

Dynamics of Buckbrush Populations Under Simulated Forest Restoration Alternatives



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Abstract—Plant population models are valuable tools for assessing ecological tradeoffs between forest management approaches. In addition, these models can provide insight on plant life history patterns and processes important for persistence and recovery of populations in changing environments. In this study, we evaluated a set of ecological restoration alternatives for their long-term effects on buckbrush (*Ceanothus fendleri* Gray), a shrub common in understories of ponderosa pine (*Pinus ponderosa* Laws. var. *scopulorum* Engelm.) forests of the southwestern United States. The field data were collected from a set of forest restoration units located on the Fort Valley Experimental Forest. We constructed simple stage-based models in order to simulate 25-year population dynamics. Results showed that scenarios that included overstory thinning, herbivore protection, and prescribed fire resulted in buckbrush populations with significantly greater numbers of aboveground stems than populations in the other alternatives. Vegetative stem recruitment, flowering, and seedling emergence were important in producing these results. For alternatives that included protection from herbivores, burning at 2-year frequencies resulted in populations with significantly greater numbers of aboveground stems than scenarios with longer intervals between burning. In contrast, frequent burning in alternatives without herbivore protection resulted in population decline. These results indicate that protecting buckbrush from large herbivores allowed plants to complete life cycles and fully express these life history traits. This research demonstrates that population modeling can help illuminate ecological tradeoffs associated with land management alternatives.

Introduction

Buckbrush is a common shrub found in northern Arizona ponderosa pine forests. It is capable of nitrogen-fixation, provides important browse for wildlife such as mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), and adds structural diversity to predominantly herbaceous understories of these ecosystems (Allen 1996, Story 1974, Urness et al. 1975).

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Plant life history traits are adaptive strategies that influence a species' potential for survival, growth, and reproduction in a changing environment (Bellingham and Sparrow 2000). Life history traits include characteristic seed germination requirements, rates of growth and development of individuals, patterns of flowering, and recruitment of new individuals (Barbour et al. 1999). With an understanding of how life history traits and environmental conditions interact, models of long-term plant population dynamics may be constructed. Such models can be useful in evaluating potential effects of various land management alternatives. Our objectives in this study were the following: (1) to construct population models that describe demographic responses of buckbrush (*Ceanothus fendleri* Gray) to various treatment alternatives used to restore southwestern ponderosa pine forests. (2) to use these models to analyze long-term effects of restoration alternatives on buckbrush populations; and (3) to interpret model results in order to provide information useful to ecologists and forest managers.

Methods

Demographic and Life Stage Data

To build buckbrush population models, we used life history and demographic data derived from field and laboratory experiments conducted 1999-2002. Field experiments were conducted on the Fort Valley Experimental Forest about 7 km northwest of Flagstaff. We established a total of 210 buckbrush-centered plots in three experimental forest restoration units and three untreated units (see Fulé et al. 2001 for forest restoration experiment details). Buckbrush plots were 2 x 2 m in size. We randomly assigned each plot to one of five treatments: (1) no thinning, no herbivore protection, no prescribed fire (control); (2) overstory thinning only (thin-only); (3) overstory thinning plus herbivore protection (thin-protect); (4) overstory thinning plus prescribed burning (thin-burn); and (5) overstory thinning plus herbivore protection plus prescribed burning (thin-protect-burn). Herbivore protection was provided by wire fence exclosures built around plots. Plots were burned with prescribed, low-intensity fire in April-May, 2000 and 2001. Field data were collected each year 1999-2002 and included measurements of flowering, seed production, stem density, and seedling density (see Huffman 2003 for details). In addition, seed germination characteristics, including response to heat and cold stratification, were determined in the laboratory.

Simulation Modeling and Analysis

To model management effects on population dynamics, the life cycle of buckbrush was simplified into four discrete stages (Figure 1). Seeds and aerial stems were chosen as the population units of analysis. Aerial stems were defined as individuals that arose singularly from the soil surface but with various amounts of aboveground branching. Stage-based transition matrices (Caswell 2001) were built from 1999-2002 field and laboratory data. Vital rates for stage elements were calculated as the average of the annual changes for each life stage transition over the four years of field study. Separate transition matrices were constructed for buckbrush

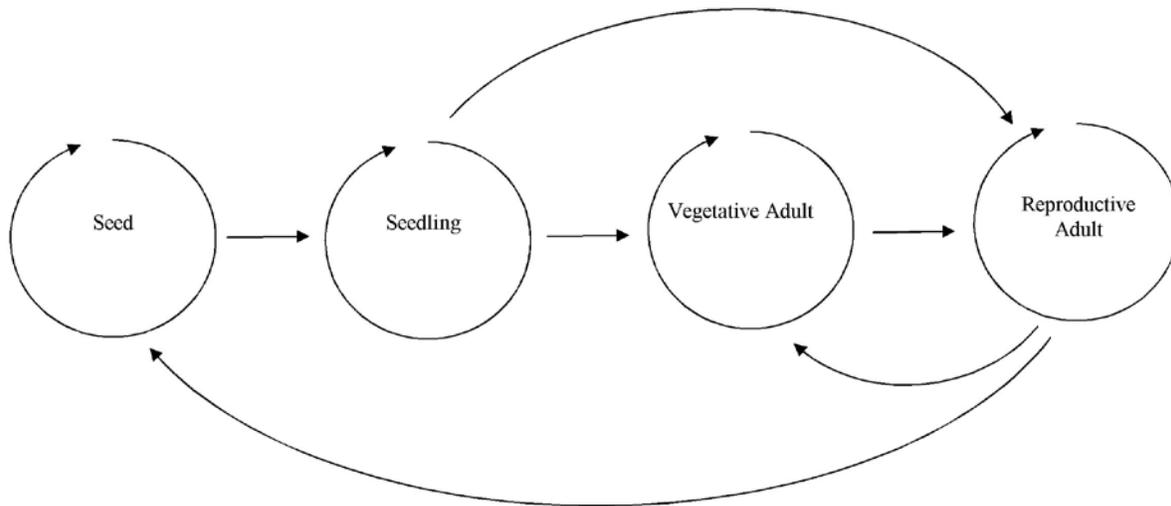


Figure 1. Simplified life cycle of buckbrush (*Ceanothus fendleri*) based on field observations. Seedlings are identified by size and presence of cotyledons (seed leaves). Vegetative stems produce no flowers whereas reproductive stems do flower. Arrows indicate probable life stage transitions, including seed contributions from reproductive adult stems.

field data from each experimental forest unit ($n=3$) and were used as replicates in our analysis. Details of vital rate assumptions and calculations are described in Huffman (2003). Buckbrush population dynamics for the five management scenarios were modeled using the computer software RAMAS Metapop (Akçakaya 1998). Model parameters, including stochasticity, initial population structure, and density dependence, are found in Huffman (2003). One-year time step and 25-year duration was used for all simulations. Prescribed burning scenarios were modeled by treating fire as a probabilistic “catastrophe” in the plant population sense of the word (Harper 1977). In years when fire occurred, we adjusted vital rates to reflect values derived from field and laboratory observations of fire response. In addition to analyzing 25-year buckbrush dynamics for the five restoration alternatives, we also examined effects of 2, 5, 10, and 25-year prescribed fire intervals for overstory thinning alternatives with and without herbivore protection by varying fire probabilities in our model.

We used analysis of variance (ANOVA) and Bonferroni adjusted pairwise comparisons to test effects of restoration alternatives on the following model outputs: (1) total abundance (population size including seeds); (2) total number of above-ground plants (not including seeds); and (3) relative abundance of each life stage at the end of the 25-year period. Output values analyzed were the average of 1000 simulations for each restoration alternative and P -values less than 0.05 were considered statistically significant.

Results

Restoration alternatives that included protection from large herbivores had significantly greater rates of population increase ($\lambda=1.33$) than those that did not include protection ($\lambda=0.99-1.06$) (Table 1). Prescribed fire did not change model estimates of λ . Population trajectories showed considerably different patterns among the five

management scenarios (Figure 2). At the end of the 25-year period, the thin-protect alternative had significantly greater total population abundance (aerial stems plus seeds) than control and thin-burn alternatives (Table 2). Thin-protect-burn and thin-only had significantly greater total abundance than thin-burn. Restoration scenarios also affected abundance of individuals in the four life stages (Table 2). For example, thin-protect-burn had significantly greater number of aerial stems and relatively more seedlings and reproductive stems than all other alternatives (Table 2).

Fire frequency and protection from herbivores interacted to affect buckbrush population size and structure (Figure 3). Total population abundances of protected and unprotected populations at the end of the simulated period were significantly greater under the 25-year prescribed fire interval than under the 2-year interval. Both protected and unprotected populations showed a pattern of increasing seed abundance with longer intervals between fires (Figure 3). However, herbivore protection and fire interval interacted to affect abundance of other life stages. For example, seedling, vegetative and reproductive stem abundances tended to decline in protected populations but increase in unprotected populations as fire interval decreased (Figure 3).

Table 1. Mean values and standard error (SEM) of finite rate of increase (λ) for simulated management scenarios of buckbrush (*Ceanothus fendleri*). Prescribed fire did not affect values of λ . Different letters associated with values denote statistically different means at $P \leq 0.05$.

Restoration Alternative	λ	SEM
Control	0.99 b	0.001
Thin-only	1.06 b	0.036
Thin-protect	1.33 a	0.044

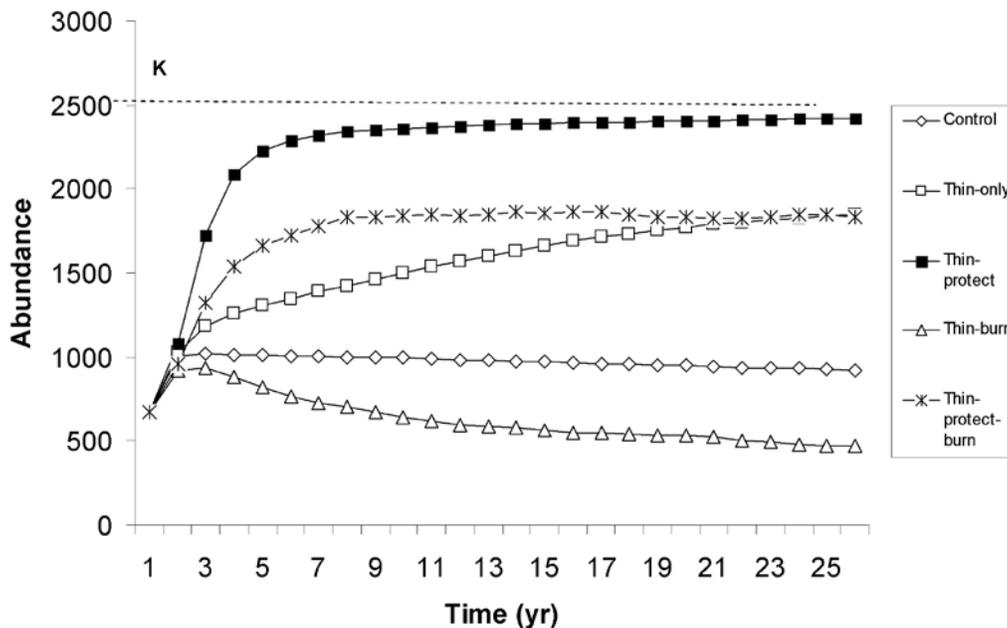


Figure 2. Buckbrush (*Ceanothus fendleri*) population trajectories for five restoration management scenarios. Abundance is total number in population, including dormant seeds. Chart shows carrying capacity (K) “ceiling” for abundance, which was a user-defined model parameter.

Table 2. Mean characteristics of buckbrush populations (*Ceanothus fendleri*) after 25-year simulations of five restoration alternatives. Different letters read across management scenarios denote statistically different means at $P \leq 0.05$.

Characteristic	Restoration Alternative				
	Control	Thin-only	Thin-protect	Thin-burn	Thin-protect-burn
<u>Number in Population:</u>					
Aerial stems ¹	25.6 b	198.4 b	119.4 b	175.9 b	575.8 a
Total ²	922.3 bc	1847.1 ab	2420.0 a	468.2 c	1832.4 ab
<u>Relative Abundance in Population (%):</u>					
Seeds	97.2 a	90.6 a	95.0 a	58.3 b	68.6 b
Seedlings	1.3 b	1.1 b	1.0 b	8.9 a	10.3 a
Vegetative	1.4 b	8.0 ab	2.4 b	31.8 a	16.3 ab
Reproductive	<0.01 c	0.3 bc	1.6 b	1.1 bc	5.8 a

¹ Number of aerial stems in population—does not include seeds.

² Number in population; total aerial stems plus seeds.

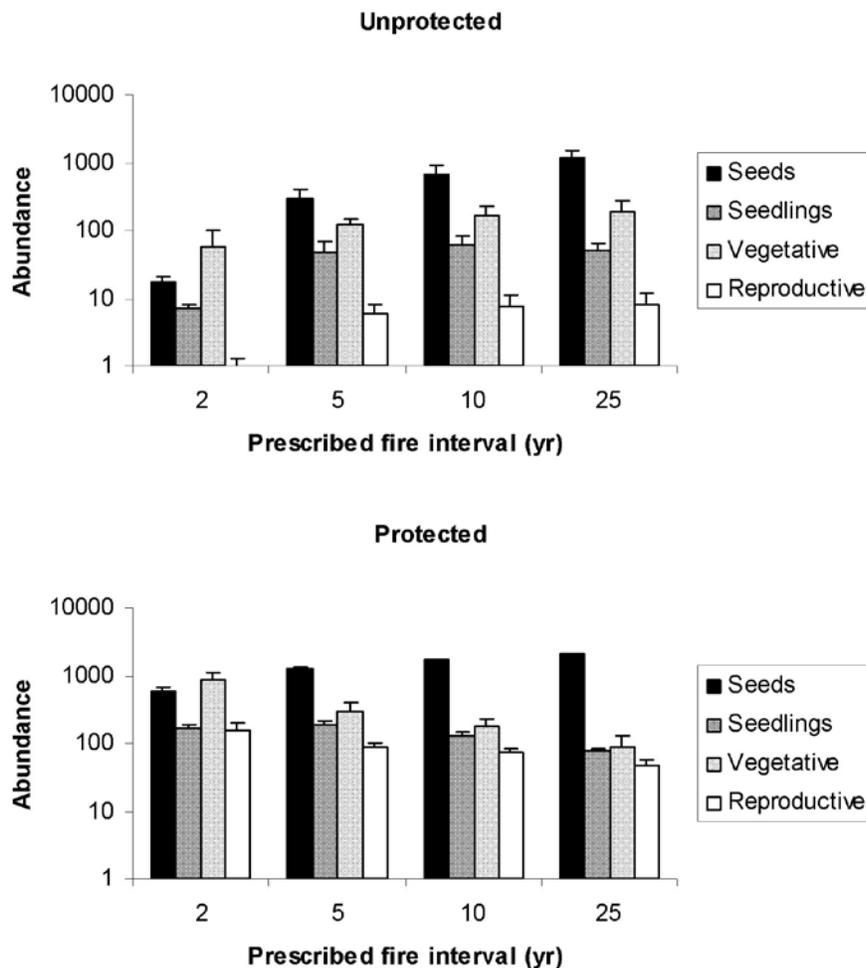


Figure 3. Life stage abundances (number in population) for buckbrush populations protected and unprotected from large herbivores under four simulated prescribed fire intervals.

Discussion and Conclusions

Results of this study indicated that buckbrush populations benefit most from restoration alternatives that include overstory thinning, prescribed fire, and protection from large herbivores. These results reflected responses linked to the life history of this species. Important responses were the following: (1) seedling emergence in years of fire due to heat scarification of seeds (Huffman 2006); (2) recruitment of vegetative stems from belowground buds in both fire and no-fire years; and (3) recruitment of reproductive stems in years without fire. For control populations, aerial stems showed gradual attrition, although seed survival in seed banks may represent potential for eventual population recovery. These responses demonstrated evolutionary characteristics that allow buckbrush to thrive in open forests with frequent, low-severity fire regimes (Arnold 1950, Fulé et al. 1997). Protecting buckbrush from large herbivores appeared to allow plants to complete life cycles and fully express life history traits. Prescribed fire facilitated recruitment of new individuals, a process that may enhance population viability by increasing genetic variation. In contrast, intensive use by large herbivores such as Rocky Mountain elk appeared to constrain long-term population growth and simplify population structure. This research demonstrates that population modeling can help provide insights concerning ecological tradeoffs associated with land management alternatives.

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