EFFECTS OF FIRE DISTURBANCE ON TERRESTRIAL SALAMANDERS IN MIXED-CONIFEROUS FORESTS OF THE KLAMATH/SISKIYOU REGION OF THE PACIFIC NORTHWEST

by

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ABSTRACT

Effects of Fire Disturbance on Terrestrial Salamanders in Mixed-Coniferous Forests of the Klamath/Siskiyou Region of the Pacific Northwest

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An effective examination of fire disturbance on floral and faunal components requires research that integrates knowledge from multiple disciplines to understand the pattern and process controls affecting organisms in a complex system. However, current fire effects research typically focuses on the pattern response of organisms or their habitats with little integration of the dynamic fire process that created the pattern. This dissertation integrates an analysis of the processes of fire disturbance with terrestrial salamander ecology in a fire-dependent forest ecosystem, Klamath Province, California, USA.

In Chapter 1, I begin with a comprehensive review of disturbance ecology, focusing primarily on fire in forested ecosystems. Next, I discuss the current state of knowledge regarding effects of fire from the scale-extent of ground-dwelling vertebrate habitats through forested landscapes. Finally, I conclude with a oveview of my specific research objectives.

In Chapter 2, I examine multi-scale vegetative responses to fire disturbance. Specifically, I characterize micro- and macro-scale forest structure and physical site characteristics across various fire disturbances. Finally, I discuss the concept of a fire refugium and examine potential fire effects in current and future forest dynamics of these critical environments.

In Chapter 3, I characterize a fire exclusion legacy in a fire-dependent forest system. Specifically, I quantify fire exclusion legacy in stands perturbed by fire. Next, I estimate and characterize potential fuel structure and biomass associated with post-fire forest structure. To conclude, I explore the implications of a hypothetical legacy-mediated disturbance model on future fire severity and forest resilience.

In Chapter 4, I explore faunal responses to fire disturbance through the examination of processes directly and indirectly affecting terrestrial salamander populations. I use classification tree models to compare various population metrics at the micro- and macro-scale. I also examine associations between animal presence and multi-scale forest structure, physical site characteristics, and fire disturbances.

I conclude with a synthesis that examines the applicability of a salamander-based fire severity model (Chapter 5). Specifically, I examine the utility of predictive models to integrate fire processes and the effects of fire on terrestrial salamanders. Finally, I discuss the application of my results to future management and conservation of terrestrial salamanders.

(123 pages)

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CHAPTER 1

INTRODUCTION

NATURAL DISTURBANCE

Natural disturbance plays a critical role in the successional dynamics of biological systems (White 1979). White and Pickett (1985: 3) defined disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Disturbances can range from major destructive events to subtle environmental fluctuations (Nielson and Wullstein 1983). Therefore, adequate characterizations of the effects of disturbance on biological systems must include information on the type of disturbance and the frequency and severity of the event (i.e., disturbance regime) (White and Pickett 1985).

In many ecosystems, disturbances can occur as frequent events, often spatially patchy and temporally discontinuous or disjunct, that act to modify both the abiotic and biotic environment (White 1979, White and Pickett 1985). The range of heterogeneity in the post-disturbance environment is dependent on the state of the community prior to the disturbance (White 1979). As a result, the natural landscape is a mosaic of successional patches of varying size (Whittaker 1953). Thompson (1978) introduced the term "patch" to spatially classify subsets of the environmental mosaic found in ecosystems. Internal processes associated with these patches (patch dynamics) result from both the pattern of disturbance (i.e., disturbance regimes) and the ensuing successional pathway (Watt 1947, Pickett and Thompson 1978). In addition, natural disturbance and patch dynamics occur on a wide range of temporal and spatial scales (Delcourt et al. 1983). Therefore, patches and associated patch dynamics provide a quantitative framework to examine the dynamic process of disturbance in ecological studies (Wiens 1976, 1985, White and Pickett 1985).

Disturbance in forest ecosystems

Forest systems are affected by many types of natural disturbance encompassing both major catastrophic events (e.g., crown fire, hurricanes, windthrow) and minor, less extensive events (e.g., surface fire, insect infestations, lightning strikes, individual tree-fall, disease, and anthropogenic impacts) events (Oliver 1981). The frequency of disturbance relative to the life-span of many tree species indicates current forests in many regions are largely the result of past disturbance events (Hough and Forbes 1943, Jones 1945, Watt 1947, Franklin and Waring 1979, Agee and Huff 1980). For example, in the Cascades of western Washington and Oregon, large relatively homogenous even-aged Douglas-fir stands are thought to result from large, infrequent (+300 year), high severity fires that kill most trees (Hemstrom and Franklin 1982). Similar results documenting the time since last fire disturbance and forest age have also been reported for other northern coniferous forests (Heinselman 1973) and eastern mesophytic forests (Runkle 1982). Further, disturbance regimes and associated variability in timing, severity, and duration of disturbance events are important in producing the vegetative mosaic and pattern of development and dynamics in forest communities and systems (Runkle 1985, Wiens 1985, Turner 1987, 1989, Zimmerman et al. 1996, Turner et al. 1997).

FIRE IN FOREST ECOSYSTEMS

In North America, fire is a primary disturbance process in many ecosystems. The functional role of fire as a natural disturbance has been documented in numerous aquatic and terrestrial ecosystems (Knapp 1974, Grubb 1977, Miles 1979, White 1979, Pickett 1980, Oliver 1981, Runkle 1985). Fire, alone or combined with other disturbances, can alter the spatial mosaic and future severity of subsequent disturbance events (Runkle 1985, Lotan et al. 1985). Interactions between forest management and alteration of fire patterns has also been examined. For example, forest harvest practices (i.e., clearcutting) that increase landscape level fragmentation can reduce the aerial extent of fires (Green 1989, Turner 1989, Turner et al. 1994). In fire-dependent systems in the northwestern U.S., Spies et al. (1994) reconstructed historic forest patterns and demonstrated differences in forest patch mosaics between reconstructed historic and current human altered forest patterns. Therefore, disturbance may account for a large part of the spatial and temporal variation observed in populations, communities, and ecosystems (White 1979, Sousa 1984, 1985, White and Pickett 1985).

Fire regimes

The historic role of fire in forested ecosystems can provide a framework for understanding the dynamics of current, and future forest conditions (Morgan et al. 1994). Fire can vary widely in frequency, seasonality, extent, and severity and manifest itself as patterns over long time periods. These patterns are used to define fire regimes. Central to this definition is a recognition of the feedback relationship between the biotic assembly, fire regime, and pattern of fire severity (Pyne 1996). Therefore, alteration of an ecosystem component(s) will likely alter the fire regime (Kauffman 1985).

Descriptions of fire regimes are often generalized due to the high degree of temporal and spatial variability in fires (Whelan 1995). Fire frequency and severity are commonly used to characterize fire regimes (Kilgore 1971, Heinselman 1973). Fire frequency is defined by both fire return interval (years between fires at a given location) and fire cycle (years required to completely burn over a specified area) (Heinselman 1970, 1973). Pickett and White (1985) define fire severity as the degree to which the pre-disturbance vegetation has been damaged and ecosystem properties have been disrupted. In general, fire severity is often categorized into broadly defined classes ranging from fine-scale soil response (Hungerford 1996) or coarse-scale percentages of total area burned by severity class (Wells et al. 1979). Adequate classification of fire regimes is often limited by the impacted vegetation communities and their associated tolerance (or intolerance) to fire (Agee 1991, 1993, Pyne 1996).

In coniferous forests of the Pacific Northwest, fire regimes are classified along gradients of temperature and moisture stress (Agee 1991, 1993). Specifically, these gradients include the growing environment (temperature and moisture regime), ignition pattern (lightning, anthropogenic), and plant species characteristics (fuel accumulations, adaptations to fire). The resulting fire regime classification for the Pacific Northwest depicts three broad categories of fire severity: high, mixed, and low, with each category corresponding to a portion of the fire severity continuum and associated post-fire forest stand structure (Agee 1993). For example, high severity fire regimes are characterized by long fire return intervals of 100 to 300+ years and combinations of crown fires and severe surface fire. Historically, these fire disturbances were often large in spatial extent (10^3 - 10^4 hectares) with most of the area affected by severe stand-replacement fire. This disturbance pattern results in large, relatively homogenous similar aged forest communities. In contrast, low severity fire regimes are characterized by fire return intervals of 10 to 60 years and low to moderate severity surface fires, often over large areas. Forest communities in this regime are often characterized by mosaics of different stand ages and forest types.

Fire regimes and their associated severity levels are responsible for the observed patterns of plant community structure, composition, and diversity (Franklin and Dyrness 1973, Agee 1981, 1991, 1993, Stewart 1989). However, most fire effects work has focused primarily on stand-level vegetation changes and associated fire fuels dynamics. Little attention has been given to the dynamics of those forest floor environments typically used by vertebrates (e.g., large down wood). Therefore, the spatial and temporal aspects of forest stand dynamics, fire regime, and resulting fire severity are inevitably linked to both the pre-fire community and its associated vegetation structure and composition (Forman and Godron 1981, Turner et al. 1994).

Fire effects on forest stands and associated forest floor structure

Fire regimes and their associated range of severity can affect forest stands by modifying structural components of the forest floor (low-moderate severity), forest canopy (high severity) or both (stand replacement events). Forest stand structure is an important factor affecting many ecological processes (Franklin and Hemstrom 1981). These include habitat suitability for wildlife (Morrison et al. 1992), wildlife corridors

(Maser et al. 1979), and fire behavior (Williams and Gill 1995). Many of the structural and functional elements of the forest floor are potentially more vulnerable to fire than other components of the forest system (Page-Dumroese et al. 1991). The forest floor is important in ecological processes such as decomposition and nutrient cycling (Odum 1969, Maser and Trappe 1984). Coarse woody debris is particularly important in the long-term function and dynamics of the forest floor (Franklin et al. 1991, Maser and Trappe 1984). A majority of coarse woody debris arises from disturbance (Harmon et al. 1986). Due to the patchy behavior of fire within and across forest stands, down woody debris is often highly variable in space, time, and rate of decay (Harmon et al. 1986, Franklin et al. 1991). The resulting heterogeneous forest floor environment could have profound effects on species dependent on coarse woody debris (Maser and Trappe 1984).

Structure and composition of fire-dependent Douglas-fir forests of the Pacific Northwest are strongly influenced by natural disturbances such as fire, windthrow, insect attack, and volcanism. Of these, fires have affected most areas with the greatest frequency (Agee 1981). Fires shape a complex mosaic of stand sizes and ages, forest floor environments, vegetation structure, and plant species occurrence across the landscape; the resulting environmental heterogeneity has a strong influence on the resident animals (Lyon et al. 1978, 2000, Agee 1993).

Role of fire in forest management

Long-term fire exclusion in forested systems has prompted concern over issues of forest health. Fire suppression activities have resulted in compositional and structural changes in forest fuels resulting in larger, more catastrophic fires (Albini 1976, Agee

1993). Agee (1981) found a significant relationship between increased fuel loadings and wildland fire intensity in fire-suppressed coniferous forests of the Pacific Northwest. Similar relationships were also documented in ponderosa pine forests (Mutch et al. 1993, Wilson and Baker 1998), and western montane forests (Brown and Bevins 1986). In these studies, it was generally concluded that fire suppression activities had significantly altered the historic fire regimes of these systems. Finally, the resulting natural and anthropogenic changes associated with altered fire regimes could significantly alter vegetation patterns and forest stand structure and composition (Fosberg et al. 1993, McKenzie et al. 1996).

EFFECTS OF FIRE ON FOREST FLOOR VERTEBRATES

Direct and indirect effects

Although much work has been done regarding the effects of fire on large, more mobile vertebrate groups such as ungulates and birds (see reviews by Bendell 1974, Lyon et al. 1978, Smith 2000), limited information is available on small vertebrate species, especially those inhabiting the ground-surface environment in terrestrial systems. In studies of fire effects on small mammals a variety of outcomes have been documented. Wright and Bailey (1982) described direct mortality from burning or suffocation; suggesting that survival within a burn was dependent on 1) uniformity, intensity and severity, size, and duration of the burn; 2) mobility of the animal; and 3) position of the animal relative to the exposed soil surface during passage of the flame front. Ford et al. (1999) found no evidence of significant direct mortality in small mammals resulting from a high intensity prescribed burn in a southern Appalahcian forest. Burrow-dwelling small mammals survived a stand replacing fire during summer in an ungrazed sagebrush-steppe system in eastern Washington (Hedlund and Rickard 1981). In contrast, Ver Steeg et al. (1983) found a high incidence of direct mortality in meadow voles after an early spring fire in Illinois grasslands. Similar results were also reported in wildland and prescribed fires in Australian malee and heathlands (Friend 1993). Ambient temperatures over 63° C are lethal to small mammals and likely other small vertebrates (Howard et al. 1959). Therefore, uniformly severe wildfire over large areas is potentially the most deleterious to small animals that are unable to escape underground and avoid the direct effects of the fire. In contrast, small mammal species that use other forms of cover (e.g., burrows) show different responses. In a review of fire effects on small mammals, Ream (1981) concluded that populations of ground squirrels (*Spermophilous spp.*), pocket gophers (*Geomys spp.*), and deer mice (*Peromyscus maniculatus*) generally increased after stand replacement fire. Kaufman et al. (1982) found similar post-fire increases in deer mouse populations on 1- and 2-year old burns than in unburned tallgrass prairie and suggested the species' high reproductive rate allowed for the observed recovery.

Indirect effects of fire on forest floor vertebrates likely result from habitat modifications to the post-fire environment and the adaptive capabilities of the impacted species. For example, numerous small vertebrates use coarse woody debris for food, cover, or shelter. Campbell and Tanton (1981) found a positive relationship between animal abundance under logs and the dimensions, decay state, and depth of accumulated litter around the log prior to burning, suggesting the importance of coarse woody debris in providing a more stable thermal and moisture environment during fire.

Effects of fire on amphibians

Amphibians have received little attention regarding their responses to wildland and prescribed fire (Means and Campbell 1981, Harlow and Van Lear 1981, 1987, deMaynadier and Hunter 1995). Literature reviewing the effect of fire on amphibian diversity and abundance suggests highly variable fire effects across individual, population, and community levels (Lyon et al. 1978, Russel 1999, Bury et al. 2002). Individual response to fire ranges from direct mortality (Cole et al. 1997, Driscoll and Roberts 1997) to speculated survival resulting from behavioural adaptations such as burrowing (Friend 1993), refuge in burrows of other animals (Komarek 1969, Means and Campbell 1981, Lipps 1991) or aquatic habitats (Vogl 1973), and movement away from fire (Komarek 1969). Given the potential magnitude of the range of amphibian responses, Lyon et al. (1978) speculated that direct effects of fire on mortality and survival appear to be strongest in low vagility species with restricted home ranges and species requiring specialized habitats.

Fire can indirectly affect amphibian populations by modifying habitat structure and distribution (Lyon et al. 1978, 2000, Russel 1999, Bury et al. 2002). In a review of fire effects on amphibian populations, the degree of patchiness associated with fires of low to moderate severity was thought to reduce fire effects by providing unburned patches to serve as refugia (Lyon et al. 1978). Ford et al. (1999) found only minimal effects of prescribed burning on amphibian populations in southern Appalachian forests, suggesting that micro-site variability within the burns may protect herpetofauna from direct injury or mortality. Similar results were documented in wetland-associated amphibians in southeastern pine and pine/hardwood forests (Vogl 1973, Means and Campbell 1981, Russel 1999).

Information is needed on the effects of fire-induced habitat modification for amphibian species with specialized habitat requirements (Lyon et al. 1978, 2000, Petranka 1999). In Pacific Northwest forests, many salamander species are strongly associated with structural elements of the forest floor (i.e., coarse woody debris, moss, and surface/sub-surface rock) (Bury and Corn 1988, 1990, Welsh and Lind 1991, 1995). These forest floor components are vulnerable to fire. In contrast to other systems where previous fire effects studies have been conducted, many Northwestern salamander species are only active for short times (weeks to 2+ months) during the cool wet periods. The cool temperatures during activity periods of these ectothermic animals result in less mobility than salamanders found in more temperate and tropical environments.

MODELING FOREST RESPONSE TO FIRE

The development of models that predict the behavior and effects of fire on stand-level vegetation and successional dynamics in terrestrial ecosystems has received considerable attention (e.g., Andrews 1986, van Wagner 1987, Keane et al. 1989, 1994, Ottmar et al. 1992, Clark et al. 1994, Finney 1995, Finney and Ryan 1995). In a review exploring uses and limitations of predictive fire models, McKenzie et al. (1996) described three categories of models used to predict the effects of fire on vegetation. These include 1) stand-level mechanistic fire behavior models, and first-order fire-effects models, 2) stand-level successional models incorporating fire stochastically, and 3) landscape-level models of disturbance. Fire-behavior models (e.g., BEHAVE [(Andrews 1986)], FARSITE [(Finney 1994, 1995, Finney and Ryan 1995)]) are typically used to quantitatively determine fire hazard and provide information on fire intensity and rates of spread (Schmoldt et al. 1999). These models rely on linkages between fuels and vegetation, weather, and topography to predict behavioural characteristics of single fires at the landscape-level (Rothermal 1972, 1991, Andrews 1986). Fire-effects models (e.g., CONSUME [Ottmar et al. 1992], FOFEM [Keane et al. 1994, Reinhardt et al. 1996]) consider not only fire behavior, but also attempt to incorporate the impact of fire severity and resulting post-fire resource conditions on short-term vegetation development.

Although moderately reliable at the stand-level, fire-behavior and fire-effects models assume homogeneity of inputs (fuels, vegetation structure, etc.) over the spatial extent to which they are applied (Kercher and Axelrod 1984, Peterson and Ryan 1986, Keane et al. 1989, 1996). Vegetation succession models commonly simulate vegetation dynamics at the stand-level (Shugart and West 1980). At larger spatial extents, vegetation dynamics have been examined in "gap phase" models (Botkin 1993) and landscape models examining fire dynamics (Keane et al. 1989, 1996, Baker 1993). These models predict disturbance mediated succession within or across forest stands at various spatial and temporal resolutions and extents. However, the magnitude of empirical data required to test these larger spatially explicit models is limited by the spatial resolution of data acquisition, data aggregation, and error-propagation associated with stand-level extrapolation (Keane et al. 1996).

Stand-level fire effects data have been used to examine community succession (Guerin 1993), ecosystem process (Weber 1987), and population dynamics (Borchert 1989). However, this work specifically focused on vegetation dynamics with little attention on linkages between fire dynamics and ecological impacts on non-plant biota (Peterson and Ryan 1986, Agee 1993, McKenzie et al. 2000). Fire dynamics are critical in examining fire effects on ecosystems and associated ecological function (Schmoldt et al. 1999). Research attempting to predict the effects of a fire or series of fires within a specific fire regime are often limited by scale dependence and assumptions of homogeneity of fire effects. This is of particular concern for forest floor biota such as amphibians, that function at scales smaller than a forest stand.

RESEARCH OVERVIEW

A current trend in ecology focuses on disturbance and its associated effects on structure and function of communities and populations. Natural and anthropogenic disturbances play a major role in shaping the mosaic of biotic and abiotic environments; however, a comprehensive understanding of the range of effects on communities and populations remains elusive (White 1979). In order to understand the ecological role of disturbance, information on type of disturbance, range of variability in the frequency and severity of the event (i.e., disturbance regime), and patterns of vegetative heterogeneity (pre- and post-disturbance) must be characterized (White and Pickett 1985). In combination, this baseline information is vital to understanding causative relationships and determining ecological linkages between disturbance and ecosystem function.

In fire-adapted forests of the western U.S., forest health issues resulting from altered fire regimes have prompted federal forest managers to consider the reintroduction of fire into these systems. Prescribed fire has been proposed as a primary restoration activity to reduce accumulated forest fuels and associated risk of catestrophic fire.

However, the effects of seasonality and frequency of prescribed fire on forest ecosystems, forest floor structure and associated wildlife species, and ecological processes associated with the forest floor environment remain largely unknown (Page-Dumroese et al. 1991, Tiedemann et al. 2000).

Information is also limited on the effects of fire on forest floor vertebrates (e.g., herpetofauna, small mammals) and their habitats (Lyon et al. 1978, Russel 1999, Bury et al. 2002). The greatest succeptibility to fire is found in low vagility species and species strongly associated with specific components of the forest floor (e.g., duff/litter, downed wood, etc.) (Russel 1999, Bury et al. 2002). Amphibians are highly sensitive to habitat change (Bury et al. 1995), in part because they have moist, permeable skin and restricted home ranges. In addition, many terrestrial salamander species (Genus Plethodon) are strongly associated with downed woody material (Bury and Corn 1990). Thus, terrestrial salamanders are an excellent candidate to examine the direct and indirect effects of fire.

In the mixed coniferous forests of the Klamath Ecoregion (Fig. 2-1), terrestrial salamanders (*Genus-Plethodontidae*) inhabit talus fields and surrounding dense canopy mature forest habitat (Welsh and Lind 1991, 1995). It has been speculated that talus environments provide critical refugia for these species during the warm-dry summer period, with animal use of the adjacent forest floor environment during the cool-wet periods of spring and fall. Historically, frequent fires of low to moderate severity worked in concert to create a patch mosaic of both forest stand and forest floor environments in this fire-dependent system. Most of these fires occurred during the dry period of late summer and early fall, after the salamanders had retreated into the talus slopes. Given the narrow range of environmental conditions suitable for these species, persistence of these populations may depend on the quantity and quality of cover available on the forest floor, how the forest floor environment limits movement of animals between talus fields, and the suitability of newly colonized areas.

OBJECTIVES

I examined the effects of fire type and severity level on habitat relationships and population ecology of an endemic terrestrial salamander species (Del Norte salamander *Plethodon elongatus*) in the Klamath/Siskiyou region of the Pacific Northwest. Specifically, my research objectives are: 1) Quantify the effects resulting from long periods of fire exclusion on current forest structure and composition; 2) Compare the effects of fire-type and severity on stand structure and composition in fire excluded forests; 3) Quantify and compare the effects of fire (type and severity) on salamander habitats in these forests; 4) Model salamander presence/absence across forest, fuels, and habitat components; 5) Model terrestrial salamander responses to simulated changes in forest floor “habitats" under different fire intensity/severity conditions.

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CHAPTER 2

THE ROLE OF FIRE DISTURBANCE IN STAND STRUCTURE OF DRY DOUGLAS-FIR / TANOAK FOREST ECOSYSTEMS

INTRODUCTION

In fire-adapted forests of the western U.S., forest health issues resulting from altered fire regimes have prompted federal forest managers to consider the reintroduction of fire into these systems. Prescribed fire has been proposed as one of several restoration techniques to reduce accumulated forest fuels and the associated risk of wildland fire. However, the effects of seasonality and severity of prescribed fire on forest ecosystems, forest floor structure, and ecological processes associated with the forest floor environment remain largely unknown (Page-Dumroese et al. 1991, Tiedemann et al. 2000). Further, comparative information on natural fire disturbance effects is also needed to evaluate fire-mediated changes in vertical and forest floor woody structure resulting from periods of fire exclusion.

Fire disturbance and associated fire regimes, play an important role in the structure, composition, and dynamics of Douglas-fir forests of the Pacific Northwest (Franklin and Dyrness 1973, Agee 1981, 1991, 1993, Morrison and Swanson 1990, Spies and Franklin 1991). However, past research has focused largely on Douglas-fir forests in the central and northern portions of its range only. Fire disturbance in these forests are generally infrequent (200-1000+ years), high severity stand-replacing fires (Agee 1993). Relatively little information is available on the fire ecology of the dry Douglas-fir / tanoak forests of northern California and southern Oregon. Recent studies include examination of stand structure and composition using fire history reconstructions (Wills and Stuart 1994, Skinner 1997), stand dynamics (Hunter 1991, 1997), and quantification of landscape level patch dynamics (Skinner 1995, Agee 1998). However, information is lacking on fire-mediated changes in stand structure, modifications of forest down woody structure, and the role of fire exclusion in current and future stand dynamics. Moreover, the value of using coarse level canopy burn severity categories to characterize fire effects on overstory, understory, and surface structure and composition is unknown.

The dry Douglas-fir / tanoak forests of northern California and southern Oregon are characterized as a mixed severity fire regime with fires occurring at relatively frequent intervals (Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998). Forest structure/composition can vary dramatically across a landscape, ranging from relatively open understory to a multi-layered, multi-age understory. Fire history reconstructions in these forests suggest fire occurrence in these forests is edaphically regulated; that is being most frequent on ridge-tops and mid-slopes of south and east facing slopes, and least frequent at lower elevations with generally northern aspects (Taylor and Skinner 1998). Taylor and Skinner (1998) speculated that forests in areas of lower fire frequency might function as a fire refugium for this forest community.

Camp et al. (1995: 9) defined a *fire refugia* as "a landscape/forest patch that is affected differently by the disturbance (fire) regime characteristic of the surrounding matrix." A fire refugia differs structurally and compositionally from the matrix (Hessburg et al. 1994), typically resulting from less frequent fire return intervals and greater fire severity levels. As part of a larger study examining fire effects on terrestrial salamanders, I explored fire-mediated effects on endemic terrestrial salamander species in these potential fire refugia.

Here, I report the effects of fire type and burn severity level on dry Douglas-fir / tanoak forest ecosystems. Specifically, the objectives of my study were to: 1) Compare the effects of disturbance type and canopy burn severity level on components of stand structure and composition; 2) Evaluate the use of a composite burn severity index (CBSI) to assess fire-mediated ecological impacts within this forest system; 3) Discuss the role of fire in current and future forest dynamics of these potential fire refugia.

METHODS

Study area and site selection

This study was conducted in portions of the Clear, Dillon, and Swillup Creek watersheds in the Klamath National Forest, near Happy Camp, California (Fig. 2-1). I examined late-seral dry Douglas-fir (*Pseudotsuga menziesii*) / tanoak (*Lithocarpus densiflorus*) dominated forest community in the Sierran Steppe – Mixed Forest – Coniferous Forest Ecological Province: Klamath Section (Kuchler 1975, Bailey et al. 1994). The Klamath Ecoregion is noted for its complex terrain with varied and often abrupt changes in bedrock geology, soils, elevation, and climatic regimes. Topography is characterized as steep slopes ($\bar{x}$ = 60%, range 45-85%) (USDA Forest Service 1990). Elevation ranges from approximately 250 m to 2400 m. The climate is considered to be modified Mediterranean, and is characterized by hot, dry summers and cool, wet winters. Average annual precipitation ranges from 1120 mm to 2000 mm, typically increasing with elevation (USDA Forest Service 1990). Most precipitation (~ 90%) falls from October through May; the remainder occurs with occasional summer thunderstorms. The dry summer period typically creates severe fire weather between July and September (Wills 1991).

I selected study sites identified as unmanaged mature-old dry Douglas-fir / tanoak vegetation type. Natural fire disturbance in these communities is described as a mixed-severity fire regime (Agee 1990), with median fire return intervals of approximately 6-16 years (Taylor and Skinner 1998). I define unmanaged forests as naturally regenerated stands created by historic fire events (i.e., prior to European-man fire suppression activities). I examined unmanaged forest stands under the following categories: 1) Disturbance Type - wildland fire (*WF*), prescribed fire (*PF*), and no fire (*NF*); and 2) Canopy Burn Severity – Low: <25% canopy mortality, Moderate: 25-75% canopy mortality, and High: >75% canopy mortality. Canopy burn severity is commonly used in evaluating fire effects and associated rehabilitation efforts by visually quantifying post-burn tree canopy mortality (percent loss of foliage and/or brown leaves/needles) within a predefined forest stand boundary (USDA Forest Service 2001).

Study site selection criteria included the following physical site characteristics: forest stand size > 10 ha, generally northern aspect, moderate to steep slopes (25-55%), and talus covering ~20% of site. Environmental compliance restrictions associated with prescribed burning on Federal lands limited the range and characteristics of prescribed fire sites available for this study. Further, wildland fire study sites were limited to Douglas-fir / tanoak stands available in wildland fires that burned during the 2001 and 2002 fire years.

Study design

I used a retrospective study design to examine the effects of both fire type and burn severity on stand structure of current Douglas-fir / tanoak forests. Study sites were selected using a systematic random sampling design. Sites meeting the selection criteria were identified within the three disturbance types (NF, WF, PF). Within burned sites (WF and PF sites), I attempted to sample up to three sites in each of the three canopy burn severity levels (Low, Moderate, High). I selected sites based on availability within recent wildfires (≤ 6 months post-fire) or prescribed burning activities (≤1 year post-fire). Sites were sampled in 2001 and 2002.

I examined forest stand structure and composition using combined fixed plot and variable area sampling techniques. I located sampling points to effectively cover the entire stand using the criteria of one sampling point per 1.0 ha of stand area (e.g., stand size = 20 ha would receive up to n = 20 sampling points). Slope aspects, slope angles, and elevation were determined for each sample point and averaged for each site. Horizontal canopy cover percentage was recorded at each sample point using a spherical densiometer. A single canopy cover estimate was recorded 1-m above ground, facing due North, with the densiometer leveled and approximately 50 cm away from the body (Wenger 1984).

Tree species, size, and density estimates were sampled using the variable plot method. Using a hand-held prism (BAF=20, Forestry Suppliers, Inc.) at sample point center, I tallied trees and recorded information on species diameter breast height (dbh), height, and condition. In addition, I recorded data on tree fire scorch (presence or absence) and scorch height (m) in burned sites.

Forest regeneration was sampled in a nested 3.0 m radius fixed area plot centered on each sampling point. Stems < 7.6 cm dbh were tallied by species on each 3-m plot and grouped into six height classes: 30 cm, 60 cm, 90 cm, 120 cm, 150 cm, >150 cm. Shrub cover and herbaceous species density were measured on seven 1-m^2 sub-plots per plot. I visually estimated shrub cover (0-100 percent) in each 1 m^2 sub-plot. Counts of individuals (by group: herb or grass) and percent cover were also recorded in the 1-m^2 sub-plot.

I measured both fire fuels (1-1000 hr fine fuels) and litter/duff depths along three 15-m transects established in a “Mercedes (Y) Array” from sample point center. Fire fuels were tallied following the planar intersect method of Brown (1974). I recorded litter and duff depth (cm) at 1-m intervals along each 15 transect. Large down woody material (≥ 10 cm dbh) was measured (log length and diameter at both ends) and classified into decay condition class following Maser et al. (1979). Woody fuels and down wood biomass were calculated using procedures in Brown et al. (1982) and Sackett (1979).

Analysis

I examined three components of forest stand structure and composition: 1) overstory species composition, density, and basal area, 2) diameter distributions, and 3) forest fuels structure. Tree metrics included trees per hectare (TPHa), basal area (BA), and quadratic mean DBH (Dq) and were computed using common forest mensuration equations (Wenger 1984).

I used descriptive statistics to characterize the structure and composition of stand and forest floor environments. Histograms, normal score plots, and measures of skewness and kurtosis (SAS 2000) were used to assess normality assumptions of the variables. If deviations were present, I corrected by appropriate transformations (e.g., arcsine, log, square root: (Sokal and Rohlf 1981). Stand structure and forest floor data were analyzed using a multi-factorial AVOVA (SAS 2000). Because of unequal sample sizes among disturbance type and canopy burn severity classes, I used ANOVA with contrasts to analyze within and among the following seven factor-level combinations (NF, WF-Low, WF-Mod, WF-High, PF-Low, PF-Mod, PF-High). Finally, strengths of association for specific stand components were examined with regression analyses.

Composite burn severity index

I evaluated fire-mediated effects on stand-level vertical woody structure using a composite burn severity index (CBSI). CBSI integrates components of vertical and horizontal stand structure, fire fuels profile, and measures of fire intensity (e.g., flame scorch height) to rate fire severity. This index operates on a scale of 0 (no severity) to 3.0 (highest severity). I modified aspects of the CBSI developed by Key and Benson (1999) to assess plot and stand-level burn severity within three vertical strata: *Overstory* (Dominant/Co-dominant canopy), *Understory* (Understory/Shrub), and *Surface* (surface fuels and down woody material). Because plot specific pre/post data on fuel consumption rates were unavailable, I used average values from unburned stands to approximate “pre-fire” conditions (Table A1). Relative consumption rates were computed using the following formula:

$$\text{Proportion Consumed} = \left(\frac{\text{Reference Value of variable } x - \text{Plot Value of variable } x}{\text{Reference Value of variable } x} \right) * 100$$

I compared relative proportion consumed to "pre-fire" conditions to produce an average plot and total stand CBSI score for each burned plot/site (Table A1). CBSI values were compared among fire types (WF, PF) and within canopy burn severity (Low, Moderate, High) using a multivariate analysis of variance (SAS 2000). Multiple-range tests used *t*-tests of the least-squares means. Least-squares means are the expected values of means, if the sample design was balanced.

RESULTS

Overstory species composition, density, and basal area

Stand structure/composition was analyzed from a total of n=19 stands (n =166 plots). Tanoak (*Lithocarpus densiflorus*) and Douglas-fir (*Pseudotsuga menziesii*) had the greatest occurrence of all tree species encountered within the sampling plots, occurring in 72.3% and 92.3%, respectively (Figure 2-2). Douglas-fir and tanoak were co-dominant overstory species in both unburned and burned forests (Figure 2-3). Douglas-fir accounted for an average of 61.5% of the basal area and 30.5% of trees ≥ 10 cm dbh and tanoak for 31.5% of the basal area and 63.0% of trees ≥ 10 cm dbh (Table 2-1). Other species including Pacific madrone (*Arbutus menziesii*), chinkapin (*Castanopsis *chrysophylla*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), canyon live Oak (*Quercus chrysolepis*), and black Oak (*Quercus kelloggii*) were also recorded in sample plots. However, these species exhibited low and variable occurrence (<20% of plots and <10% total tree density, basal area, and quadratic mean dbh) and were not included in any of the following analyses (Table 2-1).

Stand-level tree density, basal area, and quadratic mean diameter estimates were highly variable among disturbance types. Tanoak and Douglas-fir density decreased from no fire to wildland fire to prescribed fire (Table 2-1). Tanoak average tree density ranged from 103 to 236 trees per hectare (TPHa) in prescribed fire and unburned reference stands, respectively. Douglas-fir had the next highest tree density, ranging from 61 to 114 TPHa. No statistically significant differences were found in tanoak or Douglas-fir tree density among disturbance types; however, a clear trend in reduced trees per hectare was observed from the No fire to Wildland fire to Prescribed fire categories.

Total stand-level mean basal area ranged from 18.9 to 29.4 m^2/ha, with the lowest basal areas found in Prescribed fire sites (Table 2-1). Douglas-fir mean basal area was significantly lower in stands perturbed by Wildland fire than in either No Fire or Prescribed fire sites. Douglas-fir mean basal area ranged from 10.8 to 18.1 m^2/ha. Tanoak mean basal area was notably lower (range 5.4 to 9.3 m^2/ha) but showed a similar response among disturbance types (Table 2-1). Mean basal area of Douglas-fir and tanoak remained generally constant across the three disturbance types, representing ~60% and ~30% of the total, respectively. However, the trend in Douglas-fir was from No fire to Prescribed fire to Wildland fire. In contrast, tanoak mean basal area was highest in No fire followed next by Wildland fire and Prescribed fire.

Douglas-fir average quadratic mean diameter (Dq) was reduced in both Prescribed fire and Wildland fire sites. Average Dq for Douglas-fir ranged from 44.1 to 55.4 (cm) and accounted for >75% and 58% of total Dq across disturbance types. I observed contrasting trends in mean Dq of tanoak, with this species exhibiting reductions in Prescribed fire and increases in Wildland fire sites (Table 2-1).

Douglas-fir and tanoak mean density and basal area were only minimally affected by increasing canopy burn severity level in both prescribed and wildland fire sites (Table 2-2). Douglas-fir accounted for an average of <70% of the basal area and 32.5% of trees ≥ 10 cm dbh and tanoak for 30.0% of the basal area and >70.0% of trees ≥ 10 cm dbh (Table 2-2). Tanoak mean tree density ranged from 189 to <2 trees per hectare from low to high canopy burn severity sites, respectively. There was a trend in reduced Douglas-fir density across canopy severity, however this change was not statistically significant in either prescribed or wildland fire sites. Douglas-fir average quadratic mean dbh (Dq) increased from low to high canopy burn severity in prescribed fire sites; however, a significant decrease in average Dq was observed in high canopy burn severity wildland fire sites (Table 2-2). In contrast, Tanoak mean Dq was greatest in moderate canopy burn severity sites of both prescribed and wildland fire.

Diameter distributions

Tanoak, in unburned sites, exhibited a typical reverse J-shaped curve with 75% of the trees occurring in the 10 to 30 cm dbh size classes (Figure 2-4). In contrast, Douglas-fir exhibited a skewed uni-modal distribution characterized by high tree density in the 15 cm dbh class and relatively low densities across medium and large diameter classes. I found shifts in size class distributions of tree density and basal area across both prescribed and wildland fire stands (Figures 2-4 & 2-5).

Increasing canopy burn severity level resulted in pronounced diameter distribution changes in tanoak and Douglas-fir across prescribed and wildland fire sites (Figures 2-6 and 2-7). In Prescribed fire sites, tanoak diameter distributions shifted from a reverse J-shaped curve (75% of trees in diameter class 5 and 15) in low canopy burn severity to a more uni-modal bell shaped curve in moderate and high canopy burn severity level. In contrast, Douglas-fir diameter distributions shifted from a reverse J-shaped curve in low and moderate canopy burn severity to a more uni-modal bell-shaped curve in the high canopy burn severity level. In Wildland fire sites, tanoak diameter distributions exhibited a somewhat skewed (Poisson) shape curve in low and moderate canopy severity levels with greatest tree density in the 15-cm diameter class. Sites with high canopy burn severity levels exhibited a uni-modal curve representing trees in the 45cm and greater diameter classes. Similar to results found in Prescribed sites, Douglas-fir diameter distributions shifted from a reverse J-shaped curve in low and moderate canopy burn severity to a more uni-modal bell shaped curve in the high canopy burn severity level in Wildland fire sites. Concomitant with the observed burn severity mediated distributional shifts in Prescribed fire and Wildland fire sites, both tanoak and Douglas-fir lost entire size classes; corresponding to small diameter classes in tanoak and both small and large diameter classes in Douglas-fir.

Tanoak basal area distributional changes across canopy burn severity showed generally similar reapportioning patterns of mean basal area, shifting from small to larger dbh size classes in low and moderate canopy burn severity levels of both Prescribed and

Wildland sites (Figure 2-7). In high severity Wildland fires, extremely high mortality resulted in all tanoak basal area to be located in a single diameter class (diameter class 65). Douglas-fir exhibited a more pronounced distributional shift in mean basal area allocation from small to larger diameter size classes; most pronounced in high severity Prescribed and moderate severity Wildland fire sites (Figure 2-7).

Forest fuels – woody fuels and forest floor depth

Woody fuels and forest floor depth were significantly reduced in both Wildland and Prescribed fire sites (Table 2-3). Total forest floor woody fuels ranged from 25.5 tons/ha in No fire sites to 9.0 tons/ha in Wildland fire sites. Ten-hour Fine Fuels (2.5-7.6 cm diameter) accounted for the highest fuel loading, representing 63%, 54%, and 39% percent of total woody fuels in No fire, Wildland fire, and Prescribed fire sites, respectively. There was a significant difference among all fire types in Rotten 1000-hour fuels (logs >7.6 cm diameter), with the greatest reductions occurring in Wildland fire sites. Wildland and prescribed fire sites had significantly reduced litter and duff depths compared to the No fire sites (Table 2-3).

Composition and biomass of woody fuels and forest floor depth showed different responses to increasing canopy burn severity levels within and among Wildland fire and Prescribed fire sites (Table 2-4). In Prescribed fire sites, moderate canopy burn severity levels resulted in the greatest reductions of woody fuels, accounting for a 42% reduction from levels observed in low canopy burn severity sites. Total woody fuel loadings ranged from 9.1 to 22.0 tons/ha. One hundred-hr fuels (2.5-7.6 cm diameter) represented the highest fuel loading in low and high canopy burn severity sites; accounting for 45%

and 54% of total woody fuels, respectively. Sound 1000-hr fuels (>7.6 cm diameter) represented the highest fuel loading in moderate canopy burn severity Prescribed fire sites. In Wildland fire sites, high canopy burn severity levels resulted in the greatest reductions of woody fuels accounting for 59% reduction from levels observed in low canopy burn severity sites. A clear trend in reduced litter depth was observed across increasing canopy burn severity levels in both fire types; however, no statistical differences were found. Duff depth was significantly reduced in moderate and high canopy burn severity levels of both Prescribed and Wildland fire sites.

Increasing canopy burn severity resulted in reductions of woody fuels and forest floor depth; although these trends differed among prescribed and Wildland fire sites. Low severity Wildland fire sites had significanly lower 100 and 1000 hr Fine Fuels and rotten logs >7.6 cm diameter than in the prescribed-Low sites. Moderate severity prescribed fire sites had significantly higher 1000 hr Fine Fuels than in corresponding Wildland fire sites. Limited sample size precluded comparisons of high canopy burn severity by fire type; however, Wildland fire sites typically exhibited lower levels of all woody fuels and forest floor depth components (Table 2-4).

Forest fuels – sapling densities

Sapling densities of tanoak declined in both Wildland and Prescribed fire sites, accounting for reductions of 94% and 72%, respectively, from average sapling densities found in the No fire sites. Significant reductions in Douglas-fir sapling density were observed with complete sapling removal observed in all Prescribed fire sites and most of the Wildland fire sites (Figure 2-8). Sapling height distributions shifted from typically small average heights in No fire sites to fewer taller individuals in the burned sites.

Increasing canopy burn severity resulted in significant declines in sapling densities of both Douglas-fir and tanoak; the highest sapling mortality observed in high canopy burn severity sites. Tanoak saplings were represented in all stem height classes. Tanoak re-sprout density differed by fire type with significantly greater re-sprouts across all canopy burn severity levels in Wildland fire sites. Re-sprouting vigor of tanoak appeared to be greatest in moderate severity burn plots as many clumps attaining >25 cm height were observed within a few months post fire (D. Major, pers. obsv.).

Composite burn severity index

Comparison of categorical index strata and total composite burn severity scores across Wildland fire and Prescribed fire exhibited interesting patterns within the vertical stand structure. Stand-level mean CBSI ranged from 1.6 to 1.8 and 1.8 to 2.0 in Prescribed fire and Wildland fire sites, respectively. CBSI values were highest in moderate canopy burn severity sites in Prescribed fire and high canopy burn severity sites in Wildland fire. High canopy burn severity Wildland fire sites had significantly higher stand-level CBSI scores than corresponding Prescribed fire sites (t= 1.799, df=3, p=0.08).

Comparisons of CBSI among the three stand strata revealed some trends both among fire type and within canopy burn severity levels (Figure 2-9). Overstory strata (OS) mean CBSI scores ranged from 1.4 to 2.1 in Prescribed fire sites, representing moderate increases from low to high canopy burn severity; however, statistical comparisons were unavailable due to small sample size. I found no differences in mean CBSI scores across canopy burn severity levels in Wildland fire sites. Understory strata mean CBSI scores ranged from 1.8 to 3.0 and 2.5 to 3.0 in Prescribed fire and Wildland fire sites, respectively. No significant differences in Understory CBSI scores existed within canopy burn severity levels. Surface Fuels represented the lowest CBSI values; accounting for scores below 1.5 in both Prescribed and Wildland fire sites. Understory strata had the highest CBSI scores across all canopy burn severity levels in both Prescribed fire and Wildland fire sites (Figure 2-9).

Canopy and composite burn severity relationships

I observed contrasting patterns in canopy cover loss across canopy burn severity categories: resulting in significantly higher canopy cover loss in moderate severity wildfire and significantly lower canopy cover loss in high severity prescribed fires (Figure 2-10). In contrast, CBSI ratings were moderately associated with fire behavior. In particular, fire scorch heights (an indication of fireline intensity) on Douglas-fir and tanoak trees were positively assocated with CBSI values; however, the two tree species exhibited very different response profiles (Figure 2-11).

DISCUSSION

The no fire sites examined in this study suggested some possible effects of fire exclusion in the dry Douglas-fir / tanoak forest system. Of particular note, tanoak sapling density was exceptionally high and likely the result of extended periods without fire that afford increased seedling/sapling survival. In contrast, Douglas-fir saplings were typically observed at low densities, often spatially clumped within the stand. Examination of Douglas-fir diameter distributions showed a prominent increase in tree density in the 15 cm dbh class. I speculate that this size class represents seedling establishment after the last fire event. Although tree age data were not recorded in my study, tree size/age relationships should be similar to those reported by Taylor and Skinner (1998) as part of fire history reconstruction work in the same general area. The presence of scattered large Douglas-fir (>80 cm dbh) and tanoak (> 50cm dbh) trees were indicative of old (> 250 yrs) fire resistant legacy trees and trees that survived in unburned patches during past fires, respectively. The dominance of large diameter fuels and large sound/rotten logs is not surprising as atypically long periods of fire exclusion would allow the build-up of additional fuels.

Diameter distributions

Fire disturbance (type and severity) resulted in significant changes in the Douglas-fir / tanoak forest composition and structure, with some species lost while others lost entire size classes. Similar fire-mediated composition and structure changes have been observed in other fire reconstruction studies (Wills and Stuart 1994, Taylor and Skinner 1998). Tree species diversity was moderate in my study sites. Higher species diversity has been documented in similar edaphic postions (Taylor and Skinner 1998) and other more mesic environments of the Douglas-fir / Hardwood zone (Bingham and Sawyer 1991, Hunter 1997). The moderate but highly variable species diversity in my sites may be due to the generally northern aspects and low to moderate elevation range (500-1000 m) of the sites. Moreover, as a potential fire refugia, these forests would have a relatively longer fire return interval that would allow survival of a few shade-tolerant and intolerant species. Other tree species encountered in the study sites represent single isolated fire resistant species (*Pinus* spp.), or species capable of establishing in small-scale disturbance patches afforded by past fires or tree-fall gaps (e.g., Pacific madrone, chinkapin). Given the low density and relatively large diameter of these species in my sites, these individual trees have probably survived numerous fire events.

The fire-mediated reduction/removal of size classes resulted in changes to stand-level tree density, basal area and quadratic mean diameter across fire disturbance types. It was interesting that although size class reductions/eliminations occurred in both Douglas-fir and tanoak, the relative proportions (Trees/ha: Douglas-fir-30%, tanoak-60%; Basal area: Douglas-fir-60%, tanoak-30%) remained similar across both fire type and burn severity levels. Maintenance of these proportions will likely result in continued dominance of Douglas-fir in the upper canopy and a new wave of tanoak occupying the lower canopy. However, the structure afforded by the remaining size classes and possible structural attributes associated with fire exclusion could result in a significant change in the fire generated multi-cohort structure of these forests (see Chapter 3).

Forest fuels

I found small differences in consumption of woody structure across Prescribed fire and Wildland fire sites. However, Wildland fire sites had notably higher within-stand variability in forest floor woody structure (Table 2-3). Given the contrasting seasonality and potentially different environmental and fire weather conditions of these two fire types, I expected greater woody material consumption during the extreme xeric conditions present during a wildland fire. One reason for the observed difference may result from the spatial mosaic of fire behavior. Post-burn observations on the effects of the Dillon Fire (1987, California, ca. 90,000 acres) and more recently the Biscuit Fire (2002, Oregon, ca. 110,000 acres) reported wildland fire behavior in Conifer/Hardwood forests resulting in a generally heterogeneous burn mosaic (Tom Atzet, pers. com.). In contrast, flame front height and associated intensity levels are typically manipulated in prescribed fires and thus result in a larger, more homogenous burn pattern and forest floor fuel consumption. This may account for the contrasting variability observed between Prescribed fire and Wildland fire sites.

There was a positive trend in increased consumption of forest floor structure across increased canopy burn severity in wildland fires, primarily affecting 10 – 100 hr fuels and large log components (1000-hr fuels) of forest floor woody material. However, the greatest overall reductions occurred in moderate severity prescribed fire sites. This may be due, again in part, to the typically homogenous burn characteristics of prescribed fire. However, the larger range of the moderate canopy burn category (between 25% and 75%) could also influence variability estimates as a greater difference between fuels consumption and associated fire behavior likely exists. However, small sample sizes precluded effective assessment of high severity fires, thus limiting interpretations. Litter and duff depths were also reduced with increasing burn severity. However, some accumulations in fuels (e.g., leaves, twigs, branches, etc.) and large logs (fire-killed and root-burnouts) were observed in high severity burns of both fire types. Moderate to high amounts of leaf cast from top-killed tanoaks were observed in many of my sites; often completely covering the forest floor in sites burned at moderate and high severity. I surveyed all burned sites within a few months post-burn; therefore, some error in estimates of forest floor woody structure and litter/duff depths is likely.

Fire regime influence on future dynamics of Douglas-fir / tanoak forests

Natural establishment and associated competitive pressures among Douglas-fir and tanoak are dependent upon dominance of the immediate post-fire environment. Tanoak is a fire-adapted species, capable of re-sprouting shortly after a fire (Jepson 1910). Douglas-fir requires a scarified seedbed and open canopy for seedling establishment (Minore 1979, Burns and Honkala 1990). Fire history reconstruction work by Wills (1991), Wills and Stuart (1994) and Taylor and Skinner (1998) reported highest Douglas-fir seedling establishment occurred after moderate to high severity fire. In my study, Douglas-fir seedlings were rarely encountered in burned plots, occurring primarily in small patches associated with extreme hot spots. Within these small patches, seedlings were typically located at the base of large Douglas-fir trees that survived the burn. Tanoak vegetative regeneration quickly dominated the understory in all burned sites, with the highest growth/density observed in the moderate and high severity fire sites. Tappeiner et al. (1992) reported a similar understory dominance of tanoak in young regeneration stands in southern Oregon.

The synergism between stand dynamics and fire processes is critical to the maintenance of the dry Douglas-fir / tanoak system (Skinner 1995). The loss or significant reduction in size classes of both Douglas-fir and tanoak could have profound effects on future stand dynamics. Establishment of Douglas-fir in these forests is typically episodic and survival of saplings is dependent on the severity of subsequent fire(s) (Wills and Stewart 1994, Taylor and Skinner 1998). Fortunately, a few large fire-resistant Douglas-fir trees remain as potential seed sources in all of my study sites.

Unfortunately, altered fuels profiles resulting from fire exclusion legacy in low and moderate severity burned stands may predispose these forests to burn at much higher severities during the next fire event (especially those burned with prescribed fires) (see Chapter 3).

Impacts to a potential fire refugium

Camp et al. (1995) described site characteristics of a fire refugia to include areas (patches) that exhibit a high diversity of shade-tolerant climax species and longer fire return intervals, higher fuel loadings, and generally high burn severity than occurs in the rest of the forest community (matrix). The dry Douglas-fir / tanoak forests examined in this study appear to posses some of these characteristics. For example, presence of large diameter shade-tolerant *Pinus* species at low to moderate densities and generally high fuel loadings across the fuels profile were common in many of my sites. However, I was able to find sites representing the entire range of canopy burn severity levels (Low to High) in both wildland and prescribed fires. Therefore, some of my sites may not be, or do not currently function as a fire refugia.

Arguably, not all environments meeting the narrow edaphic characteristics described above currently support a fire refugia, nor is this edaphic characterization pertinent to all forested environments. Further, fire exclusion can result in the creation of patches that are structurally and compositionally similar to those found in a fire refugia. Fire refugia are temporally limited as fuel loadings, fuel condition, and associated fire behavior in these environments can be altered by stand senescence or extended periods of drought (Hessburg et. al. 1994, Camp 1999). Decreased fire frequency in stands due to the presence of talus (a site selection criteria for this study) or cliff environments can also favor shade tolerant species. However, they may or may not develop the structural /compositional attributes typically associated with a fire refugium (Camp 1999). Therefore, an effective evaluation of a fire refugium requires not only the exploration of structural and compositional attributes, but also the functional role that these components play in stand dynamics and associated fire regimes.

Fire management in these dynamic and somewhat atypical fire regimes will require an understanding of fire effects and associated stand dynamics at scales ranging from a fire refugia patch to surrounding vegetation communities to entire landscapes. While a high severity, often stand-replacing, fire may be required to "reset" succession in these fire refugia, the altered fuel profiles resulting from fire exclusion in the matrix could potentially result in a similar fire "reset" of the matrix. The result would be a relatively homogenous landscape; much different from the mosaic of stand age, composition, and sizes that characterized the historic fire regime of this forest. Persistence of these ecologically important areas is dependent on reliable identification of fire refugia and effective fire and fire-surrogate strategies. Further, these fire refugia may also function as a refugium for endemic flora/fauna. Therefore, efforts should be made to evaluate the effects of management practices designed to "reset" fire refugia on the locally endemic species.

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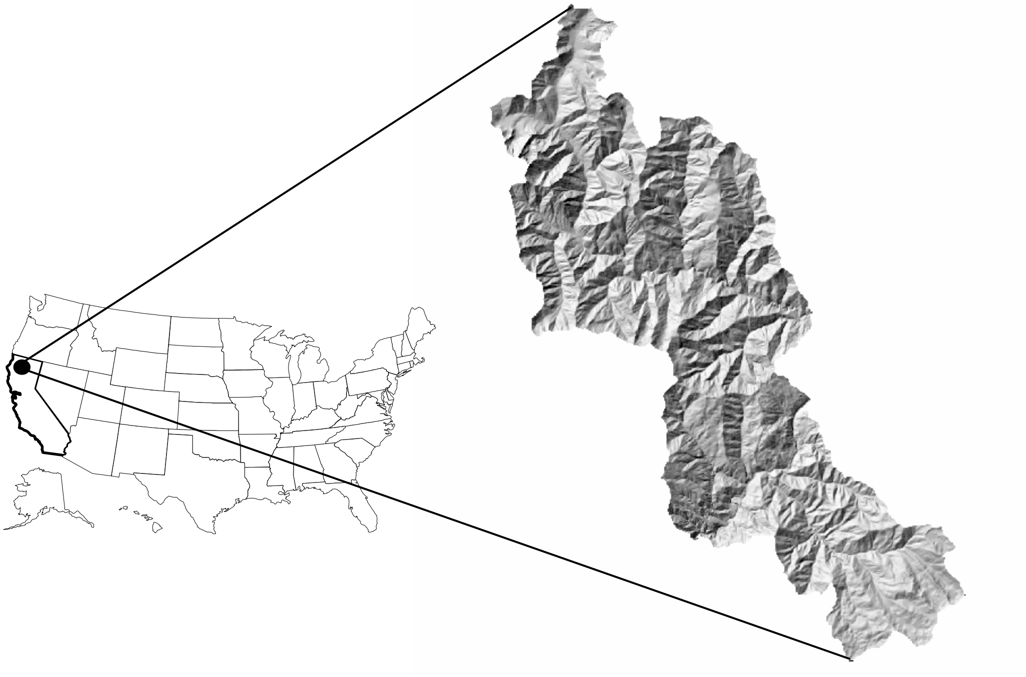


Figure 2-1. Study area location in the Klamath National Forest, Happy Camp California, USA. Expansion schematic represents shaded relief map of the combined Dillon Creek, Clear Creek, and Swillup Creek watersheds.

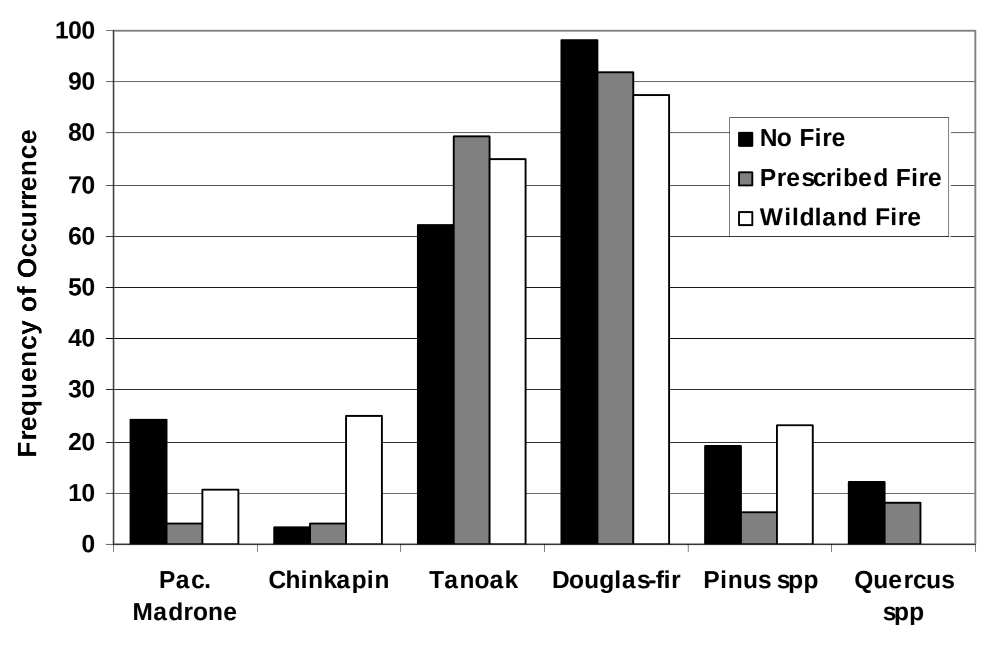


Figure 2-2. Tree species occurrence by fire disturbance type in plots sampled in the Douglas-fir (Pseudotpsuge menziesii) / tanoak (Lithocarpus densiflorus) forests.

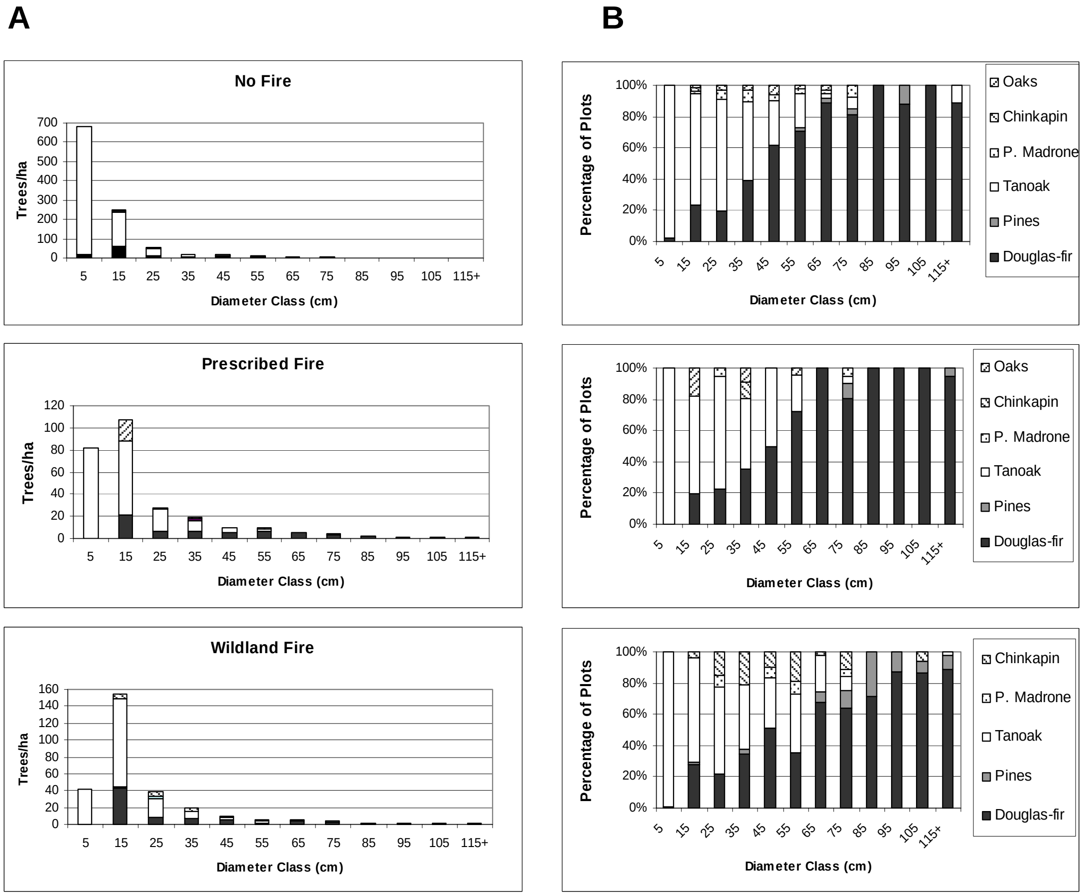
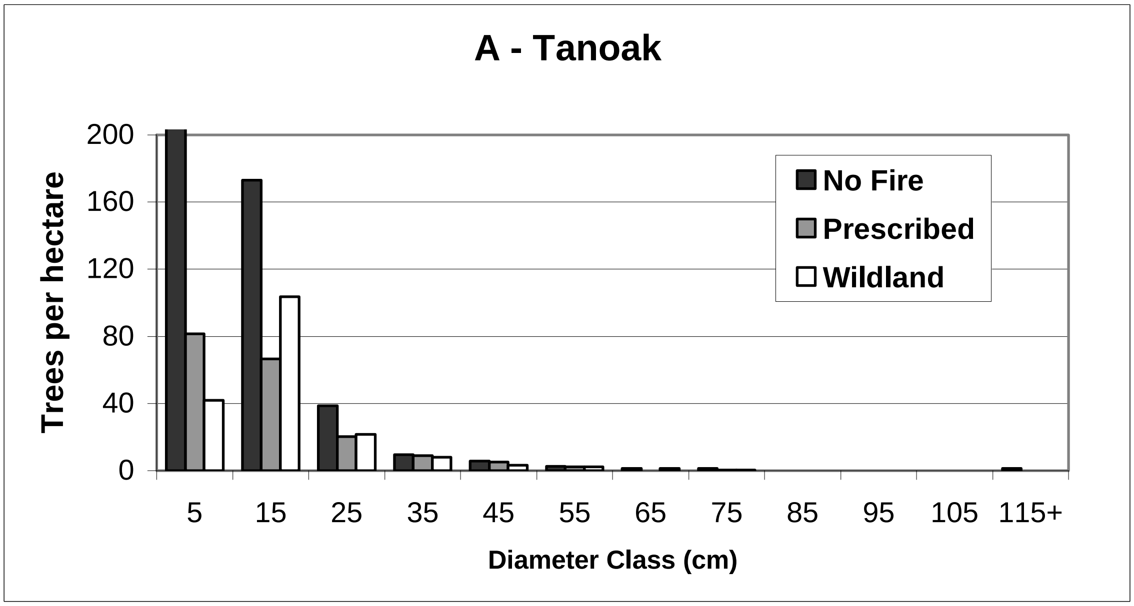


Figure 2-3. Diameter density (A) and relative density (B) of tree species by disturbance type.



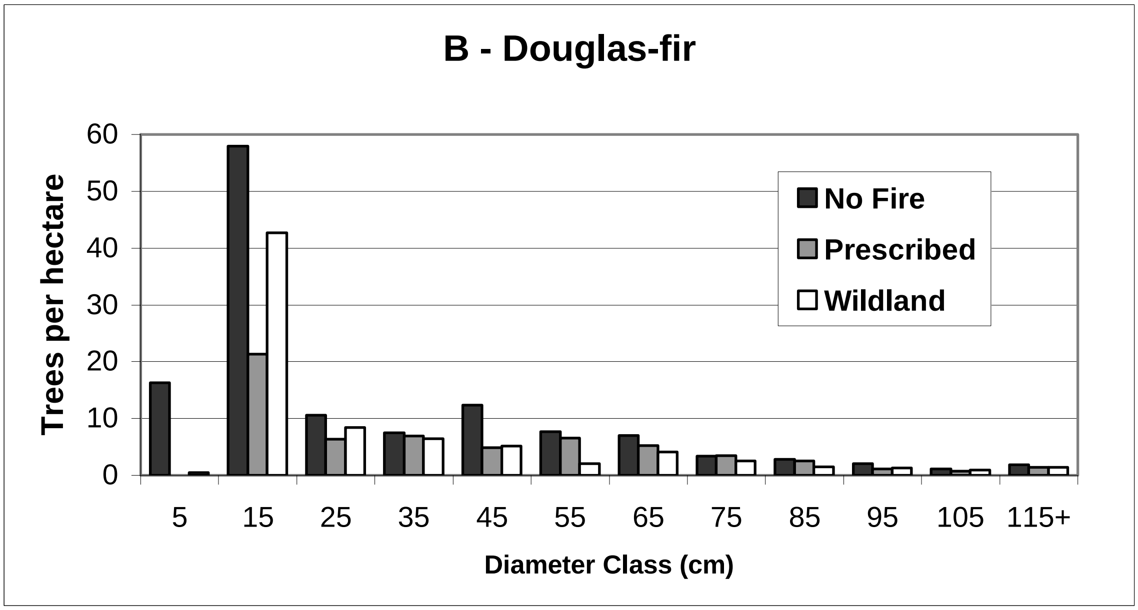
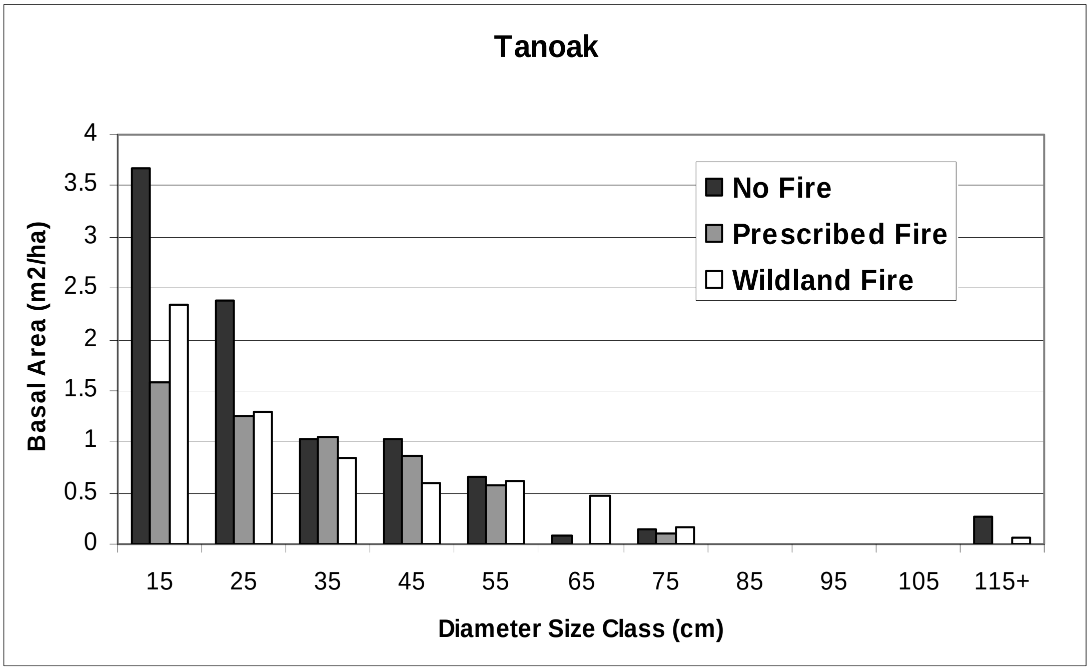


Figure 2-4. Effects of fire disturbance type on density (trees/ha) diameter distributions of (A) tanoak (Lithocarpus densiflorus) and (B) Douglas-fir (Pseudotsuga menzeisii).



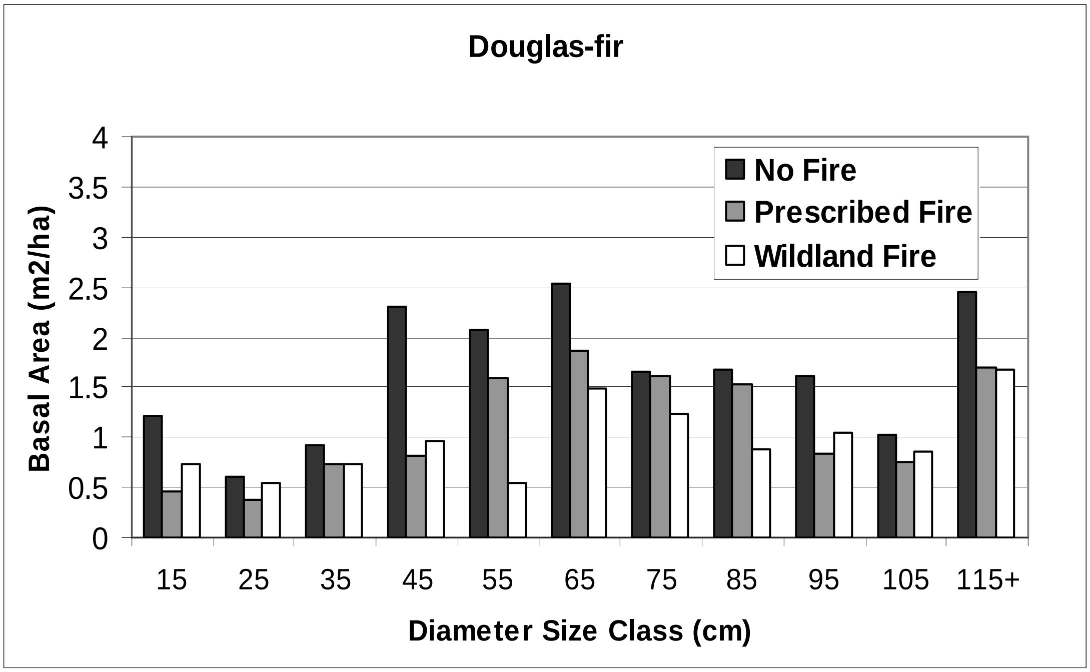


Figure 2-5. Comparison of Douglas-fir and tanoak mean basal area (m^2/hectare) by tree diameter size class across fire type.

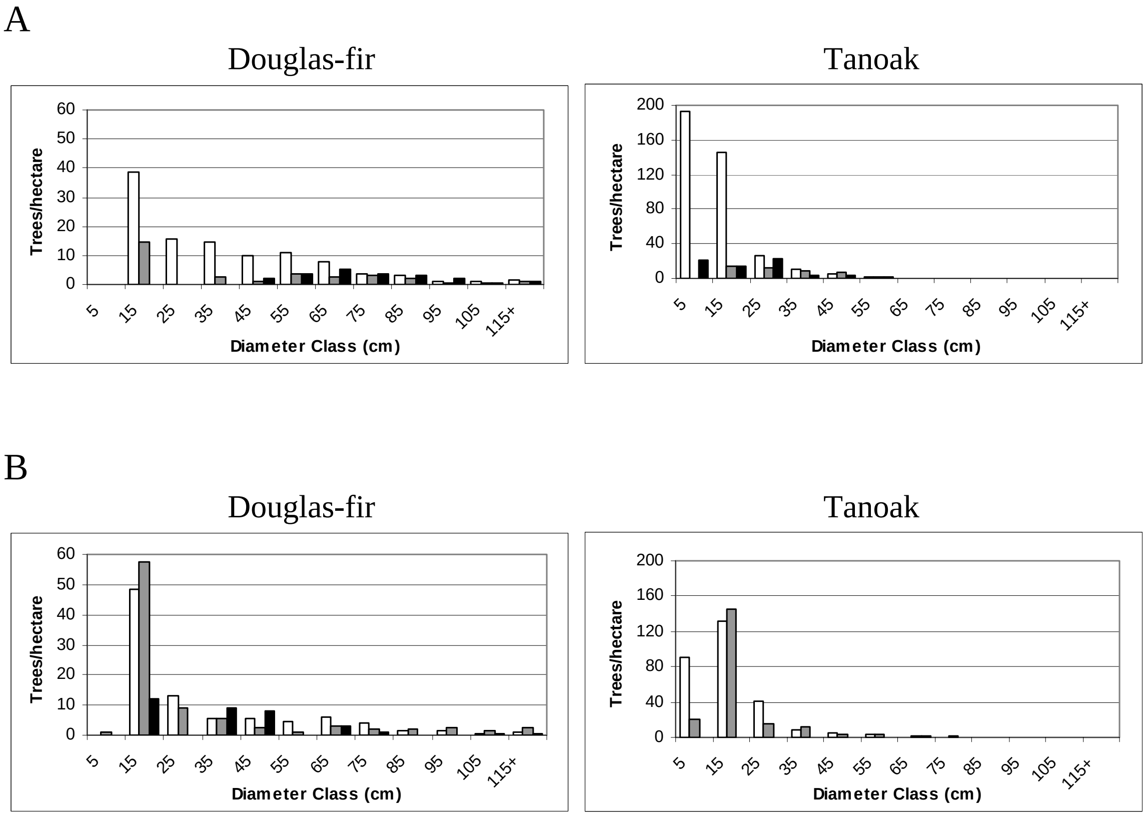


Figure 2-6. Comparison of density (trees/ha) diameter distributions across canopy burn severity levels. A - Prescribed Fire B – Wildland Fire. Canopy burn severity levels: Low (white), Moderate (grey), and High (black).

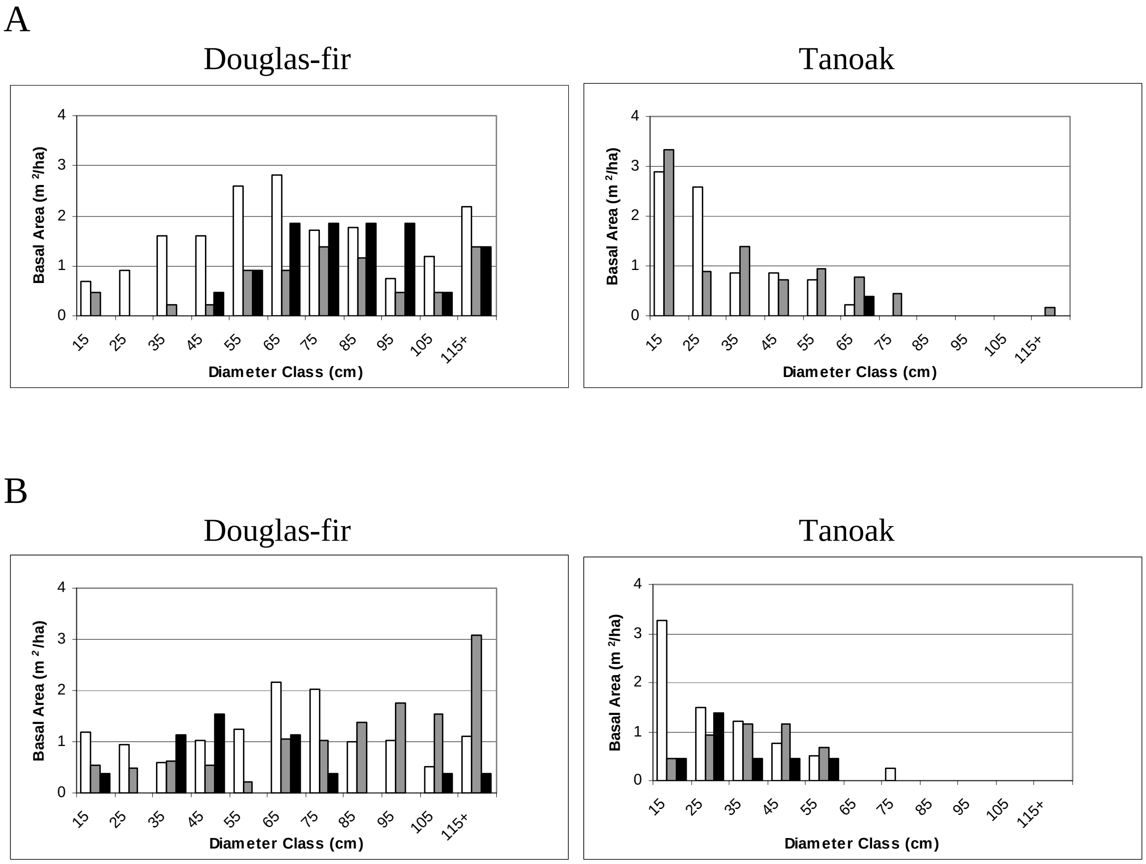


Figure 2-7. Comparison of basal area (m2/ha) diameter distributions across canopy burn severity levels. A – Prescribed Fire; B – Wildland Fire. Canopy burn severity levels: Low (white), Moderate (grey), and High (black).

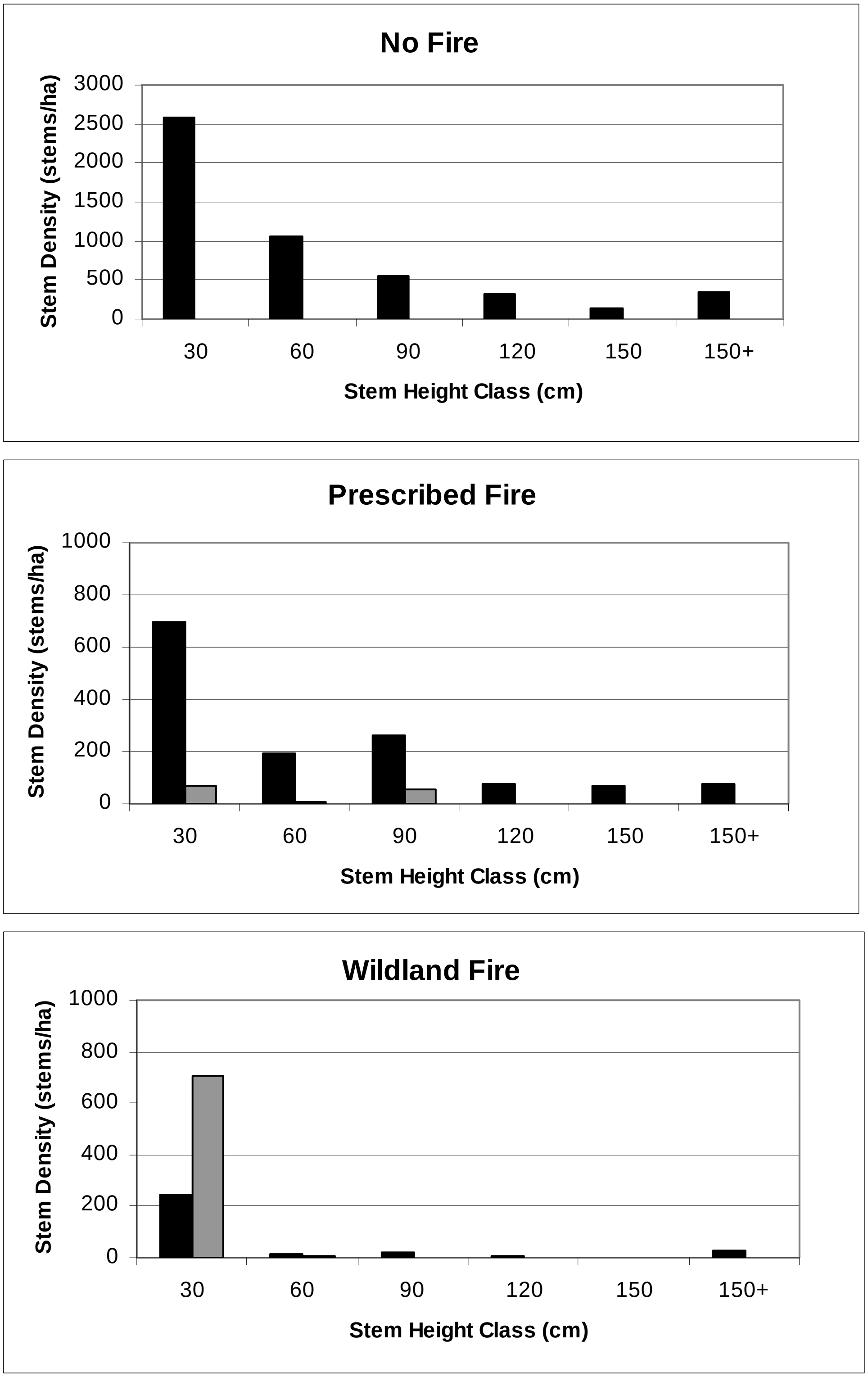


Figure 2-8. Tanoak and Douglas-fir sapling (black) and resprout (grey) density by fire type and height class.

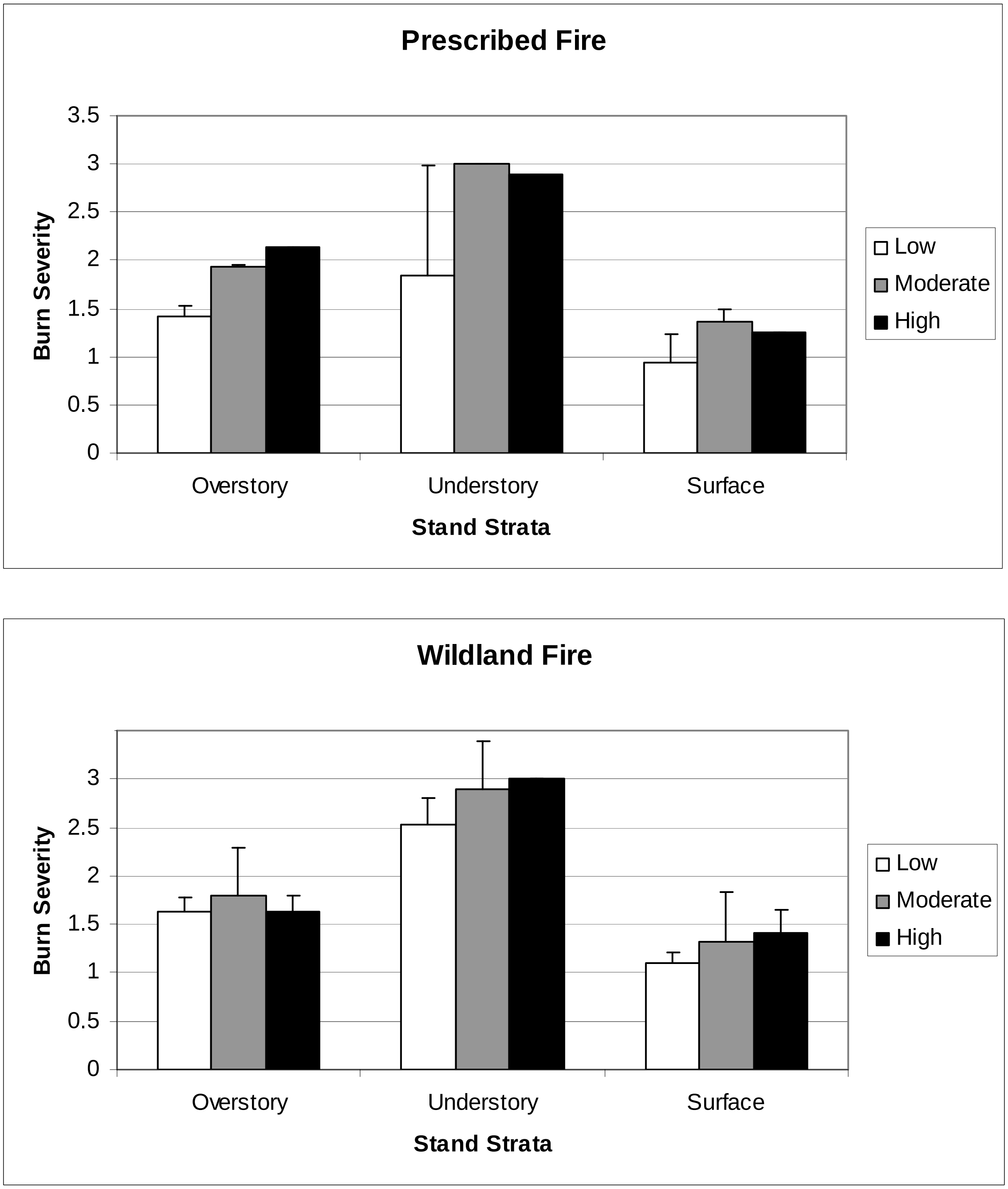


Figure 2-9. Comparisons of CBSI stand strata components by canopy burn severity levels in wildland and prescribed fire types.

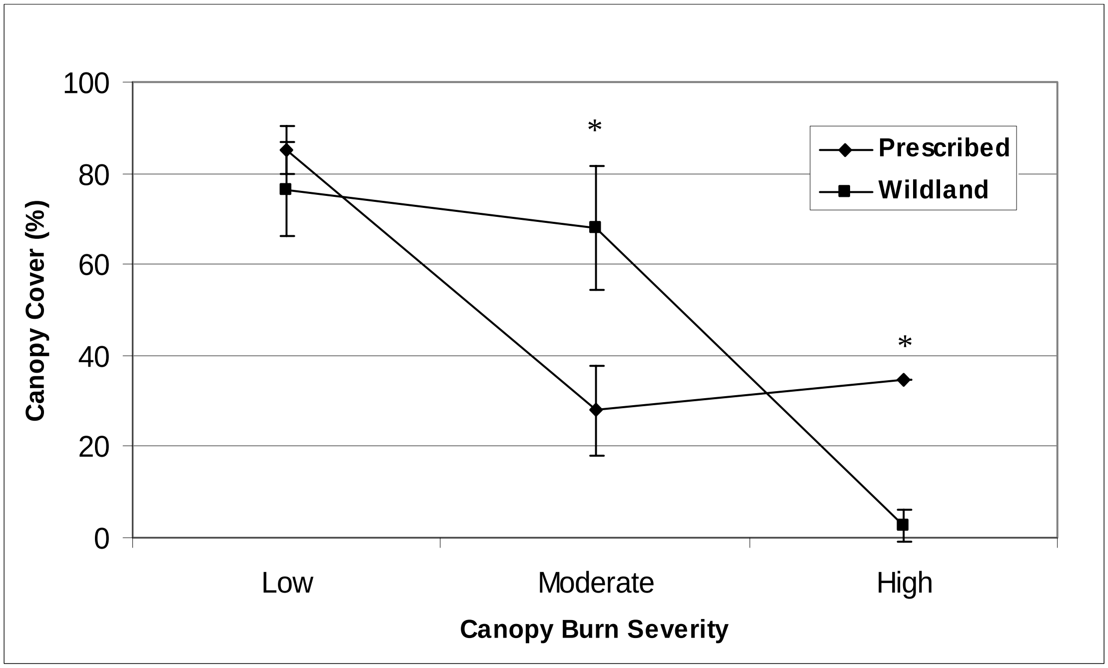
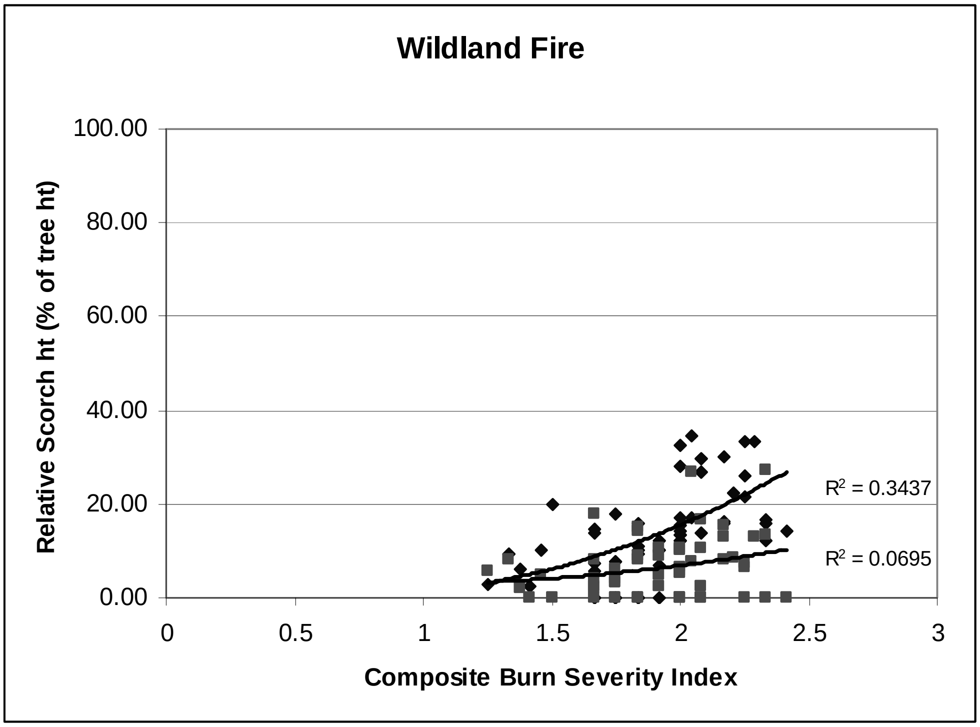


Figure 2-10. Response of overstory canopy cover to canopy burn severity level.
* significant $p < 0.05$



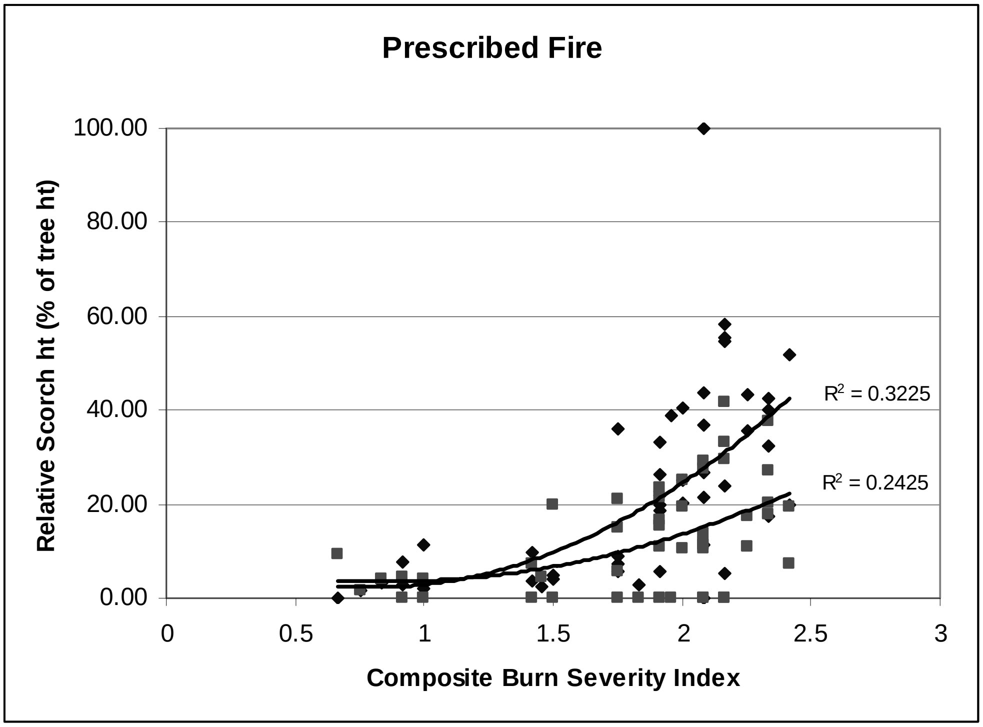


Figure 2-11. Relationship between Douglas-fir and tanoak fire scorch height and Composite Burn Severity Index (CBSI) across fire disturbance type. Douglas-fir (diamonds), tanoak (squares).

CHAPTER 3

FIRE EXCLUSION LEGACY IN MIXED-CONIFER FORESTS: IMPLICATIONS FOR FUEL DYNAMICS AND FUTURE ECOSYSTEM RESILIENCE

INTRODUCTION

Considerable attention has been given to the effects of fire suppression on forested ecosystems. In North America, fire suppression activities have significantly increased time since last fire (fire exclusion period) in many forest and non-forest systems (Heinselman 1973, Pyne 1996). Long periods of fire exclusion, in combination with other biotic (forest harvest, insect, disease) and abiotic (climate change, ENSO) factors, has resulted in altered fire regimes (i.e., type, intensity, return interval, and extent of fire) in many fire-dependent systems (Swetnam and Bentancourt 1990, Agee 1993, Covington and Moore 1994, Swetnam and Baisan 1996). Future fires in these ecosystems result in historically unprecedented catastrophic disturbance events (Pyne 1996). In fire dependent conifer forests of the West, identification of factors affecting fire regimes typically focus on pre-fire stand structure and composition associated with fire exclusion (Allen 1989, Covington and Moore 1994). However, little information exists on the role of fire exclusion in structuring post-fire fuel dynamics, potential fire behavior and ensuing fire regime characterization in these systems. Moreover, information is lacking on the potential long-term affects of altered disturbance regimes on ecosystem dynamics.

Research examining the effects of fire exclusion on stand structure and composition typically describe pre-fire dead surface fuel loadings (litter, duff, 10 to 1000-hr fuels) and density/composition of live young regeneration trees (ladder fuels). However, little attention is given to changes in above-ground biomass associated with other stand structure components; specifically, the biomass associated with changes in tree age/size distributions resulting from the loss of one to several fire cycles. Here, I define the term *fire exclusion legacy* to describe changes in stand structure, biomass, etc. related to these size/age distributional shifts in tree densities (Figure 3-1). Identification of post-fire fuel structure, composition, and loadings associated with a fire exclusion legacy is critical to understanding stand-level fuel dynamics and associated fire regime characterization. Further, this information may help elucidate trends in forest community dynamics in these fire-dependent ecosystems.

In western coniferous forests, forest health issues resulting from fire suppression/exclusion in fire-dependent forests has prompted land managers to explore the re-introduction of fire (or fire surrogates) into these systems. High priority ecosystems warranting fuels management activities include fire-dependent systems historically characterized by short fire return intervals and low to moderate severity fires (USDI/USDA 2001). In the dry Douglas-fir / hardwood forests of Northern California and southern Oregon, fire exclusion has resulted in significant alteration of forest structure and dynamics (Agee 1993, 1998, Taylor and Skinner 1998). Moreover, these forests exhibit contrasting vegetative dynamics; wherein two co-dominant tree species posses resistance or adaptation to fire. Little information exists describing the effects of fire exclusion in these communities and the influence of these divergent adaptive strategies in modifying the post-burn fire regime. Further, given the current mandate to re-introduce fire into these fire-dependent systems, an understanding of a fire exclusion legacy and its potential impacts on future forest resilience is warranted.

Here, I examine the effects of fire and fire exclusion legacy in the dry Douglas-fir / tanoak forests of the Klamath Province, Northern California. Specifically, I quantify fire exclusion legacy in stands perturbed by wildland and prescribed fire. Next, I estimate and characterize potential fuel biomass associated with post-fire forest structure. Then, I present a conceptual model to summarize the implications of this legacy on future fire severity and fire regime characterization. To conclude, I explore the implications of a hypothetical legacy-mediated disturbance model on future forest resilience.

Current system: Klamath Douglas-fir (Pseudotsuga menzesii) / tanoak (Lithocarpus densiflorus) forests

The dry Douglas-fir / tanoak (DF/TO) forest occurs within the Klamath Mixed conifer Ecological Province of Northern California and southern Oregon. DF/TO forests occupy generally north facing slopes from sea-level to about 2500 m. Whittaker (1953) described the DF/TO forests community as a transitional "ecotone" encompassing the fire resistant Douglas-fir and the fire adapted tanoak vegetation communities. Fire is the primary disturbance factor in these systems and is driven primarily by gradients of temperature- and moisture-stress (Agee 1993). Specifically, these included the growing environment (temperature and moisture regime), ignition pattern (lightning, anthropogenic), and plant species characteristics (adaptations to fire, fuel deposition). These forests develop under a mixed-severity fire regime characterized by frequent fires of generally low to moderate severity (Agee 1991, Wills 1991, Wills and Stuart 1994).

Median fire return intervals range from 8 to 16 years and were strongly influenced by local biotic/abiotic conditions (Taylor and Skinner 1998). DF/TO structure/composition can vary dramatically across the landscape, ranging from relatively open to multi-layered, multi-aged understories.

Given the frequency of fire in these forests combined with divergent fire adaptation strategies of the co-dominant tree species, I explored the following hypotheses:

1. In fire excluded Douglas-fir / tanoak forests, the fire exclusion legacy is dominated by biomass associated with increased growth and survival rates of the fire-adapted species (i.e., tanoak);
2. Fire exclusion legacy results in an altered fuels profile that *decreases* the potential time to next fire and *increases* the potential for crown fire behavior during the next fire event, thus resulting in higher mortality in the fire resistant species (Douglas-fir);
3. Legacy-altered fire fuels profiles in the post-burn forest will result in the removal/reduction of Douglas-fir during the next fire event;
4. The removal/reduction of Douglas-fir combined with the short-term competitive advantage in tanoak establishment could exceed resilience thresholds and result in a system shift to a tanoak-dominated forest. The resulting tanoak forest would be perpetuated by a generally high frequency and low to moderate severity fire regime.

METHODS

Fuel biomass estimation

I examined changes in DF/TO forest fuel loadings across three fire disturbance types: unburned current forests (n=5 sites), forests burned by wildland fire (n=7), and forests managed with prescribed burning (n=4 sites). I define stand level forest fuels as two types: 1) current surface fuel biomass (10-1000 hr fuels, logs 10-15 cm dbh), and 2) potential fuel biomass from standing dead/top-killed trees (fine fuels, branches, canopy foliage). Estimates of current surface fuel loadings and stand structure (tree density distributions) were collected as part of a larger fire effects study examining fuels/habitat dynamics and terrestrial salamanders (see Chapter 2). Data were collected within 3-6 months post-fire for wildland fire sites and within 1 year for prescribed burn sites.

To estimate total number of standing dead/top-killed trees, I quantified differences in tree density (trees per ha) by diameter breast height (dbh) size classes between burned and unburned forest stands (e.g., Unburned Current forest tree density by dbh class – Wildland fire tree density by dbh class = estimate of standing dead/top-killed trees). Next, I estimated fuel biomass by tree diameter class from species-specific allometric equations. Species-level regression equations were used to determine fine fuels, branches 10-15 cm, and canopy/foliar biomass for tanoak (Snell 1979). Douglas-fir biomass estimates (crown and foliar) were predicted using equations contained in Gholz et al. (1979) and Brown (1974). For trees <10 cm dbh (i.e., regeneration cohort), I used stand-level mean dbh values: tanoak dbh=3.5 cm, Douglas-fir dbh=8.0 cm.

RESULTS

Fuels biomass

Total post-fire surface fuel biomass ranged from 2,333 kg/ha in wildland fire sites to 7,963 kg/ha in unburned current forests (Table 3-1). Among burned sites, prescribed fire sites had higher fuels biomass associated with both fine fuels and logs 10-15cm categories than in the wildland fire sites. Both fire types contained significantly lower fuels biomass than Unburned Current forests. All fire types exhibited similar patterns in proportion of live regeneration fuels biomass contributed by conifer and tanoak tree species (Table 3-1). Potential fire exclusion legacy trees came from different portions of the two tree species diameter density profiles (Figure 3-2:A and B). Tanoak tree density ranged from to 1 – 1,554 trees per hectare (TPHa) and was distributed across 5 – 100 cm diameter classes. However, fire exclusion legacy was represented in the 5 – 40 cm diameter class. In contrast, Douglas-fir fire exclusion tree density was much lower (1 to 55 TPHa) and was distributed across the 5 – 100 cm diameter classes. Differences existed in the contribution of each tree species to estimated fuels biomass related to fire exclusion legacy (Table 3-2). Tanoak contributed significantly higher fuels biomass than Douglas-fir. Total fuel biomass ranged from 4,198 to 17,719 kg/ha (Table 3-2). Among burned sites, total biomass was greatest in prescribed fire sites; with biomass levels approaching 72% of pre-fire conditions (Table 3-2).

Fire exclusion legacy

In the dry Douglas-fir / tanoak forests, fire exclusion has resulted in significant changes in stand structure; specifically, a shift in tanoak size distributions and associated increase in stand biomass. This fire exclusion legacy component is an important factor defining the range and magnitude of fire intensity during the next fire event, subsequent post-fire burn severity, and ensuing fuels dynamics. Fire exclusion legacy was most prominent in sites managed with Prescribed burning. I suspect this is a result of the relatively homogeneous application of fire employed in prescribed burning. Wildland fire sites burned in more of a mosaic pattern, with patches of live/unburned trees distributed across the stand. Finally, fuel biomass associated with fire exclusion legacy resulted in significant ladder fuel biomass in the post-burn stand. Fire history studies in mixed conifer hardwood forests describe low to moderate intensity ground fires with ladder-mediated torching and crown-fire behavior confined to smaller patches within a stand (Skinner 1995, Agee 1998, Taylor and Skinner 1998). Further, tree growth/development and biomass production (limited by the short fire return intervals of the historic fire regime) would contribute minimally to the legacy component. Therefore, I suspect that the fuels profiles reported in my post-fire stands represent novel conditions in these forests. The effects of these atypical fuel loadings on future fuels dynamics and associated fire regime(s) will be examined in the following sections.

A conceptual model

To examine the effects of fire exclusion legacy on system stability, I developed a conceptual model of forest fuel dynamics. The model is based on ecological resilience theory (Walker et al. 1969, Holling 1996); that suggests system stability is governed by variation in a critical variable(s) (Holling 1973). However, resilience is defined in the context of *reduced/minimal levels or pools* of a critical variable(s) (Webster et al. 1975). Therefore, I modified the resilience model to better reflect the nature of fire exclusion (i.e., *increased* fuel loadings) (see Waide 1988, Vose 2000).

Figure 3-3 illustrates my conceptual model of fuel biomass dynamics developed for the DF/TO system. Initial conditions represent current post-fire fuel biomass pool (results above). Fuel biomass response is separated into three components: surface fuels, potential ladder fuels (regeneration fuels), and potential ladder fuels from top-killed trees (standing fuels). "Historic range" is used to represent a hypothetical range of fuel loadings (by category) characteristic of this system.

DISCUSSION

Surface fuels recover quickly as leaf-cast inputs from standing dead/topkilled trees add to residual fuels unconsumed in the previous fire. Next, a slow reduction resulting from a slow breakdown of vertical fuels is offset by surface fuel decomposition. Finally, fuels representing mortality in competing regeneration stems would add to the surface fuels. Regeneration likely recovers quickly as existing tanoak root biomass profile reflects the tree diameter development associated with fire exclusion legacy (i.e., larger root systems = greater energy reserves for vegetative re-sprouting=greater resprout biomass). Thereafter, inputs to surface fuels would be small incremental increases. Given the generally short (<16 yrs) fire return interval, regeneration ladder fuels would likely exist as small diameter, relatively short trees or stem clusters (typical of this system). The greatest proportion of fuel biomass in the post-fire system would be in the form of standing dead/topkilled trees (predominantly tanoak). Within the first few years, a slight increase in fuel biomass would occur as a small number of trees significantly stressed by the fire, succumb. Thereafter, this fuel component would steadily decline at a moderate rate.

Effects in the Douglas-fir / tanoak fire regime

Failure to account for fuels biomass associated with fire exclusion legacy could have profound effects on predictions of future fire behavior and severity. Given the potentially fast rebound in surface fuels, a continuous fuel bed could develop in only a few years, thereby decreasing the time to next fire. I observed leaf-cast of several cm in depth and continuous across the forest floor in DF/TO forests within two years post-burn (pers. obsv.). The high proportion of ladder fuels present in the post-fire system could result in conditions favorable to crown fire. Post-fire ladder fuels occur not as typical small diameter young regeneration, but taller trees with larger canopies. During the next fire event, this altered fuels profile would allow flames to move up into the Douglas-fir canopy; resulting in an atypically high mortality rate. The increased isolation of individual Douglas-fir combined with the highly competitive vegetative reproduction in Tanoak would reduce seedling availability and establishment rates for this species. The result would be a potential system shift from a mixed conifer/hardwood to a generally monoculture Tanoak forest (Figure 3-4). However, once the standing legacy component is removed/consumed, the forest may return to a co-dominant system if conifer seed pools remain in the vicinity and future fire(s) allow suitable growth and survival.

Model assumptions and limitations

I must concede the following assumptions and limitations of both quantitative and qualitative data. First, the retrospective nature of the larger study allows only generalized pre- vs. post-fire forest conditions. Further, failure to collect plot-level tree mortality data likely affected results. However, given the magnitude of difference in my estimates, it is likely that some level of ecologically significant change has occurred. The proportion of standing dead trees was not adjusted for fire severity; however, only a few sites characterized as high burn severity were included in this study. Tanoak biomass estimates for all fuel categories were based on equations derived from a relatively small number of tree samples. Conifer biomass estimates were based on “generic” coarse level equations. However, I observed limited Douglas-fir mortality in most study sites; thus affirming this species’ high resistance to low to moderate severity fires. Next, I assumed that all live trees persist until the next fire event and fuels resulting from partial canopy scorch, etc are not included in fuel estimates. This is unlikely because a small degree of post-fire tree mortality likely occurs, thus fire exclusion legacy estimates would be underestimated. Prior to European settlement, aboriginal burning was common in this region (Agee 1993, Atzet and Wheeler 1982). The effects of this disturbance type on Douglas-fir / tanoak stand structure are unknown. Finally, the study area was in its fourth year of a drought. The effect of this exogenous stressor on tree growth, fuels dynamics, and associated stand structure is unknown.

Management implications

Clearly, our current unburned forests are not typical of “historic” conditions. In order to manage them effectively, an ecological understanding of the effects of fire exclusion is warranted. The conceptual fuel dynamics model developed here provides insights on current and potential stand structure, fuels dynamics, and the associated fire regime(s). Moreover, the hypothetical context presented here could serve as a valuable fire management model. For example, silvicultural prescriptions targeting removal of specific fire exclusion legacy components could be implemented and monitored to ascertain future fire effects. Further, a suite of sub-models incorporating spatial and temporal fuels dynamics with system resilience thresholds could be identified to examine effective fire/fuels management strategies capable of maintaining forest-floor dependent faunal species.

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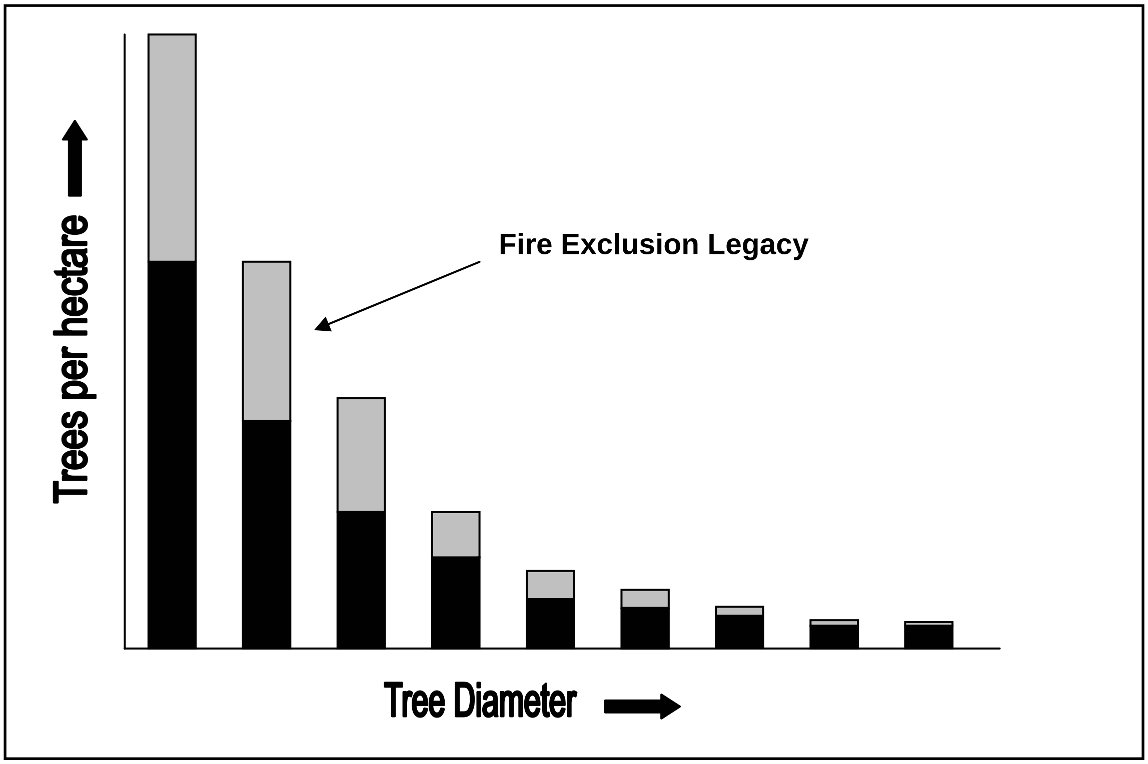
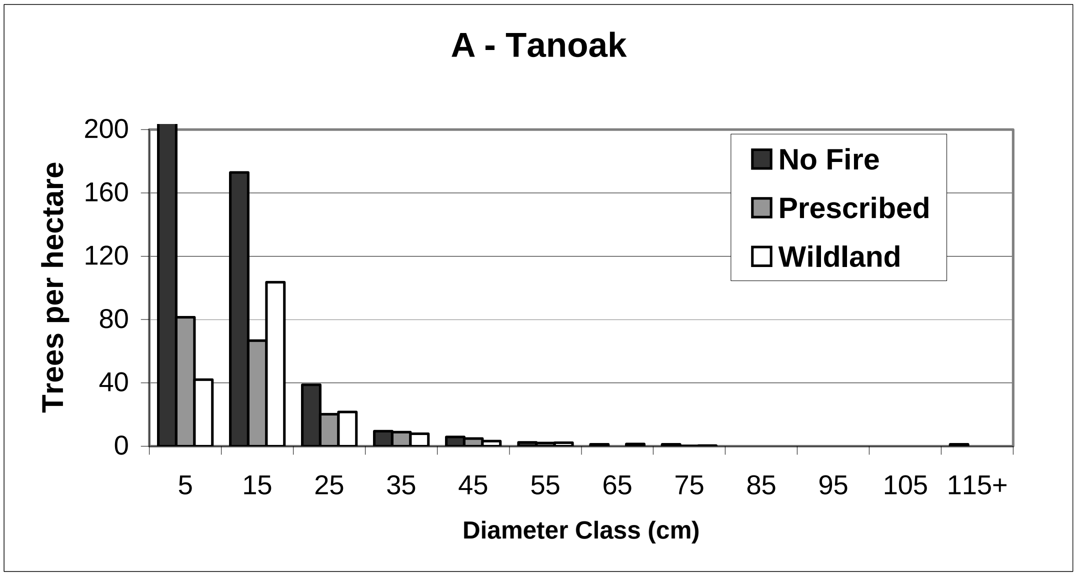


Figure 3-1. Schematic diagram depicting a fire exclusion legacy (grey portion) resulting from shifting stand size class distributions associated with increased tree survival under the loss of historic fire cycle(s).



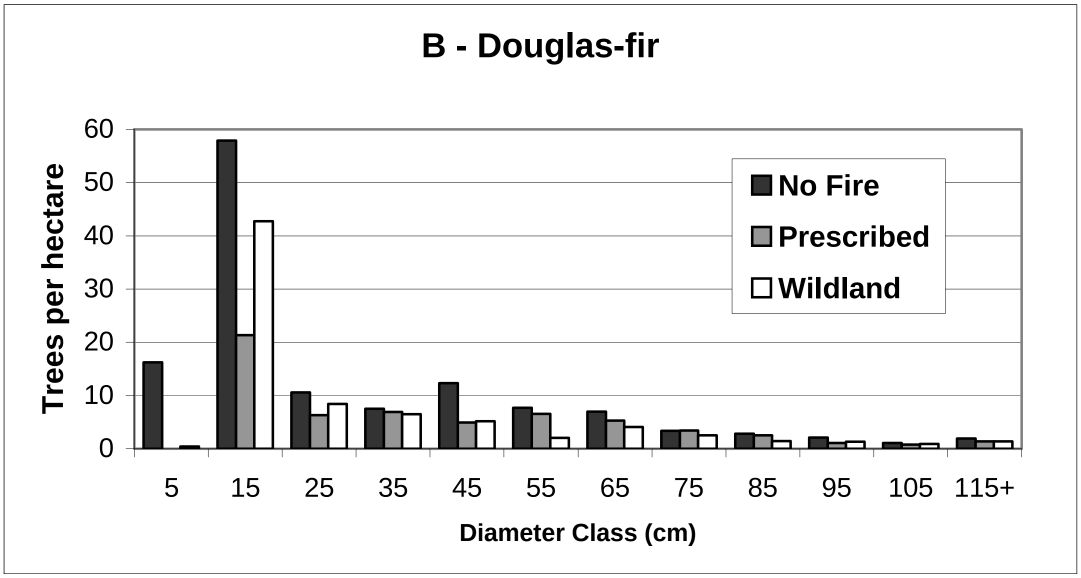


Figure 3-2: A and B. Comparison of diameter distributions by tree species across disturbance types: No fire, Wildland fire, and Prescribed fire.

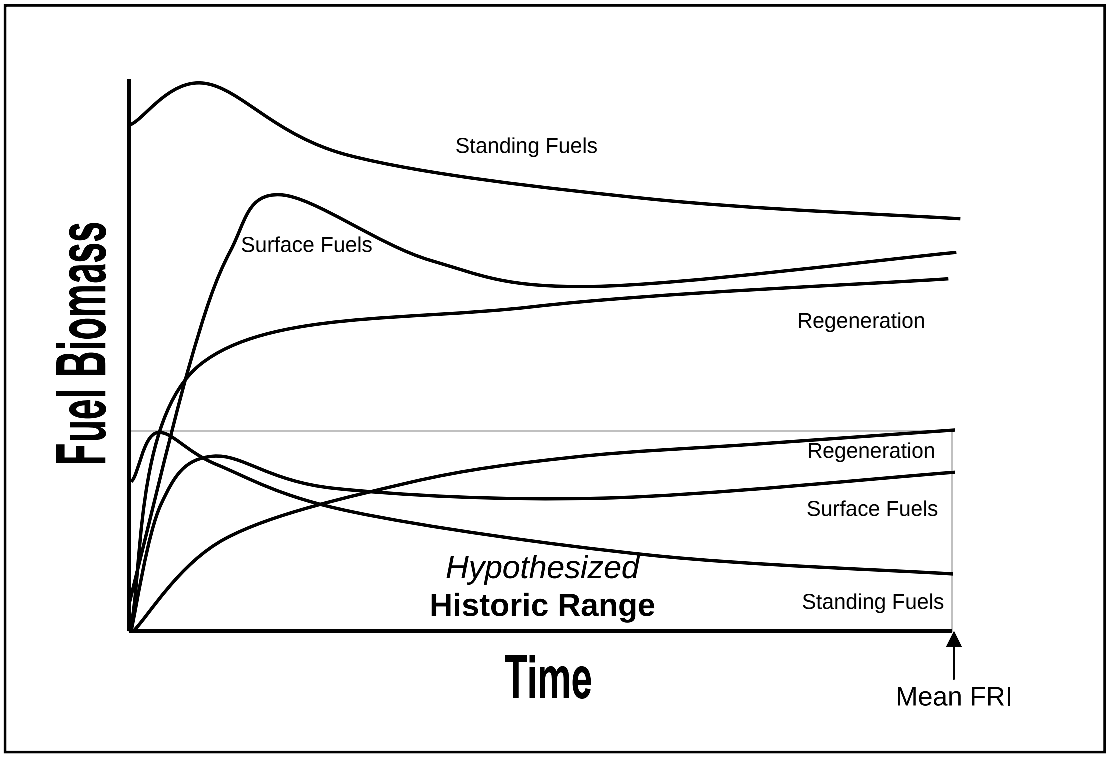


Figure 3-3. Conceptual fuel dynamics model for the Douglas-fir/tanoak forest system. Note potential for subsequent fire w/in a few years as surface and standing fuels (ladder) exceed historic range and allocation within the fuels profile.

CHAPTER 4

CLASSIFICATION-TREE MODELING OF DEL NORTE SALAMANDER (*PLETHODON ELONGATUS*) HABITATS ACROSS FIRE SEVERITY LEVELS IN DRY DOUGLAS-FIR / TANOAK FORESTS

INTRODUCTION

Research examining the effects of fire on forest salamanders and their habitats is limited (Lyon et al. 1978, 2000, Russel 1999, Bury et al. 2002). Available research suggests greatest succeptibility to fire is found in low vagility species and species strongly associated with specific components of the forest floor (e.g., duff/litter, downed wood, etc.) (Russel 1999). Fire can affect forest floor salamanders by direct animal mortality (heating) or through habitat loss/alteration (consumption). Amphibians are highly sensitive to habitat change (Bury et al. 1995), in part because they have moist, permeable skin and restricted home ranges. In addition, many terrestrial salamander species (Genus *Plethodon*) are strongly associated with down woody material (Bury and Corn 1990). Thus, terrestrial salamanders are well suited as resident wildlife to measure responses resulting from natural and managed fire.

In the Pacific Northwest, investigations documenting habitat associations of forest salamanders have focused primarily on animals inhabiting mature and managed forests and associated human perturbations. Long periods of fire-exclusion in these forests have likely resulted in atypical stand and forest floor conditions in the fire-dependent forest ecosystems (Agee 1991, Skinner 2002). Knowledge of factors important to permit both salamander persistence and effective fuel management strategies requires the exploration of relationships between these forest floor inhabitants and their abiotic and biotic environment. Past investigations examining salamander habitat associations may reflect fire suppressed forests systems, with little information available on habitat requirements of these species under historic fire regimes. Characterization of occupied and unoccupied patches may provide critical baseline information to adequately assess population and meta-population dynamics.

In fire-adapted forests of the western U.S., forest health issues resulting from altered fire regimes have prompted federal forest managers to consider the reintroduction of fire into these systems. Prescribed fire has been proposed as a primary restoration activity to reduce accumulated forest fuels and associated risk of wildland fire. However, the effects of seasonality and severity of prescribed fire on forest ecosystems, forest floor structure and associated wildlife species, remain largely unknown (Page-Dumroese et al. 1991, Tiedemann et al. 2000).

The dry Douglas-fir / tanoak forests of northern California and southern Oregon occupy a complex and potentially extreme portion of the Douglas-fir fire regime: representing mixed severity fires occurring at relatively frequent intervals (Agee 1991, Wills and Stuart 1994, Taylor and Skinner 1998). Forest structure/composition can vary dramatically across the landscape, ranging from relatively open understory to a multi-layered, multi-age understory. Fire history reconstructions (Taylor and Skinner 1998) suggest fire occurrence in these forests is edaphically regulated, being most frequent on ridge-tops and mid-slopes of south and east facing slopes, and least frequent at lower elevations with generally northern aspects. Taylor and Skinner (1998) speculated that forests in the lower fire frequency portion of the fire regime might function as areas of refugia for this forest community. If so, then a corresponding refugium may also exist for associated vertebrate inhabitants, primarily endemic species with restricted movements and narrow microclimatic requirements. Del Norte salamanders (*Plethodon elongatus*) possess these behavioral characteristics. Therefore, I had the opportunity to explore both the role of fire in structuring salamander habitats and the functionality of these forests as a potential refugium for this species.

I examined factors associated with presence of Del Norte salamanders (*P. elongatus*) in fire suppressed and recently burned Douglas-fir (*Pseudotsuga menziesii*) / tanoak (*Lithocarpus densiflorus*) forests. Specifically, I modeled terrestrial salamander plot occupancy as a function of habitat, forest, and fuels variables in order to develop a predictive fire effects model for salamander habitat. Knowledge of habitat requirements of this endemic salamander within fire-altered systems will help in the establishment of management strategies that provide continued persistence of these animals during activities important to returning system health and associated fire regimes to this fire-dependent forest ecosystem.

METHODS

Study area

This study was conducted in portions of the Clear, Dillon, and Swillup Creek watersheds of the Klamath National Forest, near Happy Camp, California (U.S.A.) (Fig. 2-1). I examined late-seral dry Douglas-fir (*Pseudotsuga menziesii*) / tanoak (*Lithocarpus densiflorus*) dominated forest community in the Sierran Steppe – Mixed Forest – Coniferous Forest Ecological Province: Klamath Section (Kuchler 1975, Bailey et al. 1994). The Klamath Ecoregion is noted for its complex terrain with varied and often abrupt changes in bedrock geology, soils, elevation, and climatic regimes. Topography is characterized as steep slopes (45-85%) averaging approximately 60% (USDA 1990). Elevation ranges from approximately 250 m to >2400 m (study sites – 600 to 1100m). The climate is modified Mediterranean, with hot, dry summers and cool, wet winters. Average annual precipitation ranges from 1120 mm to 2000 mm, typically increasing with elevation (USDA 1990). Most precipitation (approx. 90%) falls from October through May. The remainder occurs with occasional summer thunderstorms. The dry summer period typically creates severe fire weather conditions between July and September (Wills 1991).

Del Norte salamander ecology

The Del Norte salamander is one of two southernmost Plethodontid salamanders inhabiting forested ecosystems in the Pacific Nortwest. This species has a generally restricted distribution in southwestern Oregon and northwestern California. Population ecology reflects a patchily distributed but locally abundant species, likely the consequence of a strong association with deep rock substrates at low to moderate elevation mixed conifer-hardwood forests (Stebbins 1954, Nussbaum et al. 1983, Stebbins and Cohen 1985, Herrington 1988, Welsh and Lind 1991, Leonard et al. 1993). Availble information on habitat preference of this species indicates strong associations with rock (talus) fields and generally high (>70%) canopy cover; typical of mature - old growth forest habitats (Welsh and Lind 1991, 1995). Talus environments provide critical refugia for these species during the warm-dry summer period, with animal use of the adjacent forest floor environment during the cool-wet periods of spring and fall (Nussbaum et al. 1983). Historically, frequent fires of mixed severity worked in concert to create a patch mosaic of both forest stand and forest floor environments in this fire-dependent system. Fire season is generally confined to the dry period of late summer and early fall, after the salamanders have retreated into the micro-climatically favorable talus slope environments. Given the narrow range of environmental conditions suitable for this species, population persistence may depend on the quantity and quality of cover available on the forest floor, how the forest floor environment limits movement of animals among refugial talus patches, and the suitability of talus patches and adjacent forest floor habitat in the post-burn environment.

Site selection and sampling design

I selected sites in unmanaged mature dry Douglas-fir / tanoak vegetation type. Natural fire disturbance in these communities is characterized as a mixed-severity fire regime (Agee 1993). Median fire return intervals are approximately 6-16 years (Taylor and Skinner 1998). I define unmanaged forests as naturally regenerated stands created by historic fire events (i.e., prior to human fire suppression activities). I examined unmanaged forest stands under the following categories: 1) Disturbance Type - Wildland fire (*WF*), Prescribed fire (*PF*), and No fire (*NF*); and 2) Canopy Burn Severity – Low (*Low*): <25% canopy mortality, moderate (*Moderate*): 25-75% canopy mortality, and high (*High*): >75% canopy mortality. Canopy burn severity is commonly used in evaluating fire effects by visually identifying the tree canopy mortality (percent loss of foliage and/or brown leaves/needles) within a predefined forest stand boundary (USDA 2001).

Study site selection criteria included the following physical site characteristics: forest stand size >25 acres, generally northern aspect, moderate to steep slopes (25-55%), and talus covering ≥20% of site. Environmental compliance restrictions associated with prescribed burning on federal lands limited the range and characteristics of prescribed fire sites available for this study. Further, wildland fire study sites were limited to Douglas-fir / tanoak stands that burned during the 2001/2002 fire years.

A retrospective study was used to examine the effects of both fire type and canopy burn severity on salamander occupancy and associated habitat use within these forests. Study sites were selected using a systematic random sampling design. Sites meeting my selection criteria were identified within the three disturbance types (NF, WF, PF). For burned sites (WF and PF sites), I selected sites based on availability within recent wildfires (≤ 6 months post-fire) or prescribed burning activities (≤1 year post-fire) and attempted to select three sites representing each of the three burn severity levels. Forest structure, composition, fire fuels, and salamander habitat data were obtained from a larger fire effects study (see Chapter 2 – Forest Structure/Composition Sampling for specific details). Forest structure/composition and animal occupancy were sampled in 2001 and 2002, respectively.

Animal sampling

I conducted salamander presence/absence surveys within unburned (n=7 sites) and burned (n=12 sites) forests in the spring of 2002. I sampled salamanders using a time-constrained survey limited to the 15-m radius plots used for fire fuels and salamander habitat characterization (see Chapter 2 – Methods for details). Plots were surveyed for a maximum of 30 minutes (0.5 person hours). Surveys consisted of sampling cover objects (logs, branches, rocks, moss, litter) within each plot. To reduce disturbance in talus environments, only the top layer of rock was sampled. Animal surveys were conducted during periods of high animal activity in the spring (Bury and Corn 1990). Captured animals were retained at point of capture and released upon survey completion.

Classification tree analysis

Fifty-four variables were recorded from combined field collection and/or composite variable creation. I used descriptive statistics to examine structure and composition of stand, forest floor, fire/fuels, and salamander metrics across salamander presence/absence. To assist with reduction of the initial variable set, I used a set of variable reduction techniques to identify variables with no association, highly correlated variables (Pearson's r), assess collinearity issues (regression analysis), and evaluate composite variable applicability (principal components ananlysis). Given the high degree of association typical to forest stand vegetation data, I selected the most ecologically meaningful variable(s) from highly correlated (Pearsons $r > 0.70$) groups and attempted composite variable creation with moderately associated subsets (Table 4-1). No interpretable composite variables were found in principal components analyses. Further, given the exploratory nature of this modeling exercise I used published information on species ecology to further refine the variable set (Burnham and Anderson 1998).

I examined associations between salamander plot occupancy and patterns of stand, forest-floor, and fuel structure and composition using classification tree models (CART, Breiman et al. 1984). Tree structured methods have seen increased use in ecological studies of habitat association (Morrison et al. 1992, Venebles and Ripley 1994, Anderson et al. 2000, Lawler and Edwards 2000). Classification trees have a number of useful attributes unavailable in traditional parametric methods (Clark and Pregibon 1992). Tree-based methods require no assumptions regarding data distributions, linearity, or functional relationships between predictors and response (dependent) variables (De'ath and Fabricus 2000). Finally, tree methods are generally easy to interpret.

Classification trees typically over-fit and therefore must then be reduced or "pruned" to a meaningful model. There are several accepted methods of tree reduction (De'ath and Fabricus 2000). I pruned tree models by plotting the cross-validated deviances against the range of tree sizes and selected the tree size wherein the deviance was minimized. In cases where two or more tree sizes exhibited generally similar deviances I selected the more ecologically meaningful model based on current understanding of salamander ecology.

To maintain consistency in terminology associated with tree-based modeling I define the following terms: 1) a *case* represents the sampling unit, in these analyses it represents one of the 15-m radius sub-plots in each of the 19 study sites; 2) *response variable* represents the dependent variable. I used salamander occupancy of the plot (binary – present/not found); 3) *predictor variables* represent independent variables and consist of several groups of measurements, including stand structure, forest floor structure (including salamander habitat), and fire metrics (fuel loadings) (Table 4-1).

The presence of deep rock (talus) has been identified as a potentially limiting habitat component for Del Norte salamander occurrence (Stebbins 1954, Welsh 1993, Diller and Wallace 1994, Welsh and Lind 1995). I delineated area of rock cover (minimum 20 % of site) as part of my site selection criteria. Retaining this habitat component in the CART analysis would likely dominate the tree structure near the root node, thus reducing the contributions of highly competitive variables and their associated competing models. Further, rock cover may not be the only factor limiting these animals. Therefore, I omitted rock cover as a variable and focused the analysis on other habitat components (arguably more susceptible to fire) in the environments surrounding rock patches.

Classification tree models were developed for both unburned forests and burned forest sites (CART 1998, ver. 1.5, Salford Systems Inc.). To evaluate model performance, I used two measures of model error: (1) resubstitution (model) error; and (2) 10-fold cross-validation error (Manly 1997). Model error is calculated using the entire dataset and provides an indication of classification tree fit to the modeling data. The cross-validation technique involves partitioning the data into two sets, a larger *learning* set (consisting of 90% of the data) and a smaller *test* set. Ten separate cross-validations were run on random subsets of the data. I examined plots of tree deviance against number of terminal nodes and pruned trees using the cross-validation procedure mentioned above. The final result was a single model for fire suppressed forests (Unburned Sites) and forests perturbed by fire (Burned Sites).

RESULTS

Salamander associations in unburned forests

The classification tree model for Del Norte salamanders in unburned forests is shown in Figure 4-1. The tree algorithm selected three of the seven potential predictors specified in the model to construct the tree (Table 4-2). Much of the explanatory power of the model came from strong associations with down wood and other ground cover. Highest salamander occupancy tended to be in sites with high rotten log loadings (> 2.8 tons/ha), Fine Fuel loadings between 6.3 to 16.6 tons/ha, and litter depth below 3.4 cm. Lowest salamander occupancy tended to be in sites with low loadings of 10 cm diameter rotten logs and either high (> 0.8 tons/ha) or low (<6.3 tons/ha) total fine fuels.

Salamander associations in burned forests

The classification tree model for Del Norte salamanders in burned forests is shown in figure 4-1B. The tree algorithm selected 3 of the 12 potential predictors specified in the model to construct the tree (Table 4-3). Much of the explanatory power of the model came from strong associations with either down wood or 10-hr fine fuels, conifer density and lower canopy burn severity. Highest salamander occupancy tended to be in sites with high loadings if rotten logs (> 2.8 tons/ha), 10-hr Fine Fuel loadings > 0.75 tons/ha, conifer tree density below 285 trees/ha, and stands impacted by low or moderate canopy burn severity. Lowest salamander occupancy tended to be in sites with low volume of 10 cm diameter rotten logs and high (> 0.75 tons/ha) 10-hr fine fuels, sites characterized by high conifer density (> 285 trees/ha), or stands impacted by high canopy burn severity.

Model accuracy

Classification accuracy of the two models was generally fair to moderate. However, model error was typically lower than cross-validation error in both unburned and burned site models (Table 4-4). Burned site models performed better than their unburned site counterparts. To evaluate the ecological utility of my classification trees, I quantified plot-level averages of each predictor variable entered into the tree-based models by salamander occupancy and compared these averages to the numeric value associated with each splitting variable identified in the classification tree models (Tables 4-2 and 4-3). Splitting variables identified in the CART analysis tended to differ across occurrence (present/absent) in both unburned and burned forest. In addition, other modeled variables showed strong differences across site occupancy. In unburned sites large logs and conifer density showed strong differences across site occupancy. In contrast, large “sound” logs, hardwood resprouts, and Douglas-fir scorch height differed by site occupancy in burned sites. However, these variables typically exhibited large overlapping ranges, which likely reduced variable importance level and discriminatory power in the classification tree algorithm.

DISCUSSION

In contrast to earlier work on habitat associations of Del Norte salamanders, I found ground cover (fine fuels and litter) and downed wood to be important habitat attributes in predicting salamander occurrence in both unburned and burned forests. In a multi-scale study of Del Norte habitat associations, Welsh and Lind (1995) reported salamander occurrence limited to typically older conifer/hardwood forests characterized by closed, multi-storied canopy, with a cool moist microclimate and rocky substrates. My study was limited to a portion of the Douglas-fir / tanoak vegetation community, areas characterized as potential forest refugia with moderate levels of suitable rock. Rock is a significant indicator of animal abundance (Welsh and Lind 1991, Diller and Wallace 1994).

I specifically chose to omit rock cover data from these analyses in order to focus on examining habitat relationships of salamanders using the adjacent forest environment in both fire suppressed and fire altered mixed conifer hardwood forests. However, size, composition, and configuration of rock patches likely affects not only salamander density and movements, but also the distribution of trees and associated stand structure. Moreover, rock could also afford small-scale firebreaks resulting in modified fire behavior and associated level of severity in the burned forest sites. In this study, the effects of rock patches on fire behavior were visually apparent in only the low canopy burn severity sites (D. Major, pers. obsv.).

Another important factor possibly contributing to this relationship with ground cover and down wood is that most habitat association studies of Del Norte salamanders were conducted in forests developing under altered fire regimes. Fire exclusion activities have modified forest structure and composition in most of the mixed conifer-hardwood forest ecosystems within the Klamath Ecoregion (Atzet and Wheeler 1982, Agee 1990), an area encompassing the distributional range of this salamander species.

In this forest system, the altered fire regime likely results in a substantial increase in the amount and distribution of ground cover, surface fuels, and down wood; all potential cover objects for this forest floor salamander. For example, Welsh and Lind (1995) found strong relationships between density of small (sapling-sized) hardwoods and Del Norte salamander presence. The presence of hardwood regeneration is most likely an artifact of fire suppression, not a strong habitat component for salamanders. Further, additional cover resulting from fire exclusion could increase the amount and extent of suitable environments both around and adjacent to rock patches, thereby reducing the ability to discern habitat affinities. Wildlife-habitat studies conducted in these modified forest environments may provide only limited insights to animal-habitat relationships; particularly if the forest trajectory is far from historic forest conditions. However, results of my study are limited to the small portion of the Douglas-fir / tanoak vegetation continuum, a forest refugium; potentially the longest fire return interval for this fire regime.

In addition to forest floor attributes, conifer density was important in predicting presence of Del Norte salamanders in burned forest sites. In most forest systems, tree density is typically highly associated with canopy cover. Del Norte salamanders generally occupy sites with high (>70%) canopy cover (Welsh and Lind 1991, Diller and Wallace 1994). It is unclear why conifer density, and not canopy cover was selected in the classification tree model. Further, both conifer density and canopy cover estimates were generally lower in occupied sites versus unoccupied sites. I suspect there are important interactions in conifer density, hardwood proximity, and spatial distribution and composition of surface fuels that likely affects fire behavior and the resulting burn severity.

The composite categorical variable FTbyCB (fire type by canopy burn severity) afforded only moderate predictive power for identifying salamander occupancy in burned sites as this variable came out at the bottom of the tree. Sites characterized as low to moderate burn severity were separated from high burn severity sites, regardless of the type of fire. This suggests that prescribed and wildland fires of low to moderate burn severity may result in similar effects to salamander habitats. However, differences in the response of certain stand structure and forest floor components both among fire types and within burn severity categories have been documented in this forest system (D.J. Major – Chapter 2). I suspect that the canopy burn severity metric may provide too coarse a scale to adequately evaluate fire-salamander habitat relationships. Finally, higher variability in plot level structural attributes of sites burned by wildland fire may have reduced variable importance level and discriminatory power in the classification tree algorithm.

Management considerations

Clearly, knowledge of the habitat relationships of Del Norte salamanders present at a certain location does not provide a complete model of salamander habitat use. Other factors including relative abundance, population demographics, and animal energetics need to be effectively incorporated into future local and comparative studies. However, the habitat models reported in this study represent novel baseline examinations of the effects of both fire exclusion and fire disturbance on this forest-dependent salamander species.

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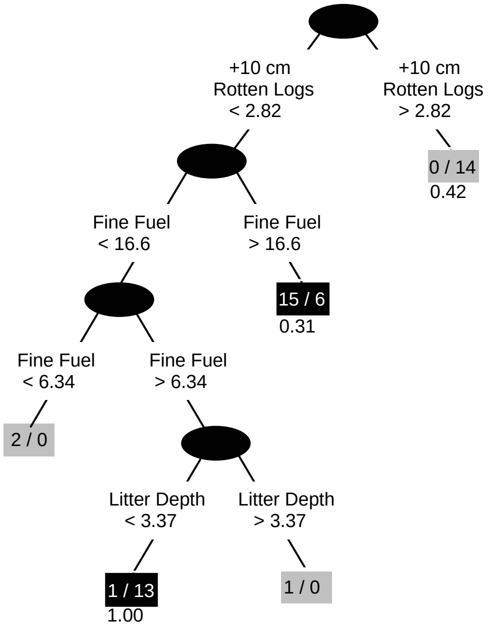

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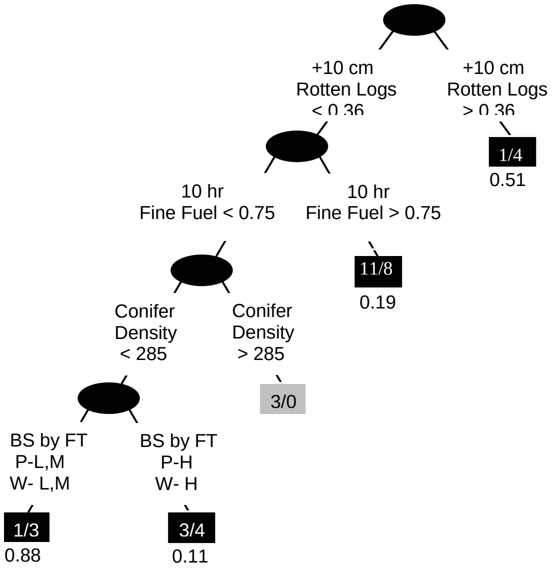

Figure 4-1. Classification trees modeling the presence of Del Norte salamanders in (a) Unburned sites and (b) sites burned by wildland or prescribed fire. Rectangles represent terminal nodes of the tree. The numbers below the rectangles are the probabilities of salamander presence calculated using the proportion of sites at each node. Numbers in the rectangles represent the number of absent and present sites at each node (absent/present).

CHAPTER 5

CONCLUSION

The three studies reported here explore aspects of the impacts of fire and fire exclusion on current/future forests and forest-associated wildlife, and contribute valuable baseline information on disturbance regimes and associated fire ecology of fire-dependent forest ecosystems. Here, I address aspects of the fire exclusion legacy and discuss the role of fire exclusion in modifying a fire-dependent forest and it's associated fire regime. Next, I examine the utility of developing predictive models that integrate fire processes and the effects of fire on terrestrial salamanders and their habitats. Finally, I evaluate the ability of these models to predict the micro- and macro-scale responses of terrestrial salamanders to various fire disturbances.

FIRE AND FIRE EXCLUSION IN FIRE-DEPENDENT FOREST SYSTEMS

In fire-dependent conifer forests of the West, identification of factors affecting fire regimes typically focus on pre-fire stand structure and composition associated with fire exclusion (Allen 1989, Covington and Moore 1994). However, little information exists on the role of fire exclusion in structuring post-fire fuel dynamics, potential fire behavior and ensuing fire regime characterization of these systems. Chapter 2 and 3 are my attempt to explore various aspects of conceptual disturbance models.

I developed the term *fire exclusion legacy* (Chapter 3) to describe changes in stand structure and biomass related to shifts in size/age distribution that occur when fire is supressed. Identification of post-fire fuel patterns (i.e., type and amount) associated with a fire exclusion legacy is critical to understanding stand-level fuel dynamics and associated fire regime characterization. Results of my study examining stand level “potential” fuel biomass documented post-fire fuel loadings approaching 70% of pre-fire conditions in prescribed fire sites. Further, I suggest that the fuels profile is altered leading to atypically higher fuels biomass on both the forest floor and in the vertical stand strata. Hypothetically, the change in amount and distribution of fuels within these forests will result in fires of higher intensity; fires capable of producing stand replacement events. However, the forest conditions described above likely constitute an extreme condition of the historic fire regime for these forests.

The forest fire refugia concept represents a novel, albeit critical, aspect of a fire regime. These stands or patches possess characteristics typically representing an extreme portion of the system’s fire regime, representing longer periods between fires and higher fuel loadings (Camp et al. 1997). These characteristics could also be important to wildlife.

Many of the unburned reference sites examined in this study had structural and compositional attributes similar to those afforded a fire refugia. However, I suspect that the altered fuels profile resulting from a fire exclusion legacy (Chapter 3) will significantly influence fire behavior during the next fire and burn these forests as stand replacing events. If these areas also function as refugia for Del Norte salamanders, survival may be compromised as deep rock substrate will constitute the only available short-term cover. Arguably, not all sites with characteristic fire refugia attributes *are* fire refugia. Therefore, research is needed to identify structural and funtional attributes common to both fire and wildlife refugia.

TOWARDS A SALAMANDER FIRE SEVERITY MODEL

In contrast to earlier work on habitat associations of Del Norte salamanders, this study found ground cover (fine fuels and litter) and down wood to be important habitat attributes in predicting salamander occurrence in both unburned and burned forests. Moreover, prescribed and wildland fires of low to moderate burn severity may result in similar effects to salamander habitats. However, I found differences in the response of certain stand structure and forest floor components typically used by these salamanders as cover both among fire types and within burn severity categories (Chapter 2). Therefore, I suspect that the canopy burn severity metric may provide too coarse of a scale to adequately evaluate fire-salamander habitat relationships. Finally, high variability in plot-level structural attributes of sites burned by wildland fire may have reduced variable importance level and discriminatory power in the classification tree algorithm.

MANAGEMENT, CONSERVATION, AND FUTURE RESEARCH

Throughout this document I have mentioned numerous ways in which the results of my studies can be applied to current forest and fuels management and wildlife conservation. However, two specific areas warrant further discussion. First, the altered fuels profile that I described in Chapters 2 and 3 suggests the management of fire-dependent forests will need to quantify fire exclusion both pre- and post-burn. Moreover, fuels management planning needs to encompass a suite of techniques and prescriptions spanning multiple fires, or fire surrogate, methods.

Second, future prescribed burning needs to employ techniques that create a mosaic of burn intensity levels. A first step should be exploring fire behavior and associated burn mosaic patterns in wildland fire. Creation of a greater array of burn intensity levels, especially forest floor fuels, will provide diverse array of forest floor characteristics ammenable to terrestrial salamanders and other forest floor biota. However, identification of fuels management approaches that benefit both fire and wildlife refugia will require additional research.

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APPENDIX

Table A1 - Composite Burn Severity Index – Modified from Key and Benson 1999.

	Stand Stratum															
	OVERSTORY				*UNDERSTORY*				*SURFACE FUELS & WOODY HABITAT*							
	A. Canopy/Sub-Canopy CO-Dominants				B. Shrubs, Small Trees				C-1. Surface Fuels				C-2. Large Woody Debris			
Severity	Canopy % Green	Canopy % Mort	LIDE Char Ht (m)	PSME Char Ht (m)	Shrub Cover (%)	LIDE <5ft cnts	LIDE >5ft cnts	Hardwood Regen Trees/m2	Litter and FF1-3	Duff	Sound <15cm cnts	Rotten <15cm cnts	Logs <15cm Tn/ha	Logs 15-25 Tn/ha	Logs 25-50 Tn/ha	Logs 50+ Tn/ha
0	100	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0
0.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1.0	95	5-10	1.8	1.8	95	20	30	20	50% Litter cons	<30 cons	20% cons	20% cons	20% cons	10% cons	5 cons	5 cons
1.5	--	--	--	--	--	--	--	--	--	--			--	--	--	--
2.0	50	30-70	4	4	50	70	80	70	100% Litter cons	50 cons	40% cons	40% cons	40 cons	25 cons	10 cons	10 cons
2.5	<10	>70	--	--	<10	80	95	80	--	--	--	--	--	--	--	--
3.0	0	100	>7	>7	0	100	100	100	*AND* 98% FF cons	100 cons	60% cons	60% cons	>60 cons	>40 cons	>20 cons	>15 cons
REFERENCE VALUES (Average values from n=58 unburned reference plots)																
0	100	0	0	0	100	13.1	1.47	0.52	2.19 14.42	0.92	4.64	2.26	10.35	9.64	31.0	89.78

LIDE – Liriodendron densifolus; PSME – Pseudotsuga menziesii

Consumption rates calculated using the following formula:

$$\text{Proportion Consumed} = \left(\frac{\text{Reference Value of variable } x - \text{Plot Value of variable } x}{\text{Reference Value of variable } x} \right) * 100$$