Modeling Controlled Burning and Trampling Reduction for Conservation of *Hudsonia montana*

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Abstract: *Populations of mountain golden heather (*Hudsonia montana*), a threatened North Carolina shrub, are declining due to the suppression of natural fires and increased trampling by hikers and campers. Consequently, proposed management strategies have focused on conducting controlled burns and restricting human traffic. To help design an optimal management plan, we used demographic data from a 5-year field study of* H. montana—*which included a controlled burn—to construct size-based population projection matrices. Using these matrices, we projected the consequences of instituting controlled burns and hiking and camping restrictions separately and in tandem. We also determined the burn frequency that would maximize* H. montana's *population growth rate. Finally, we used a stochastic model to determine how environmental fluctuations could alter the efficacy of conservation measures. Our results suggest that, although neither burning nor trampling reduction alone can reverse* H. montana's *decline, a judicious combination of the two has an excellent chance of doing so. A burn frequency of once every 6–8 years should maximize* H. montana's *population growth, although the interburn interval could be increased to 12–16 years without significantly jeopardizing the success of the management plan. Our results show that, even with the limited data available, size-based projection matrix models can be useful tools for identifying promising combinations of multiple management strategies for most threatened plants.*

Modelado de Incendios Controlados y Reducción de Pisoteo para la Conservación de *Hudsonia montana*

Resumen: *Las poblaciones del brezo dorado de montaña (*Hudsonia montana*), un arbusto de Carolina del Norte amenazado, están disminuyendo debido a la eliminación de incendios naturales y al incremento del pisoteo por escaladores y personas acampando. Consecuentemente, las estrategias de manejo propuestas se han enfocado en la conducción de quemas controladas y la restricción del tráfico de humanos. Para ayudar a diseñar un plan de manejo óptimo, utilizamos datos demográficos de 5 años de estudio de* H. montana *(incluyendo quema controlada) para construir matrices de proyección poblacional. Utilizando estas matrices proyectamos las consecuencias de instituir la quema controlada y restricciones a escaladores y campamentos en forma separada y en conjunto. También observamos la frecuencia de quema controlada que podría maximizar las tasas de crecimiento poblacional de* H. montana. *Finalmente, utilizamos un modelo estocástico para determinar cómo podrían afectar las variaciones ambientales la eficacia de estas medidas de conservación. Nuestros resultados sugieren que ni la quema ni la restricción del pisoteo pueden revertir las disminuciones de* H. montana *por si solos, pero una combinación de las dos medidas tendría excelentes posibilidades de lograrlo. Una frecuencia de quema de una vez cada 6-8 años debería maximizar el crecimiento poblacional de* H. montana, *aunque el período de interquemas podría incrementarse hasta 12-16 años sin comprometer significativamente el éxito de los planes de manejo. Nuestros resultados muestran que aún con una cantidad limitada de datos disponibles, los modelos de matrices de proyección pueden ser herramientas muy útiles para la identificación de combinaciones de estrategias de manejo múltiples prometedoras para la mayoría de las plantas amenazadas.*

Introduction

Hudsonia montana N. (mountain golden-heather, Cistaceae) is a low-growing shrub endemic to North Carolina (Radford et al. 1968). After its discovery by Thomas Nuttall (1818) at Table Rock, North Carolina, in 1816, *H. montana* went unstudied for 150 years. In the mid-1960s the species was feared to be extinct. L. E. Morse (1979) rediscovered the shrub a decade later in Linville Gorge, North Carolina, and after several years of observation warned that increased use of *H. montana*'s habitat by campers and hikers was accelerating *H. montana* mortality. Both Morse's work and a U.S. Forest Service (USFS) report (Sanders 1980) convinced the U.S. Fish and Wildlife Service (USFWS) to classify the species as threatened in 1980 (USFWS 1980). The North Carolina Department of Agriculture (NCDA) soon followed suit (Frost 1990). The USFS published a recovery plan in 1983 (Pendergrass 1983).

Along with trampling by campers, the NCDA suspected that fire suppression was contributing to *H. montana*'s decline. During the first half of this century, lightning fires in the Linville Gorge Wilderness Area occurred about once every 5–10 years (Frantz & Sutter 1987). Since the 1950s, however, fire prevention efforts have successfully eliminated forest fires (Frost 1990). Periodic fire benefits *H. montana* by subjecting its chief competitor, *Leiophyllum buxifolium* (sand myrtle, another low-lying shrub), to pulses of high mortality.

From 1985 to 1989, a manipulative field study was conducted in Linville Gorge to investigate the roles of fire and trampling in the population dynamics of *H. montana* (Frost 1990). Two hundred ten *H. montana* individuals were located and divided into three treatment groups. One group was subjected to a controlled burn in 1987, a second group was freed from above-ground competition by hand-clipping all competing plants, and the final group was left as a control. Each plant was photographed in the late summer of each year. Using these photographs, each plant's two-dimensional area was measured and its fruits were counted. In addition, causes of mortality were recorded for all shrubs that died during the study whenever diagnoses were possible.

The results of this study, summarized by Frost (1990), highlighted the role of fire in mediating competition between *H. montana* and *L. buxifolium*. *L. buxifolium* suffered higher mortality during a fire and took longer to recover its prefire ground cover than did *H. montana*. Fire also stimulated germination of *H. montana* seedlings by burning away surface litter to expose mineral soil. Burning *L. buxifolium* individuals generated flames 2–3 m high, which may have freed *H. montana* individuals from light competition by killing the foliage of encroaching large shrubs.

Frost (1990) also reported that trampling was the third highest cause of *H. montana* mortality, after drought and competition. Most shrub mortality occurred during the summer, when drought stress was most acute. *H. montana*'s demographic rates were highly dependent on environmental factors; in particular, the data suggest that *H. montana* relies on an occasional wet year to provide a burst of seedling germination. Frost (1990) concluded that a management plan for *H. montana* should include controlled burning and limitations on human access to *H. montana*'s habitat.

Although these two strategies are likely to improve the status of *H. montana*, several questions remain unanswered. First, what might be the relative contributions of controlled burns and trampling reduction in aiding recovery of *H. montana*? Are both tactics necessary, or could one or the other suffice? By making more ground area accessible to hikers and campers, burning will unintentionally increase trampling mortality. What will be the consequences of combining burning and trampling reduction into one management plan? Further, if controlled burns are initiated, what is the optimal burn frequency? Controlled burns must be timed far enough apart to allow the recovery and proliferation of *H. montana* without allowing *L. buxifolium* enough time to re-establish competitive dominance. In light of the financial cost and possible political resistance to controlled burns, how long can the interim between burns be extended without undoing the benefits of burning?

We addressed these questions by using demographic data from the field study to construct size-structured matrix population models for *H. montana*. We then used these models to investigate the long-term consequences of a suite of potential management strategies. Specifically, we projected *H. montana*'s population growth rate under management plans incorporating either controlled burns, trampling reduction, or both. We also modeled the response of *H. montana* populations to a range of burn frequencies. Because environmental fluctuations significantly affect the shrub's demographic rates, we constructed two complementary models: a deterministic model for tractable analysis of the effects of management tactics and a stochastic model to explore the impact of a capricious environment on management success.

Methods

Model Structure

Matrix population models provide a means of incorporating data on demographic processes into a structured population growth model (Caswell 1989). Specifically, demographic rates determine an annual transition matrix $\mathbf{A}$. Multiplying this matrix by a vector $\mathbf{n}_t$ containing the distribution of individuals among size classes in year t gives the resulting distribution in the following year (i.e., $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$). Successive years can be modeled by iterating this

equation. The long-term growth rate of the population is equal to the dominant eigenvalue of **A**, and the stable size distribution is given by the corresponding eigenvector.

Following most other plant population studies (Usher 1966, 1969; Werner & Caswell 1977; Huenneke & Marks 1987; Menges 1990; Silva et al. 1991; for reviews see Silvertown et al. 1993; Franco & Silvertown 1996), we used a size-based rather than an age-based projection model because size is a better predictor than age of plant mortality and fecundity (Harper & White 1974). Size-based matrices also allow for a wider range of transitions, including shrinkage from larger to smaller classes, a transition observed in *H. montana*. Our matrices were constructed using data presented in Frost (1990) and additional, unpublished data described below.

In designating size classes for our matrix, we attempted to minimize the loss of detail resulting from the assumption of homogeneity within size classes while maintaining adequate sample sizes within each class. We elected to use five size classes: seeds in the soil (Sd), seedlings and tiny shrubs (TS; ≤ 10 cm^2 of ground cover), small shrubs (SS; 10.1–60 cm^2), medium shrubs (MS; 60.1–240 cm^2), and large shrubs (LS; >240 cm^2).

Data were available for 3 years following the 1987 controlled burn. Consequently, we modeled burn effects with four matrices: a control matrix **C** (based on data from plants under control conditions) and three burn matrices (based on data from plants subjected to the burn), one for the year of the burn ($\mathbf{B_0}$) and one for each of the two years following the burn ($\mathbf{B_{+1}}$ and $\mathbf{B_{+2}}$). Each matrix describes the recruitment and subsequent size transitions during a 1-year interval between consecutive late-summer censuses (Fig. 1). From these four matrices we assembled two additional quartets of matrices, representing 50% and 100% reductions in trampling mortality.

We used the data in Frost (1990) to estimate means and variances of vital rates (Table 1). We used these vital rates in turn to compute our matrix elements (Table 2).

Estimation of Survivorship, Growth, Shrinkage, and Germination

For our stochastic projection models, we treated demographic rates as random variables; survivorship, growth, shrinkage, and germination rates were modeled as beta
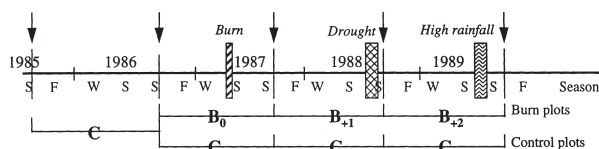
random variables (rvs; cf. Doak et al. 1994). The 4 years of data from the control plots were marginally sufficient to construct probability density functions (pdfs) for most control parameters through use of sample means and variances. Estimating pdfs for burn parameters, however, was not straightforward because only 1 year of data existed for each of the three burn matrices (Fig. 1). Consequently, we estimated burn pdfs by making two assumptions. First, we assumed that the spread of each burn pdf was identical to the spread of the corresponding control pdf. (The spread of a beta pdf [Link & Hahn 1996] is analogous to the coefficient of variation of a normal pdf.) Second, we assumed that annual environmental fluctuations caused similar deviations of observed values of burn and control demographic rates from their means. Details of how we constructed pdfs are available upon request from the corresponding author (K.G.) or the editorial office of *Conservation Biology*.

We modeled three levels of trampling reduction—no reduction, 50% reduction, and complete elimination—by increasing all survivorship parameters in accord with the expected reduction in *H. montana* mortality. In control plots, trampling accounted for 6.7%, 15.4%, 20.0%, and 0.0% of the mortality of tiny, small, medium, and large shrubs, respectively, whereas in burn plots the corresponding fractional mortalities were 9.5%, 22.2%, 40.0%, and 20.0%. Trampling mortality was more severe in burned plots because burning removes surrounding vegetative cover, making *H. montana* more vulnerable to hikers and campers. We averaged trampling mortality in the burned plots over the 3 years because it is unclear how a drought in 1988 and excess precipitation in 1989 (Fig. 1) altered *H. montana*'s vulnerability to trampling.

Because germination occurs in spring but censuses were performed in late summer (Fig. 1), germinating seeds in our models spent 7 months in the soil (September to March) and the remaining 5 months as tiny shrubs (Table 2). Because we have no information about seasonal variation in seed survival in the soil, we modeled survival during the time spent in the soil as a function of annual seed survivorship. Mortality of tiny shrubs, however, was higher and more variable during the summer months because tiny shrubs are much more susceptible to drought than larger ones (Table 2, Frost 1990). Consequently, we used separate parameters to model summer and winter survivorship of tiny shrubs. The field study did not explicitly record seasonal mortality of shrubs in other size classes, so average annual values were used. Nonetheless, because shrubs bear seeds at the beginning of the modeled time step, separating annual mortalities of these size classes into seasonal mortalities would not have changed the results of our model.

Although emergent seedlings were censused in control and burn plots for the three springs following the burn, we could not measure germination rates directly because the field study did not include seed addition experiments.

Figure 1. Time line of the major events in the H. montana *field experiment. Arrows indicate the timing of annual censuses.*

Table 1. Vital rates used to build a size-based matrix model for *H. montana*.

Parameter	Description	Stochastic form	Matrix								Elasticity[a]
			C		B_0		B_{+1}		B_{+2}		
			Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance	
$g_{sd \to ts}$	germination rate of overwintered seeds	beta random variable (rv)	0.0070	5.31×10^{-5}	0.0100	7.53×10^{-5}	0.0196	1.48×10^{-4}	0.0113	8.53×10^{-5}	0.0430
s_{sd}	annual survivorship of seeds in the soil	constant[b]	0.5012		0.5012		0.5012		0.5012		0.0699
ss_{ts}	summer survivorship of tiny shrubs	beta rv	0.5087	0.1385	0.5215	0.1385	0.8193	0.0820	0.5087	0.1385	0.1033
sw_{ts}	winter survivorship of tiny shrubs	beta rv[c]	0.9318	0.0047	0.9318[e]	0.0047	0.9318	0.0047	0.9318	0.0047	0.0602
$g_{ts \to ss}$	fraction of tiny shrubs growing given summer and winter survival	constant[d]	0.5000		0.5000		0.2000		1.0000		0.0309
s_{ss}	survivorship of small shrubs	beta rv	0.7923	0.0206	0.5515	0.0310	0.9680	0.0039	0.9066	0.0106	0.1530
$g_{ss \to ts}$	fraction of small shrubs shrinking given survival	beta rv	0.0495	0.0047	0.3080	0.0215	0.0062	6.22×10^{-4}	0.0891	0.0082	-0.0059
$g_{ss \to ms}$	fraction of small shrubs growing given survival and no shrinkage	beta rv	0.2205	0.0077	0.0749	0.0031	0.4781	0.0117	0.6628	0.0100	0.0315
s_{ms}	survivorship of medium shrubs	beta rv	0.9119	0.0029	0.7715	0.0063	0.9778	7.77×10^{-4}	0.8540	0.0046	0.3176
$g_{ms \to ts}$	fraction of medium shrubs shrinking two size classes given survival	beta rv	0.0109	3.54×10^{-4}	0.1431	0.0040	0.0254	8.15×10^{-4}	0.0069	2.27×10^{-4}	-0.0030
$g_{ms \to ss}$	fraction of medium shrubs shrinking one size class given survival and not shrinking two class sizes	beta rv	0.1056	0.0012	0.3600	0.0030	0.4647	0.0032	0.0894	0.0010	-0.0212
$g_{ms \to ls}$	fraction of medium shrubs growing given survival and no shrinkage	beta rv	0.1915	2.86×10^{-5}	0.5636	4.54×10^{-5}	0.2512	3.47×10^{-5}	0.2512	3.47×10^{-5}	0.0320
s_{ls}	survivorship of large shrubs	beta rv	0.9811	3.87×10^{-4}	0.8785	0.0022	0.9593	8.14×10^{-4}	0.9443	0.0011	0.3814
$g_{ls \to ss}$	fraction of large shrubs shrinking two size classes given survival	beta rv	0.0119	4.25×10^{-4}	0.2012	0.0058	0.0058	2.10×10^{-4}	0.0308	0.0011	-0.0032
$g_{ls \to ms}$	fraction of large shrubs shrinking one size class given survival and not shrinking two size classes	beta rv	0.1982	0.0270	0.1365	0.0200	0.4598	0.0422	0.0561	0.0090	-0.0311
f_s	viable seeds produced by a small shrub	normal rv	6.9863	0.6026	6.9863[e]	0.6026	0.8672	0.0093	1.7009	0.0357	0.0017
f_m	viable seeds produced by a medium shrub	normal rv	39.5786	215.0439	39.5786[e]	215.0439	6.9700	6.6692	17.4055	41.5892	0.0094
f_l	viable seeds produced by a large shrub	normal rv	172.1925	127.0693	172.1925[e]	127.0693	78.8107	26.6184	70.4227	21.2538	0.0320

[a]Elasticities for the control matrix (see Methods).
[b]Constant over all matrices due to lack of data.
[c]Data were insufficient to estimate effect of the burn on mean rates, so the same probability distribution was used for all matrices.
[d]Data were insufficient to construct a probability distribution about the control mean, so different constants were used for each matrix.
[e]Event occurs before burn and takes control value.

Table 2. Elements of a size-based matrix model for *H. montana*.

Matrix transition	Formula [a]
Seed → seed (Sd)	s_{sd}
Sd → tiny shrub (TS)	$(s_{sd})^{7/12} g_{sd \to ts} ss_{ts}$
TS → TS	$sw_{ts} ss_{ts} (1 - g_{ts \to ss})$
TS → small shrub (SS)	$sw_{ts} ss_{ts} g_{ts \to ss}$
SS → Sd	$f_s (1 - g_{sd \to ts}) s_{sd}$
SS → TS [b]	$f_s (s_{sd})^{7/12} g_{sd \to ts} ss_{ts} + s_{ss} g_{ss \to ts}$
SS → SS	$s_{ss} [1 - g_{ss \to ts} - g_{ss \to ms} (1 - g_{ss \to ts})]$
SS → medium shrub (MS)	$s_{ss} g_{ss \to ms} (1 - g_{ss \to ts})$
MS → Sd	$f_m (1 - g_{sd \to ts}) s_{sd}$
MS → TS [b]	$f_m (s_{sd})^{7/12} g_{sd \to ts} ss_{ts} + s_{ms} g_{ms \to ts}$
MS → SS	$s_{ms} g_{ms \to ss} (1 - g_{ms \to ts})$
MS → MS	$s_{ms} [1 - g_{ms \to ts} - g_{ms \to ss} (1 - g_{ms \to ts}) - g_{ms \to ls} (1 - g_{ms \to ts} - g_{ms \to ss} (1 - g_{ms \to ts}))]$
MS → large shrub (LS)	$s_{ms} g_{ms \to ls} [1 - g_{ms \to ts} - g_{ms \to ss} (1 - g_{ms \to ts})]$
LS → Sd	$f_l (1 - g_{sd \to ts}) s_{sd}$
LS → TS	$f_l (s_{sd})^{7/12} g_{sd \to ts} ss_{ts}$
LS → SS	$s_{ls} g_{ls \to ss}$
LS → MS	$s_{ls} g_{ls \to ms} (1 - g_{ls \to ss})$
LS → LS	$s_{ls} [1 - g_{ls \to ss} - g_{ls \to ms} (1 - g_{ls \to ss})]$

[a] *Parameter definitions given in Table 1.*
[b] *Includes both germinating new seeds and size shrinkage.*

We estimated the mean germination rate by constructing a mean control matrix with an unknown germination rate. We then tuned the germination rate to produce a slowly declining population, as observed in the field. (Specifically, a mean germination rate of 0.007 yielded an annual population growth rate of 0.9749.) Censuses of emergent seedlings in both burn and control plots for the three springs following the burn (Frost 1990) allowed us to quantify the variance in seedling emergence and the effects of burning on seedling emergence.

The field study also did not estimate long-term seed viability. Observations suggest that dormant seeds can remain viable in the seed bank for up to 10 years (C.C.F., personal observation). Thus, we computed an annual seed survival rate (0.512) that produced a small probability (0.001) of a seed surviving 10 years in the soil. We did not have enough information to estimate the variability in seed survival.

Finally, we made the growth of tiny shrubs ($g_{ts \to ss}$) a constant because the data were not sufficient to estimate the variance of a random variable. No data were collected for tiny shrub growth in the summer following the burn (1987), so we set $g_{ts \to ss}$ for $\mathbf{B}_0$ equal to the value for $\mathbf{C}$. We quantified the dependence of our model's results on these less-certain parameters by an elasticity analysis (see below).

Estimation of Fecundities

Photographs of the shrubs in the field study allowed us to count the number of fruits borne by shrubs in both burn and control plots (Frost 1990). Fruits recently collected from the field contained an average of 2.25 seeds. Frost (1990) estimates that 30% of dispersed seeds are viable. By combining these data, we estimated the number of viable seeds produced each year by shrubs in each size class.

For stochastic simulations, fecundity parameters were modeled as truncated (i.e., nonnegative) normal rvs. Control pdfs were determined by the sample means and variances of the average annual production of viable seeds by control plants in each size class. Because $\mathbf{B}_0$ includes seed set in the growing season prior to the burn (Fig. 1), fecundity parameters for $\mathbf{B}_0$ were the same as fecundity parameters for $\mathbf{C}$. Fecundities for $\mathbf{B}_{+1}$ and $\mathbf{B}_{+2}$ again presented the difficulty of constructing pdfs with only 1 year of data; we solved this problem using assumptions similar to those used to construct pdfs for burn matrix growth rates and survivorships.

Modeling Procedure

DETERMINISTIC MODEL

Mean parameter values were used to construct deterministic matrices. Because the dynamics of a population in a periodically varying environment are captured by the product of the matrices for the successive environments (Caswell 1989), population modeling was a straightforward exercise in matrix multiplication. The steady-state mean annual population growth rate (λ) for a burn cycle of length y years was calculated as the yth root of the dominant eigenvalue of the matrix product $\mathbf{P}_y = \mathbf{C}^{y-3} \mathbf{B}_{+2} \mathbf{B}_{+1} \mathbf{B}_0$ for $y \geq 4$. Not all matrices were incorporated for burn cycles shorter than 4 years: for example, $\mathbf{P}_2 = \mathbf{B}_{+1} \mathbf{B}_0$. Burn cycles ranging in length from 1 year to 20 years were modeled for each level of trampling control. We also simulated the transient dynamics for approximately the first 200 years following the initiation of management by itera-

tive matrix multiplication ($\mathbf{n}_{t+y} = \mathbf{P}_y\mathbf{n}_t$ until $t \geq 200$). The initial population vector $\mathbf{n}_0$ was set equal to the stable size distribution for the control matrix.

We quantified the dependence of our deterministic model's behavior on each parameter by performing two elasticity analyses (a parameter's elasticity value is the proportional change in λ that would be caused by a small proportional change in the parameter [Caswell 1989]). Using formulae of Caswell's (1989, equations 6.8 & 6.49), we first conducted a standard elasticity analysis of all vital rates underlying the mean control matrix. Such elasticity analyses are not easily conducted analytically for matrix products (Caswell & Trevisan 1994), so, in order to calculate approximate sensitivities for each burn-cycle matrix product, we perturbed (in turn) our less-certain parameters (e.g., germination rate, seed survivorship in the soil, and growth from tiny shrubs to small shrubs) by 0.01% and examined the resulting change in λ (Crowder et al. 1994, Appendix 2).

STOCHASTIC MODEL

Variation in environmental conditions causes correlated variation in *H. montana*'s vital rates. Frost (1990) suggested that the variances and covariances of these rates are a fundamental aspect of *H. montana*'s demography. Despite the fact that our ability to estimate correlations was limited by the duration of the field study, we chose to include the observed correlations in our model because correlations among demographic rates can considerably affect both population dynamics (Caswell 1989; Tuljapurkar 1990; Doak et al. 1994) and extinction risks (Ferson & Burgman 1995; Nakaoka 1996).

We estimated correlations between control parameters by calculating sample correlations between parameters for which we had three or more data points (data not shown). Due to lack of data, fecundities and winter survival of tiny shrubs were treated as independent variables. Construction of a separate correlation matrix for each burn matrix was impossible because only one data point was available for each burn parameter. Instead of ignoring potential correlations between burn parameters, we assumed that these correlations were identical to those between control parameters.

Generating values of correlated beta rvs is not straightforward given knowledge of only the marginal pdfs and the correlation matrix. To circumvent this difficulty, we obtained values for the beta rvs indirectly by mapping a random sample from a multivariate normal pdf onto the beta pdfs using marginal cumulative distribution functions. In so doing, we preserved the marginal pdfs of each beta rv and maintained a good approximation of each pairwise correlation. Details of this simulation method are available from K.G. or the editorial office of *Conservation Biology*. Independent parameters were drawn separately from their respective distributions.

For stochastic simulations, we began with a population of 1000 shrubs (roughly equal to the current population size) distributed among size classes in proportion to the stable size distribution of the control matrix (Table 3; 66,613 seeds, 447 tiny shrubs, 368 small shrubs, 355 medium shrubs, 277 large shrubs). Simulations were run for 200 years (beginning with a burn in year 1) plus the number of additional years necessary to complete the burn cycle in progress at year 200. Four hundred simulations were run for 39 management strategies. Specifically, for complete, partial, and no trampling control we simulated burn cycles of length 0 (i.e., no burning), 1–8, 10, 12, 15, and 20 years. The average annual population growth rate, λ, over the T years simulated was calculated from initial (N_0) and final (N_T) population sizes as

$$\lambda = \left(\frac{N_T}{N_0}\right)^{1/T}.$$

By computing λ in this way, our average annual population growth rate was a geometric and not an arithmetic mean (Lewontin & Cohen 1969). All stochastic simulations were carried out with S-PLUS (Statistical Sciences 1995).

Results

Deterministic Model

Although both controlled burns and reduction in trampling mortality increased *H. montana*'s population growth rate, neither tactic was sufficient by itself to produce a growing *H. montana* population (Fig. 2a). For all three levels of trampling reduction, population growth rates peaked at burn cycle durations of 5–8 years and asymptotically approached the control growth rate as burn frequency decreased. The intermediate optimum burn frequency suggests that the benefits of burning are maximized when the interim between burns is long enough to permit full *H. montana* recovery yet not long enough to allow *L. buxifolium* to recover as well. Burning increased λ for all three trampling-reduction schemes, but growth of the *H. montana* population was possible only when trampling

Table 3. Reproductive values and stable size distribution for a *H. montana* transition matrix under present conditons.

Size class	Reproductive value[a]	Stable size distribution[b]
Seed bank	0.023	97.874
Tiny shrubs	4.544	0.657
Small shrubs	14.145	0.541
Medium shrubs	31.063	0.521
Large shrubs	50.225	0.407

[a]*Dominant left eigenvector of the control matrix.*
[b]*Dominant right eigenvector of the control matrix.*
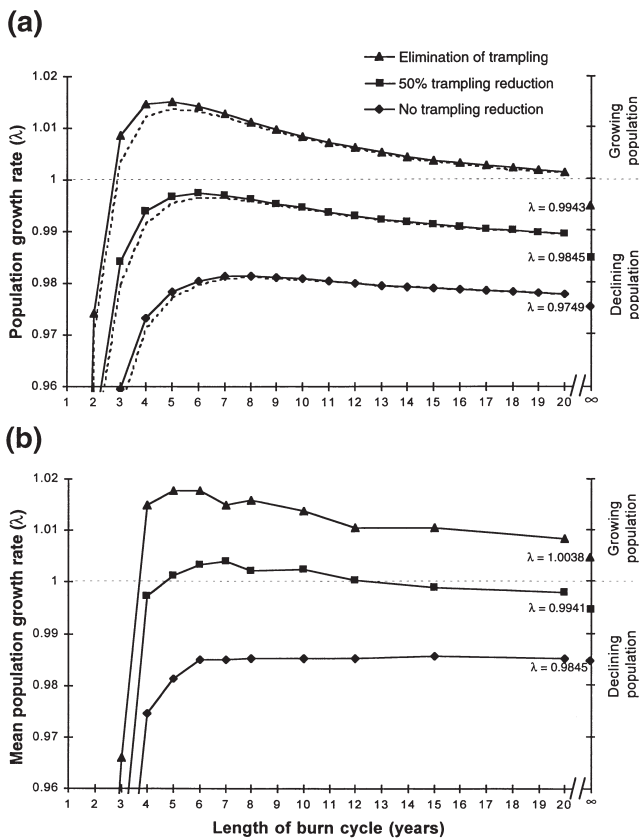
(a)

(b)

Figure 2. Annual population growth rate as a function of burn cycle length and trampling reduction for deterministic (a) and stochastic (b) models. In (a) solid lines are asymptotic rates and dashed lines show average annual population growth rates for the first 200 years of management.

Figure 3. Stable size distributions of above-ground H. montana *individuals for a subset of potential management strategies. Stable size distributions for 50% trampling reduction are intermediate between the two distributions illustrated (data not shown). Graphs do not show seeds in the soil (~98% of the population).*

was eliminated entirely. The gradual descent of λ from its peak value suggests that the positive effects of a burn persist beyond the optimal burn interval.

The stable size distribution of the control matrix represents the expected current distribution of *H. montana* individuals given the observed demographic rates (Table 3). This stable size distribution was numerically dominated by the seed bank. The number of shrubs in each size class became successively smaller with increasing shrub size. Controlled burning at short and intermediate intervals caused an increase in the proportion of individuals in the three larger size classes, whereas burning at long intervals produced only a minor shift in the stable size distribution (Fig. 3). Trampling reduction did not appreciably alter the stable size distribution. As one would anticipate, the reproductive value of the shrubs increased as the shrubs grew larger (Table 3).

The shift in the stable size distribution resulting from controlled burning caused the transient *H. montana* population growth rate to differ from the long-term, steady-state growth rate (Figs. 2a & 4). Because the initia-
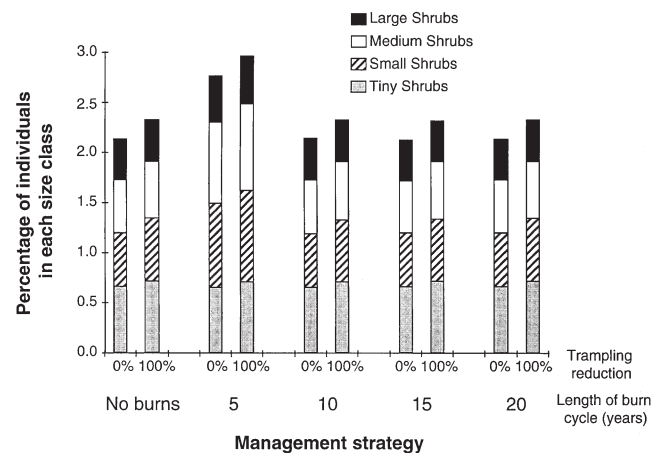
tion of burning caused a shift to a stable size distribution with more shrubs and fewer seeds, the short-term growth rate of the population of shrubs exceeded the growth rate of the whole population, and the short-term growth rate of the seed bank was less than that of the whole population. If shrub and seed populations were of roughly equal size, these effects would have canceled out. The initial seed bank, however, was nearly 70 times the size of the initial shrub population. As a result, the effect of the diminishing seed bank outweighed the exaggerated growth of the shrubs, causing the short-term growth rate of the whole population to underestimate the asymptotic rate.

Elasticity analysis of the control matrix without trampling reduction showed that the population growth rate would be most affected by small changes in the survivorship parameters (Table 1). Specifically, λ was most sensitive to the survivorship of large and medium shrubs, with the survivorship of small and tiny shrubs next in importance. Small changes in fecundity and growth parameters would alter the population growth rate the least.

The population growth rates predicted under burning scenarios were slightly more sensitive to our less-certain parameters than was the population growth rate under control conditions (data not shown). Small changes in each of our three less-certain vital rates (seed survivorship, seedling emergence, and tiny shrub growth) had the largest effect on λ predicted for a 2-year burn cycle, but the approximate elasticities for these vital rates were still much smaller than those for the survivorship of medium and large shrubs. As burn cycle length increased, elasticities for each parameter declined to control matrix values. This pattern held for all levels of trampling reduction, and λ for trampling reduction without burns had only slightly
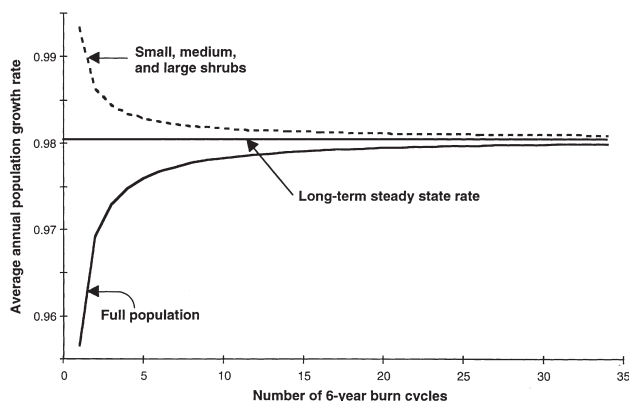
Figure 4. Transient population dynamics following the initiation of periodic burning. The dashed curve is the average population growth rate of the subpopulation of small, medium, and large shrubs, and the solid curve is the average annual population growth rate of the entire population. The horizontal line is the steady-state growth rate that will be observed when the population has reached its new stable size distribution. The dynamics shown here are for a management scheme of one burn every 6 years and no trampling reduction. Similar transient dynamics will occur for all intermediate burn frequencies that cause a shift in the population's stable size distribution (Fig. 3).
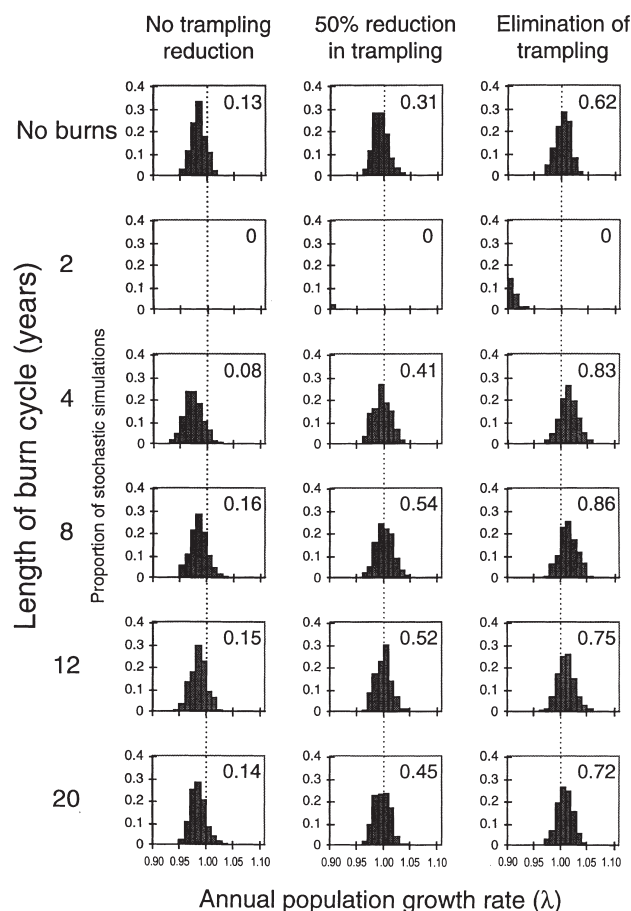

Figure 5. Frequency distributions of the annual population growth rate (λ) for a subset of burn frequencies and trampling-reduction strategies explored in stochastic simulations. The dashed line in each graph separates simulations with declining populations (left) from those with increasing populations (right). The proportion of simulations with growing populations is given in the upper right-hand corner of each histogram. Most of the simulations for a 2-year burn cycle yielded λ < 0.90; all other histograms show 400 simulations each.

(~10%) higher sensitivities to changes in uncertain parameters than did λ for the control matrix. In no case did a 1% perturbation of an uncertain parameter change the optimal burn frequency for a given level of trampling control.

Stochastic Model

The stochastic model predicted effects of burning and trampling reduction similar to those predicted by the deterministic model. Greater trampling reduction increased the average population growth rate (Fig. 2b) and the fraction of simulations with growing populations (Fig. 5). With reductions in trampling mortality, population growth rates were maximized at intermediate burn frequencies that roughly coincided with the optimal burn frequencies predicted by the deterministic model (Fig. 2). Without trampling control, the benefit of burning could barely be detected. Despite shifts in the frequency distribution of λ, its range remained roughly constant regardless of the management strategy (Fig. 5).

For the most part, the qualitative results of the stochastic model paralleled the results of the deterministic model. Both models predicted that combining high levels of trampling reduction with burn cycles of intermediate length would offer the most effective management strategy. In all cases, however, the stochastic population

growth rate was slightly (~1%) greater than the deterministic equivalent (Fig. 2). This discrepancy caused a few qualitative disagreements between the predictions of the models. Contrary to the deterministic model, the stochastic model predicted that *H. montana* population growth was possible with only a 50% reduction in trampling mortality. The stochastic model also predicted that *H. montana* populations would increase without burning if trampling were eliminated, whereas the deterministic model did not. The higher population growth rates in our stochastic model support speculation (Frost 1990) that the occasional benefits of wet years are essential to maintaining viable *H. montana* populations.

Discussion

Our results suggest that both controlled burning and the reduction of trampling will benefit populations of the threatened mountain golden heather *Hudsonia montana*. When combined, these two management tactics yield higher population growth rates than either management tactic alone. Our models indicate that it is not merely desirable but necessary to employ both strategies simultaneously in order to maximize the prospects for *H. montana* population growth. We discuss the strengths and limitations of the models and outline the implications of our results for the design of management strategies for mountain golden heather.

Performance and Limitations of the Model

Our confidence in our modeling results is bolstered by our elasticity analyses. For the control matrix, the parameters for which we had the sparsest data (seed germination rate, survival of seeds in the soil, and growth of tiny shrubs) had moderate to low elasticities (Table 1). Thus, small errors in estimating these parameters would result in only small changes in the predicted population growth rate. Moreover, the parameters with the largest elasticities were the shrub survivorships—parameters that were estimated with relatively large data sets.

Small changes in our uncertain parameters caused somewhat larger changes in the population growth rates predicted by our burn-cycle matrix products, but these changes in λ were still small compared to those caused by changes in vital rates that we were able to estimate with greater certainty (e.g., survival of larger plants). Moreover, these perturbations did not alter the optimal burn cycle lengths for any level of trampling reduction. Short burn cycles had the highest sensitivities to the less-certain parameters; predicted growth rates for longer burn cycles, including those near the optimum, were more robust to small parameter changes. Because managers are more apt to lengthen the burn cycle than to shorten it, the model's management implications are not as likely to be altered by estimation errors in our less-certain parameters.

Although these elasticity analyses examine only small perturbations of parameters (Caswell 1989), the agreement of our control model with observed *H. montana* population dynamics implies that the errors in our less-certain parameters are probably not very large. More sizable (25%) perturbations of our uncertain parameters predicted either rapid population growth or rapid decline—predictions that were at odds with observational data. Nonetheless, errors in our less-certain parameters were not insignificant; future field studies should focus on obtaining more precise empirical estimates of these rates. Given the results of our sensitivity analyses, how-

ever, we believe that these models can provide reasonable guidance for assessing management options by using the limited data available for *H. montana*.

Our models assume that subsequent burns will produce effects similar to those of the first burn. Because the experimental burn was the first fire event in approximately 40 years, the benefits of the experimental burn may well exceed those of subsequent, regularly scheduled burns. Unfortunately, we are again limited by a lack of data: multiple experimental burns have not been performed. Without an a priori expectation of how *H. montana* will respond to future burns, the best we can do is to use the available data to predict the effects of future burns. Nonetheless, it would be prudent in future work to monitor the response of *H. montana* individuals to multiple burns.

Implications for Management

Both controlled burns and trampling reduction can slow *H. montana*'s decline, but neither strategy by itself is sufficient to produce a growing *H. montana* population. According to our deterministic model, periodic burning alone could achieve an annual population growth rate of only 0.9814, a rate that would reduce the population to 2.3% of its current size in 200 years. Our stochastic model predicted that periodic burning alone would have a 17.3% chance of reversing *H. montana*'s decline. In contrast, the elimination of trampling mortality could bring *H. montana*'s population growth rate very close to 1. With trampling mortality eliminated, our deterministic model predicted an annual growth rate of 0.9943 (equivalent to a reduction to 31.9% of current population size in 200 years), and our stochastic model predicted a 62.0% chance of a growing population. Although these stochastic results may seem encouraging, full elimination of trampling is probably not feasible. Trampling elimination would require severe restrictions on recreational access to the popular Linville Gorge Wilderness Area, and logistical and political difficulties probably preclude such extreme measures. Further, even if trampling mortality could be entirely eliminated, managers would still face a nearly 40% risk of continued *H. montana* decline. Therefore, we believe that it would be unwise to focus management efforts solely on eliminating trampling-induced mortality.

Our results suggest that management strategies that integrate controlled burning with trampling reduction hold more promise. Combining the two management tactics could yield a deterministic growth rate of 1.0152 and an 88.75% chance that the *H. montana* population will grow over the next 200 years. A two-pronged management strategy is more apt to succeed in part because burning makes cliff-side habitat more accessible to hikers and campers. Consequently, without reductions in trampling, the benefits of controlled burns will be partially off-

set by increased trampling mortality. Controlled burns will be most effective when trampling reduction measures are employed simultaneously. For example, our deterministic model predicts that optimal burning will increase the population growth rate by 0.67% without trampling reduction, whereas optimal burning with trampling elimination will increase population growth by 2.10% (Fig. 2). Combining burning with trampling reduction also allows for some flexibility in choosing a specific plan; a broad range of combinations of burn schemes and levels of trampling reduction provide a reasonable chance of producing a resurgent *H. montana* population.

To achieve the maximal benefit from periodic burning, a burn frequency of once every 6–8 years is optimal. Interestingly, this burn frequency is similar to the estimated natural lightning-induced fire frequency in *H. montana*'s habitat of once every 5–10 years (Frantz & Sutter 1987). The intermediate optimum results from two opposing forces. Overly frequent fires will restrict *H. montana*'s ability to capitalize on space relinquished by *L. buxifolium* because the newly sprouted *H. montana* shrubs will encounter another fire while they are still small. Small and medium-sized shrubs have a relatively high risk of dying during a fire (Table 1), so the interim between fires must be long enough to allow new *H. montana* shrubs to grow to hardier sizes. On the other hand, if fires are too infrequent, *L. buxifolium* will have time to recover the ground cover it has lost, shading out new *H. montana* shrubs and eliminating its territorial gains. Because *L. buxifolium* is able to persist under intermediate burn frequencies, this system represents an example of Connell's (1978) intermediate disturbance hypothesis: intermediate fires allow the coexistence of a rapidly recovering inferior competitor (*H. montana*) with a more slowly recovering superior competitor (*L. buxifolium*).

The slow decline in population growth rate from its maximum with increasing length of burn cycle (Fig. 2) has favorable economic and political implications for *H. montana* management. Managers can extend the interim between burns beyond the optimum while incurring only a slight reduction in *H. montana*'s growth rate. If controlled burning is implemented, dividing *H. montana*'s habitat into blocks that are burned in an annual rotation would be more feasible, less ecologically traumatic, and less risky than attempting to burn the entire habitat in 1 year. Hiking and camping restrictions could then be instituted preferentially in recently burned areas, thus protecting those shrubs most vulnerable to trampling. If the interim between the burning of individual blocks could be extended, less ground cover would need to be burned each year, and the annual cost of burn management would decrease. Given the scarcity of human and financial resources in conservation efforts and the concerns of owners and users of neighboring land about the risks incurred by burning, halving the optimal burn frequency

from once every 6–8 years to once every 12–16 years may be desirable and prudent.

Managers should be aware of three implications of the transient dynamics that we anticipate will follow the onset of burning (Fig. 4). First, because the population of shrubs in the larger size classes will initially grow at a rate exceeding the long-term growth rate, censuses of only these shrubs are apt to overestimate the long-term benefit of the burns. Second, the diminishing rate of increase of the shrub population as more burn cycles are completed should not be interpreted as evidence of decreasing benefit from the burns; rather, this decline is only a by-product of a changing stable size distribution. Finally, 6–10 burn cycles (36–80 years with intermediate burn frequencies) may be necessary to obtain field estimates of the asymptotic *H. montana* growth rate under periodic burning (assuming that density dependence not included in our models remains negligible). Due to this long lag time, population models will be necessary to assess management strategies in a timely fashion.

Projection matrix models have been influential in guiding formation of conservation-minded legislation in the past (e.g., Crowder et al. 1994). Our models stress the necessity of conducting periodic controlled burns and curtailing mortality imposed by hikers and campers in order to revitalize *H. montana* populations. Neither tactic needs to be implemented in its most extreme form. A 60–80% reduction in trampling mortality combined with a controlled burn every 12–16 years would be compatible with conservation goals. More broadly, our models demonstrate how matrix models can use limited field data to compare management options and to identify optimal combinations of multiple strategies. Our stochastic simulations provide another example (cf. Menges 1990; Doak et al. 1994) of how species with significant annual variation in demographic rates can be modeled in a matrix framework. Finally, our results show how matrix models can help managers to adjust a management program to political and economic realities (e.g., lengthening the interval between burns) without jeopardizing the program's chance of success.

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