EFFECTS OF AN INTRODUCED PATHOGEN AND FIRE EXCLUSION ON THE DEMOGRAPHY OF SUGAR PINE

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Abstract. An introduced pathogen, white pine blister rust (*Cronartium ribicola*), has caused declines in five-needled pines throughout North America. Simultaneously, fire exclusion has resulted in dense stands in many forest types, which may create additional stress for these generally shade-intolerant pines. Fire exclusion also allows fuels to accumulate, and it is unclear how affected populations will respond to the reintroduction of fire. Although white pine blister rust and fire exclusion are widely recognized threats, long-term demographic data that document the effects of these stressors are rare. We present population trends from 2168 individuals over 5–15 years for an affected species, sugar pine (*Pinus lambertiana*), at several burned and unburned sites in the Sierra Nevada of California. Size-based matrix models indicate that most unburned populations have negative growth rates (λ range: 0.82–1.04). The growth rate of most populations was, however, indistinguishable from replacement levels (λ = 1.0), implying that, if populations are indeed declining, the progression of any such decline is slow, and longer observations are needed to clearly determine population trends. We found significant differences among population growth rates, primarily due to variation in recruitment rates. Deaths associated with blister rust and stress (i.e., resource competition) were common, suggesting significant roles for both blister rust and fire exclusion in determining population trajectories. Data from 15 prescribed fires showed that the immediate effect of burning was the death of many small trees, with the frequency of mortality returning to pre-fire levels within five years. In spite of a poor prognosis for sugar pine, our results suggest that we have time to apply and refine management strategies to protect this species.

Key words: Cronartium ribicola; *demography; fire exclusion; matrix model;* Pinus lambertiana; *population decline; prescribed fire; sugar pine; tree mortality; white pine blister rust.*

INTRODUCTION

Five-needled pines across North America are confronting evolutionarily novel stressors. The invasion of an exotic fungal pathogen, white pine blister rust (*Cronartium ribicola* J. C. Fisch. Ex Raben; hereafter blister rust), has led to massive die-offs for some affected populations (Kendall and Keane 2001). Another threat to five-needled pines is fire exclusion, which has simultaneously led to increased forest densities and fuel loading in many forest types (Agee 1993). Dense forests may reduce the potential for regeneration of generally shade-intolerant species such as five-needled pines (Mast et al. 1999, Stephenson 1999, Taylor 2000, Peterson and Hammer 2001), while fuel accumulations may lead to increased tree mortality when fire eventually reoccurs. Five-needled pines dominate many forest communities, and their decline can lead to cascading ecosystem effects (Tomback and Kendall 2001, Mattson and Merrill 2002). Although blister rust and fire exclusion are widely recognized threats, there are

relatively few data showing the demographic effects of these stressors. Long-term demographic data for perennial plants are difficult to collect (Menges 2000), but are necessary to address basic questions concerning the population-level consequences of these stressors.

A relatively large body of literature documents the range and severity of infection of blister rust (e.g., Campbell and Antos 2000, Smith and Hoffman 2000, Duriscoe and Duriscoe 2002). Such documentation is important because it is presumed that where blister rust infections occur, rapid declines in pine populations will ensue. This assumption is likely warranted; where demographic rates of infected stands have been measured, high death rates or poor recruitment have been observed (Keane and Arno 1993, Tomback et al. 1995, Kendall and Keane 2001). A more complete picture of affected species would combine measurements of reproduction, growth, and mortality. It is also important to note that many stands affected by blister rust also may be responding to fire exclusion, making it difficult to separate the relative effects of these two stressors. There is a possible relationship between disease and fire history, which could give rise to unexpected effects (Paine et al. 1998). For example, dense stands may

PLATE 1. Mature suger pine (*Pinus lambertiana*) growing in Sequoia National Park, California. Photo credit: National Park Service.

result in poor growing conditions, which in turn lead to increased susceptibility to blister rust attacks.

We use annual-resolution data from long-term monitoring plots to determine current population trends for sugar pine (*Pinus lambertiana* Doug.) in the Sierra Nevada of California, USA. This study is unique in that we conduct a demographic analysis of a species affected by blister rust and fire exclusion, and show how stands respond to prescription burning. Using size-structured matrix population models we address four questions. (1) Is sugar pine declining across our sites? (2) What distinguishes sites with different rates of population growth? (3) What are the relative effects of white pine blister rust and fire exclusion on sugar pine populations? (4) How might the reintroduction of fire affect population fates?

METHODS

Species background

Sugar pine is a coniferous tree found from the west slope of the Cascade Range in central Oregon, USA, to the northern Baja California peninsula, Mexico (Kinloch and Scheuner 1990; see Plate 1). The highest den-

sities of sugar pine are found along the western slope of the Sierra Nevada, California, USA, in ponderosa pine and white fir–mixed conifer forests at elevations between 1200 m and 2200 m (Rundel et al. 1977). Sugar pine is a moderately abundant species in both forest types, usually comprising 5% to 8% of stand densities. Sugar pine is the largest of all pines (heights may reach 60 m with diameters >150 cm), and is valued as a timber resource and for aesthetic reasons (Kinloch and Scheuner 1990). Cone production is concentrated in large (>40 cm dbh) trees (Fowells and Schubert 1956). Seeds are not stored in long-term seed banks, and this species does not reproduce vegetatively (Kinloch and Scheuner 1990). Compared to co-occurring species, sugar pine is considered moderately shade intolerant (Baker 1949).

Blister rust was first successfully introduced in western North America in 1910, and reached the southern Sierra Nevada by the early 1960s (Kinloch and Dulitz 1990). The blister rust fungus has a complex life history, and depends on currant (*Ribes* spp.) as well as five-needled pines to complete its life cycle. Eradication attempts based on *Ribes* removal have been unsuccessful, due to the small number of host *Ribes* needed to continue the propagation of the disease (Maloy 1997). Blister rust attacks pines by entering through the needles, eventually infecting the vascular tissue, leading to classic symptoms of branch swelling, needle dieback, or "flagging," and production of cankers and fruiting bodies (McDonald and Hoff 2001). Once the hyphae reach the vascular tissues in the stem, the tree will eventually become girdled, thereby killing portions of the tree distal to the infection. Small sugar pines may be killed directly by the blister rust fungi, while severe infections in larger trees may lead to bark beetle infestations (*Dendroctonus* spp.) that kill the tree (Kinloch and Dulitz 1990). Sugar pine shows little genetic resistance to blister rust (Kinloch 1992), and there is widespread concern for the long-term fate of this species (Ferrell 1996).

Field sites

Permanent study plots were established in the coniferous forest belts of Sequoia and Yosemite National Parks in the Sierra Nevada of California (Table 1, Fig. 1). We refer to these plots as the 1-ha plots to distinguish them from other plot data (see *Methods*: *Effects of fire*). The sites have never been logged. The plots encompass a range of conditions, from dry and open to mesic and closed. The climate is mediterranean, with hot, dry summers and cool, wet winters, with about half of annual precipitation falling as snow (Stephenson 1988). Average January and July air temperatures are roughly 2°C and 19°C, respectively (Major 1977). Fire was a frequent occurrence in Sierran forests prior to European settlement, but the areas containing the study plots have not burned since the late 1800s (Swetnam et al. 1992).

TABLE 1. Characteristics of 1-ha permanent forest plots.

Population and plot name	Year established	Elevation (m)	Plot size (ha)	Initial stem count†	Proportion infected by blister rust in 2001	Plot basal area in 2001 (m²/ha)	Species composition (%)‡
Suwanee Creek							
SuwABCO	1983	2035	0.9	58	0.43	74.1	ABCO 60; CADE 26; PILA 9; ABMA 5
SuwCreek	1983	2033	1.4	201	0.16	52.4	ABCO 59; CADE 21; PILA 14; ABMA 5; QUKE 1
SuwPILA	1983	2059	1.1	160	0.21	62.5	ABCO 72; PILA 17; CADE 10; QUKE 1
Crystal Road							
BBBPIPO	1992	1609	1.0	63	0.10	63.0	CADE 55; QUKE 24; ABCO 13; PILA 5; PIPO 3
CCRPIPO	1991	1637	1.1	109	0.13	58.0	ABCO 47; CADE 29; QUKE 15; PILA 5; PIPO 4
Hodgedon Meadows							
YOHOPIPO	1991	1500	1.0	753	0.21	76.3	ABCO 36; CADE 33; PILA 24; PIPO 5; PSME 1; QUKE 1
Crane Creek							
CRCRPIPO	1993	1637	1.0	324	0.37	74.7	ABCO 44; CADE 29, PILA 18, PIPO 6
Tharp Creek§							
Upper Tharp	1984	2202	1.0	7	0.33	45.9	ABCO 96; PILA 3; PIJE 1
Lower Tharp	1984	2167	1.1	94	0.43	60.5	ABCO 77; PILA 15; QUKE 8; SEGI 2; PIJE 1

† *Pinus lambertiana* (sugar pine) stems ≥1.37 m tall.

‡ Species composition of all individuals ≥1.37 m tall at time of plot establishment. Percentages may not add up to 100 due to rounding. Key to abbreviations: ABCO, *Abies concolor*; ABMA, *Abies magnifica*; CADE, *Calocedrus decurrens*; PIJE, *Pinus jeffreyi*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; QUKE, *Quercus kelloggii*; SEGI, *Sequoiadendron giganteum*.

§ Plots burned in 1990 prescribed fire; all other plots are unburned.

Data collection

In each 1-ha plot all trees ≥1.37 m in height were tagged, mapped, measured for diameter, and identified to species. We performed mortality assessments annually starting at the time the plots were established. Trees were recorded as dead only if they showed complete needle browning or loss. Dead trees were further classified by cause of death (see *Methods*: *Effects of blister rust and fire exclusion*). We took measurements of live tree stem diameter at breast height (1.37 m) typically at 5-yr intervals. Breast height was marked with a nail for precise relocation. During the measurement years, new trees (ingrowth reaching 1.37 m) were recorded as recruitment. Starting in 1999 the plots have been measured annually for new recruits. From 1999 to 2002, 9% of sugar pine recruits died before a plot measurement, suggesting that there have been a small number of uncounted "ghost" mortalities in the years preceding 1999. Since plot establishment we have kept records of live tree condition, but starting in 1998 we have explicitly tracked the presence of blister rust symptoms (i.e., branch flagging, cankers, and blister rust fruiting bodies). Beginning in 1999 we have collected data annually on seedlings (stems <1.37 m) in two 25 m² subplots within each 1-ha plot.

Matrix model construction

We removed five trees due to missing data, leaving 1847 sugar pine individuals observed over 5–15 years for the unburned data set. We organized our data into size-structured matrix population models. Caswell (2001) provides a comprehensive description of this approach. Our data supported the creation of five stem diameter classes (Table 2). These size classes roughly correspond to canopy position (i.e., sapling, understory, intermediate, co-dominant, dominant; N. Stephenson, *unpublished data*). No backward transitions or skipping size classes were permitted. Frequencies of growth and mortality were taken directly from field observations. We did not measure the fecundity of individual trees. Lacking fecundity data, we estimated reproductive output based on recruitment of new trees (see *Methods*: *Data collection*), with the assumption that only trees >40 cm dbh were responsible for the observed recruitment. This assumption is based on the results of Fowells and Schubert (1956), who found only rare instances of cone production for sugar pines <40 cm dbh in a long-term study of conifer reproduction in the central Sierra Nevada. Our method for estimating recruitment is rough, but makes few assumptions concerning the reproductive biology of this species (Har-
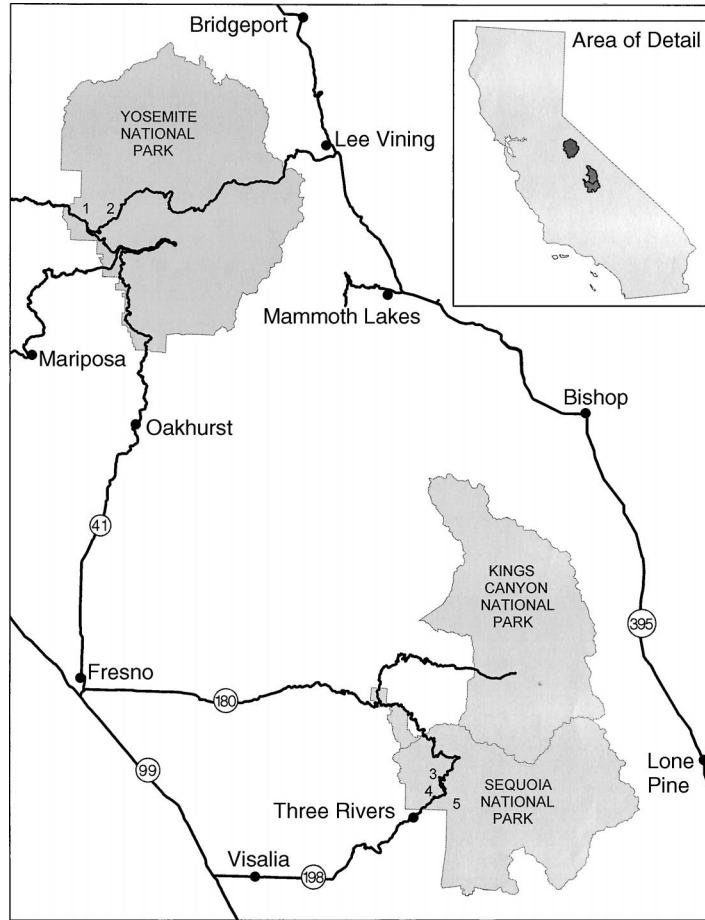
FIG. 1. Locations of 1-ha permanent plots, with numbers referring to individual plots or groups of adjacent plots: (1) Hodgedon Meadows, (2) Crane Creek, (3) Suwanee Creek, (4) Crystal Road, (5) Tharp Creek.

combe 1987, Batista et al. 1998). Seedling data were not of sufficient duration to be included in our models, although we present the results of the seedling census for 2001 relative to the number of potential parent trees (stems >40 cm dbh) in a 75-m² area encompassing each seedling subplot.

In most cases we grouped 1-ha plots that shared geographical proximity and similar elevations to estimate transition probabilities. We considered individual plots or plot groups where we could create independent models as populations (Table 1). Occasionally there were no observations of a stage transition within a population, when biologically this transition, though rare, must occur. We accounted for these transitions by calculating the probability that a "null" observation occurs in 50% of cases, given a binomial distribution and the observed sample size (Parker 2000). For example, during 1991–1996 we had seven trees >40 cm dbh in the Crystal Road population, with no observations of mortality. We calculated the binomial probability of survivorship P using the expression

$$0.5 = P^0(1 - P)^7.$$

We used this method to estimate missing transitions in

the unburned stands for six cases from a total of 80 transitions.

Matrix model analysis

The size-structured projection models took the form

$$\mathbf{n}(t + 1) = \mathbf{An}(t)$$

where $\mathbf{n}(t)$ is a vector of the abundances of each size class at time t, and $\mathbf{A}$ is the matrix containing transition probabilities (a_{ij}) that describe the frequency of survivorship, growth, or recruitment for each size class. The multiplication of $\mathbf{A}$ and $\mathbf{n}(t)$ results in the number of individuals in each size class at time $t + 1$; the sum of the size class distribution is the total number of individuals at the next time step. The 5-yr resolution of our growth and recruitment data necessitated that population matrices also be calculated at 5-yr intervals. Occasionally measurements were taken on a 6-yr interval. In these cases, we standardized the data to a 5-yr interval to calculate transition probabilities. Population growth rate (λ) measures the rate of change in the total population size when the population reaches a stable stage distribution (i.e., the proportion of individuals among size classes remains constant), with

TABLE 2. Five-year transition probabilities and population growth rate (λ) for the unburned and burned sugar pine populations.

Size class transitions, dbh (cm)†	Suwanee Creek			Crystal Road		Hodgedon Meadows		Crane Creek	Tharp Creek	
	1983–1988	1988–1994	1994–1999	1991–1996	1996–2001	1991–1996	1996–2001	1993–1998	1984–1989	1989–1994
0.1–5.0 → 0.1–5.0	0.777	0.677	0.532	0.674	0.760	0.830	0.751	0.786	0.700	0.088
0.1–5.0 → 5.1–10.0	0.107	0.086	0.081	0.120	0.070	0.038	0.018	0.056	0.100	*0.037*
5.1–10.0 → 5.1–10.0	0.806	0.754	0.596	0.679	0.667	0.850	0.788	0.794	0.714	0.118
5.1–10.0 → 10.1–20.0	0.177	0.049	0.038	0.179	0.100	0.114	0.073	0.127	0.214	*0.049*
10.1–20.0 → 10.1–20.0	0.795	0.775	0.632	0.813	*0.779*	*0.938*	0.808	0.891	0.810	0.071
10.1–20.0 → 20.1–40.0	0.115	0.028	0.070	0.094	0.194	0.050	0.068	0.054	0.143	*0.029*
20.1–40.0 → 20.1–40.0	0.878	0.773	0.684	0.643	0.833	0.824	*0.879*	0.821	*0.926*	0.440
20.1–40.0 → >40.0	0.095	0.040	0.070	0.071	0.083	0.029	0.097	0.071	0.043	0.040
>40.0 → >40.0	0.946	0.811	0.885	*0.906*	*0.917*	0.938	*0.964*	0.933	*0.957*	0.652
>40.0 → 0.1–5.0	0.075	0.042	0.090	5.429	6.500	2.056	1.105	0.733	0.087	0.000
λ		0.974	0.820	0.885	1.007	1.042	0.995	0.978	0.977	0.976	0.652
2.5% CI		0.944	0.783	0.813	0.833	0.862	0.941	0.917	0.909	0.923	0.484
97.5% CI		1.005	0.898	0.956	1.149	1.148	1.054	1.016	1.033	1.024	0.857

Notes: Estimations of ''missing'' transition probabilities are given in italics (see *Methods: Matrix model construction*). Separate matrices are given for populations with multiple observation intervals. Confidence intervals for population growth rate (λ) were generated from 3000 bootstrap samples. We do not present a matrix for the 1994–1999 interval for the Tharp Creek population due to insufficient data.

† Stem diameter at breast height (1.37 m).

λ > 1.0 indicating an increasing total population size, λ = 1.0 indicating unchanging total population sizes, and λ < 1.0 indicating a decreasing total population size. We derived 95% confidence intervals for λ by taking 3000 bootstrap samples, since population parameters such as λ are unlikely to meet the assumptions of classical statistical tests (Caswell 2001). The confidence intervals were bias corrected using the procedures in Manly (1997). We considered populations to be declining if bootstrapped confidence intervals of λ were <1.0.

We used the size-structured models to project future population sizes using both time-invariant and stochastic procedures. We obtained time-invariant results by computing simple numerical projections. We produced stochastic projections for individual populations using a random matrix selection method in cases where we had >1 matrix per population, using 3000 model iterations to generate results. The random matrix selection method insures the maintenance of the covariance pattern among the transition probabilities within each population matrix (Caswell 2001). We used the stochastic projections to estimate future changes in population size structure.

We determined the relative contribution of individual transition probabilities to λ for each projection model by calculating elasticities. Elasticity is a prospective analysis, which determines how λ would respond if individual transition probabilities change in the future (Caswell 2000). Elasticity is calculated by first computing the sensitivity (s_{ij}) of λ to each transition probability a_{ij} from

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

where v and w are the dominant right and left eigenvectors of the population matrix and $\langle \mathbf{w}, \mathbf{v} \rangle = 1$. Elasticity is then determined using the relationship

$$e_{ij} = \left(\frac{a_{ij}}{\lambda} \right) \frac{\partial \lambda}{\partial a_{ij}}$$

where e_{ij} is the elasticity of a single transition probability a_{ij} (Caswell 2001). We calculated elasticities for each projection model at all locations and observation intervals.

We conducted loglinear analyses to assess differences in demographic rates among populations during the most recent 5-yr observation interval (Horvitz and Schemske 1995, Caswell 2001). Temporal variations in demographic rates are considered elsewhere (P. J. van Mantgem and N. L. Stephenson, *unpublished manuscript*). Our loglinear analyses considered differences among states (the five size classes at *t*), fates (five size classes at *t* + 1 and death), and locations (population identity). Note that this method ignores variation arising from differences in recruitment rates. Using the terminology in Caswell (2001), the saturated model includes all terms and possible interactions for fate (*F*), state (*S*), and location (*L*) and is signified by the shorthand *FSL*. We compared the saturated model against the model *FS, SL,* which ignores interactions between fate and location. Significant differences between *FSL* and *FS, SL* show the fate and location interaction to be important, and indicate high variation in demographic rates among populations.

We used randomization tests to assess how differences in demographic rates translated into differences in λ among populations during the most recent 5-yr observation interval. Randomization methods are pref-

erable to classical statistical analysis in this instance due to the complex nature of λ (Caswell 2001). Our randomization tests consisted of 3000 random permutations used to conduct hypothesis tests for differences in λ among populations, using the test statistic

$$\theta = \text{SD}(\lambda)$$

where $\text{SD}(\lambda)$ is the standard deviation among observed values of λ (Caswell 2001).

We used a Life Table Response Experiment (LTRE), a retrospective analysis, to identify transition probabilities responsible for observed differences in λ among populations during the most recent 5-yr observation interval. The transition probabilities identified as important in prospective analyses (e.g., elasticities) may not be identical to the transition probabilities that have actually given rise to the observed differences (Caswell 2000). A LTRE reduces λ back to the variation derived from individual transition probabilities. We used a random design LTRE decomposition, given by the relationship

$$V(\lambda) \approx \sum_{ij} \sum_{kl} C(ij, kl) s_{ij} s_{kl}$$

where $V(\lambda)$ is the variance in the growth rate among population matrices, $C(ij, kl)$ are the covariances of transition probabilities a_{ij} and a_{kl} from separate population matrices, and the sensitivities s_{ij} and s_{kl} are calculated from the mean matrix (Caswell 2001). Matrix model projections, analyses, and randomization tests were carried out using PopTools, Version 2.5 (Hood 2003). All other tests were conducted with SYSTAT, Version 10.2 (SYSTAT 2002).

Effects of blister rust and fire exclusion

We assessed the importance of blister rust and fire exclusion by calculating the frequency of mortalities associated with different stressors. The process of tree death is complex and is commonly a result of numerous contributing causes acting in concert (Manion 1981). For example, blister rust infection may not directly lead to mortality, but may compromise tree defenses, leading to lethal bark beetle infestations. We therefore considered proximate mortality causes, divided into three broad classes. (1) *Mechanical* causes were assigned to trees killed by breaking or uprooting by wind or snow, or crushing by another falling tree or snag. (2) *Biotic* causes were assigned to standing dead trees that clearly had been killed by insects and fungi, or rarely mistletoes or vertebrates. We subdivided the biotic category further to distinguish deaths by blister rust and bark beetles (mostly *Dendroctonus ponderosae* Hopkins). (3) *Stress* mortality was assigned to standing dead trees that showed no definitive aboveground evidence of biotic attack. Most of the deaths in this class probably resulted from direct physiological stress due to competition (suppression), but almost certainly included some trees that died of cryptic biotic causes. We used

these data to determine overall tree mortality patterns and differences in mortality patterns among populations.

We considered the possibility that relationships exist among stressors that contribute to tree death. Fire exclusion may lead to high stand densities, which in turn could be related to the frequency of blister rust infections. Competition, measured in terms of low radial growth rates, may also predict probabilities of future blister rust infections for individual trees. We explored these relationships by correlating total stem basal area and the number of infected trees in 2001. We used logistic regression, taking the most recent growth rate measurement to predict blister rust infection within three years of the growth measurement.

Effects of fire

The 14-ha Tharp Creek watershed containing two 1-ha plots was prescribed burned by a combination of strip headfires and backing fires in October of 1990. The Tharp Creek population included 103 individuals observed for six years pre fire and 11 years post fire (Table 1). Total pre-fire fuel loads were relatively high (210 Mg/ha), primarily composed of large diameter woody fuels (58%) and litter and duff (35%). Backing fire flame lengths ranged from 0.05 m to 0.15 m, while strip headfire flame lengths were from 0.6 m to 2.4 m. Scattered areas of high fuels accumulation and standing snags occasionally ignited the canopies of nearby trees (Haggerty 1990). Following the burn the total fuel load was reduced to 31 Mg/ha (Mutch and Parsons 1998).

Demographic data for the Tharp Creek population were collected and organized as size-structured matrix population models. Observations of stage transitions for the Tharp Creek population were somewhat sparse, particularly following the fire. We had missing transitions for 1 of 10 transitions for the pre-fire interval, and 3 of 10 transitions in the immediate post-fire interval. The final post-fire interval from 1994 to 1999 required the estimation of 8 of 10 transitions, and therefore was not formally considered.

We augmented our burned plot observations with data from the fire monitoring program at Sequoia National Park (Keifer 1998, National Park Service 2001), where fire effects data were gathered from permanently marked 20×50 m plots randomly established within areas designated for prescribed burning. We refer to these plots as the 0.1-ha plots to distinguish them from the plots previously described. The 0.1-ha plot data were collected <1 mo pre fire, and 1 yr, 5 yr, and 10 yr post fire. This monitoring program provides total stem counts for trees >1.37 m in the plots. We used stem count data of 218 sugar pines from 20 monitoring plots, arrayed across 14 fires in the white fir–mixed conifer forests. The range of fuel loading and fire intensities at these sites was consistent with the plots at Tharp Creek.
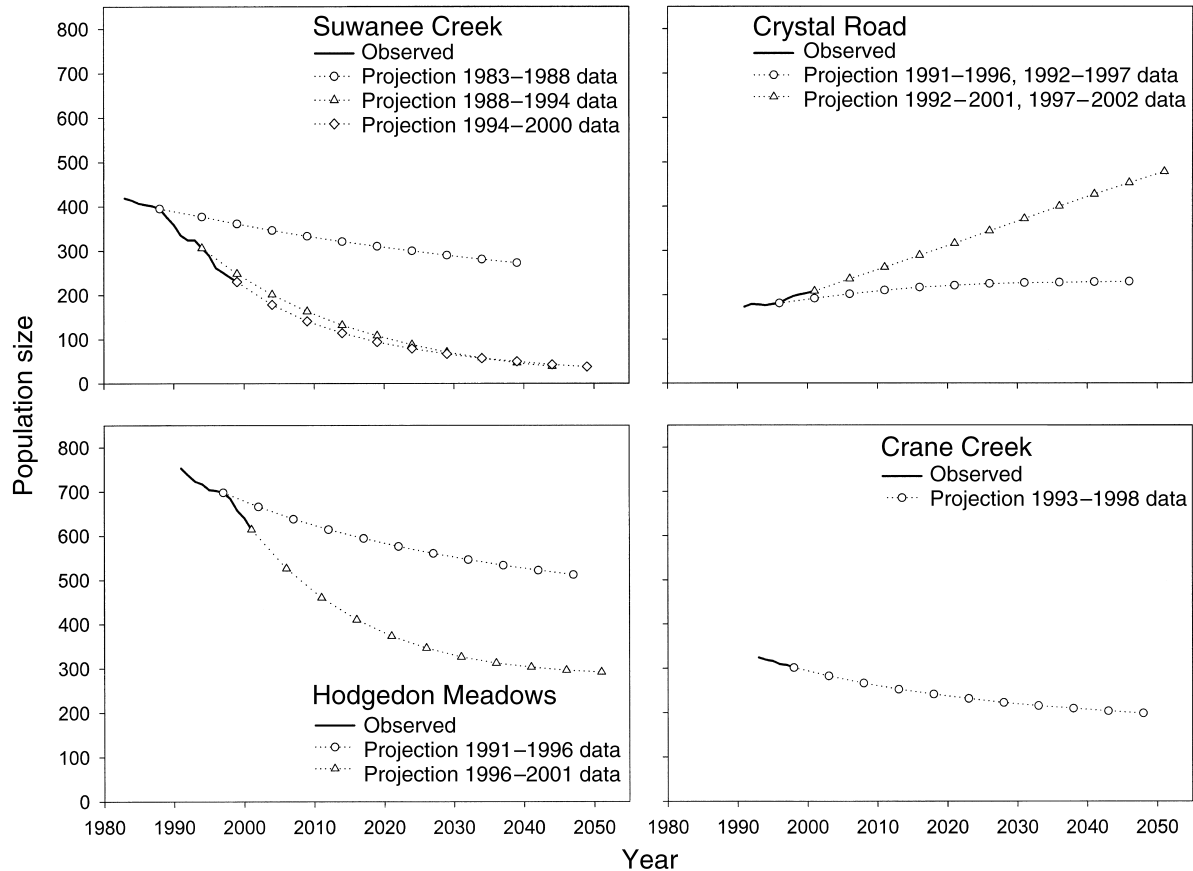
FIG. 2.   Observed population trends and time-invariant matrix model projections for unburned sugar pine populations.

RESULTS

Population trends

The total number of sugar pine individuals decreased for three of our four unburned populations (Table 2, Fig. 2). Bootstrapped confidence intervals of λ for 5-yr observation intervals range above and below 1.0 for all populations except Suwanee Creek, and therefore do not supply unequivocal evidence of either general population growth or decline. Using the entire 10-yr or 15-yr demographic records provides similar results. Time-invariant and stochastic projections of future population sizes suggest a slow, steady reduction in the overall number of sugar pine individuals over the next 50 years, with the exception of the Crystal Road population where growth is expected (Figs. 2 and 3). Size class distributions at Hodgedon Meadows and Crane Creek are expected to become less skewed as small trees are lost from the populations (Fig. 3). In contrast, the size class distributions for the Suwanee Creek and Crystal Road populations are expected to become more skewed, although the increase in skew at Suwanee Creek would arise from the almost complete loss of small trees, while high recruitment rates at Crystal Road would result in a more pronounced "reverse J-shaped" size class distribution. The ratio of seedlings

to potential parent trees in 2001 reflects the population trends (e.g., abundance of seedlings in 25 m^2 divided by the abundance of parent trees in 75 m^2: Suwanee Creek = 0.6, Crystal Road = 21.5, Hodgedon Meadows = 5.8, Crane Creek = 12.0).

Elasticity analysis shows our populations would be most sensitive to future changes in large tree survivorship, with differences in growth and reproduction being relatively unimportant (Fig. 4). Elasticity patterns are reasonably consistent across observation intervals and among populations. The degree of dependence of λ on large tree survivorship appears to increase as population decline proceeds, most easily seen in the Suwanee Creek population.

Population differences

Loglinear analyses supplied evidence for high variability in demographic rates among populations during the most recent observation interval (*FSL* vs. *FS, SL*; $G^2 = 98.85$, df = 75, $P = 0.03$). Loglinear tests were not significant if the Suwanee Creek population was removed from the analyses. Differences in demographic rates translated into significant differences in λ among unburned populations during the most recent observation interval (frequency of $\theta_{obs} \leq \theta_{randomized} =$
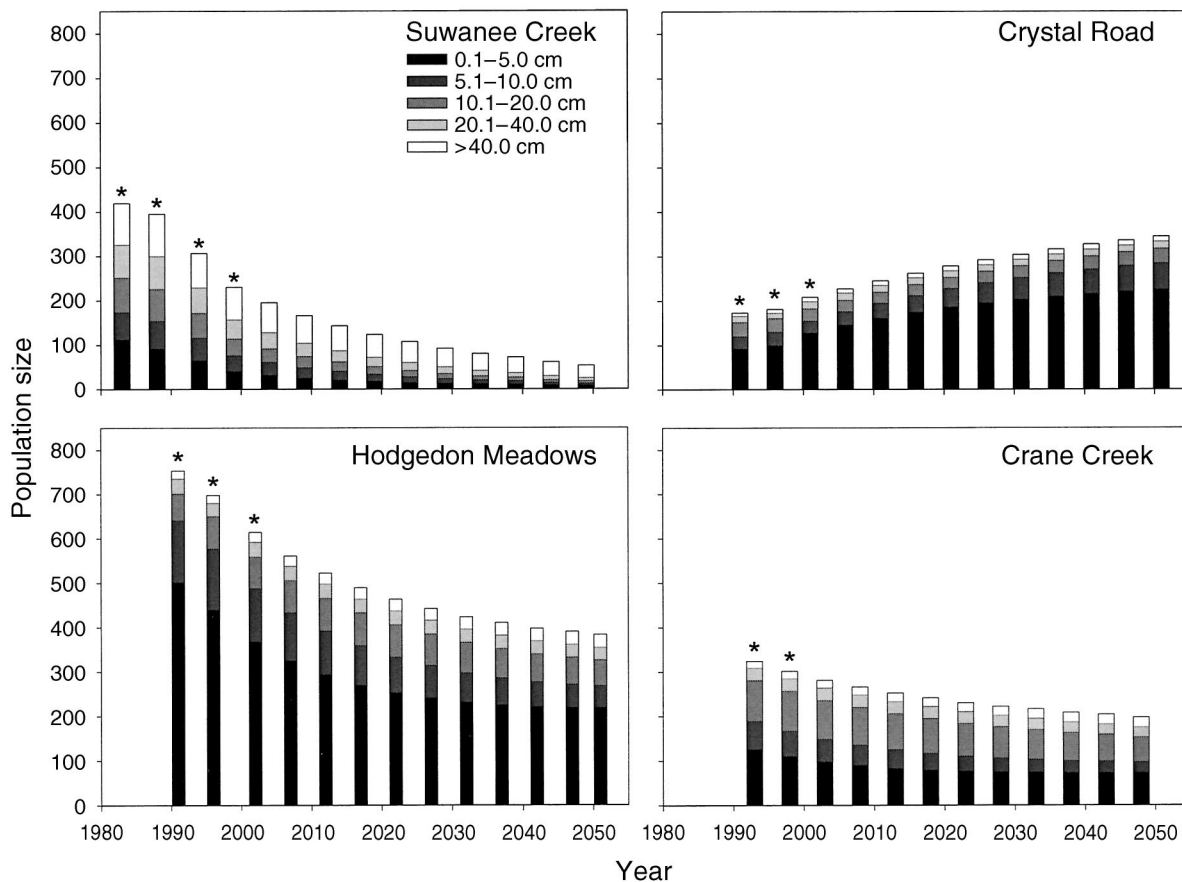
Fig. 3. Size class distributions of sugar pine for unburned populations. Bars with stars indicate observed size class distributions. Bars without stars are average projected results of 3000 stochastic model iterations (with the exception of Crane Creek, where we had insufficient data to produce stochastic projections and thus present time-invariant results). Bar shading reflects stem diameter classes.

120, 3000 random permutations, $P = 0.04$). Significant differences in λ were not found when the Suwanee Creek population was removed from the analysis (frequency of $\theta_{obs} \leq \theta_{randomized} = 1244$, 3000 random permutations, $P = 0.42$). The main factor contributing to the observed differences in λ for the unburned populations was the rate of recruitment, as shown by the LTRE variance decomposition (Fig. 5). Survivorship, particularly for large trees, also played an important, but lesser, role.

Effects of blister rust and fire exclusion

All of our stands showed high levels of blister rust infection (Table 1). During the most recent 5-yr observation interval, mortality associated with biotic attack was the most frequent cause of death, although biotic deaths were not statistically more common than stress deaths ($\chi^2 = 2.3$, df = 1, $P = 0.13$; Table 3). Within the biotic category, blister rust mortalities were more common than all other biotic deaths combined ($\chi^2 = 6.5$, df = 1, $P = 0.01$), and were associated with bark beetle attack in 38% of cases. Blister rust mortalities were more common in small (≤ 20 cm dbh) vs. large (>20 cm dbh) trees ($\chi^2 = 7.85$, df = 1, $P < 0.01$). Deaths related to bark beetle infestations were also common, and occurred in conjunction with severe blister rust infections in 29% of cases. Blister rust deaths were more common than stress deaths in the Suwanee Creek population compared to all other populations ($\chi^2 = 53.9$, df = 1, $P < 0.0001$; Table 3). This trend was driven by differences in the two smallest size classes (≤ 10.0 cm dbh, Fisher's exact test $\chi^2 = 49.0$, df = 1, $P < 0.0001$; >10.0 cm dbh, Fisher's exact test $\chi^2 = 2.1$, df = 1, $P = 0.19$).

There was no clear suggestion of a relationship between fire exclusion (i.e., high stand density) and the severity of blister rust attack. The correlation between unburned stand density and frequency of blister rust attack was not significant ($r = 0.70$, df = 5, $P < 0.10$), however our ability to detect this relationship was low ($n = 7$ plots). For individual trees there was no connection between slow growth and probability of blister rust attack within three years of the growth measurement (logistic regression likelihood ratio test statistic
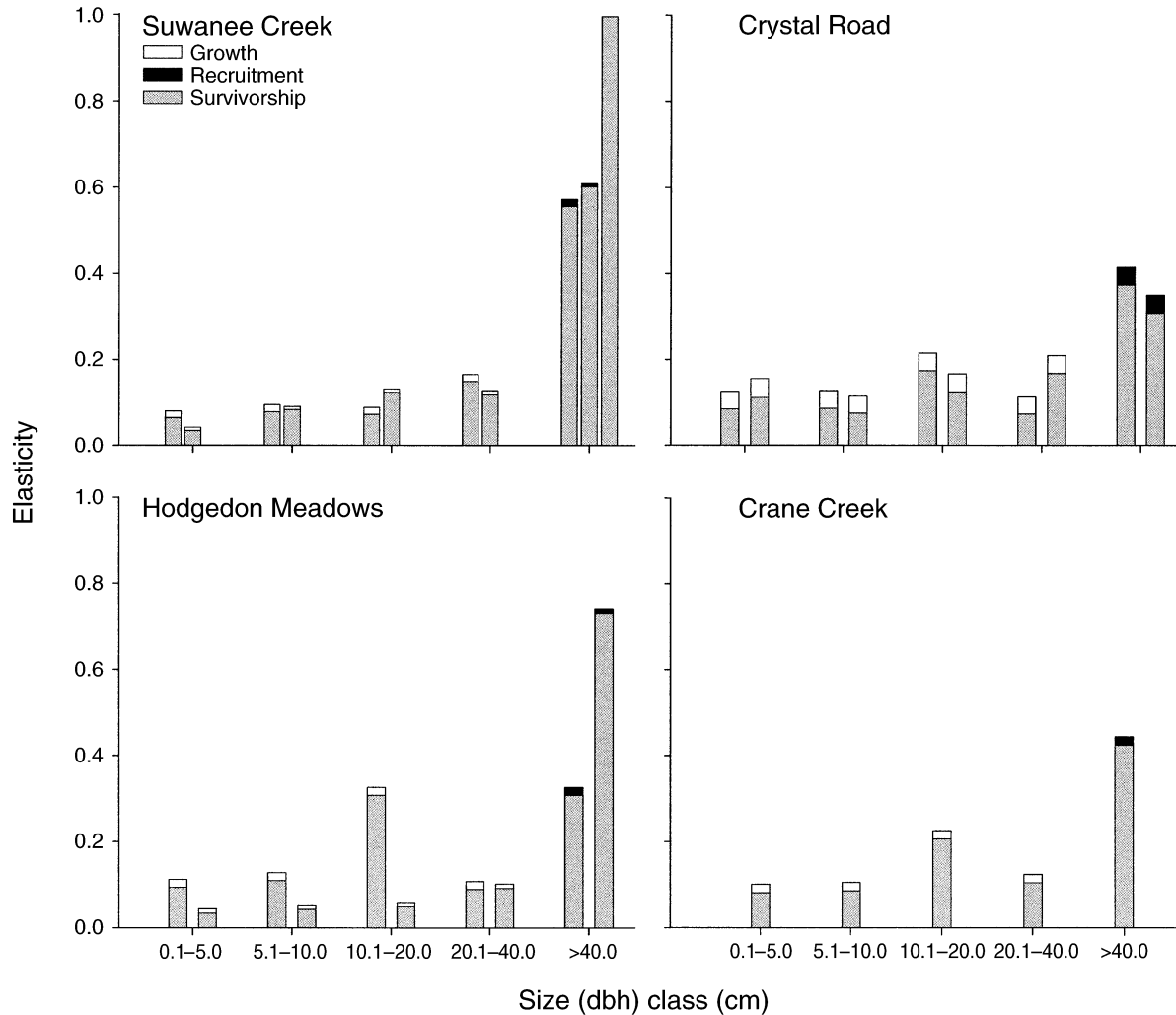
FIG. 4. Elasticities for unburned sugar pine populations over different observation periods. For each size class, each cluster of bars, reading left to right, represents the following years of observation: for Suwanee Creek, 1983–1988, 1988–1994, 1994–1999; for Crystal Road, 1992–1997, 1997–2002; for Hodgedon Meadows, 1991–1996, 1996–2001; for Crane Creek, 1993–1998.

= 0.09, df = 1, P = 0.76, n = 968). Instead, stem size appeared to be positively related to the presence of blister rust attack as shown by logistic regression relating the most recent live tree diameter to the presence of blister rust symptoms in the 2001 survey (likelihood ratio test statistic = 20.2, df = 1, P < 0.0001, n = 1193).

Responses to fire

There was a 64% reduction of sugar pine individuals within two years following the prescribed fire at Tharp Creek (Fig. 6). The resulting low λ for the years 1989–1994 reflects this sharp decline (Table 2). There was no recruitment and only one occurrence of growth to a larger size class during the first post-fire interval, so this transition matrix may not be accurate. However, replacing the three estimated transitions (see *Methods*:

Model construction and analysis) with the observed zero values had no measurable effect on λ. Trees in smaller size classes died more frequently compared to large trees (χ^2 = 22.1, df = 4, P = 0.0002), although actual mortality probabilities were best predicted by the severity of crown scorch. The increase in post-fire mortality rates was temporary, and from 1994 to 1999 there has been only one death and no observations of growth. The threat of blister rust attack has apparently not yet changed in our burned plots, with the proportion of infected trees roughly equivalent to the unburned stands (Table 1).

Pooled sugar pine stem counts from 0.1-ha plots in 14 prescribed fires in Sequoia National Park show responses similar to the Tharp Creek population. The fires caused a significant drop in total sugar pine stem counts one year following the fires (Mann-Whitney U = 145.0,
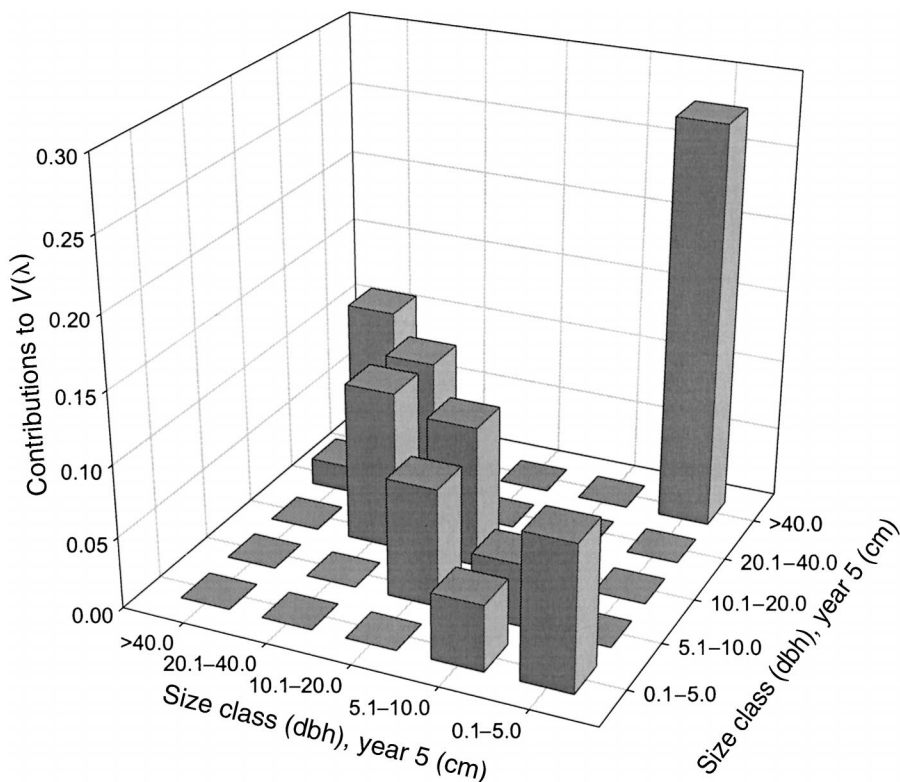
FIG. 5. Results of a random design Life Table Response Experiment among unburned populations during the most recent observation interval. Greater heights indicate greater contributions of a given transition probability to the total variation among population growth rates, $V(\lambda)$, scaled to 1.

$P = 0.03$, $n = 28$). The increased frequency of mortality was again temporary, and we did not find significant differences between observations taken 1 yr, 5 yr, and 10 yr post fire. Mortalities were more common in small trees, causing a shift in the size distribution by 1 yr post fire (using the same dbh size classes as the 1-ha plots, $\chi^2 = 18.4$, df $= 4$, $P = 0.001$).

DISCUSSION

It appears that sugar pine is responding negatively to current forest conditions, but this response is slow and not uniform among sites. We found negative growth for most, but not all, of our populations. Confidence intervals for population growth rates (λ) typically overlapped 1.0, providing equivocal evidence for general population declines. The finding that λ usually remains close to 1.0 suggests that if population declines are indeed occurring, the progression of any such declines are slow. Longer term observations are needed to clearly determine population trends for this long-lived species. High variation in demographic rates among populations may also make broad assessments

TABLE 3. Number of sugar pine deaths in unburned populations during the most recent 5-yr observation interval, by proximate causes of death.

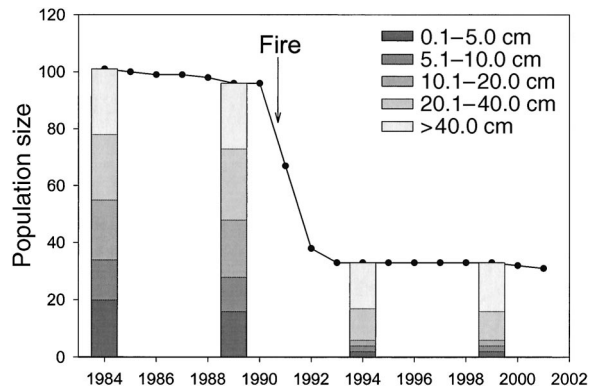| Sugar pine mortality	Suwanee Creek	Crystal Road	Hodgedon Meadows	Crane Creek	All populations
Survived	223	156	592	290	1261
Died	83	25	106	34	248
Proximate cause					
Mechanical	8	2	3	4	17
Stress	9	8	66	12	95
Biotic	66	15	37	18	136
Biotic proximate cause					
Blister rust	44	8	10	7	69
Bark beetle	21	5	23	10	59
Other	1	2	4	1	8

FIG. 6. Sugar pine population trends at Tharp Creek from 1984 to 2001. The arrow indicates the timing of a prescribed burn in 1990. Bar shading reflects stem diameter classes.

of population behavior difficult. Demographic variability was likely mediated by variability in environmental conditions; our most mesic site containing the Suwanee Creek population had the highest levels of blister rust infection, and was the only population found to be unmistakably declining. It is uncertain how well the patterns we found at our sites may reflect population trends of sugar pine across its range, although our results suggest population fates may be highly variable over space. At a regional scale the central and southern Sierra Nevada are relatively dry, and not generally conducive to the spread and development of the blister rust fungi (Kinloch and Dulitz 1990). As a result, we did not observe die-offs of the magnitude of whitebark pine (*Pinus albicaulis* Engelm.) reported in more mesic regions of western North America (Kendall and Keane 2001).

Although many of our populations are decreasing, our model projections indicate that all of our populations are likely to maintain at least more than 50 individuals over the next 50 years. Short-term assessments of viability, however, may not be adequate for long-lived organisms. For example, in spite of demographic trends that assure extinction, the American chestnut (*Castanea dentata* [Marsh.] Borkh.) and the Florida torreya (*Torreya taxifolia* [Arn.]) have persisted for long periods, albeit with highly reduced populations (Parker et al. 1993, Schwartz et al. 2000). As suggested by Schwartz (2003), generation times may be a more appropriate time scale to consider viability for long-lived plants. Assuming a mean generation time of 60 yr (U.S. Forest Service 1974), if current trends continue we could expect local extinction (total stem counts <1) of sugar pine at Suwanee Creek in approximately four generations. Other populations with negative growth are expected to develop sparse relative frequencies of small trees, which may serve as an indicator of potential future declines.

Poor recruitment was associated with negative population growth, although elasticity analysis suggests

that decreases in survivorship would have greater influences on λ. This finding underscores the distinction made by Caswell (2000) between retrospective and prospective analyses, where the observed source of demographic variation may be different from potential changes that would cause larger effects on λ. Translating the results of the elasticity analysis to management actions may prove difficult; in the absence of disturbance, large tree survivorship is already high, and may therefore make a poor target for conservation efforts. Conversely, we have established that recruitment can have a significant effect on populations, and it may prove simpler to create conditions that enhance the establishment and growth of new individuals.

The high frequency of blister rust and stress deaths suggests a significant role for blister rust and fire exclusion in determining population trajectories. Presumably these stressors are also having major effects on recruitment by causing deaths in seedlings. Blister rust infections were common in large trees, so the disease may further reduce potential recruitment by killing cone-bearing branches. Sugar pine is only moderately shade intolerant (Baker 1949) and current stand conditions allow at least limited recruitment, although the high frequency of stress-mediated deaths implies more open conditions would enhance recruitment rates. It did not appear that probabilities of blister rust attack were associated with canopy conditions, at least over the observed range of stand densities. Interestingly, prescribed fire did not appear to increase recruitment at Tharp Creek, perhaps because more than 10 years is required to observe positive recruitment responses, or high post-fire reproduction may depend on the coincidental timing of burning and mast years of seed production. Conducting longer term and more precise observations of sugar pine reproduction and seedling dynamics are key avenues of future study. In particular, the uniform failure of blister rust eradication programs (Maloy 1997) strongly implies that work should focus on how best to promote sugar pine recruitment and growth using disease resistant genotypes and forest thinning treatments.

Prescribed fire is a widely used forest-thinning tool, although protecting sugar pine populations while reintroducing fire after more than 100 years of fuels accumulation could present challenges. Post-fire mortality rates for sugar pine were high, but this response to fire is not unusual compared to other species in the Sierra Nevada (Keifer 1998, van Mantgem et al. 2003). Large individuals were resistant to damage caused by fire, in agreement with earlier work on sugar pine and other conifer species (Ryan and Reinhardt 1988, Stephens and Finney 2002). Large trees have high elasticity values, so high post-fire survivorship of these individuals may cushion populations from the effects of fire. Pre-fire fuel removal treatments designed to encourage large tree survivorship (Swezy and Agee 1991) may further protect populations. It is also likely

that second burns will have lesser effects on sugar pine populations, because as fuels are reduced through prescription burning fire severity tends to decrease in subsequent burns (van Wagtendonk 1996).

CONCLUSIONS

White pine blister rust and fire exclusion appear to be having significant effects on sugar pine populations in the central and southern Sierra Nevada of California. Although the dry conditions in this region do not readily encourage the development of the disease, our populations all had high frequencies of infected trees, and infections were linked to considerable numbers of tree mortalities. In addition, the large number of stress-related mortalities indicates that dense stand conditions may be contributing to current population trends. However, the population-level effect of these stressors was not uniform, and we found only one population to be clearly declining. At present, most populations appear to be buffered against significant declines due to relatively high survivorship of large individuals, although the increasing scarcity of smaller individuals, often due to blister rust induced mortalities and low recruitment rates, points to future problems. We have several advantages if we wish to manage for this species; large populations are found in protected areas, the threats to populations are relatively well known, and promising tactics to overcome some of these threats already exist (e.g., blister rust resistant genotypes, prescription fire to encourage recruitment and growth). Our results suggest that we have time to apply and refine management strategies to protect this species.

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