

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Effects of Extreme Drought and Megafires on Sky Island Conifer Forests of the
Peninsular Ranges, Southern California

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Geological Sciences

by

Brett Russell Goforth

December 2009

Dissertation Committee:

Dr. Richard A. Minnich, Chairperson

Dr. Robert Graham

Dr. Tom Scott

Copyright by
Brett Russell Goforth
2009

The Dissertation of Brett Russell Goforth is approved:

Committee Chairperson

University of California, Riverside

ACKNOWLEDGEMENTS

Much appreciation is expressed to Dr. Richard A. Minnich, committee chair, for guidance and advice on the research presented in this dissertation, as well as to Dr. Robert Graham and Dr. Tom Scott for their interest in my studies. I thank the members of my qualifying exam committee, chaired by Dr. David Oglesby, including Dr. Edith Allen, Dr. Douglas Morton, Dr. Al Williams, Dr. Minnich, and Dr. Graham. It has been a pleasure working with Dr. Pete Sadler, Dr. Elizabeth Cochran, Dr. Williams, and Dr. Oglesby who were mentors for my Teaching Assistant apprenticeships among their fascinating repertoire of Earth science classes taught at UC Riverside. I also wish to share my gratitude for the support of my mother and father, Paulette and Robert “Bob” Goforth, my brother Carey, David Romagnolo, Jim and Anne Kirk, the Thomas family, and the Menchacas.

The dissertation research was funded by California State Parks Interagency Agreement C0343027, with additional support of the University of California, Riverside, Department of Earth Sciences Blanchard Fund and Teaching Assistant Fellowship, as well as contributions from the John C. Dunham Summer Field Graduate Fellowships Program. I thank Jim Dice, Dr. Mike Wells, Kim Marsden, Bob Hillis, and Kirsten Winter for permissions to conduct dissertation research in the Cuyamaca Rancho State Park, Anza-Borrego Desert State Park, and the King Creek Research Natural Area of the Cleveland National Forest. Dr. Ayzik Solomesheh and Dr. Michael Barbour at the

University of California, Davis, kindly provided the archived VTM plot data, and Ken-ichi Ueda and Dr. Maggi Kelly at UC Berkeley furnished the digitized map of the Cuyamaca VTM quadrangle. I also wish to thank Dr. Walter Boyce at UC Davis, who I collaborated with in the preparation of a revised plan for prescribed burning in Cuyamaca Rancho State Park just weeks prior to its destruction in the “Cedar fire” of October 2003. I am grateful for the assistance in fieldwork by Bob G., Jerry Polletta, and Ann Bowers which contributed to this study.

Chapter 1 is reprinted from *Forest Ecology and Management*, Vol. 256, Brett R. Goforth and Richard A. Minnich, Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California, Pages 36-45, Copyright (2008), with permission from Elsevier.

DEDICATION

I wish to dedicate this dissertation to my mother and father, Paulette and Robert
“Bob” Goforth. Thank you!

ABSTRACT OF THE DISSERTATION

Effects of Extreme Drought and Megafires on Sky Island Conifer Forests of the
Peninsular Ranges, Southern California

By

Brett Russell Goforth

Doctor of Philosophy, Graduate Program in Geological Sciences
University of California, Riverside, December 2009
Dr. Richard A. Minnich, Chairperson

Conifer populations in the Peninsular Range of southern California and Baja California form isolated biogeographic “sky-islands” on mountains with high orographic precipitation. Fire suppression management altered burning patterns in southern California since ca. 1900. Significant changes in tree composition, density, and diameters are documented over a 75-year period in mixed conifer forest at Cuyamaca Mt., by replicating ground-based measurements sampled in 1932 for the Weislander Vegetation Type Map survey. Average conifer density more than doubled, from $271 \text{ trees ha}^{-1} \pm 82$ (standard error) to $716 \text{ ha}^{-1} \pm 79$. Repeat aerial photographs for 1928 and 1995 show significant increase in canopy cover from $47\% \pm 2$ to $89\% \pm 1$. Changes comprise mostly ingrowth of shade-tolerant *Calocedrus decurrens* in the smallest stem diameter class (10 cm to 29.9 cm dbh). The 1932 density of overstory conifer trees (> 60 cm dbh) and 1928 canopy cover were similar to modern mixed conifer forest in the Sierra San Pedro Mártir, ~200 km S in Baja California, Mexico, where fire-suppression had not been practiced.

The winter of 2001-2002 was the driest in southern California since instrumental records began in 1850. Whole-stand die-off of a serotinous pine (*Pinus coulteri*)

occurred over much of the northern Peninsular and eastern Transverse Ranges, before an outbreak of wildfires in 2003 extensively burned drought-killed stands. I investigated four regeneration condition classes: (1) live unburned stands (control group) and those (2) fire-killed (i.e., drought surviving but burned), (3) posthumously burned (i.e., burned after death by drought), and (4) stands with mixed mortality by drought and fire. Posthumously burned stands had an average tree to seedling ratio of 13:1, and the systematic census failed to detect any Coulter pine seedlings among two-thirds of plots. Crown-fire in drought-killed posthumously burned stands is sufficiently intense to destroy the canopy seedbank of serotinous cones. In contrast, an isolated population of Cuyamaca Cypress (*Cupresses arizonica* var. *arizonica*) successfully reproduced in King Creek and at a nearby plantation site. A significant decline in seedling and tree size was measured with distance from King Creek, suggesting that soil moisture is a likely factor limiting growth.

TABLE OF CONTENTS

	Page
Acknowledgements.....	iv
Dedication.....	vi
Abstract of the Dissertation	vii
List of Tables	xi
List of Figures.....	xii
INTRODUCTION.....	1
Significance.....	4
References.....	5
CHAPTER 1: Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park	
Abstract.....	8
Introduction.....	10
Methods.....	12
Results.....	16
Discussion.....	19
Conclusion	26
References.....	29

CHAPTER 2: Reproductive failure of a serotinous pine (*Pinus coulteri* D.Don.) in drought-killed posthumously-burned forest stands

Abstract.....49

Introduction.....51

Methods.....53

Results.....56

Discussion.....58

Conclusion61

References.....63

CHAPTER 3: Recruitment patterns of an isolated serotinous conifer (*Cupressus arizonica* var. *stephensonii* [Wolf] Little) after stand-replacement wildfire.

Abstract.....73

Introduction.....75

Methods.....77

Results.....82

Discussion.....85

Conclusion91

References.....95

CONCLUSION117

Appendix 1.....119

Appendix 2.....120

LIST OF TABLES

	Page
Table 1.1 Description of historical VTM plots and modern replicates located in the Cuyamaca Rancho State Park, southern California	47
Table 1.2 Seedling census 41 months after wildfire at Cuyamaca Rancho State Park	48
Table 3.1 Measurements of Cuyamaca cypress trees at King Creek	114
Table 3.2 Measurements of Cuyamaca cypress seedlings in the third growing season after the 2003 wildfire	115
Table 3.3 Site-specific seedling to tree ratios in Cuyamca Cypress stands in the third growing season after the 2003 wildfire	116
Table 3.4 Significant variation in the size of trees and seedlings among 10 m intervals of the slope profile belt-transect.....	116

LIST OF FIGURES

	Page
Figure 1.1 Dense stands of fire-killed conifers and top-killed oaks were completely charred by crown-fire and lacked residual surface fuels.....	39
Figure 1.2 Meteogram of weather conditions registered every 6 hours at the Julian RAWS station located 10 km north of CRSP during the “Cedar fire” of October 2003.....	40
Figure 1.3 The remaining extent of MCF in Cuyamaca Rancho State Park after stand-replacement wildfire in October 2003 (shaded area) is ~5% of the pre-fire area shown	41
Figure 1.4 Average conifer density according to stem diameter class, 1932 to 2007.....	42
Figure 1.5 Average density of tree species, 1932 to 2007	42
Figure 1.6 Average oak density according to stem diameter class, 1932 to 2007	43
Figure 1.7 Increase in average density of tree crowns, 1928 to 1995.....	43
Figure 1.8 Increase in average canopy cover, 1928 to 1995.....	44
Figure 1.9 Species-specific departure of seedling density from fire-killed trees in plots equated to massive deficiencies and extirpations	45
Figure 1.10 Extensive cover of shrubs in the forest understory, 41 months after fire.....	46
Figure 1.11 Sparse cover of exotic annuals in the forest understory, 41 months after fire.....	46

Figure 2.1 Percent of Average (POA) annual precipitation for July-June totals at individual long-term weather stations in the drought affected region of southern California	68
Figure 2.2 Repeat landscape photographs of drought-killed posthumously burned Coulter pine forest.....	69
Figure 2.3 Area-weighted average elevation of Coulter pine stand condition classes	70
Figure 2.4 Stand area histogram of Coulter pine on Bucksnot Mt. classified by slope aspect intervals	70
Figure 2.5 Stand area histogram of Coulter pine on Bucksnot Mt. classified by slope angle intervals.....	71
Figure 2.6 Coulter pine trees grown to 10 cm dbh or larger were reproductively mature	71
Figure 2.7 Summary of reproduction and fire severity metrics for stand condition classes	72
Figure 3.1 Unburned grove of Cuyamaca cypress and neighboring fire-killed stand in the native King creek population.....	104
Figure 3.2 Map of Cuyamaca cypress on Cuyamaca Mountain, southern California	105
Figure 3.3 Histogram of Cuyamaca cypress stand area classified by intervals of elevation	106
Figure 3.4 Histogram of Cuyamaca cypress stand area classified by 10° intervals	

of slope angle	106
Figure 3.5 Histogram of Cuyamaca cypress stand area classified by slope aspect intervals of 22.5° compass azimuth	107
Figure 3.6 Size-frequency distribution of tree basal diameter measurements	108
Figure 3.7 Size-frequency distribution of tree height measurements	109
Figure 3.8 Size-frequency distribution of seedling height measurements	110
Figure 3.9 Cumulative frequency of distances between individuals in Plot 1 (high seedling density) and Plot 3 (low seedling density).....	111
Figure 3.10 Post-fire cover of native and exotic herbaceous vegetation in the understory of Cuyamaca cypress stands	111
Figure 3.11 Dense mat-like cover of live and dead <i>Calystegia macrostegia</i> surrounding Cuyamaca cypress seedling and toppled fire-killed cypress tree	112
Figure 3.12 Post-fire cover of native and exotic herbaceous vegetation in the understory of Cuyamaca cypress stands	113

INTRODUCTION

Vegetation in the mountains of southern California is naturally prone to recurrent wildfires. The regional Mediterranean-type climate with cool wet winters and warm dry summers supports annual productivity of plant biomass in excess of decomposition because seasonal drought inhibits the decay of dead plant materials. Vegetation assemblages are composed of plant species having adaptations to drought, like fine sclerophyllous leaves and resinous tissues, which also result in high flammability (Christensen 1985). Periodic fires result in punctuated decomposition of accumulated plant biomass, fueled by both live vegetation and dead plant matter (see reviews in Sulgihara et al. 2006, Barbour et al. 2007).

Fire suppression management has altered patterns of burning in the mountains of southern California since ca. 1900 (Pyne 1982, Minnich 1988). Ignitions are readily suppressed under prevailing weather conditions of stable air inversion by a humid marine layer airmass with predictable diurnal patterns of adiabatic flow along slopes. Fires escape suppression to burn large patches of the vegetation landscape during extreme weather conditions like summer heat-waves or autumn Santa Ana winds when ignitions are least efficiently extinguished (Minnich and Chou 1997).

The US-Mexico international boundary separating southern California and Baja California has provided a contrast of fire patterns in paired vegetation landscapes having similar environmental gradients but different land management (Minnich 1983, Minnich and Bahre 1995). Large wildfires are more frequent in southern California, than in Baja

California where systematic fire suppression has not been practiced. Large fires are separated by broad contiguous areas which have not recently burned, in many areas since fire suppression management was initiated, unlike Baja California where fire patterns produce a fine-grained mosaic of burned patches that fragment the landscape history of time-since-fire.

A major challenge to biogeographical and ecological studies in southern California is determining how fire suppression management has altered vegetation. Long-term data which predate suppression is sparse, and limited to historical documentary sources which provide only qualitative indications of change (Goforth and Minnich 2007). Post-suppression data first collected in the early twentieth century (1920's-1930's) in the form of aerial photographs, systematic ground sampling and mapping for the Vegetation Type Map survey of California (Weislander 1935), provide a baseline reference to statistically test for changes *in situ* (Minnich et al. 1995, Albright 1998, Bouldin 1999, Stephenson and Calcarone 1999, Franklin et al 2004). Patterns of vegetation in northern Mexico provide the best approximation of an empirical control group for the effects of fire suppression management to complement studies in southwestern United States (Webster and Bahre 2001).

Conifer populations in the Peninsular Range of southern California and Baja California are isolated biogeographic "sky-islands" on mountains where orographic precipitation gradients support forest growth (Minnich 1987, Minnich et al. 2000, Minnich and Everett 2001, Minnich 2007). Intervening arid lands separating the widely disjunct forest stands are covered by southern oak woodland, chaparral, and annual

grasslands. Such distributional gaps pose a barrier to seed dispersal, resulting in lengthy lag-times for conifer migration.

The isolated conifer forests tend to exhibit three general distributional patterns in response to fires: a standing population, shifting population, and patch-mosaic population. Standing populations of mixed-aged conifers continuously reproduce from mature trees with tall stature and thick insulating bark on stems, which endure recurrent understory fires that maintain low-stand density. Mixed conifer forest (*Pinus lambertiana*, *P. ponderosa*, *P. jeffreyi*, *Abies concolor*, *Calocedrus decurrens*) exhibits a standing population distribution. Shifting populations of conifers discontinuously reproduce from serotinous cones with seed release triggered by stand-replacement wildfire, resulting in dense stands of even-aged cohorts with local stochastic recruitment failures shifting stand boundaries over time. Examples of shifting populations include closed-cone pine forest (*P. attenuata*, *P. muricata*, *P. radiata*, *P. coulteri*) and serotinous cypress stands in chaparral shrublands (*Cupressus forbesii*, *C. arizonica* var. *stephensonii*, *C. a.* var. *montana*). Patch-mosaic populations are susceptible to stand-replacement by any fire occurrence because trees lack thick bark and serotinous cones, and must recolonize burned areas by gradual seed dispersal from nearby unburned stands. Examples of patch mosaic populations of conifers include Pinyon woodlands (*Pinus monophylla*, *P. quadrifolia*) and sub-alpine forest (*P. contorta*, *P. flexilis*).

SIGNIFICANCE OF THE RESEARCH

Record drought in 2001/02 followed by massive wildfires in 2003 provided a unique opportunity to study how coupled extreme disturbance events affected conifer forests in relation to population distributional patterns. Chapter one highlights methodological approaches in the use of historical data to detect long-term change in comparison to extant conditions in mixed conifer forests, which exhibited the standing population distribution prior to the Cedar fire of 2003. The results of this study show that fire suppression management has significantly destabilized mixed conifer forests by eliminating periodic fires as a normal stand-thinning process in the understory of conifer reproduction, culminating with severe stand-replacement crown-fires which fragment its distribution to a patch mosaic population. Chapter two provides first insights into reproduction failures of a serotinous pine (*P. coulteri* D. Don.) in posthumously-burned drought-killed forest stands that had excessively aged due to fire suppression management, illuminating a punctuated contraction of population distributions which had not been previously observed. Chapter three illustrates the ironic reproductive success of an isolated population of Cuyamaca Cypress (*Cupresses arizonica* E. Greene ssp. *arizonica* [*C. stephensonii* C. B. Wolf]), despite stand-replacement of nearly its entire population in southern California, and patterns of recruitment in a shifting population distribution which are similar to other Arizona cypresses among widespread disjunct occurrences in northern Mexico and the southwestern United States.

REFERENCES

- Albright, D., 1998. Vegetation change in second-growth mixed conifer forests of western San Bernardino Mountains. M.S. thesis, Department of Earth Sciences, University of California, Riverside.
- Barbour, M., T. Keeler- Wolf, and A. Schoenherr, eds. 2007. Terrestrial Vegetation of California, third edition. University of California Press, Berkeley, CA
- Bouldin, J., 1999. Twentieth-century changes in forests of the Sierra Nevada. Ph.D. Dissertation, University of California, Davis.
- Christensen, N. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 85–100 *in* S.T.A. Pickett and P. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego.
- Franklin, J., C. Coulter, and S. Rey. 2004. Change over 70 years in a southern California chaparral community related to fire history. *Journal of Vegetation Science* 15: 701-710
- Goforth, B., and R. Minnich. 2007. Evidence, exaggeration, and error in historical accounts of chaparral wildfires in California. *Ecological Applications* 17:779-790.
- Minnich, R. 1983. Fire mosaics in southern California and Northern Baja California. *Science* 219:1287–1294.
- Minnich, R. 1987. The distribution of forest trees in northern Baja California, Mexico. *Madroño* 34:98-127.

- Minnich, R. 1988. The biogeography of fire in the San Bernardino Mountains of California: a historical study. *University of California Publications in Geography* 28:1–121.
- Minnich, R., 2007. Southern California coniferous forest. Pages 502–538 *in* M. Barbour, T. Keeler-Wolf, A. Schoenherr, eds. *Terrestrial Vegetation of California*, third edition. University of California Press, Berkeley.
- Minnich, R., and C. Bahre. 1995. Wildland fire and chaparral succession along the California–Baja California boundary. *International Journal of Wildland Fire* 5:13–24.
- Minnich, R., and Y. Chou. 1997. Wildland fire patch dynamics in the chaparral of southern California and northern Baja California. *International Journal of Wildland Fire* 7:221–249.
- Minnich, R., and R. Everett. 2001. Conifer tree distributions in southern California. *Madroño* 48:177-197.
- Minnich, R., Barbour, M., Burk, J., Fernau, R., 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9:902–914.
- Minnich, R., Barbour, M., Burk, J., Sosa-Ramírez, J., 2000. Californian mixed- conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja, California. Mexico. *Journal of Biogeography* 27: 105–129.
- Pyne, S. J. 1982. *Fire in America: a cultural history of wildland and rural fire*. Princeton University Press, Princeton.

Stephenson, J., Calcarone, G., 1999. Southern California Mountains and Foothills
Assessment. USDA Forest Service General Technical Report GTR-PSW-172.
Pacific Southwest Forest and Range Experiment Station, Berkeley.

Sugihara, N., J. Van Wagtendonk, K. Shaffer, J. Fites-Kaufman, and A. Thode, Eds.
2006. Fire in California's ecosystems. University of California Press, Berkeley.

Webster, G., and C. Bahre, eds. 2001. Changing plant life of La Frontera: observations on
vegetation in the United States/Mexico borderlands. University of New Mexico
Press, Albuquerque.

Weislander, A., 1935a. A vegetation type map of California. *Madroño* 3:140–144.

CHAPTER 1

Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California

ABSTRACT

A century of fire suppression culminated in wildfire on 28 Oct. 2003 that stand-replaced nearly an entire 4 000 ha “sky island” of mixed conifer forest (MCF) on Cuyamaca Mountain in the Peninsular Range of southern California. The fire affected Cuyamaca Rancho State Park (CRSP) represents a microcosm of the MCF covering approximately 5.5×10^6 ha (14%) of California, and was studied to evaluate how fire suppression unintentionally destabilizes this ecosystem. Significant changes in forest composition, tree density, and stem diameter class distribution are documented over a 75-year period at CRSP by replicating ground-based measurements sampled in 1932 for the Weislander Vegetation Type Map survey (VTM). Average conifer density more than doubled, from $271 \text{ trees ha}^{-1} \pm 82$ (standard error) to $716 \text{ ha}^{-1} \pm 79$. Repeat aerial photographs for 1928 and 1995 also show significant increase in canopy cover from $47\% \pm 2$ to $89\% \pm 1$. Changes comprise mostly ingrowth of shade-tolerant *Calocedrus decurrens* [Torr.] Floren. in the smallest stem diameter class (10 cm to 29.9 cm dbh). The 1932 density of overstory conifer trees (> 60 cm dbh) and 1928 canopy cover at CRSP were similar to modern MCF in the Sierra San Pedro Mártir (SSPM), ~ 200 km S in Baja California, Mexico, where fire-suppression had not been practiced, verifying that

the historical data from the early twentieth century represent a valid “baseline” for evaluating changes in forest structure. Forest successions after modern crown fires in southern California demonstrate that MCF is replaced by oak woodlands and shrubs. Post-fire regeneration in severely burned stands at CRSP include abundant basal sprouting of *Quercus chrysolepis* Liebm. and *Q. kelloggii* Newb, but only few seedlings of *Abies concolor* [Gord. and Glend.] Lindl (average $16 \text{ ha}^{-1} \pm 14$), while whole stands of *Calocedrus decurrens*, *Pinus lambertiana* Dougl., and *P. ponderosa* Laws. were extirpated. Prescribed burning failed to mitigate the crown fire hazard in MCF at CRSP because the low-intensity surface fires were small relative to the overall forest area, and did not thin the dense understory of sapling and pole-size trees. These results suggest that larger, more intense prescribed burns are needed to conserve California’s MCF.

INTRODUCTION

After a century of fire suppression management, dense stands of mixed conifer forest (MCF) have fueled high-severity wildfires over extensive areas of the southwestern United States (e.g., Graham, 2003). Wildfires were far less destructive prior to fire suppression management initiated ca. 1900. In California, open park-like stands were maintained by pre-suppression surface fires that cleared the understory of sapling and pole-sized trees (reviewed in Van Wagendonk and Fites-Kaufman, 2006; Minnich, 2007). In October 2003, massive wildfires burned ~300 000 ha across southern California, including approximately 10 000 ha of MCF. A crown fire stand-replaced nearly the entire 4 000 ha “sky island” of MCF on Cuyamaca Mountain in the Peninsular Range. Dense forest stands were completely charred, and patches of severely burned soil, conspicuously reddened with thermally produced iron oxides, covered as much as 15% of the land surface (Fig. 1.1; Goforth et al., 2005).

The fire affected Cuyamaca Rancho State Park (CRSP) represents a microcosm of the MCF covering approximately 5.5×10^6 ha (14%) of California (Barbour and Major, 1988). Previous studies have assessed how fire-suppression altered the structure of MCF in California, by relying upon indirect evidence of change, interpreted from late-nineteenth century written accounts, photographs, and survey records (e.g., Minnich, 1988; Stephens and Elliot-Fisk, 1998; Gruell, 2001), or reconstructed demographic patterns in modern stands (e.g., Vankat, 1977; Vankat and Major, 1978; Kilgore and Taylor, 1979; Parsons and DeBenedetti, 1979, Bonnicksen and Stone, 1982; Krofta, 1995), as well as by directly quantifying long-term landscape-scale change using repeat

measurements (Minnich et al., 1995; Albright, 1998; Bouldin, 1999; Stephenson and Calcarone, 1999). The availability of long-term data at CRSP provided unique opportunity to directly measure changes in forest structure and composition that culminated in stand-replacement wildfire.

Historical data collected for the Vegetation Type Map (VTM) survey of California (Weislander, 1935a, 1935b; after Minnich et al., 1995) and aerial photographs taken in 1928 were utilized as reference conditions comparable with modern repeat measurements, to quantify twentieth century changes in tree density, stem diameter-class distribution, canopy cover, and forest composition. Observations of forest change were calibrated against data obtained from a relatively unaltered MCF landscape (~40 600 ha) where fire suppression had not been practiced, located 200 km S at the Sierra San Pedro Mártir (SSPM) in Baja California, Mexico (Minnich et al. 1997, Minnich and Vizcaíno 1998, Minnich et al., 2000; Stephens and Gill, 2005; Stephens et al., 2007). Forest successional trajectories (i.e., probable long-term changes) after stand-replacement wildfire were analyzed on the basis of regeneration at CRSP, and trends observed in MCF elsewhere in California. It is hypothesized that (1) fire suppression management in the twentieth century caused increased tree density in old-growth MCF stands during the twentieth century, (2) that stand-densification broadens the size of crown fire from a process that historically developed small forest gaps, to stand-replacement of entire landscapes in modern conditions, and (3) that such large crown fires extirpate stands of non-serotinous conifers composing this ecosystem.

METHODS

Study area

The CRSP is located about 65 km east of San Diego, California, and 30 km north of the USA-Mexico international border (116° 35' W, 32° 57' N). Cuyamaca Mountain is uplifted Cretaceous intrusive igneous batholith rock within the broader Peninsular Range, which extends from Baja California, Mexico, north to the San Jacinto Mountains in southern California, USA. Soils are derived from gabbro colluvium at the study sites, and have sandy-loam to loam textures in the A horizon (Goforth et al., 2005). The Mediterranean-type climate is characterized by cold, wet winters and warm, dry summers. Average annual precipitation is 925 mm \pm 350 mm (standard deviation) over the period 1887-2006 at the Lake Cuyamaca Dam, with 87% resulting from extratropical cyclones of the North Pacific between November and April. Approximately 15% of the annual precipitation occurs as snowfall (Minnich, 1986). The annual average temperature is 11.6° C, with monthly average temperatures ranging from 4° C in January to 21° C in July.

About 4 000 ha of MCF covered Cuyamaca Mountain, over elevations ranging from 1 300 to 1 985 m. The forest was composed of white fir (*Abies concolor* [Gord. and Glend.] Lindl), incense cedar (*Calocedrus decurrens* [Torr.] Floren.), sugar pine (*Pinus lambertiana* Dougl.), Ponderosa pine (*P. ponderosa* Laws.), canyon live oak (*Quercus chrysolepis* Liebm.), and California black oak (*Q. kelloggii* Newb.). The CRSP contained 1 545 ha of old-growth protected from logging and wildfire in the twentieth century, and historical records indicate tree harvesting was limited in the nineteenth

century (e.g., Minnich, 2007, p. 509). Fire history maps show most of the study area had not burned since suppression records began in 1911, but pre-historical burning was evident from fire-scars on the base of large trees which lived for several centuries (Dodge, 1975).

VTM plot replication

Three VTM plots were located in MCF at CRSP. The sample locations are mapped at a scale resolution of ca. ± 100 m horizontal distance and ± 50 m elevation, but were not permanently marked in the field. Although it is not possible to relocate individual trees that were originally measured (Keeley, 2004), such spatial imprecision does not preclude replication of VTM plots. Rather, it necessitates a statistical resample of the local area where historical data was gathered. Sampling error was minimized by replicating measurements at multiple sites over a narrow range of environmental gradients (elevation, slope, aspect) encompassing the original VTM plot locations (after Minnich et al., 1995; Table 1). A geographical information system (GIS) was used to identify approximate latitude and longitude coordinates for each plot shown on a georeferenced digital copy of the original VTM plot map (after Bouldin, 1999). The global positioning system (GPS) was used to locate coordinate positions in the field, about which 8 replicate plots were established. The VTM data for forest trees was collected within 20×40 m rectangular plots (Weislander, 1935a), and each modern replicate plot has this same size (800 m^2). Field data was gathered 41 months after fire, precisely 75 years after the original VTM survey.

A census of trees within each plot was recorded according to tree stem diameter class protocol of the VTM survey: (10 cm - 29.9 cm, 30 cm - 59.9 cm, 60 cm - 90.9 cm, and > 91 cm). Oak trees often had multiple stems with canopy stature that branched from a common root crown base, at a height below 1.3 m where diameter is conventionally measured (diameter at breast height, dbh). Such stems were measured individually, while trees branching at dbh, or above were measured as a single stem. Therefore, stem density measurements of oaks are higher than the density of individual oak trees.

Regenerating shrub cover was estimated by line interception along the 40 m transect centerline of each plot (after Bauer, 1943). The presence or absence of exotic annual grasses and forbs was observed within five 1-m² quadrats spaced at 10 m intervals along this transect (40 quadrats total). Cover of exotic annuals and native herbaceous vegetation (live and dead) was determined by point interception along each transect (after Goodall, 1957), spaced at 1 m intervals (320 sample points total). The entire area of each plot was searched for tree seedlings (6 400 m² total).

Aerial photograph measurements

Repeat aerial photographs for 1928 (~1:7 200 scale) and 1995 (1:12 000) record changes in tree crown densities and canopy cover. Although the 1928 aerial photographs were taken using primitive photogrammetry, stereoscopic viewing was possible over about 60% of the MCF at CRSP. This coverage defined the sampling area. Ten separate aerial photograph scenes were identified close to photograph nadir points to reduce parallax distortion. Each scene was divided into a grid of 4 contiguous square cells,

giving a total of 40 replicate measurements. Scene boundaries and cell divisions were georeferenced according to the unique nearest-neighbor configuration of landmark features, and transferred from the 1928 photos onto the 1995 photos while viewed at the same scale using a Zoom Transfer Scope (ZTS).

Each scene was then independently analyzed on both 1928 and 1995 photographs under magnified stereoscopic view. Counts of tree crowns were made within scenes using gridded transparencies that further divided each cell into 25 sub-cells of equal size. Only trees in the canopy layer were counted (i.e., “crown heads” resolvable on the photographs), as sub-canopy trees were camouflaged. Hence, the density of tree crowns was expected to be lower than ground-based measurements of stem densities. Canopy cover was estimated by the extent of interception within each of the 25 sub-cells, rated from 0 (min) to 4 (max) for contribution to total cover. The sum of the 25 units gave the total cover (in percent).

Color aerial photographs taken in 1995 were used to map the forest before fire. The overstory assemblage was identified from crown form, vertical structure, and color reflectance. Surviving “unburned islands” were mapped using color aerial photography taken in November 2003 (1:12 000). Forest boundaries were transferred onto a 1:24 000 topographic quadrangle using the ZTS, and digitized into a GIS. The forest map was verified with field observation, reports of botanical collections, and other maps of conifer distributions (Griffin and Critchfield, 1972; Beauchamp, 1986; Minnich and Everett, 2001). Tree survival was checked in ground inspections aided with GPS navigation.

RESULTS

Stand-replacement wildfire

The CRSP was burned at the end of a week-long episode of dry easterly winds moving from the Great Basin to the Pacific Ocean (i.e., “Santa Ana” winds). From Oct. 24 to 28, an upper level ridge with a closed center of 6 000 m at 500 mb steered dry northeast flow over southern California (NOAA Daily Weather Maps, available online at <http://www.hpc.ncep.noaa.gov/dailywxmap/>). The winds weakened on Oct. 28 as the high pressure ridge axis shifted northward. Westerly anabatic winds along the western slope of Cuyamaca Mountain pushed the “Cedar fire” into MCF on Oct. 28 (map on file, California Dept. of Forestry, Sacramento, CA), although easterly flow aloft continued to resurface as “Santa Ana” winds at times throughout the day (Fig. 1.2; data on file, Western Regional Climate Data Center, Reno, NV). Air and fuel temperatures exceeded 30° C, relative humidity was < 15%, and wind speeds were < 20 km hr⁻¹. By Oct. 29, onshore pressure gradients produced strong sustained northwesterly winds, but humidity did not recover until Oct. 30 because the antecedent “Santa Ana” wind event displaced the moist marine layer airmass far offshore of the Pacific Ocean coastline (cf., Franklin et al., 2006). The marine layer arrived after the “Cedar fire” had spread well east where the advancing flames stopped for lack of fuel remaining after the “Pines fire” of 2002.

Over 95% of the entire MCF landscape at the CRSP was fire-killed (Fig. 1.3). Remaining “unburned islands” of MCF total just 70 ha. Rare individual trees survive within the burn along roads (not mapped).

VTM plot replication

Stem density almost doubled, from an average of $421 \text{ ha}^{-1} \pm 144$ (standard error) in 1932 to $753 \text{ ha}^{-1} \pm 75$ in 2007. Conifers comprise nearly all of the reproduction, increasing from $271 \text{ trees ha}^{-1} \pm 82$ to $716 \text{ ha}^{-1} \pm 79$. Paired distributions of stem diameter classes show significant demographic changes for conifers (Chi-square test, $\alpha = 0.05$, d.f. = 3, $\chi^2 = 64.3$, $p < 0.001$), including a 250% increase in density of pole-size trees (10 to 29.9 cm dbh), while old-growth (> 90 cm) declined by 40% (Fig. 1.4). The shade-tolerant *Calocedrus decurrens* increased by nearly a factor of 4 due to ingrowth of small trees (Fig. 1.5). Diameter class distributions of oak stems did not significantly change (Fig. 1.6; $\chi^2 = 5.2$, $p = 0.073$), and their modern average stem density ($100 \text{ ha}^{-1} \pm 43$ in) overlaps with measurements taken in 1932 ($150 \text{ ha}^{-1} \pm 80$).

Repeat aerial photography

Open stands in 1928 developed closed canopies in all of the 1995 aerial photograph scenes. Significant increases were measured in crown density (directional Mann-Whitney test, $\alpha = 0.05$, $W = 2402$, $p < 0.001$) and canopy cover ($W = 2420$, $p < 0.001$). The change in crown density paralleled trends of stem densification for conifers measured in ground-based plots, increasing from $69 \text{ ha}^{-1} \pm 4$ in 1928, to $165 \text{ ha}^{-1} \pm 6$ in 1995 (Fig. 1.7). Canopy cover similarly increased from $47\% \pm 2$ to $89\% \pm 1$ (Fig. 1.8).

Post-fire regeneration

MCF did not regenerate at CRSP, 41 months after fire (Table 2). Species-specific seedling deficiencies were as large as 937 ha^{-1} for non-serotinous conifers composing this

ecosystem, with stand extirpation of *Calocedrus decurrens*, *Pinus lambertiana*, and *P. ponderosa* (Fig. 1.9). We found only *Abies concolor* seedlings in fire-killed stands, at a density of $16 \text{ ha}^{-1} \pm 14$. Seedlings of *C. decurrens* and *P. ponderosa* were found near scorched trees that survived elsewhere (e.g., Plot A). Because oak crowns were killed, stems basally sprouted new growth regardless of diameter class ($n = 91$ stems). No acorn production had occurred on this post-fire growth, nor were oak seedlings observed.

Regenerating shrub cover ranged from 5% to 87%, averaging $63\% \pm 11$, and was almost entirely composed of *Ceanothus palmeri* Trel. (Fig. 1.10). This shrub attained reproductive maturity after only 3 growing seasons. Exotic annual grasses and forbs were absent from 68% of the 1-m^2 quadrats. Herbaceous cover ranged from 3 to 76%, averaging $21\% \pm 9$ (Fig. 1.11). Cover of exotic annuals ranged from 0 to 58%, averaging $10\% \pm 7$, with *Bromus diandrus* Roth most common. Plot A with the greatest exotic annual cover (58%) occurred within ~ 100 m of a home. Otherwise, exotic annuals were sparse in the other 7 plots, all far from disturbed land, with cover averaging only $3\% \pm 2$ (range 0-8%). We found no significant correlation of exotic annual cover with shrub cover ($\alpha = 0.05$, $p = 0.76$, $r = 0.12$) or tree density ($p = 0.11$, $r = -0.61$). Native forbs covered between 0 to 34%, averaging $11\% \pm 4$. The most prevalent native was the western mountain pea *Lathyrus vestitus* Nutt.

DISCUSSION

Forest densification

Replication of VTM forest plots and repeat aerial photography of CRSP document significant densification of stems, similar to trends reported in other studies of MCF throughout California (Vankat, 1977; Vankat and Major, 1978; Kilgore and Taylor, 1979; Parsons and DeBenedetti, 1979; Bonnicksen and Stone, 1982; McKelvey and Johnston, 1992; Minnich et al., 1995; Albright, 1998; Ansley and Battles, 1998; Bouldin, 1999; Barbour et al., 2002). Suppression of wildfire in the twentieth century prevented normal selective thinning of sapling and pole sized trees in the forest understory, permitting continuous recruitment and canopy cover by the shade-tolerant *C. decurrens*. Conifers attained local densities as high as 975 trees ha⁻¹ > 10 cm dbh (Table 1). The overabundance of sapling and pole-size trees which compete for limited soil moisture and nutrients is likely a factor causing decline of old-growth stem density in addition to air pollution injury, and such dense stands may increase the susceptibility of Pines to bark beetle infestation with mass die-off events during droughts (e.g., Savage, 1994; Minnich et al., 1995; Jones et al., 2004; Minnich, 2007).

Fire suppression records available at CRSP from 1970-1980 verify that twelve lightning initiated fires were extinguished in MCF, all less than a few hectares in size (Gaidula and Biswell, 1983). These ignitions occurred mostly in summer, from thunderstorms of the North American Monsoon (reviewed by Minnich, 2006, p. 20-24). The suppression records give an average detection rate of 1.2 lightning fires yr.⁻¹ in the 15 km² study area, or 0.08 fires km⁻² yr.⁻¹ Since the density of summer lightning strikes

averages about $3 \text{ km}^{-2} \text{ yr}^{-1}$ (Wells and McKinsey, 1993), the ignition efficiency was only 3% of strikes requiring suppression, similar to MCF elsewhere in the mountains of southern California and Baja California (Minnich et al., 1993). At this rate over 75 years, perhaps 6 lightning fires km^{-2} required suppression.

We calibrated our observations of forest change at CRSP against data gathered in the SSPM. Ground-based sampling of stand structure in the SSPM measured conifers $> 60 \text{ cm dbh}$ at densities of 27 ha^{-1} to 56 ha^{-1} (Minnich et al., 1995; Stephens and Gill, 2005) which overlaps with the VTM plot densities of 25 ha^{-1} to 63 ha^{-1} for the same size stems measured in 1932 at CRSP. Aerial photography sampling of stand structure in the SSPM measured overstory tree densities of 65 ha^{-1} to 145 ha^{-1} and cover of 25% to 45% (Minnich et al., 2000), similar to aerial photograph scenes of CRSP in 1928 showing tree crowns at densities of 39 ha^{-1} to 86 ha^{-1} with cover of 24% to 63%. These results also overlap with ground-based measurements of canopies covering 14% to 56% of stands in the SSPM (Stephens and Gill, 2005; Stephens et al., 2007). Such broad overlap of structural conditions suggests that measurements of MCF at CRSP in 1928 and 1932 do not substantially differ from pre-suppression conditions. Thus, the historical data represent a valid “baseline” for evaluating change.

Post-fire successional trajectories

Many factors may prevent regeneration of MCF after stand-replacement wildfire. The forest assemblage is composed of non-serotinous conifers whose seed borne on fire-killed trees were almost completely destroyed. The massive extent of stand-replacement

at CRSP exceeds the seed dispersal capacity of remaining live trees, and nearest-neighbor seed sources are distant within this severely burned forest. Lengthy immigration lag-times are expected because there is low probability of long-range seed dispersal within fire-killed stands, and from forests in neighboring mountain “sky islands” located tens to hundreds of km away (Minnich, 1987a; Minnich and Everett, 2001). Post-fire growth of *Ceanothus palmeri* may suppress conifer regeneration for decades (Minnich, 1978, Conard and Radosevich, 1982; Albright, 1998), and poses greater interference to recruitment than the sparse cover of exotic annual grasses and forbs reported to have invaded the burned forest stands after fire (cf., Franklin et al., 2006). While *Ceanothus* declines in abundance over decades, the shrub regenerates from a soil-stored accumulation of dormant refractory seed with germination stimulated by fire (e.g., Kauffman and Martin, 1991). It is unlikely that conifer seedlings will recruit to reproduce subsequent generations because maturation times are lengthy relative to fire recurrence intervals, and immature trees generally lack stature necessary to survive burning.

Comparable forest successions after stand-replacement wildfires in the San Bernardino Mountains may foretell likely changes at CRSP (Albright, 1998; Minnich, 1978, 1988). At Heaps Peak, dense second-growth MCF was burned by crown fire in 1922. This 1 000 ha area was subsequently mapped as a *Q. kelloggii* woodland by the VTM survey in the 1930’s (Redlands quadrangle) due to poor recruitment of conifers. Most of the area was burned by crown fire again in 1956. Although nearest seed trees were only 1.5 km away, there was very little colonization by 1974 when sampling

documented conifer densities of $< 20 \text{ ha}^{-1}$ (Minnich, 1978). Sampling in 1995 found no increase, and conifers comprised only 10% of vegetation cover (Albright, 1998). The area burned in the October 2003 firestorm, which also killed neighboring MCF, and is presently dominated by basally sprouting *Q. kelloggii* as well as shrubs of *Ceanothus*.

Increasingly fragmented MCF “sky islands” in the Peninsular Range

Stands of MCF in southern California’s Peninsular Range are widely separated by mountains and valleys covered with chaparral, oak woodland, and exotic annual grasslands (Minnich and Everett, 2001). Small unburned stands of *Pinus ponderosa* remain at CRSP, which is the southernmost distribution in the California floristic province (Griffin and Critchfield, 1972). The nearest populations are smaller groves at Pine Hills (7 km N), and Doane Valley in Palomar Mt. (46 km N, Minnich and Everett, 2001). The San Jacinto Mountains (85 km N) are presently the only large population of *P. ponderosa* remaining in the Peninsular Range. Few old-growth stems of *P. lambertiana* survived the stand-replacement wildfire at Cuyamaca Mountain (Oberbauer, 2007). Small stands grow at Hot Springs Mt. (32 km N), a small grove was recently discovered at Palomar Mt. (Goforth and Minnich, 2003), and large populations cover the San Jacinto Mountains and the SSPM (Minnich 1987a).

Did large crown fires occur in MCF prior to fire suppression and logging?

A recent book questions whether large stand-replacement wildfires occur outside of the historical range of variation (Keeley 2006, p. 380), citing earlier studies by

Minnich (1978 & 1999) as showing large pre-suppression crown fires in southern California's MCF in the late nineteenth century, and evidence of former conifer forests now occupied by chaparral indicating high-intensity crown fires prior to the twentieth century. Minnich (1978, p. 134-135) actually documents large crown fires in the late nineteenth century that occurred in dense second-growth which had been logged and was therefore already outside the range of historical variation, and Minnich (1999, p. 69) reports pre-suppression canopy fires developed numerous small forest gaps in contrast with modern stand replacement wildfires. A body of evidence indicates that large stand-replacement wildfires do not occur within the historical range of variation in MCF successions. For example, MCF does not grow in even-aged cohorts characteristic of serotinous conifers prone to crown fires (reviewed by Minnich, 2007). Dendrochronology studies in MCF report mixed ages of trees that live for several centuries, and deduce on the basis of fire scar intervals within their growth-rings, recurrence of many understory burns that stands survived prior to fire suppression beginning ca. 1900 (e.g., McBride and Laven, 1978; Kilgore and Taylor 1979; Caprio and Swetnam, 1995; Kerr, 1996; Taylor, 2000; Stephens, 2001; Everett, 2003; Stephens et al., 2003; Stephens and Collins, 2004). Written historical records such as Forest Reserve Reports of late-nineteenth century land surveys in the mountains of southern California describe pre-suppression surface fires that burned understory fuels (Lieberg 1900, p. 453). Botanical surveys emphasize a lack of damage to overstory trees in burned stands (e.g., Hall, 1902, p. 25). At the time fire-suppression records began in southern California, the State Forester wrote (Homans, 1910, p. 60):

Ground fires are the prevailing type in mature timber, crown fires being practically unknown in Southern California. They consume as fuel the litter of needles and twigs, and whatever under-growth, either brush or [conifer] reproduction, that may cover the forest floor... Ordinarily they are not difficult to control, but if not checked will run through the needles and decayed litter for miles, although seldom becoming severe enough to kill large trees. The exception is found where there is a dense stand of brush underneath the timber, or a clump of trees occurs in a chaparral area... The destructive element of the ground fire is that it kills all reproduction, leaving only a stand of mature trees.

Leiberg (1899, p. 354) observed pre-suppression crown fires limited to “scattered coniferous trees or groves among the chaparral.” Aerial photographs taken in 1938 verify small crown fires dating back to the pre-suppression period, showing stand-replacement patches in areas where trees grow with dense shrub cover, usually on steep exposed slopes subject to “fire runs” uphill, totaling ca. 5% of the old growth forest (Minnich, 1988, p. 49-52). According to Leiberg (1899, p. 354): “There is not the slightest evidence to prove that chaparral areas were covered with timber within the historic period, nor that fires increase these areas at the expense of the timbered regions.”

Similarly, without fire suppression in Baja California, Mexico, stand-replacement wildfire is localized in the SSPM and forest distributions are stable. A spatially explicit reconstruction of 865 fire perimeters in MCF mapped using repeat aerial photography since 1925 show that crown fire collectively amounts to < 16% of individual burn areas, and is limited to < 5 ha size patches mostly found on steep slopes with shrub understory fuels that generate elevated scorch heights (Minnich et al., 2000). The fire regime is characterized by countless lightning ignited surface fires, most of which burn small accumulations of leaf litter and scar the bases of individual trees, but such “micro burns” cover little cumulative area. Less frequently, only 2 or perhaps 3 times per century, an

intense surface fire spreads among stands. These “mass burns” are observed to generate scorch heights up to 10 m above ground which selectively clears the understory of sapling and pole sized trees while pruning the lower branches of overstory trees, resulting in open park-like stands mostly occupied by old-growth trees as qualitatively discussed in numerous pre-suppression accounts of MCF in California. Dense stands subject to stand-replacement wildfire in the SSPM are rare and localized, forming small fragmented areas within the landscape mosaic of previous “mass burns” at locations that have not burned in the past century due to circumstances of chance.

Many studies describe floristic and environmental similarities between MCF in the SSPM and sites in California; for example, the San Jacinto Mountains (Minnich, 2001), the San Bernardino Mountains (Minnich et al., 1995), and the eastern Sierra Nevada (Barbour et al., 2002; Stephens and Gill, 2005). The historical structure of MCF in the western Sierra Nevada may also be similar to the SSPM (Minnich et al., 2000), and requires further study. The shared demographic patterns of old-growth trees, which matured well before fire suppression was implemented, are independent of potential differences in climate suggested to preclude similarity between MCF in the SSPM and California (cf., Keeley, 2006, p. 361). These findings indicate that structural conditions of old-growth MCF in California have diverged from the SSPM in the past century because of fire-suppression practiced north of the USA-Mexico international border. The scale of stand-replacement in southern California has been linked to the large size of modern chaparral wildfires which spread into the adjoining MCF landscape as with the massive “Cedar fire” of October 2003, and trans-border comparisons of burn mosaics

indicate fire suppression is a likely factor causing these large wildfires (Minnich and Bahre, 1995; Minnich and Chou, 1997).

CONCLUSIONS

Fire suppression destabilizes MCF by allowing widespread accumulation of fuel (live and dead biomass) in the form of leaf litter accumulations, coarse woody debris, and understory growth of shrubs and conifer regeneration. Fire suppression also selects for wildfires during extreme weather states when ignitions are least efficiently extinguished as in summer “heat waves” or dry easterly “Santa Ana” winds in autumn that pushed the October 2003 firestorm across southern California (Minnich, 2006). Pre-suppression crown fire produced small forest gaps, whereas densification resulting from fire suppression promotes extensive stand-replacement wildfires involving whole MCF landscapes like at CRSP. Such large crown fires extirpate stands of non-serotinous conifers composing this ecosystem. In this context, the term “stand-replacement” somewhat misrepresents how crown fire alters MCF successions; it does not result in a replacement by like kind, but rather by oaks and shrubs that sprout new stems or germinate from dormant refractory seed stored in the soil.

In the seminal book *Prescribed Burning in California Wildlands Vegetation Management*, Harold Biswell predicted the entire CRSP would be destroyed by a single wildfire if prescribed burning was not practiced (Biswell, 1989, p. 78). A prescribed burning program was developed for the park. It relied upon use of small low-intensity

fires to reduce surface fuels (Lathrop and Martin 1982, Gaidula and Biswell, 1983). Over 20 years, 35 prescribed burns were administered treating a total of only 590 ha, and such localized results did not mitigate the hazard (Goforth and Boyce, 2003). This experience suggests it is impossible to administer enough small low-intensity burns to reduce accumulations of surface fuels in a dense forest of MCF over a landscape scale of management.

Prescribed fires in MCF need to be larger and more intense than presently envisioned, to not only reduce surface fuels over broad areas, but also to generate higher scorch heights sufficient to clear the understory of sapling and pole-sized trees while pruning the lower limbs of surviving overstory trees. Repeat aerial photography of MCF in the SSPM show that small, low-intensity surface fires do not greatly influence landscape patterns of forest demography, or the patterning of subsequent wildfires because they remove minor quantities of fuel (i.e., live and dead biomass) compared to more intense understory fires that burn among stands (Minnich et al., 2000). Since fuels gradually accumulate over decades in MCF and adjoining chaparral landscapes (e.g., Minnich and Chou, 1997; Minnich et al., 2000), only a few modest size burns are needed per century. Their placement can exploit the existing landscape mosaic of previously burned patches so that prevailing winds push flames toward recent burns which constrain further spread. Fire suppression can be relaxed in remote areas, letting unplanned ignitions burn under the observation of fire crews, even for weeks or months in summer, so that alternating smolder-and-run fire behavior develops in phase with a broad range of weather conditions, promoting heterogeneous burn severities over the landscape as

reported in numerous pre-suppression accounts (e.g., Minnich, 1987b, 1988, 2006, p. 29-32). Potential cost savings earned from these adjustments in fire management may help to reduce suppression expenses incurred in California, and elsewhere in the southwestern United States (GAO, 2007).

REFERENCES

- Albright, D., 1998. Vegetation change in second-growth mixed conifer forests of western San Bernardino Mountains. Unpublished M.S. thesis, Department of Earth Sciences, University of California, Riverside, CA, USA, 39 p.
- Ansley, J., Battles, J., 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. *Journal of the Torrey Botanical Society* 125, 297-308.
- Barbour, M., Major, J., 1988. Introduction. In: Barbour, M., Major, J. (Eds.), *Terrestrial Vegetation of California*. California Native Plant Society Special Publication 9, Sacramento, CA, USA, pp 3-10.
- Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E., Fites-Kaufmann, J., 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada. *Journal of Vegetation Science* 13, 461-472.
- Bauer, H. 1943. The statistical analysis of Chaparral and other plant communities by means of transect samples. *Ecology* 24, 45-60.
- Beauchamp, R., 1986. *A Flora of San Diego County, California*. Sweetwater River Press, National City, CA, USA, 241 p.
- Biswell, H., 1989. *Prescribed Burning in California Wildlands Vegetation Management*. University of California Press, Berkeley, CA, USA, 255 p.
- Bonnicksen, T., Stone, E., 1982. Reconstruction of a pre-settlement giant sequoia-mixed

conifer forest community using the aggregation approach. *Ecology* 63, 1134-1148.

Bouldin, J., 1999. Twentieth-century changes in forests of the Sierra Nevada.

Ph.D. Dissertation, University of California, Davis, CA, USA, 222 p.

Caprio, A., Swetnam, T., 1995. Historic fire regimes along an elevational gradient on the west slope of the Sierra Nevada, California. In: Brown, J., Mutch, R., Spoon, C., Wakimoto, R. (Eds.) Proceedings of the symposium on fire in wilderness and park management: Past lessons and future opportunities, March 30-April 1, 1993. USDA Forest Service General Technical Report INT-GTR-320, Intermountain Research Station, Ogden, UT, USA, p. 8-14.

Conard, S., Radosevich, S., 1982. Post-fire succession in white fir (*Abies concolor*) vegetation of the northern Sierra Nevada. *Madroño* 29, 42-56.

Dodge, M. 1975. Vegetational changes associated with land use and fire history in San Diego County. Ph.D. Dissertation, University of California, Riverside, CA, USA, 216 p.

Everett, R.G., 2003. Grid-based fire-scar dendrochronology and vegetation sampling in the mixed-conifer forests of the San Bernardino and San Jacinto mountains of southern California. Ph.D. Dissertation, University of California, Riverside, CA, USA, 147 p.

Franklin, J., Spears-Lebrun, L., Deutschman, D., Marsden, K., 2006. Impact of a high-

intensity fire on mixed evergreen and mixed conifer forests in the Peninsular ranges of southern California, USA. *Forest Ecology and Management* 235, 18-29.

Gaidula, P., Biswell, H., 1983. Prescribed fire management program for Cuyamaca Rancho State Park. Unpublished report, California Department of Parks and Recreation, Sacramento, CA, USA, 185 p.

GAO, 2007. Wildland fire management: Lack of clear goals or a strategy hinders Federal agencies' efforts to contain the costs of fighting fires. United States Government Accountability Office Report GAO-07-655, Washington DC, USA, 52 p.

Goforth, B., Boyce, W., 2003. Prescribed fire management plan for Cuyamaca Rancho State Park, second edition. Unpublished report, California Department of Parks and Recreation, Sacramento, CA, USA, 76 p.

Goforth, B., Minnich, R., 2003. Noteworthy collection of *Pinus lambertiana* (Pinaceae) at Palomar Mountain. *Madroño* 50, 53.

Goforth, B., Graham, R., Hubbert, K., Zanner, C., Minnich, R., 2005. Spatial distribution and properties of ash and thermally altered soils after high-severity forest fire, southern California. *International Journal of Wildland Fire* 14, 343-354.

Goodall, D., 1957. Some considerations in the use of point quadrat methods for the analysis of vegetation. *Australian Journal of Biological Science* 5, 1-41.

Graham, R. (Ed.), 2003. Hayman fire case study. USDA Forest Service General

- Technical Report RMRS-GTR-114. Rocky Mountain Research Station, Ogden, UT, USA, 396 p.
- Gruell, G., 2001. Fire in Sierra Nevada Forests: A Photographic Interpretation of Ecological Change Since 1849. Mountain Press Publishing, Missoula, MT, USA, 238 p.
- Griffin, J., Critchfield, W., 1972. The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA, 114 p.
- Hall, H., 1902. A botanical survey of San Jacinto Mountain. University of California Publications in Botany 1, 1-139.
- Homans, G., 1910. Southern California, character of fires. In: Third Biennial Report of the State Forester, California Division of Forestry, Sacramento, CA, USA, 160 p.
- Jones, M., Paine, T., Fenn, M., Poth, M. 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *Forest Ecology and Management* 200, 67–76.
- Kauffman, J., Martin, R. 1991. Factors influencing the scarification and germination of three montane Sierra Nevada shrubs. *Northwest Science* 65, 180-187.
- Keeley, J., 2004. VTM plots as evidence of historical change: goldmine or landmine? *Madroño* 51, 372-378.
- Keeley, J., 2006. South coast bioregion. In: Sugihara, N., Van Wagtenonk, J., Shaffer, K., Fites-Kaufman, J., Thode, A. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, CA, USA, pp. 350-390.

- Kerr, R., 1996. The fire regime of Mt. Gleason, California as a function of climate and vegetation. Unpublished M.S. thesis. California State University, Northridge, CA, USA, 84 p.
- Kilgore, B., 1973. The ecological role of fire in Sierran conifer forests: its application to National Park management. *Quaternary Research* 3, 496–513.
- Kilgore, B., Taylor, D., 1979. Fire history in a sequoia-mixed conifer forest. *Ecology* 60, 129-142.
- Krofta, D., 1995. Stand structure and composition of mixed conifer-hardwood forest in Cuyamaca Rancho State Park, San Diego County, California. Unpublished M.S. thesis. San Diego State University, San Diego, CA, USA, 137 p.
- Lathrop, E., and B. Martin. 1982. Response of understory vegetation to prescribed burning in yellow pine forests of Cuyamaca Rancho State Park. *Aliso* 10:329-343
- Leiberg, J., 1899. San Gabriel, San Bernardino, and San Jacinto Forest Reserves. In: Gannett, H. (Ed.), Nineteenth annual report of the U.S. Geological Survey to the Secretary of Interior, Part 5, Forest Reserves. US Government Printing Office, Washington, D.C., USA, pp. 351-371.
- Leiberg, J., 1900. San Gabriel, San Bernardino, and San Jacinto Forest Reserves. In: Gannett, H. (Ed.), Twentieth annual report of the U.S. Geological Survey to the Secretary of Interior, Part 5, Forest Reserves. US Government Printing Office, Washington, D.C., USA, pp. 411-479.
- McBride, J., Laven, R., 1976. Scars as indicators of fire frequency in the San Bernardino Mountains, California. *Journal of Forestry* 74, 439–442.

- Minnich, R., 1978. The geography of fire and conifer forests in the eastern Transverse ranges, California. Ph.D. Dissertation, University of California, Los Angeles, CA, USA, 395 p.
- Minnich, R., 1986. Snow levels and amounts in the mountains of southern California. *Journal of Hydrology* 89, 37-58.
- Minnich, R., 1987a. The distribution of forest trees in northern Baja California, Mexico. *Madroño* 34, 98-127.
- Minnich, R., 1987b. Fire behavior in southern California chaparral before fire control: the Mount Wilson burns at the turn of the century. *Annals of the Association of American Geographers* 77, 599-618.
- Minnich, R., 1988. The biogeography of fire in the San Bernardino Mountains of California: a historical study. *University of California Publications in Geography* 27, 1-121.
- Minnich, R., 1999. Vegetation, fire regimes, and forest dynamics. In: Miller, P., McBride, J. (Eds.), *Oxidant Air Pollution Impacts in the Montane Forests of Southern California*. Springer-Verlag, New York, NY, USA, pp. 44-78.
- Minnich, R., 2001. Fire and elevational zonation of chaparral and conifer forests in the peninsular ranges of La Frontera. In: Webster, G., and Bahre, C. (Eds.), *Changing Plant Life of La Frontera: Observations on Vegetation in the U.S./Mexico Borderlands*. University of New Mexico Press, Albuquerque, NM, USA, pp. 120-142.
- Minnich, R., 2006. California climate and fire weather. In: Sugihara, N., Van

- Wagtendonk, J., Shaffer, K., Fites-Kaufman, J., Thode, A. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, USA, pp. 13-37.
- Minnich, R., 2007. Southern California coniferous forest. In: Barbour, M., Keeler-Wolf, T., and Schoenherr, A. (Eds.). Terrestrial Vegetation of California, 3rd edition. University of California Press, Berkeley, CA, USA, pp. 502-538.
- Minnich, R., and Bahre, C., 1995. Wildland fire and chaparral succession along the California–Baja California boundary. *International Journal of Wildland Fire* 5, 13–24.
- Minnich, R., Barbour, M., Burk, J., Fernau, R., 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conservation Biology* 9, 902–914.
- Minnich, R., Barbour, M., Burk, J., Sosa-Ramírez, J., 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Mártir, Baja, California. Mexico. *Journal of Biogeography* 27, 105–129.
- Minnich, R., Chou, Y., 1997. Wildland fire patch dynamics in the chaparral of southern California and northern Baja California. *International Journal of Wildland Fire* 7, 221–249.
- Minnich, R., Everett, R., 2001. Conifer tree distributions in southern California. *Madroño* 48, 177-197.
- Minnich, R., Franco-Vizcaíno, E., 1998. Land of chamise and pines: Historical accounts

- and current status of northern Baja California's vegetation, University of California Publications in Botany 80, 1–166.
- Minnich, R., Franco-Vizcaíno, E., Sosa-Ramírez, J., Burk, J., Barry, W., Barbour, M., de la Cueva-Salcedo, H., 1997. A land above: protecting Baja California's Sierra San Pedro Mártir within a Biosphere Reserve. *Journal of the Southwest* 39, 613–695.
- Minnich, R., Franco-Vizcaíno, E., Sosa-Ramírez, J., Chou, Y., 1993. Lightning detection rates and wildland fire occurrence in the mountains of northern Baja California. *Atmósfera* 6, 235-253.
- Oberbauer, T. Loss of 500-year-old sugar pines during October 2003 fire storms. *Fremontia* 35, 18-23.
- Parsons, D., DeBenedetti, S., 1979. Impact of fire suppression on a mixed conifer forest. *Forest Ecology and Management* 2, 21–33.
- Savage, M. 1994. Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Canadian Journal of Forest Research* 24, 1149-1159.
- Stephens, S., 2001. Fire history of adjacent Jeffrey pine and upper montane forests in the eastern Sierra Nevada. *International Journal of Wildland Fire* 10, 161–176.
- Stephens, S., Collins, B., 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Science* 78, 12–23.
- Stephens, S., Elliot-Fisk, 1998; *Sequoiadendron giganteum*-mixed conifer forest structure in 1900-1901 from the southern Sierra Nevada, CA. *Madroño* 45, 221-230.
- Stephens, S., Fry, D., Franco-Vizcaíno, E., Collins, Moghaddas, J., 2007. Coarse woody

- debris and canopy cover in an old-growth Jeffrey pine-mixed conifer forest from the Sierra San Pedro Martír, Mexico. *Forest Ecology and Management* 240, 87-95.
- Stephens, S., Gill, S., 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in northwestern Mexico. *Forest Ecology and Management* 205, 15–28.
- Stephens, S., Skinner, C., Gill, S., 2003. Dendrochronology-based fire history of Jeffrey pine- mixed conifer forests in the Sierra San Pedro Martír, Mexico. *Canadian Journal of Forest Research* 33, 1090–1101.
- Stevenson, J., Calcreone, G., 1999. Southern California Mountains and Foothills Assessment. USDA Forest Service General Technical Report GTR-PSW-172. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA, 402 p.
- Taylor, A., 2000. Fire regime and forest change in mid and upper montane forests of the Southern Cascades, Lassen Volcanic National Park, California, USA. *Journal of Biogeography* 27, 87–104.
- Van Wagtenonk, J., Fites-Kaufman, J., 2006. Sierra Nevada bioregion. In: N. Sugihara, N., Van Wagtenonk, J., Shaffer, K., Fites-Kaufman, J., Thode, A. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, CA, USA, pp. 264-294.
- Vankat, J., 1977. Fire and man in Sequoia National Park. *Annals of the Association of American Geographers* 67, 17-27.

Vankat, J., Major, J., 1978. Vegetation changes in Sequoia National Park, California.

Journal of Biogeography 5, 377-402.

Weislander, A., 1935a. A vegetation type map of California. Madroño 3, 140–144.

Weislander, A., 1935b. First steps of the forest survey in California. Journal of Forestry
33, 877-884.

Wells, M., McKinsey, D., 1993. The spatial and temporal distribution of lightning strikes
in San Diego County, California. In: Proceedings GIS/LIS '93, Volume 2:
November 2-4, 1993. American Congress on surveying and mapping,
Minneapolis, MN, USA, pp. 768-777.



Figure 1.1 Dense stands of fire-killed conifers and top-killed oaks were completely charred by crown-fire and lacked residual surface fuels. Photograph taken 54 days after fire in CRSP.

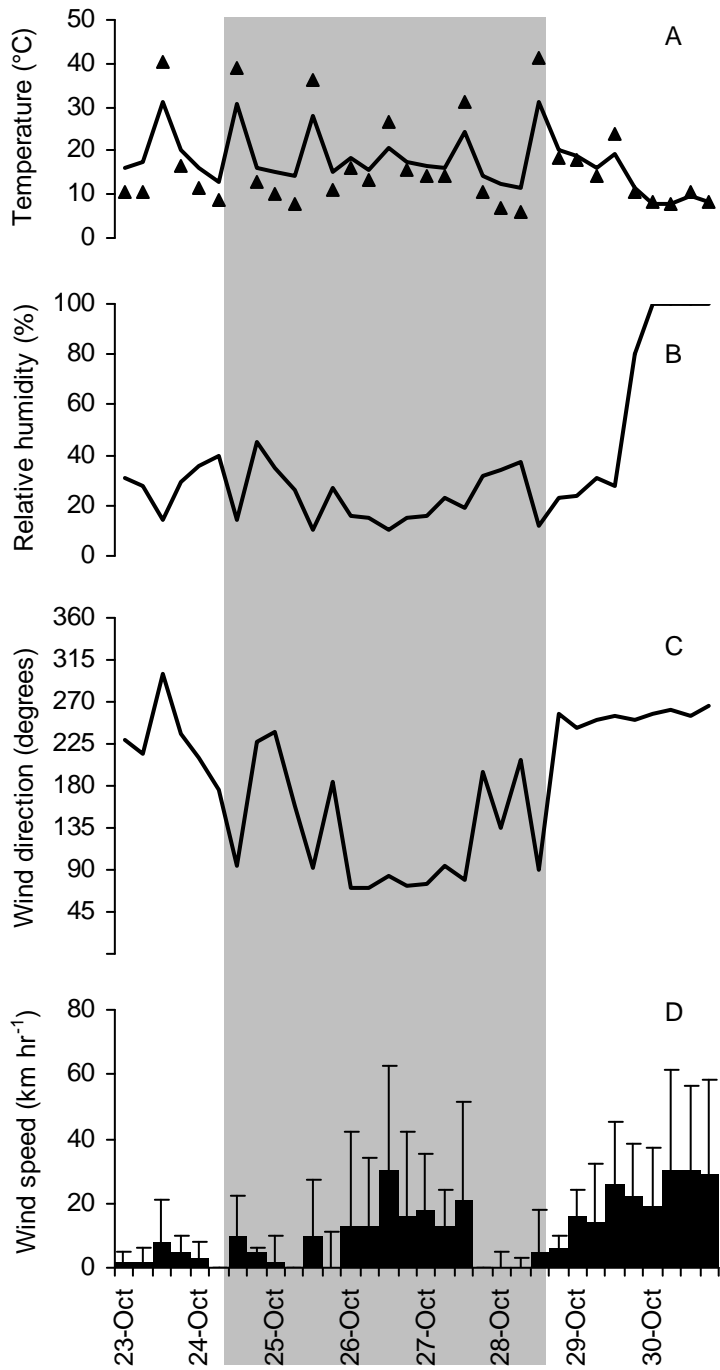


Figure 1.2 Meteogram of weather conditions registered every 6 hours at the Julian RAWS station located 10 km north of CRSP during the “Cedar fire” of October 2003. “Santa Ana” winds occurred from 24 Oct. to 28 Oct. (shaded window). (A) Air temperature is shown by trend line, while temperature of 10-hr. woody fuels (1.3 cm dia) is plotted by the symbol ▲. (B) Relative humidity. (C) Azimuths of wind direction where 0° is north. (D) Sustained wind speed and maximum gusts.

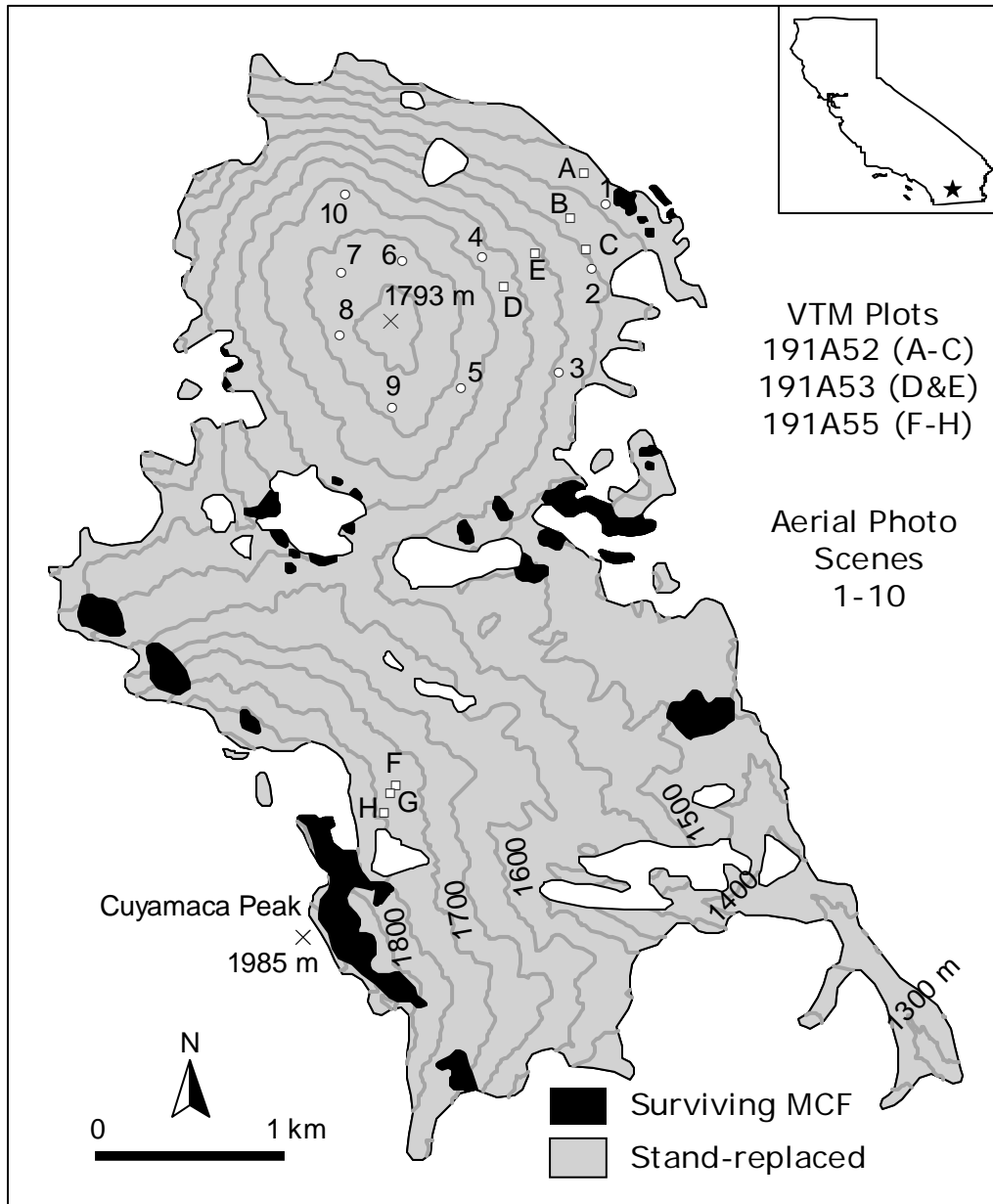


Figure 1.3 The remaining extent of MCF in Cuyamaca Rancho State Park after stand-replacement wildfire in October 2003 (shaded area) is ~5% of the pre-fire area shown. Locations of replicated VTM plots (A-H) and repeat aerial photograph scenes (1-10) are indicated for reference.

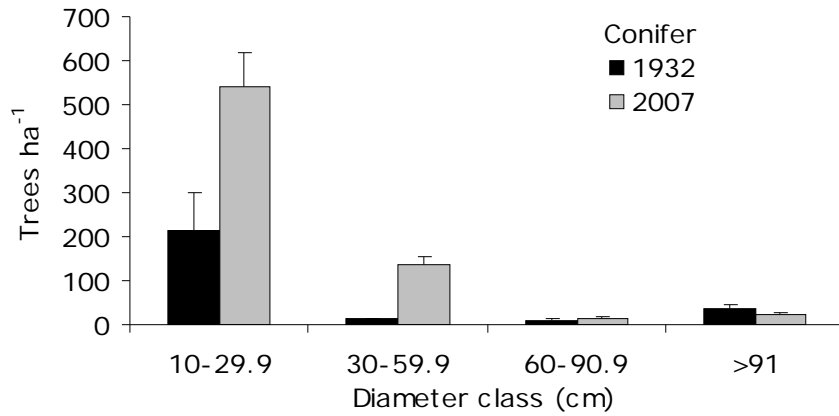


Figure 1.4 Average conifer density according to stem diameter class, 1932 to 2007. Error bars indicate one standard error.

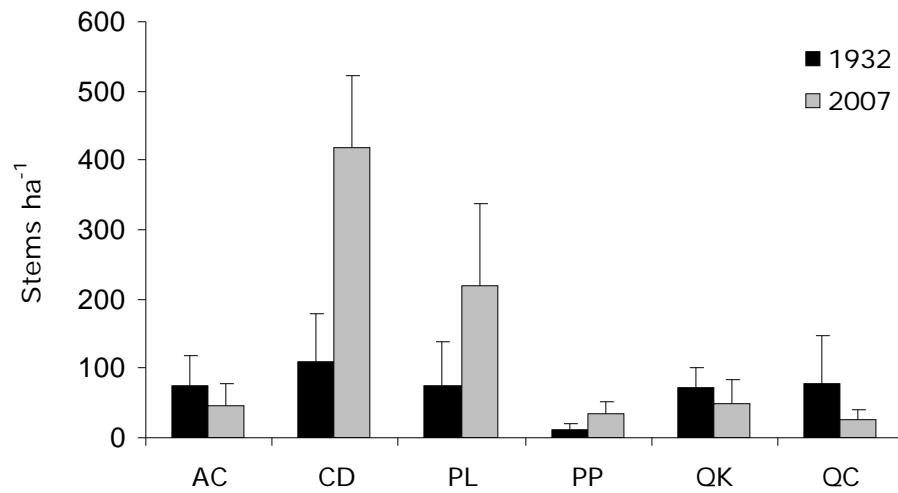


Figure 1.5 Average density of tree species, 1932 to 2007. AC, *Abies concolor*; CD, *Calocedrus decurrens*; PL, *Pinus lambertiana*; PP, *P. ponderosa*; QC, *Quercus chrysolepis*; QK, *Q. kelloggii*

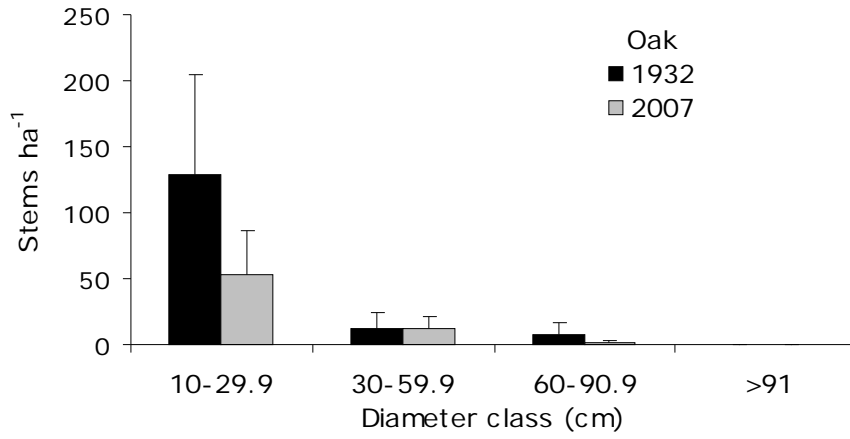


Figure 1.6 Average oak density according to stem diameter class, 1932 to 2007.

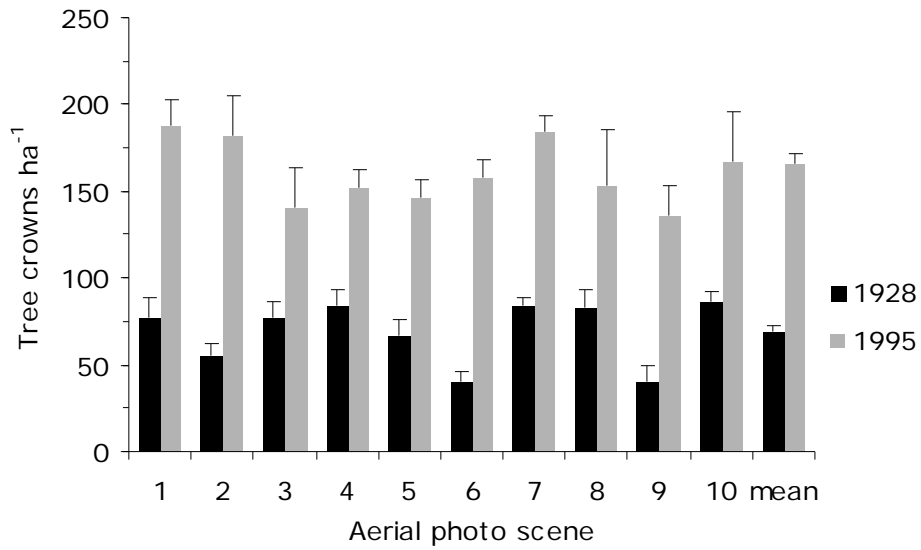


Figure 1.7 Increase in average density of tree crowns, 1928 to 1995.

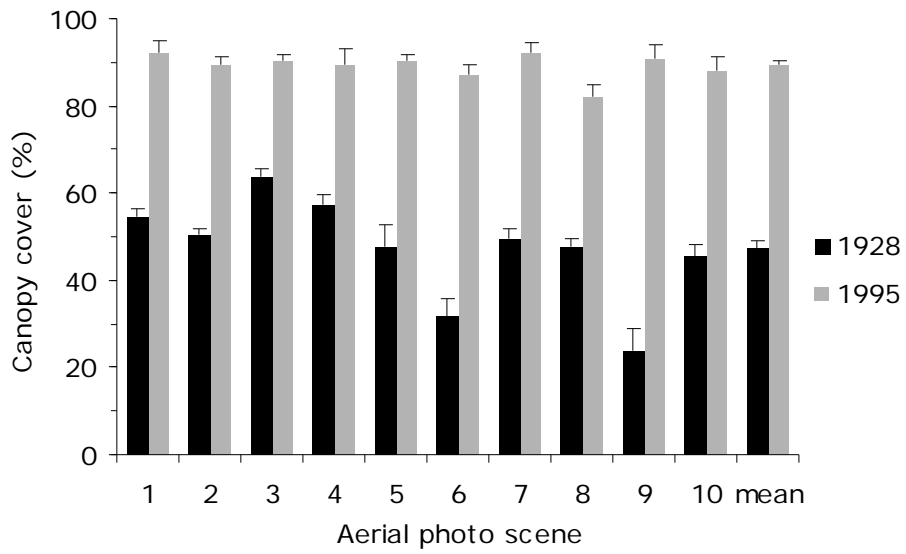


Figure 1.8 Increase in average canopy cover, 1928 to 1995.

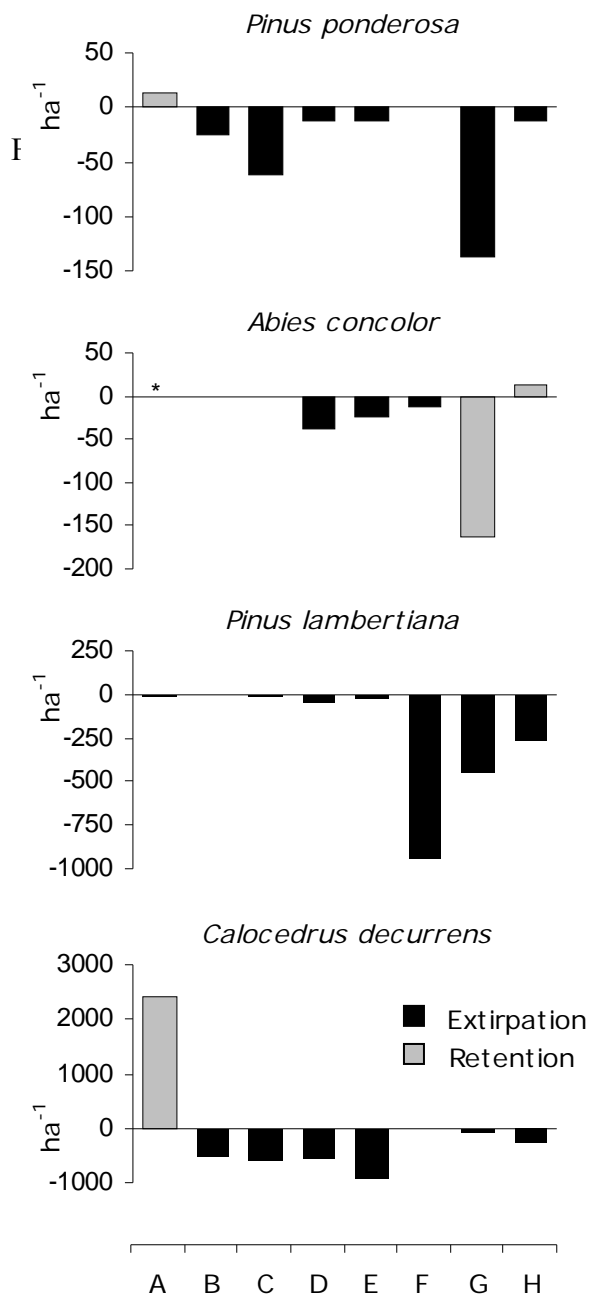


Figure 1.9 Species-specific departure of seedling density from fire-killed trees in plots equated to massive deficiencies and extirpations. The asterisk (*) indicates no change due to matching density of mortality and regeneration, while missing bars indicate species absence from plot.

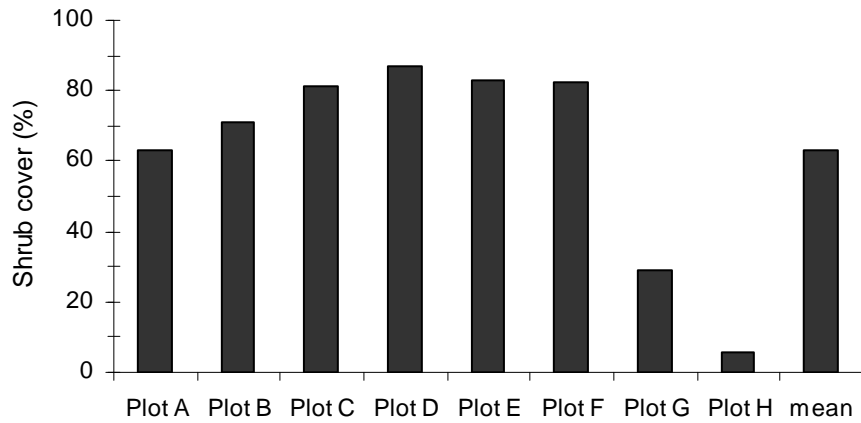


Figure 1.10 Extensive cover of shrubs in the forest understory, 41 months after fire. Shrub cover was almost entirely *Ceanothus palmeri*.

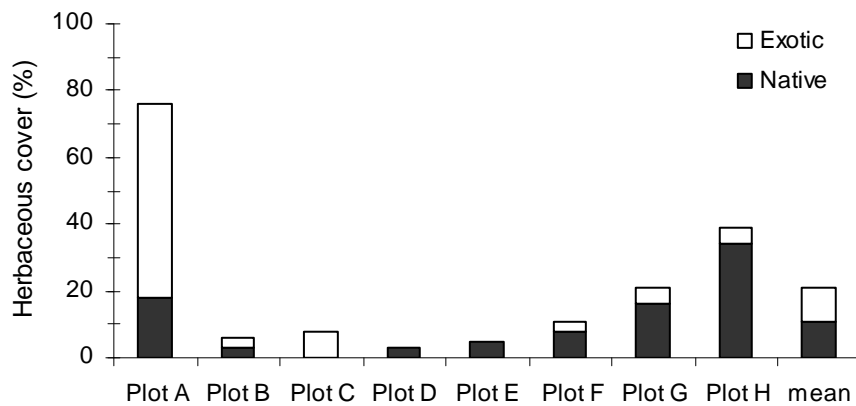


Figure 1.11 Sparse cover of exotic annuals in the forest understory, 41 months after fire. Nearly all exotic cover present was the annual grass *Bromus diandrus*.

Table 1.1 Description of historical VTM plots and modern replicates located in the Cuyamaca Rancho State Park, southern California.

Plot	Sample Date	Location ^A	Elevation ^B (m)	Slope (%)	Aspect	Stems ^C ha ⁻¹		Forest Composition ^D (%)
						Oak	Conifers	
191A52	April 1932	32° 59.16' N, 116° 35.28' W	1495 ± 50	30	E	25	113	CD, 37; QK, 9; AC, 27; QC, 9; PP, 18; PL, 0
A	April 2007	32° 59.304' N, 116° 35.274' W	1450	35	E	138	387	CD, 65; QK, 21; AC, 5; QC, 5; PP, 2; PL, 2
B	April 2007	32° 59.160' N, 116° 35.322' W	1500	30	E	38	562	CD, 90; QK, 4; AC, 0; QC, 2, PP, 4; PL, 0
C	April 2007	32° 59.058' N, 116° 35.262' W	1530	25	E	24	688	CD, 86; QK, 2; AC, 0; QC, 2, PP, 9; PL, 2
191A53	April 1932	32° 58.95' N, 116° 35.58' W	1585 ± 50	25	E	300	313	CD, 41; QC, 35; QK, 14; PL, 4; AC, 4; PP 2
D	April 2007	32° 58.932' N, 116° 35.586' W	1645	35	E	300	675	CD, 59; QC, 29; QK, 2; PL, 5; AC, 4; PP 1
E	April 2007	32° 59.046' N, 116° 35.466' W	1600	30	E	37	975	CD, 90; QC, 1; QK, 3; PL, 2; AC, 3; PP 1
191A55	April 1932	32° 57.25' N, 116° 36.04' W	1755 ± 50	30	E	125	388	PL, 40; AC, 31; QK, 22; CD, 5; QC, 2, PP, 0
F	April 2007	32° 57.295' N, 116° 36.014' W	1750	15	E	63	975	PL, 90; AC, 1; QK, 5; CD, 2; QC, 2; PP, 0
G	April 2007	32° 57.264' N, 116° 36.036' W	1765	25	E	0	937	PL, 48; AC, 28; QK, 0; CD, 9; QC, 0; PP, 15
H	April 2007	32° 57.204' N, 116° 36.060' W	1775	20	E	0	525	PL, 50; AC, 0; QK, 0; CD, 48; QC, 0; PP, 2

^A Sample locations coordinates in 1932 were estimated from a digitized copy of the original VTM plot map (quadrangle 191) using a GIS.

^B Elevation of plots established in 1932 have a 50 m range of uncertainty due to spatial imprecision of the locations shown on the original map.

^C Stems > 10 cm diameter at breast height

^D Species: AC, *Abies concolor*; CD, *Calocedrus decurrens*; PL, *Pinus lambertiana*; PP, *P. ponderosa*; QC, *Quercus chrysolepis*; QK, *Q. kelloggii*

Table 1.2 Seedling census 41 months after wildfire at Cuyamaca Rancho State Park.

Species	Plot							
	A ^A	B	C	D	E	F	G	H
<i>Abies concolor</i>	2	0	0	0	0	0	8	1
<i>Calocedrus decurrens</i>	219	0	0	0	0	0	0	0
<i>Pinus lambertiana</i>	0	0	0	0	0	0	0	0
<i>P. ponderosa</i>	1	0	0	0	0	0	0	0
<i>Quercus chrysolepis</i>	0	0	0	0	0	0	0	0
<i>Q. kelloggii</i>	0	0	0	0	0	0	0	0
total	222	0	0	0	0	0	8	1
density ha ⁻¹	2775	0	0	0	0	0	100	13

^A Only replicate plot with surviving overstory trees.

CHAPTER 2

Reproductive failure of a serotinous pine (*Pinus coulteri* D.Don.) in drought-killed posthumously-burned forest stands.

ABSTRACT

The winter of 2001-2002 was the driest in the northern Peninsular and eastern Transverse Ranges of southern California mountains since instrumental records began in 1850. Whole-stand dieoff of Coulter pine (*Pinus coulteri* D.Don.) occurred over much of the southern California distribution, a forest area of ~25,000 hectares. An outbreak of wildfires in 2003 extensively burned drought-killed stands of Coulter pine as well as stands that had survived the drought, leaving a unique mosaic of stand regeneration conditions. Coulter pine regenerates from retained seed that are released from serotinous cones after fire. No study has evaluated reproduction in drought-killed posthumously-burned stands, for this species or any other serotinous conifer in North America. I investigated four regeneration condition classes: (1) live unburned stands (control group) and those (2) fire-killed (i.e., drought surviving but burned), (3) posthumously burned (i.e., burned after death by drought), and (4) stands with mixed mortality by drought and fire. The results of this study indicate that regeneration was significantly deficient to replace the parent generation in all sampled posthumously burned stands, which had an average tree to seedling ratio of 13:1, and the systematic census failed to detect any Coulter pine seedlings among two-thirds of plots. In contrast, normal stand-replacement

regeneration occurred in drought-surviving fire-killed stands which had an average seedling to tree ratio of 3:1. The dead crown fuels of drought-killed trees combusted with unusually high severity, such that crown-fire was sufficiently intense to destroy the canopy seedbank of serotinous cones throughout posthumously burned stands.

INTRODUCTION

The winter of 2001-2002 was the driest in the eastern Transverse Range and northern Peninsular Range of southern California mountains since local instrumental climate records began in 1850, with only 17% to 30% of normal precipitation throughout the region (Fig. 2.1). Record low rainfall culminated a four-year long drought, which triggered vast outbreaks of conifer forest mortality including whole-stand die-offs (Jones et al. 2004). Then in 2003, after decades of fire suppression management, massive wildfires burned much of the drought-killed forest, providing unique opportunity to observe changes in conifer populations at risk of potentially widespread extirpations.

Coulter pine (*Pinus coulteri* D.Don) is a serotinous conifer which generally forms even-aged monotypic forest stands on dry rocky slopes associated with understory shrubs in montane chaparral (Griffin and Critchfield 1972, Minnich and Everett 2001). Coulter pine forests experienced historically unprecedented pandemic mortality in the record drought (Fig. 2.2). Drought stress was so severe that surviving trees produced anomalously small cones containing aborted seed (see herbarium collections UCR126499 & IRVC28538, B.R. Goforth, 30 Mar 2003).

Coulter pine cones are the most massive in the genus *Pinus* (Kral 1993) and have serotinous morphology, i.e., seed release is delayed because cones tend to remain closed for years to decades, which synchronizes ontogeny with periodic wildfires (Lamont et al. 1991). Wildfires normally cause stand-replacement of Coulter pine populations by a cohort of seedling progeny that establish in the first growing season after fire (Vale 1979, Griffin 1982). Mature trees often have low branches that closely overhang understory

shrubs, providing a fuel ladder for canopy ignition (Keeley and Zedler 1998). Crown-fires typically result in tree mortality from intense scorching of perenniating buds in the canopy, and vascular cambium tissue beneath bark on the trunk (Borchert et al. 2002). Stands associated with oak woodlands can have variable overstory tree survival of surface fires in places where understory shrub fuels are sparse (Talley and Griffin 1980, Borchert 1985, Wells 2001).

Heat generated by crown-fire triggers the opening of serotinous cones held in the canopy, by volatilizing resins that seal cone scales shut, and dehydrating cone tissues, causing the scales to contract and reflex away from the cone rachis (Johnson et al. 2003). The large, heavy winged seed readily dislodges from opened cones, copiously falling onto exposed mineral soil within meters of the parent tree where it may be further dispersed through caching activity by rodents (Borchert et al. 2003), and perhaps birds. Fallen seed lies dormant for months, until germination is stimulated by soil moisture and temperature conditions which occur in the first growing season after fire. Seedling establishment in fire-killed stands diminishes in successive growing seasons after fire as opened cones are depleted of seed, and regenerating shrubs cast shade and leaf litter over the soil surface which inhibits germination (Borchert 1985). Places where overstory trees survive fire have mixed aged stands as a result of reproduction both immediately after fire from scorched cones, and intermittently for decades later as unburned cones gradually open (Talley and Griffin 1980, Borchert 1985, Wells 2001). Seedlings grown in open exposure recruit to reproductive maturity as soon as 10 years after fire (Minnich 1988). Mature trees usually live for less than a century because sites are likely to

experience 2 or 3 wildfires per century (see reviews by Minnich 1999, Minnich and Everett 2001, Davis and Borchert 2006, Barbour 2007).

Post-fire regeneration and recruitment of serotinous conifers like Coulter pine were previously studied only in normal fire-killed stands (e.g., Johnstone et al. 2009, Schoennagel 2004, Turner et al. 1997; see also review by Keeley and Zedler 1998). Since Coulter pine formed monotypic forest stands of even-aged cohorts in the mountains of southern California, it was possible to control for variation in stand age to analyze patterns of reproduction over a mosaic of forest stands having differing drought mortality conditions. A systematic census of trees and seedlings was conducted among four stand regeneration condition classes: (1) live unburned stands (control group), (2) fire-killed (i.e., drought surviving but burned), (3) posthumously burned (i.e., burned after death by drought), and those with (4) mixed mortality by drought and fire. The null hypothesis was that regeneration would not significantly differ among the burned stand conditions (classes 2-4), and would be significantly greater than the control group condition of live unburned trees with unopened serotinous cones (class 1).

METHODS

Study site

Field sampling was conducted over 30,000 m² total area of tenth-hectare circular quadrats (30 plots) from elevations of 1400 m to 1888 m at Lost Valley and Bucksnot Mt. in the Peninsular range, about 80 km northeast of San Diego, California (116° 36' W, 33° 23' N). The Mediterranean-type climate is characterized by cool, wet winters and warm, dry summers. A weather station at the nearby Sky Oaks Field Station (SDSU

Global Change Research Group) registered an average annual precipitation of 400 mm, and annual temperature of 15° C (*data available online*).¹ Wildfire perimeter maps in the Cal Fire FRAP database show the Coulter pine forest had aged 75 years since previously burned in 1928 (*data available online*).² Coulter pine occurred in a mixed chaparral assemblage of shrubs (*Adenostoma fasciculatum*, *A. sparsifolium*, *Arctostaphylos glandulosa*, *Ceanothus leucodermis*, *C. greggii*, *Cercocarpus betuloides*, *Rhamnus californica*, and *Yucca whipplei*) with canyon live oak (*Quercus chrysolepis*) trees locally on northern polar-facing slopes. For additional site description, see Schmalbach et al. (2007).

Repeat Aerial Photography

Color aerial photographs (1:32,000 scale) were taken of the study area on 16 May 2003 (I.K. Curtis Aerial Photography, Inc., Burbank, CA, USA), precisely one month before lightning ignited a wildfire which burned 7570 ha between Lost Valley and Bucksnot Mt. from 16-24 July 2003. Pre-fire aerial photographs were examined to identify patterns of drought mortality and survivorship on each landscape scene. Scenes were georeferenced to unique nearest neighbor configuration of natural landmarks on a digital base map of orthographic rectified aerial photographs using a computer geographical information system (GIS) in ArcGIS 9.2 (ESRI, Redlands, CA, USA). Stands were delineated on the base map as drought surviving, drought killed, or mixed classes. This procedure was repeated using post-fire aerial photography taken 15 Sept 2004 (1:24:000 scale) to map the distribution of unburned vegetation. Merging the pre-

¹ (<http://gcrg.sdsu.edu/>)

² (<http://frap.cdf.ca.gov/>)

fire and post-fire map layers produced a composite map of four stand regeneration condition classes: (1) drought surviving unburned (live control group), (2) fire-killed (i.e., drought surviving but burned), (3) posthumously burned (i.e., burned after death by drought), and (4) mixed mortality by drought and fire. A GIS procedure was used to intersect the condition classes with terrain attributes (elevation, aspect, slope) extracted from a 10 m digital elevation model of the USGS Buscksnort Mt. 7.5 min quadrangle.

Field Sampling

A census of all trees and seedlings was conducted within tenth-hectare (1,000 m²) circular plots at 30 sites among stand condition classes. Twenty-five plots were established on Bucksnort Mt. in the third growing season after fire (2006) among all stand regeneration condition classes, and five additional posthumously burned stands were sampled at Lost Valley in the fifth growing season (2008). In contiguous forest stands, each plot center was systematically established using global positioning system navigation, separated at cardinal directions over approximately 100 m intervals from a random starting point, and referenced to the stand condition class map. Measurements were collected for trees and seedlings within plots, and the presence or absence of cones was noted. Trunk diameter was conventionally measured at 1.3 m height above ground level on upslope side of trees (diameter at breast height, dbh). Coulter pine generally has excurrent branching which forms a broad pyramidal or asymmetrical crown (Munz 1974). Tree height measurements were recorded using a digital hypsometer with ± 10 cm precision (Vertex III, Haglöf, Sweden), including a maximum height of the apical trunk stem, the height to lowest remaining canopy branch, the canopy scorch height, and height

of exposed charred wood on the trunk. Seedling stem heights were measured by tape with ± 1 mm precision. Regenerating shrub cover was sampled in each stand condition class by line interception (after Bauer 1943) along three transects extended from a plot center to the radius (each 17.85 m). A random azimuth was identified for the first transect using a calculator number generator, with the remaining two transects separated by 120° .

RESULTS

Coulter pine occurred over approximately 170 ha at Bucksnot Mt., half of which (85 ha) had experienced whole-stand tree mortality in the 2001/02 drought (Appendix 1). Drought survivorship was greatest at higher elevations (Fig. 2.3). Most forest area was distributed on polar-facing northern slope aspects (Fig. 2.4), which at lower elevations, were mostly the drought-killed posthumously burned stands. Drought survival and mortality were similarly proportioned across gradients of terrain steepness (Fig. 2.5).

Plots established on Bucksnot Mt. contained an average of 21 trees > 10 cm dbh (range: 4 to 37). The residual condition of trees differed between stands that were fire-killed and those which had posthumously burned. Fire-killed trees had intact charred bark on stems, and scorched crowns retaining dead foliage. Posthumously burned trees more resembled telephone poles because most canopy branches had completely combusted, and the bark on the remaining trunk had burned away leaving deeply charred xylem tissue (charred wood). No cones occurred among two-thirds of plots in posthumously burned stands, while all plots in the fire-killed stand condition class had trees with opened cones. In particular, cones were lacking from small trees (< 10 cm dbh) in fire-killed stands (Fig. 2.6).

Measurements of tree skeletal remains indicate burn severity was lower in fire-killed stands compared to drought-killed trees which had posthumously burned (Fig. 2.7). Fire-killed trees had an average tree height to trunk diameter ratio of 43:1, nearly double the ratio of posthumously burned trees, despite that dbh did not significantly differ between these condition classes (two sample t test, $\alpha = 0.05$, $t = -1.64$, $P = 0.10$). The branches of posthumously burned trees had been fire-pruned up an average 99% of their remaining trunk heights, 3 times the height of fire-killed trees. Although scorch heights were >90% of the total height of all burned trees, exposed charred wood averaged 60% of the tree trunk height in posthumously burned stands while <1% of height in fire-killed stands.

Seedlings had grown to an average height of 30 cm (range: 3 to 96 cm) when surveyed 3 years after fire, and were conspicuous where present because regenerating shrub cover was on average only 32% (range: 9 to 46%). Seedling abundance significantly declined as burn severity increased in stands (Fig. 2.7). Plots in fire-killed stands had seedling densities ranging from 130 to 2,180 ha⁻¹ (average 655 ha⁻¹ \pm 162 standard error), and seedling:tree ratios (trees > 10 cm dbh) ranging from 0.8:1 to 9:1 (average 3:1). In contrast, plots in posthumously burned stands on Bucksnot Mt. had an average seedling density of only 17 ha⁻¹ \pm 14. Two-thirds of plots in posthumously burned stands had no seedlings whatsoever, despite containing an average of 24 trees > 10 cm dbh, resulting in a tree:seedling ratio of 13:1. Regeneration was so scarce in posthumously burned stands that it did not significantly differ from the control group of live unburned trees which had closed serotinous cones ($t = 0.42$, $P = 0.69$). Expansion of the field survey into five posthumously burned stands at Lost Valley in 2008 failed to

detect a single seedling, despite that this census covered 5,000 m² of plot area which contained 35 trees > 10 cm dbh at an average stand density of 70 ha⁻¹ (range: 50 to 100 ha⁻¹).

DISCUSSION

This is the first study of reproduction in drought-killed posthumously-burned stands of serotinous conifer forest. Reproduction failures in posthumously burned stands are likely the result of unusually severe crown-fire due to tinder-dry fuels of dead trees, which combusted with enhanced intensities sufficient to destroy the canopy seedbank of serotinous cones. The finding of reproduction failures in posthumously burned stand conditions sharply contrasted with patterns of regeneration observed in normal fire-killed stands, which were subject to less intense crown-fire because of greater moisture content of live foliage and stem fuels. For example, Vale (1979) observed variability in Coulter pine seedling densities among fire-killed stands with differing severities of canopy scorch, but not reproduction failures. Borchert et al. (2003) found that seedling density did not significantly correlate with burn severity in fire-killed stands of Coulter pine where rodents cached and dispersed seed released by the serotinous cones soon after fire. Long-term computer model projections of Coulter pine stand dynamics in southern California using the LANDIS program (Franklin et al. 2005) were not calibrated for the extreme effects of drought coupled with posthumous burning as observed in this study. Reproduction failures in posthumously burned stands provide new insights for

interpreting dispersal processes that affect genetic diversity patterns observed among extant populations of Coulter pine (Ledig 2000).

Population decline and stand-scale extirpations occurred in response to disturbance by extreme drought followed by wildfire. It is unlikely that the failure to detect seedlings in posthumously burned stands was an outcome caused by the systematic sampling approach used in this study. The sharp contrast in regeneration was observed among nearest neighbor plots in fire-killed and posthumously burned stands separated by as little as 100 m. All plots on Bucksnot Mt. and in Lost Valley contained tree densities well within the range of measurements for Coulter pine forest sampled elsewhere in California (Vale 1979, Talley and Griffin 1980, Griffin 1982, Borchert 1985, Wells 2001, Borchert et al. 2003). Seedlings had grown to prominent size when the field surveys were conducted, and post-fire successions of regenerating vegetation formed a sparse cover that had not inhibited seedling recruitment.

Geographic distributions of the serotinous pines in California (e.g., *Pinus attenuata*, *P. coulteri*, *P. muricata*, *P. radiata*, *P. torreyana*) are highly fragmented, likely because of pre-historic recruitment failures in drought-killed posthumously-burned forests. Coulter pine occurs in an irregular pattern across the southern California mountains where it is lacking from extensive areas of suitable habitat, with stand boundaries frequently unrelated to local environmental gradients (Vogl et al. 1988, Minnich and Everett 2001, Minnich 2007). Fossil localities of serotinous pines in southern California do not overlap with extant distributions, suggesting a more widespread occurrence in moister glacial climates before the drier modern Holocene climate (e.g., Axelrod 1986). Recolonization of posthumously burned stands is expected

to lag behind changes in constraining environmental conditions because cone-serotiny restricts seed dispersal, resulting in long-term isolation of surviving populations (after Sauer 1988).

Landscape patterns of Coulter pine drought mortality and survivorship require further study. The extreme drought stress, coupled with chronic injury from atmospheric pollution, caused decreased resin production and perhaps changed resin content which reduced the resistance of pines to pandemic infestations by bark beetles, resulting in widespread mortality synchronized with the record drought year (Jones et al. 2004). Yet, drought surviving stands were not isolated from bark beetles or atmospheric air pollution.

Patterns of drought survivorship likely reflect gradients of diminished drought stress. Potential evapotranspiration is known to increase with time-since-fire in chaparral watersheds of southern California (Turner 1991, Loáiciga et al. 2001). Drought mortality was extensive within the 75 year old forest stands at Bucksnot Mt. and Lost Valley. Site-specific terrain factors appear to have reduced drought stress in local old stands. Summit stands had the least drought mortality, reflecting a gradient toward lower potential evapotranspiration at higher elevations with cooler year-round temperatures and greater orographic precipitation than lower terrain. Stands also survived drought on exposed bedrock outcrops, which function like a cistern to intercept precipitation, concentrating watering deep into the regolith within fractures that Coulter pine tree roots penetrate, and deep moisture storage in turn reduces water loss by direct evaporation.

The distribution of Coulter pine in the Peninsular Ranges mostly occurs on uplifted Cretaceous Granitic batholith rock which has been tectonically fractured, and deeply weathered (Minnich and Everett 2001). On steep slopes where Coulter pine is

abundant, shallow surface soil horizons are typically underlain by a deep profile of weathered parent rock (e.g., saprolite) containing micropores which store moisture extractable by fine tree roots and their mychroizal hyphae (Graham et al. 1994, Sternberg et al. 1996). Micropores are saturated by percolating meteoric waters in winters with abundant rainfall, and provide a moisture source essential to tree survival because surface soil horizons are desiccated every summer dry season (Arkley 1981). Lower soil evapotranspiration immediately after fire allows Coulter pine seedlings to establish, which rapidly grow deep roots compared to other pines in order to survive drought stress (Wright 1968).

CONCLUSION

Although climate change is a potential factor associated with widespread forest mortality in the drought affected Peninsular Range (Kelly and Goulden 2008), fire suppression management has altered landscape scale demographic trends in conifer populations over the past century which may have increased the susceptibility to mass-mortality in drought. The serotinous cones of Coulter pine inhibit continual reproduction, limiting forest densification between fires as a resource competition factor which would otherwise intensify drought stress while stands age (Savage 1994). If fire suppression has allowed cohorts to live longer over broad areas, the landscape scale age-class distribution may have been shifted toward older stands experiencing higher evapotranspiration. A time-series of spatially explicit fire perimeter data mapped from 1920 to 1971 using repeat aerial photography of the US Mexico Border region shows that burned patches are

larger in southern California than in northern Baja California where fires are not suppressed, the largest of which differ by more than an order of magnitude (Minnich and Chou 1997). The difference in patch size is abruptly observed at the political boundary between the United States and Mexico, where lands on either side of the border otherwise share similar environmental gradients and vegetation distributions (Minnich and Bahre 1995). Further study is needed of Coulter pine populations in Baja California which can serve as the best approximation of an empirical control for effects of fire suppression management, to evaluate drought mortality patterns of Coulter pine as a “phytometer” of global climate change. Reproduction failures in posthumously-burned stands illustrated by this study may foretell widespread outcomes in remaining drought-killed unburned Coulter pine forests of the eastern Transverse Range and northern Peninsular Range, as well as in serotinous conifer forests of Lodgepole pine (*Pinus contorta*) across the western United States where drought-kill has been extensive in the past decade.

REFERENCES

- Arkley, R. 1981. Soil moisture use by mixed conifer forest in a summer-dry climate. *Soil Science Society of America Journal* 45, 423-427.
- Axelrod, D. 1986. Cenozoic history of some western American pines. *Annals of the Missouri Botanical Garden* 73, 565-641.
- Barbour, M. 2007. Closed-cone pine and cypress forests. Pages 296-312 in M. Barbour, T. Keeler-Wolf, and A. Schoenherr, eds. *Terrestrial Vegetation of California*, third edition. University of California Press, Berkeley.
- Bauer, H. 1943. The statistical analysis of Chaparral and other plant communities by means of transect samples. *Ecology* 24:45-60.
- Borchert, M. 1985. Serotiny and cone-habit variation in populations of *Pinus coulteri* (Pinaceae) in the southern Coast ranges of California. *Madroño* 32:29-48.
- Borchert, M., D. Schreiner, T. Knowd, and T. Plumb. 2002. Predicting post-fire survival in Coulter pine (*Pinus coulteri*) and Gray pine (*Pinus sabiniana*) after wildfire in Central California. *Western Journal of Applied Forestry* 17:134-138.
- Borchert, M., M. Johnson, D. Schreiner, and S. VanderWall. 2003. Early postfire seed dispersal, seedling establishment, and seedling mortality of *Pinus coulteri* (D. Don) in central coastal California, USA. *Plant Ecology* 168:207-220.
- Davis, F., and M. Borchert. 2006. Central coast bioregion. Pages 321-390 in N. Sugihara, J. Van Wagendonk, K. Shaffer, J. Fites-Kaufman, and A. Thode, eds. *Fire in California's Ecosystems*, University of California Press, Berkeley.
- Franklin, J., A. Syphard, H. He, and D. Mladenoff. 2005. Altered fire regimes affect

- landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8:885-898.
- Graham, R., K. Rice, and W. Guertal. 1994. The pedologic nature of weathered rock. Pages 21-40 in Cremeens, R. Brown, and J. Huddleston, eds. *Whole Regolith Pedology*, SSSA special publication 34, Soil Science Society of America, Madison.
- Griffin, J. 1982. Pine seedlings, native ground cover, and *Lolium multiflorum* on the Marble-Cone burn, Santa Lucia Range, California. *Madroño* 29:177-188.
- Griffin, J., and W. Critchfield. 1972. The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82, Pacific Southwest Forest and Range Experiment Station, Berkeley.
- Johnson, M., S. VanderWall, and M. Borchert. 2003. A comparative analysis of seed and cone characteristics and seed-dispersal strategies of three pines in the subsection *Sabinianae*. *Plant Ecology* 168:69-84.
- Johnstone, J. L. Boby, E. Tissier, M. Mack, D. Verbyla, and X. Walker. 2009. Post-fire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Canadian Journal of Forest Research* 39:1575-1588.
- Jones, M., T. Paine, M. Fenn, and M. Poth. 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *Forest Ecology and Management* 200:67-76
- Keeley, J., and P. Zedler. 1998. Evolution of life histories in pines. Pages 220-248 in D. Richardson and R. Cowling, eds. *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge.

- Kelly, A.E., and M. L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Science* 105: 11823–11826.
- Kral, R. 1993. *Pinus*. Pages 373-398 in *Flora of North America* Editorial Committee, eds. *Flora of North America, north of Mexico, Volume 2*. Oxford University Press, New York and Oxford.
- Lamont, B., D. Le Maitre, R. Cowling, and N. Enright. 1991. Canopy seed storage in woody plants. *Botanical Review* 57:277-317.
- Ledig, F. 2000. Founder effects and the genetic structure of Coulter pine. *Journal of Heredity* 91:308-315.
- Loáiciga, H., D. Pedreros, and D. Roberts. 2001. Wildfire-streamflow interactions in a chaparral watershed. *Advances in Environmental Research* 5:295-395.
- Minnich, R. 1988. The biogeography of fire in the San Bernardino Mountains of California. *University of California Publications in Geography* 28:1-121.
- Minnich, R. 1999. Vegetation, fire regimes, and forest dynamics. Pages 44-78 in P. Miller and J. McBride, eds. *Ecological studies 134: Oxidant air pollution impacts in the montane forests of southern California*. Springer-Verlag, Inc. New York.
- Minnich, R. 2007. Southern California coniferous forest. Pages 502-538 in M. Barbour, T. Keeler-Wolf, and A. Schoenherr, eds. *Terrestrial Vegetation of California*, third edition. University of California Press, Berkeley.
- Minnich, R., and C. Bahre. 1995. Wildland fire and Chaparral succession along the California-Baja California boundary. *International Journal of Wildland Fire* 5: 13-24.

- Minnich, R., and Y. Chou. 1997. Wildland fire patch dynamics in the chaparral of southern California and Northern Baja California. *International Journal of Wildland Fire* 7:221-249.
- Minnich, R., and R. Everett. 2001. Conifer tree distributions in southern California. *Madroño* 48:177-197.
- Munz, P.A. 1974. A flora of southern California. University of California Press, Berkeley.
- Sauer, J.D. 1988. Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Berkeley, CA.
- Savage, M. 1994. Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. *Canadian Journal of Forest Research* 24:1149-1159.
- Schmalbach, H., J. Franklin and J. F. O'Leary, 2007, Patterns of post-fire regeneration in a southern California mixed chaparral community, *Madroño* 54:1-12
- Schoennagel, T., M.G. Turner, and W.H. Romme. 2004. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone national park. *Ecology* 84:2967–2978
- Sternberg, P., M. Anderson, R. Graham, J. Beyers, and K. Rice. Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma* 72, 89-98.
- Talley, S.N., and J.R. Griffin. 1980. Fire ecology of a montane pine forest, Junipero Serra Peak, California. *Madroño* 27:49-60.
- Turner, K. 1991. Annual evapotranspiration of native vegetation in a Mediterranean-type

- climate. *Water Resources Bulletin* 27:1-6.
- Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone national park. *Ecological Monographs* 67:411–433
- Vale, R. 1979. *Pinus coulteri* and wildfire on Mt. Diablo, California. *Madroño* 26:135-140.
- Vogl, R., K. White, W. Armstrong, and K. Cole. 1988. The closed-cone pines and Cypresses. Pages 295-358 in M. Barbour and J. Major, eds. *Terrestrial Vegetation of California*, second edition. Special Publication 9, California Native Plant Society, Sacramento.
- Wells, M. 2001. Human altered fire regimes and the development of stand structure in *Macrocarpe* pines. Ph.D. dissertation, University of California, Santa Barbara.
- Wright, R.D. 1968. Lower elevational limits of montane trees. II. Environment-keyed responses of three conifer species. *Botanical Gazette* 129:219-226.

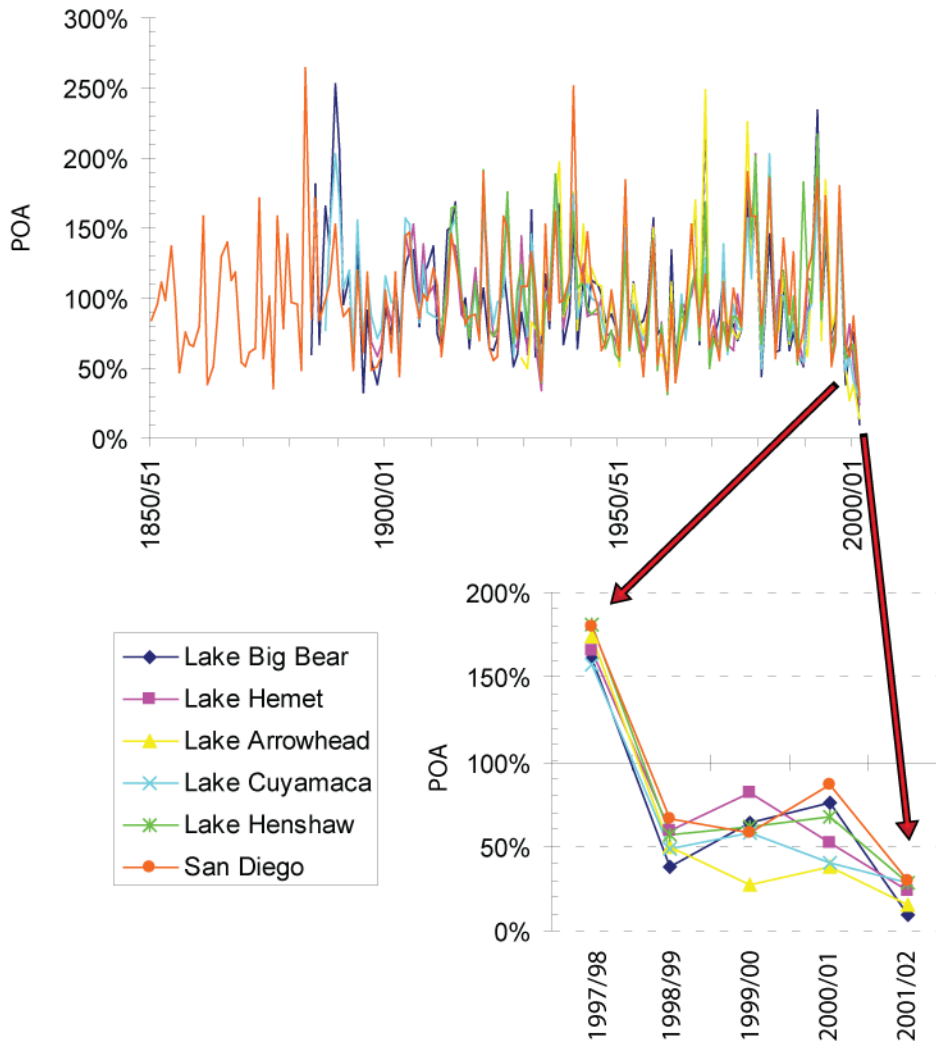


Figure 2.1 Percent of Average (POA) annual precipitation for July-June totals at individual long-term weather stations in the drought affected region of southern California. POA was calculated for each station using the period of record mean annual total at Lake Big Bear (1884-2002), Lake Hemet (1896-2002), Lake Arrowhead (1929-2002), Lake Cuyamaca (1887-2002), Lake Henshaw (1912-2002) and San Diego (1850-2002) with data provided by NOAA National Climate Data Center, San Bernardino County Flood Control District, and Riverside County Flood Control District. Above average precipitation occurred in the 1997/08 year associated with El Niño conditions in the Pacific Ocean, while subsequent drought years were La Niña conditions.

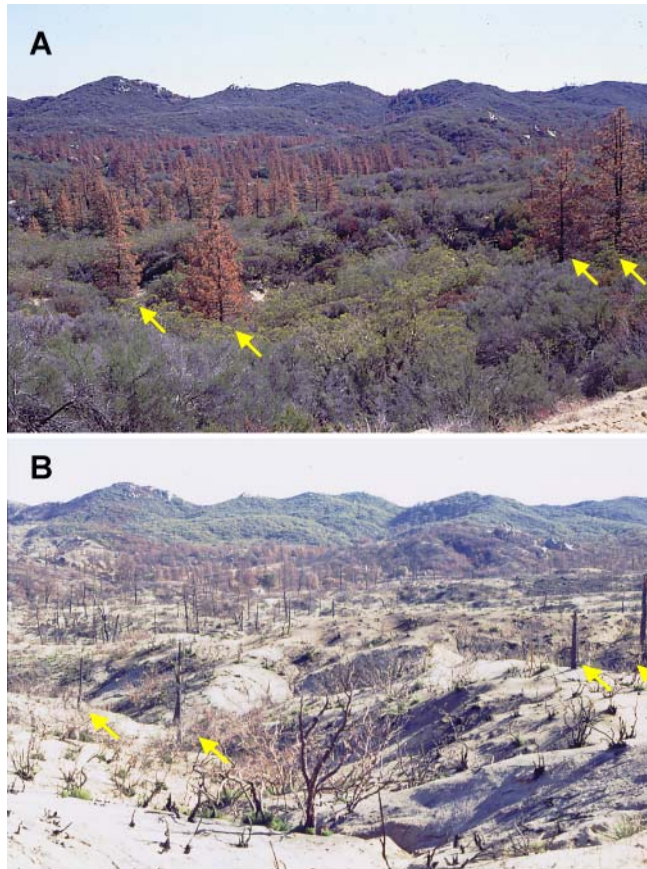


Figure 2.2 Repeat landscape photographs of drought-killed posthumously burned Coulter pine forest. (A) Photo taken on Jan 2003 of Coulter pine drought mortality at Lost Valley in the Peninsular Ranges, San Diego County. (B) The repeat photograph was taken on Jan 2004, six months after the drought-killed stand was posthumously burned by the July 2003 wildfire.

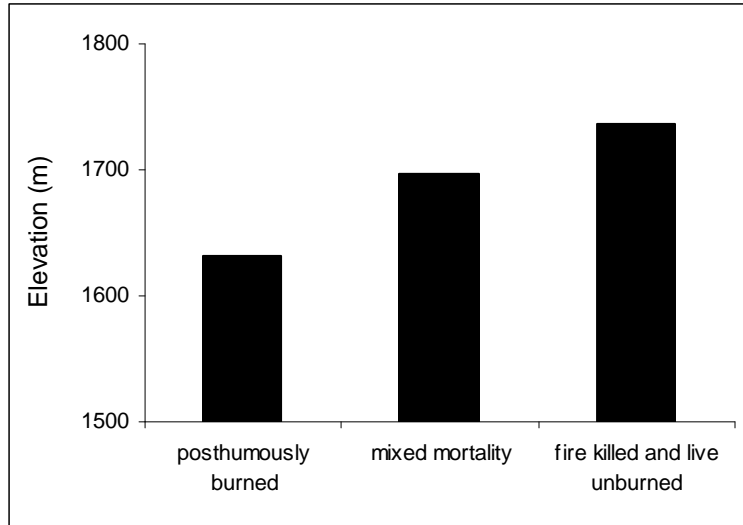


Figure 2.3. Area-weighted average elevation of Coulter pine stand condition classes. Drought survival increased with higher elevation on Bucksnot Mt., paralleling a decline in evapotranspiration with higher elevation.

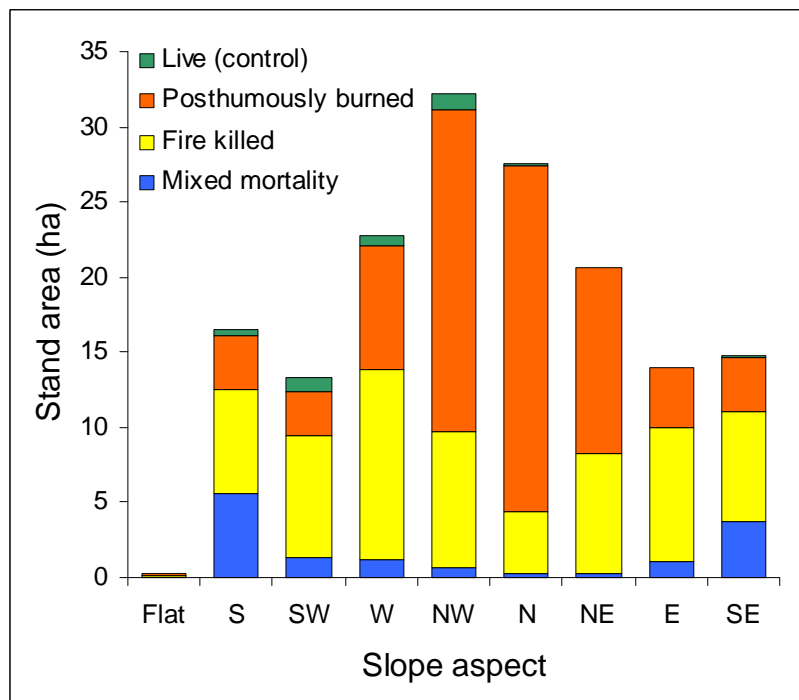


Figure 2.4. Stand area histogram of Coulter pine on Bucksnot Mt. classified by slope aspect intervals. Most forest area, hence most drought mortality, occurred on polar facing northern slopes. Legend shows stacked order of stand condition classes.

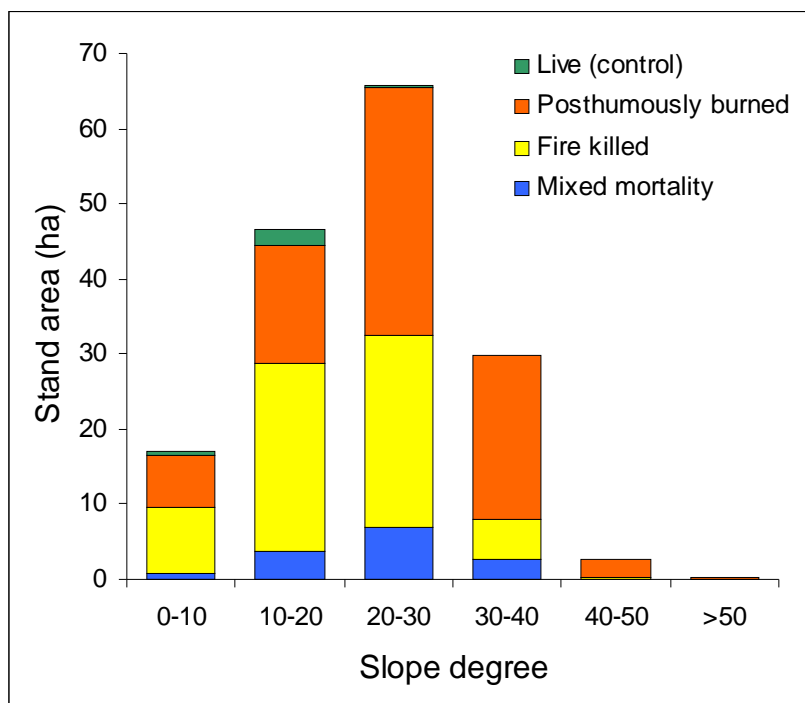


Figure 2.5 Stand area histogram of Coulter pine on Bucksnot Mt. classified by slope angle intervals. Drought survival and mortality were similarly proportioned among terrain steepness conditions of forest.

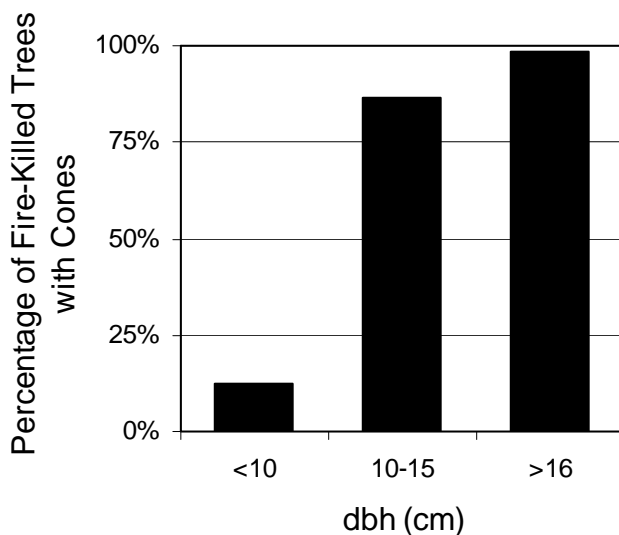


Figure 2.6 Coulter pine trees grown to 10 cm dbh or larger were reproductively mature.

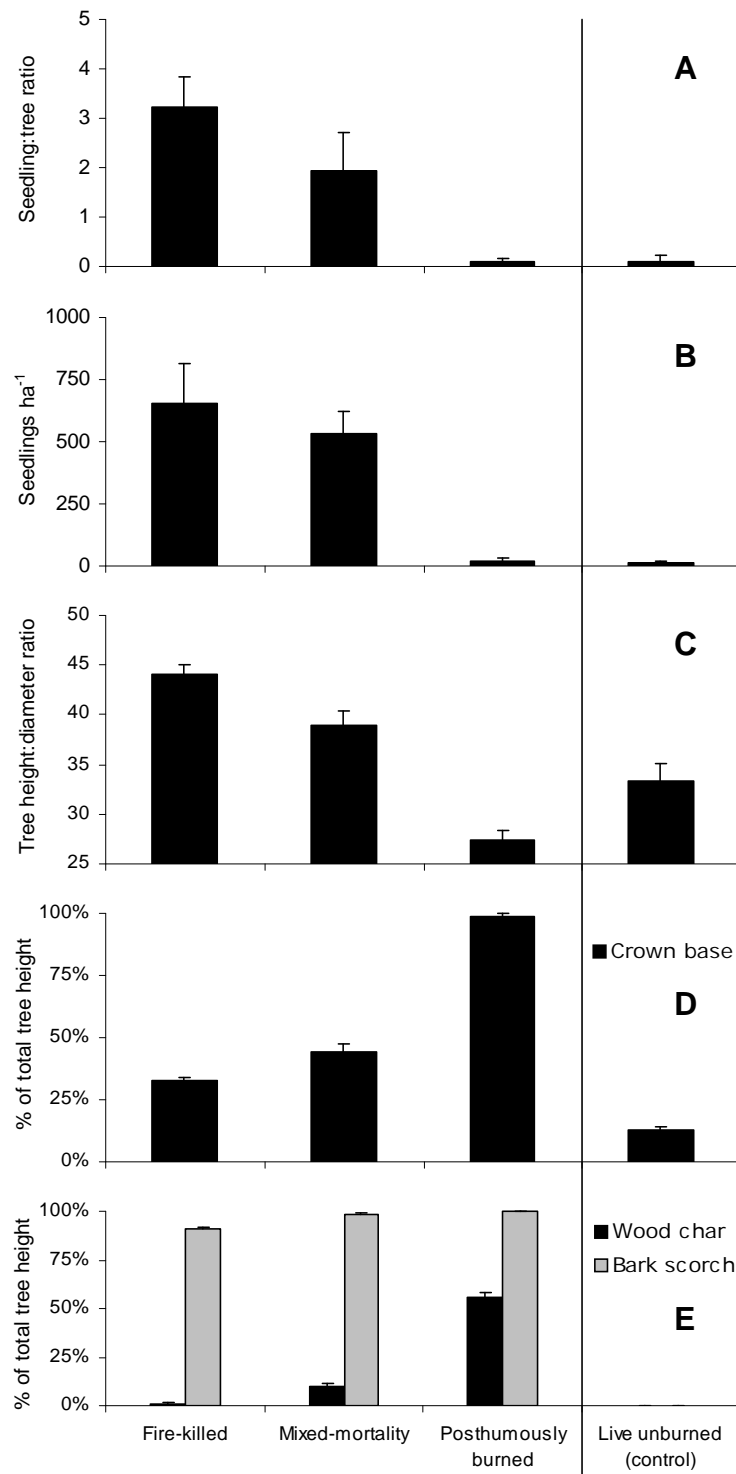


Figure 2.7 Summary of reproduction and fire severity metrics for stand condition classes. (A) The average ratio of seedlings to trees. (B) Average seedling density. (C) Average tree height to diameter ratio. (D) Average height of fire-pruned branches (crown base) as a percentage of total tree height. (E) average height of trunk stem with wood char and bark scorch expressed as a percentage of total tree height. Error bars indicate the range of one standard error. Note that reproduction declines with increased burn severity.

CHAPTER 3

Recruitment patterns of an isolated serotinous conifer (*Cupressus arizonica* var. *stephensonii* [Wolf] Little) after stand-replacement wildfire.

ABSTRACT

In the arid southwestern United States, cypresses tend to have serotinous cones, and occur in disjunct “sky-island” populations in mountainous habitats with enhanced orographic precipitation and fog condensation, as well as edaphic conditions that restrict the growth of vegetation. Isolated populations with discontinuous reproduction are subject to pandemic disturbance events of drought and wildfire, and risk potential recruitment failures. The isolated population of Cuyamaca Cypress (*Cupressus arizonica* var. *stephensonii* [Wolf] Little) in San Diego County, California, was recently subjected to an extreme sequence of disturbance events. A record severe drought was followed by stand-replacement wildfire across nearly the entire population. The population survived drought, and copiously reproduced after fire, providing a unique opportunity to study patterns of post-fire recruitment in this isolated population. The cypress population was mapped and its distribution was analyzed using a geographical information system (GIS) including terrain attributes extracted from a 10 m digital elevation model. A systematic method of sampling was used to survey patterns of recruitment, to compare variability in the abundance and growth of seedling progeny with characteristics of the fire-killed

population, as well as to abiotic habitat conditions, and interactions with regenerating vegetation successions. The results of the GIS analyses indicate Cuyamaca cypress occurs on steep, rocky, well-drained slopes having equatorial facing aspects, which are subject to high potential evapotranspiration. A significant decline in seedling heights and tree sizes was measured with distance uphill from King Creek in the belt-transect along a slope profile, suggesting that soil moisture is a likely factor limiting growth of Cuyamaca cypress. Site-specific seedling:tree ratios were as high as 108:1, while one plot had deficient recruitment overall to replace the density of fire killed trees. Cuyamaca cypress exhibits a “shifting population” pattern of reproduction and recruitment where local declines in stand density may occur in different places after every burn due to stochastic variability in reproduction, which is characteristic of other serotinous conifers in southern California. Increased seedling density observed between the 2006 and 2008 census indicate that seed release from the serotinous cones of Cuyamaca cypress can be delayed for several years after crown fire. Successful reproduction of Cuyamaca cypress in a nearby plantation which had also burned provided a rare example of conifer naturalization at a non-native locality in the southern California mountains. The fire regime in Cuyamaca cypress stands has been altered over the past century by systematic fire suppression management. Comparative study of the Cuyamaca cypress population in Baja California, where systematic fire suppression is not practiced, is needed to evaluate the effects of fire suppression on reproduction and recruitment patterns.

INTRODUCTION

Serotinous cones delay seed release for years to decades after fertilization, resulting in the retention of a canopy seed bank (Lamont et al. 1991). Mass releases of seed are triggered by disturbance of the canopy seed bank among serotinous conifers in the genus *Pinus* (pines) and *Cupressus* (cypresses), such as by stand-replacement crown-fire, resulting in synchronized recruitment and ontogeny of cohorts (see reviews by Keeley and Zedler 1999, Barbour 2007). For example, in the arid southwestern United States where cypresses tend to have serotinous cones, species occur in disjunct “sky-island” populations in mountainous habitats with enhanced orographic precipitation and fog condensation as well as edaphic conditions that restrict the growth of vegetation (e.g., Wolf 1948, McMillan 1956, Whittaker and Niering 1965, Griffin and Critchfield 1974, Vogl et al. 1989). Such isolated populations with discontinuous reproduction are subject to pandemic disturbance events of drought and wildfire, and risk potential recruitment failures. For example, recruitment can fail if frequent wildfires reoccur before cohorts of reproduction attain reproductive maturity, i.e., “immaturity risk” (after Zedler 1995). On the other hand, populations risk attrition and die-off if mass reproduction and recruitment are dependent upon disturbance opportunities which infrequently occur at longer intervals than the life span of mature cohorts and viability of seed stored in serotinous cones, i.e., “senescence risk.”

An isolated population of Cuyamaca Cypress (*Cupressus arizonica* var. *stephensonii* [Wolf] Little) occurs along King Creek on Cuyamaca Mt. in the Peninsular

Range of southern California, USA (Griffin and Critchfield, 1972), 150 km from the nearest stand in the Sierra Juárez of Baja California, Mexico (Moran 1972, Minnich 1987). Taxonomic and phylogenetic studies classify Cuyamaca cypress as one of the rarest cypresses in the world (e.g., Wolf 1948, Little 2006). Cuyamaca cypress was recently subjected to the most extreme sequence of disturbance events known since its botanical discovery in 1938 by C.B. Wolf (SD41196). The King Creek population survived an extreme drought culminating in the record deficit 2001/02 hydrologic year, but subsequently burned in the massive ~110 620 ha “Cedar fire” of the October 2003 firestorm. The 2003 fire also burned a four decade old plantation of Cuyamaca cypress nearby (Cliff LaMonte, property owner, personal communication). It is thought that the King Creek population is threatened by frequent burning, and could be lost in a single fire (Armstrong 1978, Skinner and Pavlik 1994, Lanner 2002, p. 193).

Previous studies of cypress populations with serotinous cones in California have focused on demographic trends antecedent to fire, and past fire history, as deterministic factors affecting reproduction (Zedler 1977, Reveal 1978, Zedler et al. 1983, Dunn 1987, Scheid and Zedler 1989, Zedler 1995, Ne’eman et al. 1999, De Gouvenain and Ansary 2006). Since nearly the whole population of Cuyamaca cypress had burned, as well as a nearby plantation, unique opportunity was presented to study patterns of post-fire recruitment. The objective of this study was to survey patterns of recruitment, to compare variability in the abundance and growth of seedling progeny with characteristics of the fire-killed population, as well as to abiotic habitat conditions, and interactions with

regenerating vegetation successions. Seedling density in the cypress plantation served as a control for the potential effects of frequent fire in the King Creek population.

METHODS

Study sites

Field sampling was conducted at two sites; the Cuyamaca cypress population at King Creek, and the nearby plantation. The King Creek population occurs on the SW slope of Cuyamaca Mt. in the Peninsular Range of southern California (32° 55' 55.48" N, 116° 36' 44.39" W). This site is located within the Cleveland National Forest and adjoining Cuyamaca Rancho State Park, ~60 km east of the Pacific Ocean in San Diego County, California, USA, and 40 km north of the US-Mexico international border. The plantation is located about 13 km NE of the native population (33° 2' 54.93" N, 116° 34' 8.16" W).

Cuyamaca Mt. is uplifted Cretaceous intrusive-igneous batholith within the broader Peninsular Range. Cuyamaca cypress at the King Creek and plantation sites grows only on soil derived from gabbroic rock (Reveal 1978, Alexander 2007, p. 267-269). Soils have been classified as fine-loamy, mixed, superactive, mesic Ultic Haploxeralfs and fine, smectitic, thermic Typic Rhodoxeralfs (after Soil Survey Staff 1999). The A horizons have sandy-loam to loam textures. The King Creek site is characterized by steep rocky slopes with stabilized hill-slump landforms formed during moister glacial climates of the Pleistocene, as found elsewhere on gabbroic substrates of Cuyamaca Mt. (Hart and Farcas 1983), and has been eroded by active drainage channels.

Elevations range from about 1100 m to 1700 m within the native population, and the plantation is located at 1440 m above mean sea level.

The study area has a Mediterranean-type climate characterized by warm, dry summers and cool, moist winters. Orographic lift of moist westerly flow during the passage of winter season cyclones yields abundant precipitation over Cuyamaca Mt. Fog condensation augments precipitation when weather conditions cause a cool moist coastal marine layer airmass to flow inland and lift upslope against the Peninsular range. Average annual precipitation ranges from 750 mm to 900 mm along the elevation gradient spanning the native population, with 80% occurring between December and May (Reveal 1978). Average monthly temperatures are reported to range from a low of 0°C in January to a high of 32°C, with a frost free growing season occurring between May and October for an average of 150 days.

Stands of Cuyamaca cypress form dense thickets of small trees scattered in woody-evergreen sclerophyllous chaparral shrublands (Vogl et al. 1989, Sawyer and Keeler-Wolf 1995). At highest elevations of its distribution, Cuyamaca cypress intermixes with pine-oak woodlands composed of *Pinus coulteri* D. Don, *Quercus chrysolepis* Liebm., and *Q. kelloggii* Newb. The largest Cuyamaca cypress trees occur along exposed banks of King creek and tributary drainages, and at the fringes of spring-fed meadows, locally associating with woodlands of *Alnus rhombifolia* Nutt., *Plantanus racemosa* Nutt., *Q. agrifolia* Nee., *Salix laevigata* Bebb, and *S. lasiolepis* Benth. Endemic and disjunct occurrences of shrubs and herbs occur with Cuyamaca cypress and the local gabbro soils (Oberbauer 1993).

Vegetation mapping

Color aerial photographs taken in 1995 and 2004 (1:12,000 scale) aided the relocation of Cuyamaca cypress at King Creek (I.K. Curtis Aerial Photography, Inc., Burbank, CA, USA). Large individual cypress trees were identifiable on the pre-fire photographs from observations of crown form, vertical structure, and distinctive blue-grey color reflectance of foliage. The cypress distribution was mapped in the field by locating stands of fire-killed trees and live unburned trees, with generalized stand boundaries inclusive of dense stands and habitat of scattered individuals drawn onto post-fire color aerial photograph prints. Photographs were georeferenced to unique nearest neighbor configuration of natural landmarks on a digital base map of orthographic rectified aerial photographs using a computer geographical information system (GIS) in ArcGIS 9.2 (ESRI, Redlands, CA, USA). Stands were delineated as fire-killed (stand-replaced) or live (unburned) condition classes. The mapping was verified with ground inspections aided with global positioning system (GPS) navigation and comparisons to pre-fire maps by Reveal (1978) as well as Scheid and Zedler (1989). A GIS procedure was used to intersect the final map with terrain attributes (elevation, aspect, slope angle) extracted from a 10 m digital elevation model of the USGS Cuyamaca Mt. 7.5 min quadrangle.

Sampling methods

Six locations with the largest stand area were surveyed in the third post-fire growing season (June-Sept. 2006) using a systematic sample approach. A 100 m long \times 10 m wide (tenth-hectare) rectangular plot was established longitudinally through the center of each stand (6 plots total). A 100 m transect served as the plot midline, where post-fire shrub cover was inventoried using the line-intercept method at 10 cm intervals (after Bauer 1943). Herbaceous vegetation including exotic annuals (live and dead cover) were identified at 1 m intervals along the midline transect using a point-intercept method (after Goodall, 1957), and the presence or absence of exotic annual grasses and forbs was noted within 1-m² quadrats spaced at 10 m intervals (66 total). All cypress trees were counted within 10 m \times 10 m intervals of each tenth-hectare rectangular plot. Live cypress seedlings were counted within circular sub-plots of 10 m² area, established at 10 m intervals along the midline transect (66 sub-plots total). Seedling densities obtained in sub-plots located at 10 m, 30 m, 50 m, 70 m, and 90 m distance from the transect origin were referenced to tree counts in the surrounding 10 m \times 10 m plot interval for computation of site-specific seedling:tree ratios.

Individual seedlings and trees were selected for size measurement within each tenth-hectare rectangular plot using the point-centered quarter (PCQ) method (Cottam and Curtis 1956). Sampling points were established along the 100 m midline transect at 20 m intervals, starting at 10 m distance from the transect origin (5 sample points per tenth-hectare plot). The plot area surrounding each sample point was divided into quarters, and the nearest tree and live seedling in each quarter were selected for

measurement (20 trees and 20 seedlings in each tenth-hectare plot; 120 trees and seedlings total). The distance from each selected individual to the sample point was measured in each quarter. The nearest-neighbor seedling distance was additionally measured from seedlings closest to the sample points, in a plot with the lowest detected seedling density and a nearby plot with higher seedling density, to evaluate spatial dispersion as a departure from clumped or random patterns. An index of spatial dispersion (R) for seedlings was computed as a ratio of the mean distance to the expected distance, where $R = 0$ is clumping and $R = 1$ is random, while R approaches an upper limit value at 2.15 for uniformity (Krebs 1989, p.126). Since only the skeletal remains of trees burned by crown fire were available for measurement in most stands, heights were measured to the nearest 10 cm. Seedling heights were measured with 1 mm precision from the soil surface to the highest apical bud. Basal diameter of trees was measured at a constant height of 10 cm above the soil surface because trunks often had decurrent growth of multiple apical stems branched below breast height where diameter is conventionally measured for trees.

A census of seedlings (live and dead) and fire-killed cypress trees was conducted in two belt-transects, each extending 250 m² (one in the plantation, and one along a cross-sectional profile of King Creek). To survey the slope profile, an elevation control point was established in King Creek (near plot 1) using a handheld GPS device. Then, a 50 m transect was extended uphill, perpendicular to slope contour, and surveyed for change in elevation at 1 m intervals using a profile leveling traverse with ± 1 cm precision (Wolf and Brinker 1994, p. 143). This surveyed profile was a midline for the 5 m wide belt-

transect. Heights of all trees and seedlings, and tree basal diameters were recorded for each 2 m interval along the belt transect. A second census of seedlings was conducted in the King Creek belt-transect in 2008.

RESULTS

Approximately 85% of the Cuyamaca cypress stand area was burned in 2003 (Fig. 3.2). It is estimated that < 500 unburned or partly scorched live trees remained after the 2003 fire. The total stand area mapped was 13 ha. Although Cuyamaca cypress occurred over elevations ranging from 1100 m to 1700 m, nearly half of the stand area was concentrated between 1300 m and 1400 m elevation (Fig. 3.3). Slope angles within the mapped stand area ranged from 4° to 63°, with a median slope angle of 36° (Fig. 3.4). The upper King Creek watershed has a southern (equator-facing) aspect of exposure, with only 15% of stand area having west to northwest slope aspects which are partially shaded in the winter season due to low sun angles (Fig. 3.5).

The size and abundance of trees in the pre-fire population at King Creek exhibited significant variation (Table 3.1). The variability in tree trunk basal diameters spanned two orders of magnitude (range: 0.5 cm - 49.0 cm), with a pooled average of 12.2 cm ± 9.2 cm standard deviation among plots (Fig. 3.6). The tallest tree was 25 times the height of the smallest tree (range: 0.6 m - 15.8 m), with an average height of 3.9 m ± 2.3 m (Fig. 3.7). Tree densities were as high as 6 330 ha⁻¹ where trees occupied an average of 1.6 m² per individual, compared to the average of 3 500 ha⁻¹. Tree heights were not significantly

correlated with tree density ($\alpha = 0.05$, $p = 0.19$, $r = -0.24$). Basal area in the stand of lowest tree density ($11.7 \text{ m}^2 \text{ ha}^{-1}$) was less than one-quarter the basal area in the stand of highest density ($51.7 \text{ m}^2 \text{ ha}^{-1}$), but tree basal diameter was negatively correlated with tree density ($p = 0.01$, $r = -0.46$).

Post-fire recruitment exhibited significant variation in seedling size and abundance (Table 3.2). The tallest seedling was nearly 30 times the height of the smallest (range: 3.0 cm to 89.3 cm), with seedling heights averaged $16.0 \text{ cm} \pm 14.6 \text{ cm}$ (Fig. 3.8). Seedling counts in the 10 m^2 sub-plots result in an average density of 2.6 m^{-2} (range: 0 - 22.7 m^{-2}). Site-specific seedling:tree ratios were as high as 108:1 (Table 3.3). Only plot 3 had deficient recruitment overall to replace the density of fire killed trees. Seedling density was not significantly correlated with tree density ($p = 0.37$, $r = -0.16$). In fact, Plot 3 with the fewest seedlings had the greatest density of fire-killed trees. An index of dispersion (R) computed for nearest neighbor distances of seedlings in Plot 1 with high seedling density and Plot 3 suggests large departures away from clumping, toward spatial regularity (Table 3.2). Nearest-neighbor seedling distances of 0.4 m in Plot 1, and 1 m in Plot 3, coincided with the 50% cumulative frequency level, with 95% at 1.2 m and 3.8 m respectively (Fig. 3.9).

A discontinuous cover of regenerating shrubs had developed by the third growing season after fire. Line-intercept transects averaged 36% shrub cover (range: 25%-46%), and encountered 14 species (Appendix 2). The four most frequent shrubs were *Adenostoma fasciculatum* H. & A., *Arctostaphylos glandulosa* Eastw., *Ceanothus*

foliosus Parry., and *Quercus berberidifolia* Liebm. Seedling density was weakly correlated with shrub cover ($p = 0.057$, $r = 0.79$).

Non-native annual grasses and forbs were sparse (Fig. 3.10), and entirely absent from 65% of the 1-m² quadrats. Point intercept cover of non-native annuals averaged 6% (range: 0% to 24%), with *Bromus diandrus* Roth. and *B. rubens* L. most frequent. Native herbaceous cover averaged 65% (range: 39% to 85%), which is 10 times that of the exotic cover. A native western morning glory (*Calystegia macrostegia* E. Greene) was most widespread, in places forming a dense mat-like cover with cypress seedlings (Fig 3.11). Seedling density was not correlated with herbaceous cover ($p = 0.44$, $r = -0.39$).

A significant decline in seedling heights and tree sizes was measured with distance uphill from King Creek in the belt-transect along a slope profile (Table 3.4). Cypress trees and seedlings at the bank of King Creek were double the size of trees uphill in chaparral as measured by basal diameter and height (Fig. 3.12). A 1.5% increase in live seedling density was observed between the 2006 and 2008 census of the belt transect.

Fire-killed cypress trees at the plantation site also reproduced from serotinous cones. The plantation belt-transect census counted 10 fire-killed trees, and 101 seedlings for a seedling to tree ratio of 10:1. The tree density was 400 ha⁻¹ and the seedling density was 4040 ha⁻¹. Regenerating shrub cover was 32%, while herbaceous cover was 68%.

DISCUSSION

Cuyamaca cypress occurs on steep, rocky, well-drained slopes having equatorial facing aspects, which are subject to high evapotranspiration. Stands are distributed in close proximity to active drainage channels, or concave land surfaces such as stabilized hill-slumps with convergent moisture collection. Although the positive correlation of seedling density with shrub cover was marginally insignificant at the $\alpha = 0.05$ level, seedlings were often observed protruding from the canopy projection of shrubs, suggesting a “nurse plant” interrelation as observed in the recruitment of other “shade-intolerant” conifers in arid habitat (e.g., Wangler and Minnich 1995). The canopy projection of shrubs may benefit seedlings through partial shading from summer insolation in the initial growing seasons after fire when growth is allocated to maximize root depth, and may also provide shelter from winds and occasional winter snowfall. The largest trees and tallest seedlings occurred along the banks of King Creek and tributaries, and size rapidly declined with distance uphill from these water sources. Potential factors such as herbaceous cover and tree density did not significantly correlate with recruitment patterns of seedlings. This body of observations suggests that soil moisture is a likely factor limiting growth of Cuyamaca cypress.

Heterogeneity in soil pedogenesis is another likely factor which selects for vegetation patterns of composition and growth on gabbroic substrates (e.g., Kruckeberg 2002, Alexander 2007). A general tendency is for plant species to occupy more mesic (moist) sites as soil mineral composition becomes more mafic (Fe and Mg rich), as found

on gabbro parent materials (Alexander 1993). Soil conditions most productive for Cuyamaca cypress growth appear to closely parallel gradients of soil moisture within the King Creek site. For example, cypress seedlings along a steep tributary channel of King Creek in Plot 2 had grown over 2 m ht by May 2007 (only 3.5 years after fire). Erosional down-cutting nearby exposed a deep (~1 m) soil profile of finely weathered alluvium in contrast with shallow and stony colluvial and residual soils uphill where seedlings were 15 cm - 30 cm tall. Study of gabbro soil morphology within the Cuyamaca cypress population is needed to elucidate soil physical and chemical properties affecting growth, and evaluate interrelations with other proposed factors associated with edaphic endemism on the gabbroic rock substrates (Stottlemyer and Lathrop 1981, Zedler et al. 1984), as classically studied for vegetation patterns in response to serpentine soils (e.g., Whittaker 1954, 1960, Kruckeberg 1985).

Increased seedling density observed between the 2006 and 2008 census of the King Creek belt-transect indicate that seed release from the serotinous cones of Cuyamaca cypress can be delayed for several years after crown fire. Cuyamaca cypress has woody spheric-shaped cones with ovuliferous scales which interlock in a peltate form attached to a central rachis, each holding one to many ovules (Munz 1974). Dehydration results in contraction of cypress cone scale tissues, opening the cone (Scheid 1986). This can be triggered by the heat of crown scorch from wildfire (Armstrong 1968), or at ambient air temperatures if a cone-bearing branch dies and is desiccated without being burned (Lev-Yadun 1995, Barbour 2007). Opened cones initially release mass amounts of seed. However, this response does not completely deplete the canopy seedbank.

Cuyamaca cypress cones are produced at the tips of short stubby branchlets, and are often appressed against stems (Wolf 1948). Cone scales compressed against stems were observed to contain a small portion of trapped seeds in 2006 (three growing seasons after fire). Trapped seed is gradually shaken out of the cones as the dead branches blow in the wind, and dead trees topple, resulting in continued reproduction for years after stand-replacement wildfire.

Successful reproduction of Cuyamaca cypress in the plantation is a rare example of conifer naturalization at a non-native locality in the southern California mountains. Previous study of serotinous conifers planted at non-native localities found only reproduction failures after stand-replacement wildfire, even for species native to the region, suggesting that disjunct stands in the southern California mountains are constrained in occurrence by ecological factors rather than barriers to dispersal (Burns and Sauer 1992). Successful reproduction in the Cuyamaca cypress plantation illustrates that its cone serotiny imposes a barrier to plant emigration from the King Creek population, for lack of dispersal agents which could otherwise carry seed to such nearby sites of suitable habitat.

It is unclear if frequent wildfires in the past half-century have caused changes in the distribution of Cuyamaca cypress because pre-fire studies provide imprecise map data for a baseline reference. For example, Scheid and Zedler (1989) mapped a maximum area of 20.1 ha, which is 14% more area than mapped by Reveal (1978), despite that each map was produced in the same interval between fires, and delineated onto copies of the Cuyamaca Mt. USGS 7.5 minute (1:24,000 scale) topographic quadrangle. Generalized

maps of regional conifer distributions in southern California produced at smaller 1:250,000 scale using aerial photography recently estimated a minimum stand area of 5.3 ha (Minnich and Everett 2001). Systematic field surveys of Cuyamaca cypress in this study, aided with GPS, produced a map with a larger scale of detail and less perimeter generalization that records a total stand area of 13 ha and overlaps with the area of previous estimates. The map of Cuyamaca cypress will be further refined with use of remote sensing techniques (e.g., Lefsky et al. 2002).

The King Creek population of Cuyamaca cypress was resilient to 3 stand-replacement wildfires in the past half-century. A similar finding was recently obtained by a study of repeat measurements for nearby chaparral vegetation (Franklin et al. 2004). The King Creek population has regenerated from fires in 1950, 1970, and 2003, since fire suppression management was initiated ca. 1900. The cypress plantation was protected from such frequent fire, and had reproduction well within the range measured in the King Creek population.

The fire regime in Cuyamaca cypress stands has been altered over the past century by systematic fire suppression management. Previous studies suggest that the King Creek population has declined because of frequent fire return intervals. Griffin and Critchfield (1972) report recent extinction of Cuyamaca cypress at one locality, on the basis that they could not relocate a solitary tree found by Wolf (1948) at a point on King Creek several kilometers downstream from the nearest modern stand. Reveal (1978) suggested that the solitary cypress tree, and discontinuity of remaining cypress stands, were evidence of a relict distribution fragmented by overly-frequent burning in the

twentieth century. The results of this study alternatively illustrate gradients of soil moisture as a habitat factor which likely fragment the stands of Cuyamaca cypress within its King Creek distribution. In addition, the shade-intolerance of Cuyamaca cypress precludes its growth in downstream sites that might otherwise provide continuity of habitat because of overtopping canopy cover by riparian woodlands of *Alnus rhombifolia*, *Plantanus racemosa* and *Quercus agrifolia*. Although cone-serotiny is a barrier to seed dispersal, cones carried down King Creek can establish outlying individuals, such as the solitary tree found by Wolf (1948). One such seedling was located on an exposed bank of the west fork of King Creek in a canopy gap between riparian trees, nearly 1 km downstream of the lowest fire-killed cypress stand (Fig. 18, "A"). Establishment and survival of outlying individuals poorly reflects demographic trends within the population as a whole, and may not indicate relict distributions, nor fragmentation by frequent fires. In fact, extant stands were found to occur over a larger range of elevation than reported by botanical studies which predate frequent burning in the last 50 years (Wolf 1948, Armstrong 1968).

Cuyamaca cypress exhibits a "shifting population" pattern of reproduction and recruitment which is characteristic of serotinous conifers in southern California (after Minnich and Everett 2001, Minnich 2007). Local declines in stand density may occur in different places after every burn due to stochastic variability in reproduction. Since the losses are shifted from one stand to another among fire-cycles, the overall population may remain stable because only one seed is needed to replace the parent in the next generation. With the exception of Plot 3, abundant seedlings were detected, sufficient to

replace or expand the fire-killed population (Table 3.3). A similar observation was made after the 1970 wildfire by Reveal (1978), with suggestion that a stand of 20 yr old regenerating cypress (1950 cohort) had been reduced in “stocking” by 75%. Unfortunately, his estimate was based on a visual impression of low seedling density in the stand, as no counts were taken of trees or seedlings. The results of this study indicate the 1970 cohort reached maturity and copiously reproduced after the 2003 fire, with gains in density of seedling recruits that exceed the suggested population loss in the prior fire cycle.

Patterns of reproduction and recruitment observed for Cuyamaca cypress are similar to demographic trends of Arizona Cypress (*Cupresses arizonica* E. Greene). Arizona cypress is widely distributed in disjunctive populations from northwestern Mexico to Arizona and California (Rehfeldt 1997). Arizona cypress exhibits cohort reproduction following fire, forming open stands of large trees along streams and dense thickets of smaller trees on dry rocky slopes (Whittaker and Niering 1964, Whittaker and Niering 1965, Parker 1980a&b, Moir 1982, Niering and Lowe 1984).

Wolf (1948) described 5 morphologically similar “new world” Cypress species in the arid southwestern United States as members of a so-called Arizona Cypress complex of related taxa (*C. arizonica*, *C. glabra*, *C. nevadensis*, *C. montana*, and *C. stephensonii*). Little (1966) reclassified Cuyamaca cypress as a geographically isolated variety conspecific with Arizona cypress, renamed *C. arizonica* var. *stephensonii*, which is synonymous with modern identifications as *C. arizonica* ssp. *stephensonii* by Murray (1982) and Beauchamp (1986a, 1986b), or *C. arizonica* ssp. *arizonica* by Bartel (1993a,

1993b). The comprehensive *Flora of North America* recognizes Cuyamaca cypress as a geographic variety of Arizona cypress (Ekenwalder 1993). Comparison of Cuyamaca cypress to Arizona cypress grown in common garden experiments attributed morphological differences to genetic drift and inbreeding of the King Creek population during isolation in the Holocene (Rehfeldt 1997). Study of DNA by Bartel et al. (2003) found closest genetic relation between Cuyamaca cypress and the smooth-bark variety of Arizona cypress (*C. arizonica* var. *glabra* [*C. glabra*]). It is unknown if they may still interbreed. Recent discovery of a new conifer in Vietnam has advanced a proposal to split the genus *Cupressus*, with all “new world” taxa renamed *Callitropsis* (Little et al. 2004). A recent revised phylogeny classifies Cuyamaca cypress as *Callitropsis stephensonii* (Little 2006).

CONCLUSION

The “immaturity risk” and “senescence risk” heuristic models are two end-member outcomes which define the tails of a statistical distribution of fire return intervals characterizing a fire regime, and are therefore expected to be uncommon extreme events. However, fire suppression management has systematically altered fire regimes in California over the past century, increasing the chances that extreme events frequently reoccur. Landscape scale reconstruction of fire regimes in San Diego County indicate that short fire return intervals (< 20 yrs) pertaining to the “immaturity risk” outcome occur in overlap zones among recently burned patches (Wells et al. 2004). The extent of

this patch-overlap is greater in southern California than in neighboring Baja California where systematic fire suppression management is not practiced (Minnich and Chou 1997). A time-series of spatially explicit fire perimeter data mapped from 1920 to 1971 using repeat aerial photography of the US-Mexico Border region shows that burned patches are larger in southern California than in northern Baja California, and that the patch overlap is proportional to fire size in both landscapes. The difference in patch size is abruptly observed at the political boundary between the United States and Mexico, where lands on either side of the border otherwise share similar environmental gradients and vegetation distributions (Minnich and Bahre 1995).

These observations suggest that fire suppression management is a likely factor selecting for fire patterns which place cypress populations at unusual jeopardy of “immaturity risk” (more patch overlap) and “senescence risk” (delayed burning of larger old patches). Fire suppression delays ignition of patches relative to local combustion thresholds of fuel accumulation (total live and dead biomass), resulting in widespread accumulation of potential fuels. Some patches age for unusually long intervals. Fire suppression restricts burning to extreme weather states, like summer heat waves or autumn “Santa Ana” winds when ignitions are least efficiently extinguished, and the desiccated state of vegetation lowers the combustion threshold with respect to all available fuels. Extreme fire weather favors rapid rates of spread by flamelines and longer distance spot fire behavior. Larger wildfires are more frequent in occurrence, resulting in more overlap (reburn) of younger age fuels, than if fire suppression were not practiced (see Minnich and Chou 1997).

The risk of overly frequent burning appears to be greatest where post-fire vegetation successions include extensive cover of exotic annual grasses. For example, Tecate cypress (*Cupressus forbesii* Jeps.) stands were seeded with exotic annual rye grass (*Lolium multiflorum* Lam.) for erosion control after stand-replacement wildfires in the late 1970's. This altered vegetation succession fueled recurrent grass fires which killed immature seedling cohorts of Tecate cypress in local areas (Zedler et al. 1983). The cohort extirpations were localized by heterogeneity in stand age and environmental conditions which prevented fire spread into nearby cypress groves and regenerating seedling cohorts, such that a mixed-age population has developed which demographic models predict will stabilize or increase in the next fire cycle (De Gouvenain and Ansary 2006).

The “senescence risk” posed by lengthened fire return intervals appears to be more localized because fire suppression management inevitably fails to prevent fires. For example, the only large stands of Tecate cypress in California which have not burned since systematic fire suppression management was initiated ca. 1900 are on Guatay Mt. Studies which compare stand age and reproduction for Tecate cypress (Zedler 1995), and Sargent cypress (*Cupressus sargentii* Jeps.) ca. 300 km north (Ne'eman et al. 1999), find that such old stands can have diminished reproduction compared to younger stands. However, reproduction still exceeded the density of parent trees.

Cypress populations in Baja California can serve as the best approximation of an empirical control for effects of fire suppression management on patterns of demography. Comparative study of Cuyamaca cypress populations in Baja California and southern

California is needed to evaluate the effects of fire suppression on reproduction and recruitment patterns. A similar conclusion was suggested for Tecate cypress (De Gouvenain and Ansary 2006).

Widespread disjunct occurrences of the two Cuyamaca cypress populations (150 km) suggest that pre-historical events of seed dispersal by this serotinous conifer could have been unrelated to fire. Megafauna may have consumed the small cypress cones while browsing on foliage, providing a mechanism to release and disperse seed to disturbed sites. Extinct herbivore megafauna occurred in southern California during moister glacial climates in the Pleistocene (e.g., Miller 1971, Spaulding et al. 1983, Jefferson 1991, McDonald 1993), including ground sloths (e.g., *Glossotherium*), browsing camels (e.g., *Camelops*), bison (*Bison*), and mammoths (*Mammuthus*). Pleistocene fossil evidence of megafauna confirm that plant matter of conifers were a significant component of diet. For example, the coprolite (dung) of sloths and mammoths preserved in caves (Martin et al. 1961, Hansen 1978, Thompson et al. 1980, Mead et al. 1986), as well as dental boluses (plant residue impacted in teeth depressions) of camels and bison preserved in the La Brea tar pits (Akersten et al. 1988) independently contain conifer tissues identified as belonging to the Cupressaceae, which illustrates the potential for browse of cypress. On the other hand, since cones open upon desiccation, seed may be subject to dispersal by birds, even in extant stands, in which case dispersal fails in modern climate conditions because it is unsynchronized with disturbance conditions necessary for recruitment.

REFERENCES

- Akersten, W., T. Foppe, and G. Jefferson. 1988. New source of dietary data for extinct herbivores. *Quaternary Research* 30:92-97.
- Alexander, E. 1993. Gabbro and its soils. *Fremontia* 21:8-10.
- Alexander, E. 2007. *Serpentine geocology of western North America: geology, soils, and vegetation*. Oxford University Press, Oxford.
- Armstrong, W. 1966. Ecological and taxonomic relations of *Cupressus* in southern California. M.A. Thesis, California State University, Los Angeles.
- Armstrong, W. 1978. Southern California's vanishing cypresses. *Fremontia* 6:24-29.
- Barbour, M. 2007. Closed-cone pine and cypress forests. Pages 296-312 *in* M. Barbour, T. Keeler-Wolf, and A. Schoenherr, eds. *Terrestrial Vegetation of California*, third edition. University of California Press, Berkeley.
- Bartel, J. 1993a. Cupressaceae, Cypress family. *Journal of the Arizona-Nevada Academy of Science* 27:195-200.
- Bartel 1993b. Cupressaceae, Cypress family. Pages 111-114 *in* J. Hickman, ed. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.
- Bartel, J., R. Adams, S. James, L. Mumba, R. Pandey. 2003. Variation among *Cupressus* species from the western hemisphere based on random amplified polymorphic DNA. *Biochemical Systematics and Ecology* 31:693-702.
- Bauer, H. 1943. *The statistical analysis of Chaparral and other plant communities by*

- means of transect samples. *Ecology* 24:45-60.
- Beauchamp, R. 1986a. Taxonomic rearrangements proposed for a flora of San Diego County, California. *Phytologia* 59:437-438
- Beauchamp 1986b. A flora of San Diego County, California. Sweetwater River Press, National City.
- Burns, C., and J. Sauer. 1992. Resistance by natural vegetation in the San Gabriel Mountains of California to invasion by introduced conifers. *Global Ecology and Biogeography Letters* 2:46-51.
- Cottam, G., and J. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460
- De Gouvenain, R., and A. Ansary. 2006. Association between fire return interval and population dynamics in four California populations of Tecate Cypress (*Cupressus forbesii*). *Southwestern Naturalist* 51:447-454.
- Dunn, A. 1986. Population dynamics of the Tecate Cypress. Pages 367-376 in T. Elias and J. Nelson, eds. Conservation and management of rare and endangered plants. California Native Plant Society, Sacramento.
- Eckenwalder, J. 1993. Cupressaceae. Pages 405-408 in Flora of North America Editorial Committee, eds. Flora of North America, north of Mexico, Volume 2. Oxford University Press, New York and Oxford.
- Franklin, J., C. Coulter, and S. Rey. 2004. Change over 70 years in a southern California chaparral community related to fire history. *Journal of Vegetation Science* 15: 701-710

- Goodall, D., 1957. Some considerations in the use of point quadrat methods for the analysis of vegetation. *Australian Journal of Biological Science* 5, 1-41.
- Griffin, J., and W. Critchfield. 1972. The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82, Pacific Southwest Forest and Range Experiment Station, Berkeley.
- Hansen, R. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4:302-319.
- Hart, M., and A. Farcas. 1983. Reconnaissance of landslides and debris flows in the Cuyamaca Peak Gabbro, San Diego County, California. Page 71 *in* Engineering geology today and tomorrow: Association of Engineering Geologists 26th annual meeting; Abstracts and programs, Engineering Geology Today and Tomorrow volume 26.
- Jefferson, G. 1991. A catalogue of late Quaternary vertebrates from California: part two, mammals. Los Angeles County Natural History Museum Technical Reports 7:1-129.
- Keeley, J., and P. Zedler. 1998. Evolution of life histories in pines. Pages 220–248 *in* D. Richardson and R. Cowling, eds. *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge.
- Krebs, C. 1989. *Ecological Methodology*. Harper Collins Publishers, New York.
- Kruckeberg, A. 1985 California Serpentine: Flora, Vegetation, Geology, Soils, and Management Problems. *University of California Publications in Botany* 78:1-180.

- Kruckeberg, A. 2002. Geology and plant life: the effects of landforms and rock types on plants. University of Washington Press, Seattle.
- Lamont, B., D. Le Maitre, R. Cowling, and N. Enright. 1991. Canopy seed storage in woody plants. *Botanical Review* 57:277-317.
- Lanner, R. 2002. Conifers of California. Cachuma Press, Los Olivos.
- Lefsky, M., W. Cohen, G. Parker, and D. Harding. 2002. Lidar remote sensing for ecosystem studies. *Bioscience* 52:19–30.
- Lev-Yadun, S. 1995. Living serotinous cones in *Cupressus sempervirens*. *International Journal of Plant Sciences*, 156:50-54.
- Little, D. 2006. Evolution and Circumscription of the True Cypresses (Cupressaceae: *Cupressus*) *Systematic Botany* 31:461–480.
- Little, E. 1966. Varietal transfers in *Cupressus* and *Chamaecyparis*. *Madroño* 18:161-192.
- Little, D., A. Schwarzbach, R. Adams, C Hsieh. 2004. The circumscription and phylogenetic relationships of *Callitropsis* and the newly described genus *Xanthocyparis* (cupressaceae). *American Journal of Botany* 91: 1872–1881.
- Martin, P., B. Sabels, and D. Shutler. 1961. Rampart cave coprolite and ecology of the Shasta ground sloth. *American Journal of Science* 259:102-127.
- McDonald, H. 1993. Harlan's ground sloth, *Glossotherium harlani*, from Pauba Valley, Riverside County, California. San Bernardino County Museum Association Special Publication 93-1:101-103.
- McMillan, C. 1956. The edaphic restriction of *Cupressus* and *Pinus* in the Coast Ranges

- of central California. *Ecological Monographs* 26:177-212.
- Mead, J., L. Agenbroad, O. Davis, and P. Martin. 1986. Dung of *Mammuthus* in the arid southwest, North America. *Quaternary Research* 25:121-127.
- Miller, W. 1971. Pleistocene vertebrates of the Los Angeles basin and vicinity. *Los Angeles County Museum Science Series* 10:1-124.
- Moir, W. 1982. A fire history of the High Chisos, Big Bend National Park, Texas. *Southwestern Naturalist* 27:87-98.
- Moran, R. 1972. Plant notes from the Sierra Juarez of Baja California, Mexico. *Phytologia* 35:205-215.
- Minnich, R. 1987. The distribution of forest trees in northern Baja California, Mexico. *Madroño* 34:98-127.
- Minnich, R., 2007. Southern California coniferous forest. In: Barbour, M., Keeler-Wolf, T., Schoenherr, A. (Eds.), *Terrestrial Vegetation of California*. third ed. University of California Press, Berkeley, CA, USA, pp. 502–538.
- Minnich, R., and C. Bahre. 1995. Wildland fire and Chaparral succession along the California-Baja California boundary. *International Journal of Wildland Fire* 5: 13-24.
- Minnich, R., and Y. Chou. 1997. Wildland fire patch dynamics in the chaparral of southern California and Northern Baja California. *International Journal of Wildland Fire* 7:221-249.
- Minnich, R., and R. Everett. 2001. Conifer tree distributions in southern California. *Madroño* 48:177-197.

- Munz, P.A. 1974. A flora of southern California. University of California Press, Berkeley.
- Murray, E. 1982. Spermophyta notes. *Kalmia* 12:18-20.
- Ne'eman, G., C. Fotheringham, and J. Keeley. 1999. Patch to landscape patterns in post fire recruitment of a serotinous conifer. *Plant Ecology* 145:235-242.
- Niering, W., and C. Lowe. 1984. Vegetation of the Santa Catalina Mountains: community types and dynamics. *Vegetatio* 58:3-28.
- Oberbauer, T. 1993. Soils and plants of limited distribution in the Peninsular Ranges. *Fremontia* 21:3-7.
- Parker, A. 1980a. Site preferences and community characteristics of *Cupressus arizonica* Greene (Cupressaceae) in southeastern Arizona. *Southwestern Naturalist* 25:9-22.
- Parker, A. 1980b. The successional status of *Cupressus arizonica*. *Great Basin Naturalist* 40:254-264.
- Rehfeldt, G. 1997. quantitative analyses of the genetic structure of closely related conifers with disparate distributions and demographics: the *Cupressus arizonica* (Cupressaceae) complex. *American Journal of Botany* 84: 190–200.
- Reveal, J. 1978. The autecology and status of Cuyamaca Cypress (*Cupressus arizonica* var. *stephensonii*). Unpublished report, on file, Cleveland National Forest, Rancho Bernardo.
- Sawyer, J., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento.
- Scheid, G. 1986. Comparison of reproductive modes in two species of *Cupressus*:

- serotiny vs. non-serotiny. M.S. Thesis, San Diego State University, California.
- Scheid, G., and P. Zedler. 1989. Ecological studies of Cuyamaca cypress, Cuyamaca rancho state park, San Diego County: Population status and management of *Cupressus arizonica* ssp. *stephensonii*. Unpublished report, on file, California State Parks, Sacramento.
- Skinner, M., and B. Pavlik. 1994. Inventory of rare and endangered vascular plants of California, fifth edition. California Native Plant Society, Sacramento, CA.
- Soil Survey Staff. 1999. Keys to Soil Taxonomy, eighth edition. US Soil Conservation Service, Pocahontas Press, Blacksburg, VA, USA.
- Spaulding, W., E. Leopold, and T. Van Devender. 1983. Late Wisconsin paleoecology of the American southwest. Pages 259-293 in S. Porter, ed. The late Quaternary environments of the United States, volume 1: The late Pleistocene of the United States: A review. University of Minnesota Press, Minneapolis.
- Stottlemeyer, D., and E. Lathrop. 1981. Soil chemistry relationships of the Tecate Cypress in the Santa Ana Mountains, California. *Aliso* 10:59-69.
- Thompson, R., T. Van Devender, P. Martin, T. Foppe, and A. Long. 1980. Shasta ground sloth (*Nothrotheriops shastense* Hoffsetter) at shelter cave, New Mexico: Environment, diet, and extinction. *Quaternary Research* 14:360-376.
- Vogl, R., W. Armstrong, K. White, and K. Cole. 1989. The closed-cone pines and cypresses. Pages 295-358 in M. Barbour and J. Major, eds. *Terrestrial Vegetation of California*, new expanded edition. Special publication number 9, California Native Plant Society, Sacramento.

- Wangler, M., and R. Minnich 1996. Fire and succession in pinyon-juniper woodland in the San Bernardino Mountains, California. *Madroño* 43:493-514.
- Wells, M., J. O'Leary, J. Franklin, J. Michaelsen, and D. McKinsey. 2004. Variations in a regional fire regime related to vegetation type in San Diego County, California (USA). *Landscape Ecology* 19:139–152.
- Whittaker, R. 1954. The vegetational response to serpentine soils. *Ecology* 35:275-288.
- Whittaker, R. 1960. Vegetation of the Siskiyou Mountains, Oregon and California *Ecological Monographs* 30:279-338.
- Whittaker, R. and W. Niering. 1964. Vegetation of the Santa Catalina mountains, Arizona. I. Ecological classification and distribution of species. *Journal of the Arizona Academy of Science* 3:9-34.
- Whittaker, R. and W. Niering. 1965. Vegetation of the Santa Catalina mountains, Arizona: A gradient analysis of the south slope. *Ecology* 46:429-452.
- Wolf, C. 1948. Taxonomic and distributional studies of new world cypresses. *Aliso* 1:1-250.
- Wolf, P., and R. Brinker, 1994. *Elementary Surveying*, ninth edition. Harper Collins Publishers, New York.
- Zedler, P. C. Gautier, G. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California Chaparral and coastal scrub. *Ecology* 64:809-818.
- Zedler, P., C. Gautier, P. Jacks. 1984. Edaphic restriction of *Cupressus forbesii* (Tecate Cypress) in southern California, USA.-A hypothesis. Pages 237-243 *in* N.

- Margaris, M. Arianoutsou-Faraggitaki, and W. Oechel, eds. Being alive on land: proceedings of the international symposium on adaptations to the terrestrial environment held in Halkidiki, Greece. W. Junk-Kluwer Publishers, The Hague.
- Zedler, P. 1977. Life history attributes of plants and the fire cycle: A case study in chaparral dominated by *Cupressus forbesii*. Pages 451-458 in H. Mooney and C. Conrad, eds. Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. USDA Forest Service General Technical Report WO-3.
- Zedler, P. 1995. Fire frequency in southern California shrublands: Biological effects and management options. Pages 101-112 in J. Keeley and T. Scott, eds. Brushfires in California wildlands: ecology and resource management. International Association of Wildland Fire, Fairfield.



Figure 3.1 Unburned grove of Cuyamaca cypress and neighboring fire-killed stand in the native King creek population. The photograph was taken 3 years after fire. Note that the charred bark on scorched trees has exfoliated off exposing weathered stem wood having white color.

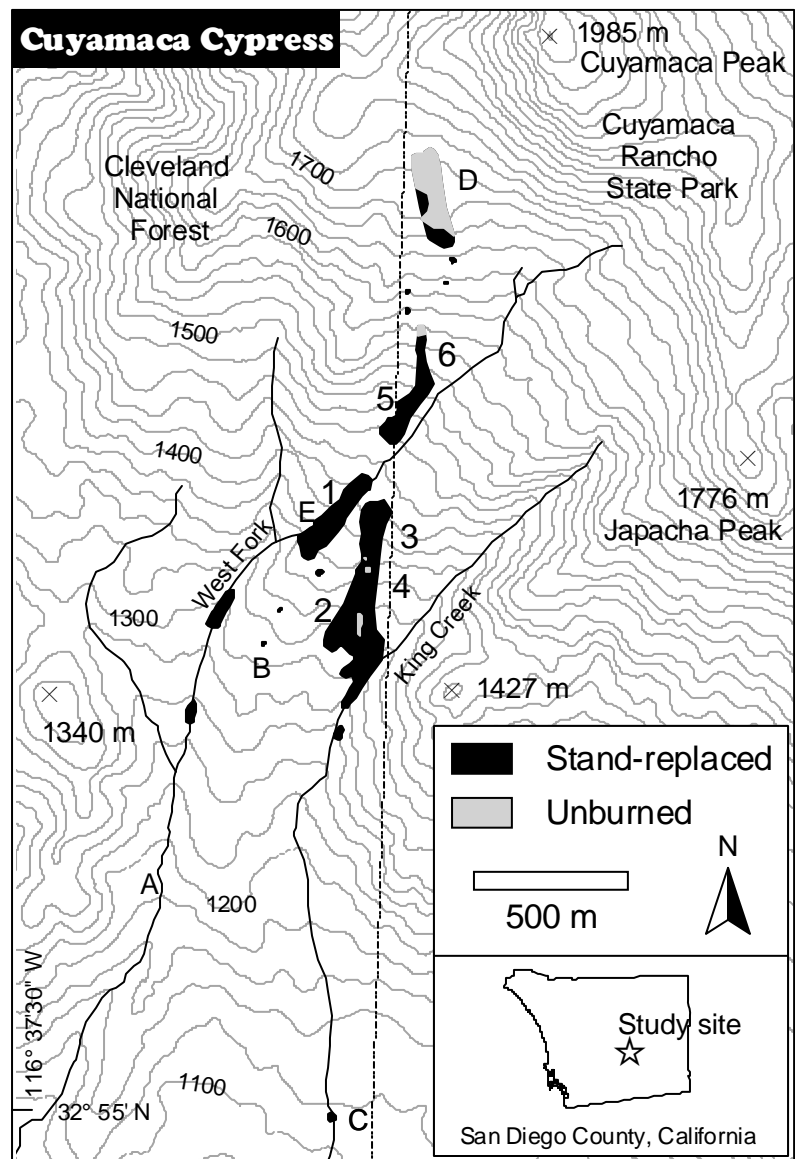


Figure 3.2 Map of Cuyamaca cypress on Cuyamaca Mountain, southern California. Unburned live trees occurred in plots 2 & 4, but also near plot 6. Map annotations: (A) Seedling located ca. 1 km downstream from nearest fire-killed stand, (B) scattered individual cypress on stabilized hill-slumps, (C) the lowest elevation stand, (D) highest stand area is scattered individual cypress on stabilized hill-slumps, (E) location of slope profile belt-transect.

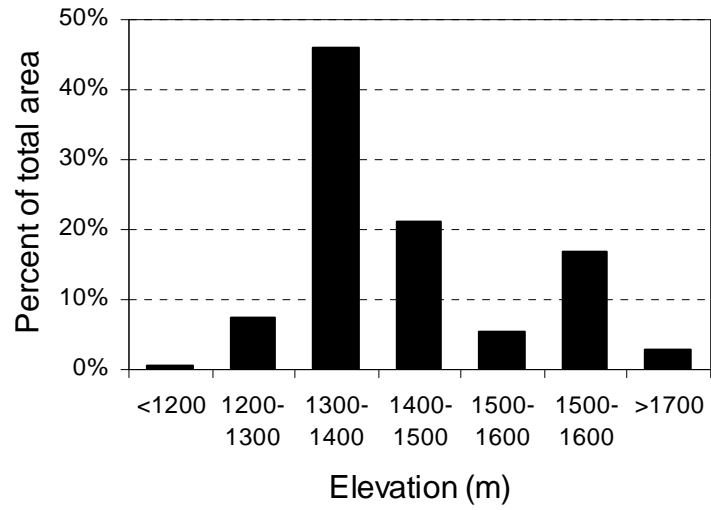


Figure 3.3 Histogram of Cuyamaca cypress stand area classified by intervals of elevation.

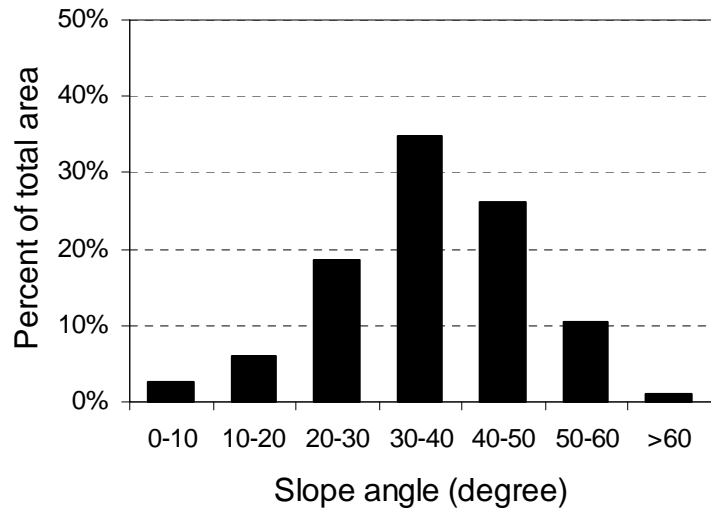


Figure 3.4 Histogram of Cuyamaca cypress stand area classified by 10° intervals of slope angle.

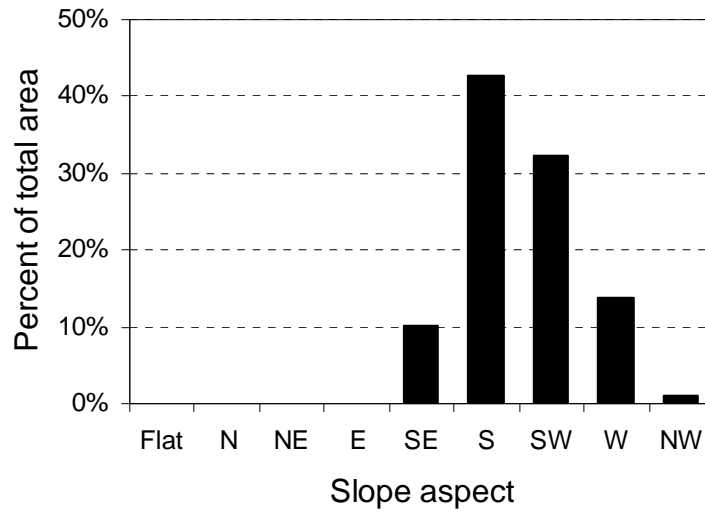


Figure 3.5 Histogram of Cuyamaca cypress stand area classified by slope aspect intervals of 22.5° compass azimuth.

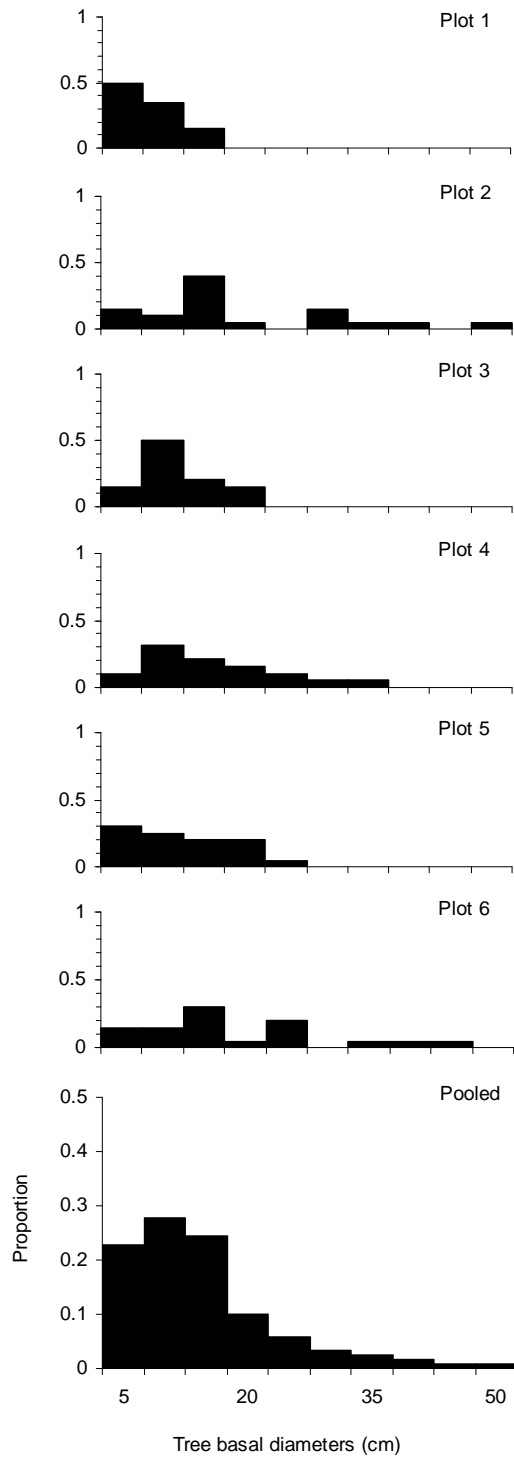


Figure 3.6 Size-frequency distribution of tree basal diameter measurements.

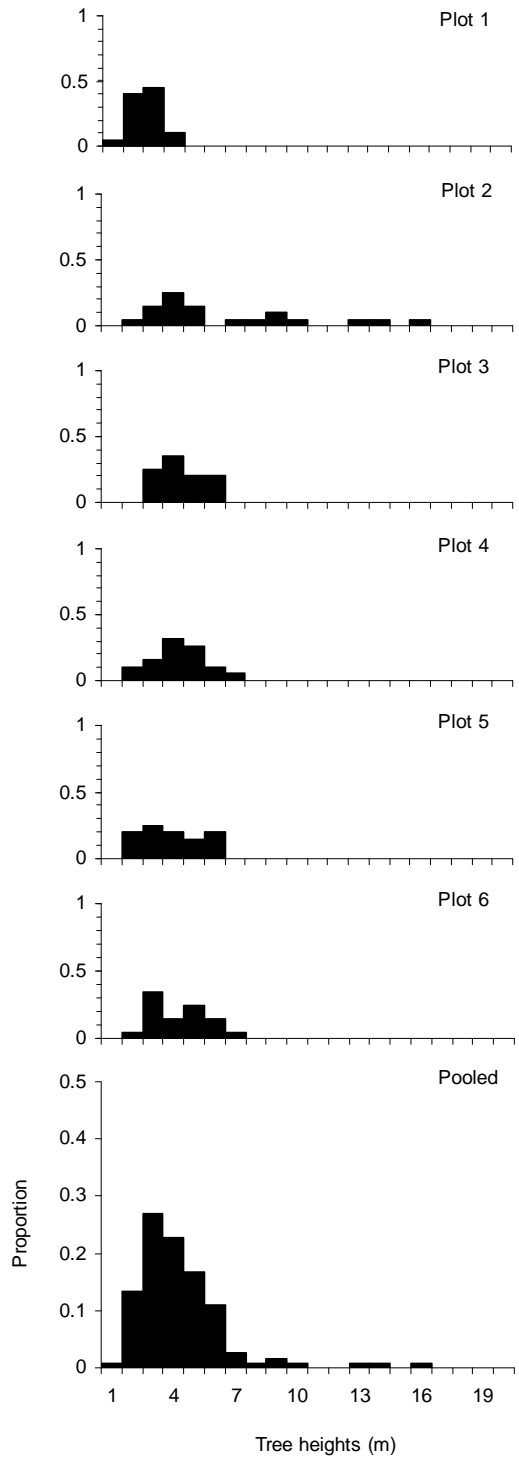


Figure 3.7 Size-frequency distribution of tree height measurements.

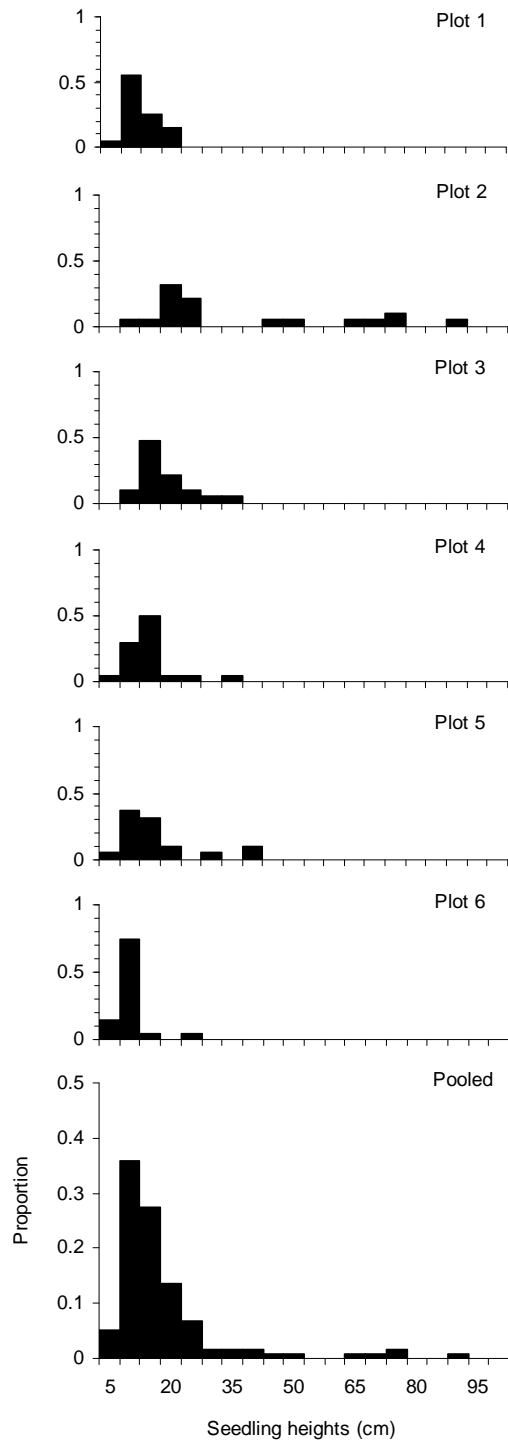


Figure 3.8 Size-frequency distribution of seedling height measurements.

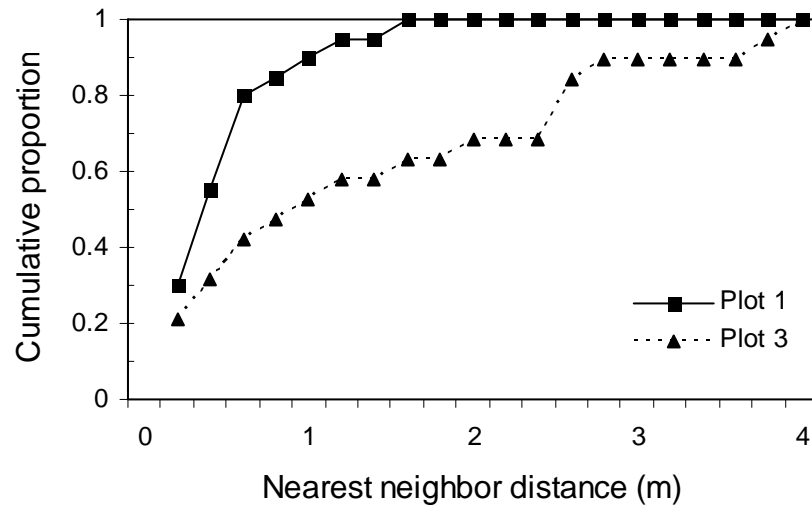


Figure 3.9 Cumulative frequency of distances between individuals in Plot 1 (high seedling density) and Plot 3 (low seedling density).

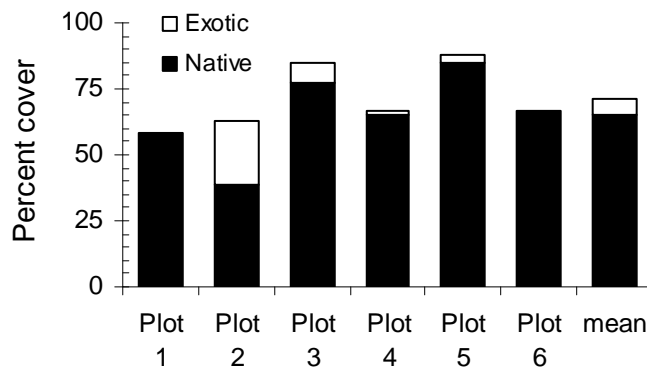


Figure 3.10 Post-fire cover of native and exotic herbaceous vegetation in the understory of Cuyamaca cypress stands.



Figure 3.11 Dense mat-like cover of live and dead *Calystegia macrostegia* surrounding Cuyamaca cypress seedling (arrow) and toppled fire-killed cypress tree. The ruler next to the seedling indicates 10 cm.

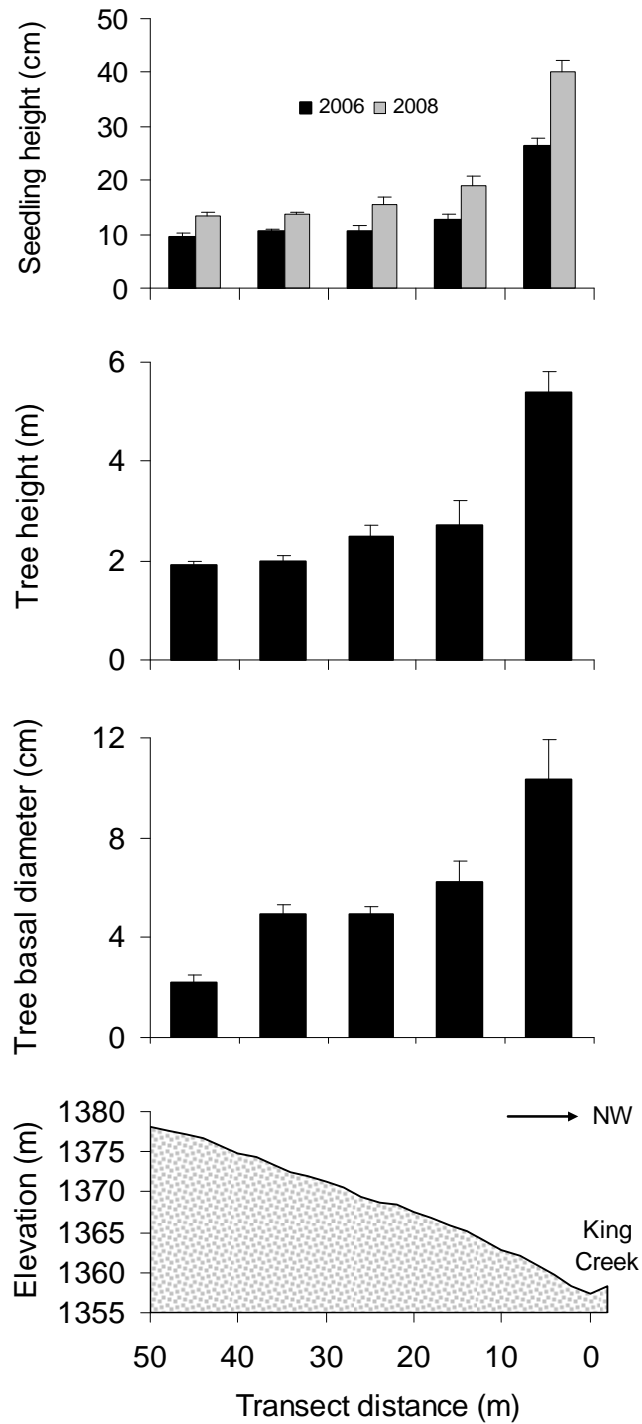


Figure 3.12 Measurement of seedling at tree size along a slope profile. Averages shown for seedling height, tree height, and tree base diameter measured along a belt-transect spanning a slope gradient from mesic conditions at King Creek to xeric conditions in chaparral uphill near Plot 1. Error bars indicate the range of one standard error.

Table 3.1 Measurements of Cuyamaca cypress trees at King Creek.

Plot	Tree density (ha ⁻¹)	m ² Tree ⁻¹ (mean) ^A	PCQ Tree distance (m) ^B		Basal diameter (cm)		Basal area (m ² ha ⁻¹)	Tree height (m)	
			mean ± SE	(range)	mean ± SE	(range)		mean ± SE	(range)
1	4910	2.0	1.4 ± 0.3	(0.3 - 4.0)	5.5 ± 0.7	(0.5 - 13.5)	11.7	2.1 ± 0.1	(0.6 - 3.4)
2	1250	8.0	2.4 ± 0.4	(0.2 - 6.5)	17.1 ± 2.8	(4.0 - 49.0)	28.7	6.3 ± 0.9	(1.8 - 15.8)
3	6330	1.6	2.5 ± 0.3	(0.5 - 4.9)	10.2 ± 1.0	(2.6 - 17.5)	51.7	3.9 ± 0.2	(2.5 - 5.7)
4	2280	4.4	2.2 ± 0.4	(0.3 - 6.6)	13.9 ± 2.1	(1.8 - 35.0)	34.6	3.8 ± 0.2	(1.5 - 6.1)
5	5000	2.0	1.9 ± 0.3	(0.4 - 4.2)	9.8 ± 1.3	(1.0 - 19.5)	37.7	3.4 ± 0.3	(1.6 - 5.7)
6	1240	8.1	3.1 ± 0.4	(0.5 - 7.6)	16.6 ± 2.5	(2.1 - 43.5)	26.8	3.8 ± 0.3	(1.9 - 6.9)

^A Mean area per individual tree is the reciprocal of density.

^B Distances to closest trees measured from point-centered quarters (PCQ) spaced at 20 m intervals along 100 m transect ($n = 20$ trees per plot). The square root of mean area per individual tree is equal to the mean PCQ tree distance if trees are randomly distributed.

Table 3.2 Measurements of Cuyamaca cypress seedlings in the third growing season after the 2003 wildfire.

Plot	Seedling density (10 m ⁻²) ^A		m ² Seedling ⁻¹ (mean) ^B	PCQ Seedling distance (m) ^C		Nearest-neighbor (m)		Dispersion index (<i>R</i>) ^D	Seedling height (cm)	
	mean ± SE	(range)		mean ± SE	(range)	mean ± SE	(range)		mean ± SE	(range)
1	20 ± 5	(6 - 58)	0.5	1.2 ± 0.2	(0.1 - 2.5)	0.4 ± 0.1	(0.0 - 1.5)	1.13	10.5 ± 0.9	(3.0 - 15.3)
2	5 ± 2	(0 - 22)	2.0	1.6 ± 0.4	(0.1 - 5.0)	--	--	--	35.9 ± 5.6	(8.5 - 89.3)
3	3 ± 1	(0 - 7)	3.3	2.9 ± 0.4	(0.7 - 6.5)	1.2 ± 0.3	(0.1 - 3.6)	1.31	16.4 ± 1.5	(8.8 - 34.1)
4	71 ± 22	(3 - 202)	0.1	1.0 ± 0.2	(0.1 - 3.8)	--	--	--	12.0 ± 1.5	(3.7 - 33.9)
5	7 ± 2	(0 - 20)	1.4	1.7 ± 0.3	(0.3 - 5.0)	--	--	--	14.3 ± 2.1	(3.5 - 39.5)
6	57 ± 19	(2 - 227)	0.2	0.8 ± 0.2	(0.1 - 2.8)	--	--	--	7.8 ± 1.0	(3.7 - 23.6)

^A Seedling counts in census of circular sub-plots established in each tenth-hectare plot ($n = 11$ sub-plots per plot).

^B Mean area per individual seedling is the reciprocal of average density.

^C Distances to closest seedlings measured from point-centered quarters (PCQ) spaced at 20 m intervals along 100 m transect ($n = 20$ seedling measurements per plot). The square root of mean area per individual is equal to the mean PCQ seedling distance if seedlings are randomly distributed.

^D Dispersion index $R = [r_A / r_E]$ where r_A is mean distance to nearest neighbor, and r_E is expected distance = $1 / 2\sqrt{\text{density}}$

Table 3.3 Site-specific seedling to tree ratios in Cuyamca Cypress stands in the third growing season after the 2003 wildfire.

Transect Interval	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
0-20 m	3.7:1	5.3:1	0.1:1	7.4:1	3.5:1	22.5:1
20-40 m	5.9:1	24.4:1	1.2:1	19.3:1	0.1:1	20.5:1
40-60 m	1.7:1	0.3:1	0.2:1	47.5:1	1.5:1	108.1:1
60-80 m	3.1:1	1.3:1	0.1:1	30.7:1	4.9:1	93.6:1
80-100 m	6.5:1	6.7:1	0.4:1	43.9:1	6.9:1	13.3:1
pooled mean	4.2:1	7.6:1	0.4:1	29.8:1	3.4:1	51.6:1

Table 3.4 Significant variation in the size of trees and seedlings among 10 m intervals of the slope profile belt-transect.

ANOVA Test	F _(df)	<i>p</i> value
Tree basal diameter	10.8 ₍₄₎	<0.000
Tree height	36.1 ₍₄₎	<0.000
Seedling height	62.4 ₍₄₎	<0.000

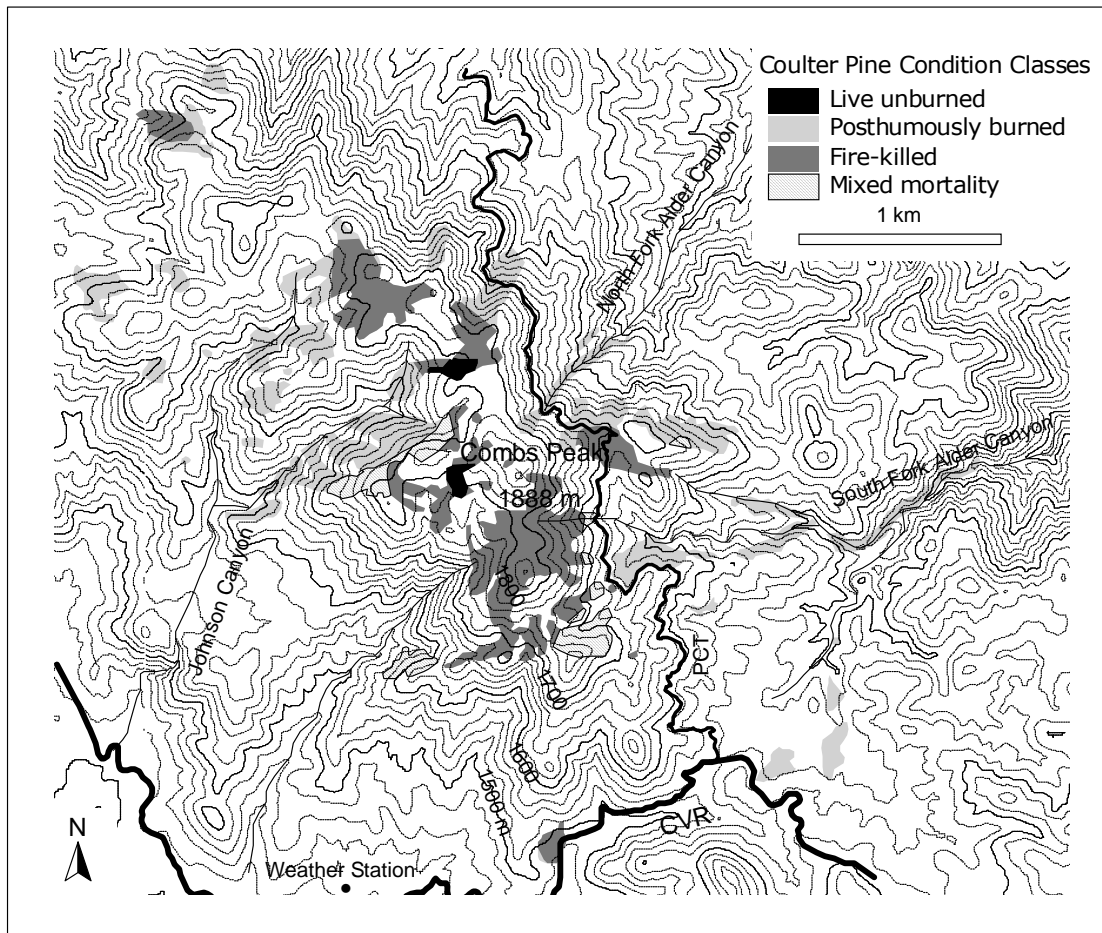
CONCLUSION

Fire suppression management has significantly altered distribution patterns of conifer forests in the mountains of southern California. The change has been most dramatic in standing populations of mixed conifer forests which have been fragmented into patch-mosaic populations whose survival is dependent upon gradual long-distance seed dispersal from nearest-neighbor populations facing similar risk of stand-replacement. Stand-replacement has broadened from a process that once cleared small forest gaps in mixed conifer forest, to an outcome which now destroys entire forest landscapes. At the same time, mixed conifer forest stands in Baja California have changed little, and forest distributions remain stable. Historical documentary sources provide qualitative indications of open park-like stands, in sharp contrast with modern post-suppression conditions. Data collected since the early twentieth century (1920's-1930's) in the form of repeat aerial photographs and ground based sampling indicate densification of stands by reproduction of shade-tolerant conifers, concomitant to large declines in the density of large overstory dominant trees. Historical reference data for tree density and canopy cover in mixed conifer forests of southern California overlap with modern conditions in Baja California, indicating fire suppression management is a likely factor attributed to the divergence in forest structure over the past century.

Fire suppression appears to select for burning patterns which place populations of serotinous conifers at greater risk of recruitment failures. In the case of Coulter pine, fire suppression management may have altered landscape scale demographic trends over the

past century by allowing cohorts to live longer over broad areas, experiencing higher evapotranspiration which may have increased population susceptibility to mortality in drought conditions, setting the stage for reproduction failures in the inevitability that stands posthumously burn. Reproduction failures by Coulter pine in posthumously-burned stands may foretell more extensive outcomes in serotinous conifer forests of Lodgepole pine (*Pinus contorta*) across the western United States where drought-kill has been extensive in the past decade. On the other hand, in places where young stands of serotinous conifers survive drought, the risk is that fire suppression unintentionally selects for more frequent large wildfires which tend to have more overlap (reburn) of younger fuel-age patches. Overly frequent burning places immature cohorts of regenerating cypress populations at jeopardy of recruitment failure, particularly in stands with extensive cover of exotic annual grasses. While reproduction failure of an entire population is the most extreme outcome possible, the more immediate trend may be toward larger shifts in the distribution of serotinous conifers subjected to fire suppression management.

Appendix 1. Map of Coulter pine stand condition classes on Bucksnot Mt., which burned on 16-24 July 2003.



Appendix 2. Regenerating shrub cover (%) in Cuyamaca cypress stands at King Creek.

Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	mean	frequency
<i>Adenostoma fasciculatum</i>	6.4	4.4	9.7	0.8	11.7	0.9	5.7	100
<i>Arctostaphylos glandulosa</i>	12.6	0	1.4	0.2	5.8	7.9	4.7	83
<i>Ceanothus greggii</i>	0.4	1.4	1.7	6.6	1.0	6.3	2.9	100
<i>Ceanothus leucodermis</i>	0.6	1.0	0	0	0	0	0.3	33
<i>Ceanothus foliosus</i>	5.5	0.4	2.4	15.5	5.2	13.6	7.1	100
<i>Cercocarpus betuloides</i>	0.1	2.5	0	7.4	0.5	0	1.8	67
<i>Ericameria arborescens</i>	0	0	0	0.4	0	0.2	0.1	33
<i>Hazardaria squarrosa</i>	0	0	0	1.3	0	1.0	0.4	33
<i>Heteromeles arbutifolia</i>	3.6	0	2.0	2.9	2.6	0	1.9	67
<i>Lonicera subspicata</i>	0	0	0	0	0.3	0.2	0.1	33
<i>Quercus berberidifolia</i>	3.2	11.0	9.0	8.9	13.5	15.7	10.2	100
<i>Rhamnus ilicifolia</i>	0.4	0	0	0.2	0.3	0	0.1	50
<i>Rhus ovata</i>	0	4.1	0	0	0.9	0	0.8	33
<i>Yucca whipplei</i>	0	0	0	0.1	0	0	0.0	17
Total	32.8	24.8	26.2	44.2	41.8	45.8	35.9	