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Revegetation after stand-replacing fire in the Lake Tahoe basin

William Henry Russell
San Jose State University

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Russell, William Henry, M.S.

San Jose State University, 1994

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Ann Arbor, MI 48106**

**REVEGETATION AFTER STAND-REPLACING FIRE
IN THE LAKE TAHOE BASIN**

A Thesis

Presented to

The Faculty of the Department of Geography and Environmental Studies
San Jose State University

In Partial Fulfilment
of the Requirements for the Degree
Master of Science

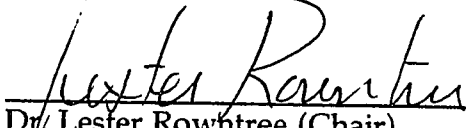
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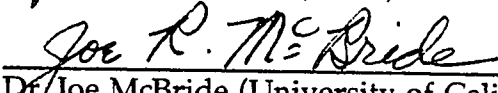
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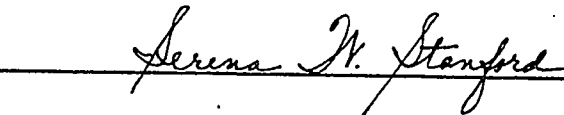


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ABSTRACT

REVEGETATION AFTER STAND-REPLACING FIRE IN THE LAKE TAHOE BASIN

by William H. Russell

Low and moderate intensity surface fires have been accepted as a natural and beneficial part of the mixed conifer forests surrounding Lake Tahoe. High intensity stand-replacing fires have not generally been considered ecologically significant. However, stand-replacing fires did occur prior to fire suppression and may have affected vegetation structure more than previously thought. The occurrence of an extensive, pre-suppression, stand-replacing fire at the south end of Lake Tahoe on Angora Ridge was confirmed.

Data gathered on the structure and composition of the current vegetation on Angora Ridge and three subsequent stand-replacing fires indicates that the four areas experienced long periods of shrub domination following the fires. Surface fuel accumulation, and the density of standing dead trees were dramatically higher on Angora Ridge than on the other fire sites. Species diversity was significantly lower. Results indicate that stand-replacing fire has a significant ecological impact in this forest type.

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TABLE OF CONTENTS

<u>Chapter 1 - Introduction</u>	1
Background	1
Problem statement	4
Summary of research problem	6
 <u>Chapter 2 - Related Research</u>	 7
General theories of disturbance	8
Disturbance as it relates to theories of succession	8
Disturbance as it relates to community dynamics	11
Fire survival traits in plants	15
Adaptations to fire	15
Specific survival traits	18
The effects of fire suppression on community composition and structure	26
Increased fire size and intensity	26
Changes in species composition	29
Changes in age structure	31
Changes in diversity: Species and habitat	32
Summary of the ecological effects of fire	35
 <u>Chapter 3 - The History of fire in the Sierra Nevada</u>	 37
Pre-European fire	38
Fire prior to human habitation	38
The Native American period	40
Post settlement fire	41
High and low intensity fire	42
Summary of Fire History	43

<u>Chapter 4 - Methods</u>	44
Incidence of stand-replacing fire	45
Historical accounts	45
Photographic evidence	47
Fire history data	47
Stand Age	47
Ecological effects of stand-replacing fire	48
Specifics on the fire sites	48
Sampling methods	50
Summary of Methods	55
 <u>Chapter 5 - Results</u>	 57
Confirmation of stand replacing fires	57
Interpretation of historical photographs	58
Fire scar analysis	66
Stand age data	66
Community composition and structure	68
Canopy cover	68
Shrub cover	69
Species diversity	71
Fuel load	76
Frequency and relative frequency	77
Density and relative density	82
Dominance and relative dominance	86
Importance value	88
Mortality	90
Summary of results	90
 <u>Chapter 6 - Summary and Conclusions</u>	 93
Ecological importance of stand-replacing fire	94
Management implications	96
Future research	98

List of References	100
Appendix - Maps of Study Areas	114

LIST OF TABLES

<u>Table</u>		<u>Page</u>
3.1	Fire Area Characteristics	50
3.2	Daubenmire Cover Class Scale	52
4.1	Average Stand Age by Species	67
4.2	Canopy Cover	68
4.3	Shrub Cover	70
4.4	Occurrence of Individual Species	72
4.5	Proportions of Individual Species	73
4.6	Fuel Load	76
4.7	Frequency - Angora Ridge	78
4.8	Frequency - Cathedral Creek	79
4.9	Frequency - Cascade Lake	80
4.10	Frequency - Luther Fire	81
4.11	Density - Angora Ridge	82
4.12	Density - Cathedral Creek	83
4.13	Density - Cascade Lake	84

4.14	Density - Luther Fire	85
4.15	Dominance - Angora Ridge and Cathedral Creek	87
4.16	Importance Value	88
4.17	Relative Density	89

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
4.1 <u>Photograph.</u> Angora Ridge Taken From the Slopes of Echo Peak Above Upper Angora Lake in 1917.	59
4.2 <u>Photograph.</u> Angora Ridge Taken in July 1940.	60
4.3 <u>Photograph.</u> Angora Ridge Taken in 1952.	62
4.4 <u>Photograph.</u> Angora Ridge Taken in 1966.	63
4.5 <u>Photograph.</u> Angora Ridge Taken in 1976.	64
4.6 <u>Photograph.</u> Angora Ridge Taken in 1983.	65
4.7 Canopy Cover	69
4.8 Shrub Cover	71
4.9 Species Richness	74
4.10 Shannon Diversity	75
4.11 Evenness	75
4.12 Fuel Load	77
4.13 Density	86
4.14 Relative Dominance	88
4.15 Density of Standing Dead Trees	90

CHAPTER 1

INTRODUCTION

Background

Historically fire has been viewed by land management agencies in the United States as a purely destructive force that should be excluded not only from areas where human property and lives are endangered, but also in the most remote areas. However, these traditional fire management practices have recently been called into question (Pyne 1992). The issue of whether fire suppression is necessary or even beneficial in wildland areas is now being discussed as the relationship of fire with other ecological factors is reevaluated.

The benefits of fire as a natural force in ecosystems have been recognized in recent years (Hendrickson 1972, Heinselman 1978). Some public lands now designate certain areas that are allowed to burn in the case of naturally occurring fires, as well as areas where prescribed burning is practiced. However, the public consternation that occurs when highly publicized fires occur, such as the Yellowstone fire of 1988, has limited the ability of public agencies to carry out a "let-burn" policy. Prescribed fire, while it can reintroduce fire to ecosystems on a regular basis, may cause further structural shifts in fire type communities¹ if management goals are directed toward fuel

¹A fire type community is any community that experiences fire at a high enough frequency that structure and composition are to some degree dependant on fire for persistence.

reduction or type conversion rather than to maintenance of an ecosystem process. In order to properly manage fire its natural role must first be understood.

Fire frequency in the Sierra Nevada varies with elevation, slope aspect, moisture, vegetation type and a variety of other factors. The mountain range as a whole, however, can be described as fire prone. Most locations historically have had relatively high fire frequencies and low intensity fires, 8-10 years on average (Kilgore 1981). Specifically, in the mixed conifer forests of the Sierra Nevada, fire frequency is thought to be between 3-11 years (Boyce 1921, Shaw and Kotock 1924).

Fire frequency data prior to the recorded history of the area is based on fire scar data. Because of this, ignition sources are uncertain. The importance of fire caused by Native American populations is a matter of current debate. It is known that Native Americans did burn in many areas, both intentionally and unintentionally, and it is believed by some that this burning had a profound effect on the ecology of some areas (Barrett and Arno 1982, Biswell 1959, Gruell 1985, Pyne 1982).

Whatever the source of fire its exclusion from fire type communities tends to result in a number of ecological changes. The dominance of shade tolerant species such as *Abies concolor* (white fir) and *A. magnifica* (red fir) may increase with time, whereas the dominance of species such as *Pinus ponderosa* (Ponderosa Pine) and *P. jeffreyi* (Jeffrey pine) that have sun loving seedlings tends to decline (Bock and Bock 1969). Seed germination of particular species of *Pinus* and *Sequoiadendron giganteum* is also inhibited by deep forest litter that under natural conditions would be removed by periodic

fires. Periodic fires also release nutrients tied up in forest floor litter improving germination conditions for some species (Whitney 1979). On a larger scale, fire within ecosystems tends to result in vegetation characterized by differences in age, density, and type. This mosaic structure allows for more habitat diversity and can support a greater variety of plant and animal species (Minnich 1983, Pickett and White 1985).

Species that persists in communities that experience recurring fire may require fire for survival and tends to be adapted for fire survival. The traits that allow plants to survive frequent fire regimes are surprisingly consistent across geographic and taxonomic boundaries (Gill 1981 a, 1981 b). These traits can be divided into two main categories.

1. Traits that help species withstand fires such as thick bark, high crown, and sprouting responses.
2. Traits that allow a species to repopulate an area rapidly such as serotinous cones, persistent seed banks, and increased flowering after fire.

The vegetation of fire prone communities in the Sierra Nevada tends to exhibit a variety of morphological and physiological fire survival traits. Species such as *Sequoiadendron giganteum*, and *Pseudotsuga menziesii* have evolved thick bark with natural fire retardants to withstand low intensity ground fires (Weaver 1974). Sprouting responses are common in species of *Sequoiadendron*, *Quercus*, *Arctostaphylos*, and *Ceanothus* (Kauffman and Martin 1989). Increased flowering and seed germination are also common for many local plant species (Sweeney 1968).

Whether fire is naturally or artificially initiated may not be an issue as long as fire occurs at appropriate intervals and intensities. Traditionally, fire

has been viewed as an ecological disturbance that can set a forest back in terms of succession, requiring that the forest then go through a series of stages leading to a Clementian type climax stage. Instead of a single forest climax stage the mixed conifer forests can be viewed of as existing in a climax cycle, or climax pattern, with fire as a part. At each stage of the cycle many of the same species will be present, though the distribution and abundance of the species will change. As the forest goes through the stages of the cycle it will inevitably reach a fire stage.

Problem Statement

This study is directed toward a clearer understanding of the ecological role of fire in the mixed-conifer forests in the Lake Tahoe Basin. The importance of fire in this region cannot be overestimated both in terms of its effects on ecological communities and its interaction with human development and management goals. Specifically, this study addresses the question: Do stand-replacing fires² have a significant ecological impact on the Lake Tahoe Basin mixed-conifer forest community in terms of the following structural and compositional factors:

1. Does the frequency, density, and dominance of species within a community vary with different periods of fire exclusion?

²Stand replacing fire is defined as any fire that results in the loss of a majority of canopy cover (Romme 1980). Stand-replacing fires are also referred to as stand-converting fires and crown fires.

2. Does species richness, diversity, and evenness vary with different periods of fire exclusion?
3. Does fuel accumulation and tree mortality vary with different periods of fire exclusion?
4. What post-fire successional patterns can be discerned by comparing the vegetative development on fire sites of varying fire exclusion?

The historical prevalence of low and moderate intensity surface fires in the forests of the Sierra Nevada is well accepted, but it has been generally assumed that due to their rarity larger stand-replacing fires were not an important ecological factor in the evolution of these forests. Though it is true that surface fires were much more common than stand-replacing fires before European settlement and fire suppression, stand-replacing fires did occur (Kilgore and Taylor 1979) and their effect on forest structure may have been profound (Agee 1974). For example, recruitment of species that have high light requirements for germination may require stand-replacing fires for the opening of canopy gaps. Habitat heterogeneity, and species diversity may also be increased by crown fires (Baker 1992, Minnich 1983, 1989) and, in general, the large, long-term gaps caused by this type of fire may add an important dimension to the structure of Sierra Nevada forests.

This study will begin with a literature review in the second chapter that includes a discussion of general theories relating to fire ecology, adaptations to fire on the organismal and community levels, and the effects of fire

suppression on community structure. In the third chapter the history of fire in the Sierra Nevada is discussed in terms of ignition sources and the frequency of fire. The fourth (experimental) chapter of this study focuses on the ecological effects of stand-replacing fires in the South Lake Tahoe area. The final chapter includes a discussion of the implications of the existence of stand-replacing fires before European settlement in terms of their effect on forests structure and diversity and the importance to the future management of Sierra Nevada forests.

Summary of Research Problem

Fire is a natural part of many ecosystems. However, for the last century it has been the policy of public agencies to suppress all wildfire. Recently, some effort has been made to reintroduce low intensity surface fire in select areas. High intensity stand-replacing fire has not generally been considered as an important ecological factor in the Sierra Nevada and is not included in most fire management plans.

The purpose of this investigation is to demonstrate the importance of stand-replacing fire in the historical and modern fire regimes of the Lake Tahoe Basin with the goal that stand-replacing fire will be considered as a tool by public land managers. Clearly it would be difficult and unpopular to institute a management program that includes high intensity crown fire. However, if not included intentionally, and managed carefully, stand-replacing fire will likely occur regardless, often in bad weather conditions when it is no longer manageable.

CHAPTER 2

RELATED RESEARCH

It is necessary to build a theoretical framework on which to base the experimental portion of this study. The concept of fire as an integral part of the ecology of biotic communities has evolved over a long period of time and has been a subject of heated debate.

Our understanding of the role of fire in the environment is closely related to theories of disturbance. In order to place fire in its proper theoretical perspective the origin of the concept of ecological disturbance will first be investigated and the historical shifts in theoretical treatment of the subject will be outlined. In particular, the goal is to demonstrate that not only can disturbance (as fire) exist in mature ecological communities, but that it also plays a roll in the formation of their structure and function.

The second section of this chapter is directed toward a further understanding of the interactive relationship between fire and vegetation in fire-prone communities. Specifically discussed are the life history strategies that allow vegetation to persist and thrive under a regime of periodic fire episodes demonstrating the depth of interrelation between fire, individual organisms, and their communities.

Once it has been established that fire has an important role in the ecology of some communities it becomes important to understand the effect of removing fire through suppression on the composition and structure of these

communities. The importance of the role of fire will be established by demonstrating that the composition and structure of fire-type communities are significantly effected by the absence of fire.

General Theories of Disturbance

Fire is often included in the broad category of ecological disturbance with a number of other physical and biological factors. In the most simplistic terms disturbance can be defined as a factor that "destroys the tranquillity or settled condition of" (The American Heritage Dictionary 1990). This definition, when applied to ecological systems, requires the assumption that ecological systems exist in a "settled condition." While ecologists have redefined the term to better fit with current successional models (White and Pickett 1985), the essential meaning of the term disturbance remains the same.

Disturbance as it relates to theories of succession

The concept of ecological disturbance is intimately connected to the development of successional theory. In the earliest works on succession disturbance was seen as an anti-successional force (Clements 1916). The way in which ecologists think about succession has changed dramatically since Clements' time, but the term disturbance is still widely used. However, the use of this word to describe rapid changes in community structure implies that the community is in an equilibrium or climax state.

In Clements' view, disturbances were regarded as anomalies which set back succession and had no place in climax formations. Clements responded disapprovingly to the assertion by researchers that disturbances may result in

unique types of climax formations (Chapman 1932). Though he admitted that disturbance was a prevalent factor in some systems, he attributed its prevalence to human activities and persisted in his belief in a system of climate-based climax communities (Clements 1936). Even in Clements' work the concept of a stable climax began to erode as examples of systems that did not meet the climax formation criteria were presented. In order to salvage his climate based monocl原因 model he was forced to devise a series of terms for communities that did not fit the model such as proclimaxes, subclimaxes, preclimaxes, postclimaxes, and disclimaxes (Clements 1936). With this new terminology, factors that Clements saw as extraneous such as disturbances, soil types, and micro climate variation could be safely kept in the category of abnormality, and non-climax.

Several of the researchers that followed Clements were dissatisfied with such a rigid construct, and attempted to alter the model to fit more closely with the natural world. The polyclimax view allowed for a wider variety of climax communities, but disturbance was still seen as a force that set back succession. Under this model a climax formation could be effected by factors such as soil types, micro-climates, and the activity of animals (Tansley 1939). This model also differed from the traditional model in the scale of time. With Clements' model, climaxes developed over geological time. However, since climates change over geological time, the polyclimax model was based on development over ecological time (Krebs 1972). In essentially every other detail, however, the polyclimax model was identical to Clements model. Vegetation was said to change in a progression of discrete predictable seres that eventually led to a self regulated climax community. With this model,

as with the monoclimate model, ecological events that slowed or prevented the progress toward the climax were viewed as disturbances to the natural system. Disturbance could not be part of a climax community (Daubenmire 1966).

In addition to efforts to alter the basic Clementian model of succession some researchers rejected the concept of discrete vegetative formations entirely (Gleason 1926). Instead, vegetation types were said to vary gradually on both spatial and temporal continuums resulting in a pattern, or mosaic, of different aged stands and vegetative associations. This point of view was perhaps best developed by Whittaker (Whittaker 1953). Whittaker's "climax pattern hypothesis" gives hope for inclusion of disturbance in an ecological succession model. Ecological events such as fire and insect attack, were seen as reducing the climax to a seral state under the traditional model of succession. Under Whittaker's model these ecological events could be seen as part of the climax for the first time. Supporting this idea is the statement that "a degree of instability is intrinsic to the climax steady-state" (Whittaker 1953).

Some ecologists who subscribe to the climax pattern model have tried to modify some of the terminology that came out of the Clementian succession model. T. C. Whitmore suggested the use of the words "gap," "building," and "mature" phases to replace "pioneer," "seral," and "climax" (Whitmore 1989), and though these terms are an improvement, they still reflect a sense of hierarchy between vegetational associations that is fundamentally at odds with the cyclic and elastic nature of floristic dynamics suggested by Whittaker. The difficulty with Whittaker's model is determining how much instability can exist within a climax before it is no longer called a climax. Possibly

Whittaker's criticism was not deep enough. By presenting the climax pattern hypothesis, he avoided attacking the concept of climax itself. As long as the concept of climax is accepted there is an inherent value judgment in regard to ecological events such as fire. Without climax, "disturbances" can be seen simply as another factor acting to shape communities.

Only recently has disturbance been accepted as a legitimate ecological factor to the point where it has been built into a successional model. The "multiple pathway model" (Cattelino et al. 1979) not only allows for disturbance within a successional system but actually bases the direction of community development, to a large extent, on the disturbance regime. And though the model is predictive there is no ultimate end point, or "climax community." Community structure is based on the ability of species to survive and reproduce themselves within the confines of a set fire frequency.

Each of the successional models described above represents an increasingly fluid view of community development. The multiple pathway model, as mentioned above, is best fitted to communities that experience fire relatively regularly. However, not all communities do experience disturbance regularly. Fire regimes, like all environmental factors, vary. Predictability is always flawed, and at best, successional models can only result in estimations.

Disturbance as it relates to community dynamics

Up to this point this paper has focused on the question of whether disturbance may be considered a natural part of ecological communities. In what follows, it is assumed that disturbance does exist as a natural part of communities and the interactions between disturbances and community

structure and function are investigated. Once it has been accepted that disturbance is not an anomaly, the substantial role that disturbance plays in ecosystems becomes apparent (Bazzaz 1983, Sprugel 1991). The effects of disturbance are extremely varied, just as the disturbances themselves are varied. Therefore, the following discussion will be limited to the effects of fire.

When considering the effects of fire on communities it is less useful to treat each fire as a discrete event than to regard the cumulative impacts of multiple repetitive events. Where a single fire may have little lasting effect on community structure, multiple fires over the same area can begin to shape the community by favoring certain species, and eliminating others. The frequency, intensity, and type of disturbance experienced by a given community is known as a disturbance regime. If a disturbance regime is fairly consistent it can have a profound impact on community structure, and on the species within a community (Cattelino et al. 1979, Hendrickson 1972).

The frequency of fires on a human time scale need not be high to have a significant effect on vegetation. For instance, the fire frequency in a *Sequoia sempervirens* forest may be as low as once per century (Greenlee and Langenheim 1990). While this may appear to be a long interval by human terms, relative to the life span of the dominant organisms it is not.

In most fire-prone communities, disturbance regimes tend to be relatively consistent over the long term, but not necessarily predictable. The impact of multiple randomly situated fires, varying in size, intensity, and season results in an inconsistent vegetative pattern over the landscape with a mosaic or patchy quality (Pickett and White 1985). This patchy quality can result in

higher diversity of both habitat and species (Phillips and Sure 1990). An example of this can be seen in studies comparing areas where fire has been differentially suppressed (Minnich 1983, 1989). In the areas where fire was not suppressed patches tended to be much smaller, and also much more numerous. This higher number of patches creates more spatial diversity and habitat diversity throughout the community (Brokaw 1985, Connell and Keough 1985, Connell and Orias 1964). Because the patch creating events vary in time of occurrence, intensity, and size, a resulting variation in stand age and vegetation types will occur.

In addition to increasing diversity in a community, fire can effect individual organisms within a community through the liberation of resources. Generally two types of resources have increased availability after fire; sunlight and mineral nutrients. This increased availability, however, is temporary. In the case of increased solar radiation, the continuing availability of sunlight at ground level is dependent on how rapidly forest canopy is replaced. With regard to mineral nutrients, the length of the resource pulse is dependent on the amount nutrients released when the area was burned, the degree to which the nutrients were volatilised during the fire (Dunn and DeBano 1977, Wright and Bailey 1982), and the amount of nutrients lost to erosion (Christensen 1977).

The ability of plants to rapidly absorb nutrients may also play a role in determining if nutrients are lost to a system after a fire. Once nutrients are mineralized, they can easily be lost through erosion. The proliferation of ephemeral plants may, in some systems, act as a nutrient bank (Rundel and Parsons 1984). After the dominant species begin to recover, nutrients that

were held in the tissues of the ephemeral organisms can be taken up by the dominants.

The variable availability of resources can effect the recruitment of new individuals. In fact, the recruitment of particular species may be dependent on the availability of certain resources. The most obvious illustration of this is sunlight requirement for the germination of some seeds. An example is the shade intolerance of species of the genus *Pinus* in the mixed conifer forests of the Sierra Nevada. Both *Pinus jeffreyi* and *P. contorta* were shown to have very high recruitment rates after canopy removal by fire (Bock, Bock and Hawthorne 1976). Conversely, the recruitment of *Abies concolor* and *A. magnifica*, both shade tolerant species, was almost nonexistent on the same plots after the burn. The recruitment of pine seedlings showed a rapid decline after the canopy began to close.

Because of the high degree of recruitment following events such as fire, disturbances are often referred to as recruitment events. However, the absence of a disturbance can also be seen as a recruitment event for species that are traditionally thought of as requiring canopy development. An example can be seen in California chaparral. Many species of *Adenostema* and *Arctostaphylos*, which are dominant chaparral species, exhibit high recruitment after fire (Keeley and Zedler 1978). However, species of *Quercus*, that tend to have shade tolerant seedlings and are also prominent in chaparral communities, generally show no recruitment after fire.

The significance of these contrasts is that different species within the same community have conflicting requirements for recruitment. The specific fire regime, therefore, is necessary for the continued survival of all species

present. The dual nature of recruitment in fire type communities was described by Keeley (1991), who referred to recruitment shortly after a fire, as the "fire recruiter syndrome," and recruitment in the absence of fire, as the "fire persister syndrome." If fire does not occur within the parameters of a fire regime, the species that are dependent on fire for recruitment will eventually be replaced by other species.

Fire Survival Traits In Plants

The continuing existence of organisms in a community that experiences regular disturbance requires specialized abilities for survival and reproduction. Strategies can include anatomical, physiological, and life history adaptations.

Adaptations to fire

Plants that persist in fire-type communities exhibit a number of traits that allow them, as a species, to survive fire. In some cases these may be protective traits such as the thick bark of *Sequoiadendron giganteum* and *Pinus ponderosa*, or the sprouting response of *Sequoia sempervirens*, and some species of *Quercus*. In other cases, plants may survive through reproductive strategies. Above ground seed storage in the serotinous cones of *Pinus contorta* and *P. rigida* is one example. The persistent seed banks in the cases of some species of *Ceanothus* and *Arctostaphylos* are another example. That these types of traits allow species to exist in fire-type communities is widely accepted (Fuller 1991, Gill 1981 a-b, Pyne 1982, Sweeney 1968, Whitney

1979, Wright and Bailey 1982). The question of the evolutionary selection of traits for fire, however, is still debated.

One area where this debate has been strongest is in regard to cone serotiny. Cone serotiny in *Pinus rigida* exhibits geographical variation, with occurrence of serotiny more concentrated in areas of high fire frequency. One group of researchers attributed the variation to gene flow (Ledig and Fryer 1971). They argued that serotiny was a pre-adaptation, and that the high frequency of serotinous cone bearing individuals in one location was not related to fire selection. The test for their argument lay in the assertion that the distribution of serotinous trees would decline gradually with distance from the highest area of concentration. Though their results do indicate this general trend, the existence of a few distant and discrete areas of high serotiny frequency weakens their argument. That these same areas have histories of high fire frequency further discredits the gene flow argument. In response Givnish (1981) argued that selection rather than gene flow was the factor responsible for the geographic variability of serotinous cones. He also argued that the ultimate selective pressure came from high fire frequency.

To test the selection model, a correlation was established between fire frequency and cone serotiny. And though Givnish makes a strong point for selection of serotiny geographically, the origin of the trait is not addressed. Logically one might surmise that serotiny is an evolutionary response to fire, but it is difficult, if not impossible to show causality between an environmental pressure and an existing morphological or physiological trait.

Another example of the debate over the evolution of fire survival traits involves shrub responses. Chaparral shrub types such as *Arctostaphylos* and

Ceanothus vary on a gradient from obligate sprouters (species that require a sprouting response to reproduce after a fire), to facultative sprouters (species that can reproduce vegetatively or from seed), and obligate seeders (species that only reproduce from seed) (Christensen 1985). Two evolutionary arguments have emerged out of this system. Wells (1969) suggested that obligate seeders evolved from sprouters as a response to fire thereby increasing the rate of evolution for seeders, because genetic recombination would occur more often, allowing for faster adaptation to fire regimes.

A more recent argument suggests that rather than fire simply selecting for the seeding trait, that either trait (sprouting or seeding) would be selected for depending on the fire frequency of the regime (Keeley and Zedler 1978). A lower frequency of fire would likely result in extensive fuel build up, and consequently increased fire intensities, resulting in a high rate of total individual mortality. A longer term between fires would also allow for the deposition of a sizable seed bank so that reproduction through seeding would be more advantageous to survival. Conversely, in regimes with high fire frequency, fuel build up would not reach the same levels, fire intensities would be lower, and sprouting species would stand a much better chance of survival. Again, as was the case with cone serotiny, this argument is logically coherent, but it is difficult to prove that an environmental pressure and a genetic or phenotypic response are causally linked.

Taking the evolution argument a step further, Mutch (1970) proposed that not only has fire acted as a selective pressure in the adaptation of fire survival mechanisms in plants, but may have also selected for more flammable characteristics (such as volatile compounds in leaves and bark). The high

flammability of *Eucalyptus obliqua* and *Pinus ponderosa* litter may contribute to the perpetuation of fire regimes. Mutch argues that these traits were selected for because the perpetuation of fire gives fire adapted plants a competitive advantage over plants that have low fire survival rates.

While these arguments for the evolution of adaptive traits with fire as the selective force may well represent the best explanation for evolution of some of these traits, they are not definitive. When studying organisms with life spans in the hundreds or even thousands of years, it is difficult to acquire compelling evidence. We are forced to accept that these traits do exist, and do allow some species to survive in various fire regimes better than others, without having definite knowledge of the traits evolutionary origins.

Specific Survival Traits

Traits that allow species to exist in fire-type communities have been categorized in several models. A. M. Gill (1981 b) divides what he calls "fire adaptive traits" into four main categories; plant survival, fire-stimulated seed dispersal, fire enhanced flowering and fire-promoted germination. Aside from these main categories, he recognizes that fire adaptive traits include "all those traits contributing to the successful completion of the life cycle of a species in a fire-prone environment" (Gill 1981 b).

A more intricate model was developed by Noble and Slatyer (1977) and was adapted to coniferous forests by Rowe (1983). In this model, post fire reproductive strategies are divided into three main categories. The first category, "vegetative-based" strategies, corresponds with Gill's plant survival category. Under the category of vegetative based strategies are two sub-

categories; V species (species that are able to sprout if burned in the juvenile stage, and W species (species able to resist fire in the adult stage but not in the juvenile stage). The second category, "disseminule-based" strategies, includes three sub-categories; D species (species with highly dispersed propagules), S species (storing long lived propagules in the soil), and C species (storing propagules in the canopy). These sub-categories are linked through "communal relationships" to other factors designated as T species (tolerants that can establish immediately after fire and can persist indefinitely thereafter without further perturbations), R species (tolerants that must wait for shade before they can become established, and I species (intolerants that can only establish immediately after a fire, and tend to die out without recurrent disturbance). These sub-categories are linked together into groups of survival strategies including, endureres, resisters, evaders, invaders, and avoiders, and are set out on moisture and fire cycle gradients.

Both of these models have merit. Where Rowe's approach is more useful for a functional understanding of the relationship of the survival traits to environmental variables, Gills less complex approach is more suitable for a descriptive analysis. I have adapted his approach to the following discussion.

- Vegetative survival traits. The most direct method of survival of fire is through protection of the above ground portion of the organism. This protection is accomplished through increased bark thickness, frequently accompanied by a decreased flammability of the bark, and an elevation of the crown. The high crown raises the vulnerable portions of the plant well above

surface levels, reducing the possibility of crown fire, and optimizing the effectiveness of the protection of the lower trunk.

An excellent example of all of these features can be seen in *Sequoiadendron giganteum*. This species, which lives in the fire prone mixed conifer forests of the Sierra Nevada, has bark which is up to two feet thick (Fuller 1991), and lacks flammable resins common in most conifer bark. The low crown to height ratio of *Sequoiadendron*, coupled with a growth height in excess of 280 feet (Peattie 1953), protects the bulk of the vulnerable leaves and stems from even fairly intense ground fires. *Sequoiadendron giganteum* is of particular interest in regard to fire adaptation due to its multiple fire adaptive traits. In addition to its protective thick bark, *Sequoiadendron* exhibits highly serotinous cones, and requires fire for seedling germination (Hartesvelt and Harvey 1968, Harvey, Shellhammer and Stecker 1980). Additional examples of trees that possess above ground tissue protection with thick bark include; *Pinus ponderosa*, *Pinus jeffreyi*, *Pseudotsuga menziesii*, and *Larix occidentalis* (Wright and Bailey 1982).

Similar in many respects to *Sequoia giganteum*, is the closely related species *S. sempervirens*. This species also exhibits protective features but also includes features that allow survival through sprouting both from above ground, and underground tissues (Peattie 1953). Regeneration from above ground tissues occurs from epicormic buds. This adaptation also occurs in species of *Quercus* (Kauffman and Martin 1989), *Eucalyptus* (Gill 1981 a), and a number of other species. Sprouting of lateral buds is triggered by a hormonal response to the removal of the apical meristem so that any number of factors

removing the meristem including fire, lightning strike, blowdown, or timber harvesting can achieve the same result.

The ability to sprout from an underground source requires one of the following morphological features; lignotubers, rootcrowns, burls, rhizomes, or lateral roots (Kauffman and Martin 1989). The ability to sprout from one source does not preclude an ability to sprout from another. *Sequoia sempervirens*, for example, can sprout both from aerial buds, and from basal burls.

Sprouting ability can vary within the lifetime of an organism. In the case of *Quercus*, sprouting is common with younger individuals, but becomes more rare as the individual ages. Eventually the sprouting strategy gives way to a strategy of above ground protection with thick bark (Kauffman and Martin 1989).

Root crown sprouting is common with chaparral shrubs including species of *Arctostaphylos*, *Ceanothus*, *Heteromeles*, and *Adenostema* (Sweeney 1968, Wright and Bailey 1982), though not all species of these genera are sprouters. Sprouting may be more prevalent in species that inhabit high frequency, low intensity fire regimes (Keeley and Zedler 1978), as sprouting response is diminished with high intensity fire due to the death of underground advantageous buds.

Coupled with fire intensity, fire type is also important in determining survival for sprouting plants. Crown fires and surface fires can be of fairly high intensity without destroying the ability of plants to sprout, if the advantageous buds are buried deep enough below the soil surface (Gill 1981 b). Ground or peat fires, however, will likely destroy most species sprouting

capability. Further protection from heat occurs with plants that have retractile roots that possess the ability to pull the plant such as *Xanthorrhoea australis* deeper into the soil as the roots dry out. This type of response is common with bulb and corm type plants.

Sprouting may also occur from rhizomes as is the case with species of *Vaccinium*, or from root buds. With the original plant destroyed, multiple sprouting responses are triggered, increasing the population in the next generation (Gill 1981 b).

- Seeding strategies. When vegetative regeneration is not an option, seed becomes the only mechanism of persistence of a species. Seed may occur in the system in two ways; it can be reintroduced from the outside, or it can exist in the form of stored seed banks, either in the soil or in the canopy.

Seed can be stored above ground in serotinous cones, or seed capsules. The cones serve as some protection by enclosing the seeds, and also by holding seeds away from the most intense heat at ground level (Givnish 1981, Ledig and Fryer 1971). These cones generally remain closed, and attached to the tree until heat is applied. Because serotinous cones are a type of seed bank, seeds generally remain viable for long periods of time, up to 20 years in the case of *Pinus banksiana* (Ahlgren 1974).

Some species vary in the degree of serotiny present in individuals. This variation may be related to high fire frequency in the area where increased serotiny occurs, as is the case with *Pinus rigida* (Givnish 1981). Other species such as *Pinus contorta*, can produce both serotinous and non-serotinous

cones on the same individual (Fuller 1991, Lotan 1975, Wright and Bailey 1982). This dual strategy allows for reproduction with or without fire.

Many of the North American species that produce serotinous cones are in the genus *Pinus*, such as those listed above, and also *P. serotina* and *P. coulteri*, and, in the Mediterranean area *P. halepensis* and *P. brutia*.

Serotinous cones are also present in other genera such as *Sequoiadendron*, and *Picea*, and families such as Cupressaceae, Casuarinaceae, Proteaceae, and Myrticaceae (Gill 1981 a, Parker and Kelley 1989). The serotinous-like strategy in eucalyptus differs in some ways from cone serotiny in pines. *Eucalyptus regnans* stores seed in seed pods that are opened by drying during fires (Gill 1981 a). Unlike serotinous cones, the time interval for seed storage in *Eucalyptus* is relatively brief.

Serotiny, at least in the case of *Pinus*, is usually accompanied by a lack of other fire survival traits. These relationships between traits indicate that post fire regeneration (exemplified by cone serotiny) represents an entirely different set of life history strategies than the protective thick bark strategy represents. The serotinous pines are relying on fire to complete their life cycles, where thick bark pines such as *P. ponderosa* tolerate fire as a method to reduce shade tolerant competitors. Serotiny may also be accompanied by fire requirements for germination. *Sequoiadendron giganteum*, for instance requires a mineral soil for germination, which is normally only provided by fire (Hartesvelt and Harvey 1968, Harvey, Shellhammer and Stecker 1980, Sweeney 1968, Wright and Bailey 1982).

The majority of plants that occur on post burn sites develop from seed (Sweeney 1968), and aside from above ground seed storage nearly all post fire

germination occurs from persistent seed banks in the soil. The only other source is dispersal of seed into a burn area from outside. This contribution, however, is generally quite low, especially in large burn areas.

Although most of the research that has been done on seed bank response to fire has focused on chaparral species (Keeley 1991, Kelly and Parker 1990, Parker and Kelly 1989), fire stimulated persistent seed banks have also been studied in coniferous forests (Archibold 1989), and grasslands (Rice 1989).

In California chaparral, a large number of species have persistent seed banks that are stimulated by fire, including some species of woody plants such as *Ceanothus* and *Arctostaphylos*, (Keeley 1991, Parker and Kelly 1989), and also herbaceous plants such as *Emmenanthe penduliflora* (Parker and Kelly 1989).

In order for propagation from soil seed bank storage to be a successful fire survival trait, seeds must be able to remain viable for long periods of time. The length of this time period depends on the frequency of fire within a given fire regime. In chaparral it has been indicated that some seeds may persist in the soil as long as 200 years (Parker and Kelly 1989). The need for a persistent seed storage is of particular importance to fire stimulated annual species because their reproductive effort is limited to a few years after fire.

For seeds to survive over long periods of time they must be stored in a state of dormancy. Often this dormancy is accompanied by a hard seed coat or thick cuticle (Gill 1981 a). Dormancy ends when the seed receives germination cues. These cues can include increased light, heat, breach of the seed coat, and leachate from charred wood (Keeley 1991, Parker and Kelly 1989). Seeds of particular species each have a unique set of requirements for

germination, yet some seeds from dormant populations may germinate without these cues. Some species, in fact, produce a variable seed population, some that experience dormancy (refractory seeds) and enter the seed bank, and others that germinate readily (non-refractory seeds).

An example of refractory seeds includes all chaparral species of *Ceanothus*. These seeds require a period of intense heat, or heat shock, to germinate (Keeley 1991). Other refractory seed producers that require heat shock include species of *Fremontodendron*, *Rhus*, and annuals such as *Lotus salsuginosus* and *Lupinus excubitus*. Examples of species that require leachate from charred wood for germination include some species of *Arctostaphylos*, *Adenostoma fasciculatum* and *Fremontodendron californicum*.

A final trait among fire resistant species is the response of increased flowering after fire. Fire stimulated flowering occurs most extensively in the prairie grasses of the United States (Fuller 1991), but also occurs in a few dicotyledonous examples from the Orchidaceae, Iridaceae, Liliaceae, Amaryllidaceae, and Xanthorrhoeaceae families (Gill 1981 b). The increase in flowering after fire can be dramatic. Fire may increase flowering of prairie grasses by as much as ten times (Old 1969). The factors that trigger this response are still unknown (Gill 1981 b).

By outlining and briefly discussing the traits that allow plants to persist and produce propagules in fire prone environments, the depth of the interrelation between fire and ecosystem components has been demonstrated. The development of fire type communities is a process that has taken thousands, if not millions of years. Therefore, fire should no longer be

viewed as a disturbance in these communities, but as an integral cyclic part of the whole.

The Effects of Fire Suppression on Community Composition and Structure

The historical view of fire as a purely negative ecological force led to the instigation of fire suppression practices on virtually all public lands in the early nineteen hundreds (Fuller 1991). Though the ecological view of fire has changed dramatically over the last few decades, the managerial view has not, and fire suppression continues in most areas (Elfring 1988). The impact of fire suppression on ecosystems is complex and not completely understood. The lack of knowledge on this subject is due in part to the relationship between the period that fire suppression has been in effect and length of the life cycle of many of the organisms effected. Long term impacts will likely become evident in time if fire suppression is continued. However, several impacts of fire suppression have already been noted; these include changes in species composition, changes in age structure, changes in species and habitat diversity, and an increase in the size and intensity of fires when they do occur.

Increased fire size and intensity

The prolonged absence of fire in fire-type communities can lead to an increase in surface fuel accumulation. This has been shown extensively in *Pinus ponderosa* forests (Biswell 1959, Gaines et al. 1958, Wagle and Eakle 1979, Weaver 1967). A wildfire was shown to be much less destructive in an

area where prescribed fire had occurred recently than in an adjacent area that had not been treated by fire (Wagel and Eakle 1979). A similar increase in fire size and intensity has been found in other vegetation types as well including mixed conifer forests (Kauffman and Martin 1989, Parsons and DeBenedetti 1979, Weaver 1974). This is the result of the accumulation of surface fuels and an increase in understory vegetation.

Increased fuel loading was shown to occur after long periods of fire suppression in Montana *Pinus ponderosa* communities (Lunan and Habeck 1973). Stands of varying ages were sampled in Glacier National Park, where fire had been suppressed, and in Selway Bitterroot Wilderness, where fire had been allowed to burn more recently. The fuel accumulation (total weight per unit area) in the Glacier National Park study sites was relatively high compared to the fuel levels in the wilderness sites indicating that there is an increase of fuels in the areas with a longer history of fire suppression. Also evident was a well developed understory, and recruitment of young trees. The development of the understory and proliferation of younger trees can act as ladder fuels increasing the probability of crown fire. Lunan and Habeck argue, citing historical evidence, that before fire suppression was put into effect ponderosa pine forests in this area were "open and park like."

In an Arizona ponderosa pine forest, research has also shown that increased fuel load can dramatically alter the effect of a wildfire (Wagle and Eakle 1979). This study looked at the differences between the effects of wildfire on a ponderosa pine forest where prescribed burning had taken place, and in surrounding areas where it had not. A fire burned a total of 59,300 acres of predominantly ponderosa pine forest, 500 acres of which had been

control burned one year prior to the fire. On three plots outside of the controlled burn area only one living tree remained standing. In the controlled burn plots the fire only killed 5 trees out of 30, and all trees that were killed were within the dbh class of 8 inches or less. Reduction of fuel in this case was shown to improve the chance of survival for mature trees.

Prescribed fire has been widely used for fuel management, and though the fire regime under a prescribed burning plan is unlikely to reflect a wildfire regime, certain analogies can be made in terms of fuel reduction. Prescribed fire has been shown to greatly reduce fuel load (Gaines et al. 1958, Kilgore 1973) both in terms of reduction in litter and duff fuels, as well as a decrease in small saplings after treatment with prescribed fire.

Prescribed fires are normally in the form of low intensity surface fires and are not used to create stand-replacing fires. In contrast, under natural conditions fire intensities tend to be irregular due to uneven distributions of fuel, fuel moisture content, and changing weather patterns, resulting in areas of canopy fire. Treatment with low-intensity surface fire is not enough to compensate for fire suppression, because it tends to favor species with fire protective mechanisms over species with germination responses to fire. The possibility of including intense fire in prescriptions for some areas has been discussed (Stephenson et al. 1991), but has not yet been put into practice.

In addition to increasing the accumulation of fuel on any given spot, fire suppression increases the probability of large scale fires. Fire is less likely to pass through areas that have recently burned (Fuller 1991) because of the existence of natural fire breaks.

The fire histories of San Diego County and Baja California chaparral communities were compared in the period between 1920 and 1971 by R. A. Minnich (1989). During this time fires in Baja California were uncontrolled with some deliberate burning occurring. In San Diego County fire suppression had been in effect for at least 80 years. The number of fires was shown to be higher where fire was not suppressed, but the average size of fires was significantly higher where fire was suppressed.

Similar trends have been determined through fire scar data (Biswell 1959, Bork 1984, Dietrich 1983, Kilgore and Taylor 1979). The suppression of fire, rather than eliminating fire from an ecosystem appears to alter the fire regime. As many communities have developed under a particular fire regime, changing the regime may also change community structure and composition.

Changes in species composition

An altered fire regime can effect vegetative communities by favoring a different set of species. The frequency of shade tolerant species, and species that do not require fire for reproduction tends to increase when fire is suppressed in fire type communities (Lunan and Habeck 1973, Phillips and Sure 1990). Stand structure data collected from sites in Glacier National park was used to determine relative frequency, density, dominance, and importance values for all species of trees (Lunan and Habeck 1973). This data indicated a lack of regeneration of *Pinus Ponderosa* since sapling sized ponderosa pines were found to have an average age of 50 years and were in a severely suppressed condition. Most of the *Pinus ponderosa* sampled were in

the much older age classes of 180 years, 230 years and 400 years. Growing among the older ponderosa pines were a variety of younger trees; spruces (*Picea* spp.), douglas-fir (*Pseudotsuga mensziesii*), western larch (*Larix occindentalis*), and lodgepole pine (*Pinus contorta*). Additionally the study sites had well developed understories.

In Sierra Nevada mixed conifer forests, a similar lack of regeneration was noted for *Sequoiadendron giganteum* in the absence of fire (Hartesvelt and Harvey 1968, Kilgore and Taylor 1979), and for sequoia-mixed conifer forests in general (Weaver 1974). As is the case in *Pinus ponderosa* forests, the absence of fire in Sierra mixed conifer forests favors shade tolerant species. With recurrent fire, this forest type tends to be dominated by species such as *Pinus ponderosa*, *Sequoiadendron giganteum*, *Pinus lambertiana*, and *Pinus contorta*, or what Weaver calls fire climax-trees. Without fire shade tolerant trees such as *Abies magnifica* and *A. concolor* begin to dominate.

The frequency of fire may play a particularly important role in determining species composition in communities such as chaparral that are composed of a number of species with a variety of fire survival traits and life history strategies (Keeley 1991). An example is the ratio of obligate seeders to obligate sprouters surviving after a fire. A low frequency of fire results in higher fuel build up and increased fire intensities, so that survival of vegetative sprouters declines. Conversely, with a high fire frequency, fuel accumulation would not reach the same levels, fire intensities would be lower, and sprouting species would stand a much better chance of survival (Keeley and Zedler 1978).

The invasion of shade tolerant species, such as *Pseudotsuga menziesii*, can also occur in chaparral communities. Fire recruiter species with seedling establishment that is restricted to the year following fire, such as *Adenostoma fasciculatum*, and species of *Arctostaphylos* and *Ceanothus*, are at a competitive disadvantage with long term fire suppression.

Other instances where fire suppression results in species changes include mountain meadows where rates of tree invasion are increased in the absence of fire (Murray 1992), and in southwestern mixed conifer forests (Dietrich 1983). Though it is difficult, if not impossible, to determine the exact fire regime that occurred prior to fire suppression, it is clear that with fire suppression species composition in fire type communities does change.

Changes in age structure

Fire suppression, that leads to changes in species composition, also tends to create a homogeneous age structure within a community. The trend from smaller low intensity fires toward larger high intensity fires results in an increase in fires that are stand replacing. A stand-replacing fire, coupled with increased intervals between fires, results in an age structure over a large area based on a single recruitment event. This is particularly true for species that require fire for reproduction.

Dietrich (1983) found the composition of a southwestern mixed conifer forest tending toward age uniformity after a 90 year fire-free interval. He argues that if the pre-suppression fire frequency of roughly 22 years (determined by fire scar data) had continued, "many age classes would have been represented because regeneration would have been nearly continuous,

and only a portion of the regenerated trees would have been destroyed by periodic fires" (Dietrich 1983 p. 28).

In Eastern Oregon similar structural effects were found in *Pinus ponderosa* stands (Weaver 1967, 1974). Weaver states that "periodic burning causes development of uneven-aged stands, comprised of even-aged groups of trees of various age classes" (Weaver 1967 p. 145). While providing canopy gaps for reproduction, periodic low intensity fire also protects some mature trees by removing undergrowth, and limiting the success of competing seedlings.

The effects of wildfire on stand structure are complex. Generally, unimpeded naturally ignited fires, by virtue of their random nature, tend to result in a more heterogeneous community. Fire is by no means the only agent of randomization. A wide variety of environmental events can contribute to community heterogeneity (White and Pickett 1985). However, where fire has played a role in the structural formation of a community over ecological, or even evolutionary time, the removal of fire from the system can result in dramatic changes.

Changes in diversity; species and habitat

Periodic fire has been said to be important in the maintenance of high species diversity, or richness (Abagov 1982, Bazzaz 1983, Huston 1979). In part diversity is increased by species that are common in an area only directly following disturbance. These species have been called "fugitive" species because they are at a competitive disadvantage as individuals of other species begin to develop (Hutchinson 1951). Some of these species exist in the

community as stored seed in soil seed banks until released by fire (Keeley 1991, Parker and Kelly 1989); others may enter the community from outside such as *Epilobium angustifolium* (fire weed).

In shrubland community types, fire has been associated with the maintenance of species diversity (Christensen 1985). Species richness tends to peak immediately after a fire and then declines rapidly after reestablishment of dominant species. However, if the species present in the seed bank are included, species diversity changes little. This pulse of species richness is exemplified in California coastal sage scrub (O'Leary 1990). In this study, peak richness was reached two years following fire. Similar increases in species diversity was also seen in African grassland communities (Belsky 1992).

In a spatial simulation model that analyzed the effects of fire suppression on a number of ecological factors in the Boundary Waters Canoe Area, Minnesota, Baker (1992) determined that fire suppression is negatively correlated to species richness. The decline in species richness can be both significant and rapid. Another study, however, involving fire suppression in southwestern mixed conifer forests tends to dispute the hypothesis that species richness declines with fire suppression (Dietrich 1983). Though stand composition and structure did change in the long term absence of fire, species diversity remained essentially unchanged. This apparent dicotomy is likely due to the lower canopy cover common to forests in the southwestern United States. The mixed-conifer forests of the Sierra Nevada tend toward high canopy cover, and prolonged fire absence would be likely to results in conditions similar to those found by Baker (1992) in the Boundary Waters Canoe Area. In the Sierra Nevada populations of species with shade

intolerant seedlings or seeds that need fire for germination gradually decline with fire suppression (Lunan and Habeck 1973, Phillips and Shure 1990). If fire is absent for an extended period of time, some of these species may become locally extinct, reducing species richness.

As mentioned previously fire suppression can also effect diversity on the community level by reducing habitat diversity (Minnich 1989). The decreased habitat heterogeneity caused by a decrease in patch size provides fewer habitat interfaces and reduced edge effect resulting in less habitat for wildlife, and lower wildlife diversity.

Traditionally, fire has been considered an ecological disturbance. However, When considering all of the effects of fire suppression on fire type communities it appears that it may be fire suppression rather than fire that is acting as a disturbance in many communities. Ecological disturbance has been defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure" (White and Pickett 1985). Much research has been done on the disruption of ecosystem, community, and population structure by fire suppression. In order to fit the definition however, fire suppression must also be seen as a discrete event in time. I would argue that in ecological time, the effects of fire suppression are quite immediate, particularly when compared to the life span of many of the dominant organisms in the communities involved.

Similar conclusions were reached by Greenlee and Langenheim (1990) in a study that investigated changing fire regimes in *Sequoia sempervirens* communities. Greenlee states that "a single fire in a fire-dependent system is

not regarded as a disturbance, but a change in fire regime may create a disturbance" (Greenlee and Langenheim 1990 p. 239).

Summary of the Ecological Effects of Fire

The intention of this chapter was to build a theoretical foundation for the experimental portion of this study. This review was not intended to include all relevant works, but instead was an attempt to present as broad range of research as possible, and to draw from this research some basic assumptions that I will be operating under. These include the following:

1. Fire is a natural part of the forest ecosystems in the Sierra Nevada, and has played a role in the formulation of their structure and function.
 2. Within communities and ecosystems continual change and variation is inevitable. Fire acts as an agent of change resulting in an increase in spatial diversity.
 3. Recurrent fire over ecological time has resulted in communities of species that are not only capable of persisting under these regimes, but may also require fire for reproduction.
 4. The removal of fire from fire-type communities results in fundamental structural and compositional changes to vegetative communities.
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Many of the basic concepts discussed in this chapter have direct bearing on the formulation of my hypotheses, my research design, and the interpretation of my field data.

CHAPTER 3

THE HISTORY OF FIRE IN THE SIERRA NEVADA

Fire frequency in the Sierra Nevada varies with elevation, vegetation type, moisture regime, slope, aspect, and a variety of other factors. The range in general, however, can be described as fire prone, in that most locations historically have had relatively high pre-suppression fire frequencies (Kilgore 1981). The most common source of ignition prior to European settlement was from lightning. However, Native Americans may have also influenced fire frequency through intentional and unintentional burning (Barrett and Arno 1982, Biswell 1959).

Though the vegetative communities of the Sierra Nevada are considered fire prone, fire intervals and intensity vary temporally and spatially. That the fire regime of the range is considered relatively regular (Wagener 1961) does not suggest that it is predictable. There are both short term and long term variables, such as climate and human fire use patterns (Pyne 1992), that have dramatically altered the pattern of burning (Cwynar 1987). Currently fire suppression and human settlement are the greatest of these variables (Greenlee 1983, Kilgore and Taylor 1979).

Pre-European Fire

The fire history of the Sierra Nevada before European settlement can be divided into two major periods. A period without anthropogenic fire, and a period that included anthropogenic fire as a factor.

Fire prior to human habitation

Because of a lack of a historical or biological record the first part of the fire history of the Sierra Nevada, which occurred prior to human habitation, is the period that we know the least about. There are two methods that have been developed to estimate the pre-human fire history.

The first involves superimposing an estimate of the current number of lightning fires on the pre-human landscape. As lightning fire was essentially the only source of fire at that time this type of estimation would seem to give a fairly accurate estimate. However, there are some problems with this approach. For the Sierra Nevada ponderosa pine forest Biswell (1959) estimated a 10 year lightning fire interval. This estimate was based on a record of lightning strikes that occurred from 1948-1958. The first weakness in this approach is Biswell's assumption that the period between 1948 and 1958 was representative of current climate patterns. With the climatic fluctuations common to California ten years is not a sufficient period of time from which to draw conclusions. The second weakness in this approach is also related to climatic fluctuation but at a greater scale. Superimposing current weather patterns on the pre-human landscape requires the assumption of a stable climate over thousands of years. From research on climate in the Sierra Nevada we know that such an assumption is not correct. Even over the last

one thousand years there have been extreme fluctuations in both temperature and precipitation (Graumlich 1993). Despite the lack of precision with this approach it continues to be used by some researchers. Greenlee and Langenheim (1990) used data on fire strikes from 1930-1979 to estimate fire frequency for the last fifteen thousand years. Though a 49 year sampling period gives a more accurate estimate of current lightning strikes than Biswell's 10 year period attempting to apply the estimate to the past fifteen thousand years does not take into account the climatic changes during that period.

The second method for determining pre-human fire frequencies involves the sampling of charcoal deposits preserved anaerobically in bogs and lakes (Mehring et al. 1977). Through sampling of fossil charcoal deposits Edlund and Byrne (1990) have shown that changes fire regimes in the Sierra Nevada over the last fifteen thousand years were related to climatic shifts and changes in vegetation types. As a result of increasingly dry summers fire frequencies have generally increased over the last ten to twelve thousand years.

The charcoal sampling method makes it clear that long term fire regimes, like all other ecological factors, are not stable. The current state of fire in the Sierra Nevada is unique, and cannot be applied retroactively. The approach of using lightning fire information for determining non-anthropogenic fire, though not useful for prehistorical fire research, may be useful for modeling current fire patterns with human factors excluded.

The Native American period.

Human beings first populated the Sierra Nevada approximately 1000 to 4000 years ago (Eargle 1986). The fire history of the period that follows the first habitation by Native Americans and ends with the settlement by Europeans can be estimated with more confidence than the proceeding period. For the latter part of this period there are not only historical accounts in the form of written records (Gruell 1985), but also records within living tree tissue. Analysis of fire scars have long been used to determine fire history (Arno and Sneek 1977, Weaver 1951), and in the Sierra Nevada where there are trees with life spans of several thousands of years, the fire records can be extensive. Even so there has been significant debate on the fire frequency of pre-European forests, and particularly on the extent that Native American activities might have effected it.

It has been generally accepted that fire was used by Native Americans as a management tool for hunting, improvement of browse for deer, increasing the quantity of food sources, and a wide variety of other uses (Anderson 1990, Aschmann 1977, Barrett 1980, Biswell 1959, Pyne 1982). Fire frequency in the Rocky Mountains, through fire scar analysis, was shown to be higher in areas that were extensively used by Native Americans (Barrett 1980). Barrett's assertion that burning was conducted by Native Americans was also supported by interviews and journals. Similar evidence has been found for aboriginal burning in the Sierra Nevada (Biswell 1959, Kilgore and Taylor 1979).

Some have argued that the human impact on fire frequency before European settlement was negligible (Wagener 1961). Wagener's argument

was based on analysis of his own fire history data collected in Sierra Nevada mixed conifer forests that showed no change in fire frequency after human settlement. The opposite conclusion was reached by Kilgore and Taylor (1979) in a similar comparison in a Sequoia mixed conifer forest.

Regardless of the historical cause of fire it is clear that fire was common in the Sierra Nevada before the settlement of Europeans. However, the average fire frequency during this period is another area of debate. This debate may be due in part to a high variation in fire frequency from site to site. An average frequency of 8 to 10 years was determined by Wagener (1961), supporting similar evidence in earlier studies (Boyce 1920, Shaw and Kotock 1924). An average fire frequency from as short as 1 to 2 years to as long as 10 years for the Sierra Nevada as a whole has been suggested by Biswell (1959, 1963). The 1 to 2 year interval was based on the possibility that low intensity fires did not cause fire scars on many trees.

Post Settlement Fire

From the period of time when Europeans began to settle in the Sierra Nevada to the present historical records are increasingly prevalent. The time at which European settlement becomes important to forest ecosystems varies considerably between locations. The most noted impacts began with large scale development associated with mining operations in the mid 1800's.

The frequency of fire in the Sierra Nevada began to decrease in the 1870's due to a decrease in Native American burning resulting from a reduction in indigenous populations (Kilgore and Taylor 1979). However, a certain amount of the intentional burning left off by the Native Americans was

supplanted by sheep and cattle ranchers that began to use the area around that time (DeBenedetti and Parsons 1979).

As European settlement increased, the occurrence of fire decreased. The fire scar record becomes almost nonexistent in the early 1900's due to the creation of the U. S. Forest Service, the development of more efficient fire fighting equipment (Kilgore and Taylor 1979), and the implementation of systematic fire suppression.

High and Low Intensity Fire

With fire suppression as the official federal and state policy, low intensity surface fires that were the most common type of fires prior to suppression (Agee et al. 1978) became almost nonexistent (Carro 1992). Surface fires reduced understory and small trees resulting in what has been referred to as open, park like pine forests (Muir 1894). With light surface fires virtually extinct in the Sierra Nevada, the majority of the fires that have occurred after the implementation of fire suppression are those too large and intense to contain.

Though it is accurate to say that the majority of fires that occurred prior to suppression were low intensity surface fires, it is not true to suggest that all fires were of that type. Infrequently there did occur high intensity crown fires (Biswell 1959), though in size they were probably smaller on average than the fires that occur today due to lower degrees of fuel build-up and understory development.

Summary of Fire History

Though there are disagreements in the literature over some of the details of the fire history of the Sierra Nevada, there is general agreement on the basic outline. Fire frequency, whether the result of lightning fire alone or also the result of aboriginal burning, was much higher before European settlement and the introduction of fire suppression. Coupled with a decrease in the average frequency of fire there has been an increase in average fire intensity. The combination of these two factors has resulted in an historic shift in the fire regime of the Sierra Nevada, and in the forests of the majority of the western United States.

The recent change in the fire regime is of primary importance to the understanding of the current state of the forests in the Sierra Nevada. The remainder of this study is directed toward a better understanding of the ecological impacts of stand-replacing fire. This type of fire has become increasingly prevalent since the implementation of fire suppression and may result in long term changes to the structure and composition the regions forests.

CHAPTER 4

METHODS

Stand-replacing fires have not, in general, been considered important to the ecology of forests in the Sierra Nevada due to their infrequency. Though rare, these fires did exist and may have played an important role in the formation of community structure. In order to study the effects of stand-replacing fires an investigation of the recent fire history of the Lake Tahoe Basin was conducted. The Lake Tahoe Basin was chosen due to its high priority as a management area. Concerns about the health of the forests surrounding Lake Tahoe have been growing in recent years due to the visible decline of a large number of forest trees, the fuel accumulation in the forests, and a growing population in what is an area of intense urban-wildland interaction. Current management strategies include some low intensity surface burning, but high intensity stand-replacing fire is still fully suppressed.

The intention of this study is to establish the existence of at least one large scale, pre-suppression, stand-replacing fire in the Lake Tahoe Basin and then to test whether such fires have a substantial effect on forest ecosystems. The first goal was accomplished through interviews with long time residents of the area, study of historical photographs, and stand age analysis. The second goal was accomplished through ground sampling of post fire revegetation on several stand-replacing fires sites of different ages in upper montane mixed

conifer forests. The fire areas were chosen to be as similar as possible, given the scarcity of such fires in the area, in terms of elevation, vegetation, ecology, and soil type.

Incidence of Stand-Replacing Fire

Several potential stand-replacing fires were located in the South Lake Tahoe Area. The existence of these fires was first suggested in conversations with personnel of the USDA Forest Service Lake Tahoe Basin Management Unit (LTBMU) Fire Management Office (Johnson 1993, Swanson 1993).

Two of the fires occurred well into the period of fire suppression, and were used in this study only to investigate the effects of stand-replacing fires, and not as evidence for pre-suppression fire.

The probable existence of two older fires, particularly a large fire that burned on Angora Ridge at the turn of the century, warranted further examination.

Historical accounts

Three long time residents of the area were interviewed in regard to the Angora Ridge and the Cathedral Creek fires. This type of evidence alone can not be decisive. However, in combination with other evidence a strong case can be made for the existence of both of these fires.

The first individual interviewed was Jim Hildinger, the proprietor of the Angora Lake Resort located at Upper Angora Lake below Echo Peak. The Hildinger family built the resort and has run it since the 1890's. Having spent nearly every summer at Angora lake for the last 68 years he has a good sense

of the changes that have occurred in the area. In regard to the Angora Ridge fire, Mr. Hildinger remarked that he could remember Angora Ridge covered with "Christmas tree" sized firs when he crossed the ridge as a boy. Though the fire occurred before his birth it was described to him by family members as a large crown fire that burned up both sides of the ridge toward Lower Angora Lake. He placed the fire at about 1890.

Bill Craven, the son of the owner and operator of the Fallen Leaf Lodge that was built in 1904, was also interviewed. He has lived his entire life (65 years) at Fallen Leaf Lake, which is located between Angora Ridge and the lower slopes of Mount Tallac. He described numerous small fires between the upper end of Fallen Leaf Lake and Lily Lake, but also recalled two larger fires adjacent to the Cathedral Creek drainage on the north side of Fallen Leaf Lake. The first of these he dated at about 1937, and the second, which he described as less intense at about 1955. The first of these is referred to as the Cathedral Creek fire in this study. He also described a large fire that had occurred on Angora Ridge before his birth. This fire was described to him by family and acquaintances as a large fire that burned both sides of the ridge leaving only a few remaining trees at the ridge line. He dated this fire between 1890 and 1900. The fire area was clearly visible for many years and he was able to render a rough sketch of its perimeter and the extent of the Cathedral Creek fire on a topographical map.

Margo Hackley Gwinn, who has owned a home on Fallen Leaf Lake since the 1920's, describes similar perimeters for the Angora Ridge fire and dates the Cathedral Creek fire at 1937. Her recollection of the precise date of this fire results from her family's evacuation.

Photographic evidence

Historical Photographs were used to confirm the existence of the two older fires. These include a photograph taken from the slopes of Echo Peak in 1917 (Scott 1973) along with a series of five aerial photographs (figures 4.1-4.6) obtained from the USDA Forest Service. Photographs taken as close as possible to the suggested dates of the fires were examined for canopy gaps, and these gaps were compared to the historical accounts of the fires.

Fire history data

Trees were sampled on Angora Ridge using the Arno and Sneek (1977) method for determining fire history in an attempt to ascertain the exact date of the Angora Ridge fire. Both sides of the ridge were surveyed for trees with visible fire scars. Trees that appeared most likely to provide a discernible fire record were selected within the following limitations set by the USDA Forest Service LTBMU (Swanson 1993). No more than four trees could be sampled in the area. Only trees a sufficient distance away from roadways and trails could be sampled, so that if a tree were to fall it would not cause an obstruction. And, no significant damage would be caused to any tree. These limitations were restrictive and did not allow an adequate sample size.

Stand age

Within the guide-lines of the plot sampling described in the following section on the ecological effects of stand-replacing fire, the average stand age for each fire area was determined for the Angora Ridge and Cathedral Creek

fire areas. This was accomplished by sampling the largest tree of each species present on each plot with an increment bore. Tree ages were counted in the field and were averaged for the entire fire area.

Ecological Effects of Stand Replacing Fire

Assuming the existence of pre-suppression stand-replacing fires, the ecological effects of this type of fire must be investigated in order to draw an accurate picture of the pre-European forest structure. In this study stand structure, species diversity, and fuel load were determined on four sites in the South Lake Tahoe area where stand-replacing fires had occurred (see maps in appendix). Before describing the method of sampling, however, it is important to give a detailed account of each fire area.

Specifics on the fire sites

(See table 3.1 for a summary of each fire areas characteristics.)

1. Angora Ridge. This fire covered approximately 250 acres, and was located on both sides of Angora Ridge between the present location of the Angora Lookout tower and Lower Angora Lake. The fire ran from 6400 to 7200 feet in elevation burning both the northwest and the southeast sides of Angora Ridge. The area's vegetation currently consists primarily of white fir (*Abies concolor*) - Jeffrey pine (*Pinus jeffreyi*) mixed conifer forest type with incense cedar (*Calocedrus deccurrens*) included at the lower elevations, red fir (*Abies magnifica*) becoming more prominent at higher elevations, and occasional occurrences of both western white pine (*Pinus monticola*) and lodgepole pine (*P. contorta* ssp. *murrayana*).

2. Cathedral Creek. This fire burned in 1937, covered approximately 53 acres, and was located in the Cathedral Creek drainage on the southeast slope above Fallen Leaf Lake, from 6400 to 7200 feet in elevation. The same forest type dominates the area surrounding both fires, and both have soils of the Meeks-Tallac formation type.

3. Cascade Lake. This fire occurred in 1978, covered approximately 16 acres, and was located on the southeast slope above Cascade Lake, from 6400 to 7200 feet in elevation. The same species of trees inhabit the area surrounding this fire area as were present on the Angora Ridge and Cathedral Creek sites. However, whereas white fir was generally dominant on the two older fire sites, Jeffrey pine was more prevalent at Cascade Lake. The soil type was also Meeks-Tallac.

4. Luther Fire. This 1987 fire covered approximately 20 acres and was located on the northwest slope above Christmas Valley, from 6600 to 7200 feet in elevation. The soil type was the same as that of the other three fire sites, and the forest type was similar to the two older fires with white fir dominant.

	Angora Ridge	Cathedral Creek	Cascade lake	Luther Fire
Date	≈1890	1937	1978	1987
Hectares	250	53	16	20
Elevation	6400-7200	6400-7200	6400-7200	6600-7200
Soil type	Meeks-Talac	Meeks-Talac	Meeks-Talac	Meeks-Talac
Forest type	Abco	Abco	Pije	Abco

Table 3.1 - Fire Area Characteristics. The forest type for all four fire areas was upper montane mixed conifer. The designations Abco and Pije stand for the dominant tree species on those sites, *Abies concolor* and *Pinus jeffreyi* respectively.

Sampling methods

The following methods were used to sample and analyze the structural and compositional factors of the vegetation on the four post fire areas.

- Sample Plot Location. Stand structure data was collected within each fire area using 33 by 66 foot rectangular plots. The location of these plots was determined by selecting elevations with a random number table (National Park Service 1991). This method of random selection was preferred due to the extreme slope on all four of the sites (45%-65%). Elevations were located using an altimeter accurate to 50 feet.

On each elevational transect the distance between plots was also selected randomly, and paced off at 100, 200, and 300 feet. Plot center was set at the end of this distance, and marked with a stake. The perimeter of the each plot was defined with flagging.

- Data Collected within 33 by 66 Foot Plots. At plot center within each 33 by 66 foot plot the elevation, slope, and aspect, were recorded and canopy cover was determined using a spherical densiometer.

Forest type was recorded in terms of the dominant species of tree for each plot. Fuel load was determined using a natural forest residue photo series (Blonski and Schramel 1981), and stand age was determined using an increment core sample from the largest tree of each species present on each plot.

The species and number of all living and dead standing trees was recorded for the 33 by 66 foot plot. Diameter at breast height (dbh) was measured for all

standing mature trees (defined as trees with a diameter greater than 4 inches). Height was measured for all trees using a clinometer.

The quantity and species of seedlings (trees less than 2 feet in height) and saplings (trees less than 4 inches in diameter) were also recorded.

- Data Collected within Nested Circular Plots. Three 6 foot diameter circular nested plots were used within each rectangular plot. One was set at plot center and one at each point where the elevational transect intersected the 33 foot side of the rectangular plot.

Within each circular plot the occurrences of all herbaceous species were recorded. For all shrubs present, species and cover class were determined using a standard cover scale developed by Daubenmire (1968) (table 3.2).

Cover Class	Range of Cover	Class Midpoints
6	95% - 100%	97.5%
5	75% - 95%	85%
4	50% - 75%	62.5%
3	25% - 50%	37.5%
2	5% - 25%	15%
1	0 %- 5%	2.5%

Table 3.2 - Daubenmire cover class scale (Daubenmire 1968)

- Canopy cover. The percent canopy cover for each fire area was determined by averaging the canopy covers of all sampled plots.

- Shrub cover. The shrub cover was calculated for each fire area by converting cover class values (Daubenmire 1968) into class midpoints

expressed in percent cover. The percent cover was averaged for shrub cover in general, and for individuals species.

- Species Diversity. Several measures of species diversity were calculated from the data including species richness, evenness, and the Shannon diversity index. Species richness describes the number of species that exist in a community, but does not address their relative abundance. Abundance is described through a measure of evenness. A diverse community has been described as one in which there are "many species, all of which are relatively rare" (Patil and Taillie 1982). In order to combine these two measures, diversity indices such as the Shannon and the Simpson have been developed (Pielou 1975). Because the Shannon index is the most commonly used (Smith 1992), it was utilized in this study .

$$\text{Shannon diversity} = \sum_{i=1}^s (p_i)(\ln p_i)$$

where s = diversity of species
 p_i = proportion of individuals of the total sample
 belonging to the i th species.

For this study, the species occurrence (which is necessary for calculating p_i), was determined from the total number of individuals of each tree species occurring on all plots. For shrub and herbaceous species totals of cover class values were used. Though these two values are not strictly compatible, the comparison of Shannon diversity between fire areas should be no less valid.

Using the Shannon diversity index evenness can be calculated using a simple formula.

$$\text{Evenness} = SD / SD_{max} = SD / \ln s$$

where SD = Shannon diversity index

s = total number of species

- Fuel load. The fuel load for each study area was calculated by averaging the natural forest residue determined on each plot (Blonski and Schramel 1981) resulting in a value of tons/acre.

- Frequency. The frequency (fraction of plots containing one or more individuals of a single species) and relative frequency was determined for all mature live and standing dead trees, and for all species of seedlings and saplings.

$$\text{frequency} = \frac{\text{number of plots in which a species occurs}}{\text{total plots sampled}}$$

$$\text{relative frequency} = \frac{\text{frequency of a single species}}{\text{total frequency of all species}} \times 100$$

- Density. Density and relative density were also determined for all species of live and dead trees present, and all species of seedlings and saplings.

$$\text{density} = \frac{\text{number of individuals}}{\text{acre}}$$

$$\text{relative density} = \frac{\text{density of a single species}}{\text{total density for all species}} \times 100$$

- Dominance. Dominance and relative dominance were calculated for mature live trees sampled on Angora Ridge and the Cathedral Creek Fire area. Dominance was not calculated for the Cascade Lake and Luther fire areas because there was not a sufficient sample size of mature trees.

$$\text{dominance} = \frac{\text{total basal area [dbh(p)] for a species}}{\text{total area sampled}}$$

$$\text{relative dominance} = \frac{\text{dominance of a single species}}{\text{total dominance for all species}} \times 100$$

- Importance. Importance values (Curtis and McIntosh 1951) were calculated only for species within the Angora Ridge and Cathedral Creek fire areas due to lack of canopy development on the other two fire sites.

$$\text{importance value} = \text{relative density} + \text{relative dominance} \\ + \text{relative frequency}$$

The accumulation of this information on the structure and composition of the present vegetation on these four fire sites is intended to facilitate a comparison between the sites. It is a temptation to configure the data in chronological sequence and treat the four fire areas as a single fire site allowing the development of a post stand-replacing fire successional model.

However, it is important to note while reviewing the data in the following chapters, that though there are numerous similarities between the fire areas, they are by no means equivalent; comparisons should be considered with this in mind.

Summary of Methods

Four study sites where stand-replacing fire had occurred within the last 100 years were selected in the Lake Tahoe Basin. Stand structure data was collected in each study area using 33 by 66 foot rectangular plots that were randomly selected within each study site. Within each plot slope, aspect, elevation, and forest type were recorded as well as information on size and species of all live and dead standing trees present. The quantity and species of seedlings and saplings were also measured. Canopy cover was determined with a spherical densiometer. Fuel load was determined using a natural forest residue photo series (Blonski and Schramel 1981), and stand age was determined using a core sample from the largest tree of each species present on each plot. Within each 33 by 66 foot plot three 6 foot diameter circular nested plots were used to sample herbaceous and shrub species. For all shrubs present, species and cover class were determined using a standard cover scale (Daubenmire 1959, 1968). The presence of all herbaceous species on 6 foot diameter circular plots was also recorded.

In the following chapter the data collected using these methods was used to calculate aspects of stand structure and composition including density, frequency, dominance, canopy cover, shrub cover, and species diversity. A chronological series of aerial photographs of the Angora Ridge is also

presented in the next chapter as evidence for the existence of a stand-replacing fire at that location and for its value in interpreting the ecological impact of such fires.

CHAPTER 5

RESULTS

This study is directed toward the question of the existence of stand-replacing fires in the pre-suppression fire regime of the Lake Tahoe basin and their effect on the structure and composition of forests communities. In this chapter the data is presented to support the existence of at least one stand-replacing fire that occurred prior to the implementation of systematic fire suppression (the Angora Ridge fire), and one stand-replacing fire that occurred at the time when fire suppression was first initiated (the Cathedral Creek fire).

Data is also presented on the structural and compositional components of the communities that have developed after these two fires, as well as two other, more recent, stand-replacing fires. This data is intended to facilitate a comparison between the various aged fires and to establish a developmental sequence.

Confirmation of Stand Replacing Fires

Four criteria were used in this study to confirm the existence of the two early fires (Angora Ridge and Cathedral Creek). These criteria are historical evidence, photographic interpretation, fire scar analysis, and average age of the oldest cohort of trees. The historical evidence was presented in the last chapter. This discussion will begin with photo interpretation.

Interpretation of historical photographs

Five aerial photographs (USDA-For. Serv. aerial photos) and one land photograph (Scott 1973) were used to support oral accounts of the existence of the two oldest fires. The earliest available photographs of the Angora Ridge plainly show an area without forest cover that matches the location, size and perimeter described by long time residents of the area (Craven 1993, Gwinn 1993, Hildinger 1993). A reconnaissance of the area also revealed several fire scarred snags and stumps in the area where the fire was thought to have occurred. Though this method of determining fire perimeter is by no means completely accurate, it is more than sufficient for the purposes of this study.

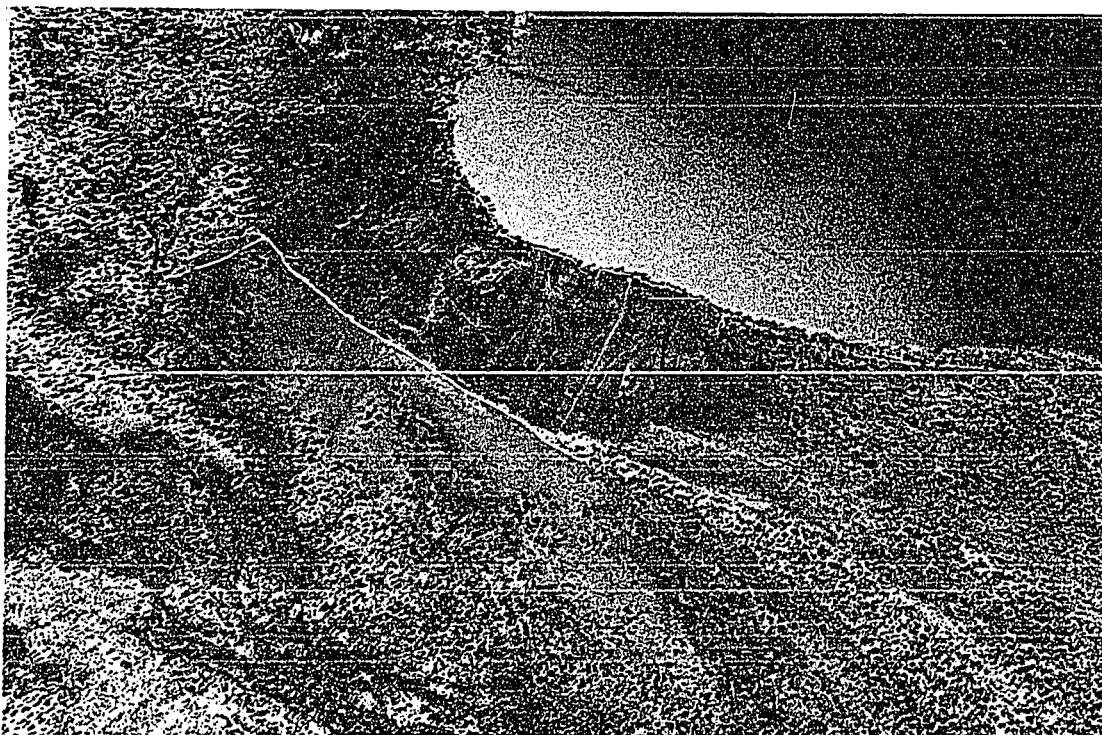
In addition to supporting the verbal report of the location of the fire, the photographs are also useful for considering the development of vegetation after the fire. The development of canopy and the period of shrub domination are particularly evident.

From the oldest available photograph of the area, the area without forest cover on the southeast side of the ridge is easily discernible (figure 4.1). The first aerial photograph gives a better view with both sides of the ridge visible (figure 4.2). In the second photograph, the southeast side of the ridge is almost completely deforested, yet some residual trees can be seen along the ridge top, and the northeast side. Many of these trees, mostly Jeffrey pine, still survive but are commonly in an advanced state of bark beetle attack.

Figure 4.1 - Angora Ridge taken from the lower slopes of Echo Peak above Upper Angora Lake in 1917 (Scott 1973).



Figure 4.2 - This is the earliest available aerial photograph of Angora Ridge taken in July 1940. The perimeter of the deforested area in this photograph matches the sketch made by Bill Craven (1993) almost exactly.



It is apparent by looking at the early photographs that the fire resulted in more complete stand-replacement on the southwest side of the ridge than on the northwest side. This may be due to a higher intensity of fire on that side, or a variety of other factors related to the pre-fire forest structure. Regardless of the cause, the total removal of canopy on the southwest side appears to have facilitated an extended period of shrub domination. As small trees begin to appear on the northwest side of the ridge, the southwest side remains deforested (figure 4.3).

Following a sixty to seventy year period of shrub domination, a high density of small trees appeared on both sides of the ridge (figure 4.4). Canopy continued to develop over the next ten years leaving only a few, relatively small shrub fields (figure 4.5).

The most recent aerial photograph of the ridge is, unfortunately, more than ten years old. It does, however, show the forest in a condition quite similar to its present state, with nearly complete canopy cover over the entire fire area (figure 4.6).

Figure 4.3 - By 1952 tree canopy began to develop on the northwest side of the ridge. The southwest side remains dominated by shrubs and small trees.

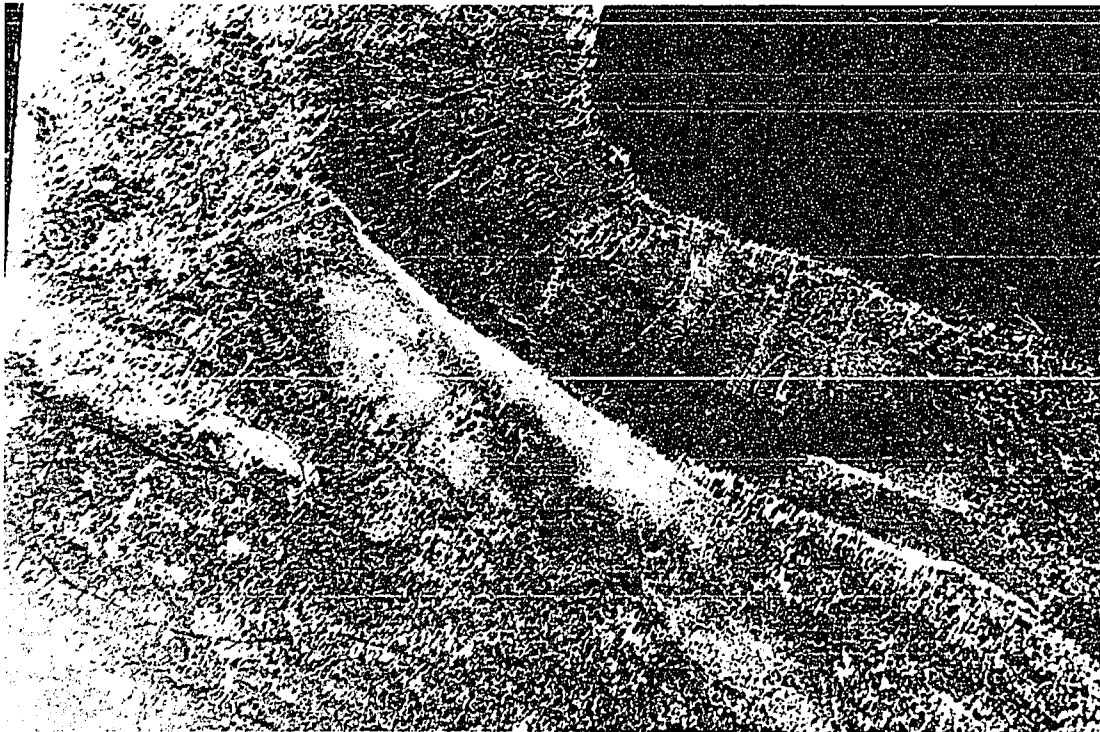


Figure 4.4 - In 1966 both sides of the ridge have a high density of small trees.

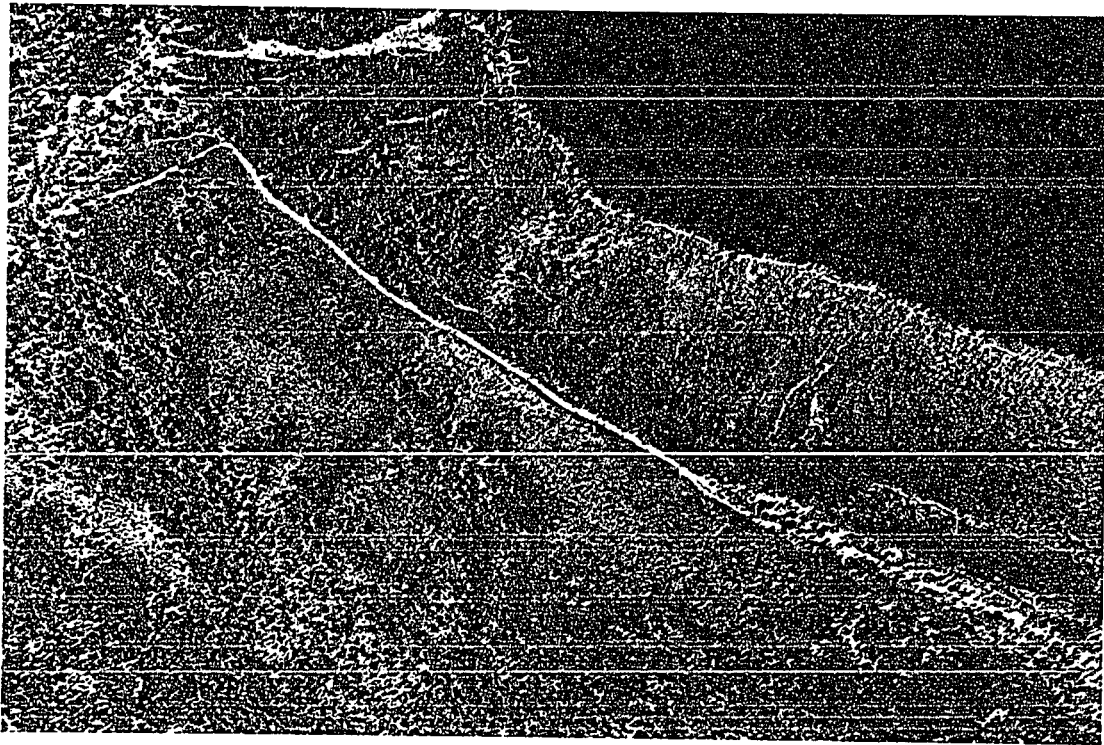
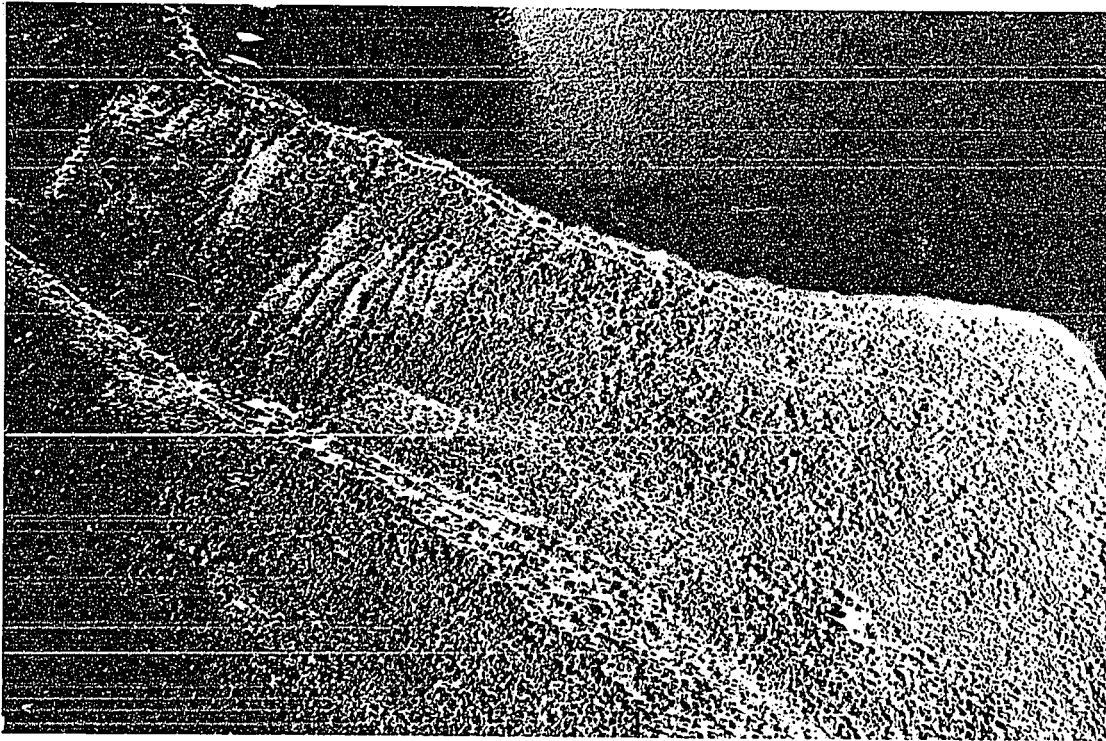


Figure 4.5 - Angora Ridge 1976, a significant canopy has developed but there are still areas of shrub domination.



Figure 4.6 - This 1983 photograph shows Angora Ridge in a state similar to its present one, with high density forests on both slopes.



Fire scar analysis

In an attempt to determine a precise date for the Angora Ridge fire, the fire history determination methods of Arno and Sneek (1977) were employed. Trees sampled included Jeffrey pine (*Pinus jeffreyi*), whitebark pine (*P. monticola*), and white fir (*Abies concolor*). Unfortunately the results from this portion of the study were inconclusive. A combination of factors resulted in a lack of usable data. A maximum of four samples were allowed by the USDA Forest Service due to the sensitive nature of the area. A lack of suitable specimens were found in areas approved for sampling. And many of the trees that displayed fire scars also suffering from acute cases of heart rot resulting in an unreadable fire record.

Stand Age Data

Stand age was determined for the two older fire areas through increment core analysis, resulting in an average dominant tree age (table 4.1). Currently average age for sampled trees on Angora ridge is 70 years with no significant difference in age between *Abies concolor*, *A. magnifica*, and *Pinus jeffreyi*. This is consistent with the existence of a 100 year old stand-replacing fire.

The average dominant tree age for the Cathedral Creek Fire area was 40 years, which is consistent with a 56 year old fire. There was no significant difference in age between *A. concolor* and *P. jeffreyi*.

Neither the Cascade Lake fire area or the Luther fire area had enough canopy development to determine stand age. Both of these fires were recent, and their age was determined through interview with USDA Forest Service fire suppression personnel (Johnson 1993).

Plot #	Angora Ridge Elevation	Abma	Abco	Pije	Cathedral Creek Elevation	Abma	Abco	Pije
1	6500'		80		6800'		57	
2	6500'		82	84	6800'		20	22
3	6500'		79		6800'			
4	6500'		70	73	6800'			
5	6600'		81		6800'			
6	6600'		95	79	6900'			50
7	6600'		95		6900'			
8	6600'	82	71	54	6900'			53
9	7000'		21	54	7000'		44	25
10	7000'			41	7000'		42	50
11	7000'		62		7000'		26	
12	7000'		34		7000'			
13	7200'		59		7000'		36	
14	7200'		89	63	7200'		54	
15	7200'		79		7200'			
16	7200'				7200'			
17					7200'			
18					7200'		42	
Mean		82	71	64			40	40
Range		0	74	43			37	31

Table 4.1. Average stand age by species. Range = the dispersion between high and low values.

The historical accounts of the Angora Ridge and Cathedral Creek fires, coupled with the historical photos and the stand age analysis are evidence that these two fires occurred and that they can be regarded as stand replacing. It is unfortunate that the fire scar analysis did not produce results, as this type of record not only would have offered further evidence for the existence of these fires, but would also have facilitated a determination of an exact fire date for the Angora Ridge. Even without this evidence, however, it can be assumed with confidence that there was stand-replacing fire in the pre-suppression fire regime.

Community Composition and Structure

With the existence of stand-replacing fires confirmed, the long term effects of such fires are presented in the following data.

Canopy Cover

The canopy cover for trees was calculated for each plot and then averaged for each fire area (table 4.2).

Plot #	Elevation	Angora Ridge	Elevation	Cathedral Creek	Elevation	Cascade Lake	Elevation	Luther Fire
1	6500'	82%	6800'	4%	6800'	38%	7100'	0%
2	6500'	90%	6800'	0%	6800'	0%	7100'	0%
3	6500'	92%	6800'	0%	6900'	20%	7100'	0%
4	6500'	48%	6800'	16%	6900'	0%	7100'	5%
5	6600'	78%	6800'	18%	6900'	3%	7100'	0%
6	6600'	72%	6900'	23%	6950'	0%	7150'	0%
7	6600'	100%	6900'	2%	6950'	0%	7150'	0%
8	6600'	89%	6900'	33%	6950'	0%	7150'	0%
9	7000'	73%	7000'	11%	6950'	0%	7150'	7%
10	7000'	34%	7000'	2%	6950'	5%	7150'	5%
11	7000'	39%	7000'	0%	7100'	0%	7250'	10%
12	7000'	100%	7000'	0%	7100'	4%	7250'	0%
13	7200'	43%	7000'	0%	7100'	0%	7250'	0%
14	7200'	95%	7200'	0%			7250'	5%
15	7200'	55%	7200'	0%			7250'	0%
16	7200'	66%	7200'	0%			7300'	0%
17			7200'	3%			7300'	0%
18			7200'	0%			7300'	4%
Mean		72%		6%		5%		2%
Standard Error		6%		2%		3%		1%
Range		66%		33%		38%		10%

Table 4.2 - Canopy cover.

The percent cover is clearly highest on the Angora Ridge (figure 4.7). Canopy cover is roughly equal on the other three fire areas. The wide range of values, particularly for the Angora Ridge fire, reflects the existence of the few remaining shrub fields on the northwest side of the ridge. The canopy cover on the Cascade Lake and Luther fires is the result of residual trees, and trees on the perimeter of the fire areas. There was no post fire canopy development on these sites.

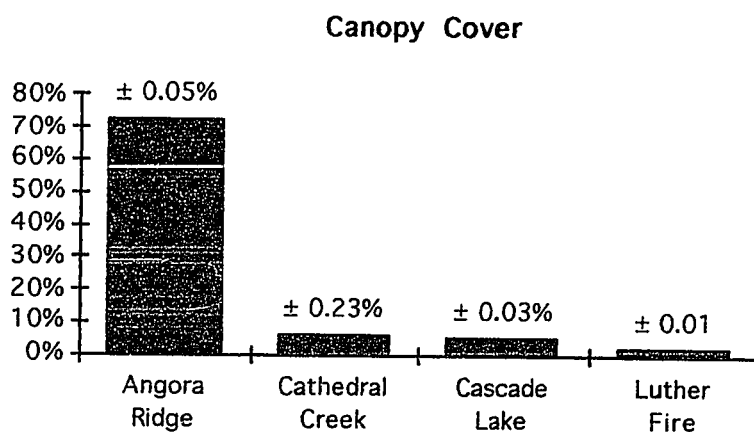


Figure 4.7 - Each value represents an average from all plots.

Shrub Cover

Shrub cover was also calculated for each plot by converting the cover class values obtained for the three nested plots (Daubenmire 1968) into class midpoints (see table 3.1) and averaging them for a single plot percent cover value (table 4.3).

Plot #	Elevation	Angora Ridge	Elevation	Cathedral Creek	Elevation	Cascade Lake	Elevation	Luther Fire
1	6500'	6%	6800'	98%	6800'	55%	7100'	98%
2	6500'	0%	6800'	86%	6800'	86%	7100'	78%
3	6500'	8%	6800'	13%	6900'	70%	7100'	86%
4	6500'	45%	6800'	93%	6900'	31%	7100'	98%
5	6600'	18%	6800'	98%	6900'	70%	7100'	73%
6	6600'	0%	6900'	98%	6950'	33%	7150'	98%
7	6600'	1%	6900'	98%	6950'	86%	7150'	93%
8	6600'	5%	6900'	98%	6950'	93%	7150'	82%
9	7000'	33%	7000'	62%	6950'	98%	7150'	98%
10	7000'	34%	7000'	86%	6950'	98%	7150'	98%
11	7000'	27%	7000'	98%	7100'	98%	7250'	86%
12	7000'	5%	7000'	86%	7100'	82%	7250'	89%
13	7200'	5%	7000'	98%	7100'	93%	7250'	98%
14	7200'	10%	7200'	98%			7250'	86%
15	7200'	0%	7200'	98%			7250'	58%
16	7200'	10%	7200'	93%			7300'	82%
17			7200'	78%			7300'	86%
18			7200'	98%			7300'	86%
Mean		13%		88%		76%		87%
Standard Error		4%		5%		7%		3%
Range		45%		85%		67%		40%

Table 4.3. Shrub cover.

The relative values for shrub cover have an inverse relationship to the canopy cover values. The shrub cover on Angora Ridge is clearly the lowest with the other three fire areas having roughly equivalent values (figure 4.8). The percent shrub cover exhibited a high degree of variability. On the older fire sites this was due primarily to areas of residual shrub domination. On the two recent fire sites the variation is due primarily to small boulder fields and steep slopes.

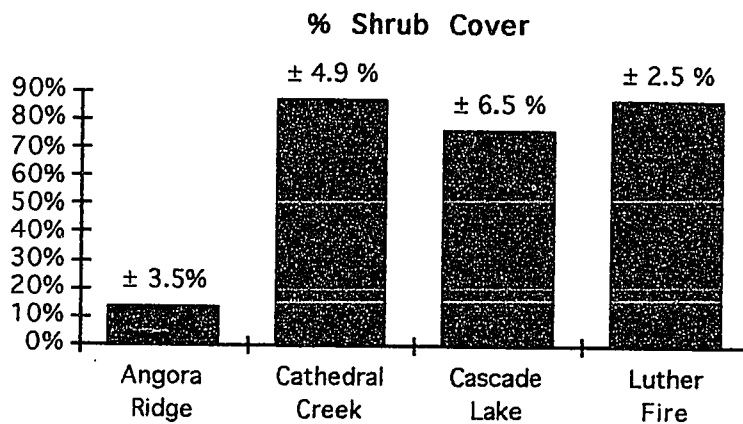


figure 4.8 - Shrub cover. Each value represents an average from all plots.

Species Diversity

Species diversity is a function of both the total number of species occurring within a community, and the evenness, or distribution, of those species. A species list was compiled for all four fire areas along with the number of occurrences of each species (table 4.4). For tree species, the number of individuals was recorded for each plot. For herbaceous and shrub species, cover class values were used (Daubenmire 1968).

		Angora Ridge	Cathedral Creek	Cascade Lake	Luther Fire
Trees	<i>Abies concolor</i>	277	285	1	12
	<i>Abies magnifica</i>	11	1		
	<i>Calocedrus decurrens</i>			1	
	<i>Pinus contorta</i> (var. <i>murrayana</i>)			1	
	<i>Pinus jeffreyi</i>	21	36	27	2
Shrubs	<i>Amelanchier alnifolia</i> (var. <i>pumila</i>)	1	16	1	
	<i>Arctostaphylos patula</i>	14	40	58	101
	<i>A. navadensis</i>		15	3	
	<i>Castanopsis sempervirens</i>	1			3
	<i>Ceanothus cordulatus</i>		8	17	56
	<i>C. velutinus</i>		2	8	2
	<i>Prunus emarginata</i>	5	2	2	4
	<i>P. virginiana</i> (var. <i>demissa</i>)		32	1	3
	<i>Quercus vaccinifolia</i>	35	170	73	105
	<i>Ribes roezlii</i>		5	3	
	<i>Salix</i> spp.			6	2
Herbs/ Forbs	<i>Achillea lanulosa</i>		1		
	<i>Aquilegia formosa</i>		1		
	<i>Aster</i> spp.			2	
	<i>Bromus</i> spp.	1		1	
	<i>Castilleja</i> spp.		1		1
	<i>Cassiope mertensiana</i>				2
	<i>Delphinium</i> spp.				1
	<i>Eriogonum umbellatum</i>				1
	<i>Festuca</i> spp.		1	1	
	<i>Gayophytum</i> spp.			2	
	<i>Lonicera</i> spp.		3	3	1
	<i>Lupinus</i> spp.		5	1	1
	<i>Linum perenne</i> (ssp. <i>lewisii</i>)		2		
	<i>Mimulus</i> spp.				1
	<i>Rubus parviflorus</i>			1	
	<i>Smilacina racemosa</i>	1	1	1	
	<i>Symphoricarpos</i> spp.	3	4	14	4

Table 4.4 - Occurrence of individual species. Each value represents the total number of individuals sampled on all plots. Trees were sampled using 33 by 66 foot plots, the shrubs and herbaceous plants were sampled on 6 foot diameter plots.

From the number of occurrences of individual species relative occurrence within each fire area, expressed as a proportion was also calculated (table 4.5).

		Angora Ridge	Cathedral Creek	Cascade Lake	Luther Fire
Trees	<i>Abies concolor</i>	0.749	0.474	0.004	0.04
	<i>Abies magnifica</i>	0.03	0.002		
	<i>Calocedrus decurrens</i>			0.004	
	<i>Pinus contorta</i> (var. <i>murrayana</i>)			0.004	
	<i>Pinus jeffreyi</i>	0.057	0.06	0.118	0.007
Shrubs	<i>Amelanchier alnifolia</i> (var. <i>pumila</i>)	0.003	0.027	0.004	
	<i>Arctostaphylos patula</i>	0.038	0.067	0.254	0.334
	<i>A. navadensis</i>		0.025	0.013	
	<i>Castanopsis sempervirens</i>	0.003			0.01
	<i>Ceanothus cordulatus</i>		0.013	0.075	0.185
	<i>C. velutinus</i>		0.003	0.035	0.007
	<i>Prunus emarginata</i>	0.014	0.003	0.009	0.013
	<i>P. virginiana</i> (var. <i>demissa</i>)		0.053	0.004	0.01
	<i>Quercus vaccinifolia</i>	0.095	0.283	0.032	0.348
	<i>Ribes roezlii</i>		0.008	0.013	
	<i>Salix</i> spp.			0.026	0.007
Herbs/ Forbs	<i>Achillea lanulosa</i>		0.002		
	<i>Aquilegia formosa</i>		0.002		
	<i>Aster</i> spp.			0.009	
	<i>Bromus</i> spp.	0.003		0.004	
	<i>Castilleja</i> spp.		0.002		0.003
	<i>Cassiope mertensiana</i>				0.007
	<i>Delphinium</i> spp.				0.003
	<i>Eriogonum umbellatum</i>				0.003
	<i>Festuca</i> spp.		0.002	0.004	
	<i>Gayophytum</i> spp.			0.009	
	<i>Lonicera</i> spp.		0.005	0.013	0.003
	<i>Lupinus</i> spp.		0.008	0.004	0.003
	<i>Linum perenne</i> (ssp. <i>lewisii</i>)		0.003		
	<i>Mimulus</i> spp.				0.003
	<i>Rubus parviflorus</i>			0.004	
	<i>Smilacina racemosa</i>	0.003	0.002	0.004	
	<i>Symphoricarpos</i> spp.	0.008	0.007	0.061	0.013

Table 4.5 - Proportions of individual species. Each value is a proportion of the occurrence of the individual species to the occurrence of all species.

From the relative occurrence values the species richness (figure 4.9), Shannon diversity index (figure 4.10), and evenness (figure 4.11) were derived for each fire area.

There is a higher species richness, evenness and Shannon diversity index measured on the three more recent fire sites compared to the Angora Ridge. All three values were similar for the recent fires.

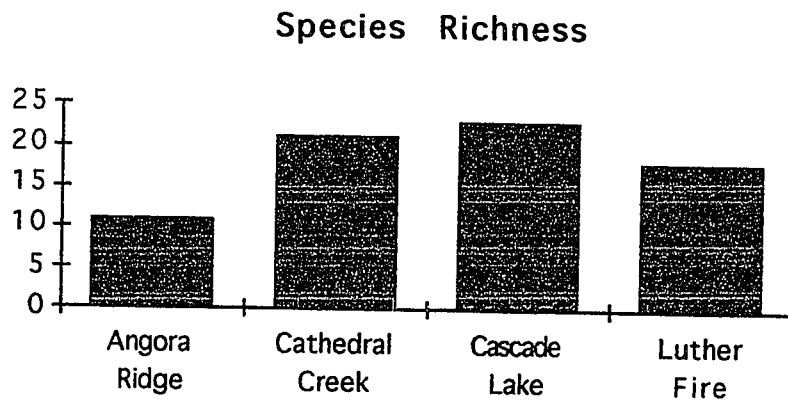


Figure 4.9 - Species richness.

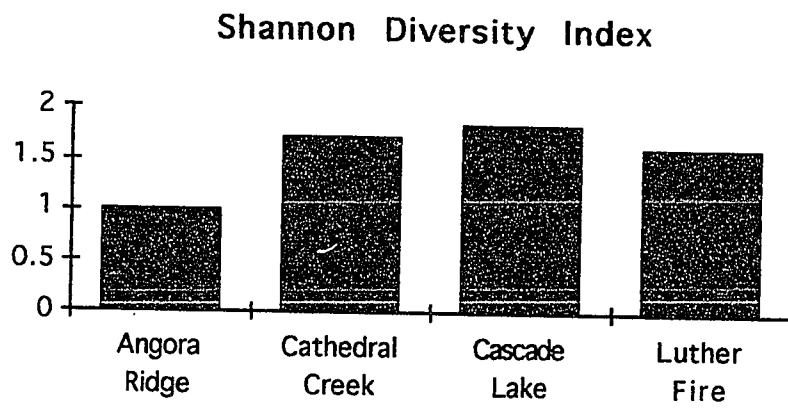


Figure 4.10 - Shannon diversity.

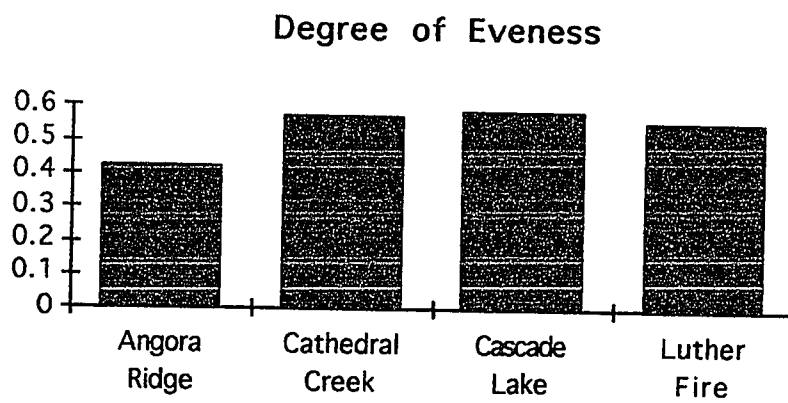


Figure 4.11 - Evenness.

Fuel Load

The amount of residual fuel, including dead and downed material, calculated for individual plots was averaged for each fire area (Table 4.6).

Plot #	Elevation	Angora Ridge	Elevation	Cathedral Creek	Elevation	Cascade Lake	Elevation	Luther Fire
1	6500'	22.9	6800'	10.1	6800'	8.8	7100'	10.1
2	6500'	10.1	6800'	10.1	6800'	3.9	7100'	10.1
3	6500'	22.9	6800'	0	6900'	3.9	7100'	10.1
4	6500'	22.9	6800'	10.1	6900'	3.9	7100'	10.1
5	6600'	16.4	6800'	10.1	6900'	8.8	7100'	10.1
6	6600'	39.2	6900'	10.1	6950'	3.9	7150'	10.1
7	6600'	16.4	6900'	10.1	6950'	3.9	7150'	10.1
8	6600'	39.2	6900'	10.1	6950'	3.9	7150'	0
9	7000'	10.1	7000'	3.9	6950'	3.9	7150'	10.1
10	7000'	10.1	7000'	3.9	6950'	3.9	7150'	10.1
11	7000'	10.1	7000'	3.9	7100'	3.9	7250'	10.1
12	7000'	16.4	7000'	3.9	7100'	12.6	7250'	10.1
13	7200'	16.4	7000'	10.1	7100'	3.9	7250'	10.1
14	7200'	16.4	7200'	10.1			7250'	10.1
15	7200'	22.9	7200'	10.1			7250'	10.1
16	7200'	16.4	7200'	10.1			7300'	0
17			7200'	16.4			7300'	10.1
18			7200'	16.4			7300'	0
Mean		19.3		8.9		5.3		8.4
Standard Error		2.3		1		0.8		0.9
Range		29.1		16.4		8.7		10.1

Table 4.6 - Fuel load. Values are expressed in tons per acre.

The fuel accumulation was highest on the Angora Ridge, with values for the other three fires being roughly equivalent (figure 4.12). The fuel accumulation value for the Cascade lake fire area was somewhat lower than that of the other two, more recent fire areas due primarily to the

domination of pine in the forests surrounding the fire. Natural residue in Jeffrey pine forests tends to be less dense than that found in white fir.

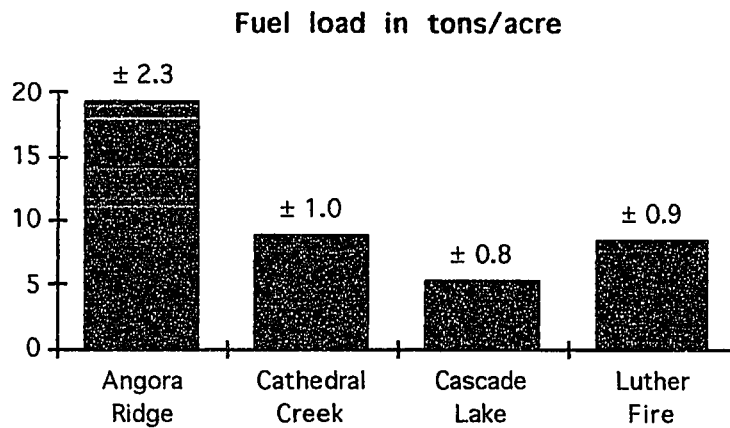


Figure 4.12. Fuel load.

Frequency and Relative Frequency

The average frequency of occurrence, or percentage of plots in which a particular species is found, was calculated separately for each fire area (tables 4.7-4.10). The frequency of each species was separated into four categories including; living (live trees greater than 4 inches dbh), dead (dead trees greater than 4 inches dbh), saplings (trees < 4 inches dbh , and > 2 feet tall), and seedlings (trees less than 2 feet tall).

Angora Ridge												
Plot #	Living			Dead			Saplings			Seedlings		
	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije
1		13			4			5			4	
2		8	2					5				
3		10			6			9				
4	1	3	2		1			5			4	
5		7			4			23			15	
6	1	4	1		1		1	11				
7	1	7		1	5			6			3	
8	3	9			1		2	11	3		6	
9		5	2					4	2			
10		6	1					1	1			
11		6	2		1			7			4	
12		10			2			18			4	
13		7								2	2	
14		9	1		9	2		4				
15		7	1		1			5			2	
16		4	3		2			3			1	
Frequency	0.25	1	0.56	0.06	0.75	0.06	0.13	0.94	0.19	0.06	0.63	0
Rel. Freq.	14%	55%	31%	7%	86%	7%	10%	75%	15%	0.09	0.91	0

Table 4.7. Frequency-Angora Ridge. Abma = *Abies magnifica*, Abco = *A. concolor*, Pije = *Pinus jeffreyi*.

Abies concolor has the highest frequency in all categories on the Angora Ridge, Cathedral Creek, and Luther fires areas. The relative frequency of pine appears to decline in the lower age classes. On the Cascade Lake fire site *Pinus jeffreyi* was the most frequent species due to its dominance in the surrounding forest.

Cathedral Creek												
Plot #	Living			Dead			Saplings			Seedlings		
	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije
1		4						19			12	
2		2	1					15	17		17	
3							1	24	1		14	1
4								32	4		39	
5								24			12	
6								8	2		6	
7			1								1	
8								12	3		2	
9			1					8			4	
10		1	1					5	2			
11		1	1					1				
12		2						3				
13		6						3	1		5	
14		1			2							
15		1										
16												
17												
18		1										
Frequency	0	9.9	5.5	0	1.1	0	1.1	13.3	7.8	0	11.1	1.1
Rel. Freq.	0%	64%	36%	0%	100%	0%	5%	60%	35%	0%	91%	9%

Table 4.8. Frequency-Cathedral Creek. Cade = *Calocedrus decurrens*, Pico = *Pinus contorta*.

Cascade Lake										
Plot #	Living			Dead		Saplings			Seedlings	
	Abco	Pije	Cade	Abco	Pije	Abco	Pije	Pico	Abco	Pije
1		2			1					
2							1	1		
3							7			
4										
5			1				2			
6							4		1	
7					1					
8										
9										
10										
11										
12		1				1	5		2	
13									2	
Frequency	0	0.15	0.8	0	0.15	0.08	0.38	0.08	0	0.23
Rel. Freq.	0%	65%	35%	0%	100%	15%	70%	15%	0%	100%

Table 4.9. Frequency-Cascade lake.

Luther Fire												
Plot #	Living			Dead			Saplings			Seedlings		
	Abco	Pije	Cade	Abco	Pije		Abco	Pije	Pico	Abco	Pije	
1								2				
2												
3												
4												
5												
6											1	
7												
8								2			1	
9												
10								1			3	
11								1				
12												
13												
14		1							1			
15												
16												
17											1	
18												
Frequency	0	0.06	0	0	0	0	0	0.22	0.06	0	0.16	0.06
Rel. Freq.	0%	100%	0%	0%	0%	0%	0%	79%	21%	0%	73%	27%

Table 4.10. Frequency-Luther fire.

Density and Relative Density

The density, or number of species per unit acre, was calculated for each plot and then averaged for the individual fire areas (Tables 4.11-4.14). *Abies concolor* had the highest density in all age classes on the Angora Ridge, Cathedral Creek, and Luther fire sites. In contrast the density of *Pinus jeffreyi* is highest on the Cascade Lake fire area.

Angora Ridge												
Plot #	Living			Dead			Saplings			Seedlings		
	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije
1		260			80			100			80	
2		160	40					100				
3		200			120			180				
4	20	60	40		20			100			80	
5		140			80			460			300	
6	20	80	20		20		20	220				
7	20	140		20	100			120			60	
8	60	180			20		40	220	60		120	
9		100	40					80	40			
10		120	20					20	20			
11		120	40		20			140			80	
12		200			40			360			80	
13		140								40	40	
14		180	20		180	40		80				
15		140	20		20			100			40	
16		80	60		40			60			20	
Mean	7.5	144	18.8	1.25	46.3	2.5	3.75	146	7.5	2.5	56.3	0
St. Error	4.03	13.1	4.99	1.25	13	2.5	2.72	30.2	4.43	2.5	19	0
Rel. Dens.	4%	85%	11%	2%	93%	5%	2%	93%	5%	4%	1%	96%

Table 4.11 - Density-Angora Ridge.

Cathedral Creek												
Plot #	Living			Dead			Saplings			Seedlings		
	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije
1		80						380			240	
2		40	20					300	340		340	
3							1	480	20		280	20
4								640	80		780	
5								480			240	
6								160	40		120	
7			20								20	
8								240	60		40	
9			20					160			80	
10		20	20					100	40			
11		20	20					20				
12		40						60				
13		120						60	20		10	
14		20			40							
15		20										
16												
17												
18		20										
Mean	0	21.1	5.56	0	2.22	0	0.06	171	33.3	0	119	1.11
St. Error	0	7.66	2.17	0	2.22	0	0.06	48	18.9	0	47.3	1.11
Rel. Dens.	0%	79%	21%	0%	100%	0%	1%	83%	16%	0%	99%	1%

Table 4.12. Density-Cathedral Creek.

Cascade Lake											
Plot #		Living			Dead		Saplings			Seedlings	
		Abco	Pije	Cade	Abco	Pije	Abco	Pije	Pico	Abco	Pije
1			40			20					
2								20	20		
3								140			
4											
5				20				40			
6								80			20
7						20					
8											
9											
10											
11											
12			20								
13								20	100		40
Mean		0	4.62	1.54	0	3.08	1.54	29.2	1.54	0	7.69
St. Error		0	3.32	1.54	0	2.08	1.54	13.1	1.54	0	4.26
Rel. Dens		0%	75%	25%	0%	100%	5%	91%	5%	0%	100%

Table 4.13. Density-Cascade Lake.

Luther Fire												
Plot #	Living			Dead			Saplings			Seedlings		
	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije	Abma	Abco	Pije
1								40				
2												
3												
4												
5												
6											20	
7												
8								40			20	
9												
10								20			60	
11								20				
12												
13												
14		20							20			
15												
16												20
17												
18												
Mean	0	1.11	0	0	0	0	0	6.67	1.11	0	5.56	1.11
St. Error	0	1.11	0	0	0	0	0	3.23	1.11	0	3.54	1.11
Rel. Dens.	0%	100%	0%	0%	0%	0%	0%	86%	14%	0%	83%	17%

Table 4.14 - Density-Luther fire.

The relative density of various size classes (i.e. mature, sapling, and seedling) are compared in figure 4.13. The most dramatic comparison is between the Angora Ridge and the Cathedral Creek fire area. Density is very low on the two most recent sites, but it is significant that some recruitment of trees is occurring. The density of seedlings and saplings is much higher on the Cathedral Creek fire than on the Angora Ridge fire, indicating a higher recruitment rate on that fire.

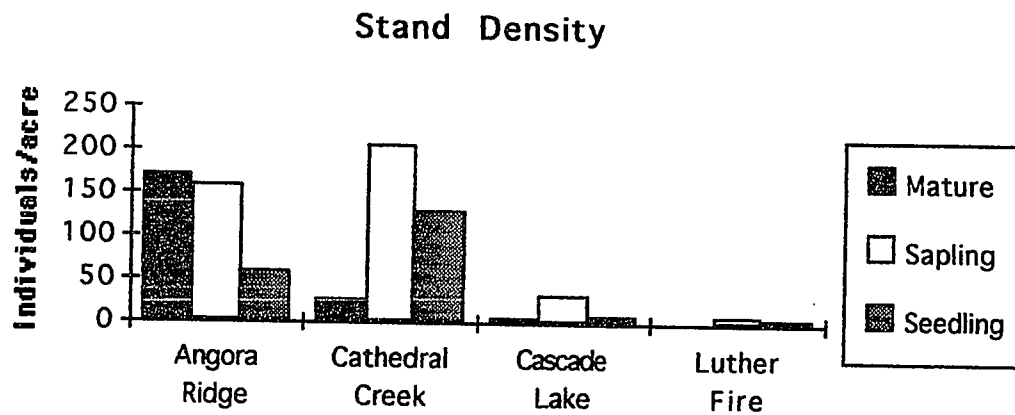


Figure 4.13 - Density.

Dominance and Relative Dominance

The dominance values of the three species of mature living trees occurring on the two older fire areas was calculated (table 4.15). No dominance values were calculated for the more recent fire areas due to a lack of mature trees.

Plot #	Angora Ridge			Cathedral Creek		
	Abma	Abco	Pije	Abma	Abco	Pije
1	0	45780	0	0	1890	0
2	0	60200	2210	0	270	80
3	0	4940	0	0	0	0
4	100	3600	2420	0	0	0
5	0	24080	0	0	0	0
6	100	19940	500	0	0	0
7	100	14060	0	0	0	400
8	1646	21480	0	0	0	0
9	0	2560	780	0	0	710
10	0	3900	300	0	270	110
11	0	9340	420	0	2020	290
12	0	36420	0	0	1350	0
13	0	12860	0	0	18420	0
14	0	56860	300	0	143	0
15	0	10980	400	0	15630	0
16	0	5940	3160	0	0	0
17				0	0	0
18				0	349	0
Dominance	121	20809	656	0	2241	88
St. Error	101	4757	252	0	1282	45
Rel.Dom.	1%	96%	3%	0%	97%	3%

Table 4.15 - Dominance. Expressed in square inches/ plot.

The relative domination of the three species of trees common to the Angora Ridge and Cathedral Creek fire areas is similar in both fire areas with *Abies concolor* dominant on both sites (figure 4.14).

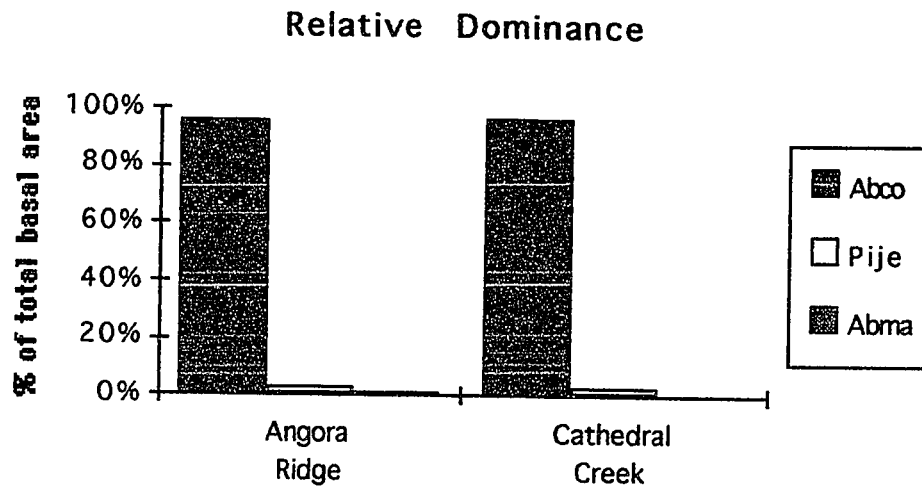


Figure 4.14 - Relative dominance.

Importance Value

Importance values were calculated for the two older fires only (table 4.16). The similarity in values of the two sites indicates that these sites have similar stand composition despite the difference in their time of development.

	Angora Ridge			Cathedral Creek		
	Abma	Abco	Pije	Abma	Abco	Pije
Rel. Frequency %	14	55	31	0	64	36
Rel. Density %	3	89	8	0	79	21
Relative Dominance %	1	96	3	0	97	3
Importance Value	19	240	42	0	240	60

Table 4.16 - Importance Value.

The results described so far are consistent with conventional models of post fire succession in mixed conifer forests (Kercher and Axelrod 1984, Lyon and Stickney 1976). In one significant aspect, however, the communities

studied differed from these models. The relative abundance of the two major genera of trees, *Abies* and *Pinus*, was approximately equivalent for Angora Ridge, Cathedral Creek, and the Luther fire with white fir clearly the dominant species. In the Cascade Lake fire area, however, *Pinus* was clearly dominant. The varying domination of *Abies* and *Pinus* on these sites appears to be proportional to available seed sources rather than a result of post fire successional patterns. This is further demonstrated by a comparison of the relative density of mature *Abies* and *Pinus* to seedlings and saplings (table 4.17). The earliest recruitment of *Abies* appears to have coincided with the earliest recruitment of *Pinus*. There does not appear to be a requisite period of pine domination on these sites as was described for a similar site in the Sierra Nevada (Bock and Bock 1969, Bock, Bock and Hawthorne 1976). The continuous regeneration of *Abies concolor* found in this study is comparable to that found by Conard and Radosevich (1982).

	Angora Ridge			Cathedral Creek			Cascade Lake			Luther Fire		
	Mat	Sap	Seed	Mat	Sap	Seed	Mat	Sap	Seed	Mat	Sap	Seed
Abma	3.5	2.3	4	-	1	-	-	-	-	-	-	-
Abco	89	93	96	79	83	99	-	4.5	-	-	86	83
Pije	8.5	4.7	-	21	16	1	-	91	100	-	14	17
Pico	-	-	-	-	-	-	-	4.5	-	-	-	-

Table 4.17 - Relative density. Expressed as the percent of mature trees, saplings, and seedlings of all species present.

Mortality

The total density of mature standing dead trees may be useful in predicting the future direction of vegetation change in the communities studied. The percentage of dead to live trees is much higher on the Angora Ridge than on the other three sites (Fig 4.15) indicating that mortality may be connected to stand density. All trees that were recorded as dead on both fire sites showed evidence of bark beetle infestation.

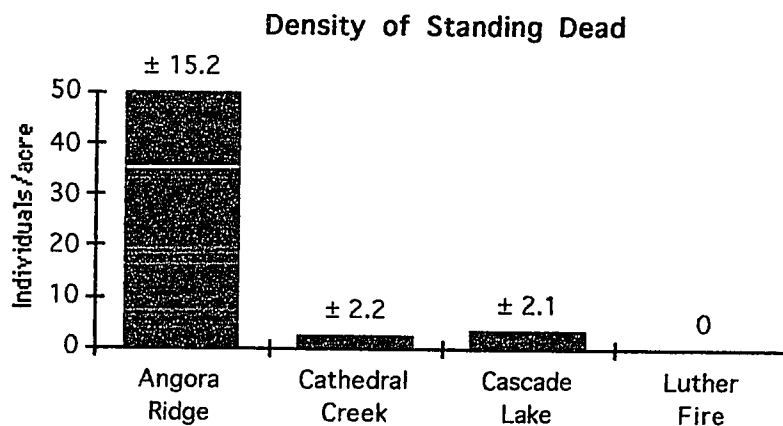


Figure 4.15 - Density of Standing dead trees.

Summary of Results

In this chapter the existence of pre-suppression stand-replacement fire in the Lake Tahoe Basin has been confirmed with historical evidence, aerial photo interpretation, and stand age data. Further, it has been shown that stand replacing fires have a significant effect on the structure and composition of ecological communities over long periods of time. Important aspects of this effect include:

1. A long period of shrub domination. Three out of the four fires sampled were currently dominated by shrub species, including the Cathedral Creek fire area, where fire had not occurred for almost sixty years. A long period of shrub domination was also evident through aerial photo interpretation, on the Angora Ridge. Significant canopy cover did not develop there until at least seventy years after fire.

2. Reduced fire potential. The Angora Ridge had significantly higher downed fuel load, standing dead, and forest density all of which increase the potential for another high intensity fire on that site. The younger fire sites had lower fuel loads due to lower stand density and less time for residue accumulation, indicating that potential is reduced for a period after stand-replacing fire.

3. Species diversity. The three measures of species diversity employed in this study (species richness, evenness, and the Shannon diversity index) all indicated separately that species diversity was highest on the three youngest fires. This result is due, most likely, to the lack of canopy on those sites.

In contrast to these effects, stand-replacing fire did not, in these instances, limit the community to a traditional seral stage. The species that existed on the mature fire sites also existed on the less mature fire sites, though in varying abundances, indicating community structure based on initial florist recruitment rather than a traditional models of succession. In addition, the

dominant species of trees (*Abies concolor*, and *Pinus jeffreyi*) appear to have been recruited simultaneously, as is shown by stand age data (table 2).

The degree to which stand-replacing fire existed in the pre-suppression forest is not addressed in this study. However, based on this data, when stand-replacing fire occurs it has a long term and significant effect on the floristic composition of the community.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Fire is clearly a natural part of the forests of the Sierra Nevada. Ignited by a variety of sources, it has burned regularly, at times moving slowly through the underbrush and other times exploding violently in the tree tops, since long before humans settled this continent. The occurrence of fire in these forests has shaped them both structurally by reducing understory and small trees and compositionally by favoring species that can tolerate fire. In the early written accounts, the forests surrounding Lake Tahoe were described as "open and park like" where a man could easily ride a horse through groves of enormous pines (Muir 1894). It is difficult to imagine riding a horse now through the thickets of fir that have replaced the park-like pine forests. The forests have changed, and an important reason for that change is the absence of fire.

In order to understand the consequences of removing fire from a community one must first understand the role that fire plays when it does occur. The ecological effects of low intensity surface fires, which were by far the most prevalent prior to fire suppression, have been studied in detail, and their importance has been widely accepted (Boyce 1921, Kilgore 1981, Show and Kotock 1924). The ecological role of high intensity stand-replacing fire, however, has been neglected in the literature. It is the conclusion of this study that despite the rarity of its occurrence, stand-replacing fire has been

historically, and remains today, an important ecological factor in the forests of the Sierra Nevada.

Ecological Importance of Stand Replacing Fire

The effects of stand-replacing fire were studied by collecting data regarding stand composition and structure on four sites in the Lake Tahoe Basin that had experienced stand-replacing fire within the last one hundred years.

The oldest fire occurred on Angora Ridge before the implementation of systematic fire suppression. The existence of this fire and the structural data collected within its perimeters indicates that not only did stand-replacing fires exist before fire suppression, but that the process of forest development after such fires can be extensive, including a long period with minimal canopy cover, and high shrub domination. This conclusion was supported by data collected on the three younger fire sites that remain dominated by shrubs after as much as fifty seven years.

It would appear from the occurrence of the shrub domination period on each fire site that stand-replacing fire was followed by a traditional type of ecological succession. However, concurrent with the domination of shrubs on the three younger sites was the emergence of all of the tree species found on the Angora Ridge, indicating that all species that exist in the mature forest community are present early after the fire. Also contradicting the possibility of traditional forest succession, the average age of mature fir and pine were approximately the same on both the Angora Ridge and Cathedral Creek fire areas (the only two fire sites with sufficient canopy development to measure average stand age). This indicates that the post-fire period served as a

recruitment event for both genera, and that relative species abundance did not appear to follow traditional successional sequence after large fires that usually includes a period of pine domination followed by increasing fir domination (Bock and Bock 1969, Bock, Bock and Hawthorne 1976, Lyon and Stickney 1976, Kercher and Axelrod 1984). It appears that there was no obligatory period of post-fire pine domination in the study areas, and that fir regenerated with as much facility as pine. However, because the recruitment rate of fir is currently much higher on the two older fire sites, the frequency of pine will likely decline without future fire.

The post fire period not only served as a recruitment period for the species that dominated the recent fire sites, but for all of the species that occurred on all fire sites. Three measures of species diversity were used in this study, including species richness, the Shannon diversity index, and evenness. In each of these measurements diversity was significantly lower on the Angora Ridge than any of the other sites. The higher species richness on the more recent fire sites is important in several ways. Most important is that species richness seems to decline as canopy cover increases. In several plots on the Angora Ridge fire site the canopy cover grew so great that shrubs and herbaceous species were completely excluded and the stand became a monoculture of white fir. In addition to the apparent increase in diversity at the community scale, stand-replacing fire also appears to increase diversity at the landscape scale through the introduction of large canopy openings. The habitat heterogeneity caused by these types of canopy gaps have been shown to be important for wildlife.

Accompanying the lower diversity and high stand density on the Angora Ridge was a higher fuel accumulation and a high density of standing dead trees. This result, though not surprising, suggests the probability of another severe fire on the same site.

The impact of these four fires on community composition and structure is significant, and it is safe to assume that stand-replacing fires that occurred prior to fire suppression also had a important impact. However, it is important to note that the community development that occurred on these sites did so with fire suppression fully implemented. Consequently, development after such fires may have been quite different if fire had been a recurring event. This is a particularly important observation in regard to the Angora Ridge where fire has been absent for the unnatural period of one hundred years. Had Angora Ridge experienced regular low intensity fire during that time, it is likely that the results of this study would have been quite different. The stand density would have been lower, the diversity higher, and the fuel kept down to level less likely to support another high-intensity crown fire. Rather than the homogenous stand now present a mosaic of stands of different ages may have developed.

Management Implications

Concern about the ecological condition of the forested lands surrounding Lake Tahoe has been growing in recent years due to the visible decline of a large number of trees. This decline is likely the result of a number of factors, including fire suppression, an extended drought coupled with species conversion from drought tolerant pine to drought susceptible fir, high forest

density, air pollution, and the influence of the Jeffrey pine beetle (*Dendroctonus jeffreyi*), the mountain pine beetle (*D. ponderosae*), the fir engraver (*Scolytus ventralis*) and the pine engraver (*Ips pini*), (Wenz and DeNitto 1983, Williams et. al 1992). The recent bark beetle outbreaks, though these beetles are a natural part of affected ecosystems, have resulted in unprecedented interest and commitment by both private citizens and public agencies toward the development of management policies and goals for the Lake Tahoe Basin forests. The TRPA (Tahoe Regional Planning Agency) Forest Health Consensus Group, which includes private land owners and representatives of public agencies, has concluded that the forests should be managed toward their pre-European state (Swanson 1993, Sweeney 1993). Exactly what the structure and composition of the pre-European forest was has not yet been determined, but it is evident that fire, at least low intensity surface fire, was an important part of this forest.

There is, in fact, already an effort by public land agencies to reintroduce low intensity fire in the Lake Tahoe basin. The California Department of Parks and Recreation has been conducting a prescribed burning program including 25 to 100 acres a year of under-burning at parks in the Lake Tahoe area with the goal of reducing fire hazard and enhancing wildlife habitat (Rice 1988 and 1990, Walker 1992). The USDA-Forest Service has also been involved in 200-900 acres per year of machine and hard-pile burning for fuel reduction on the federal lands they manage (Swanson 1993). Stand-replacing fire, however, has not been considered. Together with low-intensity surface fires, high intensity stand-replacing fires were probably instrumental in the

formation of large canopy openings, and the maintenance of habitat heterogeneity and species diversity.

In addition to its ecological importance, fire needs to be considered due to its inevitability. It appears that the structural changes that have occurred in fire type communities since the implementation of fire suppression are resulting in a new fire regime. Where small low-intensity surface fire used to predominate, large crown fires are becoming the most frequent fire type. The goal of fire suppression is to protect human life and property, yet it seems to be having the opposite effect. The fires that occur in the Sierra Nevada today, as a result of high fuel loads, are increasingly catastrophic. An example is the 22,500 acre Cleveland fire that occurred in the summer of 1992.

Including stand-replacing fire as a part of the forest management plan in an urbanizing region would likely be unpopular socially and politically, and difficult to implement. However, the possibility should be considered. Suppression of all stand-replacing fires, in the long run, may be more costly, in terms of property and lives, than their careful management.

Future Research

Including stand-replacing fire in future forest management plans will require a more extensive understanding of its ecological effects, its history, and its control. This study focused on only four fires which all occurred in similar vegetation types with analogous abiotic parameters. In order to construct a useful model of the ecological effects of stand-replacing fire in the Sierra Nevada studies such as this should be carried out in as broad a range of vegetation types as possible. A comprehensive history of stand-replacing fire

is also necessary in order to compare current fire sizes and intervals to those that occurred prior to systematic fire suppression implementation.

This study was intended to establish the importance of stand-replacing fire with the hope that it will be considered in the management of the forests of the Sierra Nevada. Fire has been a part of these forests since their formation and will remain so. The attempt to remove fire entirely has been futile resulting only in a change in the fire regime. Rather than attempting to eliminate fire it should be the goal of public agencies to manage it. Human beings must learn to build around such natural processes such as these rather than attempting to control them.

LIST OF REFERENCES

- Abagov, R. 1982. Species diversity and phasing of disturbance. Ecology 63: 289- 293.
- Agee, J. K. 1974. Environmental Impacts from Fire Management Alternatives. Nat. Park Serv., Western Regional Office, San Francisco, Ca.
- Agee, J. K., R. H. Wakimoto, and H. H. Biswell. 1978. Fire and fuel dynamics of Sierra Nevada conifers. Forest. Ecol. and Manage. 1:255-265.
- Ahlgren, C. E. 1974. Effects of fires on temperate forests: north central United States. In: Fire and Ecosystems. T. T. Kozawski and C. E. Ahlgren (eds.). Academic Press, New York, pp. 195-223.
- Anderson, M. K. 1990. California Indian horticulture. Fremontia 1990:7-14.
- Archibold, O. W. 1989. Seed banks and vegetation processes in coniferous forests. In: Ecology of Soil Seed Banks. M. A. Leck, V. T. Parker, and R. L. Simpson (eds.). Academic Press, New York.
- Arno, S. F. and K. M. Sneek. 1977. A method for determining fire history in coniferous forests of the mountain west. USDA For. Serv. Gen. Tech. Rep. INT 42.

- Aschmann, H. 1977. Aboriginal use of fire. In: proc., symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-3.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. Ecology, 73:1879-1887.
- Barrett, S. W. 1980. Indian fires in the pre-settlement forests of western Montana. In: Proceedings of the Fire History Workshop. USDA For. Serv. Gen. Tech. Rep. RM-81.
- Barrett, S. W. and S. Arno. 1982. Indian fires as an ecological influence in the northern Rockies. J. For. 80: 647-651.
- Bazzaz, F. A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. In: Disturbance and Ecosystems, Components of Response. H. A. Mooney and M. Gordon (eds.). Springer-Verlag, New York.
- Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. J. Veg. Sci. 3:187-200
- Biswell, H. H. 1959. Man and fire in the ponderosa pine in the Sierra Nevada of California. Sierra Club Bull. 44: 44-53.
- Biswell, H. H. 1963. Research in wildland fire management in California. Proc. Tall Timbers Fire Ecology Conf. 2:63-97.
- Blonski, K. S. and J. L. Schramel. 1981. Photo series for quantifying natural forest residues: southern Cascades, northern Sierra Nevada. USDA For. Ser. Gen. Tech. Rep. PSW-56.

- Bock, J. H. and C. E. Bock 1969. Natural reforestation in the northern Sierra Nevada-Donner Ridge burn. Proc. Tall Timbers Fire Ecology Conf. 9:119-129.
- Bock, J. H., C. E. Bock, and V. M. Hawthorne. 1976. Further studies of natural reforestation in the Donner Ridge burn. Proc. Tall Timber Fire Ecology Conf. 14:195-200.
- Bork, J. L. 1984. Fire History in Three Vegetation Types on the Eastern Side of the Oregon Cascades. PhD Thesis, Oregon State University.
- Boyce, J. S. 1920. The dry rot of incense cedar. U. S. Dept. Agric. Bul. 871.
- Boyce, J. S. 1921. Fire scars and decay. The Timberman 22(6):37
- Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. In: The Ecology of Natural Disturbance and Patch Dynamics. S. T. A. Pickett and P. S. White (eds.) Academic Press, Orlando, Florida.
- Carro, K. 1992. Fire effects on the vegetation of the Lake Tahoe Basin. USDA For. Serv., Lake Tahoe Basin Management Unit.
- Cattelino, P. J., I. R. Noble, R. O. Slayter, and S. R. Kessell. 1979. Predicting the multiple pathways of plant succession. Env. Mange. 3:41-50.
- Chapman, H. H. 1932. Is the longleaf type a climax? Ecology 13:328-34.

- Christensen, N. L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31:27-44.
- Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. In: The Ecology of Natural Disturbance and Patch Dynamics. S. T. A. Pickett and P. S. White (eds.) pp. 86-99. Academic Press, Orlando, Florida.
- Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Carnegie Inst. Washington Publ. No. 242.
- Clements, F. E. 1936. Nature and structure of the climax. J. Ecol. 24: 552-584.
- Conard, S. G., and S. R. Radosevich. 1982. Post fire succession in white fir (*Abies concolor*) vegetation of the northern Sierra Nevada. Madroño 29:42-56.
- Connell, J. H., and Orias, E. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399-414.
- Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: The Ecology of Natural Disturbance and Patch Dynamics. S. T. A. Pickett and P. S. White (eds.) Academic Press, Orlando, Florida.
- Craven, B. 1993. Fallen Leaf Lake. Personal communication.
- Curtis, J. P. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest boarder region of Wisconsin. Ecology 32:476-496.

- Cwynar, L. 1987. Fire and the forest history of the north Cascade range. Ecology 68:791-800.
- Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Sci. 33:43-64.
- Daubenmire, R. F. 1966. Vegetation: Identification of typical communities. Science 151: 291-298.
- Daubenmire, R. F. 1968. Plant communities: A textbook of plant synecology. Harper & Row, New York.
- DeBenedetti, S. H. and D. J. Parsons. 1979. Natural fire in subalpine meadows: A case description from the Sierra Nevada. J. of For. 77:477-479.
- Dietrich, J. H. 1983. Fire history of southwestern mixed conifer: A case study. For. Ecol. Manage. 6:13-31.
- Dunn, P. H., and L. F. DeBano. 1977. Fires effect on biological and chemical properties of chaparral soils. In: H. A. Mooney and C. E. Conrad (tech. coord.) Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Gen. Tech. Report WO-3.
- Eargle, D. 1986. The Earth is Our Mother: Guide to the Indians of California; Their Locals and Historic Sites. Trees Company Press, Los Angeles, CA.
- Edlund, E. G. and R. Byrne. 1990. Climate, fire, and late quaternary vegetation change in the central Sierra Nevada. In: Proc., Symposium on Fire and the Environment: Ecological and Cultural Perspectives. USDA For. Serv. Gen. Tech. Rep. SE-69.

- Elfring, C. 1988. Yellowstone: fire storm over fire management. Bioscience, 39:667-672.
- Fuller, M. 1991. Forest Fires: An Introduction to Wildland Fire Behavior, Management, Firefighting, and Prevention. John Wiley and sons, New York, New York.
- Gaines, E. M., H. R. Kallander, and J. W. Wagner. 1958. Controlled burning in southwestern ponderosa pine: results from the Blue Mountain plots, Fort Apache Indian Reservation. Journal of Forestry 56:323-327.
- Gill, A. M. 1981 a. Adaptive responses of Australian vascular plant species to fires. In: A. M. Gill, R. H. Groves, and I. R. Noble (eds.) Fire and the Australian Biota. Aust. Acad. Sci., Canberra, Austr., pp. 243-271.
- Gill, A. M. 1981 b. Fire adaptive traits of vascular plants. In: H. A. Mooney et al (tech. coord.) Fire regimes and Ecosystem Properties, USDA For. Serv. Gen. Tech. Rep. WO-26., pp. 208-230.
- Givnish, T. J. 1981. Serotiny, geography, and fire in the pine barrens of New Jersey. Evolution 35:101-123.
- Gleason, H. A. 1926. The individualistic concept of the plant association. Torry Bot. Club Bull. 53: 7-26.
- Graumlich, L. J. 1993. A 100-year record of temperature and precipitation in the Sierra Nevada. Quaternary Research 39:249-255.

- Greenlee, J. M. 1983. Vegetation, Fire History, and Fire Potential of Big Basin Redwoods State Park, California. Dissertation, University of California Santa Cruz.
- Greenlee, J. M. and J. H. Langenheim. 1990. Historic fire regimes and their relation to vegetation patterns in the Monterey Bay area of California. Am. Midl. Nat. 124: 239-253.
- Gruell, G. E. 1985. Fire on the early western landscape: An annotated record of wildland fires 1776-1900. Northwest Sci. 59:97-107.
- Gwinn, M. H. 1993. Fallen Leaf Lake. Personal communication.
- Hartesveldt, R. J., and H. T. Harvey. 1968. The fire ecology of Sequoia regeneration. Proc. Tall Timbers Fire Ecology Conf. 7:65-77
- Harvey, H. Thomas, Howard S. Shellhammer, Ronald E. Stecker. 1980. Giant Sequoia Ecology; Fire and Reproduction. Scientific Monograph Series No. 12. U. S. National Park Service.
- Heiselman, Miron L. 1978. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. Proc., Fire Regimes and Ecosystem Properties Conf. USDA For. Serv. Gen. Tech. Rep. WO-26.
- Hendrickson, William H. 1972. Perspective on fire and ecosystems in the United States. Fire in the Environment Symposium Proc. 1972: 29-33.
- Hildinger, J. 1993. Angora Lakes Resort. Personal communication.

- Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113: 81-101.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology 52:571-577.
- Johnson, M. 1993. USDA Forest Service, Lake Tahoe Basin Management Unit. Personal communication.
- Kauffman, J. B. and R. E. Martin 1989. Fire behavior, fuel consumption, and forest floor changes following prescribed understory fires in Sierra mixed conifer forests. Can. J. For. Res. 19(4):455-462.
- Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. Bot. Rev. 57: 81-116.
- Keeley, J. E., and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: A comparison of sprouting and seeding strategies. Amer. Midl. Natur. 99:142-161.
- Kelly, V. R. and V. T. Parker. 1990. Seed bank survival and dynamics in sprouting and nonsprouting *Arctostaphylos* species. Am. Midl. Nat. 124:114-123.
- Kercher, J. R. and M. C. Axelrod. 1984. A process model of fire ecology and succession in a mixed conifer forest. Ecology, 60:129-142.
- Kilgore, B. M. 1973. Impact of prescribed burning on a Sequoia-mixed conifer forest. Proc. Tall Timbers Fire Ecology Conf. 12:345-375.

- Kilgore, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands." In: Mooney, H.A., et al (tech. coords.). Fire regimes and ecosystem properties. USDA Gen. Tech. Rep. WO-26, pp. 58-89.
- Kilgore, B. M. and D. Taylor. 1979. Fire history of a Sequoia-mixed conifer forest. Ecology, 60:126-142.
- Krebs, C. J. 1972. Ecology: The Experimental Analysis of Distribution and Abundance. Harper and Row, New York.
- Ledig, F. T. and J. H. Fryer. 1971. A pocket of variability in *Pinus rigida*. Evolution, 26:259-266.
- Lotan, J. E. 1975. The role of cone serotiny in lodgepole pine forests." In D. M. Baumgartner (ed.) Management of Lodgepole Pine Ecosystems Symposium Proceedings. Wash. State Univ. Coop. Ext. Serv., Pullman, pp. 471-495.
- Lunan, J. S. and J. R. Habeck. 1973. The effects of fire exclusion on ponderosa pine communities in Glacier National Park, Montana. Can J. For. Res. 3:574-579.
- Lyon, L. Jack and P. F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. Proc. Tall Timbers Fire Ecology Conf. 14:355-375.
- Mehring, P., S. Arno, and K. Peterson. 1977. Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains Montana. Arctic and Alpine Res. 9:345-368.
- Minnich, R. A. 1983. Fire mosaics in Southern California and northern Baja California. Science 219:1287-1294.

- Minnich, R. A. 1989. Chaparral fire history in San Diego county and adjacent Baja California: An evaluation of natural fire regimes and the effect of suppression management, pp. 37-47. In: S. C. Keeley (ed.) The California Chaparral: paradigms reexamined. No. 34, Nat. Hist. Mus., L. A. Co.
- Muir, J. 1894. The Mountains of California. Doubleday, Garden City, New York.
- Murray, M. 1992. Suppression threatens subalpine meadows. Inner Voice 4(2):10.
- Mutch, R. W. 1970. Wildland fires and ecosystems - a hypothesis. Ecology, 51:1046-1051.
- Noble, I. R., and Slatyer, R. O. 1977. Post-Fire Succession of Plants in Mediterranean Ecosystems. USDA Forest Service Gen. Tech. Rep. WO-3, 27-36.
- O'Leary, John F. 1990. Post fire diversity patterns in two subassociations of California coastal sage scrub. J. Veg. Sci. 1:173-180.
- Old, S. 1969. Microclimate, fire and plant production in an Illinois prairie. Ecol. Monogr. 39: 355-384.
- Parker, V. T. and V. R. Kelly. 1989. Seed banks in chaparral and other mediterranean climate shrublands. In: Ecology of Soil Seed Banks. Academic Press, New York.
- Parsons, D. J., and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed conifer forest. For. Ecol. Manage. 2:21-33.

- Patil, G. P., and C. Taillie. 1982. Diversity as a concept and its measurements. J. Amer. Stat. Assoc. 77:548-561.
- Peattie, D. C. 1953. A Natural History of Western Trees. Bonanza Books, New York.
- Phillips, D. L. and D. J. Shure. 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology 71: 204-212.
- Pickett, S. T. A. and P. S. White 1985. Natural disturbance and patch dynamics: An introduction. In: The Ecology of Natural Disturbance and Patch Dynamics. (S. T. A. Pickett and P. S. White, eds.), pp. 3-9 . Academic Press, Orlando, Florida.
- Pielou, E. C. 1975. Ecological Diversity. John Wiley and Sons, New York, New York.
- Pyne, S. J. 1982. Fire in America. Princeton University Press, Princeton, N.J.
- Pyne, S. J. 1992. Feeding the flame: rethinking the role of fire. Inner Voice 4(2):1-3.
- Rice, K. J. 1989. Impacts of seedbanks on grassland community structure and population dynamics. In: Ecology of Soil Seed Banks. M. A. Leck, V. T. Parker and R. L. Simpson. Academic Press, New York.
- Rice, C. L. 1990. Fire history of the Sierra District of the California Department of Parks and Recreation. Wildland Resource Management, Walnut Creek, CA.

- Romme, W. 1980. Fire history terminology: Report to the ad hoc committee. In: Proceedings of the fire history workshop, October 20-24, 1980, Tuscon, Arizona. USDA Gen. Tech. Rep. RM-81.
- Rowe, J. S. 1983. Concepts of fire effects on individuals and species. In: The Role of Fire in Northern Circumpolar Ecosystems, R. W. Wein and D. A. MacLean, (eds.), pp. 135-154. Wiley, New York.
- Rundel, P. W., and D. J. Parsons. 1984. Post-fire uptake of nutrients by diverse ephemeral herbs in chamise chaparral. Oecologia 61:285-288.
- Scott, E. B. 1973. The Saga of Lake Tahoe, Vol II. Sierra-Tahoe Publ. Co. South Lake Tahoe , CA..
- Show, S. B. and E. I. Kotock. 1924. The Role of Fire in the California Pine Forests. USDA Bulletin 1294. Washington D.C.
- Smith, R. L. 1992. Elements of Ecology. Harper Collins publ.
- Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: What is 'natural' vegetation in a changing environment? Biol. Conserv. 58:1-18.
- Stephenson, N. L., D. J. Parsons, and T. W. Swetnam. 1991. Restoring natural fire to the sequoia-mixed conifer forest: should intense fire play a role? Proc. Tall Timbers Fire Ecol. Conf. 17:321-337
- Swanson, J. 1993. USDA Forest Service, Lake Tahoe Basin Management Unit. Personal communication.

- Sweeney, J. R. 1968. Ecology of some 'fire type' vegetation in northern California. Proc. Tall Timbers Fire Ecol. Conf. 7:110-125
- Sweeney, J. R. 1993. Incline Village, Nevada. Personal communication.
- Tansley, A. G. 1939. The British Islands and Their Vegetation. Cambridge University Press, Cambridge.
- The American Heritage Dictionary. 1990. Houghton Mifflin Company.
- USDA Forest Service Aerial Photos, courtesy of Lake Tahoe Basin Management Unit U. S. Forest Service, South Lake Tahoe, Calif.
- Wagener, W. 1961. Past Fire Incidence in the Sierra Nevada Forests. J. For. 59:739-747.
- Wagle, R. F. and T. W. Eakle. 1979. A controlled burn reduces the impact of a subsequent wildfire in a ponderosa pine vegetation type. Forest Sci. 25: 123-129.
- Walker, G. 1992. Prescribed Burn Plan; Sugar Pine Point State Park. California Dept. of Parks and Rec.
- Weaver, H. 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. J. For. 49:93-98.
- Weaver, H. 1967. Fire and its relationship to ponderosa pine. Proc. Tall Timbers Fire Ecol. Conf. 7:147-149.
- Weaver, H. 1974. Effects of fire on temperate forests: western United States. In: Fire and Ecosystems. T. T. Kozlowski and C. G. Ahlgren (eds.). Academic Press, New York.

- Wells, P. V. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23: 264-267.
- Wenz, J. and G. DeNitto. 1983. Evaluation of pest conditions in the Kiva/Taylor Creek Visitor Center Recreation Areas on the Lake Tahoe Management Unit. USDA For. Serv. For. Pest Manag. Rep. No. PSW 83-06.
- White, P. S. and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. In: Natural Disturbance and Patch Dynamics. S. T. A. Pickett and P. S. White (eds.). Academic Press, Orlando, Florida.
- Whimore, T. C. 1989. Canopy gaps and the two major groups of forest trees. Ecology 70:536-538.
- Whitney, S. 1979. The Sierra Nevada; a Sierra Club Naturalist's Guide. Sierra Club Books.
- Whittaker, R. H. 1953. A consideration of climax theory: The climax as a population and pattern. Ecol. Monogr. 23:41-78.
- Williams, C. B. , D. L. Azuma, G. T. Ferrel. 1992. Incidence and effects of endemic populations of forest pests in young mixed conifer forests of the Sierra Nevada. USDA For. Serv. Res. Paper. PSW-RP-212.
- Wright, H. A., A. W. Bailey. 1982. Fire Ecology, United States and Southern Canada. John Wiley and Sons publ.

**APPENDIX
MAPS OF STUDY SITE LOCATIONS**

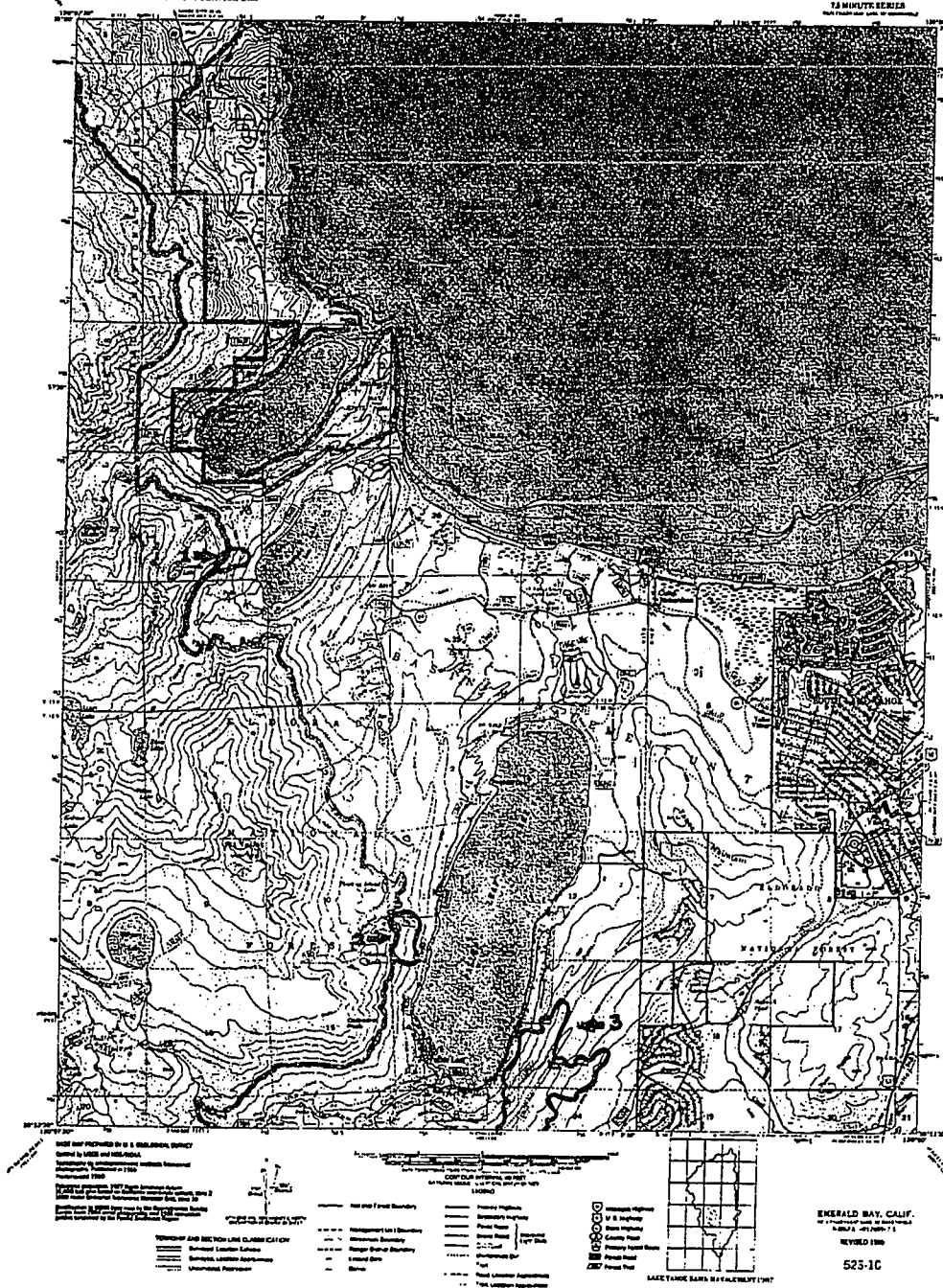
Emerald Bay Quadrangle:

1. The Cascade Lake fire. This fire burned in 1978, and covered approximately 16 acres.
2. The Cathedral Creek fire. This fire burned in 1937, and covered approximately 250 acres.
3. The Angora Ridge fire. This fire burned approximately 100 years ago, and covered 250 acres.

Echo Lake Quadrangle:

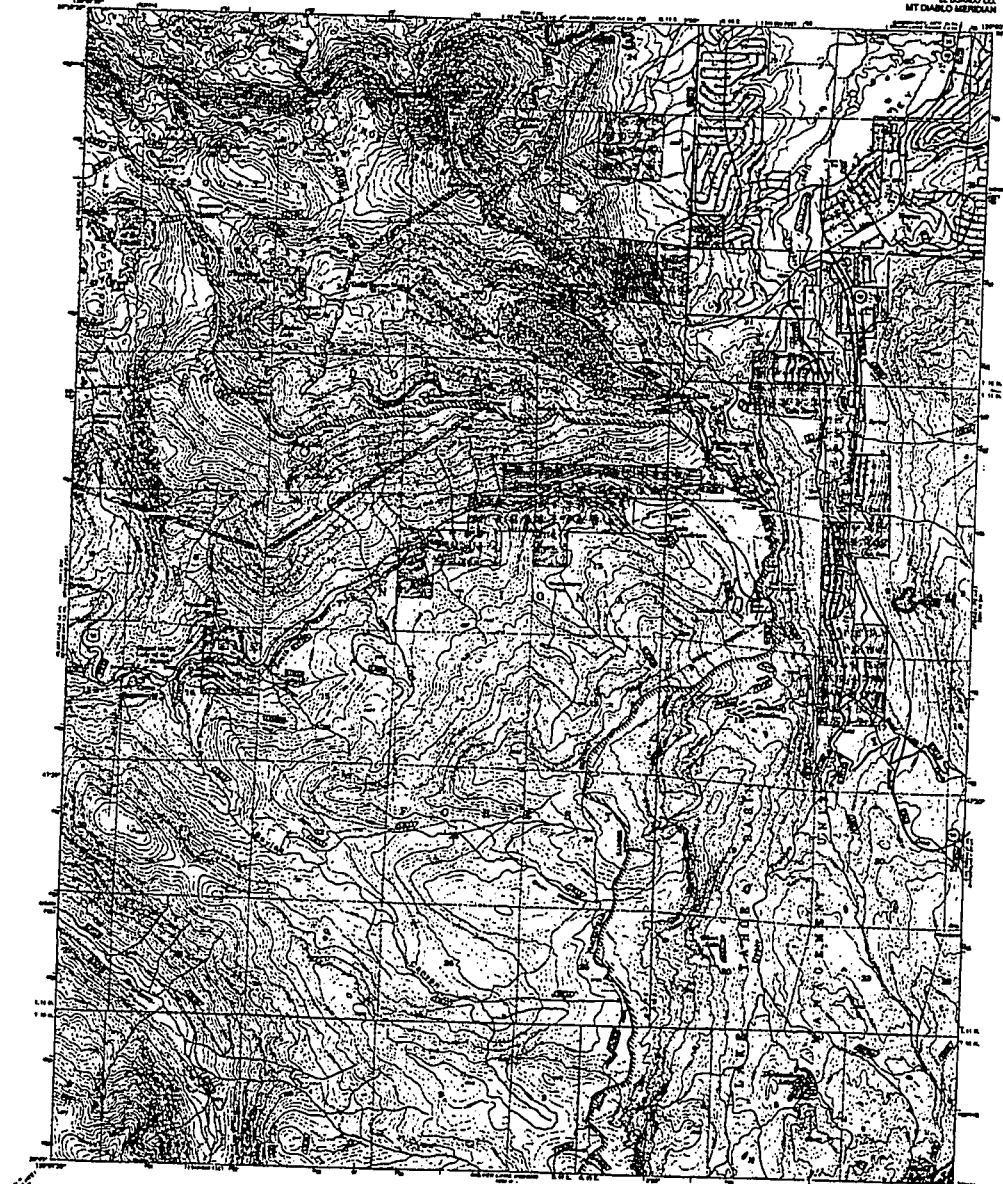
3. The Angora Ridge fire. This fire burned approximately 100 years ago, and covered 250 acres.
4. The Luther fire. This fire burned in 1987, and burned approximately 20 acres.

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- | | |
|---|---|
| <p>— Boundary Line</p> <p>— Contour Line</p> <p>— Road</p> <p>— Stream</p> <p>— Well</p> <p>— Elevation</p> <p>— Spot Elevation</p> <p>— Section Line</p> <p>— Township and Range</p> <p>— Meridian</p> <p>— Township and Range</p> <p>— Meridian</p> <p>— Township and Range</p> <p>— Meridian</p> | <p>— Boundary Line</p> <p>— Contour Line</p> <p>— Road</p> <p>— Stream</p> <p>— Well</p> <p>— Elevation</p> <p>— Spot Elevation</p> <p>— Section Line</p> <p>— Township and Range</p> <p>— Meridian</p> <p>— Township and Range</p> <p>— Meridian</p> <p>— Township and Range</p> <p>— Meridian</p> |
|---|---|



PHOTOGRAPHIC SURVEY MAP
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