrix modeling used to compare management treatments for promoting rare plant populations (Oostermeijer 1996, Lesica 1997, Gross et al. 1998, Menges and Dolan 1998). This approach has widespread applicability for assessing management actions for rare species, especially when proposed habitat alterations can be tested for two to several years prior to large-scale implementation.

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#### LITERATURE CITED

- Alverson, E. R. 1989. Use of a county soil survey to locate remnants of native grassland in the Willamette Valley, Oregon. Pages 107–112 in R. S. Mitchell, C. J. Sheviak, and D. J. Leopold, editors. Ecosystem management: Rare species and significant habitats. Proceedings 15th Annual Natural Areas Conference, New York State Museum Bulletin.
- Alverson, E. R. 1990. A survey for native grassland remnants in the mid-Willamette Valley, Oregon. Oregon Department of Agriculture, Salem, Oregon, USA.
- Aplet, G. H., R. D. Laven, and R. B. Shaw. 1994. Application of transition matrix models to the recovery of the rare Hawaiian shrub, *Tetramalopium arenarium* (Asteraceae). Natural Areas Journal 14:99–106.
- Barker, N. G., and G. B. Williamson. 1988. Effect of winter fire on *Sarracenia alata* and *S. psittacina*. American Journal of Botany 75:138–143.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62: 821–841.
- Benton, T. G., and A. Grant. 2000. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution 14:467–471.
- Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335–351.
- Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological Applications 9:1278–1287.
- Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London, UK.
- Borchert, M. 1989. Post fire demography of *Thermopsis macrophylla* H. A. var. *angina* J. T. Howell (Fabaceae), a rare perennial herb in chaparral. American Midland Naturalist 122:120–132.
- Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology 5:65–86.
- Boyd, R. 1999. Strategies of Indian burning in the Willamette Valley. Pages 94–138 in R. Boyd, editor. Indians, fire and

- the land. Oregon State University Press, Corvallis, Oregon, USA.
- Boyd, R. S., and L. L. Serafini. 1992. Reproductive attrition of the rare chaparral shrub *Fremontodendron decumbens* Lloyd (Sterculiaceae). *American Journal of Botany* **79**: 1264–1272.
- Burgman, M. A., S. Ferson, and H. R. Ackakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London, UK.
- Campbell, J. J., D. D. Taylor, M. E. Medley, and A. C. Risk. 1991. Floristic and historical evidence of fire-maintained, grassy pine-oak barrens before settlement in southeastern Kentucky. Pages 359–375 in S. C. Nodvin and T. A. Waldrop, editors. Fire and the environment: ecological and cultural perspectives. Southeastern Forest Experiment Station, Asheville, North Carolina, USA.
- Carlson, P. R., G. W. Tanner, J. M. Wood, and S. R. Humphrey. 1993. Fire in key deer habitat improves browse, prevents succession and preserves endemic herbs. *Journal of Wildlife Management* **57**:914–928.
- Caswell, H. 1986. Life cycle models for plants. *Lectures on Mathematics in the Life Sciences*. **18**:171–233.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**: 619–627.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.
- Caswell, H., and T. N. Kaye. *In press*. Stochastic demography and conservation of an endangered perennial plant *Lomatium bradshawii* in a dynamic fire environment. *Advances in Ecological Research*.
- Currier, P. J. 1984. Response of prairie fringed orchid to fire and reduction in grazing. *Restoration and Management Notes* **2**:28.
- de Kroon, H., A. Plaiser, and J. van Groenendael. 1987. Density dependent simulation of the population dynamics of a perennial grassland species, *Hypochaeris radicata*. *Oikos* **50**:3–12.
- de Kroon, H., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427–1431.
- Douglas, D. 1914. Journal kept by David Douglas during his travels in North America 1823–1827. William Wesley and Son, London, UK. Published under the direction of the Royal Horticultural Society.
- Dunwiddie, P. W. 1990. Rare plants in coastal heathlands: observations on *Corema conradii* and *Helianthemum dumosum*. *Rhodora* **92**:22–26.
- Enright, N., M. Franco, and J. Silvertown. 1995. Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. *Oecologia* **104**:79–84.
- Ferson, S. 1991. RAMAS/stage: generalized stage-based modeling for population dynamics (Version 1.4). Applied Biomathematics, Setauket, New York, USA.
- Fiedler, P. L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). *Journal of Ecology* **75**:977–995.
- Fingleton, B. 1984. Models of category counts. Cambridge University Press, Cambridge, UK.
- Finley, K. K. 1994. Hydrology and related soil features of three Willamette Valley wetland prairies. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Finley, K. K., and J. B. Kauffman. 1992. Soils and hydrology of Willamette Valley wetland prairies and ecological response of *Lomatium bradshawii* and *Erigeron decumbens* var. *decumbens* to prescribed fire. A progress report to the U.S. Army Corps of Engineers and the Bureau of Land Management, Eugene, Oregon, USA.
- Folkerts, G. W. 1977. Endangered and threatened carnivorous plants of North America. Pages 301–313 in G. T. Prance and T. S. Elias, editors. Extinction is forever: threatened and endangered species of plants in the Americas and their significance in ecosystems today and in the future. New York Botanical Garden, Bronx, New York, USA.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.
- Gankin, R., and J. Major. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. *Ecology* **45**:792–808.
- Greenlee, J., and T. N. Kaye. 1997. Stochastic matrix projections: a comparison of the effect of element and matrix selection methods on quasi-extinction risk for *Haplopappus radiatus* (Asteraceae). Pages 66–71 in T. N. Kaye, A. Liston, R. M. Love, D. Luoma, R. J. Meinke, and M. V. Wilson, editors. Conservation and management of native plants and fungi. Native Plant Society of Oregon, Corvallis, Oregon, USA.
- Gregg, K. B. 1991. Variation in behaviour of four populations of the orchid *Cleistes divaricata*, an assessment using transition matrix models. Pages 139–159 in T. C. E. Wells and J. H. Willems, editors. Population ecology of terrestrial orchids. Academic Publishing, The Hague, The Netherlands.
- Gross, K., J. R. Lockwood III, C. C. Frost, and W. F. Morris. 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biology* **12**:1291–1301.
- Habeck, J. R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. *Northwest Science* **35**:65–77.
- Hardin, D. E., and D. L. White. 1992. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. *Natural Areas Journal* **9**:234–245.
- Hartnett, D. C., and D. R. Richardson. 1989. Population biology of *Bonomia grandiflora* (Convolvulaceae): effects of fire on plant and seed bank dynamics. *American Journal of Botany* **73**:361–369.
- Hawkes, C. V., and E. S. Menges. 1995. Density and seed production of a Florida endemic, *Polygonella basiramia*, in relation to time since fire and open sand. *The American Midland Naturalist* **133**:138–145.
- Heppel, S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: methods and applications. *Ecology* **81**:605–606.
- Hessl, A., and S. Spackman. 1995. Effects of fire on threatened and endangered plants: an annotated bibliography. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.
- Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* **65**:155–192.
- Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The relative “importance” of life-history stages to population growth: prospective and retrospective studies. Pages 248–271 in S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York, New York, USA.
- Jacobs, J. 1993. New hope for the Peter’s Mountain Mallow. *Endangered Species Technical Bulletin* **18**(3):13–14.
- Jacobson, G. L., H. Almquist-Jacobson, and J. C. Winne. 1991. Conservation of rare plant habitat: insights from the recent history of vegetation and fire at Crystal Fen, northern Maine, USA. *Biological Conservation* **57**:287–314.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S.

- McWilliams. 1971. The vegetation of the Willamette Valley. *Annals of the Association of American Geography* **61**: 286–302.
- Johnson, A. F., and W. G. Abrahamson. 1990. A note on the fire responses of species in rosemary scrubs on the southern Florida Lake Wales Ridge. *Florida Scientist* **53**:138–143.
- Johnson, A. F., and A. Blyth. 1988. Re-discovery of *Calamovilfa curtissii* (Graminae) in Florida Panhandle. *Sida* **13**: 137–140.
- Kagan, J. S. 1980. The biology of *Lomatium bradshawii* (Apiaceae), a rare plant of Oregon. M.S. Thesis. University of Oregon, Eugene, Oregon, USA.
- Kaye, T. N. 1992. Bradshaw's desert-parsley: population monitoring and pollination biology. *Kalmiopsis* **2**:1–4.
- Kaye, T., K. Pendergrass, and K. K. Finley. 1994. Population biology of *Lomatium bradshawii*. I. Population viability analysis under three prairie burning treatments. Oregon Department of Agriculture, Salem, Oregon.
- Keeley, J. E., and C. J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. *Science* **276**: 1248–1250.
- Kephart, S. R., and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). *American Journal of Botany* **84**:179–189.
- Kucera, C. L., and J. H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. *Ecology* **43**: 334–336.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**:911–927.
- Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy Science* **85**:7418–7421.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* **21**:1–18.
- Lesica, P. 1997. Demography of the endangered plant, *Silene spaldingii* (Caryophyllaceae) in northwest Montana. *Madroño* **44**:347–358.
- Lesica, P. 1999. Effects of fire on the demography of the endangered, geophytic herb *Silene spaldingii* (Caryophyllaceae). *American Journal of Botany* **86**:996–1002.
- Lindsey, A. H. 1982. Floral phenology patterns and breeding systems in *Thaspium* and *Zizia* (Apiaceae). *Systematic Botany* **7**:1–12.
- Lindsey, A. H., and C. R. Bell. 1985. Reproductive biology of Apiaceae. II. Cryptic specialization and floral evolution in *Thaspium* and *Zizia*. *American Journal of Botany* **72**: 231–237.
- MacRoberts, M. H., and B. R. MacRoberts. 1990. Notes on the occurrence of *Platanthera integra* (Nutt.) A. Gray ex Beck (Orchidaceae) in West Central Louisiana. *Phytologia* **69**:378–381.
- Manders, P. T. 1987. A transition matrix model of the population dynamics of the Clanwilliam cedar (*Widdringtonia cedarbergensis*) in natural stands subject to fire. *Forest Ecology and Management* **20**:171–186.
- Maret, M. P., and M. V. Wilson. 2000. Fire and seedling population dynamics in western Oregon prairies. *Journal of Vegetation Science* **11**:307–314.
- Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. *Conservation Biology* **11**:990–999.
- McClaren, M. P., and P. C. Sundt. 1992. Population dynamics of rare orchid *Spiranthes delitescens*. *Southwestern Naturalist* **37**:299–333.
- Meagher, T. R. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two sex population projections and stable population structure. *Ecology* **63**:1701–1711.
- Menges, E. S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. *Natural Areas Journal* **6**:13–25.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* **4**:52–62.
- Menges, E. S. 1992a. Habitat preferences and response to disturbance for *Dicerandra frutescens*, a rare Lake Wales Ridge (Florida) endemic plant. *Bulletin of the Torrey Botanical Club* **119**:308–313.
- Menges, E. S. 1992b. Stochastic modeling of extinction in plant populations. Pages 253–275 in P. L. Fiedler and S. K. Jain, editors. *Conservation biology: the theory and practice of nature conservation, preservation, and management*. Chapman and Hall, New York, New York, USA.
- Menges, E. S. 1995. Factors limiting fecundity and germination in small populations of *Silene regia* (Caryophyllaceae), a rare hummingbird-pollinated prairie forb. *American Midland Naturalist* **133**:242–255.
- Menges, E. S. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution* **15**:51–56.
- Menges, E. S., and R. W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology* **86**:63–78.
- Menges, E. S., and J. Kimmich. 1996. Microhabitat and time-since-fire: effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic. *American Journal of Botany* **83**:185–191.
- Moir, W. H., and P. Mika. 1976. Prairie vegetation of the Willamette Valley, Benton, Co., Oregon. Research Work Unit 125, U.S. Forest Science Lab, Corvallis, Oregon, USA.
- Moloney, K. A. 1986. A generalized algorithm for determining category size. *Oecologia* **69**:176–180.
- Moore, R. P. 1973. Tetrazolium staining for assessing seed quality. Pages 347–366 in W. Heydecker, editor. *Seed ecology*. Butterworth and Company, London, UK.
- Myers, R. L. 1989. Condominiums, trailer parks and high intensity fires: the future of sand pine scrub preserves in Florida. Proceedings of the 17th Tall Timbers Fire Ecology Conference, Tallahassee, Florida, USA.
- Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**:5–21.
- Ojima, D. D., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry* **24**:67–84.
- Oostermeijer, G. 1996. Population viability of the rare *Gentiana pneumonanthe*. The relative importance of demography, genetics, and reproductive biology. Dissertation. Institute for Systematics and Population Biology, University of Amsterdam, The Netherlands.
- Oostermeijer, G., M. L. Brugman, E. R. de Boer, and H. C. M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology* **84**:153–166.
- Oregon Natural Heritage Program. 1998. Rare, threatened, and endangered species of Oregon. Oregon Natural Heritage Program, Portland, Oregon, USA.
- Owen, W. R., and R. Rosentreter. 1992. Monitoring rare perennial plants: techniques for demographic studies. *Natural Areas Journal* **12**:32–39.
- Parenti, R. L., A. F. Robinson, and J. S. Kagan. 1993. Bradshaw's lomatium recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Pendergrass, K. L. 1995. Vegetation composition and re-

- sponse to fire of native Willamette Valley wetland prairies. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Pendergrass, K. L., P. M. Miller, and J. B. Kauffman. 1998. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. *Restoration Ecology* **6**:303–311.
- Pendergrass, K. L., P. M. Miller, J. B. Kauffman, and T. N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. *Ecological Applications* **9**:1420–1429.
- Phillips, B. G., H. Green, S. Dudley, and R. Galeano-Popp. 1992. Prescribed fire research on Flagstaff pennyroyal (*Hedeoma diffusum* Greene). Pages 162–169 in R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern rare and endangered plant conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico, USA.
- Sarukhan, J., and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. *Journal of Ecology* **62**:921–936.
- Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**:584–606.
- Schlessman, M. A. 1978. Systematics and reproductive biology of *Lomatium farinosum* (Geyer ex Hooker) Coulter & Rose (Umbelliferae). *Madroño* **25**:1–9.
- Shaw, R. G. 1987. Density-dependence in *Salvia lyrata*: Experimental alteration of densities of established plants. *Journal of Ecology* **75**:1049–1063.
- Silva, J. F., J. Raventos, and H. Caswell. 1990. Fire and fire exclusion effects on the growth and survival of two savanna grasses. *Acta Oecologica* **11**:783–800.
- Silva, J. F., J. Raventos, H. Caswell, and M. C. Trevisan. 1991. Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. *Journal of Ecology* **79**:345–356.
- Silvertown, J., M. Franco, and E. S. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**:591–597.
- Silvertown, J., M. Franco, E. S. Menges, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography: relative importance of demographic components to the finite rate of increase in perennial plants. *Journal of Ecology* **81**:465–476.
- Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1997. Principles and procedures of statistics, a biometrical approach. Third edition. The McGraw-Hill Companies, New York, New York, USA.
- Stone, C. P., and J. M. Scott. 1985. Hawaii's terrestrial ecosystems: preservation and management. Cooperative National Park Resources and Studies Unit, University of Hawaii, Manoa, Hawaii, USA.
- Streatfield, R., and R. E. Frenkel. 1997. Ecological survey and interpretation of the Willamette Valley Floodplain Research Natural Area, W. L. Finley National Wildlife Refuge, Oregon, USA. *Natural Areas Journal* **17**:346–354.
- Thompson, J. N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. *Ecology* **66**:1608–1616.
- Tuljapurkar, S. D. 1990. Population dynamics in variable environments. Springer-Verlag, New York, New York, USA.
- Tuljapurkar, S. D., and S. H. Orzack. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theoretical Population Biology* **18**:314–342.
- Usher, M. B. 1976. Extensions to models, used in renewable resource management, which incorporate an arbitrary structure. *Journal of Environmental Management* **4**:123–140.
- Vacanti, P. L., and K. N. Geluso. 1985. Recolonization of a burned prairie by meadow voles (*Microtus pennsylvanicus*). *Prairie Naturalist* **17**:15–22.
- Vandermeer, J. 1978. Choosing category size in a stage projection matrix. *Oecologia* **32**:79–84.
- van Groenendael, J. M., and P. Slim. 1988. The contrasting dynamics of two populations of *Plantago lanceolata* classified by age and size. *Journal of Ecology* **77**:162–181.
- Warren, P. L., R. J. Frye, D. Gori, and A. Laurenzi. 1992. Population biology of *Pediocactus paradinei*, a rare cactus from northern Arizona. Pages 132–143 in R. Sivinski and K. Lightfoot, editors. Proceedings of the Southwestern rare and endangered plant conference. New Mexico Forestry Resources and Conservation Division, Santa Fe, New Mexico, USA.
- Wilson, M. V., E. R. Alverson, D. L. Clark, R. H. Hayes, C. A. Ingersoll, and M. B. Naughton. 1995. The Willamette Valley Natural Areas Network: promoting restoration through science and stewardship. *Restoration and Management Notes* **13**:26–28.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* **81**:628–641.