INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI

films the text directly from the original or copy submitted. Thus, some

thesis and dissertation copies are in typewriter face, while others may be

from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the

copy submitted. Broken or indistinct print, colored or poor quality

illustrations and photographs, print bleedthrough, substandard margins,

and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete

manuscript and there are missing pages, these will be noted. Also, if

unauthorized copyright material had to be removed, a note will indicate

the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by

sectioning the original, beginning at the upper left-hand corner and

continuing from left to right in equal sections with small overlaps. Each

original is also photographed in one exposure and is included in reduced

form at the back of the book.

Photographs included in the original manuscript have been reproduced

xerographically in this copy. Higher quality 6" x 9" black and white

photographic prints are available for any photographs or illustrations

appearing in this copy for an additional charge. Contact UMI directly to

order.

UMI

A Bell & Howell Information Company 300 North Zeeb Road, Ann Arbor MI 48106-1346 USA 313/761-4700 800/521-0600

Fire Regimes and Forest Structure in Pine Ecosystems of Arizona, U.S.A., and Durango, Mexico

by Peter Z. Fulé

A Dissertation
Submitted in Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy
in Forest Science

Northern Arizona University

December 1996

Approved:

W. Wallace Covington, Ph.D., Chair

Thomas E. Kolb, Ph.D.

Joy Mystrom Mast, Ph.D.

Margaret M./Moore, Ph.D.

Thomas G. Whitham Ph D

UMI Number: 9710194

Copyright 1996 by Fule, Peter Z.

All rights reserved.

UMI Microform 9710194 Copyright 1997, by UMI Company. All rights reserved.

This microform edition is protected against unauthorized copying under Title 17, United States Code.

300 North Zeeb Road Ann Arbor, MI 48103

ABSTRACT

Fire Regimes and Forest Structure in Pine Ecosystems of Arizona, U.S.A., and Durango, Mexico

Peter Z. Fulé

Frequent, low-intensity fire regimes are keystone ecological processes in longneedled pine forests of western North America. This study compared related ecosystems in the southwestern U.S., where extended fire exclusion has led to the development of unsustainably dense forests, and in northern Mexico, where forests have a complex mix of fire regimes. In Arizona, U.S.A., reference conditions of the historic fire disturbance regime and forest structure prior to Euro-American settlement (circa 1880 A.D.) of a Pinus ponderosa landscape were quantified. Presettlement fire return intervals averaged 4 years for all fires and 7 years for widespread fires. After excluding fire, forest density increased from an average of 148 trees/ha in 1883, an open forest dominated by relatively large pines, to 1,265 trees/ha in 1994/95, a dense forest of relatively small and young trees. Species composition has shifted toward greater dominance by Quercus and conifers less-adapted to frequent fires (Abies and Pseudotsuga). In Durango, Mexico, fire disturbance history and forest structure were compared at four unharvested or lightly-harvested long-needled pine forests. The sites had regimes of frequent, low-intensity fires, recurring between 4 to 5 years for all fires and 6 to 9 years for widespread fires, until fire exclusion began in the midtwentieth century at three sites. The remaining site has an uninterrupted frequent fire regime. Forest ecosystem structures differed in ways consistent with the thinning and fuel consuming effects of fire: extended fire exclusion led to dense stands of smaller and younger trees, high dead woody biomass loading, and thick forest floors. Spatial pattern analysis showed that the overstory developed under a frequent-fire regime was dispersed and less dense, while fire-excluded sites had clumped overstory trees with a high density of smaller trees. Dominance by sprouting *Quercus* and *Alnus* was greatest at the fire-excluded sites. The return of fire after 29 years of exclusion at one site reduced tree density but did not restore pre-fire-exclusion structure. Strategies for sustainable management of long-needled pine ecosystems should recognize the keystone role of fire, and the effect of fire exclusion in changing forest density, composition, and fire severity.

© 1996 Peter Z. Fulé

ACKNOWLEDGMENTS

For their continuing professional and personal support over many years, making this research and many other things possible, I thank Wally Covington and Margaret Moore. I would like to thank the other members of my graduate committee, Tom Kolb, Joy Nystrom Mast, and Tom Whitham, as well as David "Sam" Sandberg, and Doc Smith. Concepts, procedures, and software for studying fire regimes developed by Tom Swetnam, Chris Baisan, and Henri Grissino-Mayer were invaluable to this research.

For research at Camp Navajo (chapter 3), I thank Donald Hack, Jr., John Morrow, and Elizabeth Gilman, of the Arizona Army National Guard. Field and laboratory work was carried out with the help of Tom Heinlein, John Paul Roccaforte, Judy Springer, and Amy Martin Waltz. Forest management history was provided by Teri Cleeland of the Kaibab National Forest. At Northern Arizona University, thanks to David Hammond and Tina Ayers of the Deaver Herbarium for assistance in identifying plant specimens and the Special Collections and Archives staff of the Cline Library, particularly Bruce Hooper, for help with the Navajo Army Depot collection. Tom Swetnam and an anonymous reviewer provided helpful comments. The Camp Navajo project was supported by a grant from the Arizona Army National Guard.

For research in Mexico (chapters 4 and 5), I thank the Ejido Salto de Camellones, the Ejido Topia, and the Ejido Hacienditas for permission to sample the study sites. The Unión de Ejidos y Comunidades "General Emiliano Zapata," the Unidad de Conservación y Desarrollo Forestal Integral (UCDFI) #12 "Topia" and UCDFI #2 "Santiago Papasquiaro," Carlos Zapata Pérez, and Daniel Trujano Thome provided extensive and invaluable assistance and cooperation. Reynaldo Hernández aided in establishing the project. Field work was carried out under sometimes difficult conditions with the help of Brad Ruess, J. Guadalupe Paredes Pérez, Martín Lozano Vargas, Jerónimo Corral Chaidez, Fernando Salazar Jiménez, Angel Almodovar Varela, Armando Alanís de la Rosa, José Luís Leco Romero, Valentín Reyes Hernández, and Marcelo Hernández Martínez. Dr. M. Socorro González Elizondo identified several plant specimens and gave taxonomic clarification. Amy Martin Waltz, John Paul Roccaforte, and Joy Nystrom Mast assisted with laboratory analysis. Weather records were provided by Minera Mexicana La Cienega, S.A. de C.V. Financial and in-kind support for data collection was provided by the Unión de Ejidos y Comunidades "General Emiliano Zapata" and the Northern Arizona University School of Forestry. This research was supported by grants from the USDA Forest Service, Pacific Northwest Experiment Station, Global Environmental Protection program (cooperative agreement PNW 93-0456), the National Science Foundation (DEB-9322706 and INT-9417560), and the USDI Bureau of Land Management, Arizona State Office (cooperative agreement 1422-A950-A6-001).

TABLE OF CONTENTS

LIST OF TA	ABLES	ix
LIST OF FI	GURES	xii
DEDICATION	ON	•
DD 55 . 65		xiv
PREFACE		xv
1. INTROD	UCTION	i
1.1	Fire regimes and forest structure	1
1.2	Research design questions	3
1.3	Significance	4
2. LITERAT	URE REVIEW AND RESEARCH DESIGN	6
2.1	Fire in western long-needled pine ecosystems	6
	2.1.1 Southwestern U.S.	7
	2.1.2 Northern Mexico	11
2.2	Ecosystem management	16
	2.2.1 Hierarchical scaling	18
	2.2.2 Keystone processes and structures	21
	2.2.3 Reference conditions	23
	2.2.4 Ecological restoration	27
2.3	Large-scale research design	29
	2.3.1 Methodology	30
	2.3.2 Conceptual research approach	33
3. DETERMI	NING REFERENCE CONDITIONS FOR ECOSYSTEM	27
MANA	AGEMENT IN SOUTHWESTERN PONDEROSA PINE	37
FORE	STS	
3.1	Introduction	27
3.2	Study area	37
3.3	Methods	39
	3.3.1 Field sampling	40
	3.3.2 Dendrochronologyfire disturbance history	41
	3.3.3 Age structure	43
	3.3.4 Reconstruction of presettlement structure	43
	3.3.5 Statistical analysis	44
3.4	Results	48
	3.4.1 Fire disturbance history	49
	3.4.2 Changes in forest structure	49
	G	51

3.5	Discussion	53
	3.5.1 Context of changes in fire regime and forest structure	53
	3.5.2 Ecosystem management: (1) comparison to	56
	contemporary conditions	30
	3.5.3 Ecosystem management: (2) ecological	58
	restoration	30
4. FIRE RE	GIMES AND FOREST STRUCTURE IN THE SIERRA	72
MAI	DRE OCCIDENTAL, DURANGO, MEXICO	, 2
4.1	Introduction	72
4.2		74
4.3	- · · · · · · · · · · · · · · · · · · ·	75
4.4		77
	4.4.1 Field sampling	77
	4.4.2 Analysis	79
4.5	Results	83
	4.5.1 Fire disturbance history	83
	4.5.2 Forest structure	90
4.6	Discussion	94
	4.6.1 Patterns of fire occurrence	94
	4.6.2 Fire and forest structure	97
4.7	Conclusions	100
5. TREE PA	TTERNS IN TEMPERATE MEXICAN FORESTS UNDER	123
DIFF	ERENT FIRE REGIMES	
5.1	Introduction	123
5.2	Methods	126
	5.2.1 Study area	126
	5.2.2 Sampling and analysis	127
5.3	Results	129
5.4	Discussion	132
5.5	Implications	135
6. DISCUSS	ION	149
6.1	Differences between Arizona and Durango ecosystems	149
6.2	Parallels between Arizona and Durango ecosystems	152
6.3	Ecosystem management implications and future directions	153
. LITERATI	URE CITED	156

LIST OF TABLES

Table 3.1. Fire return intervals over the period 1637 to 1883.	61
Table 3.2. Seasonal distribution of fires based on the position of the fire injury within the ring. Total number of scars = 457.	61
Table 3.3. Presettlement forest structure reconstruction in 1883 compared with contemporary forest structure from 1994/95 inventory at Camp Navajo, AZ. Presettlement New Mexican locust shrub structure could not be reconstructed so locust is not included in the totals. Sample size n = 62. Within-row means followed by asterisks are significantly different (p < .05). S.E.M. = standard error of the mean.	62
Table 3.4. Regeneration density (stems/ha) by species and height class. Sample size $n = 62$, $100-m^2$ plots. S.E.M. = standard error of the mean.	63
Table 3.5. Frequency of the 20 most-encountered herbaceous species and percent herbaceous cover. Frequencies of all other herbaceous species were below 1%. S.E.M. = standard error of the mean.	64
Table 3.6. Dead woody biomass and forest floor depth. Sample size $n = 62$, 15-m planar intersect transects. S.E.M. = standard error of the mean.	65
Table 4.1. Study site characteristics.	103
Table 4.2. Fire return intervals at the four study sites. Statistical analysis was carried out in three categories: (1) all fire years, including those represented by a single fire scar; (2) fire years in which 10% or more of the recording trees were scarred; and (3) fire years in which 25% or more of the recording trees were scarred. For those sites where a disruption of the long-term fire regime was identified (sites AV, CB, and SP), fire return intervals are presented both for the pre-disruption period as well as the full historical recording period.	104
Table 4.3. Seasonal distribution (number and percent) of fire scars at the four study sites based on the position of the fire injury within the scarred tree ring.	106
Table 4.4. Regional fire interval analysis comparing fire years over all four sites. The analysis period is 1797-1993.	107
Table 4.5. Major regional fire years based on the percentage of fire occurrence at the four study sites.	108

Table 4.6. Tree species encountered on the study sites. Nomenclature follows González et al. (1991).	109
Table 4.7. Forest structural characteristics (basal area and density) of living overstory trees and regeneneration density at the four study sites. Within-row means followed by different letters are significantly different ($p < .05$). $N = 30$ at all sites.	110
Table 4.8. Forest structural characteristics (basal area and density) of snags, dead/down trees, and cut stumps at the four study sites. Within-row means followed by different letters are significantly different (p < .05). N = 30 at all sites. "Recent" snags have intact bark and branches (condition class 3); "older" snags are in more advanced conditions of decay (condition classes 4 through 7).	111
Table 4.9. Dead woody biomass, forest floor, and herbaceous cover at the four study sites. Within-row means followed by different letters are significantly different $(p < .05)$. $N = 30$ at all sites.	113
Table 5.1. Tree species encountered on the study sites. Nomenclature follows González et al. (1991).	137
Table 5.2. Forest structure of live trees over 1.3 m on stem-mapped plots at sites AL $(n = 4)$, AV $(n = 4)$, and SP $(n = 2)$. S.E.M. = standard error of the mean.	138
Table 5.3. Forest structure of dead trees over 1.3 m on stem-mapped plots at sites AL $(n = 4)$, AV $(n = 4)$, and SP $(n = 2)$. S.E.M. = standard error of the mean.	139
Table 5.4. Density of trees under 1.3 m on stem-mapped plots at sites AL ($n = 4$), AV ($n = 4$), and SP ($n = 2$). S.E.M. = standard error of the mean.	140
Table 5.5. Spatial distribution [K(t)] of live trees under 1.3 m on stemmapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and () for dispersed patterns; blank values indicate random pattern. $N =$ number of trees. Tree groups not shown have $N < 20$. Asterisks indicate smaller plot size (* = 20 X 20 m, ** = 15 X 15 m) analyzed where $N >$ 1000 on the full plot; $n/a = t$ not applicable on plots smaller than 25 X 25 m.	141
Table 5.6. Spatial distribution [K(t)] of live trees over 1.3 m on stem-mapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and () for dispersed patterns; blank values	143

indicate random pattern. N = number of trees. Tree groups not shown have N < 20.

Table 5.7. Spatial distribution [K(t)] of dead trees on stem-mapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and (--) for dispersed patterns; blank values indicate random pattern. N = number of trees. Sites and tree groups not shown have N < 20. The dead/live group at site SP is the combination of recently killed trees and live trees. Asterisk indicates smaller plot size (15 X 15 m) analyzed where N > 1000 on the full plot; n/a = t not applicable on plots smaller than 25 X 25 m.

144

LIST OF FIGURES

Figure 2.1. Range of long-needled pines in North America.	36
Figure 3.1. Study area map showing fire scar and forest structure sampling locations.	66
Figure 3.2. Composite master fire chart for the Camp Navajo study area. Each horizontal line in the graph corresponds to a fire-scarred sample. Dashed lines show where the sample is not considered a recording tree (e.g., before the first fire scar forms), and continuous lines show recording periods. Fire dates are indicated by short vertical lines and the dates are displayed along the lower axis. Frequent fires were interrupted after 1883, the year in which the transcontinental railroad was completed across the northern edge of the study area. The top to bottom order of samples runs roughly from north to south.	67
Figure 3.3. 1883 and 1994/95 diameter distributions of all trees (labeled diameters are the endpoints of 5 cm dbh classes, n = 2981 trees).	68
Figure 3.4. Age distribution of living trees in 1994/95 showing tree center date at the 40 cm above-ground sampling height (labeled dates are the endpoints of 10 year classes, n = 718 trees aged).	69
Figure 3.5a. September 1, 1942, forest scene 3.5 km south of the study area (center of T21NR5ES20, view east). This scene is typical of many in the 1942 photo archives: a very open residual ponderosa pine stand with numerous scattered stumps and logs from railroad-logging in the 1920's. In the background, especially at right center, dense patches of small seedlings can be seen. The full crowns of the residual trees suggest that the stand was probably not very dense even prior to logging.	70
Figure 3.5b. August 15, 1995, scene from approximately the same location. A dense sapling to pole-sized ponderosa pine stand dominates the area. Grassy openings remain but herbaceous density appears to be substantially less than in 1942.	71
Figure 4.1. Map of study area and sampling site locations.	114
Figure 4.2. Map of forest sampling plots and fire scar sampling locations.	115
Figure 4.3a. Composite master fire chart for Site AV (Arroyo Verde). The last widespread fire at this site occurred in 1945. Fires in 1962 and 1986 were limited to the northwest corner of the study site.	116

Figure 4.3b. Composite master fire chart for Site CB (Cebadillas). Frequent fires were interrupted at this site after 1951. This forest area, supporting Abies and Pseudotsuga in addition to pine and oak, was the only study site to have undergone selective harvesting of pines (circa 1970).	117
Figure 4.3c. Composite master fire chart for Site SP (Salsipuedes). Frequent fires were interrupted at this site after 1955. After a fire-free period of 29 years, widespread fires returned in 1984 and 1993.	118
Figure 4.3d. Composite master fire chart for Site AL (Arroyo Laureles). This site has continued to burn frequently up to the present, although there is some evidence of fire regime changes in the twentieth century, notably the 14-year gap from 1951 to 1965.	119
Figure 4.4. Comparison of fire occurrence at all four study sites in three categories: (1) all fire years; (2) years in which 10% or more of recording samples were scarred; and (3) years in which 25% or more of recording samples were scarred at each site.	120
Figure 4.5. Live overstory tree diameter distribution at sites (a) AV (b) CB (c) SP and (d) AL.	121
Figure 4.6. Center date distribution of conifers over 6 cm dbh at sites (a) AV (b) CB (c) SP and (d) AL.	122
Figure 5.1. Map of study site and weather station locations.	145
Figure 5.2. Diameter distributions of living (white) and dead (black) trees at the three study sites. Labeled diameters are the upper endpoints of 10-cm classes.	146

DEDICATION

This dissertation is dedicated to my wife, Mary, my children, Cameron and Emily, and to my parents, Aurelia and Zoltan.

xiv

PREFACE

The dissertation contains manuscript chapters intended for publication in several journals. The manuscripts are chapter 3, "Determining reference conditions" (accepted by *Ecological Applications*), chapter 4, "Fire regimes and forest structure" (*Journal of Forestry* 94(10):33-38, 1996), and chapter 5, "Tree patterns." Wherever possible, the text has been edited to minimize redundancy between chapters due to the manuscript format. Because the manuscript chapters are collaborative publications, the plural pronoun "we" is used to refer to the authors.

1. INTRODUCTION

1.1 Fire regimes and forest structure

Fire is a keystone ecological process (sensu Holling 1992) in the long-needled pine forests of the western cordillera of North America. The evolutionary environment of these ecosystems was influenced by hot, dry, windy climates with dense lightning, favoring frequent fires. Long-needled pine ecosystems appear to have been self-regulating (sensu Perry 1995), with rapid production of continuous fine grasses and flammable leaf litter carrying fire, which in turn maintained relatively open forests and savannas in which the dominant pine and perennial grass species, well-adapted to resist low-intensity fire, thrived (Covington et al. 1994).

In the greater Southwest, the southern range of long-needled pines extends from Durango, Mexico, through Arizona and New Mexico, U.S.A. Fire occurrence north of the Mexican border declined sharply when large herds of domestic animals were introduced by Euro-American settlers in the late nineteenth century. Livestock consumed grasses and rapidly broke fuel continuity over virtually all southwestern U.S. forests, stopping most frequent fire regimes by 1900 A.D. (Swetnam and Baisan 1996). Shortly thereafter, a policy of complete fire suppression was adopted throughout the region. In northern Mexico, however, with a distinctly different cultural context, frequent fire regimes continued in many areas (Leopold 1937, Minnich et al. 1995). The research described here compares some effects of this far-reaching "unplanned experiment" in fire exclusion on related long-needled pine ecosystems in the greater Southwest in order to

develop information on ecological structure, function, and composition relevant to sustainable management of these ecosystems.

Concerns over deleterious changes, such as increasing tree density and wildfire severity associated with fire exclusion in the southwestern U.S., have increased through the twentieth century (Leopold 1937, Weaver 1951, Cooper 1960, Covington and Moore 1994a), coinciding with a broader rise in attention paid to a variety of ecological and environmental issues such as harvesting of old-growth trees, fragmentation of wildlife habitat, and changes in patterns of natural resource use by society. The contemporary paradigm of ecosystem management, adopted in recent years by both the scientific and management communities, seeks to perpetuate ecosystems by integrating ecological science and social interests (Kaufmann et al. 1994, Ecological Society of America 1996). Management decisions should be based on solid understanding of ecosystem reference conditions, that is, the range of variability in natural structure and function in the context of recent evolutionary history prior to impacts associated with industrial society (Morgan et al. 1994, Swanson et al. 1994). A reference is necessary to evaluate contemporary ecosystem conditions as well as the effects of alternative management actions (Kaufmann et al. 1994). Reference conditions can also serve as the target for ecological restoration of degraded ecosystems (Covington et al. in press).

Although most long-needled pine forests in the southwestern U.S. have been substantially altered by recent human activity, reference conditions of key ecological processes (e.g., the frequent-fire disturbance regime), and ecosystem structure (e.g., species composition, density, size, and age of trees), can be reconstructed through

retrospective dendroecological methods (Fritts and Swetnam 1989, Baisan and Swetnam 1990, Covington and Moore 1994a, Kaufmann et al. 1994). Application of these methods in a hierarchical sampling design over a northern Arizona, U.S.A., ponderosa pine landscape is the topic of chapter 3.

Intact ecosystems, where they remain, are invaluable points of reference for natural process and structure. The recent and sporadic initiation of fire exclusion in Mexico has created 'natural experiments' (sensu Carpenter 1990) where ecosystems under continuing frequent fire regimes may be compared with fire-excluded ecosystems. In chapters 4 and 5, several unharvested forest tracts in Durango, Mexico, measured in a consistent sampling and analysis design (Gosz 1992), are compared in terms of fire regime, forest structure, composition, and spatial pattern. Finally, the differences and parallels between the Arizona and Durango sites are discussed in chapter 6.

1.2 Research design questions

The goal of this research was to quantify patterns of fire occurrence and forest structure across a broad area of the southern range of long-needled pines, assess how structures and fire disturbance processes had changed, and develop some recommendations for sustainable management of these ecosystems. The initial questions in designing research about fire regimes and forest structure in long-needled pine ecosystems were: what are the important variables, which ones should be measured, and how? These questions structured the methodology, analysis, and limits of interpretation of the results. The research design, described in chapter 2, drew on the background of

existing knowledge about long-needled pine ecosystems, as well as consideration of hierarchy theory (O'Neill et al. 1986), the role of keystone structures and processes (Holling 1992), and concepts in large-scale environmental studies (Eberhardt and Thomas 1991), to address the following questions:

- (1) What were the temporal and spatial patterns of presettlement fire in a ponderosa pine forest of the southwestern U.S.? What was the presettlement forest structure and how has it changed?
- (2) What are past and present patterns of fire occurrence in long-needled pine ecosystems of northern Mexico representing a range of fire regimes, including continued frequent fire? Are forest structures correlated with recent changes in fire regime and do these relationships match the pattern of increasing forest density and fuel loading observed in the U.S.?
- (3) How can this information be applied to support sustainable management of long-needled pine ecosystems?

1.3 Significance

Quantitative measurements of changes in fire regimes and forest structure are essential baseline information for long-needled pine ecosystem management. Although several investigations of fire history and forest change have been carried out in the southwestern U.S. (e.g., Covington and Moore 1994a, Swetnam and Baisan 1996), studies are needed which link sampling of key disturbance regime and structural elements in a hierarchical framework, contributing to improving the procedures for determining

reference presettlement conditions (Kaufmann et al. 1994) and designing ecological restoration treatments (Covington et al. in press). Studies in northern Mexico focus on regions where scientific investigation, especially of the role of disturbance in forest dynamics, is almost nonexistent (González-Cabán and Sandberg 1989). Baseline information from unharvested forests will become increasingly valuable as these forests are harvested. Conservation of some intact ecosystems, which remains a possibility in this region of Mexico, will be aided by this quantitative data. The continuing evolution of fire policies in Mexico will also be served by evidence of the long-term role of frequent fire in long-needled temperate ecosystems, as the nation moves from an inadequately understood and inconsistently applied fire suppression policy (Rodríguez Trejo and Sierra Pineda 1992) toward fire management. Finally, the broad biogeographical approach taken here has added to a network of studies that are contributing to a clearer understanding of the relationship between ecological process and pattern (Levin 1992) in long-needled pine forests on a sub-continental scale.

2. LITERATURE REVIEW AND RESEARCH DESIGN

This chapter reviews the ecological and management context of the dissertation.

The role of fire in long-needled pine ecosystems of the greater Southwest, with particular attention to long-term fire exclusion in the U.S. and the contrasting patchy pattern of continuing frequent fire or recent fire exclusion in Mexico, is presented in section 2.1.

The next section (2.2) describes the ecosystem management paradigm, an integrated approach to sustainable management based on understanding of the evolutionary environment and historic reference conditions of ecosystems. In the final section (2.3), appropriate methods for landscape-scale research are presented and the specific research of chapters 3 through 5 is placed in a large-scale research perspective.

2.1 Fire in Western Long-Needled Pine Ecosystems

Ecosystems dominated by closely-related, long-needled pines dominate the western cordillera of North America in a nearly continuous band from southern Canada to northern Mexico (Figure 2.1). Members of the taxonomic section Ponderosae (or subsection, [Lauria 1991]), important species include ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), Durango pine (*P. durangensis*), Arizona pine (*P. arizonica*), and Apache pine (*P. engelmannii*) (Perry 1991). Beyond sharing a common evolutionary lineage, these species form an ecological group well-adapted to disturbance regimes of frequent, low-intensity fires (McCune 1988). Adaptations such as thick, insulating bark. protected growing buds, resilience to crown scorch, and the production of highly

flammable litter are interpreted as evidence that these species have evolved under the dry, windy conditions and frequent lightning of their mountainous habitats (Mutch 1970, McCune 1988). The following discussion is focused on the greater Southwest, a region defined here as extending further south than the area covered by Brown (1982) in order to match the southern range of the long-needled pines, roughly from Durango, Mexico, through southern Utah and Colorado, U.S. Many of the characteristic ecosystem responses to fire exclusion are analogous in the northern and Pacific coastal ranges of long-needled pines as well (Covington et al. 1994, Arno et al. 1995b, Minnich et al. 1995).

2.1.1 Southwestern U.S.

Frequent fire, recurring every 2 to 20 years in long-needled pine forests prior to Euro-American settlement (Weaver 1951, Biswell 1972, Kilgore 1981, Knight 1987, Swetnam and Betancourt 1990, Covington et al. 1994, Arno et al. 1995b, Swetnam and Baisan 1996), has played a key role in the evolution of the biota of these ecosystems. Frequent fires appear to be essential in southwestern ponderosa pine forests for maintaining open, park-like forests by controlling pine tree population irruptions and forest floor accumulations (Covington et al. 1994) and by maintaining high levels of nutrient availability (Covington and Sackett 1984, 1990). Flammability has even been hypothesized to be an adaptive characteristic favored by natural selection in ponderosa pine, producing traits such as long needles with high resin content and exceptionally slow decomposition rates (Hart et al. 1992), characteristics which facilitate frequent fires,

thereby reducing establishment of, and competition from, other trees less adapted to frequent fires (Mutch 1970, Bond and Midgley 1995).

Although Native Americans "settled" North America long before Euro-Americans, for the sake of brevity the term <u>presettlement</u> will be used here to refer to conditions prior to Euro-American settlement and the term <u>postsettlement</u> to refer to conditions after Euro-Americans began intensive alteration of the southwestern U.S. landscape in the late nineteenth century.

Presettlement long-needled pine fire regimes in the southwestern U.S. have been studied primarily through dendrochronological analysis of fire-scarred trees (Baisan and Swetnam 1990), supported by the limited historical and anecdotal record (Leopold 1924, Cooper 1960, Bahre 1985, 1991). In a comparison of fire-scar chronologies from 63 sites across Arizona and New Mexico, Swetnam and Baisan (1996) found that mean fire intervals (MFIs) between 1700 and 1990 A.D. ranged from 2.1 to 25.2 years with 80% of the sites having an MFI below 10 years. Considering only fire years in which 25% or more of the samples were scarred, probably representing larger or more intense fires, the MFI_{25%} ranged from 4.1 to 36.2 years. Fire occurrence was linked to regional climatic factors which synchronized fires at many sites in dry years. Wet climatic conditions, presumably encouraging herbaceous growth, were often followed in 2-3 years by large regional fires (Swetnam and Betancourt 1990). Human ignitions may have been locally important at specific times and places (Leopold 1937, Pyne 1982, Bahre 1985). However, Swetnam and Baisan (1996) argued that high lightning density was sufficient to ignite historical fires throughout most of the southwestern ponderosa pine types.

Many presettlement fires burned over large areas in the absence of fire suppression. Swetnam and Dieterich (1985) suggested that many presettlement fires in the Gila National Forest, New Mexico, burned over several thousand hectares. Woolsey (1911) reported that a 1910 fire in the same region covered 60 square miles (15,540 ha). Lang and Stewart (1910) described evidence of old fires of various sizes up to several square miles (1 square mile = 259 ha) on the Kaibab Plateau, Arizona.

Presettlement ponderosa and Jeffrey pine forests were relatively open in structure and dominated by large-diameter pines (Cooper 1960, Covington et al. 1994, Covington and Moore 1994a,b, Arno et al. 1995b, Minnich et al. 1995). Covington and Moore (1994b) compared forest densities reported in early forest inventories and retrospective studies in Arizona, New Mexico, and southern Utah, ranging from 7 to 116 pines/ha. Arno et al. (1995b) found higher densities, from 116 to 290 trees/ha, in reconstructions of pre-1900 Montana ponderosa pine/Douglas-fir forests. Perennial grasses and other herbaceous plants and shrubs dominated the presettlement forest understories in the southwestern U.S., carrying the flaming front of low-intensity fires and helping to limit tree regeneration (Cooper 1960, White 1985, Covington and Moore 1994a).

Soon after Euro-American settlement of the southwestern U.S. in the 1870-1890 period, heavy livestock grazing broke grass fuel continuity and eliminated the presettlement fire regime through most of the ponderosa pine type (Cooper 1960, Dieterich 1980, Swetnam and Baisan 1996). Subsequent fire suppression practices maintained fire exclusion in most forests until the present, except for sites burned under prescription and the increasing area burned by wildfire (Swetnam 1990). Pine ecosystems

adapted to short-return-interval disturbance regimes have been quick to show the effects of disturbance regime disruption (Leopold 1937, Weaver 1951, Covington et al. 1994).

Substantial changes have occurred following fire exclusion, including: (1) an increase in density of small diameter trees; (2) a decrease in herbaceous and shrub production; (3) accumulation of pine litter as forest floor fuels; (4) disruption of nutrient cycling as nutrients remain in the forest floor and unavailable to plants; (5) increased crown fuel loading and increased crown closure; (6) increased fuel ladders or vertical fuel continuity; (7) increased patch and landscape crownfire hazard and occurrence; (8) decreased tree vigor; (9) increased tree mortality from pathogens which attack trees of low vigor; (10) increased dominance by tree species less-adapted to frequent fire, including fir (*Abies*) and Douglas-fir (*Pseudotsuga*) on mesic sites and oak (*Quercus*) on xeric sites (Cooper 1960, Covington and Sackett 1984, Swetnam 1990, Covington et al. 1994, Covington and Moore 1994a,b, Kolb et al. 1994, Barton 1995, Minnich 1995, Wilson and Tkacz 1995, Swetnam and Baisan 1996).

Increased tree density and the cessation of fires were welcomed by forest managers early in the 20th century (Covington et al. 1994), particularly because the "understocked" condition of the presettlement forest had been blamed on frequent fires (Lang and Stewart 1910, Woolsey 1911), but the deleterious character of many of the forest changes were soon recognized (Leopold 1924, Weaver 1951, Cooper 1960, 1961). Increasing size and severity of wildfires (Swetnam 1990, Swetnam and Betancourt 1990) has raised concern among land managers and the public. The drought of 1995-96 led to several of the largest and most intense fires in the recorded history of the southwestern

U.S., including the Bridger and Hochderffer fires in northern Arizona and the Dome and Hondo fires in northern New Mexico.

Acknowledging the extent of ecosystem problems (Covington et al. 1994, Jensen and Bourgeron 1994, Kaufmann et al. 1994), current research and management approaches include evaluation of ecosystem health in the context of the evolutionary environment (Kolb et al. 1994) and restoration of structure and function in some pine ecosystems to emulate historic reference conditions (Covington and Moore 1994a, Covington et al. in press) within the framework of ecosystem management (Kaufmann et al. 1994), the prevailing contemporary land management paradigm. These approaches are discussed in section 2.2 below.

2.1.2 Northern Mexico

Although temperate long-needled pine forests of northern Mexico are composed of fire-adapted species closely related to those further north, and thousands of fires burn each year in the Mexican mountains, high-intensity crownfires remain rare (González-Cabán and Sandberg 1989, SARH 1994). Why does the ecosystem which extends seamlessly across political boundaries exhibit such different characteristics north and south of the border?

Fire plays an important ecological role in the forests of northern Mexico. Within these diverse but little-studied ecosystems are areas where frequent, low-intensity fires have continued up to the present, or where fire regime disruption has only recently begun. These forests have great potential for long-term conservation of ecological processes,

such as fire disturbance regimes, together with ecosystem structures. Furthermore, the Mexican forests can serve as one benchmark for the ecological restoration of related fire-adapted forests elsewhere in North America.

In northern Mexico, long-needled pine forests follow the upper elevations of the Sierra Madre Occidental (Martínez 1948, Perry 1991). This mountain range begins in the "sky islands", or Madrean archipelago, of isolated peaks in southern Arizona, then consolidates into a broad, high landmass dissected by steep canyons and river valleys through the states of Chihuahua and Durango, merging into the central Mexican highlands further south. On the western slopes of the range, down to the Pacific coastal plain in Sonora, Sinaloa, and Nayarit, dams provide water for intensive irrigated agriculture. In the rain shadow to the east lie dry foothills and desert. There are no large cities in the Sierra, but the resources of the mountain range, primarily water but also mineral mining, timber, livestock grazing, and other agricultural production, are essential to the economy of northern Mexico. Considered over evolutionary time, the mountain range has been a corridor to connect temperate and tropical ecosystems of North America, serving as a migratory pathway and a center of endemism (Perry 1991, Manuel and de Jesús 1993, Felger and Wilson 1995).

Despite many similarities, the long-needled pine forests of northern Mexico are also distinct from the related ecosystems farther north. First, a wealth of biological diversity exists in the Madrean forests (Felger and Wilson 1995). Combining the tropical influences of the southern latitude with the great elevational gradients of the canyons, highly diverse ecosystems flourish in the Sierra Madre. Twenty or more overstory tree

species may occur in an area of a few hectares: seven or eight species of pines, a similar number of oaks, and other trees including alder (*Alnus*), aspen (*Populus*), juniper (*Juniperus*) and madrone (*Arbutus*). In this respect, the Sierra Madre is a microcosm of Mexico, one of the three most biologically diverse nations with approximately half the world's species in the genera *Pinus* and *Quercus* (Perry 1991, Nixon 1993, Felger and Wilson 1995). Taken as a whole, plant communities of the Madrean pine-oak forests are considered comparable in species richness to tropical rainforests and contain numerous plants with valuable medicinal properties (Felger and Wilson 1995).

A second important distinction between Madrean forests and those farther north is the persistence of frequent, low-intensity fire regimes. While lightning has continued on both sides of the border, the cultural context in which humans interact with ecosystems has been quite different in northern Mexico than in the U.S. and Canada.

Indigenous peoples have lived in the Sierra Madre Occidental for thousands of years. The two prominent groups of the forested highlands were the Tarahumara (Rarámuri) people, of present-day Chihuahua, and the Tepehuán people further south (Pennington 1963, 1969, Gerhard 1982). Among the adaptations these people made to life in a fire-prone ecosystem was the frequent application of fire. Traditional uses of fire included clearing of agricultural plots, flushing animals from cover, and warfare (Pennington 1963, 1969), similar to Apache and other Native American uses of fire in the southwestern U.S. (Bahre 1985).

Spanish influence came early to the Sierra Madre because of its famous mineral riches: gold, silver, and copper. Spanish towns and mines were established as long as 400

years ago. Except where minerals were discovered, the Spanish were not interested in colonizing the inhospitable Sierra; European diseases such as smallpox, however, spread more rapidly than armies among the indigenous populations. The indigenous population of north-central Durango, for example, declined by 95% in the first two centuries following contact with Europeans (Gerhard 1982). The less accessible areas of the Sierra Madre remained sparsely populated well into the twentieth century. Large tracts were finally settled in the twentieth century as *ejidos*, communally-held land grants.

Spanish and Mexican settlers continued to apply fire in the Madrean forests, using fire to clear fields and spur herbaceous growth. These fires generally spread into the woods, in addition to fires started by lightning, cooking and campfires, and cigarettes (see González-Caban and Sandberg [1989] for discussion of human-caused fires in Mexico). Until recently, little attention has been paid to fire suppression, probably for a combination of reasons. From the perspective of miners, farmers, and ranchers, the effects of fire in reducing tree density and fertilizing herbaceous growth are highly positive. The trees themselves were often not especially valued, since little infrastructure existed for timber extraction, and in any event neither the government nor the local populations had the economic resources to train, equip, and pay wildland firefighters. A similar lack of infrastructure and investment kept the mountains (though not the valleys) of northern Mexico free from the immense herds of cattle and sheep which were introduced to Arizona and New Mexico following the railroads (Leopold 1937).

The traditional Mexican attitude toward wildfire contrasted sharply with the concerns of Anglo-American settlers in the western U.S., especially after the

establishment of the Forest Service. Under Gifford Pinchot and his successors, the new agency decried the devastating effects of wildfire and seized upon fire control as a defining symbol of the forestry profession, applying extensive government resources to the task (Pyne 1982).

Differences between Mexican and American policies were apparent early on. In 1937 (p. 119) Aldo Leopold contrasted the open forests, lush grasslands, and flowing streams of the Chihuahua mountains with the dense trees, heavy fuels, and dry, eroded soils of the southwestern U.S., commenting that the "Sierras burn over every few years. There are no ill effects...But the watersheds are intact, whereas our own watersheds, sedulously protected from fire, but mercilessly grazed before the forests were created, and much too hard since, are a wreck." Twenty-five years later, Joe Marshall (1962:76) reinforced Leopold's observations, saying:

"If we grant that this contrast is too abrupt and too coincident with the international boundary to be due exclusively to climate, then we must look for man-made causes of the difference in vegetation. The outstanding cause seems to be fire... There has until very recently been no protection on the Mexico side from naturally occurring fires. These sweep through the grass, killing young junipers, eliminating debris, and leaving unscathed the tall clear trunks of the widely spaced pines."

Although ecologists have commented on the importance of fire in forested ecosystems of northern Mexico for some time, relatively few studies have been done to quantify the forest structures and disturbance regimes (Gonzáles-Cabán and Sandberg 1989, Rodríguez Trejo and Sierra Pineda 1992). Most data comes from sites adjacent to the U.S. border. Frequent fires, with a mean fire return interval (MFI) around 4 years, continued up the 1970's in the Sierra de los Ajos of Sonora, just south of the Arizona border (Dieterich 1983a, Baisan and Swetnam 1994). Minnich (1983) compared

chaparral ecosystems in southern California and northern Baja California, showing that fire exclusion on the U.S. side had created vast contiguous fuelbeds of mature, flammable chaparral, in contrast to the mosaic of fuel patches maintained by frequent small fires in Mexico.

Most recently, Minnich et al. (1995) compared coniferous forests in the San Bernadino Mountains (California, U.S.) with similar forests of the Sierra San Pedro Mártir (Baja California Norte, Mexico). Density of trees over 12 cm diameter at breast height increased nearly 80% since an early 1929-35 forest survey and species composition changed from dominance by pines to *Abies* and *Calocedrus* in the fire-excluded U.S. forest. The Mexican forest, where unmanaged fire regimes continued, remained relatively open and dominated by pines. Minnich et al. (1995) recommended restoration of historic forest structure to reverse the decline in native bird habitat and increased risk of high-intensity fire in the U.S. forest, as well as conservation of the frequent fire regime in the Mexican forest.

2.2 Ecosystem Management

Ecosystem management is an attempt to deal with the complexity and dynamics of nature and society by making decisions which integrate ecological science and human welfare to sustain the function, structure, and composition of ecosystems. Definitions of ecosystem management are themselves complex; the Ecological Society of America (1996) lists eight principal elements: (1) intergenerational <u>sustainability</u>; (2) measurable goals; (3) sound <u>ecological models and understanding</u>; (4) <u>complexity</u> (diversity) and

connectedness; (5) dynamic character of ecosystems; (6) context and scale; (7) humans as ecosystem components; and (8) adaptability and accountability. Lackey (1995) stressed the role of humans in setting values and priorities, while Kaufmann et al. (1994) argued for sustaining natural ecosystem structures and processes, but both concurred that ecosystem management has evolved from past land management practices, rather than representing a radical or novel departure.

The model methodology suggested for implementing ecosystem management is the adaptive management design (Walters 1986, Walters and Holling 1990, Kaufmann et al. 1994, Ecological Society of America 1996). Adaptive management recognizes that actions are undertaken in an environment of uncertainty. Rather than adopt a "trial and error" approach or rely exclusively on the best information that happens to be available when the initial management decision is made, Walters and Holling (1990) argue that the superior method is an active adaptive approach in which deliberate monitoring and evaluation feed back into ongoing management activities. This "learning by doing" approach integrates research and management efforts.

Kaufmann et al. (1994) presented an analytic framework for assessing ecosystem characteristics needed for sustainable management, including: (1) determining hierarchical spatial and temporal scales of ecosystems, (2) identifying key structural patterns and processes at various scales, and (3) comparing contemporary patterns and processes to historic reference conditions. Management alternatives can be evaluated in terms of their relative departure from reference conditions, or ecological restoration to reference conditions can be a goal of management. The next sections outline the

characteristics of southwestern long-needled pine ecosystems within this analytic framework.

2.2.1 Hierarchical scaling

Hierarchical ecological structures can be defined in space and time (Delcourt and Delcourt 1988) but are often ignored or treated as an unchanging "background" in ecological research (Gosz 1992). To the considerable extent that ecological knowledge is advanced by detailed study of interactions among one or a few variables on small plots over short periods of time, scale considerations may be avoided. To address the sustainability of long-needled pine ecosystems, however, management alternatives must be evaluated for ecosystems covering millions of hectares, composed of species with a recent evolutionary history extending back thousands to millions of years (Millar 1993). Furthermore, these ecosystems occur in landscapes which have already been subjected to a massive unplanned experiment (sensu Carpenter 1990) in the form of fire exclusion and other changes associated with Euro-American settlement.

A general hierarchy of spatial and temporal scales can be briefly outlined for long-needled pine ecosystems. The broadest spatial scale is the range of long-needled pines, from northern Mexico to southwestern Canada. In the greater Southwest, comprising roughly the southern half of this area, long-needled pines dominate forest vegetation at mid to upper elevations. Both natural and cultural differences divide the Southwest. First, from north going south, growing seasons lengthen and species diversity increases. Second, nearly ubiquitous grazing and fire exclusion began in the late nineteenth century

on the U.S. side, but generally later and in more sporadic fashion on the Mexican side. Inside the overall boundaries of the pine-dominated area are meadows, sagebrush or shrub communities, "stringers" of xeric pinyon and juniper woodland or mesic mixed conifer forest, and stands of oaks, aspen, locust, or alder. Pine-dominated stands themselves are clumpy with varying species, densities, and sizes of trees. Individual plants may range in size from 30-m dominants to seedlings. Sub-plant scales include leaves, stems, and roots, with the finest definable spatial scales probably occurring at the level of soil biochemistry. Disturbance patterns vary in scale from fires that may cover the entire forest, to small patchy fires or clumps of bark beetle mortality, down to individual mortality of plants or plant parts (defoliation).

The evolutionary history of long-needled pine ecosystems, extending back to the Mesozoic, is believed to be strongly associated with the development of seasonality and mountain-building, creating new arid environments (Axelrod 1986, Millar 1993).

Although the Mexican mountains served as pine refugia and centers of speciation since the Eocene (Axelrod 1986, Millar 1993), ponderosa pine appeared in the southwestern U.S. in the Holocene period (past 10,000 years), a time characterized by glacial retreat and northward and upward colonization of long-needled pines (Anderson 1989).

Climatic fluctuations during the Holocene isolated many higher-elevation southwestern ecosystems from related forests, creating "sky islands" of varying size (e.g., Kaibab Plateau, Mt. Trumbull), while other ranges remained connected (e.g., Sangre de Cristo, Sierra Madre Occidental). Time periods associated with biological activities range from 600+ years (tree lifespans, perhaps effectively much longer for clonal species), to 20-40

year pulses of pine establishment, to years to decades lifespans of understory plants and dominant animals. Organisms are affected by seasonal and daily change, with the finest definable scales ranging down to the rates of chemical processes (photosynthesis, combustion). Disturbance patterns also have varying cycles in a hierarchy of time, ranging from daily and seasonal changes (fire behavior, fire season), to annual or multi-year occurrence (fire frequency), to large-scale patterns related to multi-year or multi-century climate patterns (Swetnam and Betancourt 1990, Swetnam 1993). Some insect disturbance patterns are similarly cyclic (Myers 1988, Swetnam and Lynch 1993).

Trophic hierarchies can be defined at differing levels of detail as well, ranging from a broad general view (autotroph-herbivore-predator-detritivore) to an extremely fine separation of subspecies and races. At the finest level of detail there are likely to be organisms which have never been identified (fungi, microorganisms). An intermediate trophic categorization may be based on functional attributes, e.g., aggregating animals into guilds based on their feeding behavior.

Can appropriate and practical studies be designed to address the overwhelming diversity of ecosystems? This question is not only of theoretical interest. Ecologists have tended to focus on particular ecosystem attributes, usually framed by the scales of human perception and often drawing arbitrary distinctions between structural and functional characteristics (O'Neill et al. 1986).

Hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) has been proposed as an organizing ecosystem paradigm. Ecosystems are composed of interdependent entities aggregated at varying levels, in which the numerous, fast processes at one level (e.g., leaf

photosynthesis) collectively comprise the fewer, slower processes at the next level (e.g., individual plant production). In turn, the higher levels (e.g., climate) constrain the lower ones (e.g., plant distribution). O'Neill et al. (1986) present a theoretical approach to hierarchical classification based on differences in the rates of processes, suggesting that sharp rate differences occur at natural hierarchical breaks, such as the skin of an animal or the boundary of a plant distribution. Patterns which appear heterogeneous or nonequilibrium at one scale may appear to be in equilibrium when aggregated at a higher scale (O'Neill et al. 1986, Levin 1992).

2.2.2 Keystone processes and structures

An understanding of the fact that there can be no inherently correct scale at which to view the hierarchical assemblage of ecosystems (O'Neill et al. 1986, Levin 1992) can help place subjective choices of scale in the context of alternative possibilities (Frost et al. 1988); we select scales appropriate to the questions of interest. Holling (1992) argued that certain scales and ecological thresholds are controlled by a small group of keystone organisms and abiotic processes. This structuring set, in turn, strongly affects its own environment and entrains the other members of the community. Dominant species and predominant contagious disturbance regimes maintain this self-reinforcing (Perry 1995) hierarchical pattern of ecosystem structure and function across the landscape at the mesoscales in between the small-scale biochemical and individual organism processes and the large-scale climatic and geomorphological processes (Holling 1992).

Furthermore, structuring organisms and processes tend to be clustered at characteristic

spatial scales and temporal frequencies. Imbalances in the system—such as exclusion of disturbance—can culminate at a critical reorganization threshold in which the fast, lower-level processes overwhelm the slow, higher-level processes and convert the system to a different stable form (Gosz 1992, Holling 1992, Turner et al. 1994), as when a high-intensity fire in accumulated fuels kills dominants adapted to frequent, low-intensity fire, thereby converting the forest to shrubland.

Despite much recent attention to theories of ecological hierarchies and keystone variables, the complexity and dynamics of natural systems remain difficult to categorize. Holling (1996:734) emphasized that scaling relationships are nonlinear, that destabilizing forces frequently move ecosystems far from equilibrium, and that "knowledge of the system we deal with is always incomplete. Surprise is inevitable." In light of such uncertainty, I feel that the following discussion of key variables and scales for longneedled pine ecosystems is a logical, but necessarily incomplete, list. Long-term monitoring and adaptive research and management practices remain essential to permit flexibility in the face of new knowledge or changes in the environmental or social context (Holling 1996).

In long-needled pine ecosystems, the predominant contagious disturbance process, fire, is a key variable. Disturbance forces which may be less ubiquitous but have locally important effects on dominant trees include bark beetles (e.g., *Dendroctonus* spp.), defoliators (e.g., sawflies, pandora moth), parasites (e.g., dwarf mistletoe), disease (e.g., *Armillaria*, *Annosus*), and abiotic mortality agents (e.g., lightning, windthrow). In recent times, the disturbance force with the greatest impact is human impact (Holling 1992).

Human activities appear to be the major underlying cause of fire exclusion and large-scale ecosystem changes over the past century in long-needled pines. Similarly, dominant structuring organisms can be identified (e.g., pines, oaks, perennial grasses) as well as entrained organisms (e.g., many herbaceous plants, insects, vertebrates). Holling (1992) notes that these distinctions do not reflect relative ecological importance (nor are ecological roles fully understood), but keystone structures and processes should form the core of ecosystem measurements.

Scales of study should be related to the relevant spatial scales of the key variables (e.g., pine distribution, fire size) as well as the temporal scales (slowest organismic variable in the system, e.g., 600+ year age of oldest trees). It may not be possible to distinguish effects of ecological changes on organisms which range at scales beyond the maximum extent of the long-needled pine ecosystems, such as large herbivores, carnivores, or raptors. Frost et al. (1988) define a third scale, degree of resolution, showing that errors can arise when variables are inappropriately aggregated. Such errors must be weighed against the inefficiency or impossibility of exhaustive measurement. In general, the larger the scale of investigation, the fewer variables are needed for prediction (Frost et al. 1988) and in fact excessive detail can obscure important cross-scale patterns (Levin 1992).

2.2.3 Reference conditions

Reference conditions are the historic pattern of ecosystem structure and function, usually prior to large-scale alteration by industrial human society. The range of

variability in reference conditions can serve either as a goal for ecosystem restoration or as a point of comparison to evaluate how far contemporary or forecast ecosystem conditions have diverged from the historic state (Swanson et al. 1994, Morgan et al. 1994). "Historic" does not refer to the human historical record but to specific conditions that existed in the past; the term "natural range of variability" has been used synonymously (Swanson et al. 1994, Morgan et al. 1994). Threats to conservation of biological diversity of the plants and animals which evolved together in a specific ecological context increase when ecosystem conditions become far removed from the range of historic variability (Swanson et al. 1994). In contrast, management actions which tend to restore reference conditions are believed to generally benefit the assemblage of species, although this "coarse-filter" approach may have to be supplemented by "fine-filter" species-specific actions for rare or threatened species (Swanson et al. 1994, Bourgeron and Jensen 1994).

The concept of forest ecosystem health is a useful complement to the idea of reference conditions. A utilitarian definition of forest health, representing the traditional approach of "forest protection," is that a healthy forest is one which achieves management goals. Wagner (1993) pointed out that this view is tautological if maintenance of a healthy forest is taken as a management goal. Kolb et al. (1994) developed an ecologically-based definition with four essential characteristics of a healthy forest: (1) the presence of the physical, biological, and trophic elements of the ecosystem: (2) resistance to catastrophic change; (3) functional equilibrium of supply and demand for essential resources: (4) diversity in seral stages and habitats. They argued that

historic reference conditions of long-needled pine ecosystems met these criteria, but contemporary southwestern ponderosa pine forests fit only the first characteristic of a healthy forest.

The use of adjectives such as "healthy" or "degraded" to describe ecosystems has been criticized by Lackey (1995), who argued that such terms are "value-laden" and misleading unless evaluated in terms of a benchmark, a defined desired condition set by society. To the degree supported by the available evidence, reference conditions comprise such a quantitative benchmark, permitting assessment of relative ecosystem health or degradation.

To determine reference conditions where no intact or undisrupted ecosystems are available for study, as is essentially the case for long-needled pine ecosystems in the U.S. except for isolated patches (e.g., Madany and West 1983, Grissino-Mayer 1995), Kaufmann et al. (1994) and Covington and Moore (1992, 1994a) recommended using multiple intersecting lines of evidence to reconstruct past conditions. For example, dendroecological reconstructions of the intensity, frequency, and size of past disturbance events (e.g., Veblen et al. 1994, Swetnam et al. 1995) or patterns of forest structure (e.g., Covington and Moore 1994a) provide quantitative estimates of historic conditions. Such data should be compared with independent data from historic photos (e.g., Veblen and Lorenz 1991), early inventory data (e.g., Minnich 1995), anecdotal or historical accounts (e.g., Cooper 1960, Bahre 1991), and contemporary measurement of sites where ecosystem structure and function remain intact (e.g., Minnich 1995).

Quantitative estimates of historic ecosystem structure can conflict with theoretical conditions or those extrapolated from other ecosystems. In southwestern ponderosa pine forests, for example, "old-growth stands" have been described as including old trees but also characterized by other characteristic features of mesic oldgrowth forests of the Pacific Northwest such as multi-layered canopies, relatively dense growth and canopy closure, and abundant snags and downed material (e.g., Moir and Dieterich 1988, Moir 1992, Mehl 1992). Although dense multi-layered canopies and heavy dead organic matter accumulations do exist in contemporary ponderosa pine forests, Covington and Moore (1992, 1994b) argued that the well-documented disruption in frequent fire regimes and subsequent increase in tree density have created a contemporary forest quite different from any which existed on a broad scale over the previous evolutionary history of ponderosa pine ecosystems. They go on to state that closed-canopy stands with high snag densities and heavy loadings of dead woody material are more likely to be an artifact of fire exclusion than representative of natural conditions in presettlement forests. Adoption of an inappropriate or inaccurate reference condition could cause substantial harm, because dense ponderosa forests are likely to be unsustainable over the long term, despite the best efforts of managers, due to their vulnerability to high-intensity fire or biological pathogens (Covington et al. 1994, Kolb et al. 1994).

The value of reference conditions as a key concept of ecosystem management has been questioned in two ways. First, few ecosystems have escaped substantial recent human impact, such as fire exclusion, (Swanson et al. 1994) and pre-industrial human

activities have influenced some evolutionary environments for tens of thousands of years (e.g., aboriginal burning in Australia [Pyne 1995]). Even where direct human impact has been minimal, certain ecosystem elements have probably been lost (e.g., Mexican wolf), exotic elements have been added (e.g., *Tamarix, Verbascum, Linaria*), and changes in climate and atmospheric composition may affect ecosystem structure and function (Kaufmann et al. 1994, Covington et al. 1994, Hobbs and Norton 1996). However, although natural areas are "less than pristine" and historical data or reconstruction methods are imperfect, they still comprise the best baseline data source available (Ecological Society of America 1996). A second concern is that rigid application of a reference historical condition may impose a static snapshot as an unrealistic and unreproducible baseline for contemporary management (Hobbs and Norton 1996). In the absence of examples, this problem may be mostly hypothetical. In practice, research has focused on variability in historical conditions, including dynamics of past disturbance regimes and ecosystem structural change (Veblen et al. 1994, Morgan et al. 1994).

2.2.4 Ecological restoration

The science and practice of ecological restoration, "reestablishing to the extent possible the structure, function, and integrity of indigenous ecosystems and the sustaining habitats that they provide" (Clewell et al. 1993:206), can be an important component of ecosystem management of long-needled pine forests in several ways (Covington and Moore 1994a). First, by recreating "a sample of what we had to begin with" (Leopold 1934), restoration to historic conditions prior to fire regime disruption can provide a

living example of reference conditions, serving as a scientific resource and an ecological baseline for evaluating management alternatives. Second, restoration can help sustain species not adapted to novel ecosystem characteristics such as dense forests and high-intensity fires. Third, restoration has high value for human society by enhancing the resource value and aesthetic appeal of long-needled pine forests, reducing the threat of crownfire and the costs of firefighting, and providing the mechanism to achieve the mandate of park and wilderness management for natural conditions.

The restoration process, summarized by MacMahon and Jordan (1994), begins with acknowledging that human activity has altered an ecosystem. After deciding to restore a specific historic condition, deliberate management intervention is required to recreate, as far as possible, the structure and function of the ecosystem. The need to intervene differentiates restoration from recovery, a more passive process in which the stressing factors which are causing ecosystem degradation are removed (e.g., remove grazing livestock), allowing the ecosystem to recover on its own.

The same criticisms leveled at the concept of reference conditions (section 2.2.3 above) have been applied to ecological restoration: first, ecosystems have changed irrevocably due to extinctions, atmospheric change, etc., and second, restoration to a static "target" condition is unrealistic (Hobbs and Norton 1996). The spectrum of views on restoration ranges from close adherence to pre-degradation reference conditions (Morgan et al. 1994, Swanson et al. 1995) to acceptance of a relatively broad range of reference conditions considered generally suitable and desirable for the site (Hobbs and Norton 1996).

Ecological restoration is a relatively new concept in management of long-needled pine forests and different approaches are being tried. Covington et al. (in press) treated a 3.2 ha ponderosa pine forest in northern Arizona by closely following reconstructed reference conditions in 1876, prior to fire exclusion. The approach involved conserving living presettlement trees, removing most postsettlement trees but retaining replacements for dead presettlement trees (snags, downed trees, stumps), removing accumulated forest floor fuels, creating a fuelbed of mown native grasses and pine litter, and then reintroducing fire. A subsequent operational-scale treatment has been initiated in northwestern Arizona (W.W. Covington, M.M. Moore, and P.Z. Fulé, unpublished data). Other treatments have not intensively emulated reference conditions, seeking in more general terms to re-introduce fire (Harrington 1996, Sackett et al. 1996) or to apply silvicultural techniques to create tree densities and age distributions relatively similar to those of presettlement forests (Fiedler 1996, Fiedler et al. 1996).

2.3 Large-scale research

Useful research and effective management must address the broad spatial and temporal scales of ecosystems. However, adherence to traditional experimental methodology can limit both the ability of investigators to draw conclusions from large-scale unplanned experiments and their ability to design planned ecosystem-level experiments (Carpenter 1990, Walters and Holling 1990, Eberhardt and Thomas 1991). Several options proposed for dealing with the analysis of large-scale experiments are

discussed in section 2.3.1. Application of selected methods to the specific dissertation studies is presented in the final section, 2.3.2.

2.3.1 Methodology

Eberhardt and Thomas (1991) categorized environmental studies along a spectrum from analytical experiments, where replicated events are controlled by the observer and strong statistical cause-and-effect inference is possible, to descriptive sampling, where measurements following uncontrolled events provide weak to nonexistent support for causal inference. In the middle of this statistical hierarchy lies "intervention analysis" of distinct, uncontrolled treatments, also called natural or unplanned experiments (Carpenter 1990). A variety of relatively complicated statistical procedures may be required to draw inferences from unreplicated perturbations (Eberhardt and Thomas 1991, Stewart-Oaten et al. 1992). However, Stewart-Oaten et al. (1992:1402) stress that "the important questions are how large the effects are, and whether they matter. The main statistical tasks are estimating effect sizes and estimating the precision of these estimates, not hypothesis testing."

Randomized, replicated experimental designs provide the strongest evidence for statistical inference (Carpenter 1990), although even these experimental designs may not prove useful if the manipulated samples or the range of treatments are not adequately representative of the broad range of conditions (Frost et al. 1988). Even when replicated experimentation is possible, baseline information should be collected outside the experimental area to provide a context in which the experimental results may be viewed

(Frost et al. 1988, Eberhardt and Thomas 1991, Morgan et al. 1994). The high cost of large-scale replication often limits experimenters to only two or a few replicates, greatly diminishing the power of statistical tests. Eberhardt and Thomas (1991) note that investigators in this situation should consider adopting a higher alpha level in order to increase power. Otherwise the low power of experiments with few replicates makes it unlikely that a reasonable level of treatment effect can be detected (Eberhardt and Thomas 1991).

At large scales, experimental replication becomes impractical or impossible either because of cost constraints or because of the ubiquitous nature of the treatment, such as air pollution increases or whole-lake studies (Frost et al. 1988, Carpenter 1990).

Carpenter (1990) offers two possibilities for evaluating effects of large-scale perturbations. First, intervention analysis demonstrates change over time, without the capability to infer cause-and-effect. Inferences can be substantially strengthened by obtaining measurements before as well as after the treatment, especially on paired treated and control sites as described below (Eberhardt and Thomas 1991, Stewart-Oaten et al. 1992). Second, Bayesian statistical methods can also support causal inference. In Bayesian methods a pre-treatment prior probability is assigned to the outcomes suggested by alternative hypotheses, reflecting previous knowledge or intuition about the likelihood of each outcome (Iversen 1984). The post-treatment posterior probability applies to the specific event studied, rather than to a population of similar events as in traditional statistical inference (Iversen 1984).

Comparison with one or preferably several untreated areas is a third approach to the analysis of large-scale experiments (Frost et al. 1988). No within-treatment error term exists, but the multiple comparison can help support the argument for a treatment effect. If treated areas are paired with untreated controls and pre-treatment baseline data collected, the treatment effect can be assessed in terms of altered ratios among the pairs following treatment (Eberhardt and Thomas 1991). This "station-pairs" design can be applied either to unreplicated experiments (the treatment was controlled by the investigator) or to intervention analysis (a definable treatment occurred outside the investigator's control) (Eberhardt and Thomas 1991, Stewart-Oaten et al. 1992). As an extension of the multiple comparison idea, a variety of experimental or observational studies across a broad region or over a period of time can be analyzed jointly. The cumulative result may provide evidence for changes which appear more subtle in the individual studies (Gosz 1992) or even lead to the reassessment of some of the individual study conclusions (Eberhardt and Thomas 1991). Such comparisons are particularly powerful if common sampling designs and methods were used in the individual studies (Gosz 1992).

A final consideration is the scaling relationship among ecosystem components (Levin 1992). Hierarchy theory suggests that spatial extent of sampling should match that of the key structures and processes of interest (Frost et al. 1988). Taking advantage of the spatial autocorrelation of most ecological communities (Rossi et al. 1992), spatial information can be applied to interpolate measured ecosystem characteristics across larger scales. Mapped data can be analyzed from the point-pattern level, to investigate small-

scale interactions and ecological processes (Kenkel 1988, Duncan 1991), up to landscape scales (Turner and Gardner 1991). Where the sample data set is sufficiently large, spatially dense, and detailed enough for modeling, interpolation methods such as kriging and stochastic simulation (Deutsch and Journel 1992) can be used to map ecosystem variability at large scales.

2.3.2 Conceptual research approach

The goal of this research was to quantify patterns of fire occurrence and forest structure across a broad area of the southern range of long-needled pines, assess how structures and fire disturbance processes have changed, and develop some recommendations for sustainable management of these ecosystems. Within the limits of available time and resources, and considering hierarchical scales and keystone variables, this project was designed to meet this goal and lay the foundation for future work. This section summarizes the research concept in terms of the discussion of ecological, management, and theoretical considerations presented above. Methodological details, as distinct from the conceptual design, are presented in the individual Chapters 3 through 5.

The U.S./Mexico border divides the greater Southwest into regions of distinctly different human cultures. For the long-needled pines, this division has created a vast "natural experiment" in which the exclusion of frequent fire has been a drastic change in the natural disturbance regime in virtually all the U.S. forests. At the broadest biogeographical scale of this hierarchy, two approaches were selected to examine the effects of this treatment. First, reference conditions prior to fire exclusion were

reconstructed in a ponderosa pine forest in northern Arizona, U.S.A., and compared with contemporary conditions in the analytical framework of ecosystem management (Kaufmann et al. 1994) (Chapter 3). Second, a related ecosystem was sampled in northern Durango, Mexico, which contained unharvested tracts representing several different recent fire regimes, including a site with an uninterrupted frequent fire regime (Chapters 4 and 5). Reference conditions at this site can therefore be measured directly in an intact ecosystem. Comparisons in an intervention analysis context (Eberhardt and Thomas 1991) among the Mexican sites support inferences about effects of fire exclusion in these forests (Chapters 4 and 5). Comparisons between the U.S. and Mexican study areas illustrate similarities in conditions both prior to fire regime disruption (compare reconstructed presettlement reference conditions in Arizona with measured reference conditions on frequent-fire Durango site) and after disruption (compare contemporary Arizona conditions with fire-excluded Durango conditions) (Chapter 6). Finally, differences between study areas, reflecting different climates, species composition, and human social context, can be contrasted (Chapter 6).

Hierarchy theory and the keystone hypothesis (Holling 1992) provide a framework from which to view the ecosystem and to select variables for measurement. Given uncertainty and limited knowledge about ecosystems (Holling 1996), as well as limited research resources, exhaustive sampling is not possible. However, the key variables sampled, those discussed in section 2.2.2 (fire disturbance history, vegetation composition and structure, and dead biomass), are essential components of ecosystem function and structure which create and regulate habitats. In practical terms, information

about these variables is central to designing and implementing plans to manage these ecosystems.

Within the study areas, a hierarchical sampling design was selected to cover scales up to the landscape level in Arizona (over 600 ha) and up to the maximum size of available study sites in Mexico (up to 70 ha/site). A sampling grid was used at all study areas to spatially reference measurements of structure and fire disturbance history (Arno et al. 1993). Appropriately-scaled sampling plots were sized to measure variability in different ecosystem components (overstory trees, forest floor fuels, etc.). Consistent methods were used to facilitate cross-site comparisons (Gosz 1992). Small-scale spatial relationships were measured on stem-mapped plots (Chapter 5). Temporal scale was addressed through dendrochronological analysis of fire history and the application of tree-ring data to reconstruct past forest structure (Fritts and Swetnam 1989).

Finally, the sampling sites and procedures applied in the following three chapters do not stand in isolation, but form part of a broader network of collaborative studies across the range of western long-needled pines. Continuing research and future directions are outlined in Chapter 6.

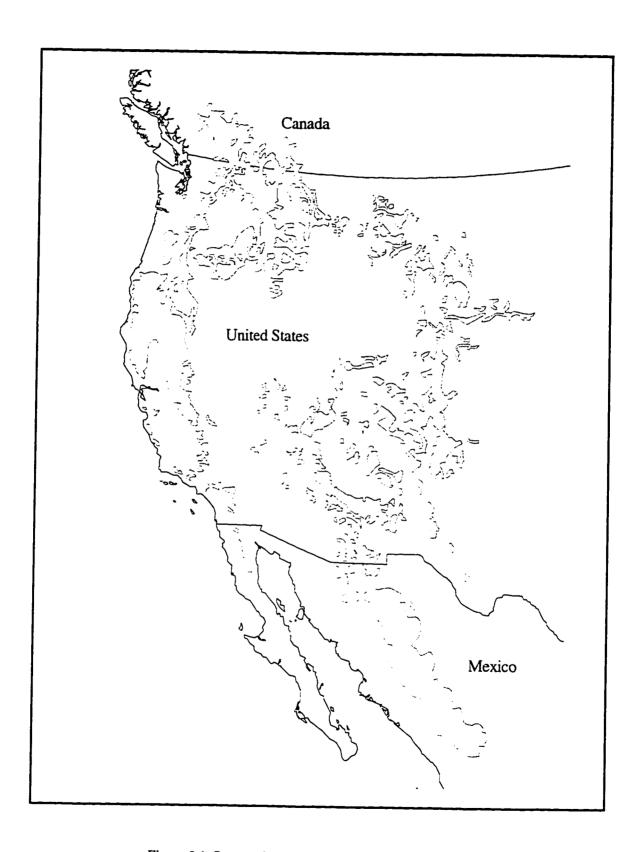


Figure 2.1. Range of long-needled pines in North America

3. DETERMINING REFERENCE CONDITIONS FOR ECOSYSTEM MANAGEMENT OF SOUTHWESTERN PONDEROSA PINE FORESTS

3.1 Introduction

We present an integrated method for determining reference conditions of key ecosystem functional and structural components in a southwestern ponderosa pine forest prior to Euro-American settlement; then we apply the reference data in an ecosystem management context. Reference conditions are the range of historic (or natural) variability in ecological structures and processes, reflecting recent evolutionary history and the dynamic interplay of biotic and abiotic conditions and disturbance patterns (Swanson et al. 1994, Morgan et al. 1994). These conditions form the basis for comparison with contemporary ecosystem processes and structures and are a frame of reference for designing ecological restoration treatments and conservation plans (Grumbine 1992, Covington and Moore 1992, 1994a, Swanson et al. 1994, Morgan et al. 1994, Kaufmann et al. 1994). Almost no ecosystems remain undisturbed by industrial human society, and early historical documentation of past conditions is commonly quite limited, so quantifying reference conditions is a key initial challenge for ecosystem management (Swanson et al. 1994, Kaufmann et al. 1994, Ecological Society of America 1996).

Fires recurred every 2 to 20 years in southwestern ponderosa forests prior to Euro-American settlement around 1870 to 1890 (comparison of 63 fire chronologies in Swetnam and Baisan 1996). Fire has been a keystone ecological process (sensu Holling 1992) regulating the density, species composition, and amount and structure of dead

biomass, maintaining open forests, and promoting nutrient cycling in presettlement ponderosa pine ecosystems (Cooper 1960, Covington and Sackett 1990, Covington and Moore 1994a,b). Although we recognize that Native Americans "settled" North America long before Euro-Americans, for the sake of brevity the term presettlement will be used here to refer to conditions prior to Euro-American settlement and the term postsettlement to refer to conditions after Euro-Americans began the intensive alteration of the landscape which resulted in fire exclusion.

The century-long exclusion of frequent, low-intensity fires has led to striking and rapid changes in ecosystems that evolved under frequent disturbance: trees less adapted to frequent fire (e.g., Abies, Pseudotsuga) have invaded at the expense of other plants, and pine (Pinus) tree biomass, both live and dead, has steadily accumulated, contributing to progressively declining herbaceous productivity, increasing susceptibility to insect and disease epidemics, and supporting a shift from frequent, low-intensity surface fires to increasingly larger crown fires (Cooper 1960, Swetnam 1990, Covington and Moore 1994a,b, Kolb et al. 1994, Swetnam and Baisan 1994). Similar deleterious changes seen in related long-needled pine ecosystems throughout western North America (Covington et al. 1994) form much of the impetus behind increasingly urgent calls for biological conservation, ecological restoration, and ecosystem management (Leopold 1937, Grumbine 1992, Covington et al. 1994, Kaufmann et al. 1994, Arno et al. 1995a).

Keystone ecosystem variables for presettlement ponderosa pine reference conditions include the autotrophic organisms and the predominant contagious disturbance process, fire. These variables regulate their own environment through positive feedback

interactions (sensu Perry 1995) and in turn constrain other components of the ecosystem (sensu Holling 1992); therefore they form the basis for management intervention.

The questions addressed by this study are: what were the temporal and spatial patterns of presettlement fire in a southwestern ponderosa pine forest? What was the presettlement forest structure and how has it changed following fire exclusion and other human-caused perturbations? Finally, how can this information be applied to support sustainable management of southwestern ponderosa pine ecosystems?

3.2 Study Area

The study area is approximately 700 ha of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.)—Gambel oak (*Quercus gambelii* Nutt.) forest at Camp Navajo, an Arizona Army National Guard facility 16 km west of Flagstaff, AZ (Figure 3.1), latitude 35°15'N, longitude 111°52'W. Average annual precipitation at the Flagstaff weather station, elevation 2,134 m, is 502.9 mm, with a distinct dry period in May and June (average 31 mm), followed by the summer monsoon in July and August (average 134.8 mm) (Sellers and Hill 1974). The study area has a gently rolling topography with a single large hill, Volunteer Mountain; elevations range from 2,175 to 2,453 meters. Most soils are of volcanic origin but soils derived from underlying limestone and sandstone formations occur at lower elevations (Soil Conservation Service 1970). Ponderosa pine and Gambel oak are the dominant trees, with scattered alligator juniper (*Juniperus deppeana* Steud.). On mesic, north-facing slopes, Douglas-fir (*Pseudotsuga menziesii* (Mirb.)) and white fir (*Abies concolor* (Gord. & Glen.) Lindl.) are also encountered. New

Mexican locust (Robinia neomexicana Gray) thickets occur in the southern part of the study area.

Evidence of human occupancy dates from the archaic period (approximately 5,500 BC - 100 AD) (Grenda 1993). Large-scale timber extraction became profitable when the transcontinental railroad arrived in 1882 and logging for ties and pilings began around 1885 (Timber Atlas, on file at Kaibab National Forest Supervisor's Office, Williams, AZ). Livestock grazing began in the same period. The area was transferred from mixed National Forest and private ownership to military use in 1942 and has formed part of the undeveloped buffer zone around the military facilities to the present.

3.3 Methods

Quantitative procedures were selected to reconstruct past fire regimes and forest structures. Comparative studies of fire scar analysis methods concur that the most reliable fire histories in forests with low-intensity fire regimes are based on crossdated fire-scarred samples from trees, stumps, and logs (Madany et al. 1982, Baisan and Swetnam 1990). In ponderosa pine forests where direct evidence (stumps, logs, old-growth trees) of past forest structure still exists due to the very slow wood decomposition rate in the absence of fire, direct measurement of presettlement-era remnant wood together with contemporary forest structure is possible (Habeck 1990, Covington and Moore 1994a,b, Arno et al. 1995b). We applied dendroecological reconstruction (Fritts and Swetnam 1989) in a hierarchical sampling framework scaled to different forest structural components (e.g., presettlement pine clumps, regeneration, coarse woody fuels)

to determine reference conditions and compare them to contemporary conditions across a relatively large forest landscape.

3.3.1 Field sampling

A 300 X 300 m systematic sampling grid was established in the study area and sample points were assessed for suitability according to the following criteria: A) suitable soil type for ponderosa pine forest based on Soil Conservation Service (1970) soil survey; B) at least 10% forest cover in presettlement times, with ponderosa pine a dominant species, based on the presence of presettlement-era trees, snags, stumps, or logs; and C) at least 20 m from a road to minimize disturbance to living trees and dead woody material. A total of 62 plots covering 558 ha was sampled in 1994 and 1995.

Sample plots were laid out as a series of nested plots of different sizes. At the largest scale, fire scar samples were collected and their locations mapped (Figure 3.1) throughout each 9 ha area centered on the sampling grid points, effectively searching the entire study area. Cross-section samples of fire-scarred tree catfaces were collected from trees, stumps, or logs apparently recording the oldest scars and/or the best preserved record of multiple fires (Baisan and Swetnam 1990).

Overstory vegetation was sampled on circular plots 400 m² (11.28 m radius) centered on each sample point. Species, condition, diameter at stump height (dsh, 40 cm above ground level), and a preliminary field classification of presettlement or postsettlement origin, were recorded for all live and dead trees over 1.37 m (breast height) in height, as well as for stumps and downed trees which surpassed breast height

while alive. Tree condition classes were assigned based on a tree, snag and log classification system (Maser et al. 1979, Thomas et al. 1979) widely applied in ponderosa pine forests (Covington and Moore 1994a,b, Lundquist 1995). The nine condition classes (1-living, 2-declining, 3-recent snag, 4-loose bark snag, 5-clean snag, 6-snag broken above 1.37 m, 7-snag broken below 1.37 m, 8-downed, 9-cut stump) were used to determine dead tree structure and to estimate the death date of presettlement-era snags and logs, as described below. Potentially presettlement ponderosa pine trees were identified based on size (dsh > 40 cm) or yellowed bark (White 1985). Trees of all other species were considered as potentially presettlement if dsh > 40 cm, or dsh > 20 cm for oaks and junipers (Barger and Ffolliott 1972). All potentially presettlement trees, as well as a random 20% subsample of other trees, were cored with an increment borer at 40 cm above ground level to determine age and past size, as described below. Diameter at breast height (dbh) was recorded for all cored trees.

Seedlings or sprouts of tree species were tallied on nested 100 m^2 (5.64 m radius) plots. Stems below 1.37 m in height were tallied on the nested 100 m^2 plot by species and condition in three height classes: (1) $\leq 40 \text{ cm}$; (2) 40.1-80 cm; and (3) 80.1-137 cm.

Herbaceous and shrubby species were measured on two 1 m² subplots per plot.

The frequency (presence/absence) of dominant plants and percent herbaceous cover were recorded.

Forest floor fuels and litter and duff depths were measured along 15-m planar intersect transects (Brown 1974) established in random directions from each plot center.

Woody fuel biomass was calculated using procedures in Brown (1974) and Sackett (1980).

3.3.2 Dendrochronology--fire disturbance history

In the laboratory, fire scar samples were surfaced and crossdated (Stokes and Smiley 1968) with master tree-ring chronologies from the region (Graybill 1987). Ring widths of all samples were measured and dating of each sample was checked with the COFECHA program (Grissino-Mayer and Holmes 1993). A 20% subset of samples was also checked through independent visual crossdating by another dendrochronologist. To identify the season of occurrence of fires (Baisan and Swetnam 1990), the relative position of each fire scar within the ring was recorded using the following categories: EE (early earlywood), ME (middle earlywood), LE (late earlywood), L (latewood), and D (dormant season, scar occurring between the cessation of latewood growth and the beginning of the next year's earlywood growth). Dormant scars are considered to represent spring fires in the Southwest (Baisan and Swetnam 1990).

Fire history was reconstructed from analysis of 473 fire scars from 51 ponderosa pine samples and 1 white fir sample. The majority of the samples was cut from dead trees but samples from several live trees brought the fire history up to 1995.

3.3.3 Age structure

Tree increment cores were surfaced and crossdated (Stokes and Smiley 1968) with local tree-ring chronologies (Graybill 1987). Rings were counted on cores which could

not be crossdated. The accuracy of ring counting was tested with a set of counted and crossdated presettlement cores, finding a mean error of 0.9 years (std. dev. 2.1 years). We concluded that grouping tree ages into 10-year classes was reasonable. Additional years to the center were estimated with a pith locator (concentric circles matched to the curvature and density of the inner rings) for cores which missed the pith. Tree center dates are at the 40-cm sampling height; as few as 3 years (Sackett 1984) or as many as 8-10 years (Cormier 1990) may be required for ponderosa pine seedlings to reach 40 cm in the Flagstaff area.

3.3.4 Reconstruction of presettlement forest structure

The year 1883, in which the final fire of the presettlement frequent-fire regime occurred, was chosen as the date for reconstruction of presettlement forest structure. Reconstruction of forest structure at an earlier date would present greater difficulties because the frequent fires during this era probably consumed much rotten woody material.

The field determination of presettlement or postsettlement tree status was confirmed or rejected using the age data. Several large trees turned out to be of postsettlement origin and the data were adjusted accordingly. However, no trees field-classified as 'postsettlement' turned out to be of presettlement age. For each cored presettlement tree, the 1883-1994 radial growth increment was measured on the core and the 1883 diameter calculated. Species-specific equations developed by Myers (1963) and Hann (1976) in the Southwest were used to estimate bark thickness and to predict dbh

based on the inside-bark diameter of stumps. Site-specific regressions were developed from the data set to predict dbh from dsh for all species.

The year of death of presettlement snags and logs was estimated based on tree diameter and condition class. Dead trees were not crossdated in this study, but a companion study in which all dead material was crossdated at the Gus Pearson Natural Area, approximately 15 km NE of Camp Navajo, found that all dead wood classified in the field as 'presettlement' based on size and decay was of presettlement origin (J.N. Mast and others, unpublished data). However, direct determination of death date was precluded by sapwood rot on almost all of those samples. Harvest dates for stumps were determined from timber harvest and forest inventory records of the Tusayan Forest Reserve (on file in the Supervisor's Office, Kaibab National Forest). The records were spatially detailed and corresponded well with field observations of the high stumps (up to 1 m) in the initially-logged areas (1885) and lower stumps in areas harvested later (1925 and 1933).

Rates of snagfall and movement from class to class were summarized by Rogers et al. (1984) who combined data from Cunningham et al. (1980) and Avery et al. (1976) to calibrate for northern Arizona the tree decomposition model developed by Thomas et al. (1979). Because of high variability among substrates and environmental conditions, as well as the extremely long time span required for research, the dynamics of tree decomposition are poorly understood (Harmon et al. 1985) and mathematical models based on observed decomposition classes are likely to be highly imprecise. To assess the effect of such variability on the presettlement forest reconstruction, a sensitivity analysis

was carried out by using three different decomposition rate percentiles, 25%, 50%, and 75%, to examine the effect of slower or faster decomposition on the estimates of death date and 1883 structure. For example, a 65-cm dbh snag in condition class 5 would be assigned a death date of 1950 assuming the 50th percentile of the distribution of decomposing trees. At the 25th and 75th percentiles, the assigned death dates would be 1906 and 1976, respectively. Presettlement forest structure based on each of the three percentiles was calculated to determine the relative effect of model imprecision.

To determine the 1883 diameter of dead trees, growth estimates for the period from 1883 to death date were subtracted from the measured diameter, adjusted for the loss of bark where appropriate. In the case of ponderosa pine, where an increment core data set adequate for modeling was obtained in the study, a site-specific predictive regression relationship between diameter and basal area increment was developed for presettlement trees ($r^2 = .70$). As is often the case, pine diameter proved to be an inadequate predictor of radial increment ($r^2 = .07$). For other species, published diameter-dependent growth regression equations were applied to determine 1883 diameter (Rogers et al. 1984).

A potential source of error in this reconstruction approach is missing presettlement-era woody material, which would lead to an underestimate of presettlement forest density. Fire consumption of wood was controlled as much as possible by selecting 1883, the year of the last widespread fire on the site, as the reconstruction year. Complete decomposition of resinous woody material in the absence of fire is likely to take longer than 112 years (1883 to 1995) due to the very slow decomposition rate of ponderosa pine

(Jenny et al. 1949, Hart et al. 1992). Fire history sampling included many stumps harvested circa 1885 which had endured for 110 years. Juniper and Douglas-fir wood is also highly resistant to decay. Gambel oak and white fir may decompose more quickly, often beginning with heart rot in the living trees (Barger and Ffolliott 1972, Burns and Honkala 1990), but old oak and fir stumps and logs were also found on sample plots. Some wood removal may have occurred in slash disposal, but this rarely affects the stumps and root crowns needed for presettlement reconstruction.

Because small-diameter pines rot quickly (Harmon et al. 1985, Arno et al. 1995b), it could be argued that small trees or even doghair thickets which were alive in the settlement year but died soon thereafter would be missed. However, there is no evidence in historical accounts, photographs, or early inventories for the existence of numerous small trees in presettlement northern Arizona—quite the contrary (Cooper 1960). Nor does it seem likely that such thickets could have become established under frequent fire regimes (White 1985). Finally, there is no reason to believe that such trees would have died in high numbers following fire exclusion, especially in light of the remarkable persistence of small trees in stressed postsettlement doghair thickets (Schubert 1974, Avery et al. 1976, White 1985). In sum, while the possible underestimation of some small presettlement trees that left no trace cannot be dismissed, such trees are unlikely to have formed a substantial component of presettlement forest structure.

3.3.5 Statistical analysis

Statistical analysis of the fire history data was carried out with the FHX2 fire history analysis software developed by Grissino-Mayer (1995). The areal extent and intensity of presettlement fires are difficult or impossible to reconstruct in ecosystems characterized by frequent, low-intensity fire where forest stand boundaries do not correspond with fire edges (Swetnam and Dieterich 1985). However, relative fire extent and/or fire intensity within the sampled area can be inferred to some degree from the percentage of samples scarred and their spatial distribution. Therefore, fire return intervals were analyzed statistically in different sub-categories. First, all fire years, even those represented by a single scar, were considered. Then only those fire years were included in which 10% or more, and 25% or more, respectively, of the recording samples were scarred.

Statistical comparison of the 1883 and contemporary forest structure was carried out with the SYSTAT software (Wilkinson 1988). Alpha level for all analyses was .05. Multivariate analysis of variance (Tabachnick and Fidell 1983, p. 222-291) was used to determine differences in mean density, basal area, and quadratic mean diameter on the entire set of tree species. If a significant difference was found between the presettlement and contemporary forests (Wilk's lambda statistic), then Bonferroni-adjusted univariate F statistics were compared by species.

3.4 Results

3.4.1 Fire Disturbance History

Fire was frequent in the period 1637-1883, with a mean fire return interval (MFI) of 3.7 years, but only a single fire scar, in 1951, was recorded after 1883 (Figure 3.2). The year 1637 was selected as the initial year for fire history analysis because it was the earliest fire year deemed to have an adequate sample depth (5 recorder trees, about 10% of the total sample size) to confidently evaluate fire occurrence (Grissino-Mayer et al. 1994).

The statistical analysis of fire return intervals in Table 3.1 includes the mean fire interval (average number of years between fires), the median, and the Weibull median probability interval (WMPI), used to model asymmetrical fire interval distributions and to express fire return intervals in probabilistic terms (Johnson 1992, Grissino-Mayer 1995). All three measures of central tendency over the 1637-1883 period were in close agreement and distributions were asymmetrical, positively skewed with a clumped distribution of short fire return intervals and fewer long intervals.

Spatial patterns of fire were inferred from the similarity of MFI values from both the all-scar and 10%-scar distributions, 3.7 and 4.6 years, respectively, and identical median value of 4 years for both (Table 3.1). The measures of central tendency in the 25%-scar distribution, possibly representing more widespread fires, are only about 1.5 times greater than the all-scar and 10% distributions (Table 3.1) and no significant difference in fire return intervals or percentage of scarring for the fire interval distributions between the north and south halves of the study area over the period 1684-

1883. Fire years were not statistically independent in the north and south and, in all but the 25%-scar distribution, the number of synchronous dates was significantly greater than the number of asynchronous dates. Overall, these results support the inference of a spatially homogeneous fire regime, consistent with the lack of topographic or vegetative barriers to fire spread on the site and the fact that fires could have persisted for extended periods in the absence of fire suppression activities.

The presettlement fire regime was also temporally homogeneous. No statistically significant differences found in fire interval means, variances, or distributions between the periods 1637-1759 and 1760-1883, although the fire history overlapped with the major regional climatic trend, the Little Ice Age, a period of warming beginning from a cold extreme in 1600 until 1850 (D'Arrigo and Jacoby 1991). The lack of significant long-term fire regime change appears to correspond with the short-term nature of climatic fluctuations within this period (Meko et al. 1995). On a shorter time scale, however, fire occurrence appeared to be linked to annual climatic factors, with fires occurring in the study area during some of the largest presettlement regional fire years in the Southwest, based on a comparison of 63 southwestern fire chronologies for the period 1700-1900 (Swetnam and Baisan 1996). Fires burned at Camp Navajo in 8 of the 20 major regional fire years; in the top two regional years, 1748 and 1851, fires scarred 63% and 44%, respectively, of the recording sample trees. Climatic influences over broad geographic regions are considered responsible for this synchrony (Swetnam and Baisan 1996).

Seasonal data on fire occurrence (Table 3.2) showed that approximately 40% of presettlement fires occurred in the spring (approximately late April to June [Baisan and

Swetnam 1990]) and 60% in the summer (July to early September), without evidence of burning during latewood formation. This seasonal pattern is consistent with regional fire weather and lightning ignition patterns (Swetnam and Baisan 1996). Fire season could not be determined on approximately 40% of the scars (Table 3.2), often due to narrow rings, possibly biasing the seasonal determination toward years in which better conditions for tree growth led to wider rings.

3.4.2 Changes in Forest Structure

Pine and oak density increased significantly and pine quadratic mean diameter decreased significantly from 1883 to 1994 (Table 3.3). The average density of ponderosa pine was 65.3 trees/ha with quadratic mean diameter of 41.6 cm in 1883, as compared with 720.2 trees/ha and quadratic mean diameter of 22.8 cm in 1994; pine basal area increased from 11.7 m²/ha to 18.2 m²/ha. Thus the pine population has changed from fewer, larger trees to numerous, smaller trees (Figure 3.3). Density and basal area of oaks both increased (Table 3.3). Other species had such low and variable occurrence that no statistically significant changes were observed, although all trended toward increasing density. Living presettlement-era trees comprise only 7% of contemporary tree density but make up 33.9% of contemporary basal area despite their sparse distribution.

New Mexican locusts found on the study area were small and young, so no estimation of presettlement locust density could be made and locust was excluded from the totals in Table 3.3. However, New Mexican locust does sprout readily following

removal of overstory pines (Gottfried 1980) and dense locust thickets were observed surrounding old pine stumps, suggesting that locust density has increased since 1883.

The sensitivity analysis on modeling of tree decomposition showed that estimates of 1883 tree density were robust. Only under the slowest modeled decomposition conditions, the 25th percentile, were a few trees assigned death dates prior to 1883 (3 out of 54 dead presettlement trees, 5.6%) and no death dates prior to 1883 were calculated using the 50th and 75th percentiles, leaving the estimated 1883 forest density unchanged. Estimates of tree size in 1883 were also relatively robust. The 25th percentile model estimated the 1883 basal area at 13.7 m²/ha, a 7% increase above the 50th percentile model, while the 75% percentile model estimated the 1883 basal area at 12.4 m²/ha, a 4% decrease. The narrow range of differences in estimated 1883 structure, compared with the wide differences in decomposition rate percentiles and associated tree death dates, indicates that the 1883 reconstruction is relatively insensitive to decomposition model imprecision.

Distributions of size and age (Figures 3 and 4) show that the contemporary forest is dominated by relatively smaller, younger trees. Large pulses of tree establishment (Figure 3.4) occurred in the late 19th century for oaks (1885-1914) and in the early 20th century for pines. Given 3-10 years to reach the 40-cm sampling height, many of the pines in the largest center-date class (1935-1944) may have originated in the 1920's. Contemporary woody seedling density (Table 3.4) is highly variable but averages several thousand stems per hectare, mostly oak and locust.

Grasses were the dominant herbaceous understory plants in the contemporary forest, followed by composites, legumes, and sedges (Table 3.5). All identified species were native to northern Arizona. Percent cover by herbaceous species averaged 19%.

Changes in tree and grass structure over the mid-twentieth century are illustrated in Figure 3.5. The 1942 photograph, the earliest available scene from Camp Navajo, shows a very open forest structure with many stumps after railroad logging in the 1920's. Herbaceous plants were dense but numerous patches of pine seedlings are evident, corresponding with the large increase in tree establishment during this period (Figure 3.4). By 1995 the site was dominated by small-diameter pines with an apparent decrease in herbaceous density.

Contemporary dead woody biomass was highly variable on the study site (Table 3.6) but forest floor depth was more consistent. In terms of potential fire behavior, these fuel data imply that continuous fuels to carry the flaming front are found throughout the study area, while heavy fuels that may support intense fire behavior occur in scattered patches.

3.5 Discussion

3.5.1 Context of changes in fire disturbance regime and forest structure

The beginning of effective fire exclusion in the study area after 1883 is coincident with the construction of the transcontinental railroad across northern Arizona from 1882 through 1884 and the initiation of heavy commercial logging in the region (Cline 1994). The date is also consistent with the cessation of frequent fires throughout most of the

Southwest by 1900, with a substantial decline in fire occurrence beginning in the 1870's and 1880's (Swetnam 1990, Swetnam and Baisan 1996). Heavy livestock grazing was associated with fire exclusion at Chimney Spring, approximately 15 km east of the study area (Dieterich 1980). The date of initiation of livestock grazing at Camp Navajo is not known, but nearby Rogers Lake was impounded to water livestock in 1878 (Grenda 1993).

Comparing presettlement forest structure to that of nearby areas, presettlement pine and oak densities on the study area were greater than the 43 pines/ha and 4 oaks/ha found by Covington and Moore (1994a) at Bar-M Canyon, but pine density was close to the 61 pines/ha at the Gus Pearson Natural Area (Covington et al. in press). Presettlement pine density at the study area also falls within the range of 7 to 116 pines/ha reported in several early National Forest inventories and other studies in the region (see Covington and Moore [1994b] for comparison). In particular, Woolsey (1911) reported a mean of 26 pines over 15.2 cm dbh per hectare on "average" stands in timber-sale areas on the Tusayan National Forest (which then included the study area) and a mean density of 85 pines over 10.2 cm dbh per hectare on "maximum" stands in the adjacent Coconino National Forest. The 1883 Camp Navajo reconstruction is within this range with 61 pines/ha over 15.2 cm dbh and 63 pines/ha over 10.2 cm dbh. There is no evidence in the reconstructed forest structure data that dense stands existed in the study area: the maximum presettlement tree density was 500 trees/ha, less than 40% of the mean contemporary tree density of 1,265 trees/ha (Table 3.3).

Relatively high densities of small-diameter oaks were observed in the 1883 forest, comprising 94% of all trees under 10 cm dbh. Because Gambel oak is a prolific sprouter but highly susceptible to fire, especially small-diameter trees (Harrington 1985), it is likely that many or most of these small trees would have been thinned had fires continued after 1883. The density of oaks over 5 cm dbh, 48 oaks/ha, or the density over 10 cm dbh, 33 oaks/ha, may be more representative of the long-term average oak density under a continuing frequent fire regime.

The increase in density of all tree species at the study area by 1994 is consistent with the structural changes in ponderosa pine ecosystems since Euro-American settlement in Arizona (Cooper 1960, White 1985, Covington and Moore 1994a,b) and in related long-needled pine ecosystems throughout western North America (Arno et al. 1995b, Covington et al. 1994). The contemporary density of ponderosa pine is very close to the 1985 Arizona average of 776 trees/ha (Garrett et al. 1990) but less than the 1,900 ponderosa pines/ha reported by Covington and Moore (1994a) at Bar-M Canyon, and well below the 3,098 pines/ha at the Gus Pearson Natural Area where logging, thinning, and firewood cutting have been excluded (Covington et al. in press). Contemporary oak density in Table 3.3 is over three times greater than the 156 oaks/ha at Bar-M Canyon (Covington and Moore 1994a) and higher than oak densities averaging 138 to 182 oaks/ha in a central Arizona ponderosa forest (Barger and Ffolliott 1972). Juniper density at the study area is lower than the 27 junipers/ha at Bar-M Canyon (Covington and Moore 1994a) and lower than the average of 88 junipers/ha in central Arizona (Barger and Ffolliott 1972).

In the northern part of the study area, adjacent to the railroad, the impact of early logging may have been a factor in limiting pine establishment. On the 15 northern plots, presettlement pine stump density averaged 33 per ha, while living presettlement trees averaged 3 per ha. The heavy pine removal at the end of the nineteenth century may have eliminated seed sources and precluded the regeneration flushes that followed good regional seed years such as 1919 (Schubert 1974). However, the period of favorable moisture conditions in the Southwest extended from 1905 to 1928 (D'Arrigo and Jacoby 1991). Later logging in the southern part of the study area (circa 1933), may have damaged seedlings, contributing to the relatively late pine regeneration pulse (Figure 3.4). Logging may also explain the relatively slow increase in ponderosa pine basal area from 1883 to 1994 despite the manyfold increase in tree density.

3.5.2 Ecosystem management: (1) comparison to contemporary conditions

The reference presettlement conditions can be applied to management of this ecosystem as (1) a benchmark against which to evaluate contemporary conditions and future alternatives (Swanson et al. 1994, Kaufmann et al. 1994), and (2) a goal for ecological restoration treatments (Covington et al. in press). Taking the 1883 forest structure as the reference condition, the contemporary structure has tree densities far higher than the mean and increased variability in both absolute and relative terms (Table 3.3). The mean 1994 density of 720.2 pines/ha is well outside even the 99th percentile of the 1883 pine distribution (1883 mean + 3 standard deviations = 231 pines/ha) and pine

densities on the sample plots in 1883 ranged from 0 to 250 pines/ha, as opposed to the broader range of 0 to 6250 pines/ha in 1994.

Mesic conifer density has increased. Although some presettlement-era mixed conifer forest existed on the north-facing slopes of Volunteer Mountain, no presettlement Douglas-fir and only two presettlement white firs were encountered on the sampling plots. By 1994 these species made up 5% of the total tree density and dominated the north-facing slopes, with white fir reaching a maximum density of 2,225 firs/ha.

Contemporary forest floor fuel loading is probably higher than in presettlement times. With fires occurring every 3-6 years in presettlement times, small-diameter woody fuels would have been consumed quickly. Larger diameter rotten woody fuels would have been consumed as well (Covington and Sackett 1984). In contrast to presettlement conditions, currently there is ample fuel to support high-intensity fire behavior, including torching through live fuel ladders and crown fire, in hot, dry, windy weather. However, herbaceous fuel loading is probably greatly reduced in the contemporary forest.

Presettlement regeneration patterns may be inferred to some extent from the age structure of living presettlement trees (Figure 3.4). White (1985) argued that presettlement pine regeneration would most likely have required "safe sites," such as in the ash bed left by a completely consumed log, until seedlings grew above the lethal scorch height of a fast-moving surface fire. Ponderosa pine regeneration is also linked to sporadic periods of favorable climatic conditions, even if favorable establishment sites exist (Savage and Swetnam 1990). Under such limitations, the relatively normal distribution of presettlement pine diameters may be explained by the few establishment

opportunities for seedlings but the high survivorship among young trees which grew above the lethal effect of the flames and benefited from uncrowded growing conditions (Figure 3.3).

Postsettlement woody regeneration patterns (Table 3.4) are likely to differ from presettlement patterns on the study area, because herbaceous competition has been reduced or eliminated, fire has not played a role in thinning, harvesting has preferentially removed pines, and the relatively dense canopy may favor shade-tolerant species.

3.5.3 Ecosystem management: (2) ecological restoration

Although restoration to conditions resembling those of presettlement times is not necessarily a feasible or desirable management goal on all forest lands (Kaufmann et al. 1995), managers of the Camp Navajo study area have agreed that an ecosystem management approach based on restoration of ecosystem function and structure similar to that characteristic of recent evolutionary history (Covington et al. 1994) is consistent with the training uses and buffer zone function of this site. Detailed description of ecological restoration in southwestern ponderosa pine forests requires an extended treatment (Covington et al. in press, W. Covington, in preparation) but key points are summarized here.

The challenge for management is to conserve existing presettlement-era resources, design treatments that restore ecosystem structure, and permit the re-introduction of frequent, low-intensity fires. These are not simple tasks. Even conservation of living presettlement trees presents problems: growth rates of old ponderosa pine trees at the

Gus Pearson Natural Area have slowed sharply, despite the exclusion of logging and grazing and without evidence of changing climate (Sutherland 1983, Kolb et al. 1994, Biondi et al. 1995, Biondi in press). These authors suggested that a primary cause of mortality of old trees is increased stress from competition with dense thickets of younger trees following fire exclusion. Re-introduction of fire without fuel treatment can also kill old-growth trees. Experimental prescribed fires beginning in 1976 at Chimney Spring, approximately 15 km NE of Camp Navajo, led to mortality of over 60% of the living presettlement pines, attributed to the lethal temperatures produced at the root collars of old trees by slow smoldering consumption of accumulated fuels (Harrington and Sackett 1990).

The underlying premise of restoration ecology is that ecosystems function best under the conditions to which they adapted over evolutionary time (Swanson et al 1994). In the case of southwestern ponderosa pine, the open, park-like forests, productive herbaceous understory, and frequent fire regime are key characteristics of this long-term evolutionary environment. Applying the reference condition data as a guide, we suggest that restoration treatments (Covington et al. in press) should include (1) establishment of permanent monitoring plots for evaluation and modification of treatments in an "adaptive ecosystem management" framework (Walters and Holling 1990); (2) restoration of overstory structure by conserving living presettlement trees and replacing dead presettlement trees; (3) protection of old trees from excessive cambial heating by reducing fuels around the boles; (4) re-introduction of fire disturbance through prescribed

burning; and (5) restoration of the herbaceous and shrub understory through seeding or planting of native species where natural regeneration is inadequate.

We expect the balance of fire and vegetation in the restored ecosystem to ultimately return to the self-regulating patterns and rhythms of the presettlement forest because the keystone natural mechanisms controlling structure and function will be able to operate. However, while extensive information exists on the small-scale (plot-level) response of woody and herbaceous plants to thinning and burning, the effectiveness of an integrated large-scale (landscape-level) restoration treatment in ponderosa pine forests has only begun to be examined (Covington and Moore 1994a, Arno et al. 1995a, Covington et al. in press). Continued monitoring of these treatments is essential and ongoing management intervention and adaptive new approaches will be necessary over time as we evaluate and learn from our first attempts at restoration and ecosystem management of landscapes.

Table 3.1. Fire return intervals over the period 1637 to 1883.

Percent of Recording Trees Scarred	Number of Intervals	Mean (MFI)	Median	Standard Deviation	Minimum	Maximum	Skewness	Kurtosis	WMPI ²
All scars Over 10% scarred Over 25% scarred	66 53 37	3.7 4.6 6.5	4 4 9	1.42 2.19 3.45	2 2 2	8 13 15	0.94 1.94 0.76	0.92 4.41 -0.46	3.7 4.6 6.2

MFI = Mean fire interval
 WMPI = Weibull median probability interval

Table 3.2. Seasonal distribution of fires based on the position of the fire injury within the ring. Total number of sears = 457,

Season Dormant Early Middle Late Latewood Dormant + Early Middle + Late Undetermined Earlywood Earlywood Earlywood (= Spring fires) (= Summer fires)	180 52 59 125 41 0 111 166 39.4 18.8 21.3 45.1 14.8 0 40.1 59.9
Dormant E	52 18.8
Season Determined	Number 277 Percent 60.6

Table 3.3. Presettlement forest structure reconstruction in 1883 compared with contemporary forest structure from 1994/95 inventory at Camp Navajo, AZ. Presettlement New Mexican locust shrub structure could not be reconstructed so locust is not included in the totals. Sample size n=62. Within-row means followed by asterisks are significantly different (p < .05). S.E.M. = standard error of the mean.

	Presettleme	ent 1883	Contempora	ary 1994
	Trees per hectare			
Species	Mean	S.E.M.	Mean	S.E.M.
Ponderosa pine	65.3 *	7.0	720.2 *	129.0
Douglas-fir	0		3.6	2.1
White fir	0.8	0.8	62.5	42.3
Juniper species	2.4	1.7	7.7	3.4
Gambel oak	79.4 *	13.6	471.4 *	77.0
New Mexican locust		13.0	[489.9	178.2]
TOTAL	148.0	14.3	1265.3	173.1
		Basal area	(m²/ha)	
Ponderosa pine	11.7 *	1.4	18.2 *	1.6
Douglas-fir	0		0.2	0.1
White fir	0.2	0.2	1.0	0.8
Juniper species	0.02	0.01	0.2	0.2
Gambel oak	1.0 *	0.2	6.6 *	1.0
New Mexican locust		0.2	[0.1	0.1]
TOTAL	12.9	1.4	26.2	1.7
		Quadratic mean	diameter (cm)	
Ponderosa pine	41.6 *	2.7	22.8 *	1.3
Douglas-fir	0		1.2	0.7
White fir	0.8	0.8	0.8	0.4
uniper species	0.3	0.2	1.6	0.7
Sambel oak	6.7	1.0	10.6	1.2
New Mexican locust		1.0	[0.3	0.1]

Table 3.4. Regeneration density (stems/ha) by species and height class. Sample size n = 62, $100-m^2$ plots. S.E.M. = standard error of the mean.

	Height: 0-40 cm 40.1-80 cm		cm	80.1-137 cm		
Species	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M
TREES						
Ponderosa pine	66.1	21.7	62.9	32.1	45.2	27.9
Douglas-fir	11.3	9.8	1.6	1.6	0	>
White fir	9.7	8.2	4.8	3.6	3.2	3.2
Juniper species	4.8	2.8	4.8	2.78	1.6	1.6
Gambel oak	3966.1	1149.8	582.3	197.6	80.7	33.6
SHRUBS						
New Mexican locust	714.5	236.1	1085.5	357.7	517.7	179.2
Service berry	4.8	4.8	1.6	1.6	0	
TOTAL	4777.4	1204.59	1743.6	427.1	648.4	195.2

Table 3.5. Frequency of the 20 most-encountered herbaceous species and percent herbaceous cover. Frequencies of all other herbaceous species were below 1%. S.E.M. = standard error of the mean.

Species name	Frequency (%)	
Grasses		
Sitanion hystrix	17.1	
Muhlenbergia montana	16.6	
Festuca arizonica	14.5	
Bouteloua gracilis	4.4	
Poa fendleriana	2.8	
Aristida sp.	1.3	
Composites		
Cirsium sp.	7.8	
Unknown composite sp.	2.8	
Erigeron sp.	2.3	
Senecio sp.	1.8	
Achillea lanulosa	1.6	
Lactuca sp.	1.6	
Erigeron flagellaris	1	
Antennaria sp.	0.8	
Legumes		
Vicia sp.	3.1	
Astragalus sp.	1.8	
Lathyrus arizonicus	1	
Sedge		
Carex sp.	3.9	
Other		
Unknown forb sp.	3.1	
Ceanothus fendleri	1	
	Herbaceous Cover	***********************
n = 59 plots mean = 18.8 %		
range 0 to 78%		
S.E.M. = 2.5%		
3.E.IVI. = 2.370		

Table 3.6. Dead woody biomass and forest floor depth. Sample size n = 62, 15-m planar intersect transects.

	Mean	Minimum	Maximum	S.E.M.
		Metric ton	/ha	
Woody Fuels				
0.0-0.6 cm diameter	0.19	0	2.18	0.04
0.6-2.5 cm diameter	0.95	0	5.57	0.14
2.5-7.6 cm diameter	2.16	0	16.87	0.42
>7.6 cm diameter sound	3.57	0	114.67	1.92
>7.6 cm diameter rotten	7.89	0	99.05	2.44
TOTAL	14.76	0	214.27	3.88
	**********	cm -		
Forest Floor Depth				
Litter	1.48	0.31	3.18	0.09
Duff	2.59	0.16	8.65	0.24
TOTAL	4.06	0.48	11.11	0.30

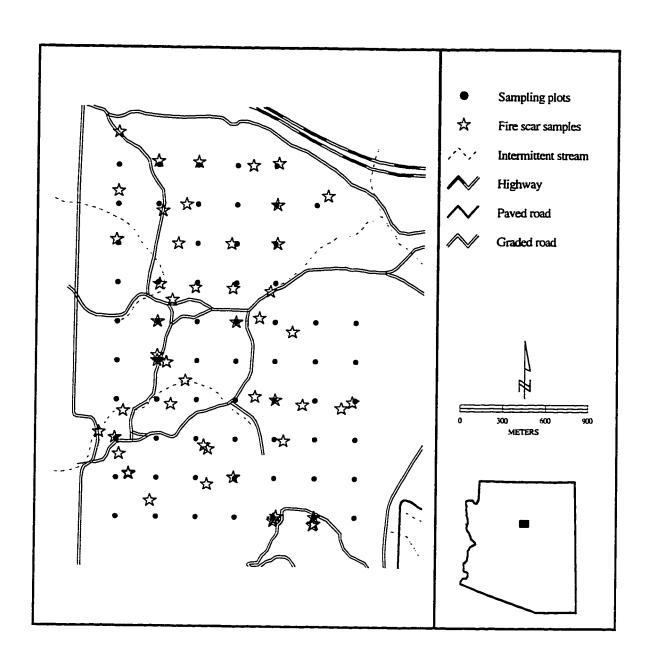
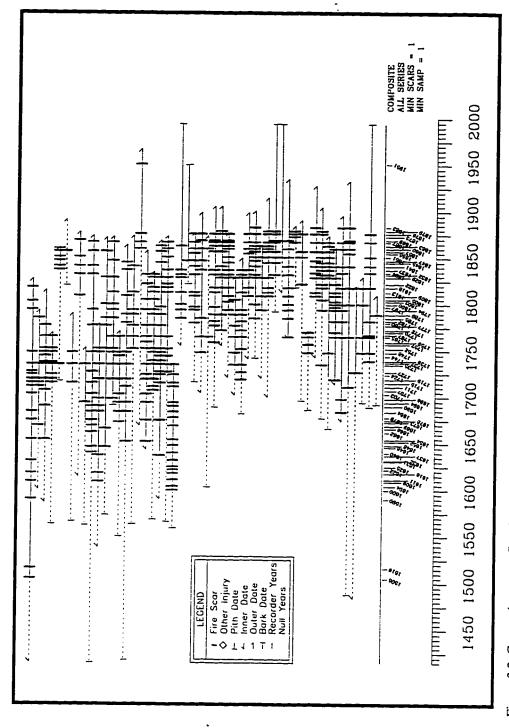


Figure 3.1. Study area map showing fire scar and forest structure sampling locations.



continuous lines show recording periods. Fire dates are indicated by short vertical lines and the dates are displayed along the lower axis. Frequent fires were interrupted after 1883, the year in which the transcontinental railroad was completed across the northern scarred sample. Dashed lines show where the sample is not considered a recording tree (e.g., before the first fire scar forms), and Figure 3.2. Composite master fire chart for the Camp Navajo study area. Each horizontal line in the graph corresponds to a fireedge of the study area. The top to bottom order of samples runs roughly from north to south.

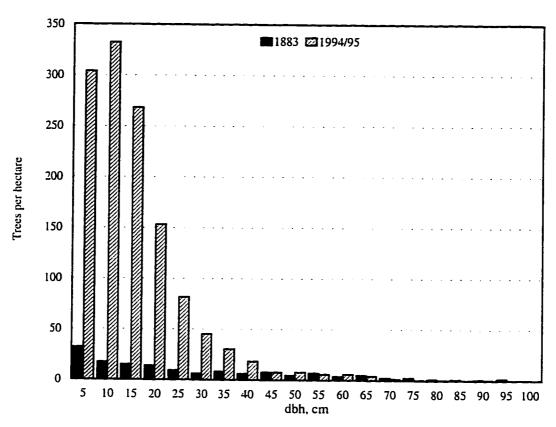


Figure 3.3. 1883 and 1994/95 diameter distributions of all trees (labeled diameters are the endpoints of 5 cm dbh classes, n = 2981 trees).

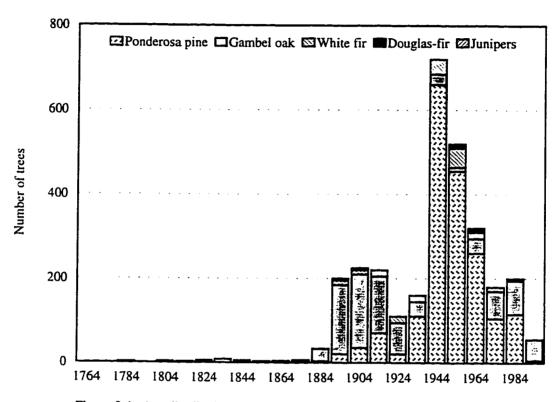


Figure 3.4. Age distribution of living trees in 1994/95 showing tree center date at the 40 cm above-round sampling height (labeled dates are the endpoints of 10 year classes, n = 718 trees aged).

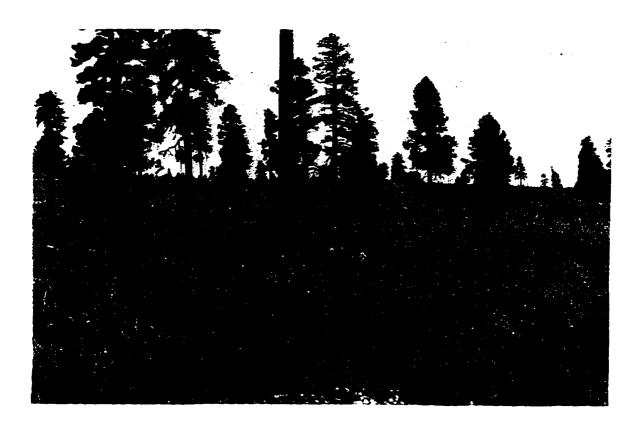


Figure 3.5a. September 1, 1942, forest scene 3.5 km south of the study area (center of T21NR5ES20, view east). This scene is typical of many in the 1942 photo archives: a very open residual ponderosa pine stand with numerous scattered stumps and logs from railroad-logging in the 1920's. In the background, especially at right center, dense patches of small seedlings can be seen. The full crowns of the residual trees suggest that the stand was probably not very dense even prior to logging. (Navajo Army Depot Collection, Cline Library, Northern Arizona University).



Figure 3.5b. August 15, 1995, scene from approximately the same location. A dense sapling to pole-sized ponderosa pine stand dominates the area. Grassy openings remain but herbaceous density appears to be substantially less than in 1942.

4. FIRE REGIMES AND FOREST STRUCTURE IN THE SIERRA MADRE OCCIDENTAL, DURANGO, MEXICO

4.1 Introduction

Disturbance regimes of frequent, low-intensity fires are a keystone ecological process (sensu Holling 1992) regulating the density, species composition, dead woody biomass, and forest floor structure of western long-needled pine ecosystems in North America (Weaver 1943, 1951, Cooper 1960, Covington et al. 1994, Swetnam and Baisan 1996, Arno et al. 1995b). These long-needled pines (Pinus ponderosa, P. durangensis, P. engelmannii., P. arizonica, P. jeffreyi, P. washoensis, and others) form a closely-related ecological group in the section Ponderosae with thick bark, insulated buds, and high capability to recover from crown scorch, all of which are considered adaptations to frequent fire (Conkle and Critchfield 1988, McCune 1988, Barton 1993). The temperate coniferous forests of northern Mexico are the most biologically diverse of these longneedled pine ecosystems (Bye 1995, Felger and Wilson 1995) and the least affected by the disruption of frequent fire regimes (Leopold 1937, Marshall 1962, Fulé and Covington 1994, Baisan and Swetnam 1995). However, with a few exceptions (e.g., Baisan and Swetnam 1995, Minnich et al. 1995, Villanueva-Díaz and McPherson 1995), little is known about the role of fire or the relationship between fire and ecosystem structure in the forests of northern Mexico.

Fire ecology studies in the coniferous forests of the southwestern United States have shown that frequent fire played a key ecological role in these ecosystems by maintaining open, park-like forests of fire-adapted species, controlling tree populations,

limiting accumulation of dead woody biomass and deep forest floors, cycling nutrients stored in dead organic material, and encouraging herbaceous production (Weaver 1951, Cooper 1960, Biswell 1972, Covington and Moore 1994a, Covington et al. 1994, Swetnam and Baisan 1996). Regimes of frequent, low-intensity fire were disrupted throughout the southwestern United States between 1880 and 1900, however, by heavy grazing of domestic animals, logging, and fire suppression associated with Euro-American settlement of the region (e.g., see Cooper 1960, Swetnam and Baisan 1996, Covington et al. 1994). In the absence of frequent fires, striking changes occurred: tree species less adapted to frequent fire (e.g., Abies, Pseudotsuga) have invaded mesic sites at the expense of other plants, and tree biomass, both live and dead, has steadily accumulated, contributing to increasing susceptibility to insect and disease epidemics and supporting a shift from frequent, low-intensity surface fires to increasingly larger crown fires (Cooper 1960, Swetnam 1990, Covington and Moore 1994a, Kolb et al. 1994, Swetnam and Baisan 1996).

In contrast, the Mexican experience with fire has been quite different from that of the United States. Deliberate agricultural burning has long been practiced by both native and Hispanic peoples in Mexico. Despite a history of official opposition to wildfire dating back to pre-Columbian times, effective fire suppression--the combination of laws, anti-fire attitudes among the public and land managers, and adequate financial and infrastructure resources needed to systematically exclude fire--has not been achieved in much of the country (Lumholtz 1902, Leopold 1937, González-Cabán and Sandberg 1989, Rodríguez Trejo and Sierra Pineda 1992, Chou et al. 1993). Striking differences

between the dense, fire-excluded forests of the southwestern United States and the open, frequently burned forests of northern Mexico were noted as early as 1937 by Leopold and later by Marshall (1957, 1962). They and others (González-Cabán and Sandberg 1989, González-Elizondo et al. 1993, Bye 1995, De Bano and Ffolliott 1995) have called repeatedly for increasing fire ecology research in Mexico. Most recently, Minnich et al. (1995) found that coniferous forests of the Sierra San Pedro Mártir (Baja California Norte), where unmanaged fire regimes continued, remained relatively open and dominated by pines. To our knowledge, however, the present study is the first to examine the relationship between fire regimes and ecosystem structures in the central Sierra Madre Occidental.

4.2 Study Questions

The goal of the present study was to compare ecosystem structures at relatively undisturbed coniferous forest sites in northern Mexico which differed in recent fire history, ranging from extended fire exclusion to continuing frequent fires. We selected study sites and sampling procedures to address the following questions: What are the past and present patterns of fire occurrence on sites representing (a) extended fire exclusion, (b) fire exclusion followed by fire return, and (c) continued frequent fire? Are fires primarily of natural or human origin? Is there a relationship between climatic factors and fire occurrence? Have forest density, basal area, regeneration density, and dead biomass all increased with fire exclusion, consistent with the changes observed in long-needled pine forests of the western U.S. following fire exclusion? Finally, what are

the implications of changing fire regimes for conservation and management of these forests?

4.3 Study Area

The Sierra Madre Occidental, part of the North American cordillera linking the Rocky Mountains with the central Mexican highlands, is an important migratory pathway and a center of endemism (Perry 1991, Manuel and De Jesús 1993). The exceptional biological diversity of the Sierra Madre is comparable to that of tropical rainforests (Felger and Wilson 1995, Bye 1995). While much of the northern Sierra Madre in Durango and Chihuahua has remained relatively undeveloped even 400 years after Spanish colonization due to the rugged and remote landscape, rapid increases in population, infrastructure development, and commercial timber exploitation, are causing substantial shifts and raising international concerns about conservation of the existing social and ecological conditions (Weaver 1993, Bojórquez-Tapia et al. 1995). The study area, a region approximately 2,000 km² in size of pine-oak forests of the Sierra Madre Occidental in northwestern Durango (Figure 4.1), was selected because the relatively recent advent of large-scale timber harvesting (circa 1970) made it possible to find examples of unharvested forest tracts for sampling. Cooperation and assistance from local landowner and forest management organizations facilitated the study.

Four study sites differing in recent fire history were chosen within the study area for fire history and forest structure sampling (Figure 4.1). Selection criteria included no (or minimal) harvesting; evidence of past fires (such as fire scars and charred wood); and

apparent differences in recent fire history ranging from extended fire exclusion to continuing frequent fire up to the present (evidenced by relative amount of fuels, forest density, and relative weathering of charred wood). The first two sites, sites AV (Arroyo Verde, lat. 25° 05' N, lon. 106° 13' W), with extended fire exclusion, and AL (Arroyo Laureles, lat. 24° 57' N, lon. 106° 13' W), with continuing frequent fire, were sampled in July and August, 1993. A preliminary comparison showed that the recent initiation of fire exclusion was associated with increased forest density and fuel accumulation (Fulé and Covington 1994). The third, site SP (Salsipuedes, lat. 25° 15' N, lon. 106° 30' W), representing fire exclusion followed by fire return, was sampled in April, 1994. All three sites were unharvested pine-oak forests. The fourth site, CB (Cebadillas, lat. 24° 53' N, lon. 106° 00' W), also with extended fire exclusion, was a mixed pine-oak-Abies-Pseudotsuga forest in which some of the larger pines had been selectively harvested approximately 15 years prior to sampling in April 1994. Table 4.1 summarizes study site characteristics.

All four study sites were communally owned, sites AV and AL by the Ejido Salto de Camellones, site SP by the Ejido Topia, and site CB by Ejido Hacienditas. Adjacent lands included both *ejido* and private holdings. Most surrounding land with accessible commercially-valuable timber had been selectively harvested at least once. Evidence of natural resource utilization observed on the study sites, in addition to the pine harvest at site CB, included grazing, scattered tree cutting for firewood, poles, shingles, and access to beehives. At the three pine-oak sites, one to several clearings, or *brechas*, for illicit cultivation were found. The *brechas* were small, ranging from 200 m² to 500 m², created

by felling a patch of trees, igniting the dried vegetation, and cultivating the plot for one or more seasons. *Brechas* were deliberately located in steep, remote, forested areas; no firebreaks existed to prevent the burns from passing into the surrounding forest.

The regional climate pattern is dry spring conditions followed by a summer rainy season. Annual precipitation at Ojito de Camellones (elevation 2400 m) is 2200 mm (9 year average), with 80% occurring between June and October. Other weather stations at lower elevations average less annual precipitation: 1540 mm (11 year average) at San Miguel del Cantil (2250 m elevation), 1150 mm (5 year average) at Topia (1800 m elevation), and 740 mm (11 year average) at San Diego de Tensaenz (1550 m elevation). Records of temperature are less available than those of precipitation, but 1992 maximum and minimum temperatures at La Cienega, 12 km west of Ojito de Camellones at 2500 m elevation, were 18° and -8° C in January, and 28° and 7° C in August. Soils are of igneous origin, primarily rhyolitic with scattered basaltic and granitic outcrops (Guizar et al., 1992). The topography is characterized by high-elevation mesas dissected by steep canyons.

4.4 Methods

4.4.1 Field Sampling

Sampling was carried out on systematic grids designed to simultaneously measure fire history and forest structural characteristics. The grid spacing was 150 m X 150 m at sites AV and AL (total site size 70 ha each) and 100 m X 100 m at the smaller sites SP and CB (30 ha each). Figure 4.2 shows the sampling layouts at each study site.

Thirty sampling points were established at each study site and used as the center points of nested sampling plots varying in size. Fire scars were sampled at the largest scale, represented by the 150 m or 100 m interplot distance. Following a search of 75 or 50 m radius centered on each sampling point, the tree catfaces apparently containing the oldest scars and/or the best record of multiple fires were selected for sampling (Arno and Sneck 1977, Swetnam and Baisan 1996). Because of the ongoing fire regimes or recent onset of fire exclusion at the study sites, most fire scar samples were taken as partial cross sections cut from living trees, although samples from snags, logs, and stumps were also collected. The geographic location of each fire scar sample was referenced (distance and bearing) to the sample point center. Figure 4.2 maps fire scar sample locations relative to the plot sampling grid and lists sample identification numbers.

Overstory vegetation was sampled on circular plots 200 m² in size (radius = 7.98 m) centered on each sampling grid point. In the context of this study, all woody plants over 1.3 m in height were considered "overstory" vegetation, as contrasted with the woody seedlings described below. Species, condition, height, live crown ratio, presence of lightning scars, and diameter at breast height (dbh, 1.3 m above ground level) were recorded for all live and dead trees over 1.3 m in height, as well as for stumps and dead and downed trees which surpassed breast height while alive. Condition classes were assigned based on a tree, snag and log classification system originally developed in ponderosa pine/mixed conifer forests of the Blue Mountains of Oregon (Maser et al. 1979, Thomas et al. 1979) and widely applied in ponderosa pine forests (Rogers et al. 1984, Covington and Moore 1994a,b, Lundquist 1995). Condition classes were (1) live;

(2) declining; (3) recent snag; (4) loose bark snag; (5) clean snag; (6) snag broken above dbh; (7) snag broken below dbh; (8) downed dead tree; and (9) cut stump. Increment cores were taken at 45 cm above ground level from all living conifers over 6 cm dbh.

Woody regeneration, defined as tree seedlings below 1.3 in height, was sampled on nested circular plots 40 m^2 in size (radius = 3.57 m). The number of woody stems on each plot was tallied by species. Percent cover by herbaceous species was also estimated visually on each 40 m^2 plot.

Dead woody biomass and forest floor depth were sampled along a 15-m planar transect laid out in a randomly-selected direction from the center of each sample plot (Brown 1974). Intercepts of the transects with woody fuels in the diameter classes 0-0.6 cm, 0.6-2.5 cm, and 2.5-7.6 cm were tallied along the first 5 m; diameters of sound and rotten fuels larger than 7.6 cm were measured along the entire transect. Depth of litter and duff was recorded every 5 m.

4.4.2 Analysis

Dendrochronology--fire scar samples

In the laboratory, fire scar samples were surfaced, mounted on plywood backing, and sanded with increasingly finer belts up to 400 grit abrasive. A total of 105 fire scar samples was crossdated (Stokes and Smiley 1968) with master tree-ring chronologies previously developed in the region (Harlan 1973) and others developed in the present study. Most samples were less than 200 years old and could be crossdated visually using characteristic patterns of narrow marker years, especially in the twentieth century: 1860,

62, 87, 1902, 04, 09, 25, 34, 43, 51, 56, 63, 71, 74. Several samples from dead trees were initially dated as floating tree-ring width series with the COFECHA program (Grissino-Mayer and Holmes 1993), then dating was confirmed visually on each sample. After dating, ring widths of all samples were measured and dating was checked with COFECHA as well as by independent visual crossdating of a 20% to 30% subset of samples by another dendrochronologist. To measure the season of occurrence of fires (Baisan and Swetnam 1990), the relative position of each fire scar within the ring was recorded using the following categories: EE (early earlywood), ME (middle earlywood), LE (late earlywood), L (latewood), and D (dormant season, scar occurring between the cessation of latewood growth and the beginning of the next year's earlywood growth). The assumption that dormant season scars are generally spring fires in the southwestern United States (Baisan and Swetnam 1990) appeared valid for the similar climate patterns and spring fire season of the central Sierra Madre Occidental, although the possibility of dormant scars forming in the fall following latewood growth cannot be excluded. From the four study sites, a total of 637 fire scars were dated to the year and season (if determinable) of origin.

Forest structure analysis

Overstory age structure was determined from ring counts of surfaced and mounted increment core samples, using known patterns of narrow marker years to correct ring counts by visual crossdating whenever possible. The ring counting provides a rapid age estimate highly accurate within 10-year age classes, adequate for the purposes of this

study in which approximately 1,000 cores were collected for age determination. For cores which missed the pith, a pith locator consisting of a transparent overlay of concentric circles was used. An appropriate circle set was selected based on the curvature of the rings nearest the center and the average growth rate of rings near the center. "Tree age" in the following sections refers to total age at the 45 cm coring height.

Dead woody biomass was calculated from the planar transect intercept tallies using the method of Sánchez and Zerecero (1983), which is analogous to the method of Brown (1974) and is commonly applied in Mexican temperate forests. Basal area (m²/ha) and density (number/ha) were calculated for living overstory trees, recent snags, older snags, dead and downed trees, and stumps, and density of regeneration was also calculated.

Statistical analysis

Statistical analysis of the fire history data was facilitated by the capabilities of the FHX2 fire analysis software developed by Grissino-Mayer (1995). Fire return intervals were analyzed statistically beginning in the first year in which an adequate sample depth of recording trees occurred at each site (Grissino-Mayer et al. 1994). The minimum sample depth was taken to be the first fire year with three recording trees (10% or more of the total sample size at each site). Fire return intervals were analyzed statistically in different sub-categories. First, all fire years, even those represented by a single scar, were considered. Then only those fire years were included in which respectively 10% or more, and 25% or more, of the recording samples were scarred. These categories help define 'widespread' fires which may have been larger in area or more intense (Grissino-Mayer

1995). The statistical analysis of fire return intervals includes several measures of central tendency: the mean fire interval (average number of years between fires), the median, and the Weibull median probability interval (WMPI). The latter statistic is a central measure in the Weibull distribution, which is useful to model asymmetric fire interval distributions and to express fire return intervals in probabilistic terms (Johnson 1992, Grissino-Mayer et al. 1994, Swetnam and Baisan 1996). Finally, the maximum hazard fire interval (100% Hazard) is the time in years at which the 100% probability level is reached in the Weibull distribution. Theoretically, the hazard interval represents the maximum fire-free period possible in the modeled distribution, and may be compared with the actual maximum fire return intervals (see Grissino-Mayer 1995 for discussion of the properties of the Weibull distribution).

Statistical analysis of forest structure was carried out with the SYSTAT software (Wilkinson 1988). Alpha level for all analyses was .05. Multivariate analysis of variance (Tabachnick and Fidell 1983, p. 222-291) was used to determine differences between sites on intercorrelated measured variables, such as the suite of dead woody biomass variables. If a significant difference was found between sites (Wilk's lambda statistic), then Tukey's honest significant difference (HSD) test (Zar 1984, p. 186, Day and Quinn 1989) was used for multiple comparisons among means at the four study sites.

4.5 Results

4.5.1 Fire Disturbance History

The fire history results confirmed that all four study sites burned frequently in the past but periods of extended fire exclusion in the twentieth century occurred at 3 of the sites, while the fourth continued to burn frequently up to the present. The fire disturbance histories at the four study sites are summarized in the master fire charts shown in Figure 4.3a-d and compared graphically in Figure 4.4. The horizontal lines in each chart represent individual fire scar samples. The sample identification numbers at the right are the same as those shown in the fire scar sample map (Figure 4.2). The horizontal lines are dashed when the sample is not considered a recording tree, usually before the first scar forms an open wound susceptible to repeated scarring from subsequent fires, or during periods in which fire scars have been burnt away completely (Swetnam and Baisan 1996, Grissino-Mayer 1995). Continuous lines indicate recording periods. Short vertical bars show the years in which each sample was scarred. Beneath the individual samples, a composite line lists all the fire years at the site. The time span of the fire histories is relatively short (maximum 196 years) compared to fire histories from the southwestern United States (Swetnam and Baisan 1996, Grissino-Mayer 1995); this is due to a combination of the relatively short lifespan of trees at the study sites (see age distribution below) as well as to the fact that recurring fires up to the mid-twentieth century or to the present have consumed relict wood which often is used to extend U.S. fire histories into the past (Baisan and Swetnam 1990).

Prior to fire regime disruption, all four sites had mean fire return intervals of less than 5 years (Table 4.2) when all fire years are included and mean fire return intervals of 9 or fewer years for widespread fires (scarring 25% or more of the recording trees). The three measures of central tendency in Table 4.2 agreed closely when the number of fire return intervals was high (e.g., the all-scar and 10%-scarred distributions), but showed less agreement when the number of intervals was low (e.g., the 25%-scarred distribution). Similarly, the 100% hazard value of Weibull distribution agreed less closely with the observed maximum fire-free interval when the number of intervals was low (e.g., the 25%-scarred distribution).

The areal extent and intensity of past fires affect the scale and nature of fire effects on ecosystem structures but spatial fire patterns are difficult to estimate in ecosystems characterized by frequent, low-intensity fire where forest stand boundaries do not correspond with fire edges (Swetnam and Dieterich 1985, Swetnam and Baisan 1996). Since fires are frequently not recorded even on trees with open fire scars (Dieterich and Swetnam 1984), a direct relationship between the percent of fire scarring and the size or intensity of a given fire cannot be drawn. Still, some connection logically exists between the extent of scarring and fire behavior in terms of areal extent of spread and/or intensity of burning. Furthermore, because sampling systematically covered each study area, the grid-based fire scar sampling design (Figure 4.2) helps support spatial interpretations of fire spread since sampling covers the entire area (see Arno et al. 1993 for a similar approach).

Spatially homogeneous fire regimes prevailed at all four sites, consistent with the lack of topographic or vegetative barriers to fire spread on the sites and the fact that fires could have persisted for extended periods in the absence of fire suppression activities. Spatial homogeneity of the fire regimes was examined by dividing each area along its shortest axis into two roughly equal sections. Fire return intervals and percentage of scarring between the two sections of each study site for the all-scar, 10%-scar, and 25%scar distributions were tested for significantly different means (t-test), variances (F-test), and distributions (Kolmogorov-Smirnov test). Alpha level for all tests was .05. No consistent pattern of significant differences between sections within study sites was found, although a few individual test statistics were marginally significant at site AL (see discussion below). In addition, the synchroneity of fire years in the two sections of each site was tested (chi-square test, 2 X 2 contingency table, Grissino-Mayer 1995). The null hypothesis of statistically independent fire chronologies between sections was rejected for all three test distributions at all sites. Although no spatial differences were observed at this scale of comparison, some smaller-scale spatial patterns of fire were detected at sites AV and AL (see below).

Seasonal patterns of fire occurrence (Table 4.3) show that 60%-77% of fires burned in the spring and the remainder in the summer. At no site did late earlywood scars exceed 10% of the total and no latewood fires were observed. This seasonal distribution is similar to patterns observed in Arizona (Baisan and Swetnam 1990) and New Mexico (Allen et al. 1995, Grissino-Mayer 1995).

Site AV (Arroyo Verde): 47 years fire exclusion

The fire history at site AV was characterized by a disruption of the fire regime after 1945 (Figure 4.3a). Although the first recorded fire occurred in 1764, the analysis period begins with 1801, the first fire year for which 3 recording trees exist in the data set. A pattern of frequent fires is seen from 1801 to 1945 (MFI for all scars = 3.79 years, Table 4.2), although an unusually long fire-free interval of 12 years occurred between 1929 and 1941. Since the 1941 fire was only recorded on a single sample, the effective fire-free period comprised the 16 years between 1929 and 1945. However, the 1945 fire burned across the entire site, scarring 63% of the recording trees. The site has not experienced a widespread burn scarring 25% or more of recording trees in the 47 years from 1945 to the sampling date, although fires scarring over 10% of the recording trees did burn in 1962 and 1986. A comparison of the sample identification numbers in the master fire chart (Figure 4.3a) with the fire sample map (Figure 4.2) shows that the scarred trees in 1962 and 1986 were confined to the northwest quadrant of the study site, an area where evidence of 2-3 brechas was encountered during sampling.

Patterns of fire exclusion are commonly "messy": Swetnam and Baisan (1994) compared 63 fire histories from the southwestern United States which frequently evidenced a period of reduced fire frequency and sporadic post-disruption burns even after the regional trend of fire exclusion had become firmly established. The identification of a fire regime disruption at site AV is not unequivocal, as would be the case if no fire scars at all were found after 1945. The year 1929 could also be reasonably

¹ A previous comparison of fire regimes at the Arroyo Verde and Arroyo Laureles sites was based on fewer fire scar samples so fire interval results were slightly different (Fulé and Covington 1994). The conclusions about fire regime patterns remain valid.

selected as a disruption date, because of the long fire-free interval which followed.

However, the conclusion that the 1945 fire had important ecological impacts on the ecosystem, while the 1962 and 1986 fires did not impact most of the site, is supported by the forest structure data, particularly the age and size distributions described below.

Site CB (Cebadillas): mixed conifer site, 42 years fire exclusion

Site CB, the high-elevation site with Abies and Pseudotsuga, had clear evidence of recent fire regime disruption, with a fire-free period of 42 years to the present following the last widespread fire in 1951 (Figure 4.3b). The only evidence of post-1951 fire is a single fire scar in 1974. As with site AV, there is also evidence of some earlier fire-regime disruption due to the gap of 22 years between the 1924 and 1946 fires, broken only by the 1934 fire which scarred 13% of the recording trees. Over the analysis period 1797-1951 (Table 4.2), the MFI for all fires (4.97 years) was about 60% less than the MFI for fires scarring 25% or more of the recording trees (8.56 years). These values are only slightly higher than the comparable pre-disruption fire return intervals at the pine-oak sites (Table 4.2), showing that the mixed-conifer site CB, on a high, relatively mesic, north-facing slope, burned at nearly the same frequency as the lower-elevation, relatively xeric sites on southwestern and western aspects. This result contrasts with the longer fire return intervals averaging 52 years for mixed conifer forests of the Sierra San Pedro Mártir in Baja California Norte (Minnich 1993). However, the study by Minnich (1993) was based on identification of fire perimeters from a time series (1942-1991) of aerial photographs, a method that may be less likely to identify frequent, low-intensity fires. In

the southwestern United States, fire history studies based on fire scars in mixed conifer forests have shown pre-disruption (presettlement) MFI values for widespread fires (scarring 20% or more of recording trees) of 22 years (Dieterich 1983a), 11 years (Grissino-Mayer et al. 1995), and 9.9 years (Baisan and Swetnam 1990). Grissino-Mayer et al. (1995) concluded that the fire regime at a mixed-conifer site in southern Arizona was very similar to that of lower-elevation ponderosa pine forests.

Site SP (Salsipuedes): fire exclusion and return

A pattern of recurring fire at site SP (1812-1955 MFI = 4.09 years, Table 4.2) was interrupted by a 29-year period with no widespread fires after 1955 (Figure 4.3c). Single recording trees were scarred in 1963, 1980, and 1982, but widespread fire returned to site SP in 1984, scarring 95% of the recording trees. Nine years later, in 1993, another widespread fire burned the site. Evidence of several *brechas*, including one with a fence surrounding the planted area, was observed at site SP during sampling in 1994. Since site SP is the least accessible of the four study sites, it may have been favored in recent years for illicit cultivation, possibly causing the 1984 and 1993 fires.

Site AL (Arroyo Laureles): frequent fire up to the present

Site AL is the only site which has burned up to the present without a clear period of fire exclusion (Figure 4.3d), providing one of the few examples of a continued frequent forest fire regime in North America (for comparison, see Dieterich 1983a, Swetnam and Baisan 1996). Even at site AL, relatively long gaps of 14 years and 11 years appear

between 1951-1965, and 1969-1980, respectively. But these gaps do not exceed the predisruption maximum fire-free intervals at the other three sites, suggesting that these periods remain within the range of natural variability of undisrupted fire regimes. However, although the 1980 and 1986 fires were widespread (Figure 4.3d), they did not scar trees in approximately the northwestern third of the site. Several of the individual test statistics for spatial differences in fire regime at site AL showed marginal statistical significance (e.g., $p \approx .03-.04$), the only site where some statistical evidence of spatial heterogeneity was observed. If this portion of the study site did not burn between 1965 and 1991, the accumulation of fuel over 26 years may explain the high-intensity 1991 fire behavior evidenced by tree mortality adjacent to the northern site boundary (Fulé and Covington 1994). Site AL was commercially logged in 1994.

Site comparison

Fire histories at the four study sites are compared graphically in Figure 4.4, with twentieth-century fire exclusion increasing in impact from the all-scar comparison (top), which shows a minimal level of recurring fire at most sites up to the present, through the 25%-scarred comparison (bottom), which shows the complete exclusion of widespread fire from sites AV and CB as well as the 29-year exclusion period at site SP. The period 1955-1980 was particularly free of widespread fire, except for the 1965 fire at site AL (Figure 4.4). The regional fire interval analysis including all sites (Table 4.4) for the period 1797-1993 shows that the MFI for fire scarring at least one tree on at least one site was 2.11 years, rising to 15.40 years for fires scarring at least three of the four sites. The

ten years in which three or all four of the sites burned are listed as major regional fire years, from 1835 to 1951, in Table 4.5. These years do not correspond with the 6 major regional fire years identified by Swetnam and Baisan (1994) in the southwestern United States during the overlapping period of their analysis, 1835-1879, possibly reflecting different patterns of climate and ignition as well as the small sample size (4 sites) of the present study. However, half of the major fire years in Table 4.5 (1862, 1887, 1909, 1921, and 1934) correspond to years in which positive winter Southern Oscillation index (SOI) extremes were reconstructed from dendrochronological data in the Sierra Madre Occidental by Stahle and Cleaveland (1993). The positive SOI extremes are associated with cold/dry weather conditions, unfavorable for tree growth but possibly conducive to fire. None of the major fire years in Table 4.5 corresponded to years with negative (warm/wet) SOI extremes (Stahle and Cleaveland 1993). These results are in agreement with the findings of Swetnam and Betancourt (1990), who showed that area burned in the southwestern United States was greatest in years with high positive SOI values and least in low SOI (El Niño) years (Swetnam and Betancourt 1990).

4.5.2 Forest Structure

Species composition

A variety of tree species was encountered on the sampling plots (Table 4.6). For purposes of analysis, trees were grouped as (1) pines (family Pinaceae, including *Abies* and *Pseudotsuga*), (2) oaks (family Fagaceae), and (3) others. Pines, oaks, and *Arbutus* (madrone) were found at all four study areas; other species occurred sporadically.

Live tree structure

Live overstory trees differed significantly in density between sites in a pattern consistent with the thinning effects of fire: sites AV and CB, with extended fire exclusion, had the highest mean densities, up to 2733 trees/ha, while sites SP and AL, with recent fires, had mean densities an order of magnitude lower (Table 4.7). However, basal area was not correlated with density: the most dense site, AL, had the lowest basal area, while there was no statistically significant difference between basal areas at the other three sites (Table 4.7). Site AV was therefore dominated by numerous small trees (quadratic mean diameter 10.4 cm) while sites SP and AL are characterized by fewer, larger trees (quadratic mean diameters 29.0 cm and 27.1 cm respectively). Site CB falls in between (quadratic mean diameter 17.7 cm). The diameter distributions of live trees at the four sites (Figure 4.5a-d) confirm these relationships, with the fire-excluded sites AV and CB having distinct reverse-J shaped distribution curves. Diameters at sites SP and AL, though still positively-skewed, were more normally distributed. All three analysis groups (pines, oaks, and other) generally shared the same relative patterns of diameter distribution at each site (Figure 4.5a-d).

Rates of lightning scarring of live overstory trees were below 3% at all sites, even considering only trees larger than 20 cm dbh. No lightning-scarred trees were encountered at site CB.

Age structure of conifers over 6 cm dbh at the four sites (Figure 4.6a-d) shows the relatively young age of the trees, with the oldest individual (a *Pinus durangensis*) dating

to the mid-1600's and the great majority of trees less than 100 years old. The ages shown in Figure 4.6 at at the sampling height of 45 cm above ground level; the actual age of the trees includes additional years required to grow to this height. Seedling growth rates at the study sites are not known, but southwestern ponderosa pine seedlings may take from 3 to 10 years to reach this height (Sackett 1984, Cormier 1990). Some effects of fire and fire exclusion are reflected in the age distributions, but the patterns are mixed. For example, the overwhelming majority of conifers at site AV (Figure 4.5a) established after the last widespread fire in 1945, but most conifers at site CB (Figure 4.5b) were already well-established before fire exclusion began following the 1951 fire. The gap in the age distribution at site AL (Figure 4.5d) in the mid-twentieth century may be an effect of the widespread 1965 fire killing trees in the younger age classes, but no analogous gap appears in the age distribution at site SP (Figure 4.5c) after the 1984 fire.

The high regeneration density at all sites (several thousand/ha), compared with the low overstory density at the burned sites SP and AL, is consistent with the thinning effect of recent fires at those sites (Table 4.7). Although all tree seedlings below 1.3 m were tallied together in this study, qualitative differences were observed between the sites. Regeneration at the fire-excluded sites AV and CB consisted mainly of dense seedlings and sprouts between 0.5 and 1.3 m, while regeneration at sites SP (last fire 1993) and AL (last fire 1991) typically consisted of very small, young seedlings and sprouts. Numerous pine seedlings at site AL were still shedding seed coats at the time of sampling in August, 1993.

Dead tree structure

Dead tree structure—snags, dead and downed trees, and stumps—is summarized in Table 4.8. Density of recent snags, those with branches and bark still intact, was significantly highest at site SP, where it was evident in the field that the return of fires in 1984 and 1993 after a 29-year fire-free period killed numerous trees. In some parts of site SP, mature oaks or alders appeared to have been killed in 1984. The subsequent thickets of sprouts around the snags were then killed or thinned by the 1993 fire. Older snags were more dense at the fire-excluded sites, reflecting the combustion of older dead material by recent fires at sites SP and AL. Stump density was generally low since three of the four sites had never been harvested on a large scale. Pines at the fourth site, CB, had been selectively harvested at a mean density of 13.3 trees/ha (Table 4.8). Although the majority of dead trees at all sites was in smaller diameter classes (Figure 4.7a-d), the densities of the smallest snags were sharply higher at the recently burned sites SP and AL, consistent with the thinning effect of fire.

Dead woody biomass and herbaceous cover

Dead woody biomass ranged from a low of 7.1 metric tons/ha at site SP to a high of 53.2 metric tons/ha at site CB (Table 4.9). The fire-excluded sites had higher dead woody biomass loads than the recently burned sites, although only the very high loading at site CB was statistically significantly different. The biggest difference was in rotten woody biomass, where the fire-excluded sites had loadings several times those of the recently burned sites. Litter depth was similar at all sites, but duff depth was significantly

lower at the recently burned sites. These characteristics, particularly the rotten woody loading and duff depth, match the expected effects of fire in consuming these fuels. The comparable levels of forest litter suggest that burned and unburned sites both have continuous fine fuels which can support fire, and that even recently burned sites (site SP burned 1 year before sampling, site AL 2 years before sampling) can quickly recover fine fuel loadings similar to those of unburned sites. The heavy fuel loadings at the unburned sites, particularly of flammable rotten fuels, indicate that the fire-excluded sites have accumulated fuel beyond the range normally found in burned forests, fuels which can support high-intensity fire. Herbaceous cover was relatively low at all four sites, ranging from 10% to 20%, but tended to be higher at the recently burned sites, as expected, given their lower overstory densities.

4.6 Discussion

4.6.1 Patterns of Fire Occurrence

The high frequency of fire in the Sierra Madre Occidental indicates that sources of ignition, weather patterns favorable to fire spread, and adequate contiguous fuels exist across the region. Evidence of both lightning and human-caused ignition (*brechas*) was observed directly on the study sites, except for site CB. The rates of these sources of direct ignition were apparently relatively low compared to the high frequency of fire (less than 3% lightning scarring of trees; one to several *brechas* per site), but the general absence of natural or artificial firebreaks around the study sites would permit fires to enter from outside the sites and cross large areas without impediment. The perennial streams

forming the downslope boundaries of sites AV and AL were narrow enough (5-10 m) for fires to spot across readily under windy conditions. Roads came close to sites AV, CB, and AL, but they are of recent construction (post-1970) and are also relatively narrow (\approx 3-4 m) and often covered with fine fuels consisting of leaves and needles from the surrounding forest.

Foresters and landowners in the study area ascribe most fire starts to humancaused ignitions, resulting from burning of pastures and agricultural fields, brechas, campfires, and smoking, a widely-held view in Mexico. Both official statistics (González-Cabán 1989, SARH 1994) as well as some botanical and ecological studies of Mexican forests (e.g., Loock 1950, Perry 1991, Fisher et al. 1995) reflect this attitude, grounded in documented cases of deforestation caused by repeated agricultural burning, primarily in the heavily-populated central Mexican states (Martínez 1948, Perry 1991). Prior to Spanish colonization, indigenous inhabitants of the study area, including Acaxee, Xixime, and Tepehuán peoples (Pennington 1969, Gerhard 1982), also used fire. Ethnographic studies of the historic Tepehuán (who no longer inhabit the study area) and Rarámuri (Tarahumara) people, who live in similar forest and canyon ecosystems within 100 km of the study area, describe fire use for clearing agricultural fields, hunting, and warfare (Lumholtz 1902, Pennington 1963, 1969). Lightning is broadly considered a minor source of ignition both at the national level (SARH 1994) and in the study area (J.G. Paredes Pérez, Forester, personal communication 1993) because it is generally accompanied by heavy rain and high humidity.

However, the role of natural ignitions may in fact be very significant in maintaining frequent fire regimes in the central Sierra Madre Occidental. Lightning ignitions in the study area can smolder until favorable burning conditions return (P.Z. Fulé, personal observation 1994). Furthermore, the human population of the study area has changed substantially since Spanish colonization, with the indigenous population in the region of the study area falling from an estimated 10,000 in 1500 A.D. to 500 by 1700 A.D. (Gerhard 1982). Although the Spanish city of Santiago Papasquiaro was founded in 1593 A.D. and mining exploration in the Sierra Madre began shortly afterward, Hispanic settlement across much of the central Sierra Madre Occidental was limited until the expansion of ejidos into government-controlled forest land after the Second World War. Considering the relatively stable pattern of pre-disruption fires found at the four study sites in this study from approximately 1800 through the 1920's to 1950's, despite low and fluctuating human populations, it seems likely that lightning has been an important ignition source. When longer fire chronologies are developed from the Sierra Madre, more detailed comparisons of changes in fire frequency and human presence can be carried out

While recent human activities are probably related to the patterns of fire exclusion at the four study sites, specific reasons for the differing patterns of fire exclusion are not known. Fire exclusion at sites AV and CB, and the 29-year fire exclusion period at site SP, may be due to changes in grazing, roads, or agricultural practices and may be associated with the establishment of *ejidos*. At least some of the recent fires at sites AV, AL, and SP, however, appear to be due to the deliberate burning of *brechas*.

Climatic factors appear to influence fire regimes in the study area in a manner similar to climate-fire relations in the southwestern United States. Both the spring-summer fire season, as well as the apparently strong response of tree growth (Stahle and Cleaveland 1993) and regional fire occurrence (Table 4.5) to positive Southern Oscillation index extremes, are similar to southwestern patterns (Swetnam and Betancourt 1990, Swetnam and Baisan 1996). As additional fire history data is collected in northern Mexico, a more detailed analysis of the climate-fire relationship should be developed to increase understanding of past and present ecological conditions as well as to improve prediction of short-term and long-term changes in fire frequency and intensity (Swetnam and Betancourt 1990).

4.6.2 Fire and Forest Structure

Forest ecosystem structures appeared to be closely linked to fire patterns at the four study sites. The descriptive comparison among different sites forming a chronosequence of fire exclusion in this study cannot statistically separate fire effects from the variety of other factors influencing forest structure and dynamics. However, the trend from relatively open forests of large trees at the recently burned sites AL and SP to the relatively dense forests of small trees at the fire-excluded sites AV and CB, together with the differences in regeneration, age and diameter distributions, dead tree structure, dead woody biomass loadings, and herbaceous cover, are consistent with the effects of frequent fire in thinning small, young trees and maintaining low levels of woody fuels and duff.

Fire exclusion impacts have received relatively little attention in Mexico.

Although beneficial aspects of fire as a silvicultural tool and as a natural ecological disturbance factor have been recognized within the scientific community (Sánchez Cordova and Dieterich 1983, Rodríguez Trejo and Sierra Pineda 1992), public perceptions have been influenced by anti-fire publicity (Rodríguez Trejo and Sierra Pineda 1992). In the United States, the attention of land managers and the public has been focused on the hazards of fire exclusion as a result of increasingly large, destructive, and costly wildfires in fire-excluded ecosystems (Swetnam 1990, Covington et al. 1994). By contrast, in Mexico large high-intensity fires are rare, perhaps as a consequence of low fuels from frequent burning, relatively short periods of fire exclusion, and a mosaic of forest patches burned at different times, analogous to the chaparral patterns in Baja California Norte (Minnich 1983). A recent government report on national wildfire status (SARH 1994) described Mexican forest fires as affecting the herbaceous vegetation but only rarely the tree crowns.²

As fire exclusion periods lengthen, however, wildfire behavior is likely to intensify. The high overstory densities and heavy fuel loading observed at the fire-excluded sites in this study are likely to support high-intensity fire with extensive tree mortality. Taking site SP as an example of the return of fire to a fire-excluded ecosystem, if the densities of recently-killed trees and living trees are summed as a rough approximation of forest density after 29 years of fire exclusion (total 914 trees/ha), the 1984 and 1993 fires killed up to 40% of the trees at the site. Despite this tree mortality,

² "En México los incendios forestales son de tipo superficial; es decir, afectan vegetación herbácea y rara vez la copa de los árboles."

the ecosystem at site SP remains a pine-oak forest. The outcome of the next wildfire at sites AV and CB may be different, as these fire-excluded sites have overstory densities 150% to 300% that of site SP, as well as very high woody fuel loading, so high-intensity fire could lead to heavy mortality or deforestation. The hazard is augmented through fuel structures such as flammable rotten wood, deep forest floors which burn slowly with extended periods of lethal temperatures, and fuel ladders composed of smaller and midsized trees that carry fire into the overstory crowns.

Further fire ecology research and increased application of innovative fire management practices such as prescribed burning will be invaluable in helping to reconcile the paradoxical nature of fire, seen both as an essential ecological process and as the destroyer of the forest. The contradictory nature of these perspectives on fire is evident in the Sierra Madre Occidental. As populations rise and as the infrastructure needed for timber exploitation is developed, landowners and foresters have become increasingly aware of timber values and have initiated extensive campaigns to prevent, detect, and suppress forest fires. Ejido members are proud of their contributions to fire prevention and suppression crews (P.Z. Fulé, personal observation, 1994). However, the regime of frequent, low-intensity fire which has prevailed till recently in these forests is a key ecological process contributing to the present health and low destructive potential of fuels in many of these forests today (Leopold 1937, Marshall 1962, Fulé and Covington 1994, Baisan and Swetnam 1995). Another example of a problematic fire paradigm is expressed in a recent study which concluded that these northern states are becoming deforested because the area reforested (i.e., planted) is a tiny fraction of the area burned

(Fisher et al. 1995); the authors explicitly make the unsubstantiated assumption of 100% mortality from fire. While the authors appear to be motivated by a commendable desire to preserve these unique ecosystems, the present study and numerous others suggest that the unintended consequence of a fire exclusion approach to preservation is likely to be the replacement of frequent low-intensity fires with infrequent, high-intensity, stand-killing fires.

4.7 Conclusions

Fire disturbance history and forest structure at four study sites differing in recent fire history were compared. Frequent, low-intensity fires characterized all the sites until the initiation of fire exclusion in the mid-twentieth century at three of the four sites. Two sites had fire exclusion periods of 47 and 42 years, up to the present, the third site underwent fire exclusion for 29 years before widespread fires returned, and the final site had frequent fires recurring up to the present. Pre-disruption fire return intervals were notably similar at all sites, between 4 to 5 years for all fires and 6 to 9 years for widespread fires. A mixed conifer site had fire frequencies very similar to those of the three pine-oak sites, until disruption of the frequent fire regime. The fire return intervals closely match pre-disruption fire frequencies in the southwestern United States, but fire regime disruption appeared 50 to 70 years later (circa 1945-1955) in the Sierra Madre Occidental.

Although most fires in the study area are ascribed to human ignitions, evidence of both lightning and human-caused burning was observed on the study sites. Since the

present study found a relatively stable long-term pattern of frequent fire from approximately 1800 to the mid-twentieth century, despite low and shifting population densities during that period, the importance of lightning as an ignition source should not be discounted.

A possible connection between fire occurrence and climate was observed in the ten major fire years in which 3 or all 4 of the study sites burned from 1835 to 1951. Five of these regional fire years corresponded to years in which positive extremes of the Southern Oscillation index (SOI) were observed or reconstructed from dendrochronological data, suggesting that the cold/dry conditions associated with positive SOI extremes may have influenced regional fire occurrence. None of the regional fires corresponded with negative SOI extremes, characterized by warm/wet conditions.

Forest ecosystem structures differed in ways consistent with the thinning and fuel consuming effects of fire. Sites with extended fire exclusion were characterized by relatively dense stands of smaller trees, high dead woody biomass loading, and deeper forest floors. In contrast, the site which had burned following a 29-year fire exclusion period, and the final site where frequent fires had continued up to the present, were both relatively open forests dominated by larger trees. The burned sites had lower dead woody biomass loading, especially of rotten woody fuels, and more shallow duff layers. Age structure distributions showed that the majority of conifers established after fire exclusion at one study site. Tree regeneration densities were roughly comparable at all sites although qualitative differences were observed between the fire-excluded and recently

burned sites. The high regeneration density but low overstory density at the recently burned sites is consistent with the thinning effect of low-intensity fire.

The dense forests with heavy fuel loading encountered at the fire-excluded sites are likely to burn with high-intensity fire in the future. At a national scale, Mexico has had relatively little problem with large, intense wildfires such as burn commonly today in fire-excluded long-needled pine forests of the western United States. The present study suggests that the relatively shorter period of fire exclusion in Mexico, combined with a mosaic of fire-excluded and recently burned sites due to the relaxed fire suppression policy, may have helped limit the development of extensive heavy fuel conditions across the landscape. Fire hazard and destructiveness in the Sierra Madre Occidental may increase, however, with further fire exclusion. We recommend further research in the ecology of fire and the potential for application of prescribed fire as a tool for management and conservation of these unique and diverse ecosystems.

Table 4.1. Study site characteristics.

Site	Size	Elevation	Slope	Aspect	Forest Type
AV	70 ha	2200-2500	37%	sw	Pine-oak unharvested
СВ	70 ha	2850-2950	32%	N	Pine-oak-Abies-Pseudotsuga selectively harvested
SP	30 ha	2300-2500	47%	W (SW & NW)	Pine-oak unharvested
AL	30 ha	2200-2500	54%	sw	Pine-oak unharvested

Table 4.2. Fire return intervals at the four study sites. Statistical analysis was carried out in three categories: (1) all fire years, including those represented by a single fire scar; (2) fire years in which 10% or more of the recording trees were scarred; and (3) fire years in which 25% or more of the recording trees were scarred. For those sites where a disruption of the long-term fire regime was identified (sites AV, CB, and SP), fire return intervals are presented both for the predisruption period as well as the full historical recording period.

Site/Analysis Period Scar Category	Number of Intervals	Mean (MFI)	Median	Standard Deviation	Minimum	Maximum	WMPI	%001 HazzeH
Site AV / 1801-1992								
All scars	42	4.55	4.0	3 38	_	12	900	-
10% scarred	33	5.79	5.0	18.4		24	60.4 00.4	4 70
25% scarred	17	11.24	7.0	10.48	. 4	47	9.63	120
Site AV / 1801-1945								
All scars	38	3.79	3.0	2.20		13	3 58	,
10% scarred	30	4.80	4.0	2.96		<u>. 5</u>	4.49	2 ,
25% scarred	91	00.6	6.5	5.15	4	81	8.47	34
Site CB / 1797-1993								
All scars	33	5.94	5.0	4.96		23	818	33
10% scarred	30	6.53	5.0	5.02		23	5.79	33
25% scarred	61	10.32	0.9	10.27		42	8.31	290
Site CB / 1797-1951								
All scars	31	4.97	4.0	3.14	_	14	4 50	2
10% scarred	28	5.50	5.0	3.19		14	5.16	<u> </u>
25% scarred	81	8.56	5.5	7.03	_	31	7.43	121

100% Hazard 7 7 10 12 18 18 æ 6 = WMPI 4.21 5.00 7.08 3.96 4.53 6.41 4.44 4.89 6.43 Maximum 17 29 29 9 9 15 4 1 1 5 Minimum - 2 6 - 2 6 355 Standard Deviation 1.90 1.98 2.84 2.91 4.70 5.34 2.87 2.88 3.32 Median 4.0 4.0 4.0 Mean (MFI) 4.535.497.54 4.09 4.61 6.50 4.67 5.09 6.59 Number of Intervals 40 33 24 35 31 22 24 22 17 10% scarred 25% scarred All scars 10% scarred 25% scarred 10% scarred 25% scarred Sitc/Analysis Period Site SP / 1812-1993 Site AL / 1879-1992 Site SP / 1812-1955 All scars All scars Scar Category

Table 4.2 continued.

Table 4.3. Seasonal distribution (number and percent) of fire scars at the four study sites based on the position of the fire injury within the scarred tree ring.

Site	Season Determined	Season Undetermined	Dormant	Early Earlywood	Middle Earlywood	Late Earlywood	Late- wood	Late- Dormant + Early Middle + Late wood (= spring fires) (= summer fires)	Middle + Late (= summer fires)
۸۸	102 (68%)	48 (32%)	(%99) L9	11 (11%)	20 (20%)	4 (4%)	0	78 (77%)	24 (23%)
CB	66 (62%)	40 (38%)	28 (42%)	15 (23%)	17 (26%)	(%6) 9	0	43 (65%)	23 (35%)
SP	166 (70%)	(%08) 89	92 (55%)	26 (16%)	47 (28%)	, (%1)1	0	118 (71%)	48 (29%)
AL	114 (78%)	33 (22%)	48 (42%)	20 (18%)	39 (34%)	7 (6%)	0	(%09) 89	46 (40%)

Table 4.4. Regional fire interval analysis comparing fire years over all four sites. The analysis period is 1797-1993.

Site/Analysis Period Scar Category	Number of Intervals	Mean (MFI)	Median	Standard Deviation	Minimum	Maximum	WMPI	100% Hazard
B	S							
Sall illes	6,6	7.11	2.0	1.27		7	1.97	2
33% or more sites	57	3.44	3.0	3.33	_	23	2.96	∞
50% or more sites	42	4.67	4.0	3.78	_	23	4.13	91
75% or more sites	01	15.40	11.5	10.74	2	38	13.68	1337

Table 4.5. Major regional fire years based on the percentage of fire occurrence at the four study sites.

Year	Number of Sites Scarred	Number of Recording Sites	Percent of Sites Burned	Fire
		Recording Sites	Sites Burlied	Interval
1835	3	3	100%	_
1860	3	3	100%	25
1862	3	3	100%	2
1887	3	4	75%	25
1898	3	4	75%	11
1909	3	4	75%	11
1921	3	4	75%	12
1934	3	4	75%	13
1945	3	4	75%	11
1951	3	4	75%	6

Table 4.6. Tree species encountered on the study sites. Nomenclature follows González et al. (1991).

Family	Species	Common Name
Betulaceae	Alnus spp.	Alder
Cupressaceae	Juniperus depeanna Steud.	Alligator juniper
	Juniperus spp.	Juniper
Ericaceae	Arbutus spp.	Madrone
Fagaceae	Quercus coccolobifolia Trel.	Encino roble
	Q. laeta Liebm.	Encino blanco
	Q. sideroxyla Humb. & Bonpl.	Encino prieto
	Quercus spp.	Encino
Pinaceae	Abies durangensis Mtz.	Durango fir
	Pinus arizonica Engelm.	Arizona pine
	P. ayacahuite K. Ehrenb.	Pino blanco
	P. durangensis Mtz.	Durango pine
	P. engelmannii Carr.	Apache pine
	P. herrerai Mtz.	
	P. leiophylla Schlect. & Cham.	Chihuahua pine
	P. lumholtzi Rob. & Fern.	Pino triste
	P. teocote Schlect. & Cham.	
	Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir
Rosaceae	Prunus serotina Ehrh.	Cerezo
	Unknowncommon name "fresno"	

Table 4.7. Forest structural characteristics (basal area and density) of living overstory trees and regeneneration density at the four study sites. Within-row means followed by different letters are significantly different (p < .05). N = 30 at all sites.

	Š	Site AV	Sic	Site CB	is	Site Sp	Sir	Cito A I
	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
Live Basal A	Live Basal Area				ha			
Pinc	12.9 a	1.2	14.2 ac	∞ :	24.8 b	3,3	22.6 bc	- E
Oak	8.9 a	6:0	18.1 b	3,3	8.9 a	1.3	13.5 ab	6
Other	1.6 ab	0.4	5.7 a	2.1	3.1 ab	6.0	1.1 b	0.4
Total	23.4 a	1.6	38.0 b	3.6	36.8 b	3.6	37.2 b	2.9
Live Tree Density	nsity			qunu	number/ha			
Pine	1499 a	235	842 b	96	288 c	40	275 c	41
Oak	980 a	107	373 b	19	167 b	26	287 b	47
Other	253 a	38	327 a	54	103 b	24	85 b	26
Total	2733 a	264	1541 b	146	558 c	19	647 c	8
Regeneration Density	Density	2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0		number/ha	cr/ha			
Pine	1525 a	695	1041 a	254	575 a	134	3542 h	040
Oak	3675 a	819	7083 a	1205	7442 a	1348	4200 a	1119
Other	675 a	141	1358 а	257	3975 b	929	983.9	703
Total	5875 a	969	9483 ab	1247	11992 b	1897	8725 ab	1333

Table 4.8. Forest structural characteristics (basal area and density) of snags, dead/down trees, and cut stumps at the four study sites. Within-row means followed by different letters are significantly different (p < .05). N = 30 at all sites. "Recent" snags have intact bark and branches (condition class 3); "older" snags are in more advanced conditions of decay (condition classes 4 through 7).

	Mean	Site AV S.E.M.	S Mean	Site CB S.E.M.	Sin Mean	Site SP S.E.M.	Site Mean	Site AL S.E.M.
Recent Snag Basal Area	Basal Area			E	m²/ha			
Pine Oak Other Total	1.0 a 0.2 a 0.01 a 1.2 ab	0.3 0.2 0.01 0.4	0.03 a 0.05 a 0.02 a 0.1 a	0.01 0.03 0.02 0.04	1.0 a 0.4 a 0.5 b 1.9 b	0.3 0.2 0.5	1.2 a 0.1 a 0.2 ab 1.5 ab	0.4 0.1 0.5
Recent Snag Density	Density	7		number/ha	er/ha			
Pine Oak Other Total	105.4 a 8.3 a 6.7 a 120.4 a	30.3 4.2 3.2 30.0	20.0 b 10.0 a 3.3 a 33.3 a	7.4 5.0 3.3	68.3 ab 151.7 a 136.7 b 356.7 b	17.9 79.1 51.5	73.3 ab 31.7 a 30.0 a	18.1 11.9 15.6
Older Snag Basal Area ^A	asal Area ^A				m²/ha		# D	
Pine Oak Other Total	1.5 0.2 0.01 1.7	0.5 0.1 0.01 0.5	2.0 0.4 0.5 2.9	1.1 0.3 0.5 1.5	1.2 0.3 0.1	0.6 0.3 0.9	0.8 0.01 1.0	0.6 0.004 0.2 0.6
Older Snag Density	ensity			number/ha	er/ha			
Pine Oak Other Total	45.8 a 6.7 a 1.7 a 54.2 a	10.2 4.0 1.7 11.9	11.7 b 11.7 a 3.2 a 26.7 ab	5.7 5.2 2.3 10.6	15.0 b 1.7 a 1.7 a 18.3 b	4.3 1.7 1.7 5.1	11.7 b 3.3 a 1.7 a 16.7 b	5.2 2.3 1.7 6.0

Table 4.8. Continued.

		Moon	Site AV	Mess	Site CB		Site SP		Site AL	
24 1.0 1.0 0.7 1.3 0.7 1.8 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0		Micall	S.E.IVI.	IMCall	S.E.M.	Mean	S.E.M.	Mean	S.E.M.	
24 1.0 1.0 0.7 1.3 0.7 1.8 0.3 0.0.9 0.3 0.0.9 0.3 0.0.9 0.0.0 0.0	Dead/Down	Basal Arca ^A			Ш	1 ² /ha				
0.04 0.04 0.4 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3 0.3	Pine	2.4	1.0	1.0	0.7	1.3	0.7	8:	0.7	
0.04 0.04 0 0 0 0 0.5 2.5 1.0 1.4 0.7 1.6 0.7 2.6 18sity 68.3a 25.1 6.7b 3.2 10.0b 4.4 31.7 ab 0.8 0.8 0 0 0 0 11.7 72.5a 25.4 10.0b 3.7 11.7b 4.6 55.0 ab 1.00 0.02 0.02 0.0 0 0 0 0.05 0.05 0.0 0 0 0 0.06 3.2 1.7 1.2 0.06 3.2 1.7 1.3 5.8 0 0 0 0 0 0 0 1.7 0 0 0 0 1.7 0 0 0 0 1.8 0 0 0 1.7 0 0 0 1.8 0 0 0 1.8 0 0 0 1.9 0 0 1.1 0 0 0 1.1 0 0 0 1.2 0 0 1.2 0 0 1.3 1.3 5.8 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Oak	0.04	0.04	0.4	0.3	0.3	0.3	0.3	0.2	
68.3a 25.1 6.7b 3.2 10.0b 4.4 31.7ab 3.3 a 2.3 1.7a 1.7a 1.7a 11.7a 11.7b 4.6 55.0ab 11.7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Other	0.04 2.5	0.04	0	0	0	0	0.5	0.3	
68.3a 25.1 6.7b 3.2 100 b 4.4 31.7 ab 3.3 a 2.3 1.7 a 11.7		<u>;</u>	2	r:	7.0	0.1	\.O	7.0	0.8	
68.3 a 25.1 6.7 b 3.2 10.0 b 4.4 31.7 ab 3.1 ab 3.3 a 2.3 1.7 a 11.7 a 11.7 a 11.7 a 0.8 0.8 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	Dead/Down	Density			unu	ber/ha				
3.3 a 2.3 3.3 a 2.3 1.7 11.7 a 11.7 a 0.8 0.8 0.8 0.8 0.0 0 0 0.0 11.7 11.7 b 0.0 0.0 0.0 11.7 11.7 b 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	Pinc	68.3 а	25.1	6.7 b	3.2	10.0 b	4.	31.7 ab	10.6	
0.8 0.8 0 0 0 11.7 72.5 a 25.4 10.0 b 3.7 11.7 b 4.6 55.0 ab ca ⁴ m ² /ha m ² /ha 1.2 0.02 0 0 1.2 0.02 0.05 0 0 0 0 0 0.06 0.06 3.2 1.7 0 0 1.2 1.7 1.3 5.8 0 0 0 0 1.7 0 0 0 0 0 0 1.7 1.7 0 0 0 0 0 1.7 1.7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Oak	3.3 а	2.3	3,3 a	2.3	1.7 a	1.7	11.7 a	5.2	
72.5 a 25.4 10.0 b 3.7 11.7 b 4.6 55.0 ab ca ⁴ 0.02 0.02 0.05 0.05 0.06 0.06 1.7 0.06 0.06 1.3.3 1.7 1.7 1.7 1.7 1.7 1.7 1	Other	8.0	8.0	0	0	0	0	11.7	4.6	
0.02 0.02 3.0 1.7 0 0 0 1.2 0.005 0.005 0.02 0.02 0.00 0 0 0.000 0.006 0.006 3.2 1.7 0 0 0 0 0.1.2 1.7 1.7 13.3 5.8 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Total	72.5 a	25.4	10.0 b	3.7	11.7 b	4.6	55.0 ab	13.4	
0.02 3.0 1.7 0 0 0.05 0 0 0 0 0 0.2 0.2 0 0 0.06 3.2 1.7 0 1.2 number/ha 1.7 1.3.3 5.8 0 0 0 1.7 0 0 0 0 0 0 0 0 0 0 0 0 0 1.7 1.7 0 0 0 0 0 0 0 0 0 3.3 3.3 15.0 6.4 0 0 8.3	Stump Basal	l Arca ^A			W	1²/ha				
0.05 0.05 0 0 0 0 0 0 0.2 0.2 0 0 0 0.06 3.2 1.7 0 1.2 number/ha 1.7 1.7 13.3 5.8 0 0 1.7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 3.3 15.0 6.4 0 0 8.3	Pine	0.02	0.02	3.0	1.7	0	0	1.2	1.2	
0 0 0 0 0 0 0.06 3.2 1.7 0 0 0 1.7 1.7 13.3 5.8 0 0 0 0 0 0 0 0 0 3.3 3.3 15.0 6.4 0 0 8.3	Oak	0.05	0.05	0	0	0	0	0	0	
0.06 3.2 1.7 0 0 1.2 number/ha 1.7 1.3.3 5.8 0 0 8.3 1.7 0 0 0 0 0 0 0 0 0 0 0 0 0 1.7 1.7 0 0 0 3.3 3.3 15.0 6.4 0 0 8.3	Other	0	0	0.2	0.2	0	0	0	0	
1.7 1.7 13.3 5.8 0 0 8.3 15.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	Total	90.0	90.0	3.2	1.7	0	0	1.2	1.2	
1.7 1.7 13.3 5.8 0 0 8.3 1.7 1.7 0 0 0 0 0 0 0 1.7 1.7 0 0 0 3.3 3.3 15.0 6.4 0 0 8.3	Stump Densi	ity^			unu	ber/ha				
1.7 1.7 0 0 0 0 0 0 0 0 1.7 1.7 0 0 0 3.3 3.3 15.0 6.4 0 0 8.3	Pine	1.7	1.7	13.3	5.8	0	0	8.3	6.8	
$\begin{pmatrix} 0 & 0 & 1.7 & 1.7 & 0 & 0 & 0 \\ 3.3 & 3.3 & 15.0 & 6.4 & 0 & 0 & 8.3 \end{pmatrix}$	Oak	1.7	1.7	0	0	0	0	0	0	
3.3 3.3 15.0 6.4 0 0 8.3	Other	0	0	1.7	1.7	0	0	0	0	
	Total	3,3	3.3	15.0	6.4	0	0	8.3	8.9	

A No significant difference found by manova between sites. B One or more groups has no variance.

Table 4.9. Dead woody biomass, forest floor, and herbaceous cover at the four study sites. Within-row means followed by different letters are significantly different (p < .05). N = 30 at all sites.

	Sice	Site AV S.E.M.	S	Site CB S.E.M.	Mean	Site SP S.E.M.	S Mean	Site AL S.E.M.
Dead woody biomass				metric ton/ha				
0-0.6 cm diameter 0.6-2.5 cm diam.	0.1 a 0.6 a	0.02	0.3 a 0.9 a	0.08	0.3 a	0.04	0.1 a	0.02
2.5-7.6 cm diam.	2.9 a	0.5	3.8 a	0.8	1.8 a	0.4	3.0 a	0.8
>7.6 cm diam. rotten	0.5 a 11.7 a	0.3 2.3	18.0 b 30.3 b	8.1 9.2	3.6 ab 0.9 a	2.0 0.3	4.3 ab 2.6 a	1.5
Total woody biomass	15.8 a	2.6	53.2 b	11.8	7.1 a	2.0	10.6 а	2.3
Forest floor depth			6 6 8 9 8 8 8 8 8 8 8	cm				ŀ
Litter Duff	2.1 a 2.2 a	0.1	2.2 a 2.7 a	0.1	2.0 a 0.9 b	0.2	2.2 a 1.1 b	0.2
Herbaceous cover							6 C E E E E E E E E E E E E E E E E E E	
	16.5 ab	1.78	10.6 а	9.1	19.7 b	2.1	20.0 b	3.0

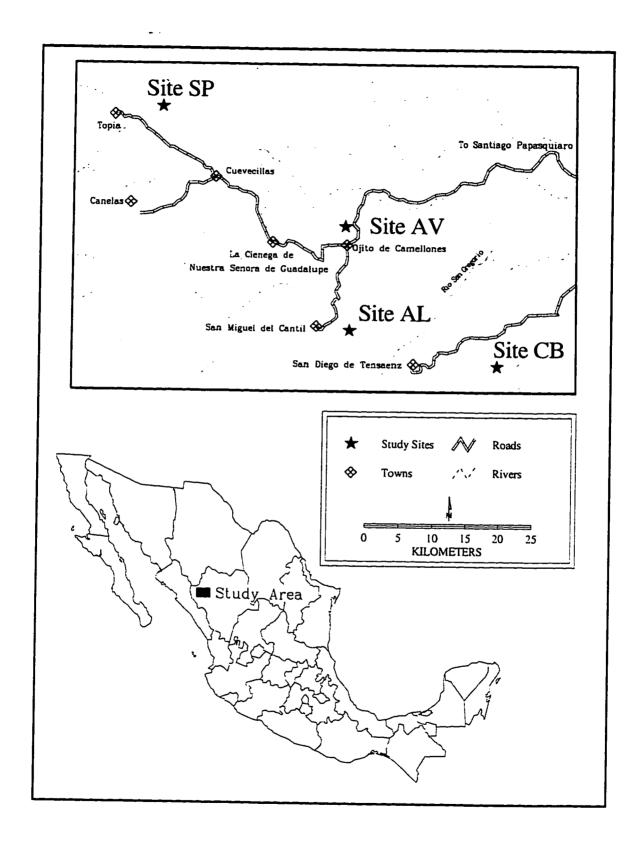


Figure 4.1. Map of study area and sampling site locations.

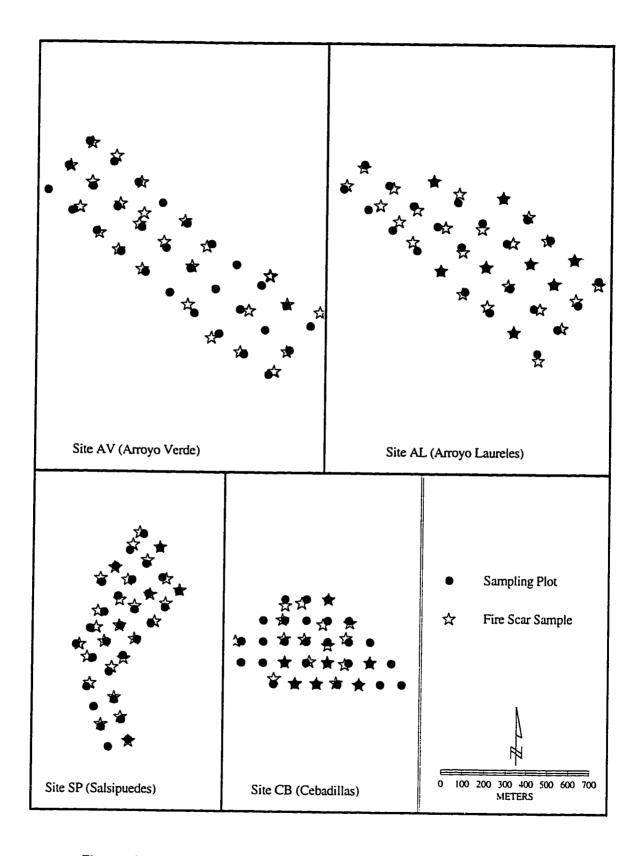


Figure 4.2. Map of forest sampling plots and fire scar sample locations.

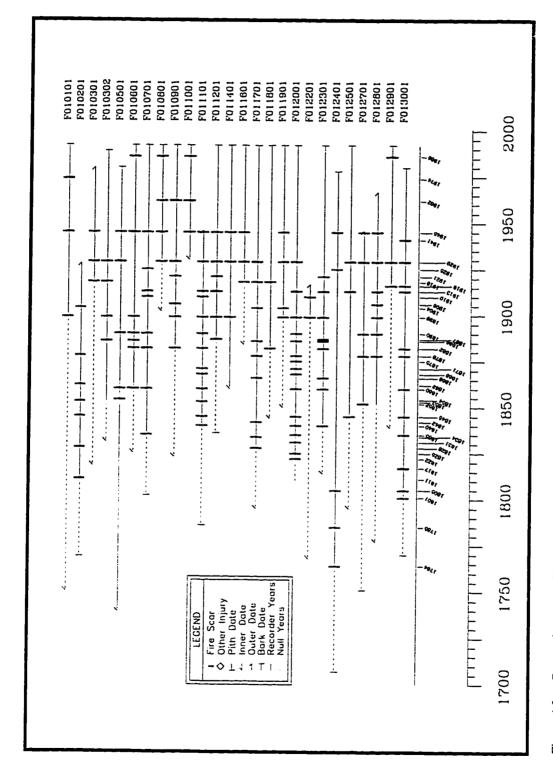


Figure 4.3a. Composite master fire chart for Site AV (Arroyo Verde). The last widespread fire at this site occurred in 1945. Fires in 1962 and 1986 were limited to the northwest corner of the study site.

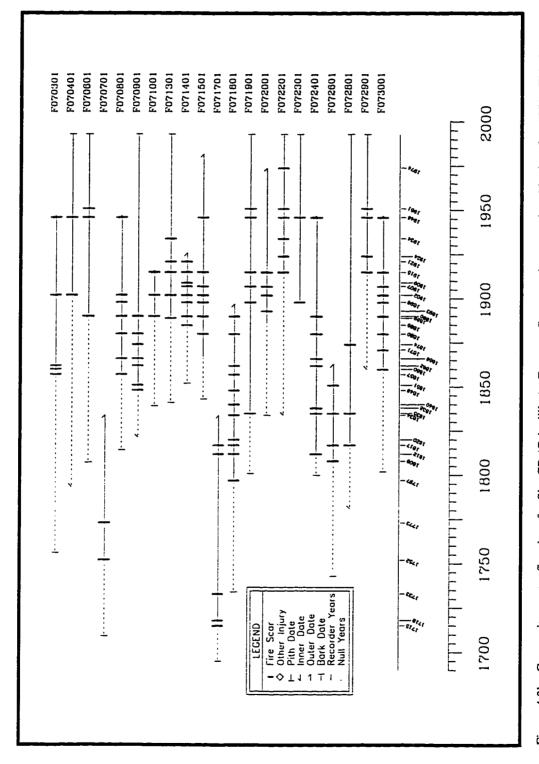


Figure 4.3b. Composite master fire chart for Site CB (Cebadillas). Frequent fires were interrupted at this site after 1951. This forest area, supporting fir and Douglas-fir in addition to pine and oak, was selectively harvested for pines circa 1970.

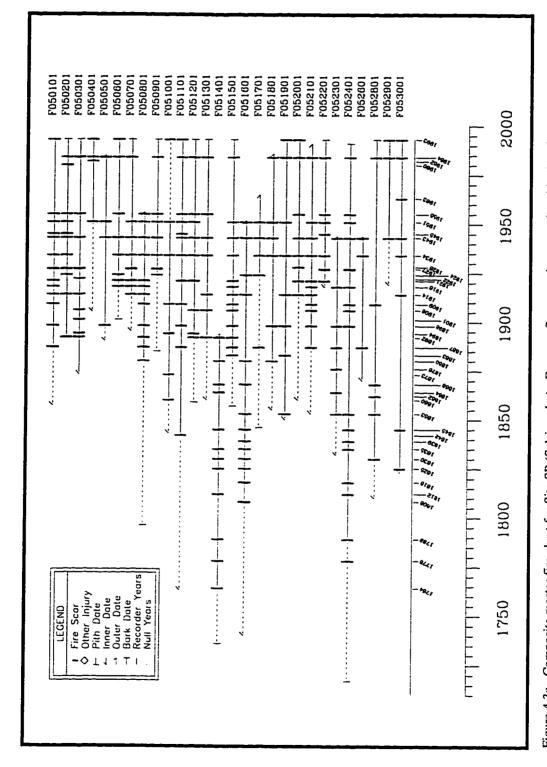


Figure 4.3c. Composite master fire chart for Site SP (Salsipuedes). Frequent fires were interrupted at this site after 1955. After a fire-free period of 29 years, widespread fires returned in 1984 and 1993.

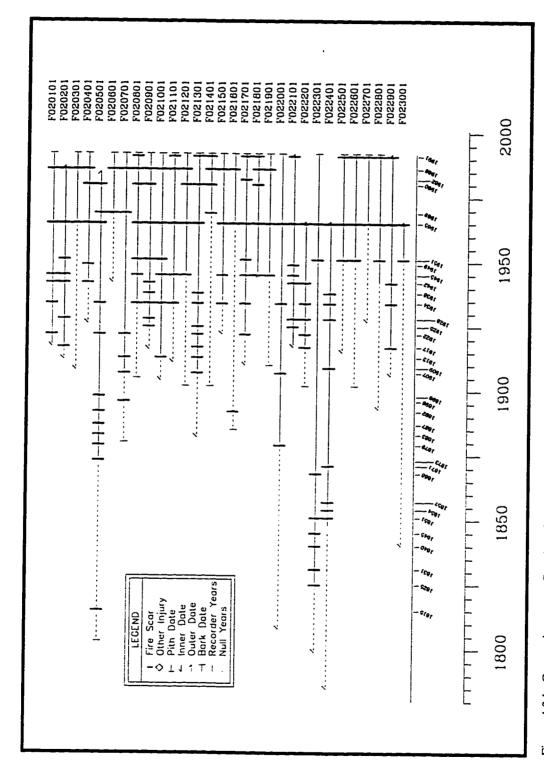


Figure 4.3d. Composite master fire chart for Site AL (Arroyo Laureles). This site has continued to burn frequently up to the present, although there is some evidence of fire regime changes in the twentieth century, notably the 14-year gap from 1951 to 1965.

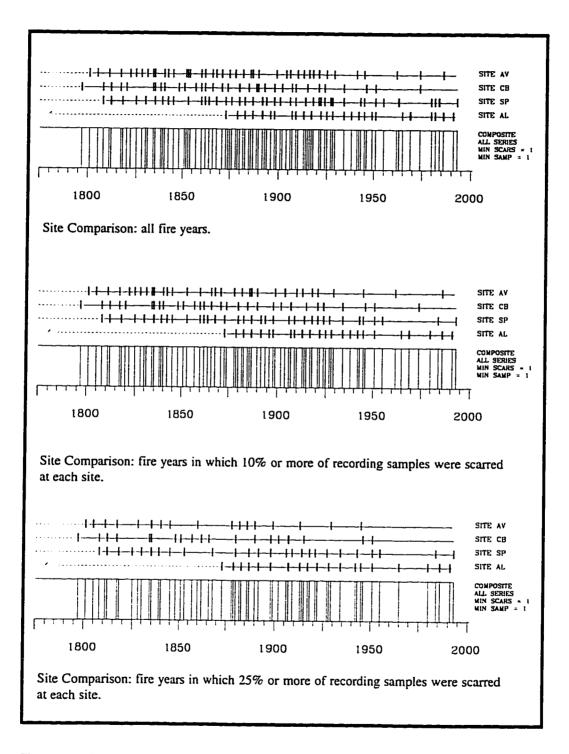


Figure 4.4. Comparison of fire occurrence at all four study sites in three categories: (1) all fire years; (2) years in which 10% or more of recording samples were scarred; and (3) years in which 25% or more of recording samples were scarred at each site.

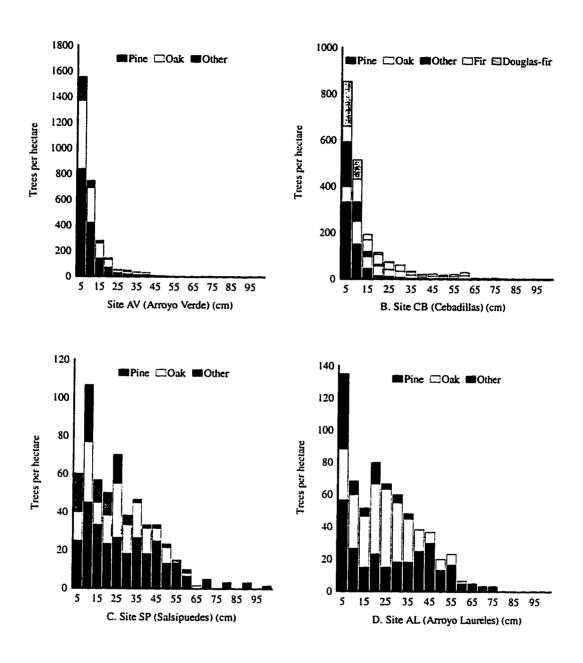


Figure 4.5. Live overstory tree diameter distribution at sites (a) AV (b) CB (c) SP and (d) AL.

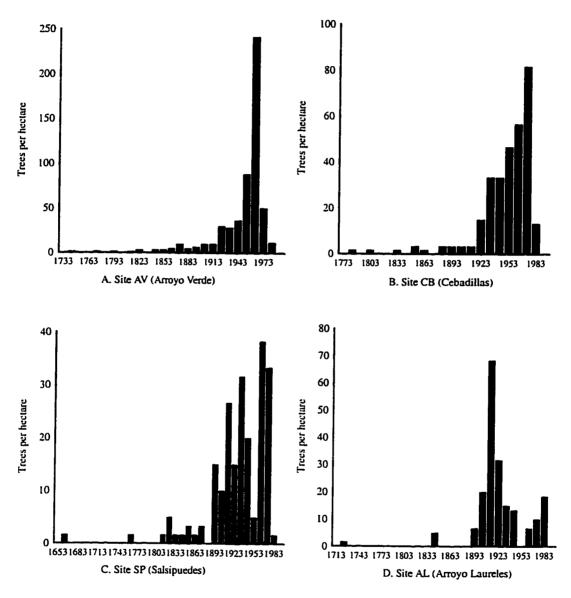


Figure 4.6. Center date distribution of conifers over 6 cm dbh at sites (a) AV (b) CB (c) SP and (d) AL.

5. TREE PATTERNS IN TEMPERATE MEXICAN FORESTS UNDER DIFFERENT FIRE REGIMES

.:

5.1 Introduction

Regimes of frequent, low-intensity fire form a keystone disturbance process (sensu Holling 1992) that regulates the structure of western long-needled pine forests (Leopold 1937, Weaver 1943, Cooper 1960, Covington et al. 1994). In the United States, where fire has been excluded for a century or more as a consequence of livestock grazing, logging, and fire suppression, ponderosa (*Pinus ponderosa*) and Jeffrey (*P. jeffreyi*) pine forests have become dense with clumps of small trees and species less-adapted to frequent fire have increased (Cooper 1960, Biondi et al. 1994, Minnich et al. 1995).

These altered ecosystems are highly vulnerable to destruction by pathogens and fire (Covington et al. 1994). In contrast, unharvested pine forests of northern Mexico have a variety of fire regimes, including continuing frequent fires as well as fire exclusion (Minnich et al. 1995, Fulé and Covington 1996). The Mexican forests present a unique opportunity to contrast patterns of virgin forests under different fire regimes.

Low-intensity fires affect forest structure by differentially thinning trees. Small pines, with thin bark and meristematic tissue close to the flames, are more vulnerable to fire mortality than larger trees (White 1985). Physiological differences between species in the insulating properties of bark and ability to withstand foliar heating are believed to contribute to the higher fire survival of pines compared with oaks in xeric Florida (Rebertus et al. 1989) and Arizona (Barton 1995) sites. Mortality also varies with fire severity fluctuations caused by local differences in fuel quantity and quality, tending to

create more severe fire behavior in heavier fuels under aggregated trees (Rebertus et al. 1989, Glitzenstein et al. 1995). The interaction of these mechanisms causes low-intensity fires to remove smaller and more fire-susceptible trees and thin clumped patches of young trees to a more random or uniform overstory spatial distribution (Rebertus et al. 1989).

Autogenic processes, rather than disturbance, may cause similar changes in spatial pattern. Competitive self-thinning in aggregated regeneration led to dispersed mature tree structure in stands of jack pine (*P. banksiana*) (Kenkel 1988), *Eucalyptus obliqua* (West 1984), and Costa Rican rainforest trees (Sterner et al. 1986). However, density-dependent mortality does not have the same effect in all forests. Resource sharing among clones may be responsible for an increase in clumping observed over time in a bigtooth aspen (*Populus grandidentata*) forest (Peterson and Squiers 1995). In western long-needled pines, the thickets of dense young trees which established following fire exclusion have shown a remarkable persistence (Cooper 1960, Covington et al. 1994). Observing this lack of self-thinning despite competitive conditions, Cooper (1961) argued that frequent fire disturbance was necessary to maintain the historic open forest.

The establishment and survival of different tree species is also affected by local scale differences in microsites leading to resource partitioning (Duncan 1991) or competitive interactions between species (Peterson and Squiers 1995). Fire influences microsites by consuming litter, increasing nutrient availability, and exposing soil (Covington and Sackett 1984). The exclusion of fire from long-needled pine forests leads to a different environment with deep litter and dense canopy cover. Under such conditions Barton (1995) found that sprouting oak species in a Madrean forest of Arizona

were able to regenerate and grow but that pine seedling establishment was reduced.

Barton (1995) suggested that alternative strategies of fire resistance (insulating bark, high scorch tolerance), associated with pines, versus fire resilience (vigorous resprouting), associated with oaks, help pines dominate under a frequent-fire regime but let oaks increase under fire exclusion.

The Sierra Madre Occidental of northern Mexico, a remote region with exceptional biological diversity, supports temperate forests dominated by pines (P. arizonica, P. durangensis, P. engelmannii) that are related to ponderosa and Jeffrey pine both taxonomically and in their adaptations to frequent fire (McCune 1988). In some areas of the Sierra Madre, harvesting and fire suppression have begun only recently and sporadically. We compared the density, species composition, and spatial distribution of trees at three unharvested sites which shared long-term frequent fire regimes but had distinct recent fire histories: (1) an uninterrupted frequent fire regime (FF), (2) fireexclusion (FE), and (3) fire exclusion followed by the return of fire (FR). We examined four hypotheses: first, that regeneration would be aggregated at all sites, especially among sprouting species. Second, that the presence or absence of fire would cause divergence in overstory pattern, with frequent fire creating a dispersed overstory of large trees but fire exclusion permitting dense small trees to survive in a clumped overstory. Third, that frequent fire would favor pine dominance while fire exclusion would lead to increases in other species, especially sprouting species. Fourth, fire return following extended fire exclusion was expected to cause relatively high, clumped mortality and favor sprouting species, leading to a forest structure quite different from the pre-exclusion condition.

5.2 Methods

5.2.1 Study area

The study sites were three unharvested pine-oak forest tracts in the Sierra Madre Occidental of northwestern Durango, Mexico (Figure 5.1). The first two sites, FF (Arroyo Laureles, lat. 24° 57' N, lon. 106° 13' W, elevation 2,300 m) and FE (Arroyo Verde, lat. 25° 05' N, lon. 106° 13' W, elevation 2,300 m), were sampled in 1993 and the third site, FR (Salsipuedes, lat. 25° 15' N, lon. 106° 30' W, elevation 2,400 m), was sampled in 1994.

In a companion study, fire history at each site was determined from fire scars and forest structure was measured (overstory, regeneration, herbaceous cover, and dead biomass) on grids of sampling plots covering 70 ha at sites FF and FE and 30 ha at site FR. All three sites had frequent fire regimes in the past, but only site FF maintained a recurring pattern of fire up to the present. The mean fire interval for widespread fires, those scarring at least 25% of the sample trees (MFI_{25%}), was 6.6 years at site FF. Site FE had an MFI_{25%} of 9.0 years prior to 1945, but had not burned with widespread fire since. Evidence of more recent fire was found on the site margin but not within 1 km of the sampling location of the present study. The MFI_{25%} at site FR was 6.5 years until 1955; the subsequent 29-year period of fire exclusion was ended by fires in 1984 and 1993. Mean forest density was related to fire regime, rising from 647 trees/ha at site FF to 2733 trees/ha at FE. Site FR had only 558 living trees/ha in 1994 but an estimated minimum of 914 trees/ha (sum of live + recently killed) before the 1993 fire. Tree size was inversely

related to density, with basal area decreasing from 37.2 m²/ha at site FF to 36.8 m²/ha at FR and 23.4 m²/ha at FE (Fulé and Covington 1996).

Regional climate follows a pattern of spring drought and summer monsoonal moisture. Annual precipitation at Ojito de Camellones (elevation 2400 m) is 2200 mm (9 year average), with 80% occurring between June and October (weather station locations are mapped in Figure 5.1). Other weather stations at lower elevations average less annual precipitation: 1540 mm (11 year average) at San Miguel del Cantil (2250 m elevation), 1150 mm (5 year average) at Topia (1800 m elevation), and 740 mm (11 year average) at San Diego de Tensaenz (1550 m elevation). Records of temperature are less available than those of precipitation, but 1992 maximum and minimum temperatures at La Cienega, at 2500 m elevation, were 18° and -8° C in January, and 28° and 7° C in August. Soils are of igneous origin, primarily rhyolitic with scattered basaltic and granitic outcrops (Guizar et al. 1992). The topography is characterized by high-elevation mesas dissected by steep canyons.

5.2.2 Sampling and analysis

Quadrats were established in areas that appeared to represent the surrounding study sites in terms of physical characteristics and vegetation structure. Tree locations were mapped to the nearest 0.1 m. Diameter at breast height (dbh, 1.3 m above ground), species, and condition class (1-living, 2-declining, 3-recent dead, 4-older dead) were recorded for each overstory tree on 50 X 50 m quadrats at sites FF and FE and on two 25 X 25 m quadrats at site FR, a more remote area where less sampling resources were

available. Understory trees, below 1.3 m in height, were assigned dbh = 0. Dead understory trees were mapped only at site FR, where they were encountered in substantial numbers. A total of 14,071 trees was mapped on the quadrats.

Trees were grouped for analysis based on taxonomy, condition, and size. Taxonomic groups (Table 5.1) were pines (non-sprouting), oaks (sprouting), alder (sprouting), and other (Arbutus and Juniperus, not observed to sprout in the study area). Pinus leiophylla, a weakly-sprouting pine (Barton 1995) encountered only at site FE, was included with the pine group because sprouting by this species was not observed on the site. Condition groups were live and dead, except at site FR where the recently killed trees were separated from older dead trees to assess mortality from the recent fires. Size classes were (1) understory (below breast height), (2) overstory (above breast height), and (3) 25+ cm dbh. The 25 cm limit was selected because 95% of conifers of this size were established before the earliest initiation of fire exclusion at any site (1945 A.D.), based on previously determined age data (Fulé and Covington 1996). Limited numbers of trees over breast height precluded further size class subdivision. Quadrats at sites FF and FE were subdivided into four 25 X 25 m plots for direct comparison with the site FR plots. However, spatial patterns of overstory trees at site FF and dead overstory trees at site FE were analyzed over the full plots because tree densities on the subdivided quadrats were too low for the spatial analysis techniques used.

To determine spatial aggregation or dispersion within and between tree groups, spatial pattern was analyzed with Ripley's K-functions (Ripley 1981, Haase 1995) using programs developed by Duncan (1990). Computed values of univariate (K[t]) or

bivariate (K12[t]) functions were compared with Monte Carlo simulations at the 95% confidence level to test the null hypothesis of random spatial distribution. Computational details are described in Haase (1995); the programs incorporate the weighted edge correction of Diggle (1983). When understory tree density on some quadrats exceeded 1000 trees/group, the limit of the programs, smaller quadrats were used for analysis. To remain consistent in interpretation, analyses were restricted to groups with a population $(N) \ge 20$. Although spatial patterns have been discerned with smaller N values elsewhere (Ripley 1981), inspection of our results from groups with small N showed wide fluctuations and abrupt changes in K(t) and significance levels.

5.3 Results

Tree structure in the mapped plots was generally representative of the surrounding forest, as measured in the companion study (Fulé and Covington 1996). Density of live trees increased from 623 trees/ha at site FF to 808 trees/ha at FR and 4,748 trees/ha at FE (Table 5.2). Only at site FE was the mapped plot density substantially different, about 73% higher, than that measured on the entire 70-ha site, indicating that a relatively dense area was selected for mapping. However, the mapped tree density was within 1.5 standard deviations of the mean 70-ha density. Dead tree density (Table 5.3) was slightly lower at site FF (215 trees/ha overall) but higher at FE (208 trees/ha overall) and FR (386 trees/ha overall). Understory tree density was uniformly higher on the mapped plots (Table 5.4) but followed the same relative ranking as on the surrounding sites (overall densities: 8,725 stems/ha at FF, 5,875 stems/ha at FE, and 11,992 stems/ha at FR).

Understory trees were highly aggregated at all three sites (Table 5.5), as expected. Pines and alders were clumped at all scales. Oaks and other trees had more variable random or dispersed patterns on several quadrats at longer scales of 9-12 m.

Differences in spatial patterns of overstory trees showed more variability but followed trends predicted by our second hypothesis, with dispersion at FF, under a continuing fire regime, and aggregation at the fire-excluded sites (Table 5.6). Site FF was clumped only at the 1-meter scale. A dispersed pattern between 5 and 10 m was statistically significant for pines and to a lesser extent (4, 5, and 10 m) for all trees and trees over 25 cm dbh; patterns of other groups and scales were not significantly different from random. In contrast, the overstory was aggregated for most groups and scales at both fire-excluded sites. Oak patterns were particularly variable on the four quadrats at site FE, ranging from random (FE-1) to clumped at shorter scales (FE-2 and 4) to clumped over the full 12 m (FE-3). The only dispersed pattern was for pines at the 11-12 m scale on FE-4 and the distribution of trees ≥ 25 cm dbh at FE was not significantly different from random. Arbutus and Juniperus trees were relatively less clumped where numbers were sufficient for analysis (FE2 and 4). Aggregation was less pronounced at site FR, which could suggest thinning by the recent fires; however, the number of overstory trees was limited and the patterns were reversed on the two quadrats, with short-scale clumping at FR-1 and long-scale clumping at FR-2.

Tree size characteristics were also consistent with fire regime differences.

Frequent-fire site FF had the fewest trees but highest basal area (Table 5.2), with the largest quadratic mean diameter of 31.5 cm. Fire-excluded sites FE and FR were

characterized by smaller trees, with quadratic mean diameters of 10.5 cm and 24.5 cm respectively. The diameter distributions (Figure 5.2) at site FF show relatively even proportions of trees across the 20 to 50 cm classes, with few small trees. Most trees at site FE, in contrast, were below 10 cm dbh.

Although pines and oaks dominated all three sites (Table 5.2), the expected increase in sprouting species at the expense of pine dominance was observed. Sprouting alders, absent from the frequent-fire FF overstory, comprised 12% and 20% of tree density at FE and FR respectively. Understory species' groups (Table 5.4) were dominated by seeding taxa at the frequent-fire site FF (pines and other, 86%) but by sprouting taxa at the fire-excluded sites (oak and alder, 68% at FE and 86% at FR). Species composition of dead trees (Table 5.3) was similar to that of live trees (Table 5.2) at all sites, except that oak mortality was relatively low at site FE, where oaks comprised 24% of live tree density but only 7% of dead tree density.

Changes at the fire return site FR also followed expected patterns. Before the return of fire, Site FR was also dominated by the smallest trees (the sum of living and dead trees in Figure 5.2) since the majority of dead trees at site FR were classed as recently-killed (90% at FR-1 and 74% at FR-2), suggesting that the site was relatively more dense with small trees prior to the 1984 and 1993 fires. Dead tree density as a proportion of living trees was highest at site FR (140%), which burned twice after 29 years of fire exclusion, followed by the frequent-fire site FF (30%) and the fire-excluded site FE (10%). Mortality concentration in the small diameter classes (Figure 5.2) was most pronounced at site FR and least evident at site FF. Dead overstory trees were

significantly clumped at all sites (Table 5.7) except FR-2 and the longer scales at FR-1. Combining the recently killed trees and live trees at FR, spatial aggregation was similar to live trees alone. Dead understory trees and the combined recently killed and live understory trees at FR were highly clumped.

No distinct spatial patterns emerged from bivariate (K12[t]) analysis among species' groups in the overstory or understory. All possible bivariate combinations (e.g., pine-oak, pine-alder, etc.) were tested wherever the group $N \ge 20$. Pines and oaks were positively associated in the FE overstory at scales of 1, 3-4, and 6-7 meters. All other overstory group pairs at FE and FF were random or had isolated positive or negative associations at one or two scales. Site FR had insufficient numbers for analysis. The greatest deviation from randomness in understory bivariate pattern was repulsion between pines and oaks at the 7-12 m scale on plot FE-1.

5.4 Discussion

Clear differences were observed in tree structure among the three study sites but the ability to draw causal inferences is limited in an unreplicated setting, a common problem in investigations of change over long time periods or due to unplanned treatments (Carpenter 1990). We closely matched the study sites (elevation, slope, slope position, soil parent material, lack of harvesting, and species composition) to limit confounding factors, thus allowing us to focus on the disturbance mechanisms influencing tree patterns. Another potential concern in studies involving fine-scale point mapping is that limited resources can preclude the collection of sufficient data to

adequately represent a large area. In the present case, however, the companion study in the surrounding forests showed that the mapped plots were reasonably representative of broader regions.

The prediction of highly aggregated regeneration was supported, although clonal species did not appear to be more clumped than seeding species. High understory tree density at all three sites indicated that trees established readily. Since almost all understory groups were clumped at scales below 9 meters and bivariate patterns were random, there was no evidence of differential regeneration due to local microsite partitioning or positive or negative interactions between groups as observed in other forests (Duncan 1991, Peterson and Squiers 1995). The longer-scale dispersion (11-12 m) of *Arbutus* and *Juniperus* understory trees might reflect distances between the sparsely distributed parent trees. Disperal away from the parents could be limited by the relatively heavy weight of seeds of these species. Similarly, the variability in long-range oak regeneration patterns may reflect clumping of oak sprouts around mother trees.

Dense, clumped overstories were consistently associated with fire exclusion, supporting the argument that continued frequent fire is the primary mechanism thinning dense regeneration to an open and dispersed overstory in these long-needled pine forests. The larger trees ($dbh \ge 25$ cm) at both sites FF and FE, those established prior to FE fire exclusion, were randomly distributed. The smaller trees, which have survived because fires ceased, are responsible for the overstory aggregation at FE.

Mortality of overstory trees was clumped at site FF, consistent with the thinning role of fire, but mortality was also aggregated at site FE, suggesting that some level of

density-dependent mortality is occurring as well. In contrast to the competitive thinning observed by Sterner et al. (1986) and Kenkel (1988), however, the degree of clumped mortality at FE is evidently insufficient to counteract the high survival of crowded young trees in the absence of fire.

Fire-excluded sites had a relatively higher proportion of sprouting species, matching the resistance/resilience hypothesis suggested by Barton (1995). The alder group was most highly correlated with fire regime, ranging from no overstory alders at frequent-fire site FF to 30% of the overstory at fire-return site FR. Alders appear to follow a fire resilience strategy, probably due to a combination of thin bark and strong sprouting. The relatively low oak mortality at the fire-excluded site FE is consistent with the observation by Barton (1995) that oaks grew relatively better than pines in dense, fire-excluded Madrean forests.

Fire following 29 years of exclusion at site FR provides an insight into the effects of altered fire regimes. The fires in 1984 and 1993 reduced tree density, especially in the smaller size classes (Figure 5.2), but the surviving overstory remained clumped and relatively dense, and had a relatively high proportion of sprouting species compared with frequent-fire site FF. The live pine:oak ratio is nearly balanced at 57% to 43% (Table 5.2), but pine mortality was relatively high (38% of dead tree density) compared with oak mortality (14%) (Table 5.3), suggesting that overstory pine dominance has declined. Sprouting oaks and alders make up 86% of understory tree density.

The comparison of sites FR and FE to the frequent-fire FF suggests that uninterrupted frequent fire is necessary for maintenance of pine dominance and dispersed

forest structure. Under fire exclusion, dense regeneration—especially of sprouting species—appears to survive into the overstory at the expense of pines. If fire returns to a fire-excluded forest, the higher fire intensity kills a high proportion of trees but the sprouters have a strong advantage in reoccupying the post-fire forest. Forest structure following the fires at site FR remains distinctly more dense and clumped with sprouters than at FF, suggesting that simply reintroducing fire does not restore the pre-fire-exclusion structure (see Sackett et al. [1996] for analogous experimental results in ponderosa pine in the southwestern U.S.).

5.5 Implications

At site FE, where tree densities are several times higher than at pre-fire FR, we have argued (Fulé and Covington 1996) that the accumulated live and dead fuels after a half-century of fire exclusion can probably support a switch to a novel disturbance: high-intensity, stand-replacing fire. Under such conditions, the post-fire dominance of sprouting species and the removal of seed sources for pines and oaks could create new vegetation patterns such as an oak-alder shrubland, an upward invasion of chaparral species (e.g., *Arctostaphylos pungens*), or an unforested brushy opening similar to those created by high-intensity fires following extended fire exclusion in ponderosa pine in the northern portion of its range (Weaver 1943, Covington et al. 1994). A reduction in site productivity may also follow because soil erosion can be severe in the region after the loss of vegetative cover. Some post-fire erosion occurred at FR and very heavy erosion,

to underlying rock, was seen at abandoned agricultural fields nearby (P.Z. Fulé, personal observation).

Conservation of key disturbance regimes can be as important as conservation of biota in order to sustain ecosystems. Vegetation manipulation may substitute to some extent for fire in terms of regulating density, species composition, and spatial arrangement, but mechanical thinning is often associated with impacts such as repeated soil disturbance, destruction of understory plants, and extraction of the largest and oldest trees. In such cases, these effects can also be detrimental to conservation of ecosystem structure and function, as well as the sustainability of soils and site productivity. Nor are the effects of fire exclusion reversed by simply re-introducing fire. Maintaining frequent fire regimes and unharvested forests, where they exist, and developing ecological restoration plans that address both the structure and function of ecosystems where conditions have changed (Covington et al. in press), would be key to perpetuating some portion of the pine-oak forest in relatively natural conditions. At present, however, the temperate forests of northern Mexico are being harvested at a rapid rate, threatening the extraordinary biological diversity of the region (Biodiversity Support Program 1995). Some balance should be struck between the need for economic development versus preservation of remnants of the intact indigenous ecosystem.

Table 5.1. Tree species encountered on the study sites. Nomenclature follows González et al. (1991).

Family	Species	Common Name
D		
Betulaceae	Alnus spp.	Alder
Cupressaceae	Juniperus depeanna Steud.	Alligator juniper
	Juniperus spp.	Juniper
Ericaceae	Arbutus spp.	Madrone
Fagaceae	Quercus coccolobifolia Trel.	Encino roble
	Q. laeta Liebm.	Encino blanco
	Q. sideroxyla Humb. & Bonpl.	Encino prieto
	Quercus spp.	Encino
Pinaceae	Pinus ayacahuite K. Ehrenb.	Pino blanco
	P. durangensis Mtz.	Durango pine
	P. herrerai Mtz.	
	P. leiophylla Schlect. & Cham.	Chihuahua pine
	P. lumholtzi Rob. & Fern.	Pino triste

Table 5.2. Forest structure of live trees over 1.3 m on stem-mapped plots at sites FF (n = 4), FE (n = 4), and FR (n = 2). S.E.M. = standard error of the mean. Site totals followed by different superscripts are significantly different (Tukey's HSD test, alpha = .10).

Site	Group	Density (trees/ha)	S.E.M.	Basal Area (m²/ha)	S.E.M.		
FF	Pine	404	13.7	42.5	3.2		
	Oak	200	24.0	6.1	0.9		
	Other	28	17.7	0.5	0.3		
	Total	632ª	28.1	49.2	3.3		
FE	Pine	2780	339.5	29.7	5.4		
	Oak	1136	239.7	9.4	1.0		
	Alder	572	124.7	1.4	0.2		
	Other	260	62.1	1.1	0.2		
	Total	4748 ^b	483.1	41.6	4.6		
FR	Pine	296	200.0	29.9	9.7		
	Oak	216	56.0	5.3	0.1		
	Alder	160	0	1.2	1.2		
	Other	136	24.0	1.9	0		
	Total	808*	280.0	38.2	11.0		

Table 5.3. Forest structure of dead trees over 1.3 m on stem-mapped plots at sites FF (n = 4), FE (n = 4), and FR (n = 2). S.E.M. = standard error of the mean. Site totals followed by different superscripts are significantly different (Tukey's HSD test, alpha = .10).

Site	Group	Density (trees/ha)	S.E.M.	Basal Area (m²/ha)	S.E.M.		
	ъ.						
FF	Pine	132	56.7	8.5	5.5		
	Oak	36	13.7	0.9	0.7		
	Alder	4	6.5	0.0	0.0		
	Other	16	4.0	0.2	0.1		
	Total	188ª	59.3	9.6	5.3		
FE	Pine	328	126.9	8.9	3.1		
	Oak	32	11.3	1.3	0.9		
	Alder	92	7.7	0.2	0.1		
	Other	12	39.4	0.1	0.1		
	Total	464 ^{ab}	129.8	10.5	3.9		
FR	Pine	432	256.0	13.4	6.7		
	Oak	160	112.0	3.2	3.1		
	Alder	344	136.0	0.3	0.1		
	Other	192	192.0	0.2	0.2		
	Total	1128 ^b	696.0	17.1	9.9		

Table 5.4. Density of trees under 1.3 m on stem-mapped plots at sites FF (n = 4), FE (n = 4), and FR (n = 2). S.E.M. = standard error of the mean. Site totals are not significantly different (Tukey's HSD test, alpha = .10).

Site	Group	Living Density (stems/ha)	S.E.M.	Dead Density (stems/ha)	S.E.M.		
CC	D:	15000					
FF	Pine	15080	2289.6				
	Oak	2240	611.9				
	Alder	156	83.5				
	Other	116	27.2				
	Total	17592	2514.6				
FE	Pine	4420	752.8				
	Oak	8916	1436.6				
	Alder	1624	421.0				
	Other	792	348.3				
	Total	15572	1861.7				
FR	Pine	1096	840.0	96	32.0		
	Oak	12248	2184.0	3560	792.0		
	Alder	8760	1080.0	2512	1088.0		
	Other	2448	1488.0	448	144.0		
	Total	24552	3432.0	6616	1704.0		

Table 5.5. Spatial distribution $\{K(t)\}$ of live trees under 1.3 m on stem-mapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and (--) for dispersed patterns; blank values indicate random pattern. N = number of trees. Tree groups not shown have N < 20. Asterisks indicate smaller plot size (* = 20 X 20 m, ** = 15 X 15 m) analyzed where N > 1000 on the full plot; n/a = t not applicable on n = t smaller than 25 X 25 m.

							Distan	ce (t) i	n mete	ers					
Site	Group	N	l	2	3	4	5	6	7	8	9	10	11	12	
FF-1	All trees	752	+	+	+	+	+	+	+	+	+	+	+	+	
	Pine	595	+	+	+	+	+	+	+	+	+	+	+	+	
	Oak	142	+	+	+	+	+	+	+	+	+	+	+	+	
FF-2	All trees	984	+	+	+	+	+	+	+	+	+	+	+	+	
	Pine	831	+	+	+	+	+	+	+	+	+	+	+	+	
	Oak	133	+	+	+	+	+	+	+	+	+		-		
FF-3	All trees*	778	+	+	+	+	+	+	+	+	+	+	n/a	n/a	
	Pine*	754	+	+	+	+	+	+	+	+	+	+	n/a	n/a	
	Oak	49	+	+	+	+	+	+	+	·	-				
FF-4	All trees**	636	+	+	+	+	+	+	+	n/a	n/a	n/a	n/a	n/a	
	Pine**	522	+	+	+	+	+	+	+	n/a	n/a	n/a	n/a	n/a	
	Oak	236	+	+	+	+	+	+	+	+	+	+	+	+	
	Alder	23	+	+	+	+	+	+	+	+	+	+	+	+	
FE-1	All trees	748	+	+	+	+	+	+	+	+	+	+	+	+	
	Pine	227	+	+	+	+	+	+	+	+	+	+	+	·	
	Oak	454	+	+	+	+	+	+	+	+	+	+	+	+	
	Alder	51	+	+	+	+	+	+	+	+	+	+	+	·	
FE-2	All trees	901	+	+	+	+	+	+	+	+	+	+	+	+	
	Pine	257	+	+	+	+	+	+	+	+	+	+	+	+	
	Oak	402	+	+	+	+	+	+	+	+	+	+	+	+	
	Alder	169	+	+	+	+	+	+	+	+	+	+	+	+	
	Other	73	+	+	+	+	+	+	+	+					
FE-3	All trees*	877	+	+	+	+	+						n/a	n/a	
	Pine	414	+	+	+	+	+	+	+	+	+	+			
	Oak	806	+	+	+	+	+	+	+	+	+	+	+	+	
	Alder	70	+	+	+	+	+	+	+	+	+				
E-4	All trees	989	+	+	+	+	+	+	+	+	+	+			
	Pine	207	+	+	+	+	+	+	+	+	+	+	+	+	
	Oak	567	+	+	+	+	+	+	+	+	+	+			
	Alder	116	+	+	+	+	+	+	+	+	+	+	+	+	
	Other	99	+	+	+	+	+	+	+	+	+				
R-I	All trees**	566	+	+	+	+	+	+	+	n/a	n/a	n/a	n/a	n/a	
	Pine	121	+	+	+	+					+	+	+	+	
	Oak	902	+	+	+	+	+	+	+	+	+	+	+	+	
	Alder	480	+	+	+	+	+	+	+	+	+	+	+	+	
	Other	246	+	+	+	+	+	+	+	+	+	+	+		

Table 5.5 continued.

		Distance (t) in meters												
Site	Group	N	I	2	3	4	5	6	7	8	9	10	11	12
FR-2	All trees*	745	+	+	+	+	+	+	+	+	+	+	n/a	n/a
	Oak	629	+	+	+	+	+	+	+	+	+	+	+	+
	Alder	615	+	+	+	+	+	+	+	+	+	+	+	+
	Other	60	+	+	+	+	+	+	+					

Table 5.6. Spatial distribution [K(t)] of live trees over 1.3 m on stem-mapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and (--) for dispersed patterns; blank values indicate random pattern. N = number of trees. Tree groups not shown have N < 20.

							Distan	ce (t) i	n mete	rs				
Site	Group	N	i	2	3	4	5	6	7	8	9	10	11	12
FF-AII	All trees	158	+											
	All ≥ 25	101										-		
	Pine	101					***							
	Oak	50	+											
FE-All	All ≥ 25	52												
FE-1	All trees	267	+	+	+	1.	•							
	Pine	162	+	+	+	+ +	+	++	+	++	+	+	+	+
	Oak	65	,	т	π-	Τ.	+	+	+	+	+	+	+	+
	Alder	34	+	+	+	+	+	+			+	+	+	+
											•	•	•	•
FE-2	All trees	347	+	+	+	+	+	+	+	+				
	Pine	161	+	+	+	+	+	+	+	+	+	+		
	Oak	106	+	+	+	+	+							
	Alder	56	+	+										
	Other	24	+	+							+	+	+	+
FE-3	All trees	347	+	+	+	+	+	+	+	+	+	+	+	+
	Pine	235	+	+	+	+	+	+	+	+	+	+	+	+
	Oak	79	+	+	+	+	+	+	+	+	+	+	+	+
FE-4	All trees	226		+	+	+	+	+	+	+	+			
	All ≥ 25	20			•	•	•	•	•	-	-			
	Pine	137		+	+	+	+	+	+	+				
	Oak	34	+	+	+	+	•	•	•	-			_	
	Alder	35			+	+					+			
	Other	20			•	·		+	+		•	+	+	+
FR-1	All trees	33	+	+	+		+							
FR-2	All trees	68						1	1					
	Pines	31		+	+	+	+	+	+	+	+	+	+	+

Table 5.7. Spatial distribution [K(t)] of dead trees on stem-mapped plots at all sites. Statistical significance at the 95% level is indicated by (+) for clumped and (--) for dispersed patterns; blank values indicate random pattern. N = number of trees. Sites and tree groups not shown have N < 20. The dead/live group at site FR is the combination of recently killed trees and live trees. Asterisk indicates smaller plot size (15 X 15 m) carryzed where N > 1000 on the full plot; n/a = t not applicable on plots smaller than 25 X 25 m.

							Distan	ce (t) i	n met	ers				
Site	Group	N	1	2	3	4	5	6	7	8	9	10	11	12
Trees ov	er 1.3 m:													
FF-All	All trees	47	+	+	+	+	+	+	+	+	+	+	+	+
	Pine	33	+	+	+	+	+	+	+	+	+	+	+	+
FE-All	All trees	116	+	+	+	+	+	+	+	+	+	+	+	+
	Pine	82	+	+	+	+	+	+	+	+	+	+	+	+
	Alder	23	+	+	+	+	+	+	+	+	+	+	·	+
FR-1	All trees	114	+	+	+	+	+							
	Pine	43	+	+	+	+	+	+	+	+	+	+	+	+
	Alder	30	+	+	+	+	+	+	+	+	+	+	+	+
	Dead/Live	136	+	+	+	+	+					·	•	•
FR-2	All trees	27												
	Dead/Live*	88						+			+			
Trees und	der 1.3 m:													
FR-1	All trees	307	+	+	+	+	÷	+	+	+	+	+	+	
	Oak	173	+	+	+	+	+	÷	+	+	•	•	•	
	Alder	89	+	+	+	+	+	+	+	+	+	+	+	+
	Other	37	+	+	+	+	+	+	+	+	+	•		<u>'</u>
	Dead/Live	658	+	+	+					n/a	n/a	n/a	n/a	n/a
FR-2	All trees	520	+	+	+	+	+	+	+	+	+	+	+	+
	Oak	272	+	+	+	+	+	+	+	+	+	+	+	+
	Alder	225	+	+	+	+	+	+	+	+	+	+	+	+
	Dead/Live*	479	+	+	+	+	+	+	•	n/a	n/a	n/a	п/a	n/a

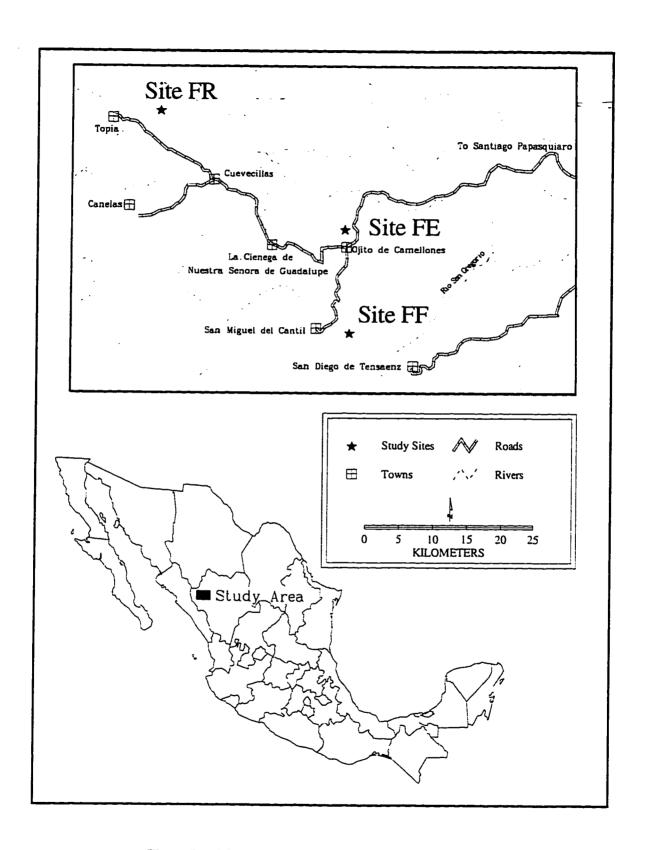


Figure 5.1. Map of study site and weather station locations.

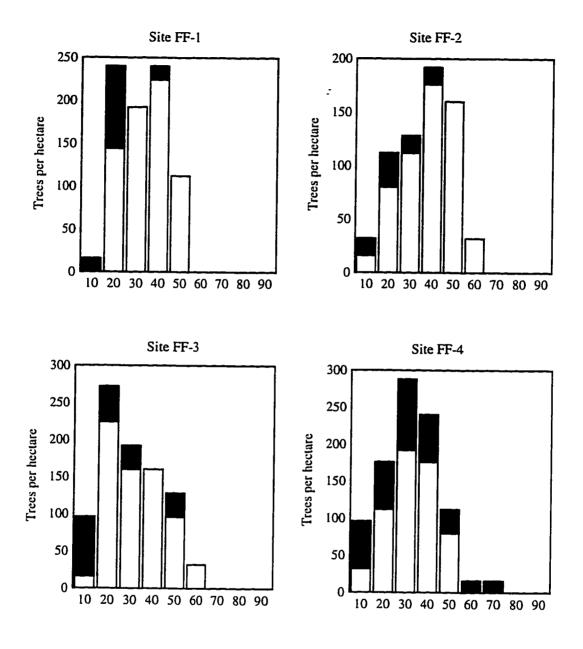


Figure 5.2. Diameter distributions of living (white) and dead (black) trees at the three study sites. Labeled diameters are the upper endpoints of 10-cm classes.

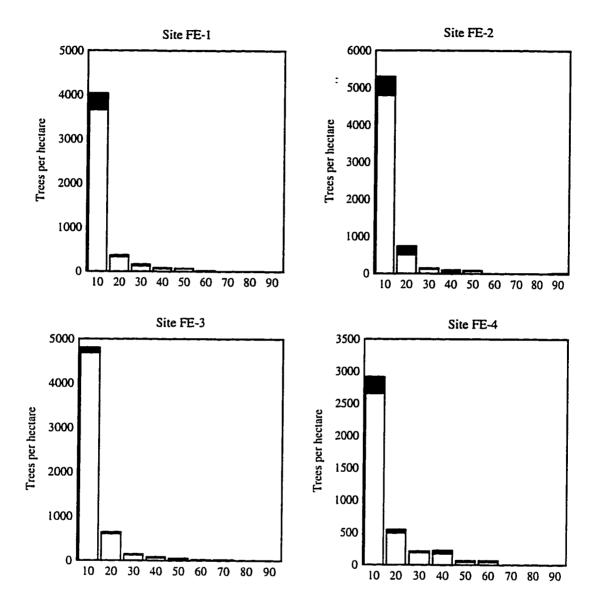


Figure 5.2. Continued.

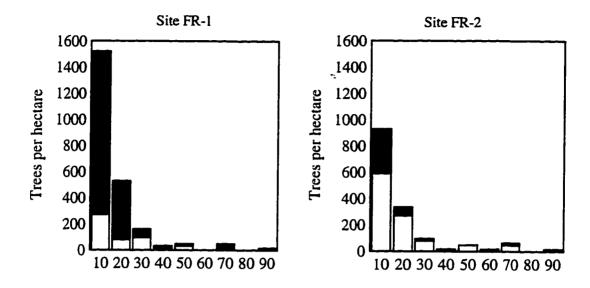


Figure 5.2. Continued.

6. DISCUSSION

The individual manuscript chapters (3 through 5) included discussions of the results and research and management implications of each study. This final chapter presents comparisons between the Arizona and Durango study sites as well as future directions for research.

6.1 Differences between Arizona and Durango ecosystems

The differences between the studied ecosystems were substantial in both social and ecological terms. Differences in culture and historic patterns of land use between the southwestern U.S. and northern Mexico, establishing the 'natural experiment' of nearly universal exclusion of fire from long-needled pine ecosystems only on the U.S. side, were reviewed in chapters 2 and 4. Ecological differences are outlined below.

Abiotic characteristics at the Durango sites included rhyolitic soil parent material, steep slopes, relatively long growing seasons, and relatively less winter precipitation. The Arizona site had primarily basaltic soil parent material, gentle slopes, and a short growing season with a strongly bimodal precipitation pattern. Consistent with the proximity to the tropics and steep elevational gradients, the diversity of plant species was greater in Durango. The Arizona site had one long-needled pine species, one oak, and a few other conifers, while the Durango site had eight pine species, several other conifers, a minimum of four oak species (the number is uncertain due to hybridization), as well as alder and madrone species.

The relationship between overstory structure and herbaceous productivity differed between the studied ecosystems. Presettlement ponderosa pine forests of northern Arizona, described as open and "park-like" (Cooper 1960), had low tree densities with pines grouped in patches separated by highly productive perennial grasses (White 1985, Covington and Moore 1994a). Presettlement forest structure at Camp Navajo matches this general description, but the Durango forests were more dense. The frequent-fire site AL had 647 trees/ha, as compared with 148 trees/ha at Camp Navajo. Overstory trees at AL, as well as pre-fire-exclusion trees at AV, had a random to uniform spatial distribution, unlike the clumped presettlement pattern in northern Arizona (White 1985). Herbaceous cover at the frequent-fire AL was only 20%, the highest of the four Durango sites but not significantly different from the others. Whether livestock grazing played a large role in creating these forest structures is not clear. Although the three Durango pine-oak sites were unharvested, they were open to grazing and had perennial (sites AL, AV) or seasonal (site SP) water available. However, dominant overstory trees ranged in age from 80 to 150 years, indicating that tree patterns were established well before the establishment of ejidos and increases in human populations in the region.

An alternative hypothesis explaining the higher tree density in Durango may be the high precipitation supporting vigorous tree growth. The study area in northwestern Durango is one of the most productive forests in the state. Sites elsewhere in the Sierra Madre Occidental with relatively more grass dominance appear to be associated with less humid environments (P. Fulé and W. Covington, unpublished data). Soil texture may be another contributing factor, with relatively heavy silt and clay soils, such as the basalt

soils of northern Arizona, tending to favor herbaceous plants, while relatively coarse-textured soils, such as the rhyolitic soils of the Mexican study sites, tend to favor trees (Covington and Moore 1994b).

Differences in the tree-grass relationship affect fuels and fire behavior in a self-regulating fashion that can determine future tree patterns. Presettlement ponderosa pine regeneration may have been limited primarily to safe sites, such as the ash bed of a consumed log, in order for the seedlings to survive grass competition and fires carried through the grass fuels until the seedlings grew above the flame height; thus by creating their own safe sites, presettlement pine groups could have been relatively self-perpetuating patches in a grass matrix (Weaver 1951, White 1985). In contrast, if tree fuels such as litter and wood served to support fires in Durango, the resulting increase in fire intensity in areas of dense trees would be expected to result in aggregated mortality patterns and a relatively uniformly-dispersed overstory, as observed on the pine-oak sites.

Regeneration patterns also differed between the Arizona and Durango sites.

Sprouting oaks (and alders in Mexico) were dense in both forests, but the mean density of pine regeneration at Camp Navajo was approximately 170 stems/ha, in contrast to the approximately 600 to 3,500 stems/ha in Durango. Sites sampled 1-year (SP) and 2-years (AL) postburn both had plentiful pine seedling regeneration. These results suggest that regeneration capability may be much less of a limiting factor of tree density in Durango, perhaps due to greater precipitation, milder climate, higher number of pine species, different soils, and reduced herbaceous competition. In Arizona, where ponderosa pine regeneration is sporadic (White 1985), the early appearance of fire exclusion due to sheep

grazing on Navajo lands was not followed by the establishment of pine thickets until favorable climatic conditions occurred that facilitated increases in tree density simultaneously throughout the region (Savage and Swetnam 1990). If regeneration can be accomplished more readily in Durango, then tree density increases following fire exclusion may occur more rapidly and consistently than in Arizona.

6.2 Parallels between Arizona and Durango ecosystems

Despite the numerous differences described above, fire exclusion was associated with increased forest density, changes in species composition, and increased fuel loading at every study site where the frequent-fire regime was disrupted (Camp Navajo, Arizona, and sites AV, CB, and SP, Durango). Under temporally and spatially similar frequentfire regimes, the Durango site AL as well as the reconstructed 1883 Camp Navajo forest were dominated by relatively few, large pines, with an important component of oaks. Following fire exclusion of approximately 50 years at the Durango sites and 112 years at the Arizona site, tree densities increased by an order of magnitude. Small-diameter trees, in highly aggregated groups, came to dominate overstory structure. Pine species declined relative to sprouting species at fire-excluded sites. Forest floor fuel loading increased, especially thick duff layers and heavy rotten woody fuels. The combination of increased dead and living fuels, with horizontal and vertical continuity, is likely to support a novel disturbance regime of high-intensity, stand-replacing fire, such as the fires which burned across landscapes of record size in Arizona and New Mexico in 1996. While the longterm effects of fires at such scales of severity and extent are still little understood, they

are clearly outside the range of variability in historic ecosystem conditions and present an important threat to sustainable management of these ecosystems.

Despite the numerous differences described above in abiotic characteristics, biotic communities, human populations, tree harvesting history, and the time of initiation of fire exclusion, a closely similar sequence of events associated with fire exclusion occurred at sites in Arizona and Durango. Ecosystem variability across this large region affects the magnitude and characteristics of the response to fire exclusion. However, the broad agreement seen in the effects of fire exclusion in this integrated set of studies supports the argument that fire is the fundamental factor controlling tree population irruptions and fuel loads in long-needled pine ecosystems of southwestern North America.

6.3 Ecosystem management implications and future directions

Quantitative information about the natural functions and structures of ecosystems is invaluable for management. Reconstructed presettlement reference conditions in northern Arizona, presented in chapter 3, were applied as a benchmark to evaluate the condition of contemporary forests and to serve as a guide for ecological restoration. In chapters 4 and 5, the intact frequent-fire ecosystem at Durango site AL was used as the point of reference against which the changes in fire-excluded ecosystems were compared.

Three key points emerged from these comparisons. First, the keystone role of regimes of frequent, low-intensity fire must be considered in management of western long-needled pine ecosystems. The role of fire cannot be easily substituted by other treatments, nor can the destructive potential of high-intensity fire in fire-excluded

ecosystems be indefinitely suppressed. Second, because extended fire exclusion leads to unsustainably dense forest structures, management alternatives aimed at preserving dense forests will not succeed. Third, simply re-introducing fire is unlikely to reverse the course of ecosystem degradation. Rather, an integrated approach based on knowledge of reference conditions and a systematic strategy of ecological restoration, such as described by Covington et al. (in press), is recommended. As human populations rise and global environments change, reference information and ecological restoration will play an increasingly important role in strategies for sustainable ecosystem management.

Future collaborative research arising from these studies will stress three main themes. First is continuation of the biogeographical approach to long-needled pine ecosystems across the southern Cordillera of North America, sampling with consistent methods at a network of sites across this gradient to investigate similarities and differences in the influence of fire regimes on forest structures. Relatively intact ecosystems of northern Mexico will remain an important focus, beginning with 1996 sampling of La Michilía Biosphere Reserve in Durango. This site is representative of the drier eastern slope of the Sierra Madre Occidental, complementing the present work in more mesic sites (P.Z. Fulé and W.W. Covington, unpublished data). A second theme is spatial analysis and landscape-scale studies, seeking to incorporate analytical tools which are relatively new to ecology and to expand the spatial scale of investigation, beginning with several collaborative projects in Arizona (W.W. Covington, M.M. Moore, J.N. Mast, and others, unpublished data). Finally, the third theme is the application of ecological science, including reference condition information, to sustainable ecosystem

management. This work is concentrating on restoration of degraded ecosystems, including the Camp Navajo forest described in chapter 3 (M.M. Moore, W.W. Covington, and others, unpublished data), the Mt. Trumbull ecosystem in northwestern Arizona, and other sites.

7. LITERATURE CITED

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: perspectives for ecological diversity. University of Chicago Press, Chicago, IL.

- Allen, C.D., R. Touchan, and T.W. Swetnam. 1995. Landscape-scale fire history studies support fire management action at Bandelier. Park Science 15(3):18-19.
- Anderson, R.S. 1989. Development of the southwestern ponderosa pine forests: what do we really know? Pages 15-22 in Tecle, A., W.W. Covington, and R.H. Hamre (tech. coords.), Multiresource management of ponderosa pine forests. USDA Forest Service General Technical Report RM-185, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Arno, S.F., and K.M. Sneck. 1977. A method for determining fire history in coniferous forests of the Mountain West. USDA Forest Service General Technical Report INT-42, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Arno, S.F., E.D. Reinhardt, and J.H. Scott. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine type: a procedure for quantifying past and present conditions. USDA Forest Service General Technical Report INT-294, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Arno, S.F., M.G. Harrington, C.E. Fiedler, and C.E. Carlson. 1995a. Restoring firedependent ponderosa pine forests in western Montana. Restoration and Management Notes 13(1):32-36.
- Arno, S.F., J.H. Scott, and M.G. Hartwell. 1995b. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. USDA Forest Service Research Paper INT-RP-481, Intermountain Research Station, Ogden, UT.
- Avery, C.C., F.R. Larson, and G.H. Schubert. 1976. Fifty-year records of virgin stand development in southwestern ponderosa pine. USDA Forest Service General Technical Report RM-22, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Axelrod, D.J. 1986. Cenozoic history of some western American pines. Annals of the Missouri Botanical Garden 73:565-641.
- Baisan, C.H., and T.W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Canadian Journal of Forest Research 20:1559-1569.

- Baisan, C.H., and T.W. Swetnam. 1995. Historical fire occurrence in remote mountains of southwestern New Mexico and northern Mexico. Pages 153-156 in Brown, J.K., and others (tech. coords.), Proceedings: Symposium on Fire in Wilderness and Park Management. USDA Forest Service General Technical Report INT-GTR-320, Intermountain Research Station, Ogden, UT.
- Bahre, C.J. 1985. Wildfire in southeastern Arizona between 1859 and 1890. Desert Plants 7(4):190-194.
- Bahre, C.J. 1991. A Legacy of Change. Historic human impact on vegetation in the Arizona borderlands. The University of Arizona Press, Tucson, AZ.
- Barger, R.L., and P.F. Ffolliott. 1972. Physical characteristics and utilization of major woodland tree species in Arizona. USDA Forest Service Research Paper RM-83, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Barton, A.M. 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. Ecological Monographs 63(4):367-397.
- Barton, A.M. 1995. Fire adaptations in pines and oaks: tree population responses to fire suppression in Arizona's Madrean forests. Pages 159-163 in Brown, J.K., Mutch, R.W., Spoon, C.W., and Wakimoto, R.H. (tech. coords.), Proceedings: symposium on fire in wilderness and park management. USDA Forest Service General Technical Report INT-GTR-320, Ogden, UT.
- Biodiversity Support Program. 1995. A regional analysis of geographic priorities for biodiversity conservation in Latin America and the Caribbean. World Wildlife Fund, Washington D.C.
- Biondi, F. in press. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse asymmetric competition? Canadian Journal of Forest Research.
- Biondi, F., D.E. Myers, and C.C. Avery. 1994. Geostatistically modeling stem size and increment in an old-growth forest. Canadian Journal of Forest Research 24:1354-1368.
- Biswell, H.H. 1972. Fire ecology in ponderosa pine--grassland. Proceedings of the Tall Timbers Fire Ecology Conference 12:69-96.
- Bojórquez-Tapia, L.A., L.A. Peña, C. Alvarez, I. Azuara, M. Alquicira, and A. Ramírez. 1995. Conservation of Madrean Archipelago and regional forest development projects in Mexico. Pages 206-213 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

- Bond, W.J., and J.J. Midgley. 1995. Kill thy neighbor: an individualistic argument for the evolution of flammability. Oikos 73:79-85.
- Bourgeron, P.S., and M.E. Jensen. 1994. An overview of ecological principles for ecosystem management. Pages 45-57 in Jensen, M.E., and P.S. Bourgeron (tech. eds.). Volume II: ecosystem management: principles and applications. USDA Forest Service General Technical Report PNW-GTR-318, Pacific Northwest Research Station, Portland, OR.
- Brown, D.E. (editor). 1982. Biotic communities of the American Southwest--United States and Mexico. Desert Plants 4(1-4):1982.
- Brown, J.K. 1974. Handbook for inventorying downed woody material. United States Department of Agriculture Forest Service General Technical Report INT-16, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Burns, R.M., and B.H. Honkala (technical coordinators). 1990. Silvics of North America. Volume 1. Conifers. USDA Forest Service Agriculture Handbook 654. Washington, D.C.
- Bye, R. 1995. Prominence of the Sierra Madre Occidental in the biological diversity of Mexico. Pages 19-27 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Carpenter, S.R. 1990. Large-scale perturbations: opportunities for innovation. Ecology 71(6):2038-2043.
- Chou, Y.H., R.A. Minnich, and R.J. Dezzani. 1993. Do fire sizes differ between southern California and Baja California? Forest Science 39:835-844.
- Clewell, A.F., D.A. Falk, and W.W. Covington. 1993. Mission statement, Society for Ecological Restoration. Restoration Ecology 1:206-207.
- Cline, P. 1994. Mountain Town: Flagstaff's First Century. Northland Press, Flagstaff, AZ.
- Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecology 42:493-499.
- Cooper, C.F. 1961. Pattern in ponderosa pine forests. Ecology 42(3):493-499.

- Conkle, M.T., and W.B. Critchfield. 1988. Genetic variation and hybridization of ponderosa pine. Pages 27-44 in Baumgartner, D.M., and J.E. Lotan (eds.), Ponderosa Pine: The Species and Its Management. Washington State University, Spokane, WA.
- Cormier, K.L. 1990. Modeling natural regeneration of even-aged ponderosa pine following shelterwood cutting in northern Arizona. M.S.F. thesis, Northern Arizona University, Flagstaff.
- Covington, W.W., and M.M. Moore. 1992. Post-settlement changes in natural disturbance regimes: implications for restoration of old-growth ponderosa pine ecosystems. Pages 81-99 In Old-growth forests in the Southwest and Rocky Mountain Region. Proceedings of the symposium. USDA Forest Service General Technical Report RM-213. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Covington, W.W., and M.M. Moore. 1994a. Southwestern ponderosa forest structure and resource conditions: changes since Euro-American settlement. Journal of Forestry 92(1):39-47.
- Covington, W.W., and M.M. Moore. 1994b. Postsettlement changes in natural fire regimes: ecological restoration of old-growth ponderosa pine forests. Journal of Sustainable Forestry 2:153-181.
- Covington, W.W., and S.S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. Forest Science 30:183-192.
- Covington, W.W., and S.S. Sackett. 1990. Fire effects on ponderosa pine soils and their management implications. Pages 105-111 in: Effects of fire management of southwestern natural resources. USDA Forest Service General Technical Report RM-191, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Covington, W.W., R.L. Everett, R.W. Steele, L.I. Irwin, T.A. Daer, and A.N.D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. Journal of Sustainable Forestry 2:13-63.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. In press. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry.
- Cunningham, J.B., R.P. Balda, and W.S. Gaud. 1980. Selection and use of snags by secondary cavity-nesting birds of the ponderosa pine forest. USDA Forest Service Research Paper RM-222. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

- D'Arrigo, R.D., and G.C. Jacoby. 1991. A 1000-year record of winter precipitation from northwestern New Mexico, USA: a reconstruction from tree-rings and its relation to El Niño and the Southern Oscillation. The Holocene 1(2):95-101.
- Day, R.W., and G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59(4):433-463.
- DeBano, L.F., and P.F. Ffolliott. 1995. The sky island conference: looking back, looking ahead. Pages 1-5 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Delcourt, H.R., and P.A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. Landscape Ecology 2(1):23-44.
- Deutsch, C.V., and A.G. Journel. 1992. GSLIB. Geostatistical software library and users's guide. Oxford University Press, New York.
- Dieterich, J.H. 1980. Chimney Spring forest fire history. USDA Forest Service Research Paper RM-220, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Dieterich, J.H. 1983a. Historia de los incendios forestales en la Sierra de los Ajos, Sonora. Nota Técnica No. 8, CIFONOR--INIF, S.F.F., S.A.R.H., Mexico.
- Dieterich, J.H. 1983b. Fire history of southwestern mixed conifer: a case study. Forest Ecology and Management 6:13-31.
- Dieterich, J.H., and T.W. Swetnam. 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Science 30:238-247.
- Diggle, P.J. 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, London.
- Duncan, R.P. 1990. Spatial analysis programmes. University of Canterbury, Christchurch, New Zealand.
- Duncan, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecology 79:1073-1084.
- Eberhardt, L.L., and J.M. Thomas. 1991. Designing environmental field studies. Ecological Monographs 61(1):53-73.

- Ecological Society of America. 1996. The scientific basis for ecosystem management. Ecological Applications 6(3):665-691.
- Felger. R.S., and M.F. Wilson. 1995. Northern Sierra Madre Occidental and its Apachian outliers: a neglected center of biodiversity. Pages 36-59 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Fiedler, C.E. 1996. Silvicultural applications: restoring ecological structure and process in ponderosa pine forests. Pages 39-40 in Hardy, C.C., and S.F. Arno (eds.), The use of fire in forest restoration. USDA Forest Service General Technical Report INT-GTR-341, Intermountain Research Station, Ogden, UT.
- Fiedler, C.E., S.F. Arno, and M.G. Harrington. 1996. Flexible silvicultural and prescribed burning approaches for improving health of ponderosa pine forests. Pages 69-74 in Covington, W.W., and P.K. Wagner (tech. coords.), Conference on adaptive ecosystem restoration and management: restoration of cordilleran conifer landscapes of North America. USDA Forest Service General Technical Report RM-GTR-278, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Fisher, J.T., P.A. Glass, and J.T. Harrington. 1995. Temperate pines of northern Mexico: their use, abuse, and regeneration. Pages 174-179 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Fritts, H.C., and T.W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Advances in Ecological Research 19:111-188.
- Frost, T.M., D.L. DeAngelis, S.M. Bartell, D.J. Hall, and S.H. Hurlbert. 1988. Scale in the design and interpretation of aquatic community research. Chapter 14 in Carpenter, S.R. (ed.), Complex Interactions in Lake Communities. Springer-Verlag, New York.
- Fulé, P.Z., and W.W. Covington. 1994. Fire regime disruption and pine-oak forest structure in the Sierra Madre Occidental, Durango, Mexico. Restoration Ecology 2(4):261-272.
- Fulé, P.Z., and W.W. Covington. 1996. Changing fire regimes in Mexican pine forests: ecological and management implications. Journal of Forestry 94(10):33-38.

- Garrett, L.D., B.E. Fox, and W.F. Stansfield. 1990. An assessment of Arizona's timber resources and forest products industry. Report to the State of Arizona, Department of Commerce. On file at School of Forestry, Northern Arizona University, Flagstaff.
- Gerhard, P. 1982. The North Frontier of New Spain. Princeton University Press, Princeton, NJ.
- Glitzenstein, J.S., W.J. Platt, and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65(4):441-476.
- González-Cabán, A., and D.V. Sandberg. 1989. Fire management and research needs in Mexico. Journal of Forestry 87:20-26.
- González Elizondo, M., S. González Elizondo, and Y. Herrera Arrieta. 1991. Listados Floristicos de México. IX. Flora de Durango. Instituto de Biología, Universidad Nacional Autónoma de México, D.F. México.
- González-Elizondo, S., M. González-Elizondo, and A. Cortés-Ortiz. 1993. Vegetación de la reserva de la biósfera "La Michilía," Durango, México. Acta Botánica Mexicana 22:1-104.
- Gosz, J.R. 1992. Gradient analysis of ecological change in time and space: implications for forest management. Ecological Applications 2(3):248-261.
- Gottfried, G.J. 1980. Control of New Mexican locust and the effect on planted ponderosa pine in central Arizona. USDA Forest Service Research Note RM-386, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Graybill, D.A. 1987. Unpublished tree-ring chronologies AZ521 and AZ547. Archived at the National Geophysical Data Center, World Data Center-A for Paleoclimatology, Boulder, CO.
- Grenda, D.R. 1993. Land use in north-central Arizona: an archaeological survey of Navajo Army Depot, Coconino County, Arizona. Statistical Research Technical Series No. 43. Tucson, AZ.
- Grissino-Mayer, H.D. 1995. Tree-ring reconstructions of climate and fire history at El Malpais National Monument, New Mexico. Ph.D. Dissertation, University of Arizona, Tucson.
- Grissino-Mayer, H.D., and R.L. Holmes. 1993. International Tree-Ring Data Bank Program Library. Laboratory of Tree-Ring Research, University of Arizona, Tucson.

- Grissino-Mayer, H.D., C.H. Baisan, and T.W. Swetnam. 1994. Fire history and age structure analyses in the mixed conifer and spruce-fir forests of Mount Graham. Final Report, Mount Graham Red Squirrel Study Committee, US Fish and Wildlife Service, Phoenix, AZ.
- Grissino-Mayer, H.D., C.H. Baisan, and T.W. Swetnam. 1995. Fire history in the Pinaleno Mountains of southeastern Arizona: effects of human-related disturbances. Pages 399-407 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Grumbine, R.E. 1992. Ghost Bears: Exploring the Biodiversity Crisis. Island Press, Washington, D.C.
- Guizar Nolazco, E., A. Benítez Paredes, and O. Bravo Bolaños. 1992. La vegetación de la Unidad de Conservación y Desarrollo Forestal "Topia", Durango. Universidad Autónoma Chapingo, División de Ciencias Forestales, Chapingo, México.
- Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. Journal of Vegetation Science 6:575-582.
- Habeck, J.R. 1990. Old-growth ponderosa pine--western larch forests in western Montana: ecology and management. The Northwest Environmental Journal 6:271-292.
- Hann, D.W. 1976. Relationship of stump diameter to diameter at breast height for seven tree species in Arizona and New Mexico. USDA Forest Service Research Note INT-212, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Harlan, T. 1973. Tree-ring chronology 43964 (La Cienega, Durango, Mexico). Laboratory of Tree-Ring Research, The University of Arizona, Tucson, AZ.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, Jr., and K.W. Cummins. 1985. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.
- Harrington, M.G. 1985. The effects of spring, summer, and fall burning on Gambel oak in a southwestern ponderosa pine stand. Forest Science 31(1):156-163.

- Harrington, M.G. 1996. Prescribed fire applications: restoring ecological structure and process in ponderosa pine forests. Page 41 in Hardy, C.C., and S.F. Arno (eds.), The use of fire in forest restoration. USDA Forest Service General Technical Report INT-GTR-341, Intermountain Research Station, Ogden, UT.
- Harrington, M.G., and S.S. Sackett. 1990. Using fire as a management tool in southwestern ponderosa pine forests. Pages 122-133 in Krammes, J.S. (tech. coord.), Effects of Fire Management of Southwestern Natural Resources.
 Proceedings of the Symposium. USDA Forest Service General Technical Report RM-191, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Hart, S.C., E.A. Paul, and M.K. Firestone. 1992. Decomposition and nutrient dynamics in ponderosa pine needles in a Mediterranean-type climate. Canadian Journal of Forest Research 22:306-314.
- Hobbs, R.J., and D.A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology 4(2):93-110.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447-502.
- Holling, C.S. 1996. Surprise for science, resilience for ecosystems, and incentives for people. Ecological Applications 6(3):733-735.
- Iversen, G.R. 1984. Bayesian statistical inference. Sage Publications, Inc., Newbury Park, CA.
- Jenny, H., S.P. Gessel, and F.T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Science 68:419-432.
- Jensen, M.E., and P.S. Bourgeron (tech. eds.). 1994. Volume II: ecosystem management: principles and applications. USDA Forest Service General Technical Report PNW-GTR-318, Pacific Northwest Research Station, Portland, OR.
- Johnson, E.A. 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, NY.
- Kaufmann, M.R., R.T. Graham, D.A. Boyce, Jr., and 8 others. 1994. An ecological basis for ecosystem management. USDA Forest Service General Technical Report RM-246, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

- Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69(4):1017-1024.
- Kilgore, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. Pages 58-89. In: Fire Regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26, Washington, D.C.
- Knight, D.H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. Pages 59-83 in Turner, M.G. (ed.), Landscape Heterogeneity and Disturbance, Springer-Verlag, New York.
- Kolb, T.E., M.R. Wagner, and W.W. Covington. 1994. Concepts of forest health. Journal of Forestry 92:10-15.
- Lackey, R.T. 1995. Seven pillars of ecosystem management. The Environmental Professional 17(4):
- Lang, D.M., and S.S. Stewart. 1910. Reconnaissance of the Kaibab National Forest. USDA Forest Service, Southwestern Region.
- Lauria, F. 1991. Taxonmy, systematics, and phylogeny of *Pinus*, subsection *Ponderosae* Loudon (*Pinaceae*). Alternative concepts. Linzer Biol. Beitr. 23(1):129-202.
- Leopold, A. 1924. Grass, brush, timber, and fire in southern Arizona. Journal of Forestry 22:1-10.
- Leopold, A. 1934. The Arboretum and the University. Parks and Recreation 18:59-60.
- Leopold, A. 1937. Conservationist in Mexico. American Forests 37:118-120, 146.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73(6):1943-1967.
- Loock, E.E.M. 1950. The pines of Mexico and British Honduras. L.S. Gray and Company, Johannesburg, South Africa.
- Lumholtz, C. 1902. Unknown Mexico. Scribner, NY.
- Lundquist, J.E. 1995. Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA. Forest Ecology and Management 74:37-48.
- MacMahon, J.A., and W.R. Jordan, III. 1994. Ecological restoration. Chapter 14 in Meffe, G.K., and C.R. Carroll, Principles of Conservation Biology. Sinauer Associates, Publishers, Sunderland, MA.

- Madany, M.H., and N.E. West. 1983. Livestock grazing--fire regime interactions within montane forests of Zion National Park. Ecology 64:661-667.
- Madany, M.H., T.W. Swetnam, and N.E. West. 1982. Comparison of two approaches for determining fire dates from tree scars. Forest Science 28:856-861.
- Manuel Toledo, V., and M. de Jesús Ordóñez. 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats. Pages 757-778 in Ramamoorthy, T.P., et al. (eds.), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, New York.
- Marshall, J.T., Jr. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pacific Coast Avifauna 32:1-125.
- Marshall, J.T., Jr. 1962. Land use and native birds of Arizona. Journal of the Arizona Academy of Science 2:75-77.
- Martínez, M. 1948. Los Pinos Mexicanos. Segunda edición, aumentada considerablemente. Ediciones Botas, México.
- Maser, C., R.G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pages 78-95 in Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. USDA Agricultural Handbook 553, Washington, D.C.
- McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany 75(3):353-368.
- Mehl, M.S. 1992. Old-growth descriptions for the major forest cover types in the Rocky Mountain region. Pages 106-120 in Old-growth forests in the Southwest and Rocky Mountain Region. Proceedings of the symposium. USDA Forest Service General Technical Report RM-213, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Meko, D., C.W. Stockton, and W.R. Boggess. 1995. The tree-ring record of severe sustained drought. Water Resources Bulletin 31(5):789-801.
- Millar, C.I. 1993. Impact of the Eocene on the evolution of *Pinus* L. Annals of the Missouri Botanical Garden 80:471-498.
- Minnich, R.A. 1983. Fire mosaics in southern California and northern Baja California. Science 219:1287-1294.

- Minnich, R.A. 1993. Reconstruction and analysis of forest and brushland fire histories using aerial photograph sequences and geographic information systems. Pages 403-418 in Proceedings of the Thirteenth Annual ESRI User Conference, Redlands, CA.
- Minnich, R.A., M.G. Barbour, J.H. Burk, and R.F. Fernau. 1995. Sixty years of change in Californian conifer forests of the San Bernadino Mountains. Conservation Biology 9(4):902-914.
- Moir, W.H. 1992. Ecological concepts in old-growth forest definition. Pages 18-23 in Old-growth forests in the Southwest and Rocky Mountain Region. Proceedings of the symposium. USDA Forest Service General Technical Report RM-213, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Moir, W.H., and J.H. Dieterich. 1988. Old-growth ponderosa pine from succession in pine-bunchgrass forests in Arizona and New Mexico. Natural Areas Journal 8(1):17-24.
- Morgan, P., G.H. Aplet, J.B. Haufler, H.C. Humphries, M.M. Moore, and W.D. Wilson. 1994. Historical range of variability: A useful tool for evaluating ecological change. Journal of Sustainable Forestry 2:87-111.
- Mutch, R.W. 1970. Wildland fires and ecosystems--a hypothesis. Ecology 51:1046-1051.
- Myers, C.A. 1963. Estimating past diameters of ponderosa pine in Arizona and New Mexico. USDA Forest Service Research Note RM-7. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Myers, J.H. 1988. Can a general hypothesis explain population cycles of forest Lepidoptera? Advances in Ecological Research 18:179-242.
- Nixon, K.C. 1993. The genus *Quercus* in Mexico. Pages 447-458 in Ramamoorthy, T.P., et al. (eds), Biological Diversity of Mexico: Origins and Distribution. Oxford University Press, New York.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, NJ.
- Pennington, C.W. 1963. The Tarahumar of Mexico. University of Utah Press, Salt Lake City.
- Pennington, C.W. 1969. The Tepehuan of Chihuahua: Their material culture. University of Utah Press, Salt Lake City.
- Perry, J.P., Jr. 1991. The pines of Mexico and Central America. Timber Press, Portland.

- Perry, D.A. 1995. Self-organizing systems across scales. Tree 10(6):241-244.
- Peterson, C.J., and E.R. Squiers. 1995. An unexpected change in spatial pattern across 10 years in an aspen—white-pine forest. Journal of Ecology 83:847-855.
- Pyne, S.J. 1982. Fire in America. A cultural history of wildland and rural fire. Princeton University Press, Princeton, NJ.
- Pyne, S.J. 1995. World Fire. The culture of fire on earth. Henry Holt and Company, Inc., New York.
- Rebertus, A.J., G.B. Williamson, and E.B. Moser. 1989. Fire-induced changes in *Quercus laevis* spatial pattern in Florida sandhills. Journal of Ecology 77:638-650.
- Ripley, B.D. 1981. Spatial Statistics. John Wiley & Sons, New York.
- Rodríguez Trejo, D.A., and A. Sierra Pineda. 1992. Bosquejo histórico sobre diversos aspectos de los incendios forestales en México. Ciencia Forestal en México 17:115-174.
- Rogers, J.J., J.M. Prosser, L.D. Garrett, and M.G. Ryan. 1984. ECOSIM: A system for projecting multiresource outputs under alternative forest management regimes. USDA Forest Service, Administrative Report, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Rossi, R.E., D.J. Mulla, A.G. Journel, and E.H. Franz. 1992. Geostatistical tools for modeling and iterpreting ecological spatial dependence. Ecological Monographs 62(2):277-314.
- Sackett, S.S. 1980. Woody fuel particle size and specific gravity of southwestern tree species. USDA Forest Service Research Note RM-389. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sackett, S.S. 1984. Observations on natural regeneration in ponderosa pine following a prescribed fire in Arizona. USDA Forest Service Research Note RM-435. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sackett, S.S., S.M. Haase, and M.G. Harrington. 1996. Lessons learned from fire use for restoring southwestern ponderosa pine ecosystems. Pages 53-60 in Covington, W., and P.K. Wagner (tech. coords.), Conference on adaptive ecosystem restoration and management: restoration of cordilleran conifer landscapes of North America. USDA Forest Service General Technical Report RM-GTR-278, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

- Sánchez Cordova, J., and J.H. Dieterich. 1983. Efecto de quemas controladas en *Pinus durangensis* en Madera, Chihuahua. Nota Técnica No. 9. CIFONOR-INIF. S.F.F., S.A.R.H., México.
- Sánchez Cordova, J, and G. Zerecero Leál. 1983. Método práctico para calcular la cantidad de combustible leñoso y hojarasca. Nota Técnica No. 3. CIFONOR-INIF. S.F.F., S.A.R.H., México.
- SARH [Secretaría de Agricultura y Recursos Hidraúlicos]. 1994. National fire statistics. Presented at the Fifth Mexico/United States Symposium, Partnerships for Sustainable Forest Ecosystem Management, October 17-20, 1994, Guadalajara, Jalisco, Mexico.
- Savage, M., and T.W. Swetnam. 1990. Early 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71:2374-2378.
- Schubert, G.H. 1974. Silviculture of southwestern ponderosa pine: the status-of-our-knowledge. USDA Forest Service Research Paper RM-123, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Sellers, W.D., and R.H. Hill. 1974. Arizona Climate 1931-1972. The University of Arizona Press, Tucson, AZ.
- Soil Conservation Service. 1970. Soil Survey, The Navajo Army Depot, Coconino County, Arizona. A special report. USDA Soil Conservation Service, DoD The Navajo Army Depot, and the Coconino Soil Conservation District. Report on file at the office of the Soil Conservation Service, Flagstaff, AZ.
- Stahle, D.W., and M.K. Cleaveland. 1993. Southern Oscillation extremes reconstructed from tree rings of the Sierra Madre Occidental and southern Great Plains. Journal of Climate 6:129-140.
- Sterner, R.W., C.A. Ribic, and G.E. Schatz. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. Journal of Ecology 74:621-633.
- Stewart-Oaten, A., J.R. Bence, and C.W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solutions. Ecology 73(4):1396-1404.
- Stokes, M.A., and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.
- Sutherland, E.K. 1983. Fire exclusion effects on ponderosa pine growth. M.S. Thesis, University of Arizona, Tucson.

- Swanson, F.J., J.A. Jones, D.A. Wallin, and J.H. Cissel. 1994. Natural variability—implications for ecosystem management. Pages 85-99 in Jensen, M.E., and P.S. Bourgeron, Eastside Forest Ecosystem Health Assessment, Vol. II, Ecosystem Management: Principles and Applications. USDA Forest Service, General Technical Report PNW-GTR-318, Pacific Northwest Research Station, Portland, OR.
- Swetnam, T.W. 1990. Fire history and climate in the southwestern United States. Pages 6-17 in Krammes, J.S. (tech. coord.), Effects of Fire Management of Southwestern Natural Resources. Proceedings of the Symposium. USDA Forest Service General Technical Report RM-191, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885-889.
- Swetnam, T.W., and C.H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11-32 in Allen, C.D. (ed.), Proceedings of the 2nd La Mesa Fire Symposium. USDA Forest Service General Technical Report RM-GTR-286, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Swetnam, T.W., and J.L. Betancourt. 1990. Fire-Southern Oscillation relations in the southwestern United States. Science 249:1017-1020.
- Swetnam, T.W., and J.H. Dieterich. 1985. Fire history of ponderosa pine forests in the Gila Wilderness, New Mexico. Pages 390-397 in Lotan, J.E., B.M. Kilgore, W.C. Fischer, and R.W. Mutch (tech. coords.), Proceedings--Symposium and Workshop on Wilderness Fire. USDA Forest Service General Technical Report INT-182, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Swetnam, T.W., and A.M. Lynch. 1993. Multi-century, regional-scale patterns of western spruce budworm outbreaks. Ecological Monographs 63(4):399-424.
- Swetnam, T.W., B.E. Wickman, H.G. Paul, and C.H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. USDA Foreset Service Research Paper PNW-RP-484, Pacific Northwest Research Station, Portland, OR.
- Tabachnick, B.G., and L.S. Fidell. 1983. Using Multivariate Statistics. Harper & Row, Publishers, Inc, New York, NY.
- Thomas, J.W., R.G. Anderson, C. Maser, and E.L. Bull. 1979. Snags. Pages 60-77 in Wildlife habitats in managed forests--the Blue Mountains of Oregon and Washington. USDA Agricultural Handbook 553, Washington, D.C.

- Turner, M.G., and R.H.: Gardner (editors). 1991. Quantitative methods in landscape ecology. Springer-Verlag, New York.
- Turner M.G., R.H. Gardner, R.V. O'Neill, and S.M. Pearson. 1994. Multiscale organization of landscape heterogeneity. Pages 73-79 in Jensen, M.E., and P.S. Bourgeron, Eastside Forest Ecosystem Health Assessment, Vol. II, Ecosystem Management: Principles and Applications. USDA Forest Service, General Technical Report PNW-GTR-318, Pacific Northwest Research Station, Portland, OR.
- Veblen, T.T., and D.C. Lorenz. 1991. The Colorado Front Range. A century of ecological change. University of Utah Press, Salt Lake City, Utah.
- Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82:125-135.
- Villanueva-Díaz, J., and G.R. McPherson. 1995. Forest stand structure in mountains of Sonora, Mexico, and New Mexico, USA. Pages 416-423 in DeBano, L.F., and P.F. Ffolliott (tech. coords.), Biodiversity and Management of the Madrean Archipelago: The Sky Islands of Southwestern United States and Northwestern Mexico. USDA Forest Service General Technical Report RM-GTR-264, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Wagner, M.R. 1994. The healthy multiple-use forest ecosystem: an impossible dream. Pages 185-188 in Covington, W.W., and L.F. DeBano (tech. coords.), Sustainable ecological systems: implementing an ecological approach to land management. USDA Forest Service General Technical Report RM-247, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Walters, C.J. 1986. Adaptive Management of Renewable Resources. McGraw Hill, New York.
- Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71(6):2060-2068.
- Weaver, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific Slope. Journal of Forestry 41(1):7-15.
- Weaver, H. 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. Journal of Forestry 49:93-98.
- West, P.W. 1984. Inter-tree competition and small-scale pattern in monoculture of *Eucalyptus obliqua* L'Herit. Australian Journal of Ecology 9:405-411.

- White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology 66(2):589-594.
- Wilson, L., and B.M. Tkacz. 1995. Historical perspectives on forest insects and pathogens in the Southwest: implications for restoration of ponderosa pine and mixed conifer forests. Pages 26-31 in Covington, W.W., and P.K. Wagner (tech. coords.), Conference on adaptive ecosystem restoration and management: restoration of cordilleran conifer landscapes of North America. USDA Forest Service General Technical Report RM-GTR-278, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Wilkinson, L. 1988. SYSTAT: The System for Statistics. SYSTAT Inc., Evanston, IL.
- Woolsey, Jr., T.S. 1911. Western yellow pine in Arizona and New Mexico. USDA Forest Service Bulletin 101, Government Printing Office, Washington D.C.
- Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ.