

AN ABSTRACT OF THE THESIS OF

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Title: Plant Community Recovery after High Severity Wildfire and Post-fire Management in the Klamath Region.

Abstract approved:

David E. Hibbs

Disturbance and microclimate interact to play a central role influencing the composition and structure of plant communities. In this thesis, I examined plant community composition and structure twenty years after high severity wildfires with and without post-fire management (salvage logging, fuel treatment, tree planting, and shrub release) under contrasting microclimatic conditions in the Klamath region of northern California. The general distribution of cover among the main life form groups: shrubs, hardwoods, and conifers, was similar between unmanaged and managed sites. The abundance of key species within each group, however, changed as a result of post-fire management. *Ceanothus integerrimus* and *Pinus ponderosa* responded positively to post-fire management, while *Arctostaphylos viscida* responded negatively. At the community level, a general pattern was a reduction of heterogeneity in managed sites in terms of both vertical structure and species composition. Based on regeneration strategies after fire, species were assigned to three regeneration behavior groups or regenerative traits, reflecting, in part, responses to disturbance. Strong positive correlations were found between species that regenerate from the seed bank and increasing levels of

heat load. Positive interactions were also found between post-fire management and aspect with the abundance of N-fixing *Ceanothus* spp., which increased in abundance on managed sites on south aspects.

In a second study, I evaluated tree composition in the same areas. Aspect and elevation were important factors controlling conifer and hardwood composition. No effect of post-fire management was detected on composition. Frequency and density of conifers were higher on north aspects relative to south aspects. Post-fire management had no significant effect on density of conifer species; however, results suggested a positive effect of post-fire management on *Pinus ponderosa*'s density on south aspects. Conifer frequency was higher on managed sites relative to unmanaged sites. These results suggest that post-fire management did not change the number of conifers but increased their spatial evenness on the sites.

Results from these studies suggest that post-fire management changed composition and structure of the early seral communities under study. Furthermore, these results suggest that post-fire management effects on plant communities were strongest on warmer, drier aspects.

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Plant Community Recovery after High Severity Wildfire and Post-fire
Management in the Klamath Region

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Maria Jose Lopez Ortiz, Author

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CONTRIBUTION OF AUTHORS

Dr. David Hibbs assisted in the study design, implementation, analysis, writing, and interpretation in Chapters 1 through 4.

Jeff Shatford assisted with data collection, analysis, writing, and interpretation in Chapters 1 through 4.

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CHAPTER 1- INTRODUCTION

Disturbances play a central role in the composition and structure of plant communities (Sousa 1984, Pickett and White 1985). Over the last decades, our knowledge about disturbance and its effect on plant community composition and structure have come from the study of large disturbance events such as wildfires, wind blows, insect outbreaks, and floods. One of the many insights that the study of these disturbances has brought to plant community ecology is the recognition that disturbances are important elements in the dynamics of plant communities (Sousa 1984, Pickett and White 1985). Furthermore, that plant communities experience repeated disturbances (Turner et al. 1998; Kulakowski and Veblen 2002; Kulakowski et al. 2003). Little is known, however, about the effects of repeated disturbances on plant community composition and structure. The main objective of this thesis was to examine changes in plant community composition and structure due to repeated disturbances, high severity wildfires alone and followed by post-fire management.

The studies presented in this thesis have been carried out in the Douglas-fir (*Pseudotsuga menziesii*) vegetation series of the Klamath region of northern California, a region that has been recognized by its diversity in vegetation and topographic patterns (Whittaker 1960, Atzet et al. 1992, Strittholt et al. 1999). The Douglas-fir series, as described by Atzet et al. (1992), is the most common series on inland sites. The series ranges in elevation from 200 to 2000 m. It occurs on all aspects and on slopes from zero to 120 percent. Changes in elevation and aspect, related with the rugged topography that characterizes the region, influence the composition and structure of plant communities (Whittaker 1960).

The structure and composition of plant communities in the region have also been shaped by recurrent fires (Taylor and Skinner 1998, 2003, Skinner et al. 2006). Historically, most large wildfires have burned at low and moderate

severities with smaller patches burning at high severity (Wills and Stuart 1994, Taylor and Skinner 1998, 2003, Odion et al. 2004, Skinner et al. 2006). The variable fire severity has created highly variable stand structures (Wills and Stuart 1994, Taylor and Skinner 1998). In recent times, when large areas have been affected by high severity fires, however, a major concern has been the ability of these areas to regenerate and recover to pre-fire conditions without human intervention (Reider 1988, Rice and Chaney 1989, Holder 1990). As a result, post-fire management has become a common practice throughout the region for the past forty years (Holder 1990, McIver and Starr 2001, Beschta et al. 2004). From an ecological perspective, perhaps one of the most important factors in examining post-fire management effects is the reality that such activities involve repeated disturbances; the fire and the subsequent management activities (Lindenmayer 2006).

To address not only the possible effects of repeated disturbances on plant community composition and structure but also the underlying patterns of species distribution driven by aspect that characterize the region, this thesis has been organized into four chapters of which this introduction is the first. Chapters 2 and 3 are presented in the basic manuscript format, both with their own introduction, methods, and discussion sections. Chapter 2 focuses on the whole plant community. Each of the major life form groups: shrubs, hardwoods, and conifers is described and used to contrast sites that were managed after high severity fires with sites that were left unmanaged. Additionally in Chapter 2, the responses of species with different regenerative traits to the microclimate of the sites and to disturbance are analyzed. Such an approach enabled me to look at the plant community as a whole before moving on to address individual groups such as conifers and hardwoods.

Conifers and hardwoods are important elements of the composition and structure of the forest in the region. Chapter 3 explores the composition and structure of these two groups twenty years after high severity fires and post-fire

management. The effects of post-fire management activities such as conifer planting on density and frequency of conifers are also addressed in Chapter 3.

Individually, each Chapter examines plant communities and their responses to repeated disturbances under contrasting microclimatic conditions. Collectively, the chapters illustrate the role of disturbances and microclimate on plant community composition and structure. Chapter 4 provides general conclusions and some comments about the possible management implications of these studies.

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CHAPTER 2: PLANT COMMUNITY COMPOSITION AND STRUCTURE TWENTY YEARS AFTER HIGH SEVERITY FIRE AND POST-FIRE MANAGEMENT IN THE KLAMATH REGION.

INTRODUCTION

Fires have been recognized as a major disturbance force in the western United States (Taylor and Skinner 1998), influencing forest structure and species composition (Agee 1993). Fire affects plant communities directly through heat and smoke and indirectly through induced changes in nutrient and light availability (Fites-Kaufman et al. 2006). Plant communities respond to these changes depending on the fire characteristics, the structure and composition of the original plant community, and the microclimate. Although each of these factors will be addressed separately in the following paragraphs, it is important to acknowledge the interactions among them.

Fire frequency and intensity within a specified area influence plant community composition and structure (Fites-Kaufman et al. 2006). Fire frequency is a measurement of temporal attributes of the fire regime and is usually described in terms of fire return intervals. Fire return interval is the average length of time between fires on a particular area of land (Van Wagendonk 2006). Fire intensity is a description of the energy release pattern and is usually measured as the amount of energy (heat) per unit length of fire front. Fire intensity is closely related to another common fire attribute, fire severity. Fire severity emphasizes the effect that fire has on the plant communities, especially on the species that characterize the ecosystem (Schmoldt et al. 1999).

The overall response of a plant community to fire is the result of the differences in the fire response of the individual species present. Variation in species responses to fire attributes determines the effect of fire on the community

(Fites-Kaufman et al. 2006). For example, in the case of fire frequency, shorter fire intervals will favor species that depend on fire for germination or species that can survive the fires. On the other hand, longer fire intervals will tend to favor species whose germination is not stimulated by fire (fire-inhibited species). Because fire intensity varies inversely with frequency, high intensity fires will favor a different array of plant species than low intensity fires.

As with any disturbance, fire rarely erases all components of the original plant community. Rather, fire leaves traces or features of the original vegetation in form of biological legacies (Hansen et al. 1991, Foster et al. 1998, Lindenmayer and McCarthy 2002). Snags, buried seeds, buds, and surviving organisms constitute examples of biological legacies after fire. These biological legacies are important not only for wildlife habitat, nutrient dynamics, and ecosystem function (Harmon et al. 1986) but also have an influence on the post-fire plant community composition and structure (Turner et al. 1998, Lindenmayer and Franklin 2002). After fires in the Klamath region, for example, the initial plant community is often dominated by species whose germination is stimulated by fire such as *Ceanothus* spp. and *Arctostaphylos* spp. (Keeley 1987), while the tree component of the community is usually dominated by hardwood species that are able to resprout (Hobbs et al. 1992).

The factors mentioned above act together rather than in isolation to influence post-fire plant community composition and structure. At the same time, the interactions among fire characteristics and vegetation are also influenced by the microclimate. At the local scale at higher latitudes, for example, slope and aspect contribute to different microclimatic conditions. Slope and aspect affect the amount of daily cycle of solar radiation at different times of the year, thus having an influence on air temperature, humidity, and soil moisture (Rosenberg et al. 1983). Differences in microclimate caused by differences in aspect influence not only plant community composition (Small and McCarthy 2002, Keeley et al.

2005) but also the frequency of major disturbances such as fire (Taylor and Skinner 1998, 2003).

In diverse fire-prone ecosystems such as the Klamath region, the relationships among fire, vegetation patterns, and microclimate have long been recognized (Whittaker 1960, Taylor and Skinner 1998, 2003, Skinner et al. 2006). After stand replacing fires on Federal lands, however, a common assumption has been that immediate actions are needed to stabilize, rehabilitate or restore the fire-damage landscape. As a result, post-fire management has been a common practice throughout the region for the past forty years (Holder 1990, McIver and Starr 2001, Beschta et al. 2004). From an ecological perspective, perhaps one of the most important factors in examining post-fire management effects is the reality that such activities involve at least two (and sometimes more) kinds of disturbances; the fire and the subsequent management activities (Lindenmayer 2006).

As separate disturbances, both wildfires and management are expected to have different impacts on vegetation (Nguyen-Xuan et al. 2000, Lindenmayer and McCarthy 2002) due, in part, to differences on the structure and presence of biological legacies (Foster et al. 1998, Lindenmayer and McCarthy 2002, Larson and Franklin 2005). Stand replacing fires increase the number of snags (Spies et al. 1988) and cause changes in plant diversity increasing the abundance of species whose germination is stimulated by fires (Keeley 1977, Halpern 1989). In contrast, management activities such as logging decrease the number of snags (Saab and Dudley 1998, Saab et al. 2007) and favor a different array of species, not necessarily those whose germination is stimulated by fire (Halpern 1989).

In the case of wildfire following management activities, there may be additive or cumulative effects that are more substantial than either a single fire event alone or traditional management in isolation (Lindenmayer 2006). However, little information is available on the effect that the combination of these two different disturbances may have on plant communities. McIver and Starr

(2001) found only 21 studies worldwide that have examined the environmental effects of post-fire logging. In particular, few studies have explored the extent to which wildfires followed by post-fire management affect plant communities and most of them have focused on the first two or three years after the fires (however, see Stuart et al. 1993). Furthermore, no information is available on the effects of these disturbances on plant community composition and structure under different microclimatic conditions within the same region.

Due to the complex interactions among plant species, disturbance characteristics, and the microenvironment, generalizations about the effects of fires or post-fire management on plant community composition and structure are not easy to achieve. However, several authors have proposed that the use of a trait-based classification instead of a species-based system would facilitate the interpretation of these complex interactions (Halpern 1989, McIntyre et al. 1999b, Lavorel and Garnier 2002, Pausas et al. 2004, Vesik et al. 2004, McGill et al. 2006). A classification scheme based on traits has been defined as groups of plants species sharing similar responses to environmental factors or disturbances (McIntyre et al. 1999a). In the case of disturbances such as fire, a major dichotomy in responses exists between species that are able to survive fires by resprouting from above or underground structures and those that are killed by the fire and rely on seeds stored in the canopy or in soil banks for persistence (Lavorel 1999, Lloret et al. 2005, Fites-Kaufman et al. 2006).

In this study, we present descriptions of the post-fire plant community composition and structure twenty years after high severity fires and more than thirteen years after post-fire management, under contrasting microclimatic conditions, in the Klamath Mountains. This description is meant to increase knowledge about plant community composition and structure beyond the first decade after stand replacing fires and post-fire management. Along with this description, we compare plant community composition and structure among sites that experienced high severity fire alone and sites that also experienced

subsequent disturbances (post-fire management). We hypothesized that many of the plant compositional differences observed would be associated with the types of disturbance and the microclimate of the sites. We supplement the observations from this study with published accounts of species life history traits and responses to fire to explain their dynamics after disturbances.

Specifically, we address the following questions: 1) after fire, does a subsequent disturbance (post-fire management) change the plant community composition? 2) If so, does the impact of a second disturbance differ with different micro-environment characteristics? 3) Does a second disturbance shift the abundance of species with different regenerative traits?

METHODS

Study Area

The Klamath Mountains bioregion of northwestern California and southwestern Oregon covers an area of approximately 22,500 km² (Skinner et al. 2006). It extends from the Cascade Range in the east to the Coast Range in the west, and from north to south for about 390 km (Whittaker 1960, Strothmann and Roy 1984, Hobbs et al. 1992, Strittholt et al. 1999). The Klamath Mountains are the result of a great mass of ancient, closely folded and faulted rocks, generally metamorphosed, and intruded by igneous rocks. The terrain is rugged and deeply incised with narrow V-shaped canyons (Palazzi et al. 1992). The varied locations and topography of the region exhibit a wide range of macro- and micro-climatic conditions (Whittaker 1960). The climate of the bioregion is broadly characterized by mild wet winters and dry summers. The duration of the wet and dry seasons, as well as the total annual precipitation, is spatially highly variable due to a strong west-to-east moisture and temperature gradient caused by proximity to the Pacific Ocean (Whittaker 1960, Skinner et al. 2006). At the local level, the microclimate is strongly influenced by topography. South-facing slopes generally experience higher temperature and light intensity and lower soil

moisture than north-facing slopes, producing differences in plant community composition (Whittaker 1960).

The Klamath Mountains are an area of exceptional floristic diversity and complexity in vegetative patterns (Whittaker 1960, Strittholt and Dellasala 2001). Various authors have classified the vegetation of the bioregion based on elevation (Whittaker 1960, Atzet et al. 1992, Skinner et al. 2006), soils (Whittaker 1960), distance to the coast (Atzet and Wheeler 1982, Atzet et al. 1992), and fire environment (Atzet and Wheeler 1982, Skinner et al. 2006). The region has been described as composed of at least 16 vegetation series (Atzet and Wheeler 1982). The most common series are the white fir (*Abies concolor*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), tanoak (*Lithocarpus densiflorus*), and mountain hemlock (*Tsuga mertensiana*) series.

This study focuses on the Douglas-fir series which ranges in elevation from 200 to 2000 m. It occurs on all aspects and on slopes from zero to 120 percent (Atzet et al. 1992). Precipitation ranges from about 1100 mm to 2000 mm; 90% of precipitation falls between October and May. The average July temperature for Happy Camp, in the center of the study area, 330 m in elevation, is 25.7°C. Fire has been a common disturbance in the study area. Taylor and Skinner (1998) reported median historic fire return intervals (FRIs) of 12-19 years in the central part of the study area.

Stand composition is variable and strongly influenced by aspect and elevation. At lower elevations on south aspects, Douglas-fir shares dominance with hardwoods such as black oak (*Quercus kelloggii*), white oak (*Quercus garryana*) and canyon live oak (*Quercus chrysolepis*). As moisture increases on north aspects, the dominant hardwoods shift from oaks to Pacific madrone (*Arbutus menziesii*) with tanoak on more mesic sites. At middle and higher elevations, Douglas-fir and white fir are canopy dominants (Whittaker 1960, Sawyer and Keeler-Wolf 1995).

Site Selection

During the last week of August of 1987, lightning started many fires that ultimately burned more than 250,000 ha of California's National Forests. Klamath National Forest accounted for almost 40% (97,466 ha) of the area burned on National Forest lands (Reider 1988, Biswell 1989). The fires burned until they were extinguished by rain or snow in late November. The large area and wide dispersal of these fires resulted in a mosaic of forest types burned under a variety of severity conditions (Weatherspoon and Skinner 1995, Taylor and Skinner 1998). Approximately 12% of the area burned at high severity (Odion et al. 2004) including some old-growth Douglas-fir-dominated forest. During the following years, many areas that burned at high severity were salvage logged and planted (Rieder, 1988; Taylor and Skinner, 1998).

We identified candidate sites among old-growth Douglas-fir-dominated forests that burned at high severity during the 1987 fires. A total of 11 fires in three Ranger Districts of the Klamath National Forest were assessed. Candidate sites were divided into two major groups: sites that were not managed (unmanaged) after the fire and sites that were logged and planted (managed). Sampling in each group was then stratified by aspect. Only north or south aspect sites ($\pm 45^\circ$ from north or south) were considered as candidates; east and west aspects were not sampled. GIS layers of topography, fire severity, and cutting activities since 1970 were overlaid to discriminate unmanaged from managed sites and to determine aspect and elevation. Aerial photographs from 1987 were assessed to confirm that the sites were burned under high severity. For managed sites, stand records were used to identify post-fire management activities. We chose managed sites that presented the most common combination of post-fire management activities: salvage, site preparation, tree planting, and manual shrub release. No additional treatments (e.g. herbicide application) were recorded.

According to stand records, sites were salvage logged within the first three years after the fire (1988 to 1990). Site preparation included felling and slashing, and reburning. Felling and slashing were carried out the same year that logging operations took place. Sites were reburned up to twelve months after salvage and planted the following spring. Thus, seedlings were planted 2-4 years after fire, often with a mixture of 60% Douglas-fir and 40% ponderosa pine (*Pinus ponderosa*) at a ~3x3 m spacing. Shrub release, the cutting of shrubs within a 2 m radius around a conifer seedling, was performed two years after seedlings were planted.

Final assessment of candidate sites was performed *in situ*. At each candidate site, we evaluated presence and diameter of snags (for unmanaged sites), and stumps (for managed sites), soils (non-ultramafic), and aspect (north or south).

Sampling

We sampled vegetation from mid June to September in 2005 and 2006, eighteen to nineteen years after the fires. A total of 62 sites (25 unmanaged and 37 managed) were sampled (Fig. 2.1). Approximately 97% of the sample sites (60 sites) were located in the Happy Camp Ranger District. Two managed sites (1 north aspect and 1 south aspect) were located in the Cave Junction Ranger District. The sampling unit (plot) was randomly located within openings created by high severity fire or high severity fire and post-fire management. The average distance to seed source (unburned forest or unburned conifer tree) at the time of sampling was 88 m (range 20-250 m). We used a 12x40 m plot comprised of 30 cells of 4x4 m. Plot level measurements included elevation, slope, aspect and geographic location (GPS coordinates, ± 20 m). We tallied trees (hardwoods and conifers) by species and measured the diameter at breast height (DBH), total height, and percentage of live crown of the dominant conifers in each cell. To estimate vegetation cover, we divided the plot into thirds. In each third, we

visually estimated percent cover of trees and shrubs by species and forbs, grasses, and ferns as life forms. We used comparison charts to aid in assessing percent cover. To reduce individual bias, two people worked together to estimate cover.

Data Analysis

We described plant community structure of unmanaged and managed sites using the average percent cover, frequency, and average height of the dominant species of each life form group: conifers, hardwoods, and shrubs. Frequency was defined as the percentage of occurrence of the species in a given group (unmanaged north, unmanaged south, managed north, and managed south). Average height of the most abundant species in each group was used to describe the vertical structure of unmanaged and managed sites. Comparison between unmanaged and managed sites was carried out using the following plant community characteristics: 1) cover of life form groups and species diversity, 2) community composition, 3) and abundance of regenerative and functional traits.

Cover of Life Form Groups and Species Diversity

We used two sample t-tests (S-plus V.7) to compare cover of the main life form groups (conifers, hardwoods, shrubs, forbs, grasses, and ferns) between unmanaged and managed sites. Bonferroni correction was used to balance individual and familywise confidence intervals. Three measures of species diversity were used: species richness (total number of species), Simpson's diversity index (Simpson 1949), and the Shannon-Wiener diversity index (MacArthur and MacArthur 1961)

Simpson's diversity index was calculated as

$$[1] D = 1 - \sum_i^S p_i^2$$

where p_i is the proportion of individuals belonging to species i and S is the total number of species. This measure emphasizes common species and is little affected by addition or loss of rare species (McCune and Grace 2002). The Shannon-Wiener index was calculated as

$$[2] H' = -\sum_i^S p_i \ln p_i$$

where p_i is the proportion of individuals belonging to species i . This measure is intermediate between species richness and Simpson's index in its sensitivity to rare species (McCune and Grace 2002). We also reported Whittaker's beta diversity (Whittaker 1972). Whittaker's beta diversity was calculated as

$$[3] \beta_w = \frac{S}{\alpha}$$

where S is the total number of species and α is the average number of species.

Community Composition

We compared community composition between unmanaged and managed sites using Nonmetric Multidimensional Scaling ordination (NMS, Kruskal 1964, Mather 1976). NMS uses an iterative search for an ordination with low stress, as measured by the relationship between ranked distances in the original multidimensional space and the ranked distance in the reduced dimensions of the ordination (McCune and Grace 2002). Ordination of community data benefits from NMS over other ordination techniques by having no assumptions of multivariate normality or linearity, and being robust to large numbers of zero values.

To reduce noise, rare species, those occurring in less than five percent of the plots (less than four plots), were deleted from the data set prior to running NMS. This action left a matrix of 62 plots and 45 species. Small seedlings of

three needled pine, *Pinus* sp., were recorded at the genus level and appeared in 4 plots. The total cover of the *Pinus* sp. across all unmanaged and managed sites was 2% and 0.1% respectively. Removing *Pinus* sp. from the sample did not change the ordination patterns, therefore *Pinus* sp. was removed for the analysis, leaving a matrix of 62 plots and 44 species. Analyses were run using Autopilot in the slow and thorough mode of NMS in PC-ORD version 5 (McCune and Mefford 1999), which used 250 runs with real data and 250 runs with randomized data for a Monte Carlo test of significance. Each NMS ordination used Sørensen's distance, and each began with a different random configuration. The best solution was assessed based on the final minimum stress and the Monte Carlo test. The data were not relativized, allowing differences in the total abundance of species to be expressed in the analysis.

Environmental and treatment variables were related to ordination results using overlay and joint plots. Environmental variables included: elevation, aspect (folded around the north-south line), slope (%), and heat load index. The heat load index represents the amount of heat a site potentially receives and is derived from models based on latitude, slope, and aspect (McCune and Keon 2002). Unmanaged and managed stand types were considered as treatments. For visual clarity, the ordination was rotated to align treatments with the horizontal axis.

Multi-response Permutation Procedure (MRPP, Mielke Jr 1984) was used to test for differences between groups defined by treatment and aspect. MRPP has the advantage of not requiring distributional assumptions such as multivariate normality and homogeneity of variance that are seldom met with ecological community data (McCune and Grace 2002). The tightness of the groups was described with an A statistic, the chance-corrected within-group agreement. When $A = 0$, the groups are no more or less different than expected by chance; when $A = 1$, all sample units are identical within each group.

Association of species within these *a priori* groups was explored with Indicator Species Analysis (ISA, Dufrene and Legendre 1997), combined with a

randomization test for significance using 5000 iterations (Monte Carlo). ISA assigns a value between 0 and 100 (100= perfect indicator). A perfect indicator of a particular group is always present and exclusive to that group.

Traits

To examine plant community assemblages from a traits perspective, the abundance of plant species based on traits was ordinated using a similar NMS approach as described above. The abundance of traits was obtained by multiplying the species abundance matrix by a binary matrix of traits. Each element of the resulting matrix represents the abundance of a specific trait on a given plot. Traits were derived from the life form data base of the USDA Forest Service (<http://www.fs.ded.us/database/feis/plants>) and from the literature. The binary matrix included regeneration strategies and the ability to fix atmospheric nitrogen.

Three primary regeneration strategies were considered: 1) seed banking, 2) resprouting, and 3) obligate seeding. When more than one type of regeneration can be used by a single species, we assigned the type according to the most common response to high severity fire mentioned in the literature. Seed banking species were defined as those species killed by the fire and whose persistence relies on seeds stored in the canopy or in soil banks. Species from the genera *Ceanothus* and *Arctostaphylos* as well as *Pinus attenuata* were included under this category. Resprouting species included hardwood and shrub species that are mentioned in the literature as able to resprout after fires. The third regenerative strategy, obligate seeding, included all species that rely on off-site seed sources after high severity fires. This category included conifer species (except *Pinus attenuata*) and *Whipplea modesta* (for responses to high severity burn for this species, see Halpern 1989). Species from the genus *Ceanothus* were coded as nitrogen fixing species.

Grouping the species by their regeneration responses increased normality in the data and our ability to use parametric statistics. We used simple linear regression (S-plus v.7) to test the hypothesis of linear relationships between environmental variables and the abundance of species with a specific regenerative trait. The abundances of seed bank and resprouting species were used as the response variable and heat load as the independent variable. Two-way ANOVA (S-plus v.7) was used to determine if management, aspect, or the interaction of management and aspect significantly affected the cover of each trait.

RESULTS

Sixty-two sites were sampled of which 25 corresponded to unmanaged areas and 37 to managed areas. Unmanaged sites included 16 on north aspects and 9 on south aspects. Managed sites included 23 on north aspects and 14 on south aspects. Elevation of the sites ranged from 374 to 1506 m. Average slope for the sites was 60% with a range from 20% to 100% (Table 2.1). A complete list of sites is presented in appendix A.

Unmanaged Sites Description

Cover

Twenty years after high severity wildfire, sites were dominated by shrubs and hardwoods. The total cover ranged from 29% to 107% with a mean of 73% (100% maximum per species). Shrubs comprised about half of the total cover (54%), hardwoods a quarter (24%), and a mix of conifers, forbs and ferns made up the remainder (Fig. 2.2). The abundance of species within each life form group (conifers, hardwoods, shrubs, forbs, grasses and ferns) varied with aspect (Table 2.2).

Ten species of conifers were present; however, only four species presented average cover values $\geq 1\%$ (Table 2.2). *Pseudotsuga menziesii* was the most abundant (cover and frequency) conifer across all sites regardless of aspect. On

north aspects, *P. menziesii* shared dominance with *Abies concolor*. On south aspects, *P. menziesii* shared dominance with *Pinus ponderosa* and *Pinus attenuata* (Table 2.2).

While ten hardwood species were recorded in unmanaged sites, only seven presented average cover values $\geq 1\%$ (Table 2.2). *Arbutus menziesii* and *Lithocarpus densiflorus* comprised 56% of the cover for the sites on north aspects. *Quercus chrysolepis* was the most abundant hardwood species on south aspects, accounting for 44% of the hardwood cover of the sites.

We recorded 40 shrub species across unmanaged sites; 34 species were present on north aspects while 27 were present on south aspects. *Ceanothus integerrimus*, *Salix scouleriana*, *Quercus vacciniifolia*, and *Symphoricarpos mollis* made up 50% of the cover of shrub species on north aspects while *Arctostaphylos viscida* and *C. integerrimus* accounted for 50% of the cover on south aspects. Ferns, grasses and forbs represented a small proportion of the total cover on the sites (6 %). A complete list of species is presented on appendix A.

Vertical Structure

Three major elements constituted the vertical structure in unmanaged sites: a continuous layer of shrubs, a discontinuous layer of hardwoods (above the shrub layer), and the presence of snags (Fig. 2.3). Shrub layer height varied with species composition. On north aspects, where the dominant shrub species were *C. integerrimus* and *S. scouleriana*, the shrub layer had an average height of 1.7 m (range 0.8 to 3.5 m). On south aspects, where sites were dominated by *A. viscida* and *C. integerrimus*, the average height of the shrub layer was 1.6 m (range 0.4-3 m). Hardwood species were scattered throughout the sites and occupied the upper layer. On north aspects, the average height of the two dominant hardwood species (*A. menziesii* and *L. densiflorus*) was 3 m (range 0.5-7 m). On south aspects, where *Q. chrysolepis* was the dominant hardwood, the average height was also 3 m (range 0.2-4 m). Snags constituted an important element of the vertical

structure in unmanaged sites. The size and density of these biological legacies varied among sites. Snag's DBH ranged from 10 cm to 115 cm with a mean of 45 cm. The mean density of snags was 125 snags/ha with a range from 21 to 229 snags/ha. Conifers occupied a range of vertical positions with an average height of 1.6 m (range 0.04-13 m) on north aspects and 1.8 m (range 0.05- 8 m) on south aspects.

Managed Sites Description

Cover

Like unmanaged sites, sites managed after high severity wildfire were dominated by shrubs and hardwoods. The total cover ranged from 45% to 124% with a mean of 83%. Shrubs comprised 55% of the total average cover in managed sites (Fig. 2.2).

Conifers comprised 13% of the total cover of managed sites. Of the nine species recorded, only three species presented average cover values $\geq 1\%$ (Table 2.2). *P. menziesii* and *P. ponderosa* were the most abundant conifer species. The frequency of these species varied with aspect. *P. menziesii* was the most frequent conifer species on north aspects, while *P. ponderosa* was most frequent on south aspects.

Similar to unmanaged sites, the number and abundance (cover and frequency) of hardwood species varied with aspect. On north aspect sites, where 9 hardwood species were present; *Q. chrysolepis* and *A. menziesii* were the most abundant species. On south aspects, 69% of the hardwood cover was comprised by *Q. chrysolepis* and *Q. kelloggii*. The most frequent species, regardless of aspect, was *A. menziesii* (Table 2.2).

Thirty four species of shrubs were recorded on managed sites; 31 were present on north aspects while 20 were present on south aspects. *Rubus parviflorus* (25%), *S. scouleriana* (19%), and *C. integerrimus* (15%) comprised more than half of the cover on north aspect sites. South aspect sites were

dominated by *C. integerrimus* which comprised more than half of the shrub cover (69%) and appeared in all sites. The second most abundant species on south aspects was *Toxicodendron diversilobum*, which accounted for 15% of the shrub cover and occurred on almost every site (Table 2.2).

Forbs, grasses and ferns made up 6% of the total cover on managed sites. A complete list of species is presented on appendix A.

Vertical Structure

Two layers made up the vertical structure of managed sites: a shrub layer and an upper layer comprised of hardwoods and conifers (Fig. 2.4). Shrub layer structure varied with aspect. On north aspects, the shrub layer could be divided in two strata: 1) a lower shrub stratum of ≤ 0.5 m dominated by *R. parviflorus*; 2) an upper stratum with average height of 1.8 m (range 0.8-3 m) dominated by *S. scouleriana* and *C. integerrimus*. On south aspects, where sites were dominated by *C. integerrimus*, shrub layer average height was 1.8 m (0.8-3 m).

Hardwoods and conifers comprised the upper vertical layer on managed sites. In general, hardwood species occupied the upper layer and were scattered throughout the sites. The average height of hardwoods was 2.5 m (range 0.5-10 m) on north aspects and 3 m (range 0.5-4 m) on south aspects. On the other hand, conifers were present in a range of vertical positions (in the shrub layer and in the upper layer). Conifer average height was 2.4 m (range 0.05-14 m) on north aspects and 3 m (0.05-8 m) on south aspects.

Unmanaged vs. Managed

Cover of Life Form Groups and Species Diversity

No significant differences in cover were detected between unmanaged and managed sites for any life form groups (conifers, hardwoods, shrubs and forbs grasses and ferns) neither on north nor on south aspects (all p-values > 0.1 ; after

Bonferroni correction; Fig. 2.2.a; Fig. 2.2.b). However, examination of dominant shrub and hardwood species cover suggested differences in abundance of species by aspect and management (Fig. 2.5; Fig.2.6). Managed sites on south aspects presented the highest level of species dominance, with one or two species representing more than 50% of the cover (e.g. *Ceanothus integerrimus* which represents 70% of the shrub cover). This is consistent with the species richness results that showed higher number of species on unmanaged sites relative to managed sites. Furthermore, north aspect sites presented higher numbers of species than south aspect sites. Species diversity indexes indicated little differences between unmanaged and managed sites (Table 2.3). Simpson's index indicates that unmanaged sites in general were slightly more diverse, but Shannon-Wiener's index showed the opposite trend. The same pattern was observed on south aspect sites, while on north aspects both Simpson's and Shannon-Wiener's indexes showed similar diversity between unmanaged and managed sites. These differences reflect the sensitivity of each index to rare or uncommon species.

Community Composition

Unmanaged sites differed from managed sites in plant community composition (Fig. 2.7.a). The NMS Autopilot in PC-ORD chose a 3-dimensional solution as providing a considerable and statistically significant reduction in stress as compared with randomized data (final stress = 15.0; $p=0.004$ for all axes). The final ordination explained 76% of the variation in the dataset and showed a distinction between unmanaged and managed sites as well as differences in community composition associated with aspect (Fig 2.7.a). Axis 2, representing 32% of the variation, was aligned with aspect, thus contrasting north and south aspects. *Rubus parviflorus* ($r=0.643$), *Pseudotsuga menziesii* ($r=0.514$), *Ribes sanguineum* ($r=0.467$), and *Rosa gymnocarpa* ($r=0.466$) were positively correlated with axis 2, hence, most strongly associated with north aspects. In

contrast, *Ceanothus integerrimus* ($r = -0.585$), *Quercus kelloggii* ($r = -0.436$), *Toxicodendron diversilobum* ($r = -0.401$), and *Quercus chrysolepis* ($r = -0.329$) showed the strongest association with south aspects. The differentiation between north and south aspects was strongest for managed sites, as indicated by the separation of managed sites by aspect in contrast with the spread of unmanaged sites on axis 2 (Fig 2.7.a). The stronger effect of aspect on managed sites compared with unmanaged sites shown graphically by the ordination, as well as the differences in community composition between unmanaged and managed sites were confirmed with the results from MRPP (Table 2.4).

Axis 1 in the ordination explained 25% of the variation and was rotated to align with management, thus contrasting managed and unmanaged sites (Fig. 2.7.a). *Ceanothus integerrimus* ($r = -0.447$), *Corylus cornuta* ($r = -0.445$), *Symphoricarpos mollis* ($r = -0.433$) and *Pinus ponderosa* ($r = -0.360$) were most strongly associated with managed areas, while *Arctostaphylos viscida* ($r = 0.550$), *Quercus vacciniifolia* ($r = 0.462$), *Whipplea modesta* ($r = 0.426$), and *Lithocarpus densiflorus* ($r = 0.353$) showed the strongest association with unmanaged sites.

Indicator species analysis corroborated the ordination correlations with *Pinus ponderosa* having higher indicator values for managed sites, while *Arctostaphylos viscida* was significant indicator species for unmanaged sites (Table 2.5). The third axis of the ordination, representing 19% of the variation, was related to elevation. No separation between unmanaged and managed sites was observed on axis 3 (Fig 2.7.b).

Traits

The ordination of plots in trait space showed an association of the abundance of seed bank species and resprouting species with aspect (Fig. 2.8). A two-dimensional ordination was chosen as the best solution, representing 95% of the community variation. Axis 2, represented 56% of the variation, was associated with aspect and heat load. Seed bank species were strongly associated ($r = 0.931$)

with south aspects while resprouter abundance was associated with north aspects ($r=0.438$). None of the environmental variables were associated with axis 1.

Simple linear regression results confirmed the association of seed banking species with drier conditions and suggested a positive linear relationship between the abundance of seed bank species and heat load on both unmanaged ($p<0.001$; $r^2=0.46$) and managed sites ($p<0.001$; $r^2=0.32$). Resprouting species showed the opposite trend, a negative linear relationship between the abundance of resprouting species and heat load (unmanaged $p=0.086$, $r^2=0.12$; managed $p=0.051$, $r^2=0.10$).

Based on two-way ANOVA, aspect ($F_{1,58}=31.73$; $p<0.001$) and management ($F_{1,58}=3.76$; $p=0.057$) had an effect on the abundance of seed bank species (Table 2.6; Fig. 2.9). We found little evidence that the abundance of resprouting species differed between unmanaged and managed sites ($F_{1,58}= 2.38$; $p=0.129$) and strong evidence of differences in cover between north and south aspects ($F_{1,58}=9.45$; $p=0.003$). There was also evidence that the interaction between management and aspect ($F_{1,58}=4.9$; $p=0.030$) significantly affected the cover of N-fixing species (*Ceanothus* spp.). Neither management nor aspect had a significant effect on cover of obligate seeding species (mainly conifers).

DISCUSSION

Our study provides evidence that the effects of post-fire management on plant community composition are influenced by the microclimate of the sites. The differences in plant species diversity, abundance, structure, and composition between unmanaged and managed sites were stronger when slope direction was considered reflecting the influence that the microclimate has on the resulting vegetation after disturbance. We address these plant community changes using as a framework the importance that past-vegetation characteristics have on the resulting vegetation after disturbance and the role of disturbance and microclimate.

The Importance of Biological Legacies

Most disturbances leave traces or features of the original plant community in the form of biological legacies (Hansen et al. 1991, Lindenmayer and Franklin 2002). In this study, seed banking species and resprouting species dominated, showing the influence that the previous plant community had on the vegetation after disturbances. Differences were observed, however, in the abundance and presence of key biological legacies between unmanaged and managed sites. The importance of these legacies and the differences in their distribution between unmanaged and managed sites are discussed in the following paragraphs.

Twenty years after high severity fire, snags were still part of the structure of unmanaged sites. Snags contributed to the heterogeneity of the vertical structure of unmanaged sites and their presence in post-fire settings can influence some important site characteristics such as soil moisture and evaporation (Sexton 1998). Snags are also important elements of wildlife habitat both directly and indirectly. Directly, snags serve as structural support for cavity-nesting birds and indirectly they represent food sources for insectivores (Canton 1996, Saab and Dudley 1998, Saab et al. 2007). Post-fire management directly affected the vertical structure of the sites by removing the snags. Although we cannot separate the effects of salvage logging on plant community composition from the other post-fire management activities, the reduction of vertical structure is a direct effect of salvage logging.

Ceanothus integerrimus and *Arctostaphylos viscida* also can be considered important biological legacies after high severity fires in the Klamath region. Both species can regenerate from the buried seed bank and their viable seeds can persist in the soil for decades, maybe centuries (Talley and Griffin 1980). Furthermore germination of their seeds is stimulated by fire. In the post-disturbance environment, both species play a variety of important roles. For example, *Ceanothus integerrimus* provides high-quality and palatable forage, for

wildlife, especially deer (Talley and Griffin 1980) and can significantly enrich soil with available forms of nitrogen (Binkley and Husted 1983, Oakley et al. 2003), while the fruits of *Arctostaphylos viscida* are consumed by many animals including bears, rabbits, and birds (Van Dersal 1938). In this study, post-fire management was associated with changes in the abundance of these two species on southerly aspects. In the case of *Ceanothus integerrimus*, post-fire management had a positive effect, increasing the abundance of the species, while decreasing the abundance of *Arctostaphylos viscida*.

The positive response of *Ceanothus* spp. to fire and management has been reported by other authors (Halpern 1989, Huffman and Moore 2004). However, Stuart et al. (1993) found less cover of *Ceanothus* on sites that were salvage logged after wildfire. Although Stuart's results differ from our findings, his results were based only on 3 northerly aspect sites; our largest differences in cover of *Ceanothus* (see N-fixing results) were on south aspects. Stuart et al. (1993) also included plantations under the same category as unmanaged stands when reporting *Ceanothus* cover which makes comparison even more difficult. Post-fire management implies soil disturbance, giving by salvage logging (Klock 1975) and also the use of fire to reduce fuels after salvage (Holder 1990). *Ceanothus* seeds require fire or mechanical scarification for germination (Keeley 1977, Keeley and Zedler 1978). Therefore, it is possible to argue that the combination of disturbances represented by high severity fire and post-fire management might have positively influenced the abundance of this species on managed sites.

Arctostaphylos viscida decreased in abundance with management. Although *Arctostaphylos* spp. responses to fire are well documented (Keeley 1977, Keeley and Zedler 1978, Odion and Davisa 2000), we found few studies that have looked at the effect of repeated disturbance on the abundance of *Arctostaphylos viscida* (Kauffman 1986, Fryer 2007). Kauffman (1986) suggested

that yearly fires prevent *Arctostaphylos viscida* seedlings from maturing and gradually reduce the residual soil seed stock.

Perhaps the differences in response to post-fire management between *Arctostaphylos viscida* and *Ceanothus integerrimus* can best be explained by the differences in germination requirements and time to reach maturity that exist between the two species. Although germination of both species is stimulated by fire, major differences exist in the ability of these species to break dormancy. While germination of *Ceanothus* spp. in controlled experiments has been observed after induce fire, *Arctostaphylos* spp. needed fire followed by scarification to germinate (Keeley 1987). Common post-fire management activities include the use of fire to reduce fuel hazards after salvage logging. The combination of salvage logging and burning might have provided sufficient stimulation to *Ceanothus integerrimus* seeds, but were insufficient to stimulate *Arctostaphylos viscida*'s seed germination. Both species also differ in their life cycle; while *Ceanothus integerrimus* can produce seeds as early as three years after germination (Haward 1992b), *Arctostaphylos viscida* reach maturity nine to ten years after germination (Detling 1961, Haward 1992a). Thus, this difference in life cycle might have given an advantage to *Ceanothus integerrimus* over *Arctostaphylos viscida* to establish after short return interval disturbances. However, further controlled experiments are needed to test these hypotheses.

The Role of Disturbances and Microclimate on Plant Community Composition

Both disturbances and microclimate have long been recognized to have important influence on the structure and composition of plant communities (Miller 1982, Sousa 1984, Pickett and White 1985, Nguyen-Xuan et al. 2000, Small and McCarthy 2002, Shea et al. 2004). In this study, microclimate influenced not only plant community composition and structure but also the effect that a disturbance such as post-fire management had on a plant community. We

address the microclimate influences on plant community as well as the microclimate-disturbance interaction in this section.

Differences in plant species diversity, community composition, and abundance of regenerative traits were associated with differences in microclimate and management. In general, north aspect sites presented higher species diversity and community heterogeneity than south aspect sites. This is an expected situation because establishment or persistence of plant species is limited by abiotic factors. South aspect sites are expected to experience higher temperatures and light intensity and lower moisture than north-facing slopes (Small and McCarthy 2002), which might have limited the establishment or persistence of some species on south slopes.

The abundance of species with different regenerative traits was also associated with differences in the microclimate of the sites (heat load). Seed banking species increased with increased values of heat load and more southerly aspects, indicative of the association between the abundance of seed bank species and drier conditions. A similar association between seed bank species and hot, dry conditions has been reported for other ecosystems with Mediterranean climate, such as California chaparral (Dell et al. 1986, Meentemeyer et al. 2001). The difference in microclimate between north and south aspects in the Klamath Mountains has also been reported to be associated with differences in fire frequency. Fire burned less frequently on north slopes than on south slopes (Taylor and Skinner 1998, 2003). Germination of the seed banking species considered in this study is fire dependent; thus fire might have acted as a sorting factor over time, favoring the abundance of seed bank species on sites with higher fire frequency. In contrast, the abundance of resprouting species was associated with decreasing levels of heat load and more northerly aspects, consistent with Keeley (1986) and Meentemeyer et al. (2001), who found more resprouters on north facing slopes in California chaparral. Resprouting is not considered to be a trait selected for by fire, but rather a general adaptation to recovery from any type

of disturbance. Therefore, inferences about the responses of resprouting species to increasing moisture levels can not be attributed to decreasing fire frequency.

Throughout this study the effect of post-fire management on plant community composition was mediated by microclimate. The differences in plant species diversity, abundance, structure, and composition between unmanaged and managed sites were stronger when aspect was considered (see, MRPP results, Table 2.4). Furthermore, positive interactions between post-fire management and microclimate were detected on the abundance of N-fixing species (*Ceanothus* spp.), which increased notably in managed sites on south aspects. This increase in abundance added to other factors, such as the decrease in abundance of *Arctostaphylos viscida* and other less dominant species (see Table 2.3 and Fig. 2.5) as well as the increase in abundance of *Pinus ponderosa* (see, Indicator Species Analysis, Table 2.5), indicates stronger effects of post-fire management on south aspect sites.

Our actual knowledge of post-fire regeneration in diverse ecosystems, such as the Klamath region, has been limited to the first five to ten years of vegetation recovery after fires. The study of individual, as well as community, plant responses to high severity fires and subsequent disturbances such as post-fire management beyond the first decade of recovery is an enormous task. This task becomes even more difficult when the underlying patterns of species distribution along environmental gradients are considered. Our study has contributed toward addressing this challenge and will hopefully lead to deeper understanding of plant community responses to high severity fires and post-fire management in diverse fire-prone ecosystems.

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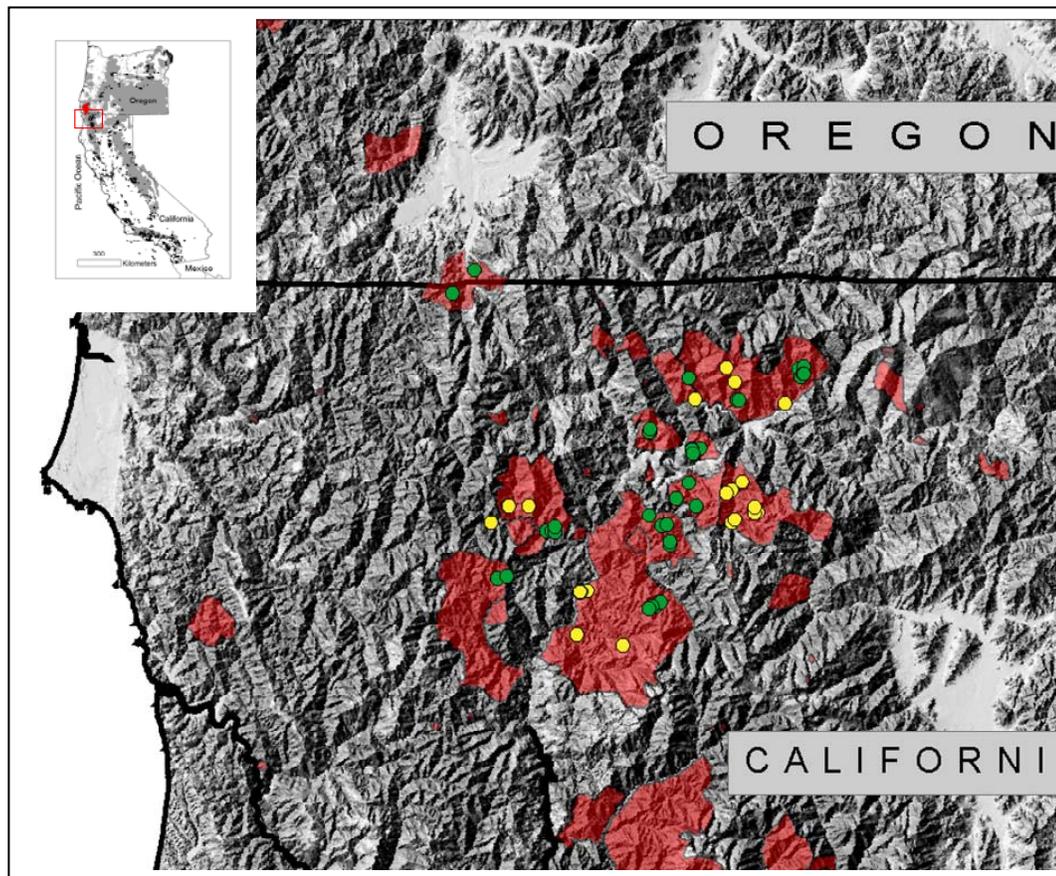


Fig. 2.1 Study site location. Yellow dots indicate unmanaged sites and green dots indicate managed sites. Red polygons indicate wildfires dating back to 1970.

Table 2.1. Summary of site characteristics. Mean values (range) are presented.

	Unmanaged	Managed
Total number of plots	25	37
North aspect	16	23
South aspect	9	14
Slope (% range)	57 (18-100)	60 (28-80)
Elevation (m range)	993 (374-1506)	913 (431-1496)

Fig. 2.2. Contribution of life form groups to the average total cover on northerly (a), and southerly aspects (b). Bars represent mean and error bars are standard errors. For a given life form group; means with the same letter are not significantly different ($p > 0.05$). Bonferroni correction was used.

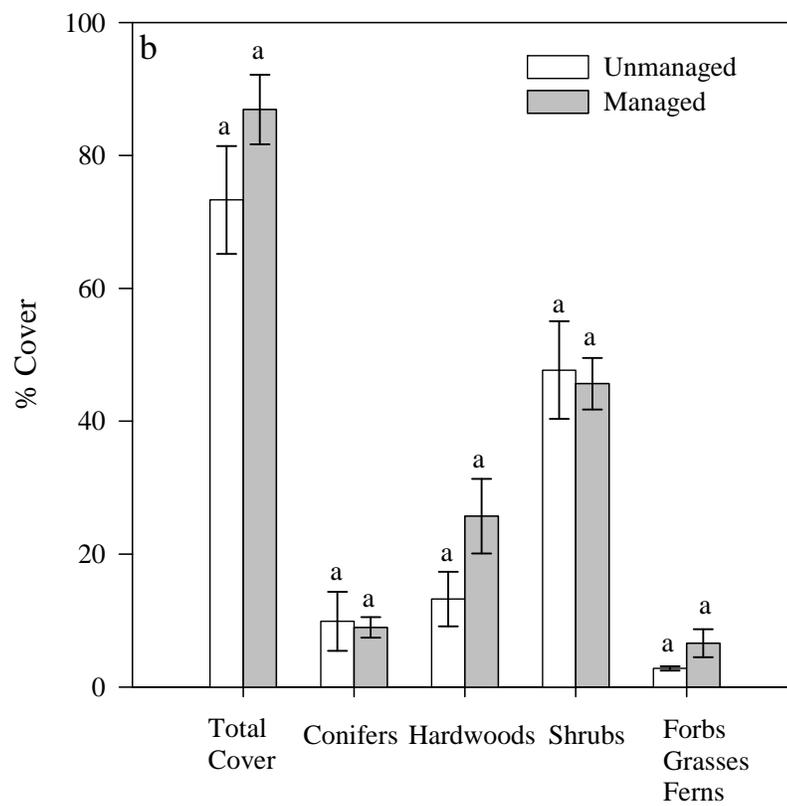
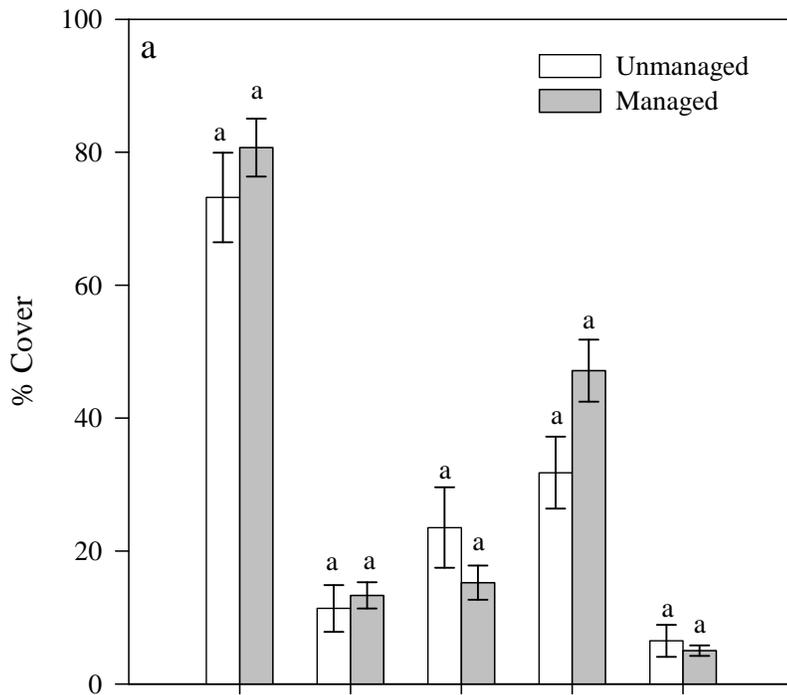


Table 2.2. Average percent cover and frequency of species on unmanaged and managed sites, stratified by life form and aspect. Species are presented in alphabetical order. Only species with cover $\geq 1\%$ in either aspect are shown.

Life Form	Species	Unmanaged				Managed			
		North Aspects		South Aspects		North Aspects		South Aspects	
		Cover (%)	Frequency (%)						
Conifer	<i>Abies concolor</i>	2.6	50	0.2	22	0.8	48	0	0
	<i>Pinus attenuata</i>	0.1	13	2.0	44	0.4	17	1.2	14
	<i>Pinus ponderosa</i>	0.3	38	2.1	67	1.0	74	4.1	93
	<i>Pseudotsuga menziesii</i>	7.8	100	5.6	67	10.7	100	3.4	79
Hardwood	<i>Acer macrophyllum</i>	0.8	19	0	0	1.5	57	0.3	7
	<i>Arbutus menziesii</i>	7.2	88	2.9	78	4.5	70	4.1	93
	<i>Chrysolepis chrysophylla</i>	1.3	38	0.3	11	0.4	22	0	0
	<i>Cornus nuttallii</i>	0.6	38	0.4	11	1.2	48	0	7
	<i>Lithocarpus densiflorus</i>	6.4	38	1.2	22	1.7	39	3.0	29
	<i>Quercus chrysolepis</i>	6.1	75	5.9	56	5.7	57	9.7	71
	<i>Quercus kelloggii</i>	0.9	19	1.1	22	0.1	17	8.1	86
Shrub	<i>Umbellularia californica</i>	0	6	1.6	33	0	0	0	0
	<i>Amelanchier alnifolia</i>	0.5	50	0.1	22	0.1	26	0	0

Table 2.2. (Continued)

Life Form	Species	Unmanaged				Managed			
		North Aspects		South Aspects		North Aspects		South Aspects	
		Cover (%)	Frequency (%)						
Shrub	<i>Arctostaphylos columbiana</i>	0.4	19	0	11	0	0	0	0
	<i>Arctostaphylos nevadensis</i>	0.4	13	1.9	11	0	0	0	0
	<i>Arctostaphylos patula</i>	0.8	25	0.9	22	0	13	0.1	14
	<i>Arctostaphylos viscida</i>	0.1	25	12.6	67	0.2	22	0.4	36
	<i>Berberis aquifolium</i>	0.1	13	0.2	22	0.1	26	0	7
	<i>Berberis nervosa</i>	1.9	38	0.1	11	2.6	70	0	0
	<i>Ceanothus integerrimus</i>	5.9	75	10.9	89	7.1	65	31.6	100
	<i>Ceanothus sanguineus</i>	0.3	25	0	0	2.3	35	0	0
	<i>Ceanothus velutinus</i>	1.2	19	0	0	4.3	22	0	0
	<i>Corylus cornuta</i>	1.3	50	0.6	22	2.4	61	1.1	36
	<i>Quercus vacciniifolia</i>	4.0	25	5.6	33	1.2	4	0	0
	<i>Ribes sanguineum</i>	0.4	56	0.1	22	1.0	65	0	7
	<i>Rubus parviflorus</i>	1.1	69	1.1	22	11.6	87	0	21
	<i>Rubus ursinus</i>	0	13	1.4	22	0.1	35	0	7
	<i>Salix scouleriana</i>	5.4	75	0	0	8.7	87	2.6	57
	<i>Symphoricarpos mollis</i>	3.3	88	0.2	33	1.4	83	1.4	21
	<i>Toxicodendron diversilobum</i>	1.1	50	0.4	67	0.9	43	6.9	86

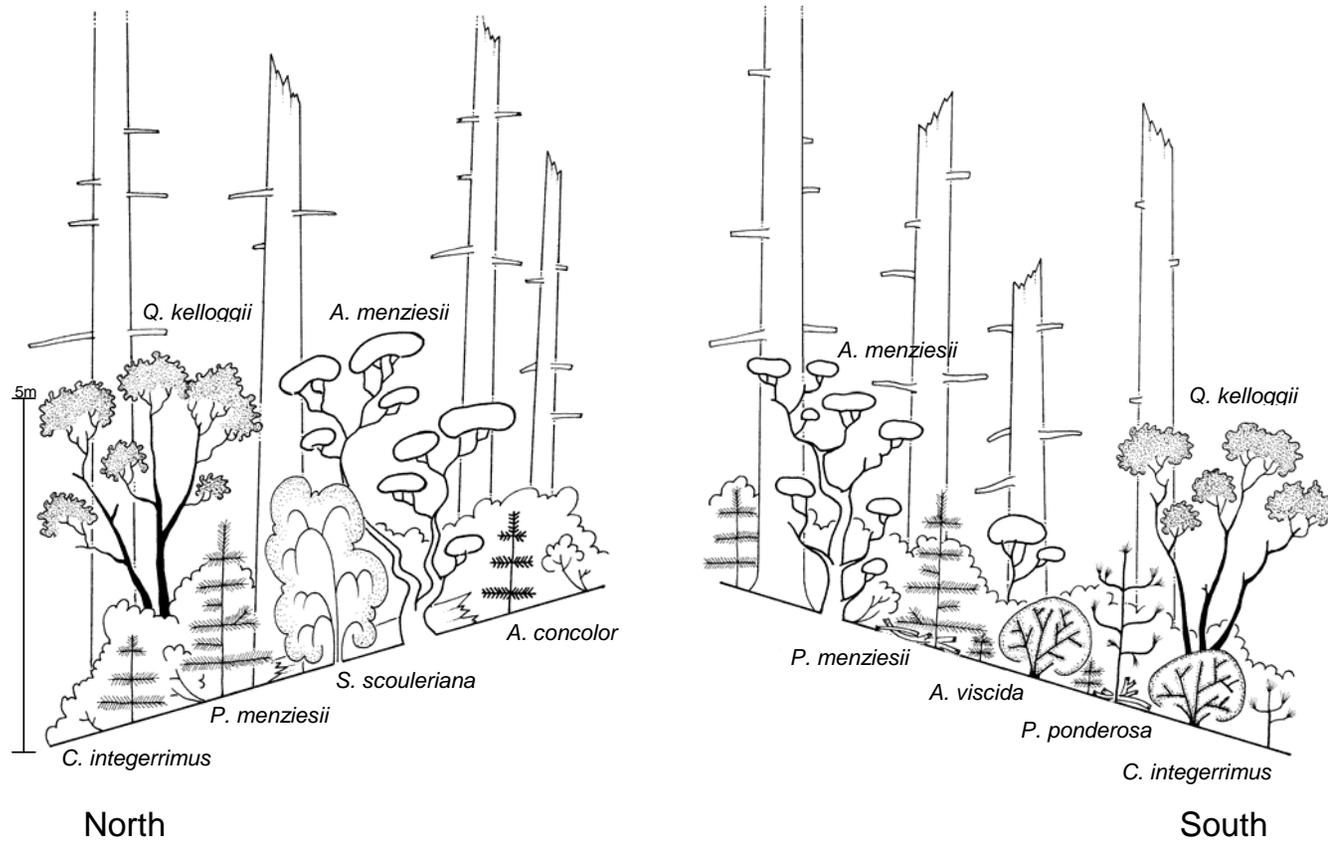


Fig. 2.3. Representation of the vertical structure of unmanaged sites on north and south aspects. Only the most abundant species are shown.

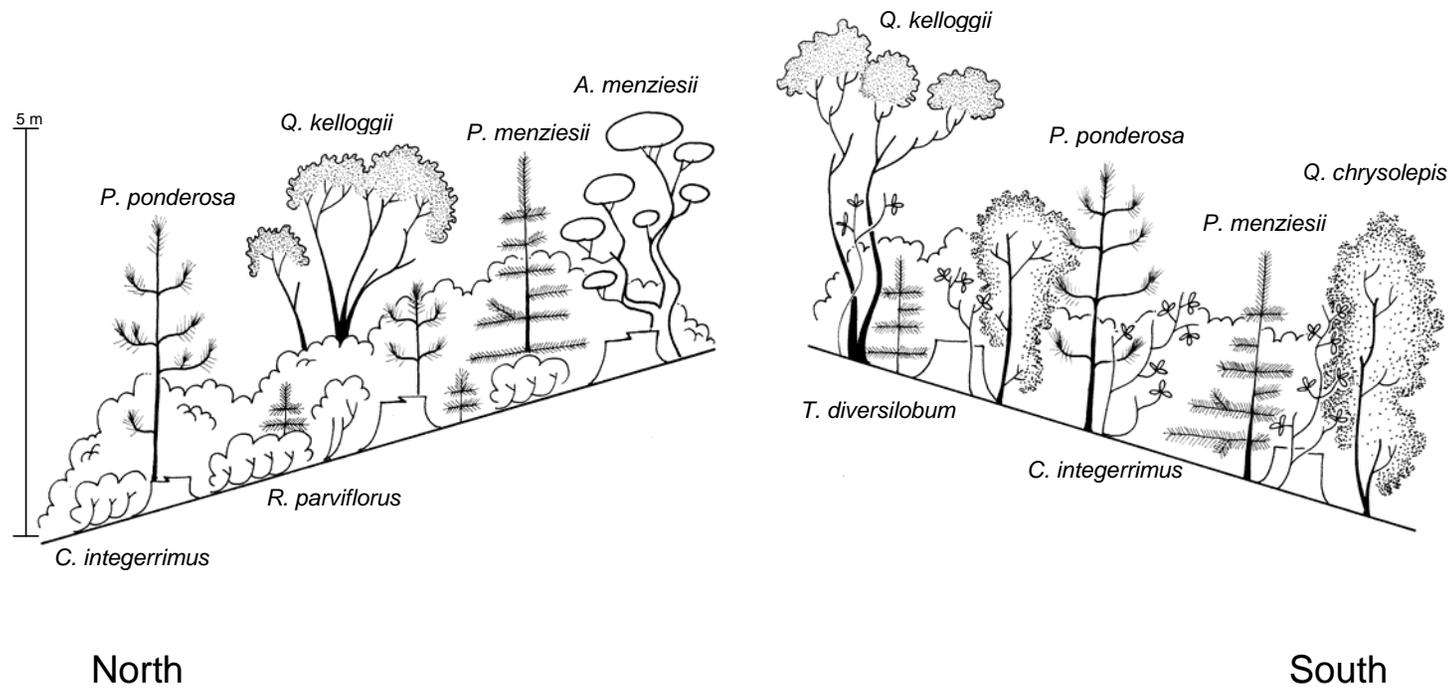


Fig. 2.4. Representation of the vertical structure of managed sites on north and south aspects. Only the most abundant species are shown.

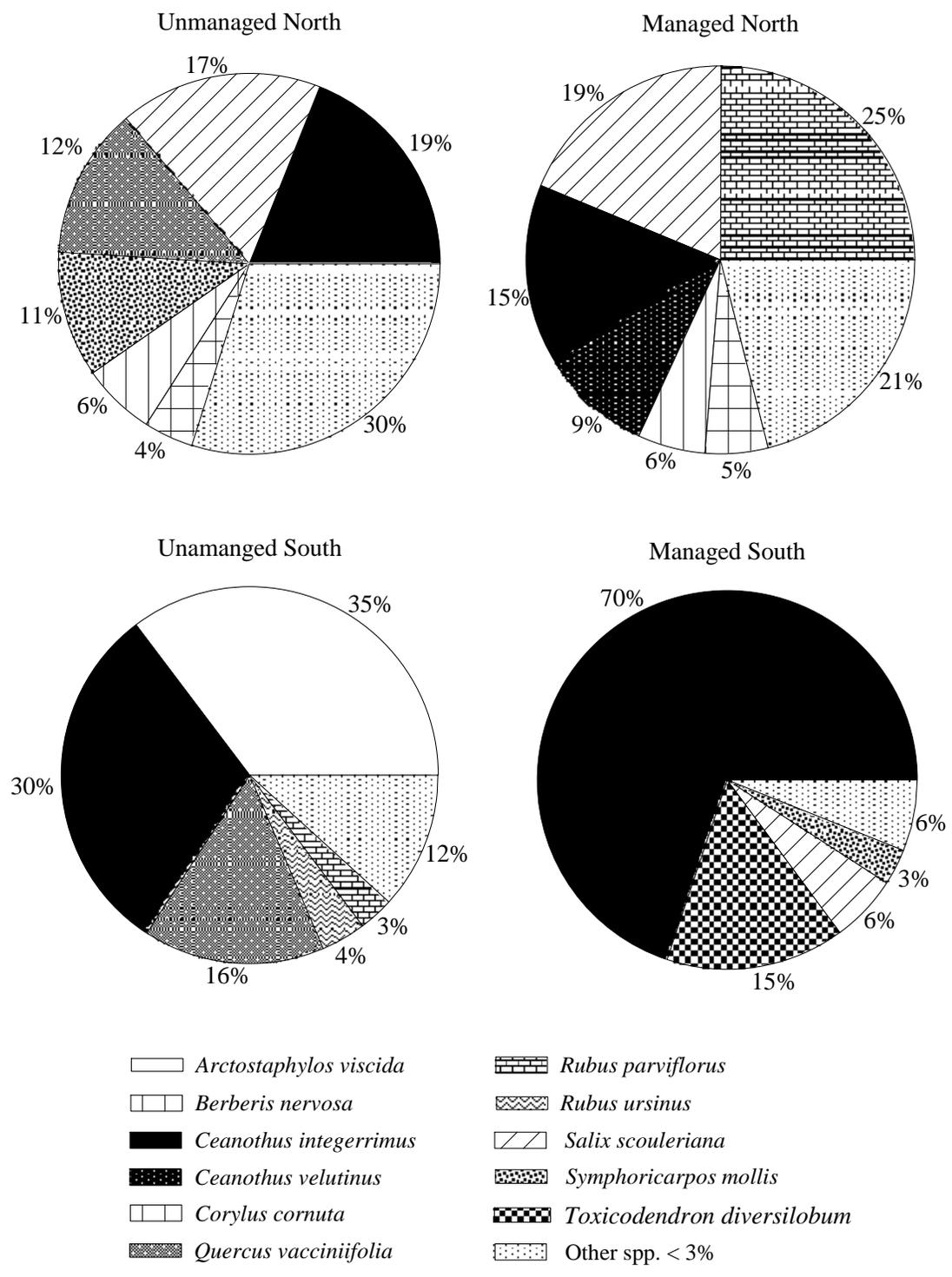


Fig. 2.5. Cover of shrub species broken down by aspect and management.

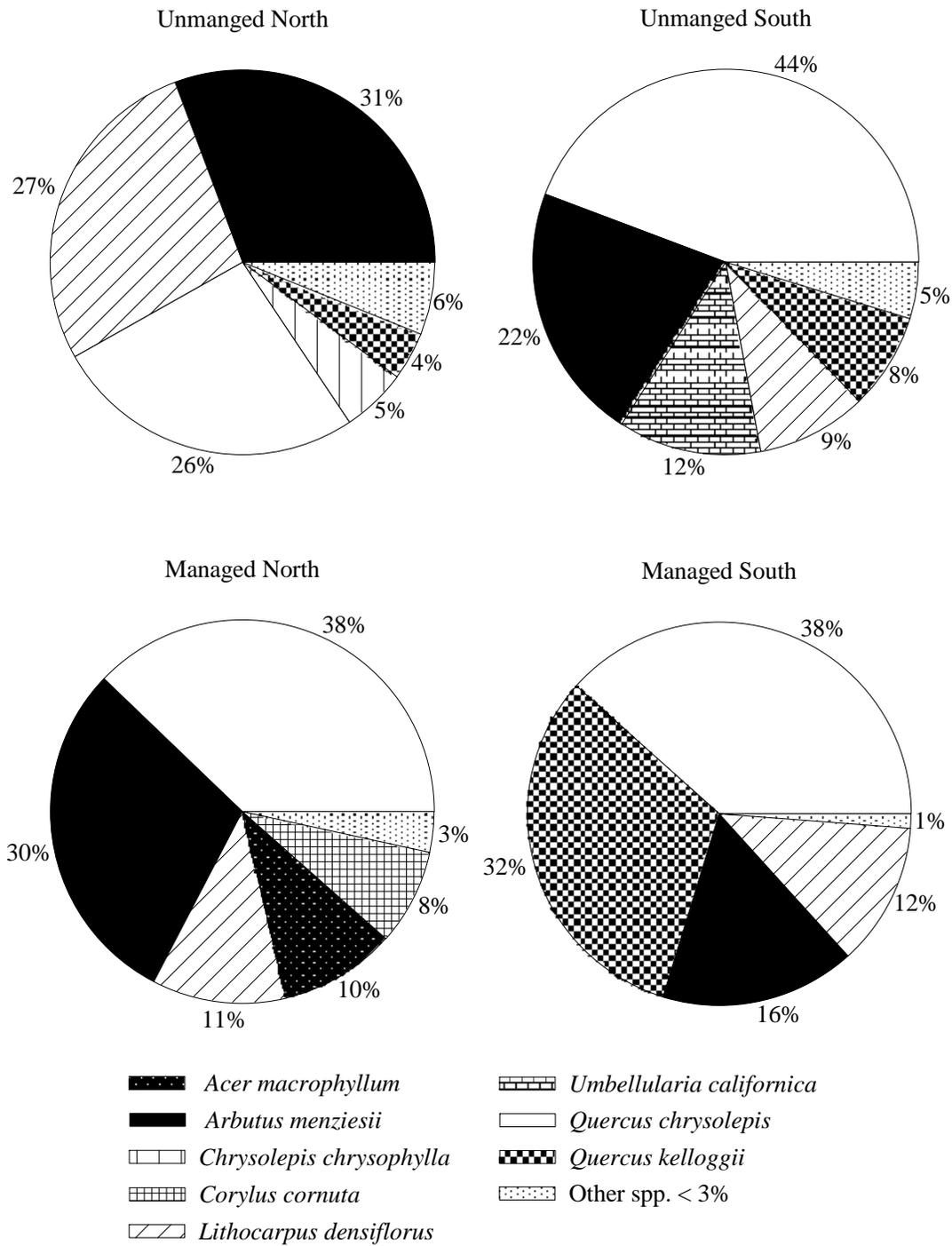


Fig. 2.6. Cover of hardwood species broken down by aspect and management.

Table 2.3. Species diversity on unmanaged and managed sites; broken down by aspect. Beta diversity (β_w) was measured as the total number of species divided by the average number of species. Simpson's index (D), Shannon-Wiener (H').

Group (sample size)	Average species richness (S.D.)	β_w	D	H'	Total number of species
Unmanaged (25)	16 (0.4)	3.8	0.724	1.784	60
Managed (37)	16 (0.4)	3.3	0.745	1.806	52
Unmanaged North (16)	18 (0.4)	3.1	0.762	1.924	55
Managed North (23)	18 (0.5)	2.8	0.761	1.924	51
Unmanaged South (9)	13 (0.4)	3.3	0.655	1.535	43
Managed South (14)	12(0.4)	2.9	0.719	1.611	35

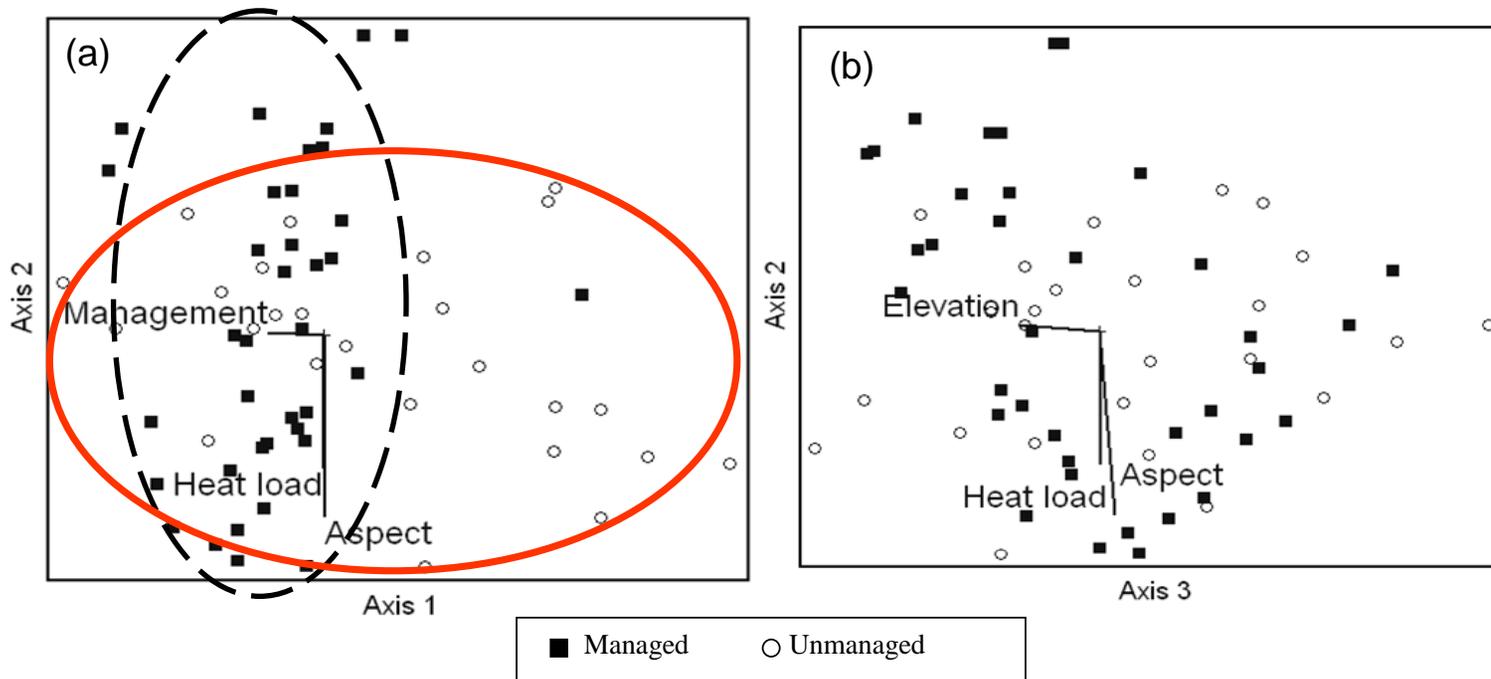


Figure 2.7. NMS ordination of sample units in species space based on 44 species that occur in more than 5% of the sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with $r^2 > 0.200$. Red line on (a) shows spread of unmanaged sites while dashed line shows aggregation of managed sites. (b) shows the desegregation of sites on axis. 3.

Table 2.4. Differences in community composition using MRPP; based on Sorensen distance; g = number of groups; A = chance corrected within-group agreement p = probability of type I error for H_0 : no difference between groups.

Grouping variable	g	A	p
Unmanaged North vs. Unmanaged South	2	0.06	0.020
Managed North vs. Managed South	2	0.27	<0.001
Unmanaged vs. Managed	2	0.03	0.006
Unmanaged vs Managed (Aspect)	4	0.22	<0.001
Unmanaged North vs. Managed North	2	0.04	0.019
Unmanaged South vs. Managed South	2	0.18	<0.001

Table 2.5. Indicator species analysis; using Monte Carlo test, only species with $p \leq 0.05$ are shown.

Group	Species	(IV)	Mean	SD	<i>p</i>
Unmanaged	<i>Arctostaphylos viscida</i>	38	24	6.3	0.04
	<i>Amelanchier alnifolia</i>	35	21	5.7	0.02
	<i>Ribes speciosum</i>	32	11	4	0.00
	<i>Quercus vacciniifolia</i>	24	11	3.9	0.01
	<i>Arctostaphylos columbiana</i>	16	8	2.9	0.02
	<i>Umbellularia californica</i>	16	8	3.5	0.06
Managed	<i>Pinus ponderosa</i>	57	42	6.7	0.03
	<i>Rubus parviflorus</i>	54	37	6.3	0.02
	<i>Ribes roezlii</i>	43	28	5.2	0.02

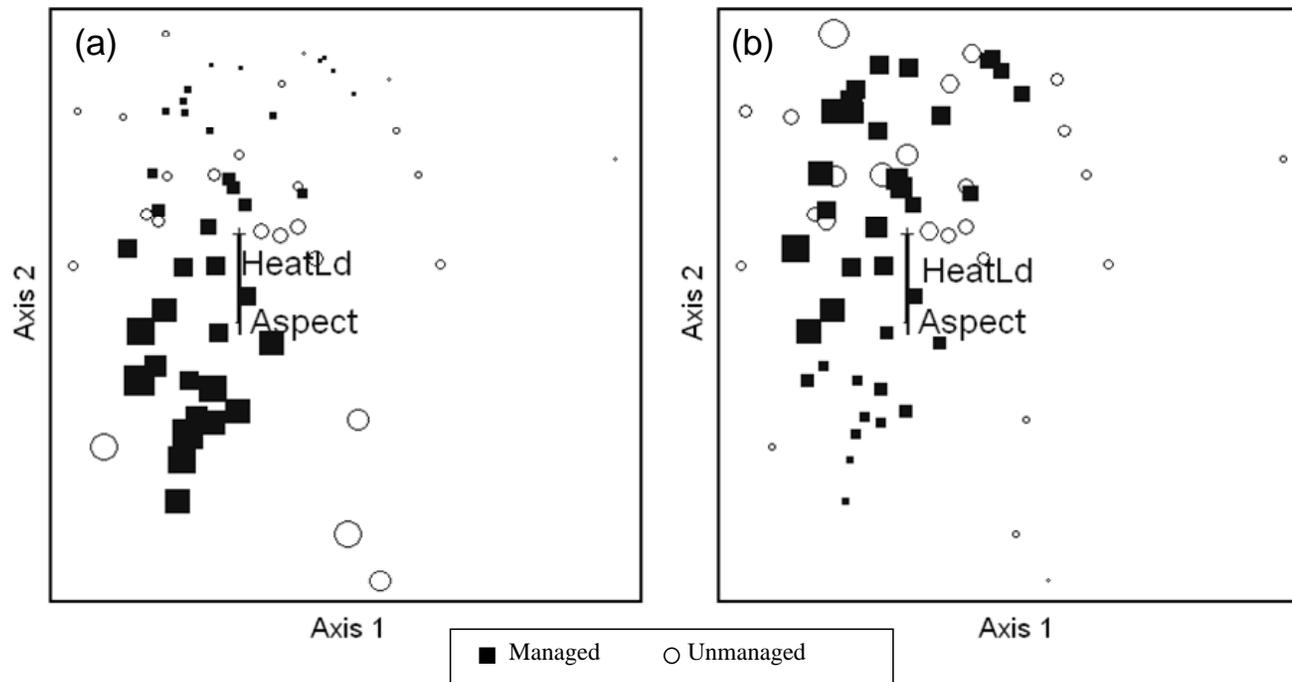


Figure 2.8. NMS ordination of plots in trait space based on 44 species that occur in more than 5% of the sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with $r^2 > 0.10$. Symbol size reflects relative cover of a trait group in a plot. (a) Seed banking species. (b) Resprouting species.

Table 2.6. Two-way ANOVA results for the effect of management and aspect on the abundance of different regenerative and functional traits.

Source of Variation	DF	SS	F	P
<i>Seed banking</i>				
Management	1	578.01	3.76	0.057
Aspect	1	4876.12	31.74	<0.001
Management x Aspect	1	8.20	0.05	0.818
Residuals	58	8910.79		
<i>Resprouting</i>				
Management	1	771.77	2.38	0.129
Aspect	1	3068.92	9.45	0.003
Management x Aspect	1	511.69	1.57	0.215
Residuals	58	18843.43		
<i>Obligate dispersal</i>				
Management	1	10.74	0.09	0.764
Aspect	1	272.65	2.31	0.134
Management x Aspect	1	17.93	0.15	0.698
Residuals	58	6834.61		
<i>N-fixing</i>				
Management	1	2039.67	13.87	<0.001
Aspect	1	2156.88	14.67	<0.001
Management x Aspect	1	721.34	4.91	0.031
Residuals	58	8526.98		

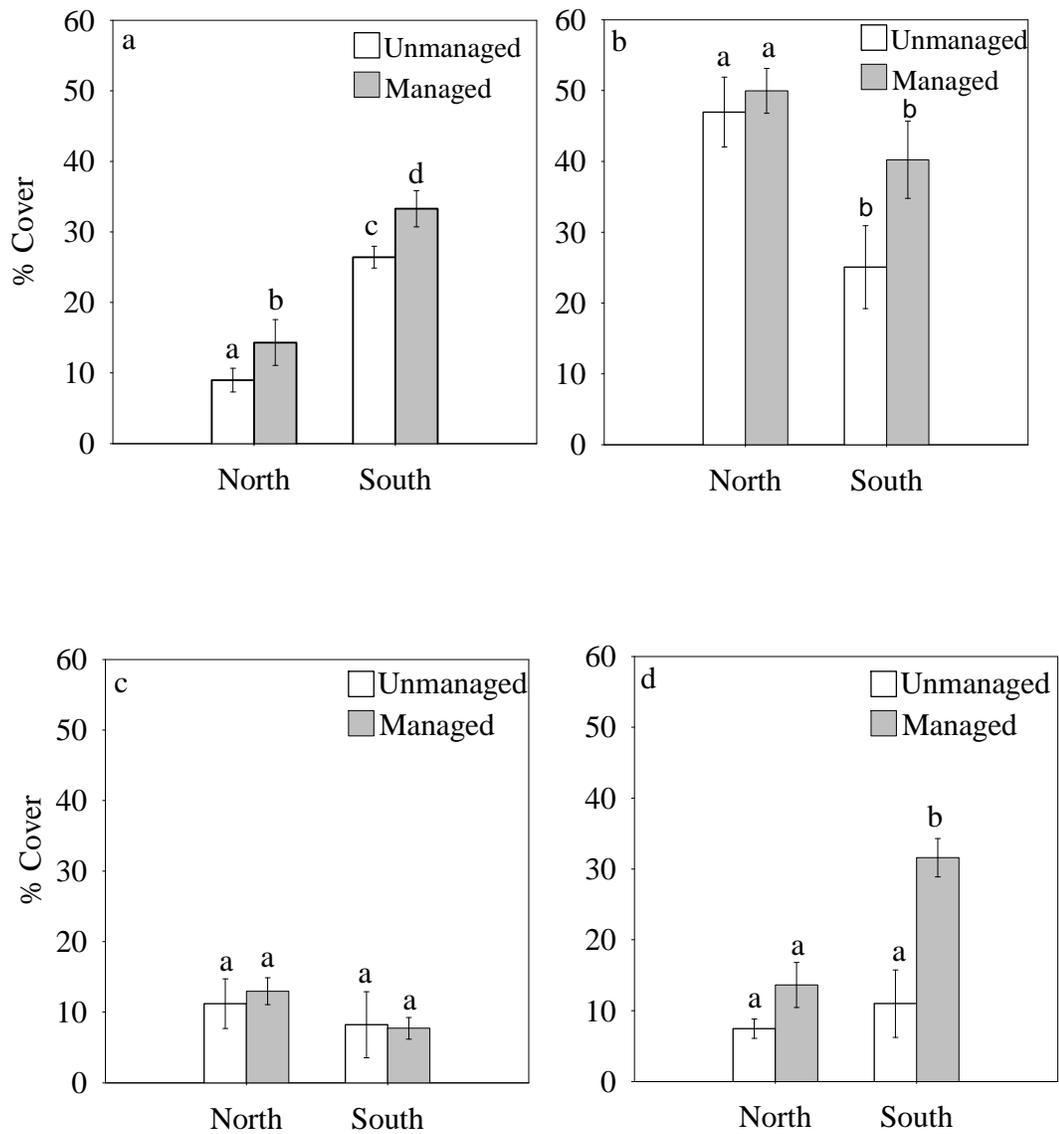


Fig. 2.9. Distribution of cover of (a) seed banking species, (b) resprouting species, (c) obligate seeding species, and (d) N-fixing species; broken down by aspect and management. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different ($p > 0.05$).

CHAPTER 3: TREE COMPOSITION TWENTY YEARS AFTER HIGH SEVERITY FIRE AND POST-FIRE MANAGEMENT IN THE DOUGLAS-FIR SERIES, KLAMATH REGION

INTRODUCTION

In the Klamath region of northern California, the distribution of tree species is strongly influenced by recurring fires (Taylor and Skinner 1998, 2003, Skinner et al. 2006). Over the last twenty years, for instance, more than 600 wildfires burned in the region. Some of these fires burned over long periods of time, killing the vegetation on hundreds of thousands of hectares. Federal land managers have dedicated many resources to control these fires first, and to restore or stabilize the fire damage landscape later. Special attention has been put into areas that have burned at high severity, where the common assumption has been that immediate actions are needed to restore (Rice and Chaney 1989, Holder 1990) and to hasten the return of complex conifer forests (Sessions et al. 2004). To best examine the possible effects of post-fire management on these forests, general patterns of species distribution related with the environmental gradient as well as the historical role of fire in the region will be addressed in the following paragraphs.

Forests in the Klamath region have a complex mix of species and vegetation types that reflect species distributions along moisture and altitudinal gradients (Whittaker 1960, Atzet et al. 1992). Atzet et al. (1992), for instance, described 16 vegetation series that occur across elevation and topographic position within the region. The Douglas-fir (*Pseudotsuga menziesii*) series, the most common on inland sites, constitutes a good example of the complex pattern of species composition that can be observed in region. This series ranges in elevation from 200 to 2000 m. It occurs on all aspects and on slopes from zero to 120 percent (Atzet et al. 1992). Changes in elevation and aspect, related with the

rugged topography that characterized the region, influence the composition of conifers and hardwoods species that share dominance with *P. menziesii*.

Forest structure and species composition in the Douglas-fir series has also been influenced by recurrent fires. Historically, most large wildfires have burned at low and moderate severities with smaller patches burning at high severity (Wills and Stuart 1994, Taylor and Skinner 1998, 2003, Odion et al. 2004, Skinner et al. 2006). The variable fire severity has created highly variable stand structures (Wills and Stuart 1994, Taylor and Skinner 1998). When large areas have been affected by high severity fires, however, major concern has arisen about the ability of these areas to regenerate and recover to pre-fire conditions without human intervention (Holder 1990). Few studies, however, have looked the patterns of tree regeneration after high severity fires in the region (Stuart et al. 1993, Hanson and Stuart 2005, Donato et al. 2006). Furthermore, only one to our knowledge has considered the influence of moisture and altitudinal gradients on natural regeneration patterns after high severity fires (Shatford et al. 2007). Shatford et al. (2007) showed that natural regeneration was abundant throughout the region and that moisture and elevation gradients played a central role influencing the distribution and abundance of conifer regeneration after high severity fires.

The uncertainty about the level of resilience that can be expected after high intensity fires in the region has resulted in a series of post-fire management activities intended to restore the fire damaged landscape. Although post-fire management activities usually vary with site characteristics and fire severity, common practices after stand replacing fires include in chronological order the removal of dead or dying trees (salvage logging), fuel reduction, conifer plantation, and shrub control (Rice and Chaney 1989, Holder 1990). Of this set of post-fire management activities, salvage logging is probably the one that has generated most attention. Salvage logging inherently involves the removal of large trees that play important roles in numerous biological processes and provide

habitat for a variety of species (Harmon et al. 1986, Canton 1996, Saab and Dudley 1998, Saab et al. 2007). Indirectly, salvage logging has been associated with soil erosion (Klock 1975) and increases in surface temperature (Sexton 1998) as well as changes in plant species diversity (Hanson and Stuart 2005) and reduction of conifer density shortly after salvage (Donato et al. 2006).

Salvage logging, however, is not carried out in isolation, but is part of a set of post-fire management activities. Conifer planting, for instance, constitutes a common activity after salvage logging. Tree planting after fire has been described as especially necessary to establish trees of specific species on areas where seed sources can be a limiting factor (Beschta et al. 2004, Franklin 2004). Few studies, however, have examined the effect of these post-fire management actions on hardwoods and conifers beyond the first decade of treatments (however, for conifers, see Bock et al. 1978). The effectiveness of planting is uncertain over time; several factors could limit conifer establishment and growth. At early stages, for instance, conifer seedling establishment and growth is sensitive to the microclimate of the sites and to shrub and hardwood competition (Hobbs 1992).

Shrubs and hardwoods have been considered a problem for conifer establishment after fires in the region (Tappeiner et al. 1992). Shrub and hardwood cover usually increases after fire through sprouting and seed germination in response to fire (Stuart et al. 1993, Hanson and Stuart 2005). Moreover, shrubs can reduce near-surface soil moisture content, limiting conifer establishment (Conard and Radosevich 1982). Several authors, however, have suggested that shrubs may aid seedling survival by reducing soil temperature or enriching available soil nitrogen (Conard and Radosevich 1982, Oakley et al. 2003, 2006). While the effects of shrubs and hardwoods on conifer establishment and growth are likely variable through time, detailed information about the density and frequency of conifer regeneration after large, intense forest fires and post-fire management has important implications for forest ecosystem in the region.

The purpose of this study was to investigate the effects of post-fire management on conifers and hardwoods under contrasting microclimatic conditions. We hypothesized that many of the tree compositional differences may be associated with post-fire management and the microclimate of the sites.

METHODS

Study Area

Our study was conducted in the Klamath National Forest, California. Forests within the study area have been classified as Douglas-fir-Sclerophyll by Whittaker (1960) and within the Douglas-fir (*Pseudotsuga menziesii*) Series by Atzet (1982). The Douglas-fir series in the Klamath region ranges in elevation from 200 to 2000 m (Atzet 1982). It occurs on all aspects and on slopes from 0 to 120 percent (Atzet et al. 1992). Fire has been a frequent disturbance in the study area. Taylor and Skinner (1998) reported median historic fire return intervals (FRIs) of 12-19 years in an area NE of Happy Camp, CA, the center of the study area. Precipitation ranges from about 1100 mm to 2000 mm; 90% of precipitation falls between October and May. The average July temperature for Happy Camp, 330 m in elevation, is 25.7°C.

Stand composition is variable and strongly influenced by aspect and elevation. At lower elevation on south aspects, Douglas-fir shares dominance with hardwoods such as black oak (*Quercus kelloggii*), white oak (*Quercus garryana*) and canyon live oak (*Quercus chrysolepis*). On northerly aspects, the hardwood component shifted from oaks to Pacific madrone (*Arbutus menziesii*) and then to tanoak (*Lithocarpus densiflorus*) on more mesic sites in the western portion of the study area. At middle and higher elevations, Douglas-fir and white fir (*Abies concolor*) are canopy dominants (Whittaker 1960, Sawyer and Keeler-Wolf 1995).

Site Selection

We identified candidate sites among old-growth Douglas-fir-dominated forests that burned at high severity during the 1987 fires. A total of 11 fires in three Ranger Districts of the Klamath National Forest were assessed. Candidate sites were divided into two major groups: sites that were not salvage logged or planted (unmanaged) after the fire and sites that were salvaged and planted (managed). Each group was then stratified by aspect. Only north or south aspect sites ($\pm 45^\circ$ from north or south) were considered as candidates; east and west aspects were not sampled. GIS layers of fire severity and cutting activities since 1970 were overlaid to identify openings created by high severity wildfire and to discriminate unmanaged from managed sites. A topographic layer was used to determine aspect and elevation. Aerial photographs from 1987 were assessed to confirm the presence of conifer snags following the fire and to indicate that the sites were burned at high severity. For managed sites, stand records were used to identify post-fire management activities. We chose managed sites that presented the most common combination of post-fire management activities: salvage, site preparation, tree planting, and shrub release. No additional treatments (e.g. herbicide application) were recorded. According to stand records, sites were salvage logged within the first three years after the fire (1988 to 1990). Site preparation included felling, slashing, and re-burning. Felling and slashing were carried out the same year that logging operations took place. Sites were re-burned to reduce fuel loads up to twelve months after salvage and then planted the following spring (Holder 1990). Seedlings were planted 2-4 years after fire, most often with a mixture of 60% Douglas-fir and 40% ponderosa pine (*Pinus ponderosa*) at a $\sim 3 \times 3$ m spacing. Shrub release, the cutting of shrubs within a 2 m radius around a conifer seedling, was performed two years after seedlings were planted.

Final evaluations were conducted on location to confirm the suitability of candidate sites prior to sampling. We evaluated the presence and diameter of conifer snags (for unmanaged sites), and stumps (for managed sites), soil type (non-ultramafic), and aspect (north or south).

Sampling

We sampled vegetation from mid June to September in 2005 and 2006, eighteen to nineteen years after the fires. A total of 62 sites (25 unmanaged and 37 managed) were sampled (Fig. 3.1; Table 3.1). Approximately 97% of the sample (60) was located in Happy Camp Ranger District. Two sites (1 unmanaged and 1 managed) were located in Cave Junction Ranger District.

The sampling plot was randomly located within openings created by high severity fire and sometimes salvage logging. Distance to seed source (unburned forest or unburned conifer tree) was never less than 20 m. We used a 12x40 m plot comprised of 30 4x4 m cells (Fig. 3.2). Plot-level measurements included elevation, slope, aspect and geographic location (UTM coordinates, model Garmin Legend). We tallied all conifers by height/DBH class and measured the diameter at breast height (DBH), total height, and percentage of live crown of the biggest conifer in each cell. For hardwood trees, species and size class data were collected on all managed sites and on 18 unmanaged sites (72% of the sites). Hardwoods were grouped in size classes with 0.5 m height intervals up to 1.5 m; trees or hardwoods clumps taller than 1.5 m were grouped in DBH classes with 2 cm intervals. In the case that hardwoods were resprouting with more than one trunk (clumps), only the biggest stem was measured and assigned to a DBH class. Hardwood cover by species as described below was estimated on all 62 sites.

Vegetation cover (%) was recorded for each species of woody plant present within the 12x40 m plot. To estimate vegetation cover, we divided the plot into thirds. In each third, we visually estimated percent cover of trees and shrubs by species. We used comparison charts to aid in assessing percent cover.

Moreover, to reduce individual bias, two people worked together to estimate cover.

Data Analysis

We divided the analysis into three sections: 1) conifers and hardwoods composition, 2) density and frequency of conifers, and 3) factors associated with the height of dominant conifers.

Hardwoods and Conifers Composition

The average number of species and diameter frequency distribution of conifers and hardwoods were used to give a general description. Differences in density of hardwoods between unmanaged and managed sites were tested using a two sample t-test (S-plus V.7). Compositional patterns of hardwoods and conifers based on cover data were examined using Nonmetrical Multidimensional Scaling (NMS, Kruskal 1964, Mather 1976). NMS uses an iterative search for an ordination solution with low stress, as measured by the relationship between ranked distances in the original multidimensional space and the ranked distance in the reduced dimensions of the ordination (McCune and Grace 2002). Ordination of community data benefits from NMS over other ordination techniques by having no assumptions of multivariate normality or linearity, and being robust to large numbers of zero values.

To reduce noise from rare species, those occurring in less than five percent of the plots (less than four plots) were deleted from the data set prior to running NMS. This action left a matrix of 62 plots and 15 species. Analyses were run using Autopilot with slow and thorough mode of NMS in PC-ORD version 5 (McCune and Mefford 1999), which used 250 runs with real data and 250 runs with randomized data for a Monte Carlo test of significance. Each NMS ordination used Sørensen's distance, and each began with a different random configuration. The best solution was assessed based on the final minimum stress

and the Monte Carlo test. The data were not relativized allowing differences in the total abundance of species to be expressed in the analysis.

Environmental and treatment variables were related to ordination results using overlay and joint plots. Environmental variables included: elevation, aspect (folded around the north-south line), slope (%), and heat load index. The heat load index represents the amount of heat a site potentially receives and is derived from models based on latitude, slope, and aspect (McCune and Keon 2002).

Unmanaged and managed were considered as treatments variables. For visual clarity, the ordination was rotated 26 degrees to align aspect with axis 2.

Non-metric Multi-response Permutation Procedure (MRPP, Mielke Jr 1984) was used to test for differences in hardwood and conifer composition between unmanaged and managed sites. MRPP has the advantage of not requiring distributional assumptions such as multivariate normality and homogeneity of variance that are seldom met with ecological community data (McCune and Grace 2002). The tightness of the groups was described with an *A* statistic, the chance-corrected within-group agreement. When $A = 0$, the groups are no more or less different than expected by chance; when $A = 1$, all sample units are identical within each group.

Density and Frequency of Conifer Regeneration

We tested for differences between unmanaged and managed sites in the density and spatial distribution of conifers. The total number of conifers per plot was used as a measure of density, while the frequency of cells in a plot with conifers gave us an idea of how the conifers were spatially distributed. Frequency was calculated as the proportion of the total number of cells on a site that were occupied by conifers (e.g. 30 cells occupied represented a frequency of 100%).

We tested for differences in density and frequency at three different levels: 1) all conifer species; 2) *Pseudotsuga menziesii* and *Pinus ponderosa* together, and 3) *Pseudotsuga menziesii* and *Pinus ponderosa* individually. Stand records of

the areas that were managed after the fires mentioned that the two species planted on the sites were *Pseudotsuga menziesii* and *Pinus ponderosa*. This stratification of the analysis allowed us to better represent the possible effect of post-fire management on the density and frequency of conifers. The term seedling in this section was used to represent not only small trees but also trees taller than 1.5 m.

In all cases, we used a two-way analysis of variance (ANOVA) with management and aspect as explanatory variables and density or frequency of conifers as a response variable. Interactions between management and aspect were tested at each level. To better meet the assumptions of normality and equal variance, transformations were performed before conducting the ANOVA; density was log-transformed, while frequency was arc-sine transformed.

Factors Associated with the Height of Dominant Conifers

We explored ways in which post-fire management, abiotic factors and biotic factors might affect the height of dominant conifers. Dominant conifers were defined as the tallest conifer in each cell (i.e. 30 cells in each plot). Heat load index was used as an abiotic index and percent cover of different life form groups (hardwoods and shrubs) were used as biotic indexes of competition for resources. Additionally, the possible influences of N-fixing species cover on height of conifers were tested. The average height of the dominant conifers in each plot was used as a response variable. In 32% of the cases the height of dominant conifers were not recorded (401 out of 1235), we estimated height using equations that predict height as a function of DBH. Parameter estimates used in the height equation were obtained from a larger data set (Shatford unpublished data; Hann unpublished data). Sample size, parameter estimate, and percentage of variation explained (R^2) are presented on Table 3.2.

A priori hypotheses were proposed (Table 3.3) and used to develop a set of candidate regression models that better explain the height of dominant conifers. All candidate models were created from some combination of the following

explanatory variables: heat load, cover of hardwoods, cover of shrubs, cover of N-fixing species, and management (Table 3.4). Management was the only categorical variables used in the models (0= unmanaged; 1= managed). The assumptions of linearity and constant variance were checked prior to examining the results by visually examining residual plots for each model and scatter plots of the response against all explanatory variables. Log-transformations were used when necessary to meet the assumptions of linearity and constant variance for a given variable.

After *a priori* hypothesis models were developed, we used a model selection technique based on Akaike's Information Criteria (AIC) with a correction factor for small sample size (AIC_c) to rank the models in terms of their ability to explain the patterns inherent to the data. AIC_c was defined as

$$AIC_c = -2(\ln L) + 2k + \frac{2k(k+1)}{n-k-1}$$

Where $\ln(L)$ is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates for a given model, k is the number of parameters from that model, and n is the sample size. We selected the best model based on minimum ΔAIC_c . Models were ranked and compared using ΔAIC_c and Akaike weights (Burnham and Anderson 1998). ΔAIC_c was calculated as the difference between any given model (i) and the model with the lowest AIC_c . Models with delta values within 2 units of the best model are considered to be supported by the data while models within 2-4 delta values of the best model are considered to be moderately supported. Akaike weights, w_i , are defined as the weight of evidence for a model (i) being the best model in the set. The weights of all models in a set sum to 1. Akaike weights represents the relative likelihood for a model given the data and the set of models tested. Regression analyses for model selection were conducted using PROC MIXED with maximum likelihood

estimation methods in SAS v9.1 (SAS Institute, Cary, NC, USA). Potential correlations between variables were examined using S-plus v.7 (Insightful Corporations, 2005). All pairs of explanatory variables had correlation coefficients below 0.5, and thus no pair of explanatory variables had strong enough intercorrelation to cause variance inflation if they occurred in the same model (Burnham and Anderson 1998).

The site selection for this study was designed so that the sample sites were representative of Douglas-fir series that burned at high severity on north and south aspects in the Klamath Mountains. However, this was an observational study, and thus causality between the explanatory variables and the response cannot be inferred.

RESULTS

Conifers and Hardwoods Composition

Ten species of conifers were present on unmanaged sites and nine species were present on managed sites (Table 3.5). The average number of conifer species per plot was 2.5 (range 1-5) on unmanaged and 2.3 (range 1-4) on managed sites. Small seedlings of three-needle pines were recorded only to genus (*Pinus* sp.). Such seedlings appeared on three unmanaged and one managed sites. Diameter frequency distribution of conifers in unmanaged and managed sites showed similar distribution patterns with larger number of individuals in the smaller diameter classes (Fig. 3.3). Ten species of hardwoods were present on unmanaged sites and nine on managed sites. The average number of hardwood species per plot was 3 (range 1-6) on unmanaged and 3.2 (range 1-7) on managed sites. Density of hardwoods was 325 trees/ha (range 0-1187) on unmanaged sites and 268 trees/ha (range 0-979) on managed sites (Table 3.5.). No significant differences were found in the density of hardwoods between unmanaged and managed sites ($p=0.8$ from a two-sample t-test). There was evidence that the frequency distribution among sizes classes differed when comparing unmanaged

and managed sites (Fig. 3.4). More data, however, would be necessary to confirm this trend.

Conifers and hardwoods are major components of forests in the Klamath region; however, twenty years after high severity wildfire, their cover was small relative to shrubs, the main component of the plant community (see Chapter 2). Mean densities of conifers and hardwoods (Table 3.5) suggested a possible effect of post-fire management on *Pinus attenuata* and *Lithocarpus densiflorus*, but the distribution of these and other less abundant species was not normal which limited our ability to establish an association between post-fire management and a shift in abundance of these species. Furthermore, ordination results described below suggest no differences in conifer and hardwood composition between unmanaged and managed sites.

Composition of conifers and hardwoods on the sites were associated with aspect and elevation (Fig. 3.5). The NMS Autopilot in PC-ORD chose a 3-dimensional solution as providing a considerable and statistically significant reduction in stress as compared with randomized data (final stress= 15.42 $p=0.004$ for all axes). The final ordination explained 78% of the variation in the data set. Axis 1, representing 24% of the variation, was aligned with elevation ($r = 0.642$). *Pinus* sp., *Pinus ponderosa*, and *Pinus lambertiana* were positively associated with elevation, while *Quercus chrysolepis*, *Arbutus menziesii*, and *Lithocarpus densiflorus* were most negatively associated with elevation (Table 3.5.). Axis 2, representing 36% of the variation, was aligned with aspect ($r = -0.444$), thus contrasting north and south aspects. *Pseudotsuga menziesii*, *Acer macrophyllum*, and *Abies concolor* were associated with north aspects while *Quercus kelloggii*, *Quercus chrysolepis*, and *Pinus attenuata* were associated with south aspects. No measured variable was associated with axis 3, which represented 18% of the variation. Furthermore, no patterns associated with post-fire management were evident on the ordination of plots in conifer and hardwood species space (Fig. 3.5). This paralleled the results from MRPP of no differences in conifer and

hardwood composition between unmanaged and managed sites ($A = 0.004$; $p = 0.158$ from MRPP).

Density and Frequency of Conifer Regeneration

Total conifer density in unmanaged sites was 4425 seedlings/ha (range 20-22062) while in managed sites was 3543 seedlings/ha (range 187-14416; Table 3.5). We found convincing evidence that aspect alone led to significant differences in conifer density ($F_{1,58} = 15.8$; $p < 0.001$), while there was no significant effect of post-fire management on conifer density at the total conifer seedling level ($F_{1,58} = 2.04$; $p = 0.158$). There was also no significant interaction between aspect and post-fire management detected at this or the two other levels (Table 3.6). *P. menziesii* and *P. ponderosa* combined densities resulted in 2407 seedlings/ha (range 0-7437) in unmanaged sites and 2383 seedlings/ha (range 41-5875) in managed sites. No significant association between the differences in density and management were detected at this level ($F_{1,58} = 3.59$; $p = 0.063$). Results at the species level varied for the two species considered. *P. menziesii* density had 2109 seedling/ha (range 0-48625) on unmanaged sites and 1976 seedlings/ha (range 20-5833) on managed sites. No evidence of post-fire management effect was detected for *P. menziesii*'s density ($F_{1,58} = 0.86$; $p = 0.357$); however, there was substantial evidence of positive north aspect effect on *P. menziesii*'s density ($F_{1,58} = 29.19$; $p < 0.001$). In contrast, both post-fire management ($F_{1,58} = 6.74$; $p = 0.011$) and aspect ($F_{1,58} = 3.90$; $p = 0.053$) led to significant differences on *P. ponderosa*'s density (Table 3.6). This suggests that post-fire management has increased the density of *P. ponderosa*, especially in south aspects (Fig. 3.6)

Average conifer frequency was 58% for unmanaged sites (range 3-100%) and 75% (range 23-100%) for managed sites. We found strong evidence that differences in frequency of conifers were associated with aspect ($F_{1,58} = 8.61$; $p = 0.004$) and management ($F_{1,58} = 11.21$; $p = 0.001$). The average frequency of *P. menziesii* and *P. ponderosa* together was 49% (range 0-100) for unmanaged sites

and 70% (7-100) for managed sites. Differences in frequency at this level were also associated with aspect and management (Table 3.7). At the species level, the effect of post-fire management was more evident on the frequency of *P. ponderosa* ($F_{1,58}=8.61$; $p=0.004$) than on the frequency of *P. menziesii* ($F_{1,58}=3.11$; $p=0.083$). The effect of aspect was significant for both species (Table 3.7; Fig. 3.7).

Factors Associated with the Height of Dominant Conifers

The average height of dominant conifers on unmanaged sites was 2.5 m (SE= 0.34 m) and 3.6 m (SE= 0.30 m) on managed sites. $\Delta AICc$ values suggest a model with two variables, management and cover of N-fixing species, as the best model for the data (Table 3.8). However, the evidence ratio (w_1/w_2) for the best model versus the second and third ranked models was 2.57 and 2.61 respectively. This relatively weak support for the best model suggests that we should expect to see considerable variation in the selected best model from sample to sample if more independent samples were considered. On the other hand, the evidence ratio for the best model versus the null model (0.394/0.0039) is 99, giving strong evidence against the null model.

Overall, $AICc$ values suggest that the cover of N-fixing species and management were important variables positively associated with the height of conifers (Table 3.8). The importance of these two variables was further supported by Akaike weights (Table 3.8). The combined Akaike weight, or importance value, of all models that included N-fixing, post-fire management (management 1), or both as predictors was 0.94 out of a possible total weight of 1.00, indicating that 94% of the weight in favor of any of the 14 candidate models was for the models containing these variables. The 95% confidence intervals for the parameter estimates of N-fixing cover (parameter estimate = 1.19; SE = 1.07) and management (parameter estimate for managed sites = 1.40; SE = 1.07) did not overlap zero providing additional support for the selection of the top candidate

model. Thus, conifer height was positively associated with the cover of N-fixing species and with post-fire management activities. Heat load also appeared in one of the top three models, but 95% confidence intervals for its parameter estimate overlapped zero (parameter estimate=0.32; SE = 0.48) providing little support for the inclusion of heat load. Models that considered shrub cover and hardwood cover as predictors had high ΔAICc values relative to the top three models which gave little support for the competition for resources hypotheses.

DISCUSSION

Throughout this study, the effect of post-fire management on tree species was mediated by the microclimate of the sites. To best examine the implications of our results, we have separated this discussion into three sections: 1) conifers and hardwood composition, 2) density and frequency of conifer regeneration, and 3) factors associated with the height of dominant conifers.

Conifers and Hardwoods Composition

The composition of conifers and hardwoods observed in this study is consistent with other studies indicating that aspect and elevation play an important role in the distribution of these species (Whittaker 1960, Atzet et al. 1992, Ohmann and Spies 1998). No effect of post-fire management was detected, however, on the composition of conifers and hardwoods. Considering that conifers and hardwoods differ in the way they colonize the sites after high severity fires, each group will be addressed separately in the following paragraphs.

Conifer establishment after high severity fires depends almost exclusively on off site seed sources (with the exception of *Pinus attenuata*). Post-fire management, is expected to have a negative influence on the abundance of conifer regeneration shortly after salvage (Sexton 1998, Donato et al. 2006), but also is expected to increase the abundance of conifers by planting activities. Thus, we

can presume that one management activity may have counteracted the other. This situation, added to the abundant natural regeneration observed in the region, may have helped to increase the similarities between unmanaged and managed sites in terms of conifer density and composition. Further review of the effect of post-fire management on conifers is presented in the next section.

On the other hand, hardwood establishment after disturbance is mainly through resprouting (Tappeiner et al. 1992, Fites-Kaufman et al. 2006), although occasional regeneration from seeds can occur. Furthermore, several authors have reported positive responses of hardwood species to logging and fires in the region (Strothmann and Roy 1984, Tappeiner et al. 1992, Wills and Stuart 1994). This capacity of hardwood species to resprout may explain the similarities in hardwood composition between unmanaged and managed sites. Post-fire management includes salvage logging and the use of fire to reduce fuels after salvage. Our results suggest that hardwoods are quite resilient to these post-fire management activities in the long term. Moreover, our results suggest that the effect of post-fire management on hardwoods could be associated with changes in the size distribution rather than in composition. More data, however, are needed to test this hypothesis.

Over the last twenty years, our view of post-disturbance plant communities has changed, mostly due to the growing accumulation of observations of extreme disturbance events. One of these changes concerns the role of hardwoods in the post-disturbance setting. We know now that hardwood species may not only contribute to stabilized soil conditions and soil microbes after high severity fires (Perry 1994) but also constitute important wildlife habitat (Apfelbaum and Haney 1981). There is, however, little information of hardwood dynamics after high severity fires, including changes in size distribution, cover composition, and distribution of hardwoods in relation to topography. Our study has provided some preliminary insights into these patterns.

Density and Frequency of Conifer Regeneration

Despite the importance of assessing the effect of post-fire management on conifer species as a function of microenvironment conditions, no previous study, to our knowledge, has studied the effects of post-fire management while taking microclimate into account. Furthermore, little information is available on the effect of post-fire management twenty or even fifteen years after the treatments. Our findings provide evidence that post-fire management has little effect on conifer density, while having strong effects on frequency, a measure of spatial distribution in this study. At the same time, our results show strong effects of differences in microclimate have on both density and frequency of conifer regeneration. We will examine the implications of these results in the following paragraphs.

Results showing similar numbers of conifers between unmanaged and post-fire managed sites were reported two years after management in southern Oregon (Sexton 1998) and fifteen years after management in northeast California (Bock et al. 1978). As in our study, Bock (1978) found that post-fire management had stronger effects on the spatial distribution of conifers than on density.

The change in spatial distribution of conifers that results from post-fire management can be seen from different perspectives; one of them is the possible influence that these changes could have on fire characteristics. Feedback between vegetation structure and frequency, spread, and severity of disturbance such as fire has been reported by various authors (Whelan 1995, Taylor and Skinner 1998, 2003, Fites-Kaufman et al. 2006). In fire-prone ecosystems, such as the mixed conifer forest in the Klamath region, feedback between vegetation structure and fire characteristics deserve even more consideration. A recent study, for instance, has suggested that areas that were salvage-logged and planted burn more severely fifteen years later than comparable unmanaged areas (Thompson et al. 2007). As explanation for this difference in severity, Thompson et al. (2007) suggested that

the changes in fuel profile compared to that found in naturally regenerated areas, may have reduced the average burn severity in unmanaged areas.

A mixed fire regime of mostly low to moderate severity fires is typical of the Douglas-fir series in the Klamath region (Taylor and Skinner 1998, 2003, Skinner et al. 2006). Whether post-fire management could lead to changes in the fire regime or not, is beyond the scope of this research. However, the changes in fuel profile, at least at the conifer level, that can be attributed to post-fire management should be considered by forest managers when planting is part of the post-fire management activities.

While the effect of post-fire management was more evident on frequency than on density, the high density of conifers on naturally regenerated sites and managed sites suggest that these forests are quite resilient with respect to intense natural disturbance. Abundant conifer regeneration has been reported to occur shortly after stand replacing fires (Donato et al. 2006) and continues to occur nineteen years after stand replacing fires in the Klamath region (Shatford et al. 2007). The dense conifer regeneration reported here in both unmanaged and managed sites, as well as the diameter frequency distributions, support the idea that natural conifer regeneration occurs continuously (Gray and Franklin 1997, Nathan and Muller-Landau 2000, Shatford et al. 2007).

At the species level, changes in density and frequency associated with post-fire management were more evident for *Pinus ponderosa* than for *Pseudotsuga menziesii*. This is not a surprising result considering that *P. menziesii* is the most abundant conifer species in the unburned forests (Rice and Chaney 1989, Holder 1990), which may also imply more available seed sources. Shatford et al. (2007), for instance, reported that within the Douglas-fir series 51% of the seedlings were *P. menziesii*, while only 14% of the seedlings were *P. ponderosa*. Hence, planting would be expected to have a stronger effect on the abundance of *P. ponderosa* than on *P. menziesii*.

Overall, conifer regeneration was strongly influenced by environmental conditions. The general pattern observed was lower conifer regeneration on southerly aspects, which is probably related to stressful environmental conditions. Drought stress and soil surface temperature will generally be higher on south aspects (Rosenberg et al. 1983). The strong effect of aspect was particularly evident for *P. menziesii*. This result is consistent with reports that found soil surface temperature to exceed temperatures lethal to *P. menziesii* seedlings on south facing clear-cuts almost twice as frequently as on north facing clear-cuts (Silen 1960). In contrast, *P. ponderosa* can survive in xeric environment by maintaining high water use efficiencies and deep root systems (Kolb and Robberecht 1996).

Factors Associated with the Height of Dominant Conifers

Our results support a facilitative effect of *Ceanothus* spp., N-fixing species, and post-fire management on conifer height; however, more specific data are required to adequately test this hypothesis. Shrubs from the genus *Ceanothus* often constitute the dominant shrub species after fires in the Klamath region (Hobbs et al. 1992, Shatford et al. 2007). Its presence on the post-fire setting can have both negative and positive effects on conifer growth. Negative effects include the reduction of conifer growth due to competition for soil moisture (Conard and Radosevich 1982, Gray et al. 2005) and light (Oakley et al. 2006). Positive effects may include facilitation of conifer establishment and growth by increasing surface soil moisture (Scott 1970). Furthermore, conifers may also benefit from enhanced soil fertility associated with an N-fixing species (Oakley et al. 2003).

Competition and facilitation are complex processes and the occurrence of one or the other depends on several factors such as life stages, densities, and sizes of the interacting species (Callaway and Walker 1997). A recent study has shown that the effects of *Ceanothus* on conifer growth was positive when the leader

remained above the *Ceanothus* crown while negative effects on growth were observed when the leader remained below the *Ceanothus* crown (Erickson and Harrington 2006). This agrees with our results, where the average height of the dominant conifers in both unmanaged and managed sites exceeded the height of *Ceanothus* (see Chapter 2).

Post-fire management was also associated with a positive effect on the height of the dominant conifers. Although significant height differences were detected between unmanaged and managed sites, a difference of a little more than one meter on average raises new questions: does a statistically significant difference in height represent also an ecological difference? Is one meter average difference a large enough difference to argue that post-fire management has accelerated the return of complex conifer forest?

Post-fire management, as any type of management, is a dynamic process. Management activities are likely to be continued in most of the managed sites analyzed in this study. These activities could lead to bigger differences between unmanaged and managed sites in terms of tree composition and, perhaps, in terms of conifer sizes. Twenty years after high severity fires and post-fire management is a short time to answer fully the questions mentioned above, but it was probably the perfect timing to see the resilience of these forests to high severity fires and post-fire management.

Fires are important factors shaping the structure of the forests in the region. Little, however, is known about the processes of recovery and structure of conifers and hardwoods beyond the first decade after high severity fires and post-fire management. We believe our study has helped to further evaluate the role of post-fire management in the recovery process.

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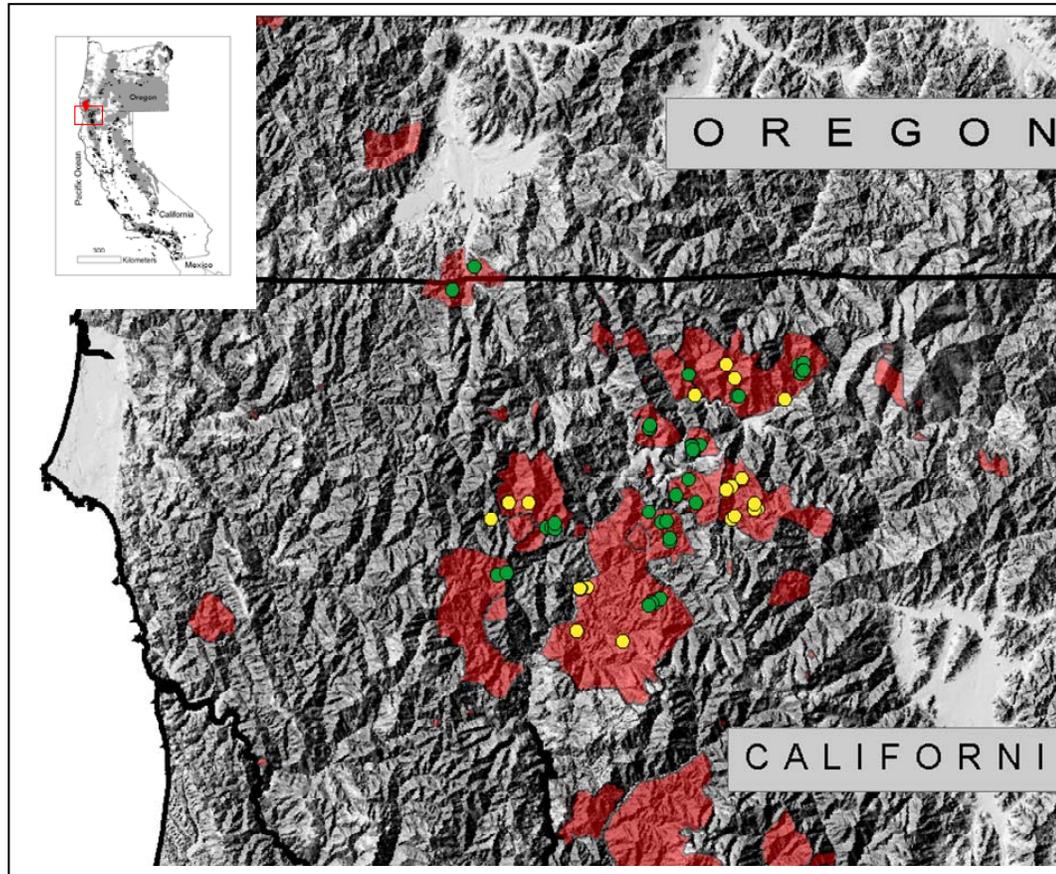


Fig. 3.1. Study site location. Yellow dots indicate unmanaged sites and green dots indicate managed sites. Red polygons indicate wildfires dating back to 1970.

Table 3.1. Summary of site characteristics. Mean values (range) are presented

	Unmanaged	Managed
Total number of plots	25	37
North aspect	16	23
South aspect	9	14
Slope (% , range)	57 (18-100)	60 (28-80)
Elevation (m, range)	993 (374-1506)	913 (431-1496)

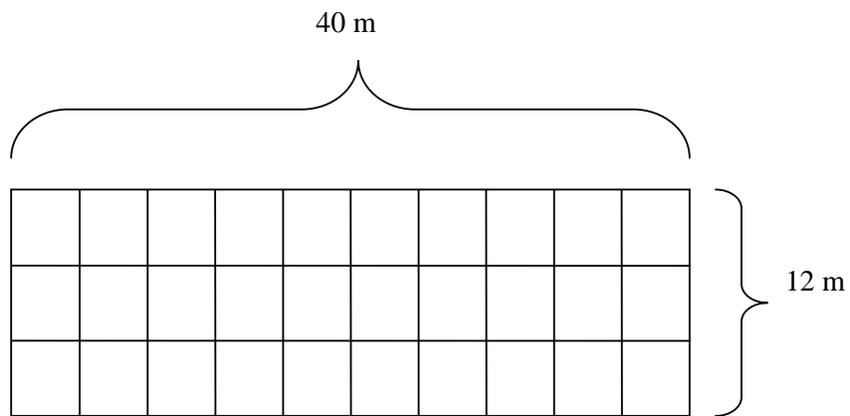


Fig. 3.2. Plot dimension with basic cell configuration for one sampling unit, a plot.

Table 3.2. Parameters used to estimate the height of conifers as a function of DBH. Equation form $\mu\{Height|DBH\} = \beta_0 + \beta_1 DBH$; where $\beta_0 = 135$; number of observations (n), parameter estimate (β_1), proportion of variation explained (R^2).

Specie	n	β_1	R^2 (%)
<i>Abies concolor</i>	112	66.49	95
<i>Calocedrus decurrens</i>	299	40.48	97
<i>Pinus ponderosa</i>	213	42.49	93
<i>Pseudotsuga menziesii</i>	2071	66.88	96

Table 3.3. List of *a priori* hypotheses used to generate AIC_c candidate models.

Hypothesis 1	Height of conifers varies with management and microclimate, with the highest conifers occurring in managed sites with low heat load index.
Hypothesis 2	Height of conifers increased with decreasing values of heat load.
Hypothesis 3	Height of conifers increased with decreasing vegetation cover (hardwood cover and shrub cover).
Hypothesis 4	Height of conifers increased with increased cover of N-fixing species

Table 3.4. Candidate models developed to test *a priori* hypotheses.**Null Model**

1) Intercept only

One factor models

2) Management

3) Heat load

4) N-fixing cover

5) Hardwood cover

6) Shrub cover

Two factor models

7) Management + Heat load

8) Management + N-fixing cover

9) Management + Hardwood cover

10) Management + Shrub cover

11) Hardwood cover + Shrub cover

12) Heat load + N-fixing cover

Three factor models

13) Management + Heat load + N-fixing cover

14) Management + Heat load + Hardwood cover

Table 3.5. Mean density (range) of conifers and hardwood species per hectare in unmanaged and managed sites. Correlations with ordination axes are also shown; only species that appeared in more than 5% of the sample (3 plots) were used in the ordination analysis.

Life Form	Species	Unmanaged		Managed		Correlation with Axis	
		North	South	North	South	1	2
Conifers	<i>Abies concolor</i>	1608 (0-18062)	12 (0-62)	909 (0-8458)	0	0.173	0.288
	<i>Abies magnifica</i>	0	2 (0-20)	0	0		
	<i>Abies procera</i>	0	0	7 (0-166)	0		
	<i>Calocedrus decurrens</i>	155 (0-1312)	30 (0-208.33)	19 (0-104)	45 (0-229)	-0.004	0.012
	<i>Pinus attenuata</i>	47 (0-375)	51 (0-166)	34 (0-520)	104 (0-1416)	-0.027	-0.167
	<i>Pinus jeffreyi</i>	16 (0-208)	0	3 (0-62)	1 (0-20)		
	<i>Pinus lambertiana</i>	30 (0-229)	7 (0-62.5)	22 (0-166)	15 (0-83)	0.195	0.136
	<i>Pinus sp*</i>	55 (0-395)	5 (0-41)	1 (0-20.8)	0	0.339	-0.054

Table 3.5. (Continued)

Life Form	Species	Unmanaged		Managed		Correlation with Axis	
		North	South	North	South	1	2
Conifer	<i>Pinus ponderosa</i>	197 (0-2562)	102 (0-479)	140 (0-666)	268 (20-937)	0.268	-0.076
	<i>Pseudotsuga menziesii</i>	1553 (20-4875)	556 (0-2416)	1704 (145-5833)	272 (20-1270)		
	<i>Taxis brevifolia</i>	1 (0-20)	0 0	0 0	0 0		
	<i>All conifers combined</i>	3661 (20-22062)	764 (20-3145)	2839 (313-14416)	704 (188-1458)		
	<i>P. menziesii and P. ponderosa</i>	1750 (20-7438)	658 (0-2896)	1844 (313-5875)	540 (42-1354)		
Hardwood	<i>Acer macrophyllum</i>	13 (0-104)	0 0	21 (0-125)	3 (0-41)	-0.119	0.351
	<i>Arbutus menziesii</i>	198 (0-1187)	24 (0-83)	79 (0-562)	80 (0-437)	-0.510	0.118
	<i>Chrysolepis chrysophylla</i>	46 (0-312)	3 (0-20)	4 (0-41)	0 0	0.156	-0.002

Table 3.5. (Continued)

Life Form	Species	Unmanaged		Managed		Correlation with Axis	
		North	South	North	South	1	2
Hardwood	<i>Cornus nuttallii</i>	8 (0-62)	0 0	0 0	0 0	0.175	-0.071
	<i>Lithocarpus densiflorus</i>	2 (0-20)	18 (0-83)	15 (0-208)	54 (0-479)	-0.403	0.162
	<i>Quercus chrysolepis</i>	158 (0-1000)	107 (0-583)	75 (0-500)	147 (0-937)	-0.557	-0.483
	<i>Quercus garryana</i>	0	0	1 (0-20)	9 (0-125)		
	<i>Quercus kelloggii</i>	2 (0-20)	21 (0-83)	3 (0-20)	91 (0-416)	-0.259	-0.377
	<i>Umbellularia californica</i>	0	9 (0-41)	0	0	-0.069	0.098
			0		0		

* Small three-needle pine seedlings

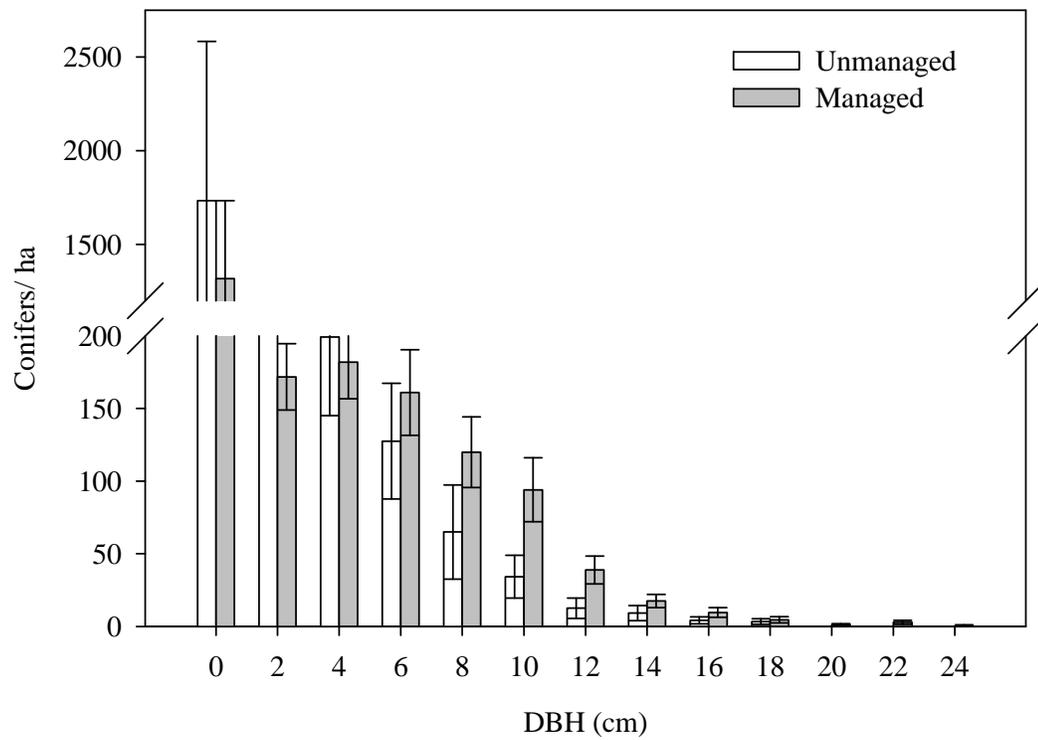


Fig. 3.3. Diameter frequency distribution of all conifer species in unmanaged and managed sites. Bars represent mean and error bars are standard errors.

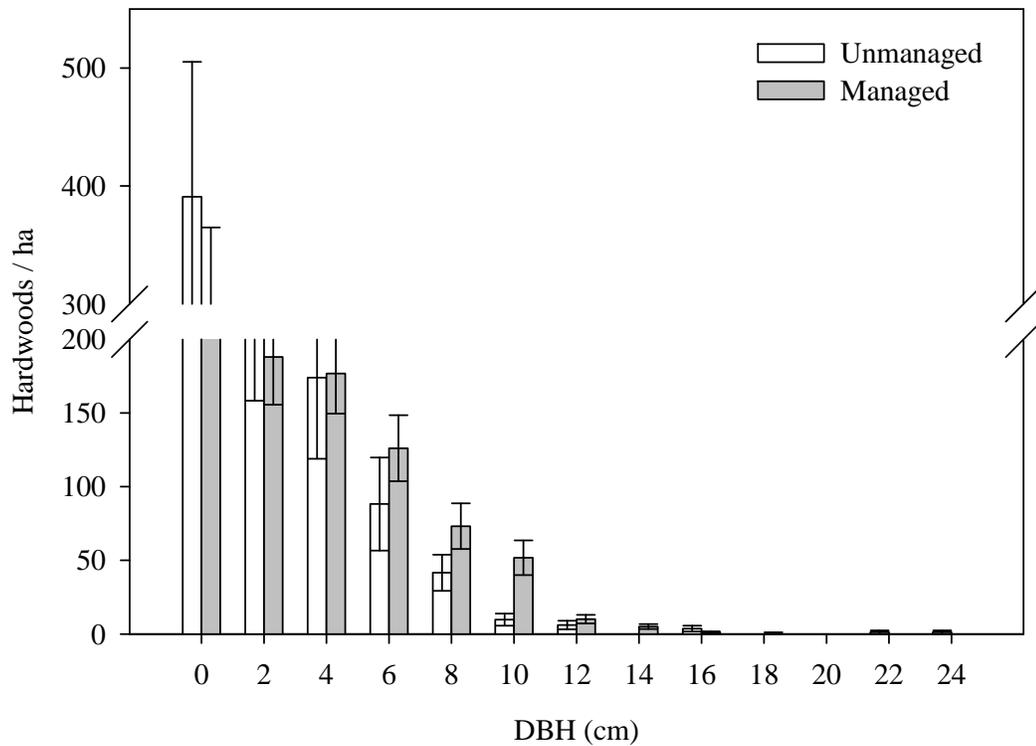


Fig. 3.4. Diameter frequency distribution of all hardwood species in unmanaged and managed sites. In case of resprouts, only the biggest stem was measured. Bars represent mean and error bars are standard errors.

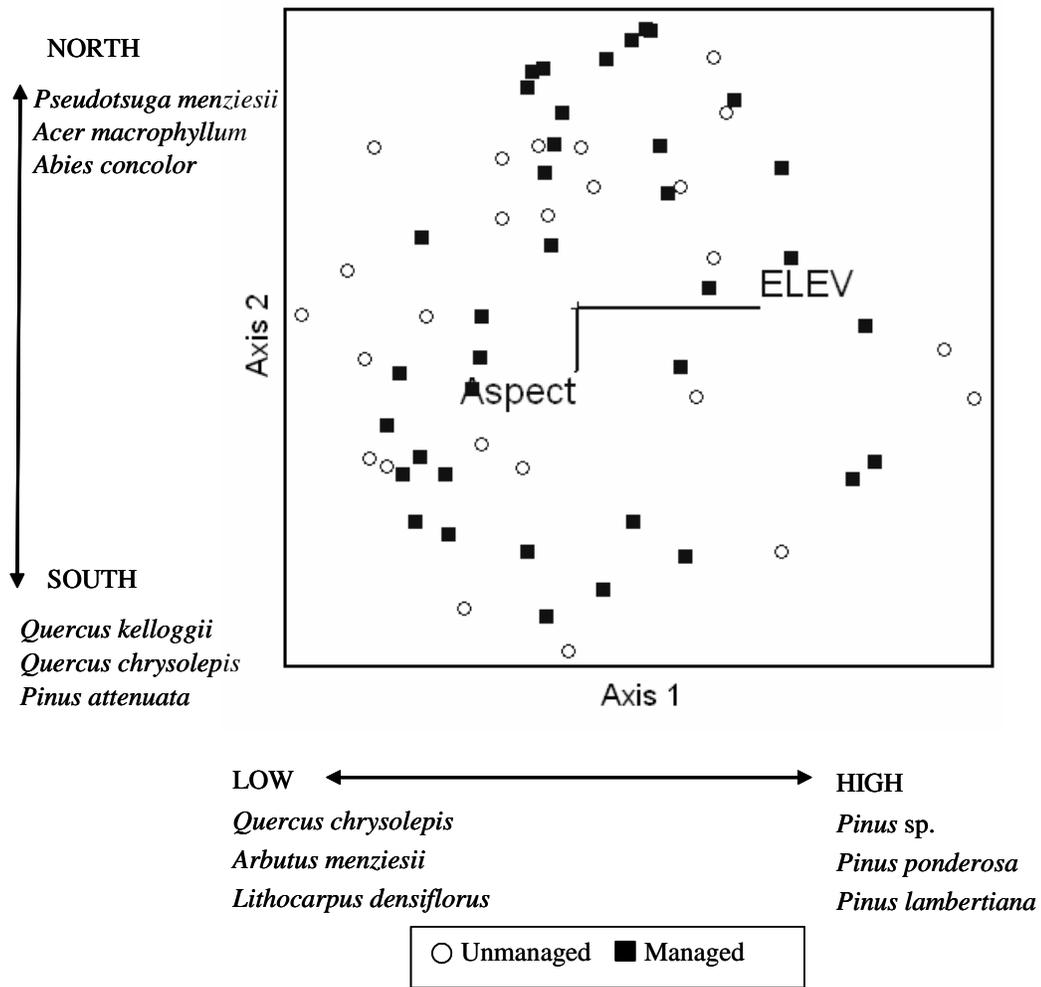


Fig. 3.5. NMS ordination of sample units in hardwood and conifers species space based on 15 species that occur in more than 5% of the sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with $r^2 > 0.100$. Ordination was rotated 26 degrees to align aspect with axis 2.

Table 3.6. Two-way ANOVA analyses of density of conifers for all conifer species, the combination of densities of *Pseudotsuga menziesii* and *Pinus ponderosa*, and *Pseudotsuga menziesii* and *Pinus ponderosa* individually. Density was log transformed.

Source of Variation	DF	SS	F	P
<i>All conifer Species</i>				
Management	1	3.12	2.04	0.158
Aspect	1	24.12	15.8	<0.001
Management x Aspect	1	0.32	0.21	0.649
Residual	58	88.52		
<i>Pseudotsuga menziesii</i> and <i>Pinus ponderosa</i>				
Management	1	4.52	3.59	0.063
Aspect	1	22.14	17.58	<0.001
Management x Aspect	1	0.07	0.04	0.832
Residuals	58	73.04		
<i>Pseudotsuga menziesii</i>				
Management	1	1.2	0.86	0.357
Aspect	1	40.84	29.19	<0.001
Management x Aspect	1	0.66	0.47	0.495
Residuals	58	81.14		
<i>Pinus ponderosa</i>				
Management	1	9.29	6.74	0.011
Aspect	1	5.37	3.9	0.053
Management x Aspect	1	1.76	1.28	0.262
Residuals	58	79.89		

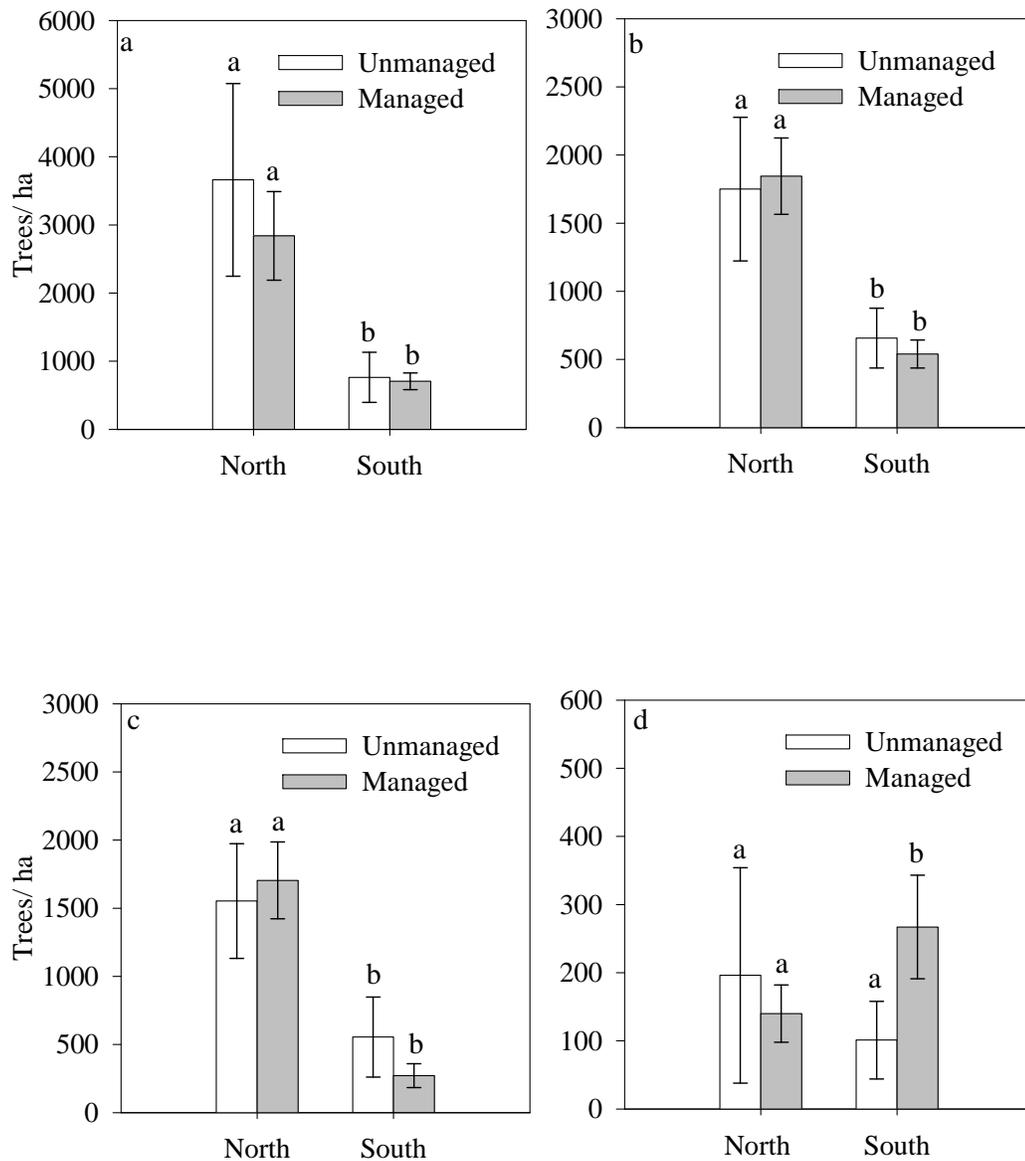


Fig. 3.6. Density of conifers (a) all conifer species combined (b) *P. menziessii* and *P. ponderosa* together (c) *P. menziessii*, and (d) *P. ponderosa*. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different ($p > 0.05$). Numbers are in the original scale.

Table 3.7. Two-way ANOVA analyses of conifer frequency for all conifer species, the combination of frequencies of *Pseudotsuga menziesii* and *Pinus ponderosa*, and *Pseudotsuga menziesii* and *Pinus ponderosa* individually. Frequency was arcsine transformed.

Source of Variation	DF	SS	F	P
<i>All conifer Species</i>				
Management	1	0.73	6.15	0.016
Aspect	1	2.45	11.21	<0.001
Management x Aspect	1	0.08	0.36	0.415
Residual	58	6.85		
<i>Pseudotsuga menziesii</i> and <i>Pinus ponderosa</i>				
Management	1	1.02	7.57	0.007
Aspect	1	2.43	18.07	<0.001
Management x Aspect	1	0.13	0.93	0.339
Residuals	58	7.80		
<i>Pseudotsuga menziesii</i>				
Management	1	0.42	3.06	0.085
Aspect	1	4.23	30.95	<0.001
Management x Aspect	1	0.31	2.31	0.133
Residuals	58	7.94		
<i>Pinus ponderosa</i>				
Management	1	0.50	5.46	0.020
Aspect	1	0.33	3.57	0.063
Management x Aspect	1	0.09	1.01	0.319
Residuals	58	5.40		

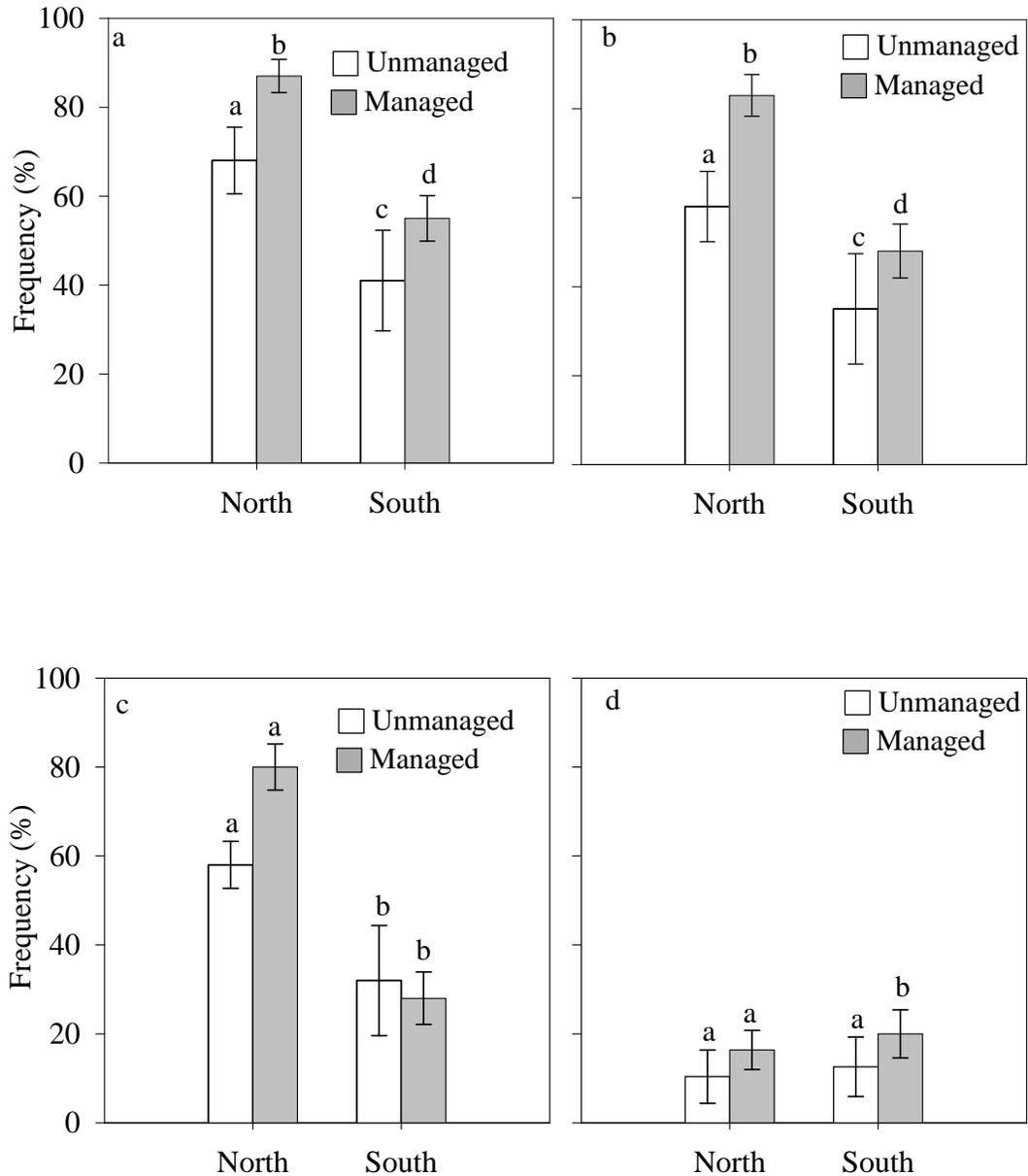


Fig. 3.7. Frequency of conifers (a) all conifer species combined (b) *P. menziessii* and *P. ponderosa* together (c) *P. menziessii*, and (d) *P. ponderosa*. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different ($p > 0.05$). Numbers are in the original scale.

Table 3.8. Summary of 14 regression models explaining height of dominant conifers, including the total number of parameters (K), the negative 2 log-likelihood (2LOGL), AIC_c values, ΔAIC_c , followed by Akaike weights (W_i). Models are ordered in terms of ΔAIC_c .

Model	K	2LOGL	AIC_c	ΔAIC_c	W_i
Management + N-fixing cover	4	113.0	121.7	0.000	0.394
N-fixing cover	3	117.2	123.6	1.891	0.153
Management + Heat load + N-fixing cover	5	112.5	123.6	1.919	0.151
Management + Shrub cover	4	116.5	125.2	3.501	0.068
Heat load + N-fixing cover	4	116.9	125.7	3.965	0.054
Management + Heat load	4	117.0	125.7	3.979	0.054
Management	3	119.4	125.8	4.085	0.051
Management + Heat load + Hardwood cover	5	116.9	128.0	6.318	0.017
Management + Hardwood cover	4	119.3	128.0	6.319	0.017
Shrub cover	3	121.8	128.2	6.507	0.015
Hardwood cover + Shrub cover	4	120.2	128.9	7.262	0.010
Heat load	3	124.4	130.8	9.090	0.004
Null Model	2	126.7	130.9	9.210	0.004
Hardwood cover	3	126.7	133.1	11.417	0.001

CHAPTER 4- CONCLUSION

The study of plant community composition and structure twenty years after high severity fires in the Klamath region, with and without post-fire management, has provided important information about plant community responses to disturbances and to microclimate and also about disturbance-microclimate interactions. In this chapter, we summarize the main conclusions presented in the preceding chapters and provide some comments on the possible management implications of our results.

In chapter 2, we showed that the general distribution of cover among the main life form groups: shrubs, hardwoods, and conifers, was similar between unmanaged and managed sites. The abundance of key species within each group, however, changed as a result of post-fire management activities. Moreover, positive, negative, and neutral responses were identified at the species level. Species such as *Ceanothus integerrimus* and *Pinus ponderosa* responded positively to post-fire management, while *Arctostaphylos viscida* responded negatively; *Pseudotsuga menziesii* was an example of neutral responses to post-fire management. At the community level, however, a general pattern was a reduction of heterogeneity in managed sites both in terms of vertical structure and species composition.

Throughout the second chapter, a strong influence of microclimate was observed on plant community composition and structure. The underlying pattern of species distribution driven by aspect was evident not only in the species abundance, but also in the abundance of species with distinct regenerative traits. A strong positive relationship between high levels of heat load and abundance of seed bank species was observed in both unmanaged and managed sites. Furthermore interactions between aspect and post-fire management influenced the

abundance of N-fixing species, *Ceanothus* spp., which increased in abundance on managed sites on south aspects.

Chapter 3 focused on the composition, abundance, and size of tree species including conifers and hardwoods. These two groups are important components of the unburned forest, although, twenty years after high severity fires both conifers and hardwoods represented a limited proportion of the total cover relative to shrubs. As in the preceding chapter, the microclimate of the sites had a strong effect on conifer and hardwood composition. Post-fire management, for instance, had a weak effect on conifer density, but a strong effect on the spatial distribution of conifers. A high abundance of conifer regeneration was observed in both unmanaged and managed sites, reflecting the resilience of these forests with respect to intense natural disturbance.

Our understanding of vegetation recovery after intense disturbances is constrained by the fact that it is difficult to establish controlled experiments at the spatial and temporal scale needed to identify causation. Observational studies such as those reported here not only provide important information about species and community responses to disturbances such as high intensity fires and post-fire management but also constitute a valuable platform for future research. Our study showed the diversity in composition and structure that can be found in plant communities twenty years after high severity fires. The importance of these diverse plant communities and their roles in ecosystem processes, as well as the effect that a reduction of heterogeneity and diversity may have on wildlife habitat, fire characteristics, or ecosystem processes are only some of the issues that need to be addressed with future research. The studies presented in this thesis provide some preliminary insights.

Management Implications

Management of forest lands or natural areas in general is a dynamic process. During this process, land managers have to find a balance among

economic, social and scientific factors. Over the last fifteen years, for instance, management objectives on Federal lands have changed from a species-based approach to an ecosystem management approach. We explore the implications of our results under the current paradigm in the following paragraphs.

Ecosystem management has been described by several authors and institutions. The Society of American Foresters (1993), for example, has defined ecosystem management as “the strategy by which, in aggregate, the full array of forest values and functions is maintained at the landscape level.” Grumbine (1994) identified five specific goals of ecosystem management: 1) maintaining viable populations, 2) maintaining ecosystem representation, 3) maintaining ecological process (i.e., natural disturbance regimes), 4) protecting evolutionary potential of species and ecosystems, and 5) accommodating human use in light of the above.

One of the major challenges to implementation of ecosystem management is the uncertainty not only about ecosystem responses to natural disturbance but also to management. This uncertainty is even bigger when large disturbances and management activities are combined. This difficult but increasingly common situation where both disturbance and management are combined has been addressed in the studies presented in this thesis. Evidence was found that areas that were managed after high severity fires were more homogeneous in plant community composition and structure than those that were left unmanaged. There is still uncertainty, however, about how such simplification of plant community will impact ecosystem processes.

Over the last twenty years, large wildfires have affected hundreds of thousands of acres in the western United States. According to predictions based on global climate models, climate change will lead to an increase in the area burned by wildfires in the region (Torn et al. 1998). Under this scenario, managers should consider the possible consequences of changes in plant community composition and structure caused by post-fire management at the

landscape level. Furthermore, if the goals of ecosystem management, mentioned above, are to be met, managers should ensure that enough representation of early seral communities without post-fire management is present on the landscape.

Post-fire management and aspect interacted to increase the abundance of N-fixing species, mostly *Ceanothus integerrimus*, on south aspect sites. The increase in abundance of a species in a certain area leads us to ask the question, what species have been replaced? Managed areas in south aspects presented the lowest levels of beta diversity, which indicates that more than one species has been negatively affected. *Ceanothus integerrimus*, however, also has the ability to fix nitrogen, which opens a new set of questions about the role of post-fire management in the recovery process. The interactions detected between post-fire management and aspect remind us of the challenges to implementation of ecosystem management in complex and diverse ecosystems such as the Klamath region.

Clearly, there are many gaps in our present understanding of the importance of early seral communities to ecosystem processes and its changes in response to post-fire management. Observational studies such as this are just the first step in developing such understanding. Intensified direct experimental research in this area is necessary to bring us beyond the few studies from which managers have to make decisions. Further, understanding the role of these early seral communities, their composition and structure will help us to develop the knowledge that is needed to achieve the goals of ecosystem management in fire-prone ecosystems.

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APPENDIX

APPENDIX A. SITE INFORMATION AND SPECIES LIST

Table A.1. Site information, including name of the fire, year of the fire (Year), aspect, elevation, slope, and type of post-fire management: unmanaged (UM) or managed (M), coordinates, and heat load.

Plot #	FIRE	Year	Aspect (°)	Elevation (m)	Slope (%)	Manage	Easting	Northing	Heat Load
1	Titus 2	1987	4	499	72	UM	463020	4611486	0.546
2	Titus 3	1987	320	547	54	UM	463062	4611450	0.586
3	Titus 14	1987	20	818	100	UM	461858	4606034	0.370
4	Grider 34	1987	210	1090	25	UM	481034	4619894	0.930
5	Titus_Ind	1987	310	424	74	UM	462288	4611318	0.467
6	Titus_Ind	1987	320	471	50	UM	462240	4611200	0.615
7	JacobsL	1987	310	1386	56	UM	467514	4604666	0.574
8	GrouseN	1987	310	1483	18	UM	468757	4472977	0.841
9	GrouseS	1987	130	1449	58	UM	469410	4472131	0.790
10	Grider	1987	310	1499	57	UM	484217	4621131	0.567
11	Grider	1987	0	1433	54	UM	483816	4620981	0.655
12	GriderNW2	1987	320	1506	67	UM	483859	4621821	0.507
13	Titus_Ind	1987	310	374	74	UM	462221	4611363	0.467
14	Portuguese	1987	210	1221	59	UM	480349	4639184	0.862
15	Lake	1987	210	1255	24	UM	481409	4620245	0.931
16	Portuguese	1987	340	1056	70	UM	481377	4637314	0.514
17	Portuguese	1987	10	1000	67	UM	481333	4637383	0.554
18	Fort Goff	1987	200	489	55	UM	476484	4635228	0.910

Table A.1. (Continued)

Plot #	FIRE	Year	Aspect (°)	Elevation (m)	Slope (%)	Manage	Easting	Northing	Heat Load
19	North Grid	1987	0	1144	75	UM	482265	4624918	0.545
20	Grider Wes	1987	50	942	71	UM	480981	4623902	0.487
21	Ten Mile	1987	230	999	56	UM	455886	4621892	0.789
22	Ten Mile W	1987	190	960	33	UM	453276	4621896	0.964
23	Ten Mile E	1987	150	940	70	UM	453352	4621921	0.836
24	Seiad Farm	1987	200	739	62	UM	487637	4634698	0.898
25	GriderTN	1987	350	1106	50	UM	480277	4623480	0.650
26	Ten Bold	1987	150	439	53	M	458095	4618821	0.876
27	Ten Bold	1987	210	431	50	M	458728	4618859	0.883
28	Ten Bold	1987	225	485	73	M	459161	4618721	0.756
29	Ten Bold	1987	200	452	67	M	459099	4619387	0.887
30	Fort Copper	1987	215	1069	78	M	489851	4638302	0.792
31	Fort Copper	1987	320	1139	54	M	489979	4638362	0.586
32	Fort Copper	1987	210	1103	68	M	489320	4638970	0.841
33	Fort Copper	1987	180	1297	53	M	489929	4639241	0.977
34	Fort Copper	1987	130	909	55	M	488137	4737651	0.782
35	Fort Copper	1987	335	932	70	M	489577	4637969	0.505
36	Slater	1987	220	611	69	M	470890	4631002	0.792
37	Slater	1987	190	643	59	M	470723	4631101	0.939
38	Slater	1987	162	819	65	M	470932	4631501	0.899

Table A.1. (Continued)

Plot #	FIRE	Year	Aspect (°)	Elevation (m)	Slope (%)	Manage	Easting	Northing	Heat Load
39	Gulch	1987	160	660	38	M	475662	4624802	0.936
40	Gulch	1987	0	758	72	M	474171	4622888	0.560
41	China	1987	10	1004	80	M	477045	4629072	0.488
42	China	1987	360	716	56	M	476100	4629049	0.642
43	China	1987	20	774	72	M	476033	4628932	0.503
44	China	1987	190	984	37	M	476164	4628375	0.962
45	Fort Copper	1987	340	947	73	M	481643	4635157	0.498
46	Fort Copper	1987	40	988	76	M	481894	4635092	0.456
47	King Titus	1987	350	801	59	M	471496	4609436	0.598
48	King Titus	1987	340	1164	59	M	472138	4610063	0.577
49	King Titus	1987	35	1359	76	M	471127	4609526	0.459
50	King Titus	1987	350	1497	51	M	470744	4609180	0.644
51	King Titus	1987	20	1028	67	M	472867	4619602	0.531
52	King Titus	1987	330	967	75	M	473367	4617081	0.470
53	King Titus	1987	350	1030	40	M	473388	4617543	0.711
54	King Titus	1987	0	1046	62	M	472325	4619434	0.610
55	King Titus	1987	25	975	76	M	472286	4619475	0.473
56	King Titus	1987	20	1020	70	M	472933	4619623	0.514
57		1987	210	943	42	M	449177	4651122	0.890

Table A.1. (Continued)

Plot #	FIRE	Year	Aspect (°)	Elevation (m)	Slope (%)	Manage	Easting	Northing	Heat Load
58	King Titus	1987	30	484	53	M	470723	4620765	0.600
59		1987	30	1048	28	M	446422	4648396	0.766
60	Gulch	1987	350	1018	61	M	476553	4621936	0.587
61	Gulch	1987	0	1055	71	M	476578	4621886	0.564
62	Fort Copper	1987	40	1212	33	M	475697	4637859	0.727

Table A .2. List of species recorded in unmanaged (UM) and managed (M) sites.
Life form: C= conifer; F= forb; FE= fern; H= hardwood; S= shrub.

Family	Species	Common Name	Life Form	UM	M
Aceraceae	<i>Acer</i> sp.	maple	H	x	
	<i>Acer glabrum</i> Torr.	mountain maple	H	x	
	<i>Acer macrophyllum</i> Pursh	big-leaf maple	H	x	x
Anacardiaceae	<i>Toxicodendron diversilobum</i> (Torr. & A. Gray) Greene	poison oak	S	x	x
Apiaceae	<i>Daucus pusillus</i> Michx.	wild carrot	F		x
	<i>Osmorhiza</i> sp.	sweet-cicely	F	x	x
Apocynaceae	<i>Apocynum androsaemifolium</i> L.	dogbane	F	x	x
Aristolochiaceae	<i>Asarum caudatum</i> Lindl.	wild ginger	F		x
Asteraceae	<i>Achillea millefolium</i> L.	yarrow	F	x	x
	<i>Achyrachaena mollis</i> Schauer	blow-wives	F	x	
	<i>Adenocaulon bicolor</i> Hook.	pathfinder	F	x	x
	<i>Anaphalis margaritaceae</i> L.	pearly everlasting	F		x
	<i>Arnica</i> sp.	arnica	F	x	
	<i>Artemisia</i> sp.	artemisia	F	x	
	<i>Balsamorhiza</i> sp.	balsamroot	F		x
	<i>Chrysothamnus nauseosus</i> (Pall. ex Pursh) Britton	rabbitbrush	F	x	
	<i>Madia</i> sp.	tarweed	F		x
	<i>Machaeranthera nutkana</i> Greene	nutcracker	F		x
Berberidaceae	<i>Achlys triphylla</i> (Sm.) DC.	vanilla leaf	F	x	x
	<i>Berberis aquifolium</i> Pursh	tall Oregon-grape	S	x	x
	<i>Berberis nervosa</i> Pursh	dull Oregon-grape	S	x	x

Table A .2. (Continued)

Family	Species	Common Name	Life Form	UM	M
Betulaceae	<i>Corylus cornuta</i> Marshall	hazelnut	S	x	x
Campanulaceae	<i>Campanula prenanthoides</i> Durand	harebell	F		x
	<i>Campanula rotundifolia</i> All. ex Steud.	bluebell bellflower	F	x	
Caprifoliaceae	<i>Lonicera hispida</i> Pall. ex Roem. & Schult.	honeysuckle	S	x	x
	<i>Sambucus caerulea</i> Raf.	blue elderberry	S		x
	<i>Symphoricarpos albus</i> (L.) S.F. Blake	common snowberry	S	x	x
	<i>Symphoricarpos mollis</i> Nutt.	trailing snowberry	S	x	x
Caryophyllaceae	<i>Cerastium arvense</i> L.	field chickweed	F		x
Celastraceae	<i>Pachistima myrsinites</i> (Pursh) Raf.	falsebox	S	x	
Clusiaceae	<i>Hypericum</i> sp.	St. John's-wort	F		x
Convolvulaceae	<i>Convolvulus</i> sp.	bindweed	F	x	x
Cornaceae	<i>Cornus nuttallii</i> Audubon	Pacific dogwood	H	x	x
	<i>Garrya fremontii</i> Torr.	Fremont silktassel	S	x	x
Crassulaceae	<i>Sedum</i> sp.	stonecrop	F	x	
Cupressaceae	<i>Calocedrus decurrens</i> (Torr.) Florin	incense-cedar	C	x	x
Dennstaedtiaceae	<i>Pteridium aquilinum</i> (L.) Kuhn	bracken fern	FE	x	x
Dryopteridaceae	<i>Polystichum munitum</i> (Kaulf.) C. Presl	sword fern	FE	x	x
Ericaceae	<i>Arctostaphylos</i> sp.	manzanita	S	x	
	<i>Arctostaphylos</i> sp.	manzanita	S	x	
	<i>Arbutus menziesii</i> Pursh	madrone	H	x	x
	<i>Arctostaphylos columbiana</i> Piper	hairy manzanita	S	x	

Table A .2. (Continued)

Family	Species	Common Name	Life Form	UM	M
Ericaceae	<i>Arctostaphylos nevadensis</i> A. Gray	pinemat manzanita	S	x	
	<i>Arctostaphylos patula</i> Greene	Greene manzanita	S	x	x
	<i>Arctostaphylos viscida</i> Parry	white manzanita	S	x	x
	<i>Chimaphila menziesii</i> (R. Br.) Spreng.	little prince's pine	F	x	
	<i>Chimaphila umbellata</i> (L.) W.P.C. Barton	prince's pine	F		x
	<i>Pyrola</i> sp.	wintergreen	F	x	x
	<i>Vaccinium parvifolium</i> Sm.	red huckleberry	S	x	x
Fabaceae	<i>Lupinus</i> sp.	lupin	F	x	x
	<i>Vicia</i> spp.	vetch	F	x	x
Fagaceae	<i>Castanopsis chrysophylla</i> (Douglas ex Hook.) A. DC.	chinquapin	H	x	x
	<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehder	tanoak	H	x	x
	<i>Quercus chrysolepis</i> Liebm.	canyon live oak	H	x	x
	<i>Quercus garryana</i> Douglas ex Hook.	white oak	H		x
	<i>Quercus kelloggii</i> Newb.	black oak	H	x	x
	<i>Quercus sadleriana</i> R. Br. ter	Sadler oak	S		x
	<i>Quercus vaccinifolia</i> Kellogg	huckleberry oak	S	x	x
Grossulariaceae	<i>Ribes</i> sp.	currant	S	x	x
	<i>Ribes roezlii</i> Regel	currant	S	x	
	<i>Ribes sanguineum</i> Pursh	redflower currant	S	x	x
	<i>Ribes speciosum</i> Pursh	currant	S	x	

Table A .2. (Continued)

Family	Species	Common Name	Life Form	UM	M
Hydrangeaceae	<i>Philadelphus lewisii</i> Pursh	mock-orange	S	x	x
	<i>Whipplea modesta</i> Torr.	whipplevine	S	x	x
Iridaceae	<i>Iris</i> sp.	iris	F	x	x
Lamiaceae	<i>Mentha</i> sp.	mint	F	x	
Lauraceae	<i>Umbellularia californica</i> (Hook. & Arn.) Nutt.	California laurel	H	x	x
Liliaceae	<i>Calochortus</i> sp.	mountain cat's-ear	F	x	
	<i>Disporum hookeri</i> (Torr.) G. Nicholson	Hooker's fairybells	F	x	x
	<i>Lilium columbianum</i> Hanson	tiger lily	F	x	x
	<i>Smilacina</i> sp.	false Solomon's-seal	F	x	
	<i>Trillium ovatum</i> Pursh	western trillium	F	x	x
	<i>Veratrum</i> sp.	hellebore	F		x
	<i>Xerophyllum tenax</i> (Pursh) Nutt.	bear-grass	F	x	x
Malvaceae	<i>Sidalcea</i> sp.	checker-mallow	F	x	
Onagraceae	<i>Epilobium angustifolium</i> L.	fireweed	F	x	x
	<i>Epilobium minutum</i> Lindl. ex Lehm. in Hook.	willowherb	F	x	x
Orquidaceae	<i>Goodyera oblongifolia</i> Raf.	rattlesnake-plantain	F		x
Pinaceae	<i>Abies concolor</i> (Gordon & Glend.) Lindl. ex Hildebr.	white fir	C	x	x
	<i>Abies magnifica</i> A. Murr.	California red fir	C	x	
	<i>Abies procera</i> Rehder	noble fir	C		x
	<i>Pinus</i> sp.	pine	C	x	x

Table A .2. (Continued)

Family	Species	Common Name	Life Form	UM	M
Pinaceae	<i>Pinus attenuata</i> Lemmon	knobcone pine	C	x	x
	<i>Pinus jeffreyi</i> Balf.	Jeffrey pine	C	x	x
	<i>Pinus lambertiana</i> Douglas	sugar pine	C	x	x
	<i>Pinus ponderosa</i> Douglas ex Lawson & C. Lawson	ponderosa pine	C	x	x
	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas fir	C	x	x
Polemoniaceae	<i>Phlox</i> sp.	phlox	F	x	
Polygonaceae	<i>Eriogonum caespitosum</i> Nutt.	silver buckwheat	F	x	x
	<i>Eriogonum</i> sp.	buckwheat	F		x
Primulaceae	<i>Trientalis latifolia</i> Hook.	western starflower	F	x	x
Rhamnaceae	<i>Ceanothus</i> sp.		S	x	
	<i>Ceanothus cuneatus</i> (Hook.) Nutt.	buck brush	S	x	x
	<i>Ceanothus integerrimus</i> Hook. & Arn.	deer brush	S	x	x
	<i>Ceanothus prostratus</i> Benth.	mahala mat	S	x	x
	<i>Ceanothus sanguineus</i> Pursh	redstem ceanothus	S	x	x
	<i>Ceanothus velutinus</i> Douglas ex Hook.	tobacco brush	S	x	x
	<i>Rhamnus californica</i> Eschsch.	California coffeeberry	S	x	
	<i>Rhamnus purshiana</i> DC.	cascara	S		x
Rosaceae	<i>Amelanchier alnifolia</i> (Nutt.) Nutt.	saskatoon	S	x	x
	<i>Fragaria virginiana</i> Mill.	wild strawberry	F	x	x
	<i>Holodiscus discolor</i> (Pursh) Maxim.	ocean spray	S	x	x

Table A .2. (Continued)

Family	Species	Common Name	Life		
			Form	UM	M
Rosaceae	<i>Oemleria cerasiformis</i> (Torr. & A. Gray ex Hook. & Arn.) J.W. Landon	indian-plum	S	x	
	<i>Prunus</i> sp.	cherry	S		x
	<i>Rosa gymnocarpa</i> Nutt.	dwarf rose	S	x	x
	<i>Rubus</i> sp.	berry	S	x	x
	<i>Rubus discolor</i> Weihe & Nees	Himalayan blackberry	S	x	x
	<i>Rubus leucodermis</i> Douglas ex Torr. & A. Gray	black raspberry	S	x	x
	<i>Rubus parviflorus</i> Nutt.	thimbleberry	S	x	x
	<i>Rubus ursinus</i> Cham. & Schltld.	trailing blackberry	S	x	x
Rubiaceae	<i>Galium</i> sp.	bedstraw	F	x	x
Salicaceae	<i>Salix scouleriana</i> Barratt ex Hook.	Scouler's willow	S	x	x
Scrophulariaceae	<i>Castilleja</i> sp.	paintbrush	F	x	x
	<i>Verbascum thapsus</i> L.	great mullein	F		x
Taxaceae	<i>Taxus brevifolia</i> Nutt.	Pacific yew	C	x	
Violaceae	<i>Viola</i> sp.	violet	F	x	x