

# Stochastic Demography and Conservation of an Endangered Perennial Plant (*Lomatium bradshawii*) in a Dynamic Fire Regime

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## I. SUMMARY

*Lomatium bradshawii* is an endangered herbaceous perennial plant found in grassland and prairie remnants in western Oregon and southwestern Washington. Fire was historically an important and highly dynamic component of the environment of *L. bradshawii*. Evaluating the demographic consequences of a dynamic environment requires a model for the environment and a coupling between that model and the vital rates of the population. In this review, we analyze in detail the effects of fire schedules on demography of *L. bradshawii*. It has been suggested that *L.*

*bradshawii* is adapted to frequent fire and that its populations would benefit from managed fires; our results support these suggestions.

We constructed size-structured population projection matrices for conditions corresponding to the year of a fire and to 1, 2 and 3 or more years post-fire, at each of two sites (Fisher Butte and Rose Prairie) in western Oregon. We used these matrices in two ways. First, we treated the population growth rate  $\lambda$  calculated from each matrix as a summary of the conditions in that environment. We found a significant decline in  $\lambda$  with time since the last fire. Second, we developed models for *L. bradshawii* in periodic and stochastic fire environments. The periodic models provide values of annual growth rate for any specified periodic burning schedule. The stochastic models describe the occurrence of fire as a two-state Markov chain specified in terms of the long-term frequency and autocorrelation of fires. The sequence of fires generates in turn a sequence of environments in terms of time since fire. From this model we calculated the stochastic growth rate  $\log \lambda_s$ ; it increases with increasing fire frequency and with negative autocorrelation.

The critical fire frequency, below which *L. bradshawii* cannot persist, is about 0.8 to 0.9 at Fisher Butte and about 0.4 to 0.5 at Rose Prairie. Extinction probability drops precipitously from 1 to near 0 as fire frequency increases through the critical value. We carried out a detailed perturbation analysis, calculating the sensitivity and elasticity of the stochastic growth rate to changes in the entries of the matrices. The sensitivity and elasticity of the stochastic growth rate are very highly correlated with the corresponding results from a deterministic model based on the mean projection matrix. Patterns of stochastic sensitivity and elasticity are also very insensitive to changes in the fire frequency. Taken together, these results show that estimates of sensitivity and elasticity are robust, and not excessively sensitive to the details of the stochastic environment. Overall, our results show that *L. bradshawii* depends on frequent fire to persist in these habitats, and that controlled burning is an attractive management tool.

## II. INTRODUCTION

Disturbance by fire affects individuals, populations, communities and ecosystems. In a given system, burning may increase the abundance of some species while reducing that of others through its effects on competitive interactions and vital rates (Noble and Slatyer, 1980). The frequency, autocorrelation, and intensity of fires are important factors that shape the population dynamics of species in many habitats (Bond and van Wilgen, 1996). Conservationists often use fire to develop and maintain

communities and populations of endangered species, especially plants (reviewed in Hessler and Spackman, 1995), but long-term studies investigating the effects of fire frequency (Glitzenstein *et al.*, 1995; Quintana-Ascencio, 1997) and time since fire (Hawkes and Menges, 1996; Menges and Kimmich, 1996) relative to such goals are comparatively rare. In this review we analyze demographic data from a series of experimental fire manipulations, to study the effects of burning, the post-fire recovery process, and the long-term frequency of fire on the population dynamics of an endangered plant.

Our analyses examine in detail the interaction between this plant and one important aspect of its environment, but the approach can also be applied to other species and other environmental factors. The essential components of our approach are (1) a stochastic model for the environment and (2) demographic data, in the form of stage-classified population projection matrices estimated in each state of the environment. Our basic tools are eigenvalue perturbation theory, life table response experiment (LTRE) analyses, and the theory of population dynamics in periodic and stochastic environments; all these methods are presented in detail in Caswell (2001).

*Lomatium bradshawii* is an endangered herbaceous perennial plant in the family Apiaceae. It exists in only 16 isolated populations, of 50–25 000 individuals, in western Oregon and southwestern Washington (Pendergrass *et al.*, 1999). It occupies grasslands and prairies that now occur only as small remnants of formerly widespread habitats (Parenti *et al.*, 1993). These habitats were, until recent times, subject to both natural and anthropogenic fires. Like other plants of frequently burned areas, *L. bradshawii* seems to have adapted to fire. Fire is an important management tool for reducing woody plants in northwestern prairies (Pendergrass *et al.*, 1998), and burning has been proposed as a management tool for *L. bradshawii* (Kaye, 1992; Parenti *et al.*, 1993). Recent research has demonstrated that fall-season burning may increase plant size and seedling recruitment, but the effect fades within a few years (Pendergrass *et al.*, 1999). In addition, populations in burned areas have higher growth rates and lower probabilities of extinction than unburned populations (Kaye *et al.*, 2001). These studies suggest that burning can be used for managing *L. bradshawii* and its habitat, but they stop short of identifying the effects of fire frequency and determining optimum fire schedules. Because insufficiently frequent fire will not maintain viable populations, and excessively frequent fire would be costly and could have detrimental side effects, it is critical to understand *L. bradshawii* demography in a dynamic fire regime.

Fire affects many environmental factors, and those factors in turn have many effects on individuals. What counts from the perspective of

conservation and management is the repercussions of those effects at the population level. In this review, we use demographic models to link the effects of fire on the survival, growth and reproduction of individuals to the resulting consequences for population growth, persistence and extinction. We do this by coupling the demography of *L. bradshawii* to a stochastic model of fire occurrence. These methods were introduced by Silva *et al.* (1991) and Canales *et al.* (1994); and subsequently used by Beissinger (1995) and Hoffmann (1999).

We describe the demography of *L. bradshawii* with a stage-classified matrix population model

$$\mathbf{n}(t + 1) = \mathbf{A}_t \mathbf{n}(t) \quad (1)$$

where  $\mathbf{n}(t)$  is a vector of stage abundances at time  $t$  and  $\mathbf{A}_t$  is a possibly time-varying population projection matrix. The variation in  $\mathbf{A}_t$  depends on the dynamics of fire. We use this model to answer three questions:

- (1) How does the time since the last fire affect population growth of *L. bradshawii*? If population growth rate depends on the time since fire, which of the vital rates are responsible for the effect?
- (2) How do population growth and extinction probability of *L. bradshawii* respond to the frequency and autocorrelation pattern of fires in a stochastic environment?
- (3) How does *L. bradshawii* respond to periodic fire regimes of the sort that might be imposed as a management tactic?

These analyses use demographic models in two ways. In the first set of analyses, we treat the projection matrix  $\mathbf{A}$  estimated in a particular environment as a probe of the conditions in that environment. We summarize the effects of the environment on the vital rates of the plant by projecting the population forward *as if* the environmental conditions remained constant, even though they cannot do so. The second set of analyses explores the consequences of a dynamic fire environment, either periodic or stochastic. Rather than projecting the consequences of a hypothetical constant environment, these analyses focus directly on environmental variability and its effects.

### III. DEMOGRAPHIC DATA

#### A. Study Sites

The data on which the models are based were obtained from a study carried out from 1988 through 1993 on lands near the city of Eugene in

Oregon's Willamette Valley. Controlled burning experiments were conducted at two sites in the Fern Ridge Research Natural Area managed by the Army Corps of Engineers. The sites are identified here as Fisher Butte (44°3' N, 123°15' W) and Rose Prairie (44°5' N, 123°15' W). Additional details on site locations, vegetation, plot establishment and data collection are available in Pendergrass *et al.* (1999) and Kaye *et al.* (2001).

## B. Fire Treatments and Time Since Fire

Plots were established in both sites, and were subjected to September or October burning treatment from 1988 through 1992. Three treatments, designed to explore different patterns of burning, were imposed. Let B and U denote years in which the population was burned and unburned, respectively. The treatments,  $T_0$ ,  $T_1$  and  $T_2$ , were

Treatment	Year					
	88	89	90	91	92	
$T_0$	U	U	U	U	U	(2)
$T_1$	B	U	U	B	U	
$T_2$	B	B	U	B	U	

Burn characteristics at each site, including flame length, height, depth and heat per unit area were recorded in 1988–89 and are reported elsewhere (Pendergrass *et al.*, 1998).

In this study, our goal is to characterize *L. bradshawii* population dynamics in terms of fire and post-fire recovery. Thus we are interested not in projection matrices based on the treatments  $T_0$ – $T_2$  (cf. Kaye *et al.*, 2001), but in matrices specific to four *environmental states* ( $E_1$ – $E_4$ ) defined as follows:

State	Definition	Treatment–year combinations
$E_1$	year of a fire	$T_1$ -88, $T_1$ -91, $T_2$ -88, $T_2$ -89, $T_2$ -91
$E_2$	1 year post-fire	$T_1$ -89, $T_1$ -92, $T_2$ -90, $T_2$ -92
$E_3$	2 years post-fire	$T_1$ -90
$E_4$	≥3 years post-fire	$T_0$ -88, $T_0$ -89, $T_0$ -90, $T_0$ -91, $T_0$ -92

Each environmental state except  $E_3$  was represented by multiple treatment–year combinations. Environment  $E_3$  was produced by only one treatment ( $T_1$ ) in one year (1990).

#### IV. POPULATION PROJECTION MATRICES

Circular plots of 2 m radius were established surrounding randomly selected mature *L. bradshawii* individuals. Ten plots per treatment were established in the Fisher Butte site. At the Rose Prairie site, there were six plots in treatments  $T_0$  and  $T_1$  and five plots in  $T_2$ . All plants within each plot were monitored annually from 1988 through 1993.

Individuals were classified into six stages based on size and reproductive status:

- $Y$  yearlings (first year vegetative plants with 1–2 leaves)
- $V_1$  vegetative plants with 1–2 leaves
- $V_2$  vegetative plants with 3 or more leaves
- $R_1$  reproductive plants with 1 umbel
- $R_2$  reproductive plants with 2 umbels
- $R_3$  reproductive plants with 3 or more umbels

The fates of individuals were recorded in each of the plots in each year. Transition matrices were constructed for each treatment in each year (1988–89, 1989–90, 1990–91, 1991–92, 1992–93) (Kaye *et al.*, 2001; see the Appendix for the complete set of matrices). The maximum likelihood estimate of the probability of transition from stage  $j$  to stage  $i$  is given by the proportion of individuals in stage  $j$  in year  $t$  that appeared in stage  $i$  in year  $t + 1$ . Stage-specific fertility was estimated as the total number of seedlings in year  $t + 1$  multiplied by the proportion of seeds produced by each stage in year  $t$  (the ‘anonymous reproduction’ method of Caswell 1989a, 2001, p. 173). The population projection matrix  $\mathbf{A}$  is produced by inserting the fertility estimates in the first row of the transition matrix.

##### A. Detailed and Averaged Matrices

Except for  $E_3$ , each environmental state is represented by more than one matrix. These matrices provide valuable information on the variability in the vital rates due to spatial and temporal variability within each environmental state. We refer to this set of 15 matrices as the *detailed matrices*.

In order to focus on the effects of time since fire, we also constructed a set of *averaged matrices*,  $\mathbf{A}^{(1)}\text{--}\mathbf{A}^{(4)}$ , one for each environmental state. Each averaged matrix was a weighted mean of the matrices for all of the treatment–year combinations corresponding to that environmental state. The weight for all elements within a column was the sample size from which that column was estimated. This construction is equivalent to pooling the transition data on all individuals in the appropriate

environmental state and calculating the maximum likelihood estimates of the matrix from the pooled data.

Sample sizes for transitions involving large reproductive plants ( $R_3$ ) were small, because these plants were rare. In some treatment-year combinations, no  $R_3$  individuals were observed at all, making it impossible to estimate these transitions. To resolve this problem, we replaced column 6 of each of the detailed matrices with column 6 of the averaged matrix for that environmental state.

The averaged matrices are shown in Tables 1 and 2. We list all the detailed matrices in the Appendix.

## V. ENVIRONMENT-SPECIFIC DEMOGRAPHY

We begin with an analysis of the population dynamic properties of the projection matrices that characterize each of the environmental states  $E_1$ – $E_4$ . We have computed population growth rates, examined the dependence of these rates on the time since the last fire, and used LTRE analysis to identify the vital rates responsible for the observed differences in population growth.

### A. Population Growth Rate

The asymptotic growth rate determined by a population projection matrix  $\mathbf{A}$  is the dominant eigenvalue  $\lambda$  of  $\mathbf{A}$ . This is the rate at which the population would grow if the conditions that produced  $\mathbf{A}$  were to remain constant.

Estimated population growth rates  $\hat{\lambda}$  for *L. bradshawii* are shown in Table 3. In the averaged matrices, which we expect to provide the best estimates of the population growth rate as a function of fire history, two trends are apparent. First,  $\hat{\lambda}$  is highest in the year of a fire, and tends to decrease with time after a fire. Second, the Rose Prairie site consistently supports more rapid population growth of *L. bradshawii* than does the Fisher Butte site.

The growth rates calculated from the detailed matrices exhibit considerable variation. In particular, the matrices calculated for the 1990–91 transition (marked with an asterisk in Table 3) exhibit consistently low values of  $\hat{\lambda}$ . This suggests that 1990 was an unusually poor year for *L. bradshawii*, in both sites and regardless of the time since fire. That presumably explains why the values of  $\hat{\lambda}$  for the averaged matrices do not decline monotonically with time since fire. Instead,  $\hat{\lambda}$  for  $E_3$  (2 years post-fire) is the lowest; this average was based on a single matrix, for treatment  $T_1$  in 1990.

**Table 1**

The averaged projection matrices for each of the environmental treatments for the Fisher Butte site

$$A^{(1)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.059 & 0.794 & 2.724 \\ 0.290 & 0.252 & 0.090 & 0.048 & 0.0 & 0.0 \\ 0.165 & 0.344 & 0.510 & 0.231 & 0.073 & 0.039 \\ 0.0 & 0.060 & 0.151 & 0.312 & 0.193 & 0.0 \\ 0.0 & 0.020 & 0.095 & 0.160 & 0.411 & 0.095 \\ 0.010 & 0.0 & 0.016 & 0.039 & 0.085 & 0.816 \end{pmatrix}$$

$$A^{(2)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.090 & 0.570 & 1.886 \\ 0.317 & 0.221 & 0.099 & 0.026 & 0.0 & 0.0 \\ 0.199 & 0.282 & 0.349 & 0.051 & 0.050 & 0.0 \\ 0.018 & 0.107 & 0.220 & 0.241 & 0.206 & 0.143 \\ 0.0 & 0.056 & 0.102 & 0.484 & 0.417 & 0.200 \\ 0.0 & 0.0 & 0.007 & 0.057 & 0.130 & 0.516 \end{pmatrix}$$

$$A^{(3)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.0 & 0.200 & 1.000 \\ 0.390 & 0.390 & 0.180 & 0.040 & 0.090 & 0.0 \\ 0.060 & 0.110 & 0.220 & 0.380 & 0.120 & 0.0 \\ 0.0 & 0.0 & 0.080 & 0.380 & 0.380 & 0.0 \\ 0.0 & 0.0 & 0.080 & 0.080 & 0.250 & 0.330 \\ 0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.330 \end{pmatrix}$$

$$A^{(4)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.291 & 1.659 & 3.080 \\ 0.222 & 0.240 & 0.056 & 0.037 & 0.043 & 0.0 \\ 0.079 & 0.207 & 0.481 & 0.213 & 0.154 & 0.235 \\ 0.013 & 0.044 & 0.167 & 0.367 & 0.301 & 0.052 \\ 0.0 & 0.017 & 0.055 & 0.172 & 0.277 & 0.177 \\ 0.0 & 0.0 & 0.002 & 0.018 & 0.058 & 0.501 \end{pmatrix}$$

**Table 2**  
The averaged matrices for each of the environmental treatments for the Rose  
Prairie site

$$A^{(1)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.919 & 4.586 & 5.940 \\ 0.379 & 0.443 & 0.080 & 0.039 & 0.023 & 0.0 \\ 0.024 & 0.202 & 0.360 & 0.186 & 0.217 & 0.415 \\ 0.017 & 0.043 & 0.242 & 0.327 & 0.114 & 0.0 \\ 0.0 & 0.009 & 0.150 & 0.350 & 0.597 & 0.479 \\ 0.0 & 0.012 & 0.0 & 0.016 & 0.037 & 0.167 \end{pmatrix}$$

$$A^{(2)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 1.062 & 4.633 & 14.90 \\ 0.185 & 0.318 & 0.031 & 0.023 & 0.021 & 0.0 \\ 0.072 & 0.173 & 0.255 & 0.134 & 0.098 & 0.0 \\ 0.017 & 0.035 & 0.260 & 0.366 & 0.339 & 0.250 \\ 0.0 & 0.035 & 0.232 & 0.378 & 0.421 & 0.250 \\ 0.0 & 0.008 & 0.0 & 0.0 & 0.029 & 0.375 \end{pmatrix}$$

$$A^{(3)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.200 & 1.400 & 2.100 \\ 0.290 & 0.300 & 0.190 & 0.190 & 0.030 & 0.500 \\ 0.010 & 0.0 & 0.190 & 0.250 & 0.170 & 0.0 \\ 0.010 & 0.0 & 0.120 & 0.250 & 0.270 & 0.0 \\ 0.0 & 0.0 & 0.0 & 0.060 & 0.300 & 0.500 \\ 0.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 \end{pmatrix}$$

$$A^{(4)} \begin{pmatrix} 0.0 & 0.0 & 0.0 & 0.367 & 2.614 & 2.100 \\ 0.079 & 0.331 & 0.104 & 0.0 & 0.0 & 0.0 \\ 0.065 & 0.114 & 0.418 & 0.233 & 0.055 & 0.0 \\ 0.020 & 0.0 & 0.270 & 0.418 & 0.601 & 0.0 \\ 0.0 & 0.0 & 0.034 & 0.187 & 0.289 & 0.500 \\ 0.0 & 0.0 & 0.0 & 0.0 & 0.053 & 0.500 \end{pmatrix}$$

**Table 3**

The population growth rate  $\lambda$  calculated from the averaged and the detailed matrices for *L. bradshawii*, and the corresponding 95% bootstrap confidence intervals. Asterisks (\*) denote growth rates calculated from matrices for the years 1990–91

## (a) Averaged matrices

Years post-fire	Fisher Butte			Rose Prairie		
	$\hat{\lambda}$	$SE(\hat{\lambda})$	CI	$\lambda$	$SE(\hat{\lambda})$	CI
0	1.020	0.0092	[1.0009, 1.0369]	1.155	0.0093	[1.1363, 1.1727]
1	0.984	0.0093	[0.9654, 1.0022]	1.118	0.0077	[1.1024, 1.1325]
2	0.662	0.0022	[0.6574, 0.6659]	0.483	0.0016	[0.4800, 0.4864]
$\geq 3$	0.869	0.0049	[0.8593, 0.8786]	0.906	0.0054	[0.8956, 0.9169]

## (b) Detailed matrices

Fisher Butte, years post-fire				Rose Prairie, years post-fire			
0	1	2	$\geq 3$	0	1	2	$\geq 3$
0.864	1.233	0.662*	0.839	1.007	1.428	0.483*	0.912
0.923	1.044		1.288	1.211	1.285		1.079
1.119	0.564*		0.690*	1.348	0.523*		0.664*
1.196	1.049		0.827	1.444	1.221		0.824
1.074			1.045	1.204			1.245

We used the bootstrap (Efron and Tibshirani, 1993) to associate confidence intervals (CIs) with the estimated growth rate  $\hat{\lambda}$  for each of the four averaged matrices. Because we did not have convenient access to the original data, we used a parametric bootstrap, as follows. The matrix  $\mathbf{A}$  contains fertilities (the first row) and transition probabilities (the rest of the matrix); thus the estimated projection matrix can be written

$$\hat{\mathbf{A}} = \hat{\mathbf{T}} + \hat{\mathbf{F}} \quad (3)$$

where  $\mathbf{F}$  contains fertilities in the first row and zeros elsewhere, and  $\mathbf{T}$  contains only transition probabilities. We generate a bootstrap sample  $\hat{\mathbf{A}}^*$  as

$$\hat{\mathbf{A}}^* = \hat{\mathbf{T}}^* + \hat{\mathbf{F}}^* \quad (4)$$

Column  $j$  of the transition matrix  $\mathbf{T}$  was estimated by noting the fates (including death), of the  $N_j$  individuals present at the beginning of the

interval. Each column was estimated independently. A bootstrap estimate of column  $j$  of  $\mathbf{T}$  is obtained by drawing a sample of size  $N_j$  from a multinomial distribution defined by the probabilities

$$\begin{pmatrix} \hat{t}_{1j} \\ \hat{t}_{2j} \\ \vdots \\ \hat{t}_{6j} \\ 1 - \sum_i \hat{t}_{ij} \end{pmatrix} \quad (5)$$

The observed fertilities in  $\hat{\mathbf{F}}$  are the mean number of offspring produced per individual in each stage. In the absence of information to the contrary, we assumed that seed production was randomly and independently distributed among individuals, which implies that offspring production follows a Poisson distribution with mean equal to the observed mean. Thus we generated a bootstrap fertility estimate for stage  $j$  as the mean of  $N_j$  Poisson random variates with mean  $\hat{f}_{1j}$ .

The bootstrap procedure was applied to each of the detailed matrices, which were then combined in the same way that we combined the real estimates. The result was a set of bootstrap estimates of the averaged matrices,  $\hat{\mathbf{A}}^*(i)$ ,  $i = 1, \dots, 3000$ , which yielded a set of 3000 bootstrap estimates  $\hat{\lambda}^*(i)$  of the population growth rate. We calculated 95% confidence intervals for  $\hat{\lambda}$  as the 2.5th and 97.5th percentiles of this bootstrap distribution.

The bootstrap results in Table 3 show that  $\lambda$  is estimated with excellent precision by these data. The standard error in  $\hat{\lambda}$  is less than 1% growth per year, typical of good demographic data (Caswell, 2001). The confidence intervals for  $\hat{\lambda}$  from  $\mathbf{A}^{(3)}$  and  $\mathbf{A}^{(4)}$  do not include 1.0, so we conclude that *L. bradshawii* would be unable to persist at either site under the environmental conditions produced 2 or more years post-fire.

To evaluate the statistical significance of the decline in  $\lambda$  during the process of recovery from fire, we used a bootstrap test. We computed regressions of  $\lambda$  and  $\log \lambda$  against time since last fire. The slope of these lines measures the rate of improvement (if positive) or deterioration (if negative) of environmental conditions for *L. bradshawii* following a fire. We computed these slopes for each of 3000 bootstrap samples. The 2.5th and 97.5th percentiles of the bootstrap distribution give a 95% confidence interval on this slope. If this confidence interval does not include zero, we can reject the null hypothesis of no trend at the  $\alpha = 0.05$  level.

Because  $\lambda$  was particularly low for the single matrix in environmental state  $E_3$ , we repeated the regression calculation using only states  $E_1$ ,  $E_2$  and  $E_4$ .

The slopes of the regressions of  $\lambda$  and  $\log \lambda$  against time since fire are given, together with their 95% confidence intervals, in Table 4. In all cases, the estimated slopes are negative and none of the 95% confidence intervals include 0. In fact, none of the 3000 bootstrap estimates of the slope exceeded 0, implying that the null hypothesis could be rejected at the  $\alpha = 0.0003$  level.

Populations in the Rose Prairie site are more sensitive to the fire recovery process than those at Fisher Butte, because  $\lambda$  and  $\log \lambda$  decrease more there with each year since the last fire.

## B. LTRE Analysis

The differences in  $\lambda$  among environmental states are the integrated result of the effects of recovery from fire on all the vital rates. These effects are diverse (some vital rates respond much more than others), which is why  $\lambda$  is so useful as a statistic in such life table response experiments (LTREs; Caswell 1989a,b, 1996a,b, 2000, 2001). In a LTRE analysis, the environmental states are viewed as ‘treatments’, and the goal is to determine how much each of the vital rates contributes to the observed effect of each treatment on  $\lambda$ . If  $\lambda$  is especially *insensitive* to variation in a particular vital rate, then even large treatment effects on that vital rate will contribute little to effects on  $\lambda$ . Conversely, even small effects on a vital rate to which  $\lambda$  is very sensitive can make a large contribution to effects on  $\lambda$ .

Because the entries in the matrix  $\mathbf{A}$  include both survival and growth, we chose to decompose treatment effects into contributions from lower-level parameters (Caswell, 1996b). To do this, we use the decomposition  $\mathbf{A} = \mathbf{T} + \mathbf{F}$ . We write the transition probabilities as

$$t_{ij} = \sigma_j \gamma_{ij} \quad (6)$$

**Table 4**  
The slopes of linear and logarithmic regressions of  $\lambda$  (from the averaged matrices) on years since fire, and the 95% parametric bootstrap confidence intervals on those slopes

Regression	Fisher Butte		Rose Prairie	
	Slope	CI	Slope	CI
Linear	-0.0775	[-0.0837, -0.0704]	-0.1382	[-0.1445, -0.1318]
Logarithmic	-0.0877	[-0.0941, -0.0804]	-0.1568	[-0.1626, -0.1507]

where  $\sigma_j$  is the survival probability for stage  $j$  and  $\gamma_{ij}$  is the probability of growth from stage  $j$  to stage  $i$ , given survival. The sensitivities of  $\lambda$  to changes in  $\sigma_j$  and  $\gamma_{ij}$  are

$$\frac{\partial \lambda}{\partial \sigma_j} = \sum_i \gamma_{ij} \frac{\partial \lambda}{\partial t_{ij}} \quad (7)$$

$$\frac{\partial \lambda}{\partial \gamma_{ij}} = \sigma_j \frac{\partial \lambda}{\partial t_{ij}} \quad (8)$$

Since  $\mathbf{F}$  contains non-zero entries only in its first row, the sensitivities of  $\lambda$  to the  $t_{ij}$  are just

$$\frac{\partial \lambda}{\partial t_{ij}} = \begin{cases} \frac{\partial \lambda}{\partial a_{ij}} & i=2, \dots, 6 \\ 0 & i=1 \end{cases} \quad (9)$$

In turn, the sensitivity of  $\lambda$  to changes in  $a_{ij}$  is given by

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (10)$$

where  $\mathbf{w}$  and  $\mathbf{v}$  are the right and left eigenvectors corresponding to  $\lambda$  and  $\langle \rangle$  denotes the scalar product (Caswell 1978, 2001).

We use the matrix  $\mathbf{A}^{(1)}$  in the year of a fire as the reference matrix, and measure effects relative to it. To first order, the growth rate in the other treatments,  $\lambda^{(m)}$ ,  $m = 2, 3, 4$ , can be written

$$\begin{aligned} \lambda^{(m)} &\approx \lambda^{(1)} + \sum_{ij} (\gamma_{ij}^{(m)} - \gamma_{ij}^{(1)}) \frac{\partial \lambda}{\partial \gamma_{ij}} \\ &+ \sum_j (f_{1j}^{(m)} - f_{1j}^{(1)}) \frac{\partial \lambda}{\partial f_{1j}} \\ &+ \sum_j (\sigma_j^{(m)} - \sigma_j^{(1)}) \frac{\partial \lambda}{\partial \sigma_j} \end{aligned} \quad (11)$$

The terms in these summations give the contributions of effects on stage-specific growth, survival and fertility to the effect on  $\lambda$ .

The contributions can be added to obtain the contribution of *groups* of vital rates. We combined them into five groups:

- (1) **survival:** the contribution of survival effects is the sum of the contributions of survival of all stages:

$$\sum_j (\sigma_j^{(m)} - \sigma_j^{(1)}) \frac{\partial \lambda}{\partial \sigma_j} \quad (12)$$

- (2) **fertility:** the net contribution of fertility effects is sum of the contributions of all entries in the first row of  $\mathbf{A}$ :

$$\sum_j (f_{1j}^{(m)} - f_{1j}^{(1)}) \frac{\partial \lambda}{\partial f_{1j}} \quad (13)$$

- (3) **shrinkage:** the contribution of effects on shrinkage probabilities is obtained by adding the contributions of all the  $\gamma_{ij}$  with  $i < j$ ; i.e. of the transitions from larger to smaller size classes:

$$\sum_{\substack{i,j \\ i < j}} (\gamma_{ij}^{(m)} - \gamma_{ij}^{(1)}) \frac{\partial \lambda}{\partial \gamma_{ij}} \quad (14)$$

- (4) **stasis:** the contribution of effects on the probability of stasis is the sum of the contributions of the  $\gamma_{ij}$ :

$$\sum_i (\gamma_{ii}^{(m)} - \gamma_{ii}^{(1)}) \frac{\partial \lambda}{\partial \gamma_{ii}} \quad (15)$$

- (5) **growth:** the contribution of effects on growth is given by sum of the contributions of the  $\gamma_{ij}$  with  $i > j$ ; i.e. of transitions from smaller to larger size classes:

$$\sum_{\substack{i,j \\ i > j}} (\gamma_{ij}^{(m)} - \gamma_{ij}^{(1)}) \frac{\partial \lambda}{\partial \gamma_{ij}} \quad (16)$$

Unlike the components into which elasticities of  $\lambda$  are often divided (e.g. Franco and Silvertown, 1996), these contributions actually separate survival, reproduction and the different directions of individual growth (increase, stasis, shrinkage).

Table 5 shows the results of the LTRE analysis. Time since fire affects  $\lambda$  mainly through effects on survival and growth; effects on fertility make a much smaller contribution. The contributions of shrinkage are positive, indicating that shrinkage rates increased following a fire. The contributions of stasis and growth are mostly negative, indicating that those probabilities declined following fire. The largest negative contributions are those for growth and for survival in states  $E_3$  and  $E_4$  (i.e. 2 and 3 or more years post-fire). Thus, in both sites, we conclude that the process of fire recovery affects  $\lambda$  mainly through reductions in survival and in the probability of growing to larger size classes.

## VI. DEMOGRAPHY IN A DYNAMIC FIRE ENVIRONMENT

So far, our analyses have used  $\lambda$  calculated from the matrices  $\mathbf{A}^{(1)} - \mathbf{A}^{(4)}$  as an index of environmental conditions in the years following a fire. These growth rates are hypothetical projections, since the environment cannot remain in one of these states (except if a plot was burned every year, or never burned, in which case it would remain in state  $E_1$  or  $E_4$  forever). But since they show that conditions for *L. bradshawii* deteriorate with increasing time since the last fire, it makes sense to suspect that population growth

**Table 5**

The summed contributions of environmental effects on stage-specific survival, fertility, shrinkage, stasis, and growth, to the effect on  $\lambda$ . The conditions in the year of a fire are used as reference conditions, so effects are measured in terms of years since fire

(a) Fisher Butte

Years post-fire	Survival	Fertility	Shrinkage	Stasis	Growth
1	-0.0070	-0.0320	0.0034	-0.1041	0.1114
2	-0.1322	-0.0552	0.0911	-0.0948	-0.1744
$\geq 3$	-0.0682	0.0375	0.0300	-0.0837	-0.0656

(b) Rose Prairie

Years post-fire	Survival	Fertility	Shrinkage	Stasis	Growth
1	-0.1425	0.0203	0.0237	-0.0452	0.1079
2	-0.2995	-0.0891	0.0741	-0.0448	-0.2954
$\geq 3$	-0.1513	-0.0605	0.0794	-0.0292	-0.0793

of *L. bradshawii* is probably affected by the frequency and temporal pattern of fire.

To explore this suspicion, we need to construct a model in which fire is a dynamic, rather than a static, component of the environment. Such models contain three components: a model for the environment, a model that assigns a projection matrix to each state of the environment, and a sequence of population vectors  $\mathbf{n}(t)$ ,  $t = 0, 1, \dots$  generated by the sequence of matrices (Cohen, 1979b; Caswell, 2001).

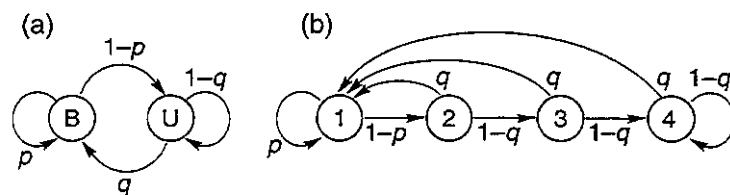
We will consider both stochastic and periodic fire environments. The stochastic model generates fire sequences according to a simple two-state Markov chain. The periodic model specifies a deterministic sequence of burned and unburned years that repeats itself indefinitely. The natural environment of *L. bradshawii* is obviously stochastic, but management strategies are likely to call for periodic fires.

## A. Models for the Environment

Our fire environment models have two parts. First, they specify a sequence of years with and without fires ('burned' and 'unburned' years). Second, they translate that sequence into a sequence of environmental states ( $E_1$ – $E_4$ ) and the corresponding sequence of matrices ( $\mathbf{A}^{(1)}$ – $\mathbf{A}^{(4)}$ ).

### 1. Stochastic Environments

In a stochastic environment, the sequence of burned and unburned years is generated by a two-state Markov chain, the transition graph of which is shown in Figure 1. A plot is burned with probability  $p$  if it was burned the year before, and  $q$  if it was not. The resulting transition matrix is



**Fig. 1.** The transition graphs for (a) the fire process and (b) the corresponding environmental states. In (a), B and U correspond to burned and unburned years. In (b), environmental states 1–4 correspond to the year of a fire, and 1–3 years after a fire, respectively. The probability of a fire in any year is  $p$  if the previous year was burned and  $q$  if not.

$$\mathbf{P} = \begin{pmatrix} p & q \\ 1-p & 1-q \end{pmatrix} \quad (17)$$

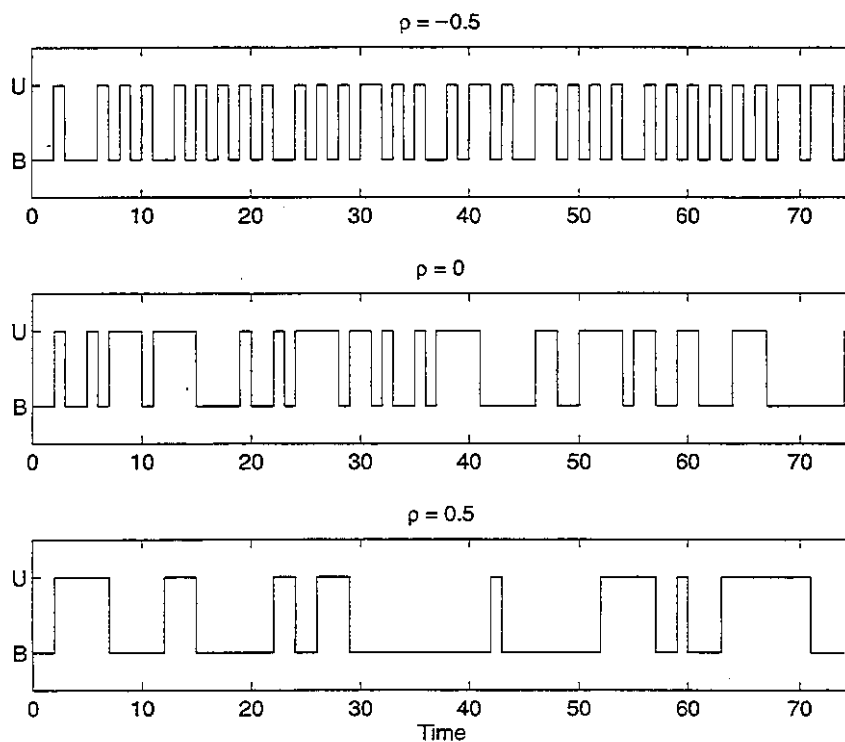
In terms of these probabilities, the long-term frequency of fire is

$$f = \frac{q}{1-p+q} \quad (18)$$

and the autocorrelation is

$$\rho = p - q \quad (19)$$

When  $\rho = 0$ , the occurrence of a fire is independent of whether a fire occurred the previous year; fires are then said to be independently and identically distributed (iid). When  $\rho < 0$  there is a tendency for burned and unburned years to alternate; when  $\rho > 0$  there are frequent long sequences of burned and of unburned years. Figure 2 shows typical stochastic realizations for  $\rho = -0.5$ ,  $\rho = 0$  and  $\rho = 0.5$ .



**Fig. 2.** Typical sequence of burned (B) and unburned (U) years generated by the two-state Markov chain model for autocorrelation values of  $\rho = -0.5$  (top),  $\rho = 0$  (middle) and  $\rho = 0.5$  (bottom). In all three cases, the long-term fire frequency is 0.5.

The entries in the transition matrix  $\mathbf{P}$  can be calculated from the fire frequency and the autocorrelation (Silva *et al.*, 1991; Tuljapurkar, 1997)

$$p = f(1 - \rho) + \rho \quad (20)$$

$$q = f(1 - \rho) \quad (21)$$

If the autocorrelation is negative, not all values of  $f$  are possible; the relations in equation (21) require that  $f$  satisfies

$$\frac{-\rho}{1 - \rho} \leq f \leq \frac{1}{1 - \rho} \quad (22)$$

so in our calculations for  $\rho = -0.5$  the fire frequency will be restricted to  $f \in [\frac{1}{3}, \frac{2}{3}]$ .

This is an admittedly simple fire model, but it captures some of the important aspects of more detailed models. Johnson and Gutsell (1994), for example, discuss the Weibull distribution as a model for inter-fire intervals; it has a hazard function (i.e. the probability of fire in a given year, dependent on the time since the last fire) that can increase or decrease with time, or, as a special case, remain constant. Our iid model has a constant fire hazard. The autocorrelated model has a hazard that increases ( $\rho < 0$ ) or decreases ( $\rho > 0$ ) in a crude fashion. It is impossible to do better than this with a model with only two states, but, crude as it may be, the comparison gives us the ability to say something about the potential effect of fire in more sophisticated models.

As fires occur, the environment moves among the states  $E_1-E_4$ . Figure 1 shows the transition probabilities among the four environmental states generated by the two-state Markov model for fire. Of course, more sophisticated models of fire could be constructed by making the probability of fire depend explicitly on the environmental state. Accumulation of fuel with the time since the last fire is one mechanism that could generate such an effect. Note that even when *fires* are iid, the *environment* is autocorrelated, because the environmental states depend on how long it has been since the last fire.

## 2. Periodic Environments

One way to specify a periodic environment is in terms of fire frequency, either in terms of the interval between burned years:

Sequence	Fire frequency
BBBBBB . . .	1.00
BUBUBU . . .	0.50
BUUBUU . . .	0.33
BUUUBU . . .	0.25
etc.	

or in terms of the interval between unburned years (needed to fill in frequencies between 0.5 and 1.0):

Sequence	Fire frequency
UBUBUB . . .	0.50
UBBUBB . . .	0.67
UBBBUB . . .	0.75
UBBBBU . . .	0.80
etc.	

The matrix applied to the population at any time is determined by the number of years since the last fire. Thus, corresponding to the fire sequence BUUUU is the sequence of environments  $E_1, E_2, E_3, E_4, E_4$ .

The fire frequency alone does not completely specify the dynamics of a periodic environment. For example, in the sequences given above a fire frequency of 0.5 is given by the sequence BUBUBUBU. . . . But the sequences

BBUUBBUUBBUU . . .  
 BBBUUUBBBUUU . . .  
 BBBBUUUUBBBB . . .

all also have a fire frequency of 0.5, and they can have dramatically different effects on population growth.

These effects can be explored by defining a fire rotation – the length of time over which the pattern repeats – and examining all possible periodic patterns with this rotation length. For example, with a rotation of 2 years, the only possible schedules are BB, UU, BU and UB (the last two, of course, being equivalent). Longer rotations have more possible schedules. Later, we will examine the population growth resulting from all  $2^{10} = 1024$  distinct fire schedules over a 10-year rotation.

## B. Stochastic Population Growth

The sequence of environments generated by the stochastic fire model generates a corresponding sequence of matrices, which projects the population from one time to the next. When using the averaged matrices, there is one matrix corresponding to each environmental state. When using the detailed matrices, at each time  $t$  a matrix is selected at random from the set of detailed matrices corresponding to that environmental state.

Population growth in a stochastic environment can be described by two indices; one measures the growth rate of average population size

$$\log \mu = \lim_{t \rightarrow \infty} \frac{1}{t} \log E(N(t)) \quad (23)$$

while the other measures the average growth rate of the population

$$\log \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} E(\log N(t)) \quad (24)$$

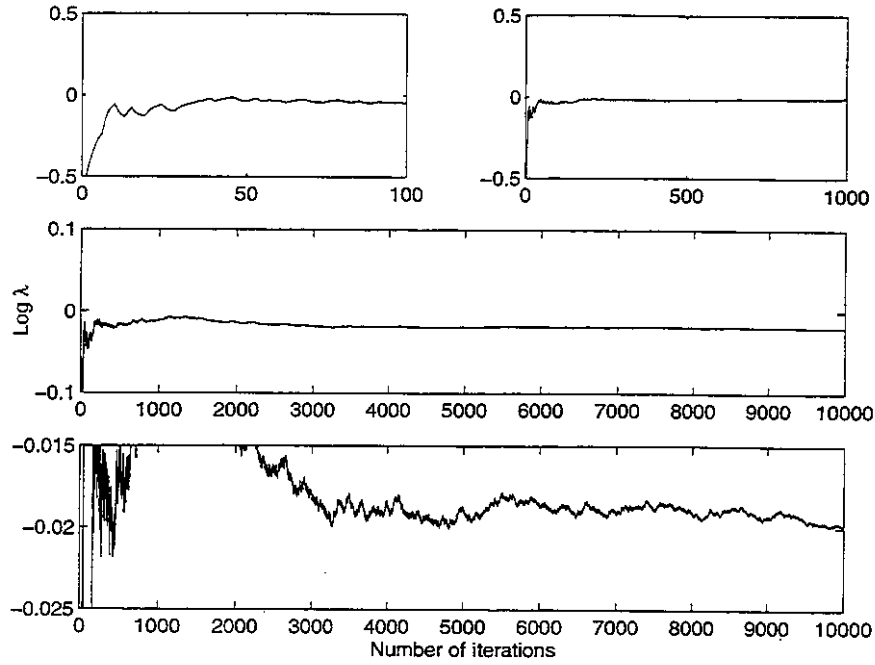
where  $N(t) = \|\mathbf{n}(t)\| = \sum_i |n_i(t)|$  is the total population size. Given some reasonable assumptions about the environment and the life history (Cohen, 1976, 1977a,b, 1979a,b; Tuljapurkar and Orzack, 1980; Tuljapurkar, 1990a, 1997), every realization of the process, with probability one, eventually grows at the rate  $\log \lambda_s$ . The quantity  $\log \lambda_s$  is called the *stochastic growth rate*. It determines the extinction (certain if  $\log \lambda_s \leq 0$ ) or persistence (with some positive probability if  $\log \lambda_s > 0$ ) of the population. It measures fitness in models of selection in stochastic environments. The theory is outlined in Caswell (2001) and detailed in Tuljapurkar (1990a).

Although it is a measure of growth rate,  $\lambda_s$  is *not* the eigenvalue of a matrix. It is estimated by simulation as

$$\widehat{\log \lambda_s} = \frac{1}{T} \sum_{t=1}^T \log \frac{N(t+1)}{N(t)} \quad (25)$$

for some large value of  $T$ . Figure 3 shows an example of the convergence of the estimate; samples of at least  $T = 5000$  seem necessary for accuracy; we used  $T = 10000$  in all our calculations.

Approximate 95% confidence intervals on the stochastic growth rate are given by



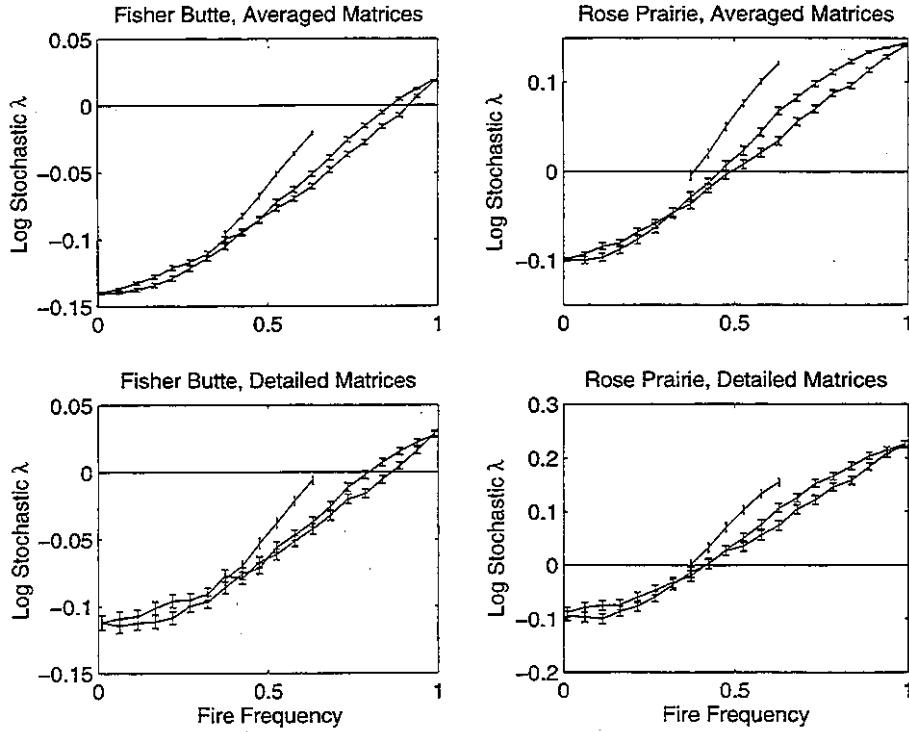
**Fig. 3.** Convergence of the estimates  $\widehat{\log \lambda_s}$  of the stochastic growth rate as a function of the length  $T$  of the simulation from which it is estimated. This example uses the averaged matrices for the Rose Prairie site with fire frequency  $f = 0.4$  and autocorrelation  $\rho = 0$ .

$$\widehat{\log \lambda_s} \pm 1.96 \sqrt{\frac{V\left(\log \frac{N(t+1)}{N(t)}\right)}{T}} \quad (26)$$

where  $V(\cdot)$  denotes the variance.

The stochastic growth rate  $\log \lambda_s$  is shown as a function of fire frequency and autocorrelation in Figure 4, for models using the averaged and the detailed matrices. It increases with fire frequency in both sites. There is little consistent difference between the results for  $\rho = 0$  and  $\rho = 0.5$ , but the stochastic growth rate is distinctly elevated at  $\rho = -0.5$ . The patterns for all three autocorrelations are similar.

The transition between certain extinction and possible persistence occurs at the fire frequency where  $\log \lambda_s = 0$ . This critical fire frequency can be estimated from Figure 4; the results are shown in Table 6. In general, the Fisher Butte site requires a fire frequency on the order of 0.8, and the Rose Prairie site a frequency on the order of 0.45, in order to support a population of *L. bradshawii*.



**Fig. 4.** The stochastic population growth rate  $\log \lambda_s$  for the two sites and both the averaged and the detailed matrices. In each graph, the upper line is  $\rho = -0.5$ , the middle line is  $\rho = 0$ , and the lower line is  $\rho = 0.5$ . Error bars in this and subsequent figures are 95% confidence intervals.

**Table 6**

The critical fire frequency required for persistence of *L. bradshawii* in a stochastic fire environment, as a function of the autocorrelation  $\rho$ , using the average and the detailed matrices

(a) Fisher Butte

$\rho$	Average	Detailed
-0.5	—	0.653
0.0	0.863	0.795
0.5	0.914	0.863

(b) Rose Prairie

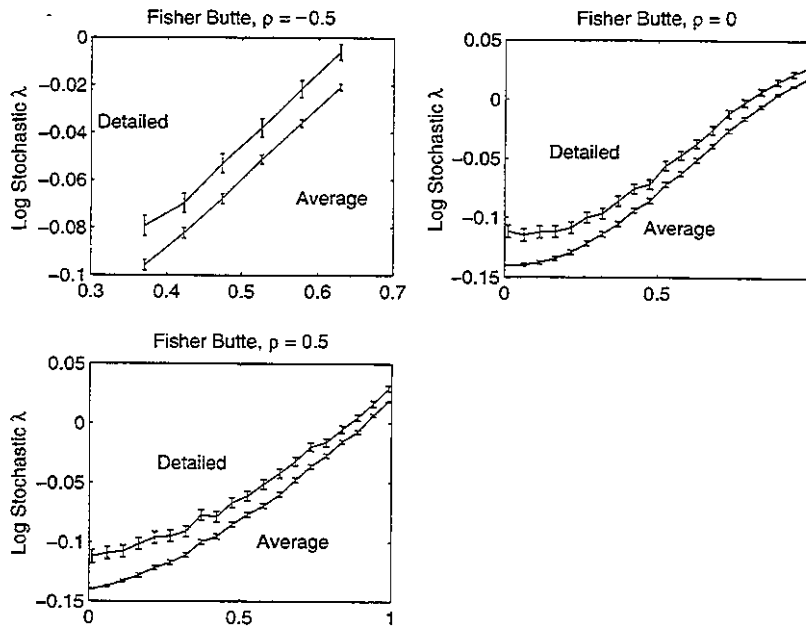
$\rho$	Average	Detailed
-0.5	0.381	0.370
0.0	0.457	0.417
0.5	0.491	0.414

Figures 5 and 6 compare the stochastic growth rates for the detailed and the average matrices. In each case, growth rates are higher for the model including the detailed matrices. This is somewhat surprising, since one might have predicted that the increased variability in the vital rates in the detailed model would reduce population growth rate.

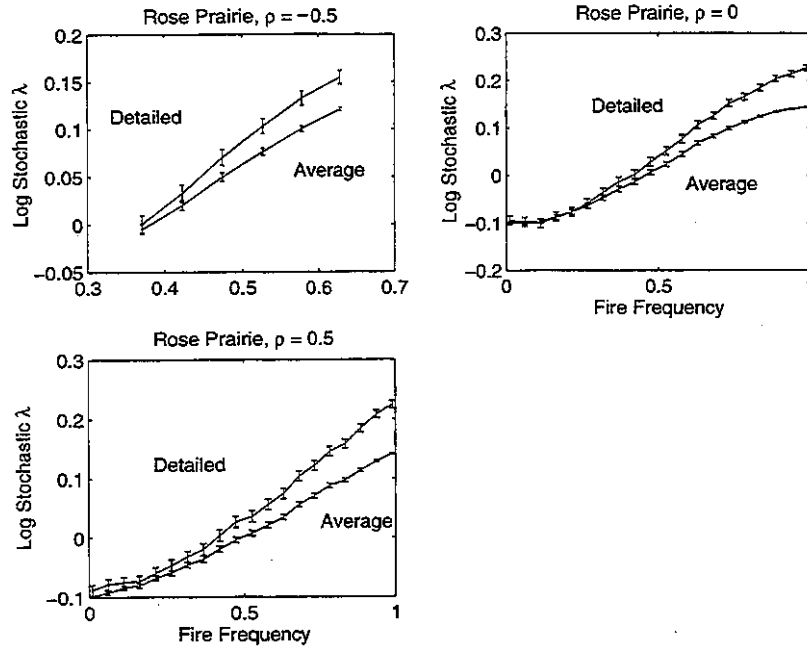
The differences between the sites can be seen more clearly in Figure 7, which shows  $\log \lambda_s$  for zero autocorrelation. As fire frequency goes to 0, the population always experiences environment  $E_4$ . In the case of the average matrices, this corresponds to the deterministic model with the matrix  $\mathbf{A}^{(4)}$ . The eigenvalues of  $\mathbf{A}^{(4)}$  in the Rose Prairie and the Fisher Butte sites are 0.91 and 0.87, respectively; the corresponding logarithms are  $-0.1$  and  $-0.14$ , corresponding to the stochastic growth rates seen at  $f = 0$  in the averaged matrix model. Similarly, when  $f = 1$ , the environment is always in state  $E_1$  and the stochastic model converges to the deterministic model with matrix  $\mathbf{A}^{(1)}$ . The logs of the eigenvalues of this matrix in Rose Prairie and Fisher Butte are 0.14 and 0.02, respectively.

### C. Quasi-extinction

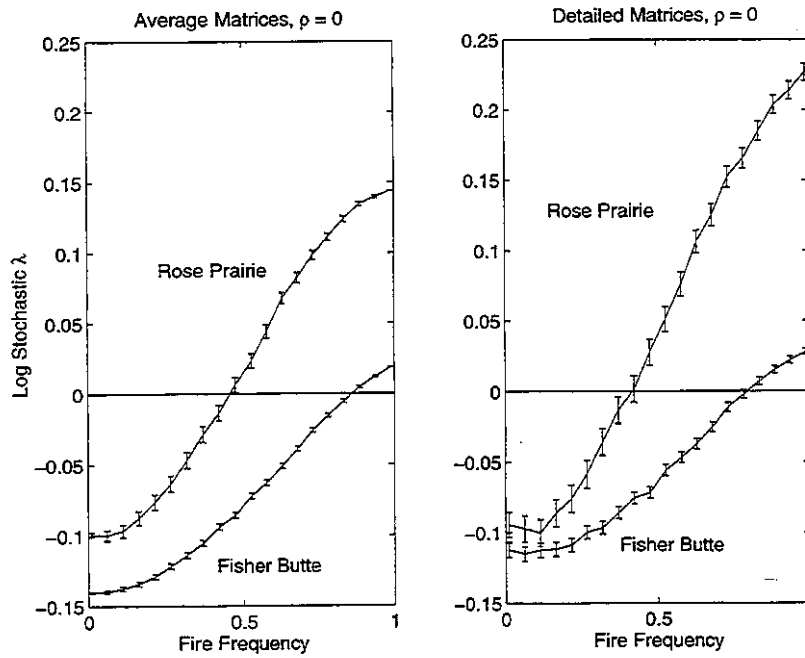
In models that include only environmental stochasticity, true extinction (reducing the population to zero) is impossible. Even if  $\lambda_s < 1$ , the



**Fig. 5.** The stochastic population growth rate  $\log \lambda_s$  for the average and the detailed matrix models, for the Fisher Butte site. Results are shown for the averaged and the detailed matrices and for all three values of the autocorrelation  $\rho$ .



**Fig. 6.** The stochastic population growth rate  $\log \lambda_s$  for the average and the detailed matrix models, for the Rose Prairie site. Results are shown for the averaged and the detailed matrices and for all three values of the autocorrelation  $\rho$ .



**Fig. 7.** Stochastic population growth rate  $\log \lambda_s$  for the two sites and the averaged (left) and the detailed (right) matrices, for  $\rho = 0$ .

population will merely decline exponentially to lower and lower densities. But these models do admit the possibility of *quasi-extinction*, defined as reduction of population size to a specified fraction of its current size (Ginzburg *et al.*, 1982; Burgman *et al.*, 1993). The fraction can be chosen to represent a level likely to result in true extinction, or a level set by management concerns.

The calculation of quasi-extinction relies on the fact (Tuljapurkar and Orzack, 1980) that  $\log N(t)$  is asymptotically normally distributed, with a mean that grows at the rate  $\log \lambda_s$  and a variance that increases at a rate  $\sigma^2$ . The variance growth rate  $\sigma^2$  can be calculated in several ways (Caswell, 2001), but the easiest relies on the fact that in the lognormal distribution the growth rate of the mean population size (i.e.  $E(N(t))$ ) rather than  $E(\log N(t))$  satisfies

$$\log \mu = \log \lambda_s + \frac{\sigma^2}{2} \quad (27)$$

Thus,  $\sigma^2$  can be estimated as

$$\widehat{\sigma^2} = 2(\widehat{\log \mu} - \widehat{\log \lambda_s}) \quad (28)$$

In turn,  $\widehat{\log \mu}$  is the log of the dominant eigenvalue of the matrix

$$\begin{pmatrix} \mathbf{A}^{(1)} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{A}^{(2)} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{A}^{(3)} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{A}^{(4)} \end{pmatrix} (\mathbf{P} \otimes \mathbf{I}) \quad (29)$$

where  $\mathbf{I}$  is an identity matrix with dimension equal to the number of stages and  $\otimes$  denotes the Kronecker product (Tuljapurkar, 1982; Caswell, 2001, Section 14.3.4).

Figure 8 shows  $\sigma^2$  as a function of fire frequency and autocorrelation. It goes to 0 when  $f = 0$  or  $f = 1$ , because the environment becomes deterministic at these limits. It is maximized at intermediate frequencies, and increases as autocorrelation becomes more positive.

Let  $N_e/N$  be the quasi-extinction threshold; e.g.  $N_e/N = 0.01$  means that quasi-extinction is defined to be reduction of the population to 1% of its current density. Then the probability of quasi-extinction is given by

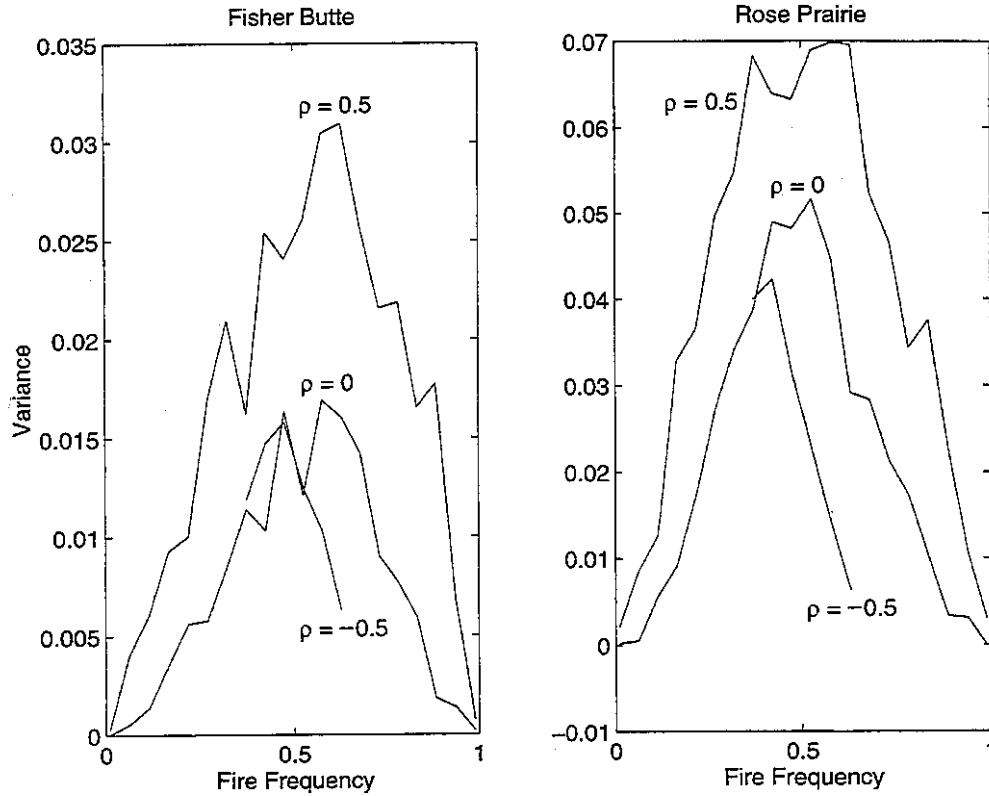


Fig. 8. The rate of growth ( $\sigma^2$ ) of the variance of  $\log N(t)$  as a function of fire frequency and autocorrelation, calculated using the averaged matrices.

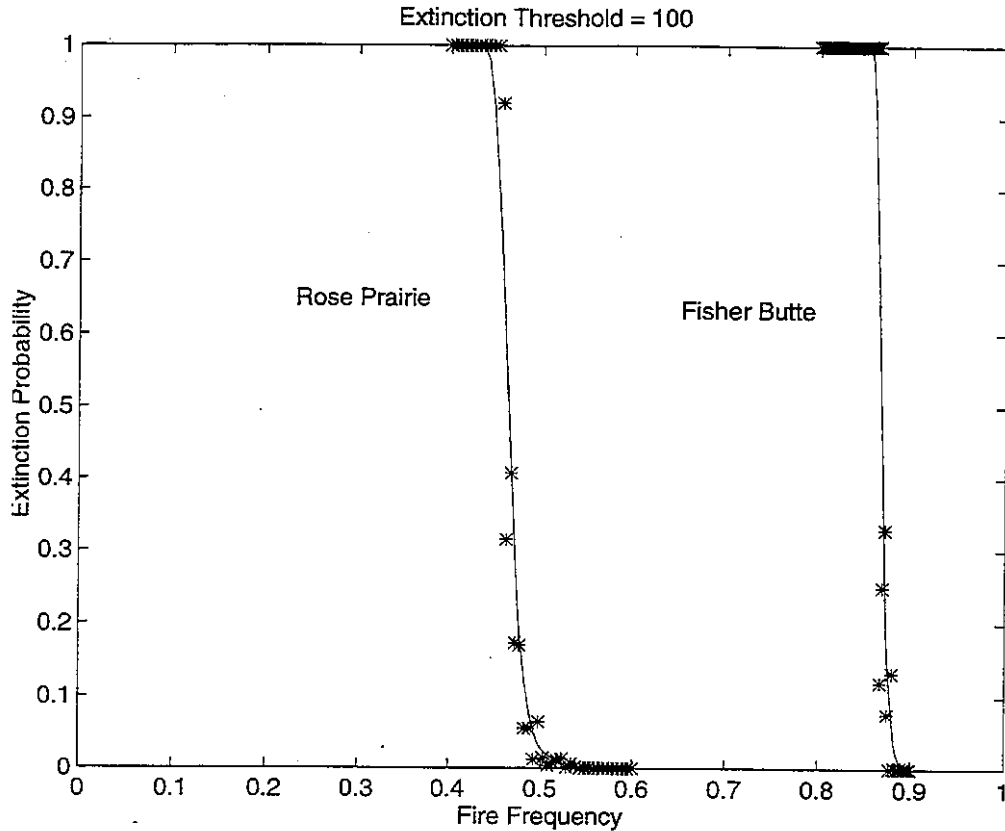
$$P_e = \begin{cases} 1 & \log \lambda_s \leq 0 \\ \exp\left(\frac{2 \log \lambda_s \log \frac{N_e}{N}}{\sigma^2}\right) & \log \lambda_s > 0 \end{cases} \quad (30)$$

(Lande and Orzack, 1988; Dennis *et al.*, 1991).

Quasi-extinction probability, for a quasi-extinction threshold of  $N_e/N = 0.01$ , is shown in Figure 9. It drops precipitously once  $\log \lambda_s$  exceeds 0. These results show that any management strategy that raises  $\log \lambda_s$  even slightly above 0 will essentially eliminate the likelihood of quasi-extinction due to environmental stochasticity.

#### D. Sensitivity and Elasticity Analysis

Perturbation analyses are an essential part of demography (Caswell, 2001). They ask what would happen *if* the vital rates were to change in certain



**Fig. 9.** The extinction probability as a function of fire frequency for an extinction threshold of 0.01 (i.e. extinction corresponds to a reduction in population size to 1% of its present size). The solid line is a non-parametric regression (loess) curve fit to the calculated points, with a bandwidth of 25% of the number of points.

ways. The effects of such changes on population growth rate are described by the sensitivity and elasticity of  $\lambda$  to changes in the matrix entries  $a_{ij}$ . The sensitivity of  $\lambda$  is given by equation (10) above. The elasticity, or proportional sensitivity, of  $\lambda$  is given by

$$\frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (31)$$

(Caswell *et al.*, 1984; de Kroon *et al.*, 1986; Caswell, 2001).

Sensitivities and elasticities have become standard parts of demographic analysis. They are used to evaluate the effects of conservation plans, pest control tactics, harvesting, environmental changes and sampling

variability. The sensitivities (though not the elasticities) give the selection gradients on the vital rates and play a critical role in life history theory.

The corresponding perturbation analysis for stochastic models was introduced by Tuljapurkar (1990a). Since the stochastic growth rate  $\lambda_s$  is not an eigenvalue, equations (10) and (31) do not apply. Instead, the sensitivities and elasticities are calculated numerically from a stochastic sequence of matrices. The algorithm is described in detail in Caswell, (2001, Section 14.4.1). Briefly, use the stochastic model to generate and store a sequence of  $T$  matrices  $\mathbf{A}_0, \mathbf{A}_1, \dots, \mathbf{A}_{T-1}$ . Pick an arbitrary non-negative vector  $\mathbf{w}(0)$ , with  $\|\mathbf{w}(0)\| = 1$ , and use the sequence of matrices to generate and store a sequence of vectors

$$\mathbf{w}(t+1) = \frac{\mathbf{A}_t \mathbf{w}(t)}{\|\mathbf{A}_t \mathbf{w}(t)\|} \quad t = 0, \dots, T-1 \quad (32)$$

and one-step growth rates

$$R_t = \|\mathbf{A}_t \mathbf{w}(t)\| \quad t = 0, \dots, T-1 \quad (33)$$

Then pick an arbitrary non-negative vector  $\mathbf{v}(T)$ , with  $\|\mathbf{v}(T)\| = 1$ , and project *backwards* using the same sequence of matrices, to generate and store the vectors

$$\mathbf{v}^\top(t-1) = \frac{\mathbf{v}^\top(t) \mathbf{A}_{t-1}}{\|\mathbf{v}^\top(t) \mathbf{A}_{t-1}\|} \quad t = T, \dots, 1 \quad (34)$$

Finally, from the sequences  $\mathbf{A}_t$ ,  $\mathbf{w}(t)$ ,  $\mathbf{v}(t)$ , and  $R_t$ , compute the sensitivity matrix for  $\log \lambda_s$  and the elasticity matrix for  $\lambda_s$

$$\left( \frac{\partial \log \lambda_s}{\partial a_{ij}} \right) = \frac{1}{T} \sum_{t=0}^{T-1} \frac{\mathbf{v}(t+1) \mathbf{w}^\top(t)}{R_t \mathbf{v}^\top(t+1) \mathbf{w}(t+1)} \quad (35)$$

$$\left( \frac{\partial \log \lambda_s}{\partial \log a_{ij}} \right) = \frac{1}{T} \sum_{t=0}^{T-1} \frac{(\mathbf{v}(t+1) \mathbf{w}^\top(t)) \circ \mathbf{A}_t}{R_t \mathbf{v}^\top(t+1) \mathbf{w}(t+1)} \quad (36)$$

where  $\circ$  denotes the Hadamard product. See Caswell (2001) for details of the derivation and MATLAB code.

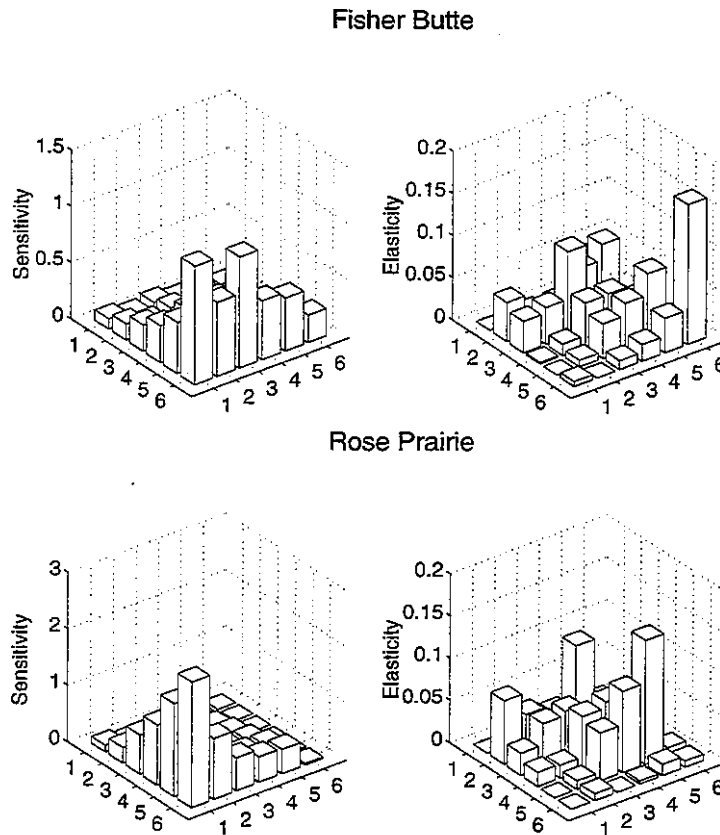
### 1. Perturbation Analysis of the Stochastic Growth Rate

The sensitivity and elasticity of the stochastic growth rate depend on the properties of the environment (the fire frequency and autocorrelation) and on the response of the vital rates to the environment (the details of the matrices  $\mathbf{A}^{(1)} - \mathbf{A}^{(4)}$ ). We will explore that dependence in detail below, but

we begin with a typical set of results, for  $f = 0.5$ ,  $\rho = 0$  (Figure 10). The sensitivities of  $\log \lambda_s$  are highest to changes in entries in the lower left corner of  $\mathbf{A}$ , corresponding to growth directly from small vegetative to large reproductive plants. The sensitivity to changes in fertility is very low in both sites.

The elasticity of  $\lambda_s$ , by contrast, is highest to survival of the largest reproductive plants (stage  $R_3$  at Fisher Butte,  $R_2$  at Rose Prairie). The elasticities of  $\lambda_s$  are also high to changes in transitions involving stages 3–5 (large vegetative and small reproductive plants), and to fertility of large reproductive plants.

It is well known that the results of perturbation analysis of deterministic models depend on the values of the  $a_{ij}$ ; this dependence is quantified in the second derivatives of  $\lambda$  (Caswell, 1996b). This has led to concern over the accuracy, precision, and/or reliability of estimated sensitivities and



**Fig. 10.** Matrices of sensitivity and elasticity of the stochastic growth rate, calculated using the average matrices. The matrices shown are for a fire frequency  $f = 0.5$  and autocorrelation  $\rho = 0$ . The sensitivities are  $\partial \log \lambda_s / \partial a_{ij}$ ; the elasticities are  $\partial \log \lambda_s / \partial \log a_{ij}$ .

elasticities, especially when used in management. If estimates are very sensitive to errors of sampling or model specification, then management recommendations based on typically imperfect data may be badly misguided. Some of the analyses of this potential problem have focused strictly on the largest elasticities, on the grounds that they represent the 'most important' parts of the life cycle (Mills *et al.*, 1999). A more detailed examination, based on patterns of sensitivity and elasticity throughout the life cycle (Caswell, 2001) concluded that perturbation analyses are remarkably robust.

In stochastic models for a dynamic environment, results depend not only on the vital rates, but also on the environment. Here we have an opportunity to investigate this dependence from several perspectives. First, we will suppose that, instead of a stochastic analysis, we constructed a deterministic model based on the average vital rates experienced by the population. Such a model would yield a value of  $\lambda$  that might differ wildly from the stochastic growth rate  $\lambda_s$ . But would the conclusions of a perturbation analysis of the deterministic model differ dramatically from those of the correct stochastic model? Second, we suppose that a stochastic model has been constructed, but that the fire frequency has not been accurately estimated. How sensitive are the conclusions of the perturbation analysis to such inaccuracies?

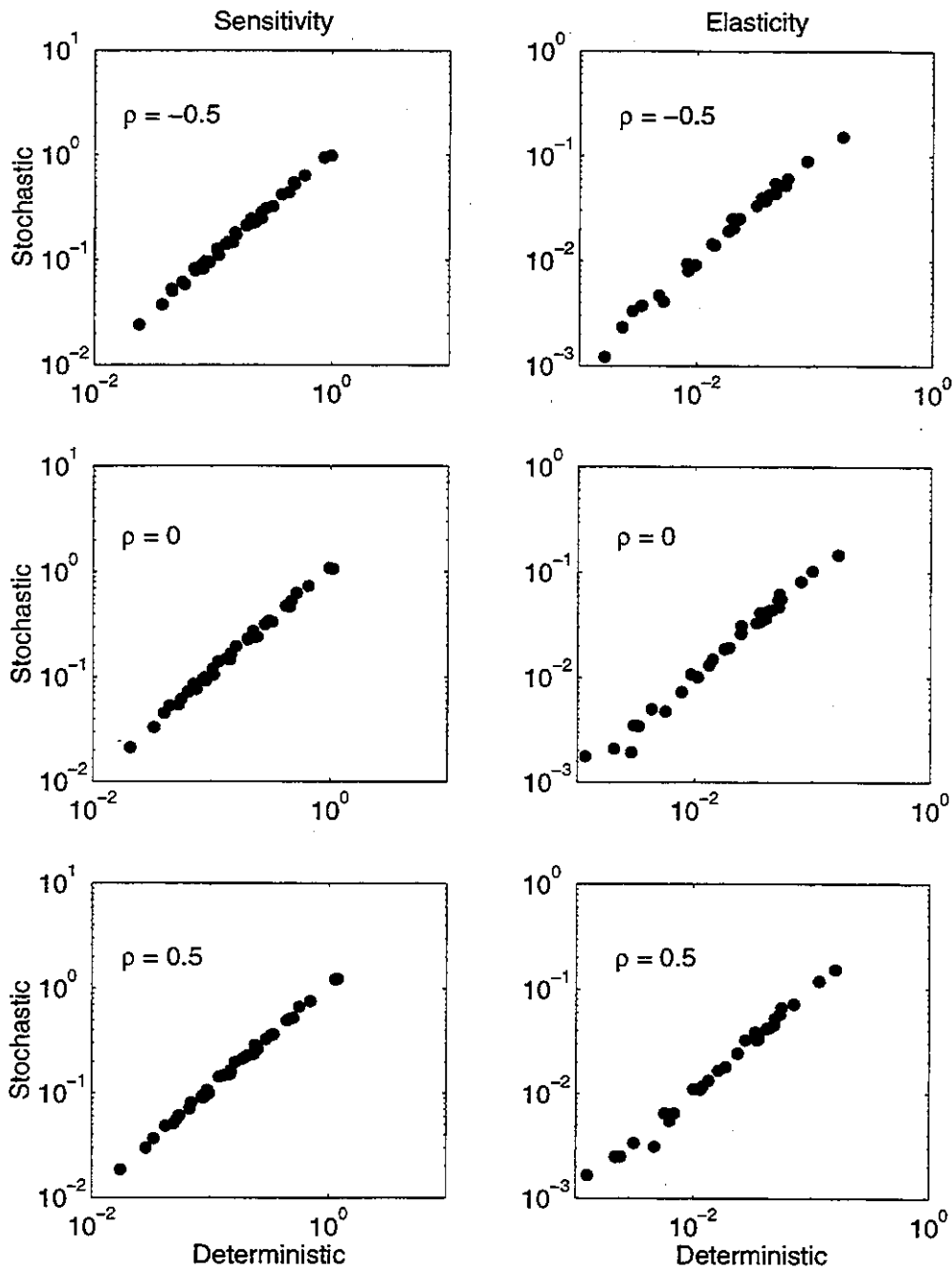
## 2. *Deterministic and Stochastic Models Compared*

The matrices in Figure 10 are very similar to the sensitivity and elasticity matrices of  $\lambda$  calculated from deterministic models. This suggests a comparison of the stochastic results shown here with those of a deterministic model based on the average matrix calculated over the stationary distribution of the environmental process. A recent detailed examination found that the perturbation analysis of stochastic and deterministic models were often very similar (Caswell, 2001).<sup>\*</sup> The model under consideration here, however, is more complex than any of those considered in Caswell (2001), so we will examine the results from several directions.

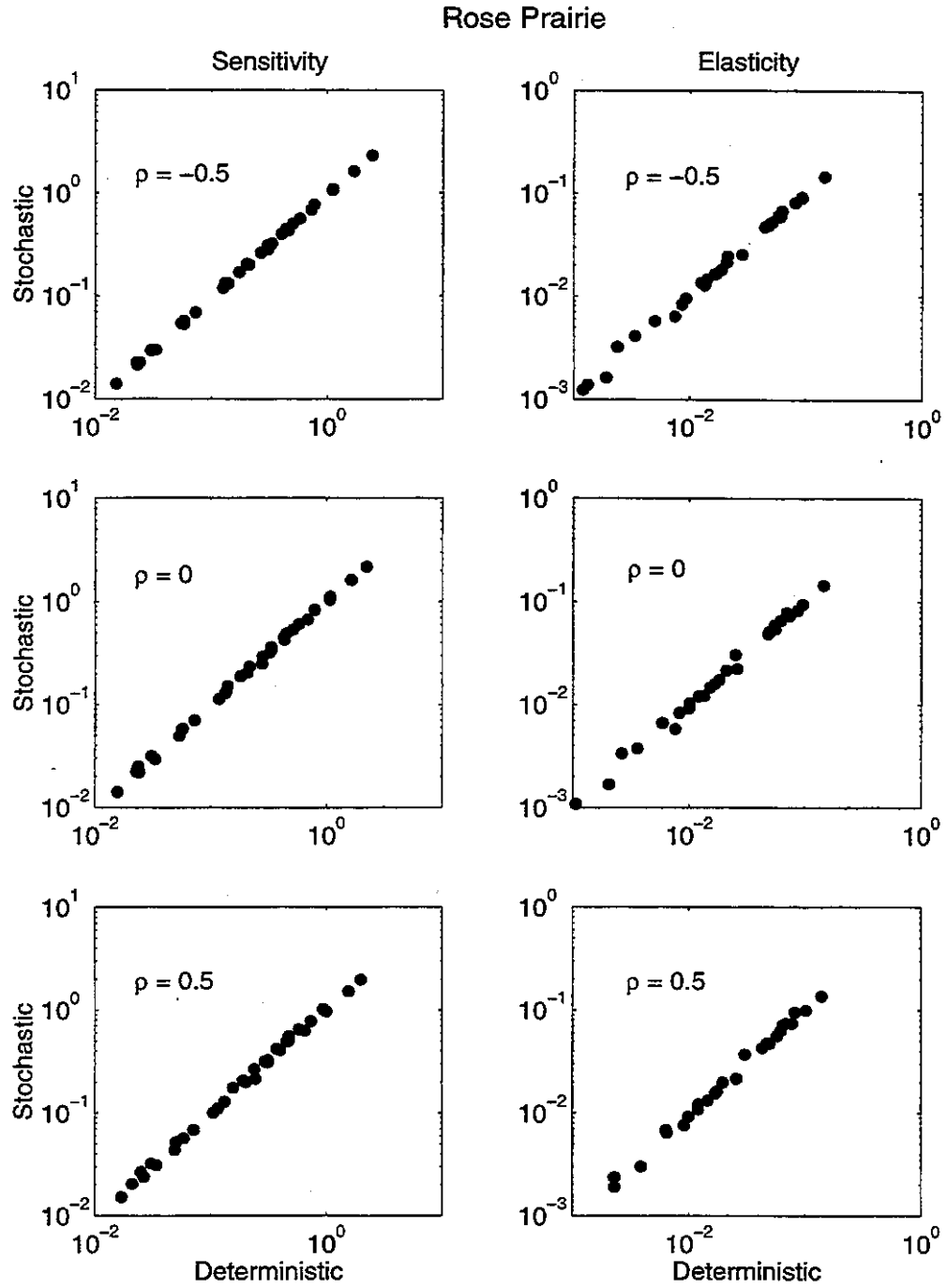
In Figures 11 and 12 the fire frequency is fixed, and the deterministic and stochastic perturbation results are compared as a function of the autocorrelation  $\rho$ . The deterministic and stochastic results are extremely closely correlated, at both sites and regardless of  $\rho$ . Table 7 shows the correlation

<sup>\*</sup>Note that in evolutionary contexts, very small differences between the deterministic and stochastic models can translate into drastically different predictions of life history evolution; see Tuljapurkar (1990b), Tuljapurkar and Istock (1993), and Caswell (2001) for examples.

## Fisher Butte



**Fig. 11.** Comparison of the deterministic and stochastic sensitivities and elasticities of population growth, calculated from the average matrices, at the Fisher Butte site. The deterministic sensitivities and elasticities,  $\partial \log \lambda / \partial a_{ij}$  and  $\partial \log \lambda / \partial \log a_{ij}$ , respectively, are calculated from the average matrix. Fire frequency  $f = 0.5$  throughout; autocorrelations as shown.



**Fig. 12.** Deterministic and stochastic sensitivities and elasticities of population growth, as in Figure 11, at the Rose Prairie site.

**Table 7**

Product-moment correlations between sensitivities and elasticities of population growth rate in the stochastic model and the corresponding sensitivities and elasticities calculated from the deterministic model based on the average matrix.  
Fire frequency  $f = 0.5$

## (a) Fisher Butte

Quantity	Matrices	$\rho = -0.5$	$\rho = 0$	$\rho = 0.5$
Sensitivity	Averaged	0.9975	0.9970	0.9986
Sensitivity	Detailed	0.9934	0.9927	0.9960
Elasticity	Averaged	0.9938	0.9929	0.9965
Elasticity	Detailed	0.9955	0.9935	0.9943

## (b) Rose Prairie

Quantity	Matrices	$\rho = -0.5$	$\rho = 0$	$\rho = 0.5$
Sensitivity	Averaged	0.9997	0.9993	0.9982
Sensitivity	Detailed	0.9981	0.9967	0.9926
Elasticity	Averaged	0.9991	0.9975	0.9955
Elasticity	Detailed	0.9852	0.9786	0.9757

**Table 8**

Product-moment correlations between sensitivities and elasticities of population growth rate in the stochastic model and the corresponding sensitivities and elasticities calculated from the deterministic model based on the average matrix.  
Autocorrelation  $\rho = 0$  throughout

## (a) Fisher Butte

Quantity	Matrices	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
Sensitivity	Averaged	1.0000	0.9972	0.9970	0.9991	1.0000
Sensitivity	Detailed	0.9965	0.9916	0.9927	0.9975	0.9997
Elasticity	Averaged	1.0000	0.9917	0.9928	0.9989	1.0000
Elasticity	Detailed	0.9884	0.9891	0.9936	0.9989	0.9997

## (b) Rose Prairie

Quantity	Matrices	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
Sensitivity	Averaged	0.9999	0.9975	0.9993	0.9999	1.0000
Sensitivity	Detailed	0.9879	0.9921	0.9967	0.9985	0.9996
Elasticity	Averaged	1.0000	0.9951	0.9975	0.9998	1.0000
Elasticity	Detailed	0.9919	0.9745	0.9788	0.9947	0.9980

coefficients for both the averaged and the detailed matrices. All are above 0.97; most are above 0.99.

Table 8 shows the result of fixing  $\rho$  and comparing deterministic and stochastic models for fire frequencies ranging from  $f = 0.01$  to  $f = 0.99$ . These correlations are also extremely high, most of them exceeding 0.99. At the extremes ( $f = 0.01$  and  $f = 0.99$ ), where the stochastic model is almost deterministic, the correlation approaches 1.0.

We conclude that the sensitivities and elasticities of the deterministic population growth rate from the mean matrix do a remarkably accurate job of predicting the same properties of the stochastic growth rate.

### 3. The Effects of Fire Frequency on Perturbation Analysis

Figure 13 compares the sensitivities of  $\log \lambda_s$  as a function of fire frequency; Figure 14 does the same for the elasticities of  $\lambda_s$ . Tables 9 and 10 show the correlations, for both the average and the detailed matrices.

Sensitivities of the stochastic growth rate are extremely *insensitive* to errors in estimation of the fire frequency. At Fisher Butte, the correlations

**Table 9**

Correlations among the sensitivities of  $\log \lambda_s$  for stochastic models as a function of fire frequency  $f$ . Values calculated using the detailed matrices are shown above the diagonal, values for the averaged matrices are shown below the diagonal. Autocorrelation  $\rho = 0$  throughout

(a) Fisher Butte

	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
$f = 0.01$	1.0000	0.9858	0.9686	0.9541	0.9288
$f = 0.25$	0.9856	1.0000	0.9931	0.9725	0.9392
$f = 0.5$	0.9684	0.9931	1.0000	0.9905	0.9651
$f = 0.75$	0.9515	0.9700	0.9889	1.0000	0.9915
$f = 0.99$	0.9194	0.9285	0.9565	0.9887	1.0000

(b) Rose Prairie

	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
$f = 0.01$	1.0000	0.9290	0.8815	0.8593	0.8347
$f = 0.25$	0.9283	1.0000	0.9926	0.9826	0.9670
$f = 0.5$	0.8755	0.9917	1.0000	0.9971	0.9857
$f = 0.75$	0.8474	0.9821	0.9979	1.0000	0.9941
$f = 0.99$	0.8157	0.9687	0.9898	0.9957	1.0000

**Table 10**

Correlations among the elasticities of  $\lambda_s$  for stochastic models as a function of fire frequency  $f$ . Values calculated using the detailed matrices are shown above the diagonal, values for the averaged matrices are shown below the diagonal. Autocorrelation  $\rho = 0$  throughout

## (a) Fisher Butte

	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
$f = 0.01$	1.0000	0.9425	0.7719	0.5831	0.4340
$f = 0.25$	0.9441	1.0000	0.9236	0.7669	0.6180
$f = 0.5$	0.7575	0.9142	1.0000	0.9501	0.8565
$f = 0.75$	0.5301	0.7282	0.9399	1.0000	0.9732
$f = 0.99$	0.3657	0.5700	0.8413	0.9738	1.0000

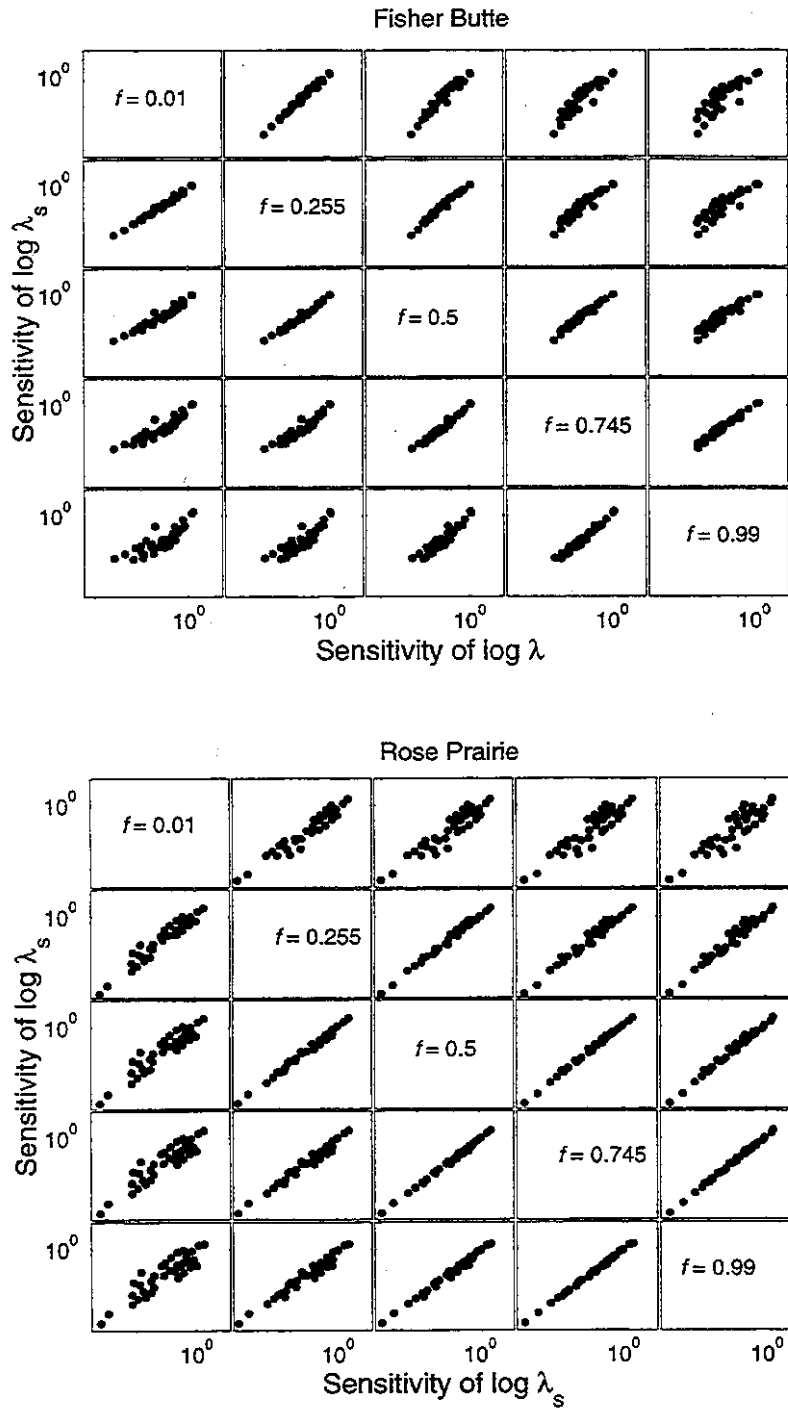
## (b) Rose Prairie

	$f = 0.01$	$f = 0.25$	$f = 0.5$	$f = 0.75$	$f = 0.99$
$f = 0.01$	1.0000	0.9082	0.6630	0.4457	0.3318
$f = 0.25$	0.9073	1.0000	0.9112	0.7661	0.6770
$f = 0.5$	0.6828	0.9251	1.0000	0.9615	0.9160
$f = 0.75$	0.5151	0.8231	0.9765	1.0000	0.9901
$f = 0.99$	0.4342	0.7653	0.9491	0.9936	1.0000

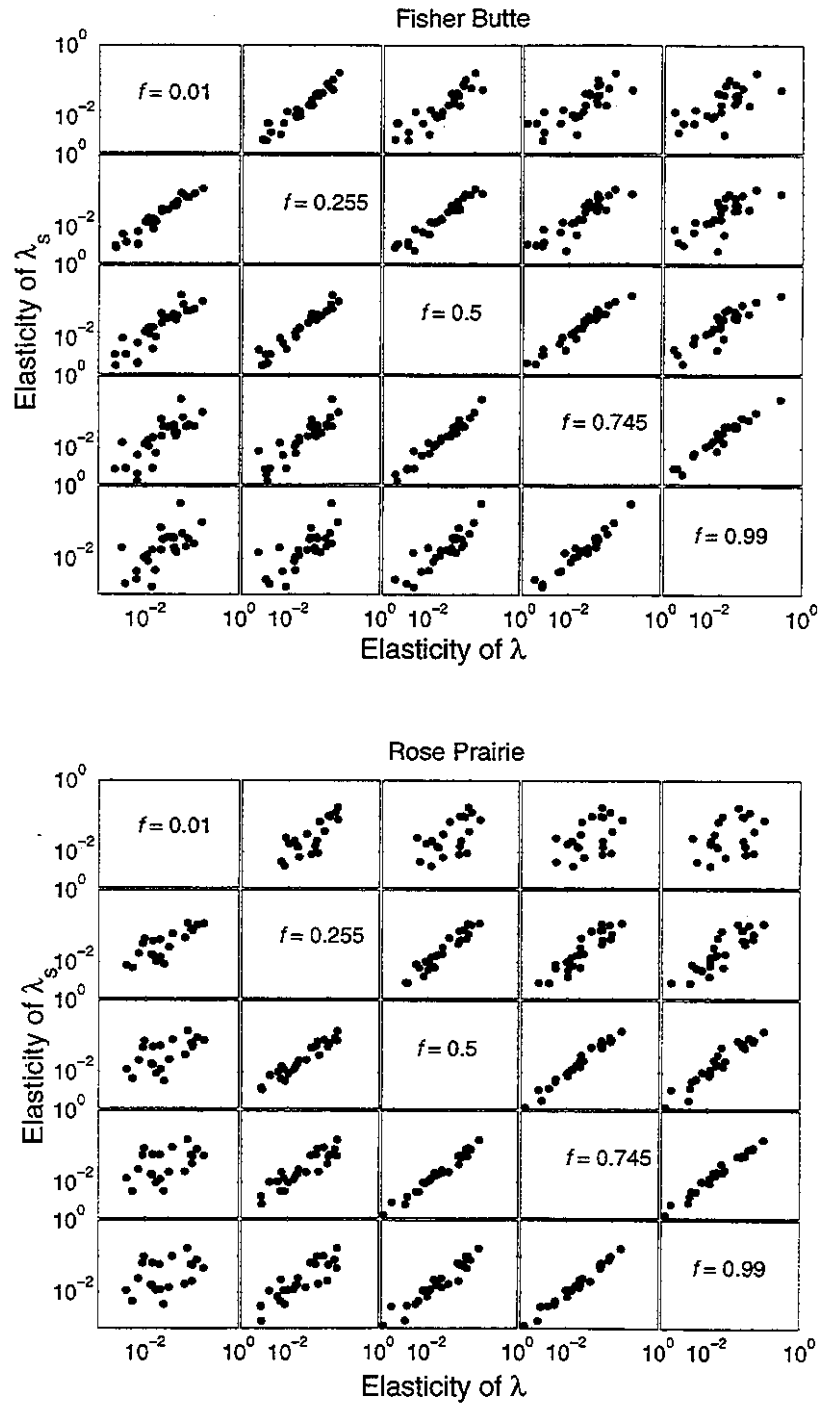
between sensitivities at different values of  $f$  exceed 0.9, even over an extremely wide range of fire frequencies ( $f = 0.01$  versus  $f = 0.99$ ). At Rose Prairie, the correlations exceed 0.8 over this range, and exceed 0.98 over the range  $0.25 \leq f \leq 0.75$ . Figures 15 and 16 show the sensitivity matrices, making clear their near-invariance under changes in  $f$ . Thus, conclusions about the effects of changes in the vital rates on the stochastic growth rate are remarkably insensitive to errors in the estimates of fire frequency.

The elasticities of  $\lambda_s$  are less robust to changes in  $f$  than are the sensitivities (Figure 14). Elasticities of  $\lambda_s$  calculated for  $f = 0.01$  do a poor job of predicting elasticities for  $f = 0.99$ . But the correlations are higher for smaller ranges of fire frequencies (Table 10). At both sites, the correlation exceeds 0.7 for  $0.25 \leq f \leq 0.75$ , and exceeds 0.9 when models are compared that differ in fire frequency by less than 0.25.

Figure 15 shows that, at Fisher Butte, as  $f$  increases, the elasticities to the survival and fertility of large flowering plants and the stasis of large vegetative plants dominate all the other elasticities. At low fire frequencies, elasticities are much more evenly distributed among the

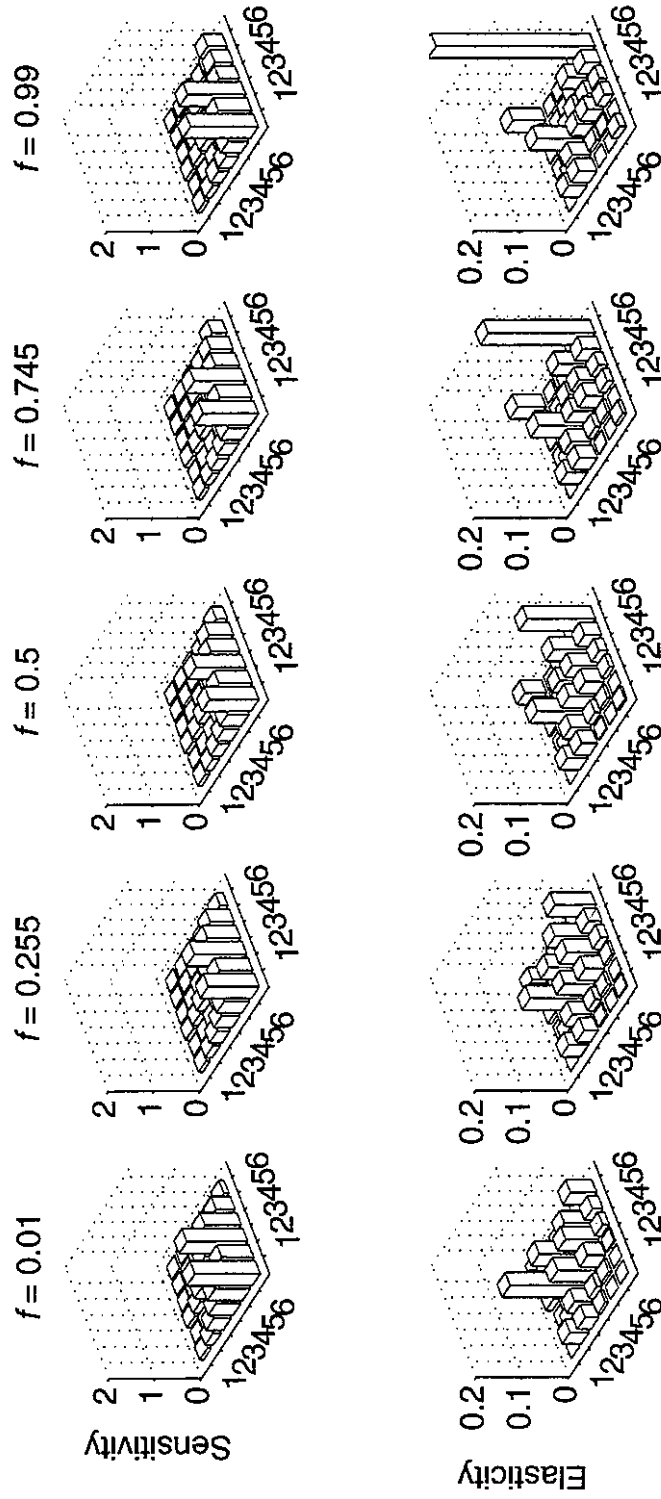


**Fig. 13.** Reliability of the sensitivity of the stochastic growth rate, across a range of fire frequencies. Calculated from the average matrices; autocorrelation  $\rho = 0$  throughout.



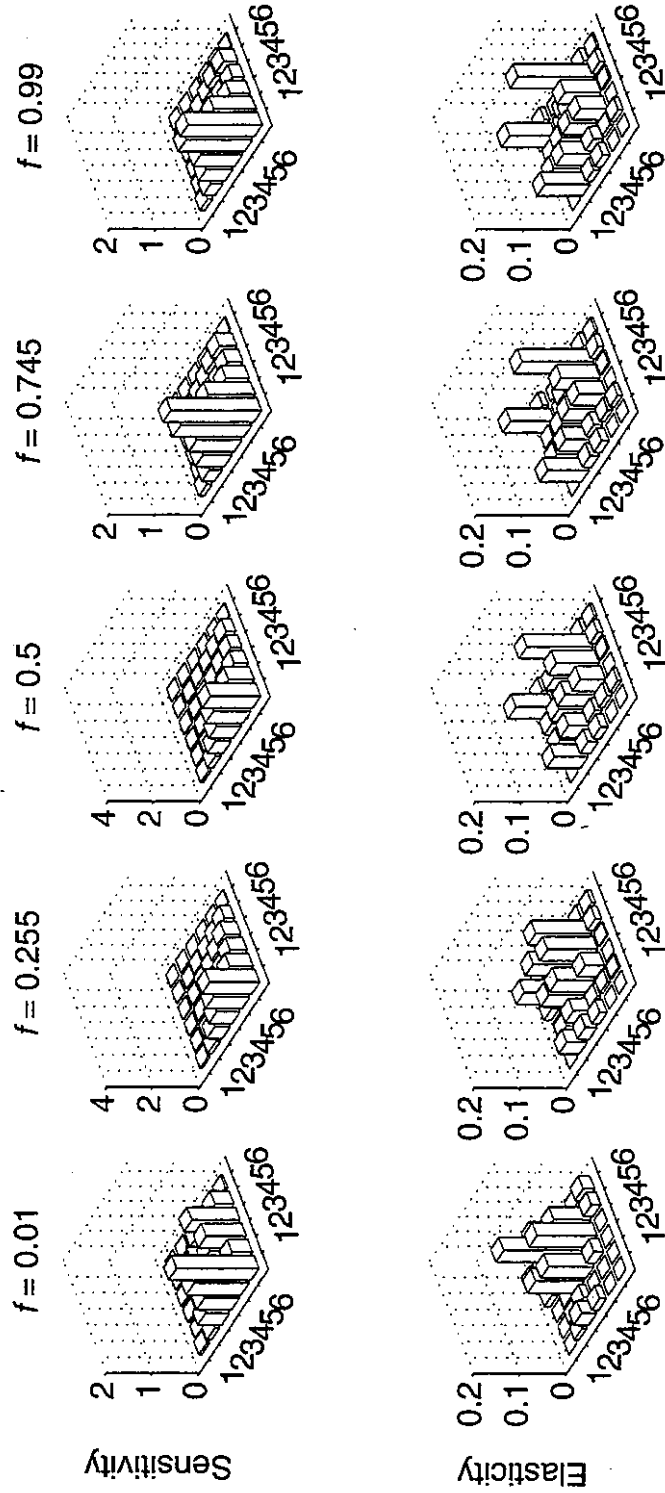
**Fig. 14.** Reliability of the elasticity of the stochastic growth rate, across a range of fire frequencies. Calculated from the average matrices; autocorrelation  $\rho = 0$  throughout.

## Fisher Butte



**Fig. 15.** Sensitivity and elasticity matrices,  $\partial \log \lambda_s / \partial a_{ij}$  and  $\partial \log \lambda_s / \partial \log a_{ij}$ , respectively, at the Fisher Butte site as a function of fire frequency. Calculated from the average matrices; autocorrelation  $\rho = 0$  throughout.

Rose Prairie



**Fig. 16.** Sensitivity and elasticity matrices,  $\partial \log \lambda_s / \partial a_{ij}$  and  $\partial \log \lambda_s / \partial \log a_{ij}$ , respectively, at the Rose Prairie site as a function of fire frequency. Calculated from the average matrices; autocorrelation  $\rho = 0$  throughout.

matrix entries. The pattern at Rose Prairie is similar (Figure 16), but with stage  $R_2$  instead of  $R_3$  playing the role of the largest reproductive size class.

In sum, conclusions about the effects on population growth of changes in the vital rates of *L. bradshawii* are extremely robust. If a management action is directed towards part of the life cycle identified as having a major impact on population growth by one model, the chances are good that it will have a major impact on population growth in a different model, whether stochastic or deterministic.

### E. Periodic Fire Environments

In a periodic environment, population growth over one cycle length is given by the dominant eigenvalue of the product of the projection matrices for each step, or 'phase' in the cycle. Suppose that the phase-specific matrices are  $\mathbf{B}^{(1)}, \mathbf{B}^{(2)}, \dots, \mathbf{B}^{(m)}$ , where  $m$  is the cycle length. Then

$$\mathbf{n}(t+m) = \mathbf{B}^{(m)} \dots \mathbf{B}^{(2)} \mathbf{B}^{(1)} \mathbf{n}(t) \quad (37)$$

$$= \mathbf{A} \mathbf{n}(t) \quad (38)$$

Population growth over an  $m$ -year cycle is given by the dominant eigenvalue,  $\lambda^{(\mathbf{A})}$ , of the product matrix  $\mathbf{A}$ . The average growth rate per year is given by

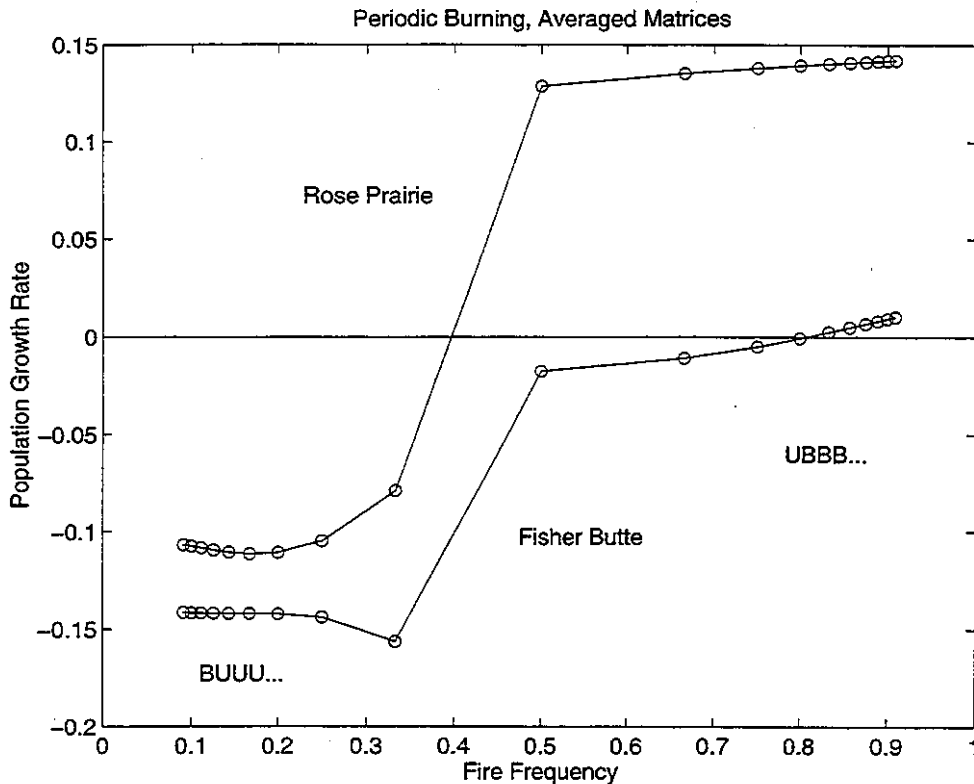
$$\text{mean annual growth rate} = (\lambda^{(\mathbf{A})})^{\frac{1}{m}} \quad (39)$$

or, changing to the more convenient continuous-time form,

$$\log \lambda = \frac{1}{m} \log \lambda^{(\mathbf{A})} \quad (40)$$

Figure 17 shows the growth rate  $\log \lambda$  in a periodic fire environment defined either by the number of years between fires (i.e. BU, BUU, BUUU, ...) or by the number of fires between unburned years (i.e. UB, UBB, UBBB, ...). The minimum fire frequencies allowing persistence under these scenarios are 0.83 for Fisher Butte (i.e. a fire regime of UBBBBB ...), and 0.5 for Rose Prairie (a fire regime of BU ...).

Periodic fire regimes can also be created by specifying the length of the fire rotation and considering all possible fire schedules of that length. For example, in a rotation of 2 years, the only possible schedules are BB, BU and UU. Longer fire rotations permit many different periodic schedules with the same frequency. In a 6-year rotation, for example, the schedules BBBUUU, BBUUBU, BUUBBU, and BUBUBU all have a fire



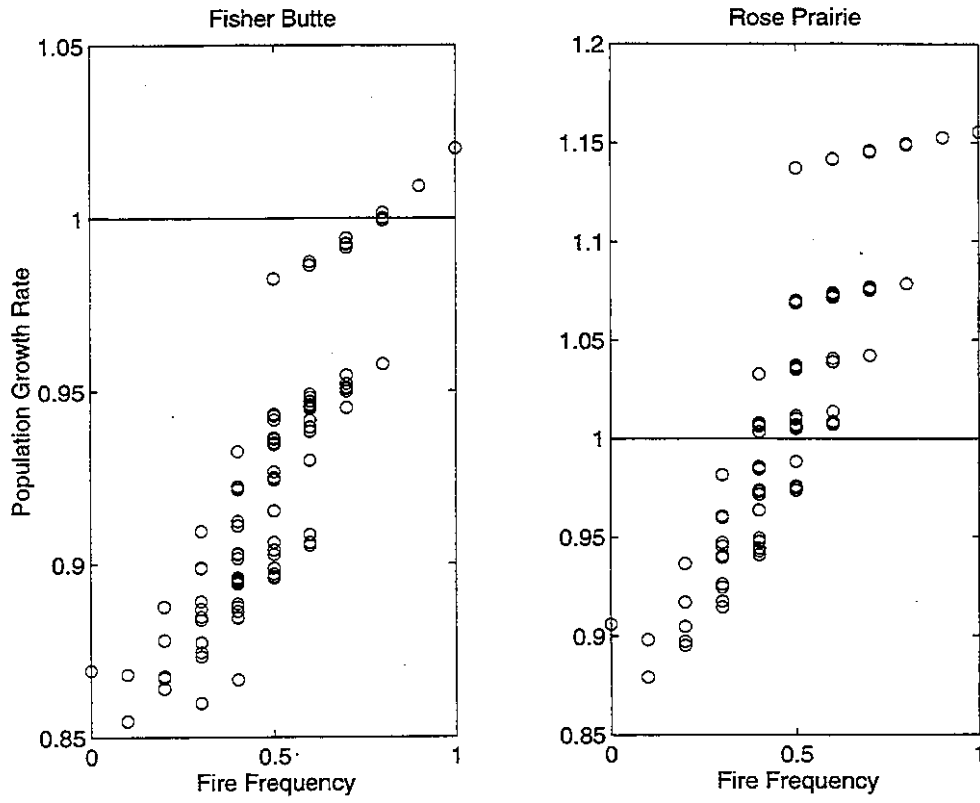
**Fig. 17.** The annual population growth rate for periodic fire regimes, based on the averaged matrices.

frequency of 0.5. Because matrix multiplication is not commutative, however, they will not, in general, produce the same growth rate.

To investigate the effect of periodic burning on a reasonably long rotation, we calculated the annual growth rate resulting from all  $2^{10} = 1024$  of the distinct fire schedules over a 10-year rotation (Figure 18). When fire frequency equals 0 or 1, there is only one possible growth rate. At intermediate frequencies, there is a range of possible growth rates associated with any one fire frequency. The schedules maximizing  $\lambda$  as a function of fire frequency are given in Table 11.

The optimal schedules at Fisher Butte always alternate, as much as possible, unburned years with burned years. The optimal schedules at Rose Prairie are the same at low frequencies, but at higher frequencies (0.6 and higher) the optimal schedules contain longer runs of burned years.

It is not clear that these differences will be significant to management, but we present them here to demonstrate how such calculations can be made. Certainly they emphasize the point that one cannot assume that any



**Fig. 18.** The annual population growth rate for all possible periodic fire regimes on a 10-year schedule, using the average matrices.

**Table 11**

The periodic burning schedules, on a 10-year rotation, that maximize the annual growth rate of *L. bradshawii* at each site

Frequency	Fisher Butte	Rose Prairie
0.1	BUUUUUUUUU	BUUUUUUUUU
0.2	BUBUUUUUUU	BUBUUUUUUU
0.3	BUBUBUUUUU	BUBUBUUUUU
0.4	BUBUBUBUUU	BUBUBUBUUU
0.5	BUBUBUBUBU	BUBUBUBUBU
0.6	BBUBUBUBU	BBUBUBUBU
0.7	BBBBUBUBU	BBUBUBUBU
0.8	BBBBBBUBU	BBBBUBUBU
0.9	BBBBBBBBBU	BBBBBBBBBU

rotation with a given fire frequency is equivalent from the point of view of *L. bradshawii*.

## VII. SUMMARY AND DISCUSSION

Fire has a substantial positive effect on the growth rate of *L. bradshawii* at both sites. The highest population growth rate would be produced by maintaining the conditions in the year of a fire, and  $\lambda$  declines with time since the last fire. This decline is due mainly to reduced survival and growth; changes in fertility make only small contributions to the effect. In a dynamic fire environment, the long-term population growth rate depends on the frequency and temporal autocorrelation of fires. High fire frequency and negative autocorrelation both increase the stochastic growth rate. Including small-scale spatial and temporal variability by using the detailed matrices produces slightly higher stochastic rates than the averaged matrices.

The two sites differed in population growth, with higher rates at the Rose Prairie site. The critical fire frequency required to maintain *L. bradshawii* populations is about 0.8–0.9 at Fisher Butte, but only 0.4–0.5 at Rose Prairie.

The causes of the differences between the sites are not clear. According to Pendergrass *et al.* (1999), the study sites had similar soils and hydrology but differed in population characteristics and associated vegetation. Prior to the initiation of burning treatments in 1988, plants at Rose Prairie were smaller and produced fewer flowering structures than at Fisher Butte, although fruit production per plant was similar at the two sites. The *Deschampsia cespitosa/Danthonia californica* community-type was present at both sites, but the *Vaccinium caespitosum* type was present only at Rose Prairie and the *Rosa nutkana/Juncus nevadensis* type was present only at Fisher Butte (Pendergrass, 1995).

Fires also differed in behavior among the study sites and years. In 1988 fires were more intense, produced greater heat per unit area, and consumed more total biomass at Fisher Butte than at Rose Prairie. The 1989 fires were similar at the two locations, but were spotty compared to the more complete 1988 burns (Pendergrass *et al.*, 1998). Differences in the response of grassland plant species to fires have been attributed to differences in fire behavior and intensity (e.g. between backfires and headfires in North American tallgrass prairies (Bidwell *et al.*, 1990) and African grassland and savanna (Trollope, 1978, 1982)). The effects of fire on *L. bradshawii* at Rose Prairie and Fisher Butte may have differed in part due to site differences in populations, associated vegetation, fire behavior or other factors.

The picture of *L. bradshawii* dynamics in a dynamic fire environment that emerges from our results agrees with other studies of plants in savanna and grassland ecosystems. Silva *et al.* (1991) and Canales *et al.* (1994) used periodic and stochastic matrix models to evaluate the effects of fire frequency on two species of grasses from tropical savannas in Venezuela (*Andropogon semiberbis* and *A. brevifolius*). Stochastic and deterministic population growth rates both increased with fire frequency, and a critical fire frequency existed in each case, below which the species would be unable to persist. Hoffman (1999) carried out a similar study on woody shrubs in savannas of Brazil. Interestingly, he found the opposite pattern: population growth rate declined with fire frequency, and he could identify a critical frequency above which species were unable to persist. Thus herbaceous and woody species seem, at least from these few examples, to respond in opposite directions to fire.

It is possible for population growth rate to be maximized at intermediate fire frequencies. Gross *et al.* (1998) found this pattern in a model for the threatened shrub *Hudsonia montana* in North Carolina. They modelled fire as a periodic, not a stochastic, process but they incorporated temporal variance in the vital rates within each environmental state (much as our detailed matrices do, although they used a different approach to include the variation). They found a population growth rate maximized at intermediate fire frequencies.

Our analysis is the first to be able to include effects of time since fire; the previous studies have included only two environmental states, corresponding to years with and without fires. Even so, our model of fire and the environmental effects it produces are relatively crude, and could be extended by incorporating effects of time since fire on the likelihood and intensity of fire.

Using fire as a management tool faces at least two restrictions. Controlled burns are expensive and may require the presence of 20–30 trained people. The cost of a burn in a Willamette Valley prairie typically ranges from \$5000 to \$10 000 (Rick Hayes, US Army Corps of Engineers, personal communication). Burning may also lead to the decline of other desirable or rare species that occur at the same location, as has been observed in other prairies (Glenn and Collins, 1992). Identifying a periodic fire regime that minimizes the number of burns needed to maintain a population of *L. bradshawii* is clearly warranted. Our results suggest that there were several periodic burn schedules that yield a stable population at both sites. These schedules, which required eight burns at Fisher Butte and four at Rose Prairie over a 10-year period, were very specific, however. Departures from these timetables could result in population decline, even if the total number of burns remained the same. To minimize the number

of burns needed, therefore, managers should identify an appropriate periodic burn schedule and commit to it.

### A. Generalizations and Methodological Issues

Our analysis of *L. bradshawii* is an example of a general approach to demography in dynamic environments, and as such it raises some important methodological issues.

First, the model can obviously be generalized to other kinds of disturbance processes. In addition to the studies of fire frequency cited earlier, such models have already been applied to floods (Beissinger, 1995), hurricanes (Batista *et al.*, 1998), and burning and trampling (Gross *et al.*, 1998).

While our analysis is based on a discrete environmental event (a fire occurs, or it does not), the approach could equally be applied to an environment described in terms of a quantitative variable such as temperature, moisture, food supply, or even the intensity of fire. Such variables can be discretized and modelled using a finite-state Markov chain, as we have done here, or can be described by autoregressive models (Tuljapurkar, 1990a; Caswell, 2001). Models for the environment play a central role in stochastic models; more work needs to be done on them. See Caswell (2001) for development of some possibly useful Markov chain models for sequences of matrices.

More sophisticated models of the environment will require the incorporation of more kinds of demographic variability. In this study, we had the option of using multiple estimates of the vital rates within each environmental state. It was conceivable that the variability within the environmental states might have swamped out the effects of the variability among those states. It did not, but this is the first case where the comparison has been made. It would be very interesting to explore the response of a population to two or more kinds of explicit environmental variability (e.g. fire and moisture) to see how they interact.

Our analysis used data from the experimental design shown as (2) (section III.B) which was intended for other purposes. It is an unfortunately unbalanced design, with estimates for  $\mathbf{A}^{(3)}$  being obtained only in one year. That year (1990) was one that led to low values of  $\lambda$  in all treatments. It is possible that the decline in performance with time elapsed since the last fire could be an artifact of this lack of balance in the design. This is highly unlikely, because the decline is still significant even if the data from environmental state  $E_3$  are excluded, and because many independent pieces of information point to the reality of this decline (Pendergrass *et al.*, 1999; Kaye *et al.*, 2001).

Still, it would be nice to have a design that would provide balanced estimates of every environmental state in every year of a study such as this one. The following design would accomplish this.

85	86	87	88	89	90	91	92	(41)
B	U	U	B	U	U	U	B	
	B	U	U	B	U	U	U	
		B	U	U	U	B	U	

This design produces the following set of environmental states:

85	86	87	88	89	90	91	92	(42)
$E_1$	$E_2$	$E_3$	$E_1$	$E_2$	$E_3$	$E_4$	$E_1$	
	$E_1$	$E_2$	$E_4$	$E_1$	$E_2$	$E_3$	$E_4$	
		$E_1$	$E_3$	$E_4$	$E_1$	$E_2$	$E_3$	
			$E_2$	$E_3$	$E_4$	$E_1$	$E_2$	

Each environmental state is present in each year, but the experiment would be more costly. It would require one additional treatment, and up to three years of preparatory treatments before the experiment *per se* begins.

Dynamic environments are the rule, not the exception. Population growth in such environments is an important problem with important implications for management and conservation. Stochastic and periodic matrix population models, with their associated growth rates and perturbation analyses, provide the tools necessary to assess the status of populations, to evaluate alternative management strategies, and to project the future of the population.

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## APPENDIX

This appendix contains the detailed matrices for the Fisher Butte and Rose Prairie sites. Each column of the following tables contains one matrix, identified by its treatment–year combination. The entries in a column of the table are the entries in each column of the matrix, stacked one above the other.

**Table A1**

This appendix contains the detailed matrices for the Fisher Butte and Rose Prairie sites. Each column of the following tables contains one matrix, identified by its treatment-year combination. The entries in a column of the table are the entries in each column of the matrix, stacked one above the other.

(a) Fisher Butte

$T_1 - 88$	$T_1 - 91$	$T_2 - 88$	$T_2 - 89$	$T_2 - 91$	$T_1 - 89$	$T_1 - 92$	$T_2 - 90$	$T_2 - 92$	$T_1 - 90$	$T_0 - 88$	$T_0 - 89$	$T_0 - 90$	$T_0 - 91$	$T_0 - 92$
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.210	0.250	0.440	0.360	0.310	0.470	0.110	0.430	0.130	0.390	0.210	0.530	0.000	0.060	0.200
0.120	0.120	0.070	0.220	0.150	0.230	0.320	0.030	0.260	0.060	0.070	0.220	0.000	0.150	0.070
0.000	0.000	0.040	0.000	0.000	0.030	0.000	0.030	0.000	0.000	0.000	0.030	0.010	0.000	0.030
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.300	0.320	0.360	0.150	0.210	0.430	0.200	0.150	0.110	0.390	0.110	0.430	0.230	0.330	0.110
0.300	0.210	0.360	0.440	0.500	0.220	0.470	0.070	0.260	0.110	0.220	0.140	0.100	0.210	0.430
0.070	0.040	0.040	0.040	0.090	0.170	0.070	0.150	0.050	0.000	0.040	0.140	0.050	0.050	0.000
0.000	0.000	0.000	0.070	0.030	0.040	0.050	0.040	0.110	0.000	0.000	0.140	0.000	0.000	0.070
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.560	0.320	0.550	0.420	0.820	0.260	0.450	0.260	0.430	0.220	0.400	0.540	0.410	0.630	0.500
0.060	0.260	0.180	0.180	0.070	0.240	0.260	0.170	0.230	0.080	0.230	0.240	0.120	0.080	0.200
0.100	0.060	0.090	0.160	0.000	0.260	0.100	0.040	0.060	0.080	0.030	0.110	0.010	0.070	0.090
0.000	0.000	0.000	0.040	0.040	0.000	0.020	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000
0.000	0.000	0.100	0.100	0.100	0.200	0.100	0.000	0.100	0.000	0.100	1.100	0.100	0.200	0.000
0.100	0.080	0.140	0.000	0.030	0.080	0.000	0.060	0.000	0.040	0.000	0.000	0.060	0.090	0.000
0.200	0.190	0.000	0.060	0.360	0.000	0.070	0.110	0.000	0.000	0.160	0.140	0.260	0.330	0.140
0.200	0.310	0.430	0.500	0.310	0.330	0.170	0.280	0.250	0.380	0.530	0.430	0.230	0.270	0.500
0.100	0.080	0.430	0.380	0.170	0.500	0.730	0.060	0.540	0.080	0.050	0.430	0.130	0.060	0.230
0.000	0.080	0.000	0.000	0.060	0.000	0.030	0.000	0.170	0.000	0.050	0.000	0.020	0.000	0.000
1.300	0.500	1.500	0.900	0.600	1.800	0.700	0.100	0.400	0.200	1.300	1.200	0.600	0.500	5.000
0.000	0.000	0.060	0.000	0.000	0.000	0.000	0.000	0.000	0.090	0.000	0.000	0.080	0.000	0.000
0.070	0.120	0.120	0.000	0.100	0.000	0.140	0.060	0.000	0.120	0.190	0.000	0.170	0.250	0.090
0.330	0.180	0.120	0.000	0.250	0.000	0.210	0.350	0.110	0.380	0.500	0.400	0.290	0.250	0.270
0.470	0.350	0.560	0.440	0.460	0.540	0.360	0.260	0.630	0.250	0.120	0.600	0.210	0.250	0.450
0.000	0.060	0.120	0.330	0.050	0.310	0.140	0.000	0.210	0.000	0.120	0.000	0.040	0.080	0.000
2.724	2.724	2.724	2.724	2.724	1.886	1.886	1.886	1.886	1.000	3.080	3.080	3.080	3.080	3.080
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.039	0.039	0.039	0.039	0.039	0.000	0.000	0.000	0.000	0.000	0.235	0.235	0.235	0.235	0.235
0.000	0.000	0.000	0.000	0.000	0.143	0.143	0.143	0.143	0.000	0.052	0.052	0.052	0.052	0.052
0.095	0.095	0.095	0.095	0.095	0.200	0.200	0.200	0.200	0.330	0.177	0.177	0.177	0.177	0.177
0.816	0.816	0.816	0.816	0.816	0.516	0.516	0.516	0.516	0.330	0.501	0.501	0.501	0.501	0.501

Table A.1 (contd.)

(b) Rose Prairie

$T_1 - 88$	$T_1 - 91$	$T_2 - 88$	$T_2 - 89$	$T_2 - 91$	$T_1 - 89$	$T_1 - 92$	$T_2 - 90$	$T_2 - 92$	$T_1 - 90$	$T_0 - 88$	$T_0 - 89$	$T_0 - 90$	$T_0 - 91$	$T_0 - 92$
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.330	0.280	0.310	0.540	0.440	0.500	0.190	0.130	0.260	0.290	0.210	0.130	0.000	0.000	0.000
0.000	0.040	0.120	0.120	0.000	0.120	0.120	0.000	0.070	0.010	0.020	0.200	0.000	0.250	0.000
0.000	0.020	0.000	0.080	0.000	0.000	0.030	0.000	0.020	0.010	0.020	0.000	0.000	0.000	0.070
0.000	0.000	0.060	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.500	0.460	0.000	0.830	0.170	0.500	0.280	0.150	0.430	0.300	0.220	0.880	0.120	0.000	0.000
0.330	0.160	0.500	0.000	0.250	0.400	0.190	0.000	0.170	0.000	0.220	0.000	0.000	0.000	0.430
0.000	0.050	0.500	0.000	0.170	0.000	0.030	0.080	0.030	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.170	0.000	0.000	0.070	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.120	0.150	0.090	0.000	0.000	0.000	0.080	0.000	0.050	0.190	0.100	0.110	0.000	0.000	0.000
0.530	0.000	0.640	0.420	0.290	0.270	0.240	0.230	0.270	0.190	0.600	0.440	0.580	0.330	0.000
0.290	0.380	0.180	0.110	0.290	0.240	0.240	0.150	0.410	0.120	0.200	0.330	0.080	0.220	0.560
0.060	0.230	0.090	0.210	0.140	0.390	0.240	0.000	0.180	0.000	0.000	0.000	0.000	0.000	0.220
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	1.200	0.100	0.400	1.300	0.800	1.500	0.300	1.300	0.200	0.300	0.600	0.100	0.500	0.400
0.000	0.130	0.000	0.000	0.000	0.070	0.000	0.000	0.000	0.190	0.000	0.000	0.000	0.000	0.000
0.200	0.070	0.330	0.330	0.230	0.070	0.140	0.500	0.000	0.250	0.400	0.120	0.210	0.290	0.120
0.600	0.200	0.330	0.000	0.310	0.330	0.360	0.250	0.500	0.250	0.600	0.560	0.210	0.290	0.500
0.200	0.400	0.330	0.670	0.310	0.530	0.360	0.000	0.400	0.060	0.000	0.250	0.140	0.290	0.250
0.000	0.070	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.600	6.900	3.900	3.800	9.100	4.400	7.300	1.700	5.500	1.400	1.100	3.800	0.500	1.400	10.40
0.000	0.080	0.000	0.000	0.000	0.000	0.000	0.070	0.000	0.030	0.000	0.000	0.000	0.000	0.000
0.380	0.000	0.250	0.000	0.000	0.140	0.110	0.070	0.080	0.170	0.220	0.000	0.000	0.000	0.000
0.120	0.080	0.000	0.170	0.000	0.070	0.210	0.570	0.460	0.270	0.670	0.500	0.750	1.000	0.000
0.500	0.580	0.500	0.750	0.670	0.710	0.530	0.140	0.380	0.300	0.110	0.000	0.250	0.000	1.000
0.000	0.170	0.250	0.000	0.000	0.070	0.050	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.000
5.940	5.940	5.940	5.940	5.940	14.90	14.90	14.90	14.90	2.100	2.100	2.100	2.100	2.100	2.100
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.000	0.000	0.000
0.415	0.415	0.415	0.415	0.415	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.250	0.250	0.250	0.250	0.000	0.000	0.000	0.000	0.000	0.000
0.479	0.479	0.479	0.479	0.479	0.250	0.250	0.250	0.250	0.500	0.500	0.500	0.500	0.500	0.500
0.167	0.167	0.167	0.167	0.167	0.375	0.375	0.375	0.375	0.000	0.500	0.500	0.500	0.500	0.500

