AN ABSTRACT OF THE THESIS OF

Amy Nathanson for the degree of Master of Science in Forest Science presented on May 16, 2011.

Title: Dead Fuels and Understory Vegetation Six Years after a Large Mixed-severity Wildfire in Southwest Oregon.

Abstract approved:

_____

Thomas A. Spies

Though the mixed-evergreen forests of the Klamath Siskiyous have a long history of large, mixed-severity fires, most research in this region has concentrated on the impacts of high-severity fire. Knowledge of the ecological effects of low- and moderate-severity areas within mixed-severity fires is important because such areas may account for over half the landscape affected by a fire. The purpose of this study was to understand the relationship of fire severity with dead fuels and understory vegetation across a full range of fire severities. Study sites were located within and just outside the boundary of the 2002 Biscuit Fire, which burned 200,000 hectares in a mosaic of burn severities.

Six years after the Biscuit Fire, the biomass and depth of litter and duff was lower on burned sites than unburned sites, and lowest on high-severity sites. This relationship was reversed for woody fuels >7.62 cm in diameter, where quantities were highest in high- and extreme-severity areas, though there was no evidence that quantities differed between low-severity and unburned sites. There was no evidence of a relationship between woody fuels 0.64-7.62 cm in diameter and fire severity, 6 years post-fire. There was no evidence that fuel quantities differed between sites that burned only in the Biscuit Fire with sites that also burned 15 years earlier in the 1987 Silver Fire. Fuel quantities and composition differed between burned and unburned sites, but these differences disappeared if litter and duff were not

considered. Fuel classes were correlated with each other within three general size classes: small (litter, duff, and fuels <2.54 cm), medium (fuels 2.54-30 cm), and large (fuels >30 cm). There was little correlation between these size classes.

Vegetation response also varied by fire severity, species, and height. Generally, density for tree seedlings <0.5 m was highest on low-severity sites and lowest on high-severity sites. For seedlings 0.5-1.37 m the relationship was reversed, with the highest seedling densities in high-severity areas. Specific seedling relationships to burn severity and other explanatory factors (e.g. shrub cover, elevation, precipitation, maxiumun August temperatures) varied by species and seedling height. Average seedling densities were above the minimum acceptable stocking levels of 333 trees per hectare (135 seedlings/acre) as identified in federal plans for the fire area. Shrub species richness and diversity did not vary with burn severity; however, shrub species and ground cover composition did differ with burn severity six years after the Biscuit Fire. The relationship of understory cover composition with burn severity aligned with species life history traits; fire-adapted, nitrogen-fixing species were more prevalent on high- and extreme-severity sites while species associated with low-severity fire or old-growth forests were more prevalent on low-severity or unburned sites. I found no evidence of difference in total graminoid or forb cover based on fire severity, but shrub quantities were lower on low-severity sites than on unburned, high-, and extreme-severity sites.

This study reveals how fuel and vegetation vary across the full range of fire severities. It demonstrates that mixed-severity fires create a mix of ecological responses. It also provides a baseline for future studies, as the relationships between fire severity and fuels or vegetation may disappear or change in subsequent decades.

Dead Fuels and Understory Vegetation Six Years after a Large Mixed-severity Wildfire in Southwest Oregon

by
Amy Nathanson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented May 16, 2011
Commencement June 2011

Master of Science thesis of Amy Nathanson presented on May 16, 2011.

APPROVED:

_____

Major Professor, representing Forest Science

_____

Head of the department of Forest Ecosystems & Society

_____

Dean of the Graduate School

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

_____

Amy Nathanson, Author

ACKNOWLEDGEMENTS

This thesis would not have been possible without the help and support of a huge number of people. I am very grateful to you all. First and foremost I would like to thank my parents: my father for fostering a love of nature by taking me for long walks in the woods, and my mother for always letting us return home, no matter how bedraggled our appearance. Their love and support have been instrumental in allowing me to pursue my dreams.

I would also like to thank my advisor, Dr. Thomas Spies, for his guidance, insightful comments, and good humor. I have learned an enormous amount during this process, and I could not have done it without his support.

I would like to express my gratitude for all the support and effort of Dr. Tom DeMeo. I appreciate all the help he has given me regarding this project, and also navigating the bewildering and sometimes byzantine aspects of the federal system.

I have been blessed with a remarkably intelligent and dynamic group of people for my committee: Dr. John Bailey, Dr. Bernard Bormann, and my Graduate Council Representative Dr. Jesse Ford. Their comments, guidance, and support were extremely helpful.

Special thanks go out to Manuela Huso for all her help with my statistical analyses. I am also grateful for her support and encouragement when my frustrations went beyond statistics.

This project would not have been possible without the extraordinary efforts of the 2008/2009 field crews: Emily Davis (2008), Ben Dawson (2008), Paul Dunnette (2008), Lyndia Hammer (2008 AND 2009!), Robert Pabst (2008), and Brett Morrissette (2009). They braved triple-digit temperatures, 100% slopes, rattlesnakes, nearly impenetrable brush, and verdant groves of poison oak to collect the data used in this project. They also taught me an enormous amount about the vegetation of southwest Oregon. I would also like to thank the

Pacific Northwest Research Station and USFS Region 6 for their financial and logistical contributions to this project.

Robert Pabst has been an enormous help to me during my time here. He always had a moment to talk, whether it was about field techniques, analytical approaches, chapter feedback, or just general encouragement. I have learned many, many things from him, not the least of which was when it is time to step away from the computer and go for a little walk outside.

One of the most powerful aspects of my experience here at OSU has been the help and support of my fellow students. There was always a plethora of people excited and eager to proofread my chapters, help me with analyses or troublesome computer programs, or just commiserate over a beverage at the local pub. The amount of support I received from them was heartwarming and humbling. I feel truly lucky to have conducted this work in such a supportive and collaborative environment. I could not have done this with without my friends at OSU and elsewhere.

Finally, I would like to thank Dr. David Kittredge for taking a chance on a young woman looking to make a career change. I could not have made this journey without him.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF TABLES

Dead Fuels and Understory Vegetation Six Years after a Large Mixed-severity Wildfire in Southwest Oregon

CHAPTER 1: INTRODUCTION

The mixed-evergreen forests of the Klamath Siskyous have a long history of large, mixed-severity fires (Agee 1993, Taylor and Skinner 1998, 2003), but factors influencing fire size, fire severity, fuel quantities and vegetation succession are poorly understood. It is unclear what effects, if any, fire suppression in the latter half of the 20th century has had on fire size and severity in the Klamath Siskiyous (Odion et al. 2004, Thompson et al. 2007) and whether fuel treatments would be effective in changing fire behavior (Brown et al. 2004, Agee and Skinner 2005, Noss et al. 2006, Spies et al. 2006).

Most work in this region has concentrated on the impacts of high-severity fire, ignoring ecological effects of low- and moderate-severity areas (Donato et al. 2006, Shatford et al. 2007, Donato et al. 2009b, Donato et al. 2009c). Though concern about high severity areas is understandable, it is not possible to evaluate ecological responses and future fire behavior of the entire fire mosaic without knowledge of conditions in low and moderate severity patches. Low- and moderate-severity fires may have limited impact on canopy trees, but the effects on understory vegetation, dead surface fuels, and soils may be extensive. Additionally, ignoring the fire effects on over half the landscape precludes understanding how areas of different burn severity interact and impact future succession and fire effects. Prior studies have found that in the mixed-evergreen forest type of the Siskiyou Mountains areas that burned at low severity tend to reburn at low severity, areas that burned at high severity tend to reburn at high severity (Thompson 2008), and areas that have not experienced fire disturbances for extended periods do not necessarily burn with high severity (Odion et al. 2004).

In an effort to better understand the ecological effects of mixed-severity fire on the mixed-evergreen forests of the Klamath Siskiyous, I investigated the response of dead fuels and understory vegetation in the northeast section of the Biscuit Fire six years post-fire. In 2002, the Biscuit Fire burned over 200,000 ha in a mosaic of burn severities in the Klamath-Siskiyou Mountains of southwest Oregon and northern California. It also completely encompassed the 40,000 ha burned by the 1987 Silver Fire, which also burned in a mosaic of burn severities. The confluence of these two disturbances, their size, and the variation in burn severity provide a unique opportunity to study fire effects for this fire regime.

Chapter 2 focuses on dead fuel responses to fire severity. I sought to address four questions: 1) Are fuel quantities correlated with burn severity six years after the Biscuit Fire? 2) What biotic, abiotic, and climatic factors are most useful in predicting current fuel quantities? 3) Is there an underlying correlational structure or relationship among the different fuel classes? And 4) do fuel quantities differ as a function of fire history (no fire disturbance for an extended period, burned once 6 years ago, and burned twice within the last 21 years)? The first question addresses the relationship of fire severity to fuel accumulation, while the second looks at other potential explanatory variables for fuel quantities. In the third question I sought to understand the multivariate relationships within the set of fuel classes to determine if fuel in one size class might be predicted from fuel in another size class. Fuel correlational structure (or lack thereof) may provide insight into what fuel classes may have similar processes and patterns of accumulation and decomposition. Finally, I was interested in whether dead fuels differ based on fire frequency. Prior to the Biscuit Fire, fuel quantities in areas burned by the Silver Fire may have been lower than unburned areas due to the relatively recent fire disturbance. However, in a highly productive ecosystem like this one, it is possible

that dead fuels may have returned to or surpassed pre-fire levels in the 15-years between the Biscuit and Silver fires. Potentially different starting conditions might lead to different post-fire conditions in areas that experienced multiple fire disturbances.

Chapter 3 focuses on understory vegetation responses to fire severity. In this chapter I sought to address three questions: 1) how does tree seedling density vary in relation to fire severity? Additionally, does seedling density vary based on species or seedling height, and what biotic, abiotic and climatic factors are most effective in predicting seedling density? 2) Does ground cover and shrub composition differ in relation to burn severity? I looked at differences in species richness and diversity metrics based on burn severity classification, as well as overall ground cover composition based on burn severity. I also investigated whether species composition differed between sites that experienced a short interval between fire disturbances (15 years, burned in both the Biscuit and Silver fires), a long interval between fire disturbances (burned only in the Biscuit Fire) and areas outside the Biscuit Fire boundary (unburned). And 3) do live fuel quantities, specifically shrubs, forbs, and graminoids, differ in relation to burn severity? Knowledge of shrub responses to fire is important for a number of reasons, including predicting fire behavior. For example, the Rothermal-based fire spread models consider two classes of live fuels: herbaceous and woody. Herbaceous fuels include annual grasses, perennial grasses, and forbs. Woody fuels include deciduous and evergreen shrubs and small trees up to 1.83 m high (Albini 1976, Anderson 1982, Rothermel 1983, Scott and Burgan 2005). The effects of live fuels on fire severity are poorly understood (Burgan 1979, Jolly 2007, Weise and Wotton 2010). They may have a dampening effect on fire when moisture content is high, but may also ignite due to drought or desiccation from fire, rapidly and drastically increasing fire severity (Burgan 1979, Weise et al. 2005). Additionally, recent

studies suggest that high severity fires in mixed-severity fire regimes tend to occur in areas with high amounts of contiguous understory vegetation including both trees and shrubs (Thompson et al. 2007, Odion et al. 2010, Thompson and Spies 2010).

Few studies investigate the fuel and vegetation responses to the full range of severities in a mixed-severity fire regime, and I am unaware of any that do so in the mixed-evergreen forests of the Klamath Siskiyou ecoregion in southwest Oregon. The answers to these questions will provide insight into fuel dynamics across the full spectrum of burn severities, and provide a baseline for comparison over time.

LITERATURE CITED

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.

Agee, J. K. and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management **211**:83-96.

Albini, F. A. 1976. Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-30, Ogden, UT, p. 92.

Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-122, Ogden, Utah, p. 22.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: Principles in the context of place. Conservation Biology **18**:903-912.

Burgan, R. E. 1979. Estimating live fuel moisture for the 1978 National Fire-Danger Rating System. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-226, Ogden, Utah, p. 17.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science **311**:352-352.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009b. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **39**:823-838.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009c. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology **97**:142-154.

Jolly, W. M. 2007. Sensitivity of a surface fire spread model and associated fire behaviour fuel models to changes in live fuel moisture. International Journal of Wildland Fire **16**:503-509.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment **4**:481-487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology **18**:927-936.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology **98**:96-105.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-143, Ogden, UT, p. 161.

Scott, J. H. and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-153, Fort Collins, CO, p. 72.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry **105**:139-146.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology **20**:351-362.

Taylor, A. H. and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111**:285-301.

Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications **13**:704-719.

Thompson, J. R. 2008. Patterns of crown damage within a large wildfire in the Klamath-Siskiyou bioregion. Dissertation. Oregon State University, Corvallis, OR.

Thompson, J. R. and T. A. Spies. 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. Landscape Ecology **25**:775-789.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America **104**:10743-10748.

Weise, D. R. and B. M. Wotton. 2010. Wildland-urban interface fire behaviour and fire modelling in live fuels. International Journal of Wildland Fire **19**:149-152.

Weise, D. R., X. Y. Zhou, L. L. Sun, and S. Mahalingam. 2005. Fire spread in chaparral - ‘go or no-go?’. International Journal of Wildland Fire **14**:99-106.

CHAPTER 2: EFFECTS OF A MIXED-SEVERITY WILDFIRE ON FUELS IN THE KLAMATH-SISKIYOU MOUNTAINS OF SOUTHWEST OREGON

ABSTRACT

The mixed-evergreen forests of the Klamath Siskyous have a long history of large, mixed-severity fires, but factors influencing fire size, fire severity, fuel quantities and vegetation succession are poorly understood. Most work in this region has concentrated on the impacts of high-severity fire, ignoring ecological effects of low- and moderate-severity areas, which may account for over half the landscape affected by fire disturbance. In an effort to understand the relationship between fuel quantities and fire severity, I looked at data from the 2002 Biscuit Fire, a large, mixed-severity fire that occurred in the Klamath-Siskiyou Mountains of southwest Oregon and northern California. This fire also completely encompassed the area burned by the 1987 Silver Fire, which also burned in a mosaic of burn severities. This study addresses four questions: 1) Are fuel quantities correlated with burn severity six years after the Biscuit Fire? 2) What biotic, abiotic, and climatic factors are most useful in predicting current fuel quantities? 3) Are fuel quantities in one size class correlated to fuel quantities in other size classes? 4) Do fuel quantities differ between areas that have not experienced a recent fire disturbance, areas that experienced a long interval between fire disturbances (burned only in the Biscuit Fire), and areas that experienced a short interval between fire disturbances (burned in both the Biscuit and Silver fires). I used the differenced Normalized Burn Ratio (dNBR), which compares pre- and post-fire Landsat imagery, as my measure of burn severity. Fuel quantities were collected on 78 plots, which spanned the full range of burn severities as well as unburned areas just outside the Biscuit Fire boundary.

I found that biomass and depth of litter and duff were lower on burned sites than unburned sites, and lowest on high-severity sites. This relationship was reversed for woody

fuels >7.62 cm in diameter, where quantities were highest in high- and extreme-severity areas, though there was no evidence that quantities differed between low-severity and unburned sites. There was no evidence of a relationship between woody fuels 0.64-7.62 cm in diameter, 6 years post-fire. There was no evidence that fuel quantities differed between short-interval and long-interval burn sites. Fuel quantities and composition differed between burned and unburned sites, but these differences disappeared if litter and duff were not considered. Fuels were correlated within three general size classes: small (litter, duff, and fuels <2.54 cm), medium (fuels 2.54-30 cm), and large (fuels >30 cm). There was little correlation between these size classes. The different relationships of fire severity to fuels of different sizes imply that the creation and decomposition of different fuel classes are governed by different processes. These relationships may change or disappear as time progresses. Future studies on fuels and fuels succession in areas with mixed-severity fire regimes should include all severities, to determine how future fuel trajectories differ based on the initial disturbance severity.

INTRODUCTION

The factors affecting fire size, fire severity, fuel quantities and vegetation succession are poorly understood. Recently, several large fires in a variety of fire-prone systems have sparked a debate over whether extremely large fires are uncharacteristic of these forest types and fire regimes or whether they are returning natural disturbance regimes to their pre-suppression conditions (Keane et al. 2008). Central to this debate is the question of how fuel accumulations due to fire suppression affect fire size and severity, and whether fuel treatments should be used to alter fire behavior. However, in areas with a mixed-severity fire regime such as the mixed-evergreen region of the Siskiyou mountains of southwest Oregon, it is unclear if

absence of fire leads to higher fire severity (Odion et al. 2004, Thompson et al. 2007) and whether fuel treatments would be effective in changing fire behavior (Brown et al. 2004, Agee and Skinner 2005, Noss et al. 2006, Spies et al. 2006).

Despite the importance of dead fuels from an ecological, management, and fire behavior perspective, relatively few studies have investigated how these fuels change over time, and how they differ in areas of different burn severities. Prior studies show that some fuel classes can return to pre-fire levels in less than a decade, though post-fire fuel trajectories vary by fuel type, fire regime, burn severity, and forest productivity (Parsons 1978, van Wagtendonk and Sydoriak 1987, Keifer et al. 2006, Keyser et al. 2008). None of these studies took place in the mixed-evergreen system of southwest Oregon, which differs in climatically and floristically, and may therefore have different rates of fuel production and decay.

Most studies that have taken place in southwest Oregon focus only on the high-severity fire areas (Donato et al. 2006, Donato 2008), or on immediate post-fire changes to fuels and carbon (Campbell et al. 2007). In a large mixed-severity fire in the mixed evergreen forests of southwest Oregon, fuel consumption was highest in high-severity areas, and also varied by fuel type (Campbell et al. 2007). A chronosequence study of fires in the mixed-evergreen forests of the Klamath-Siskiyous found that post-fire fuel accumulations followed a hump-shaped trajectory, peaking 15-20 years after a fire. Mature and old-growth stands had similar quantities of 10- and 100-hour fuels to stands that had experienced fire 17-18 years prior, and the mature/old-growth stands had lower quantities of coarse woody debris (CWD, >7.62 cm in diameter) (Donato 2008).

Comprehension of fuel dynamics across the full range of severities in a mixed-severity forest regime is critical to understanding future fire behavior. Prior studies have

found that in the mixed-evergreen forest type of the Siskiyou Mountains areas that burned at low severity tend to reburn at low severity, areas that burned at high severity tend to reburn at high severity (Thompson 2008), and areas that have not experienced fire disturbances for extended periods do not necessarily burn with high severity (Odion et al. 2004). Fuel consumption differs based on fire severity and fuel type, but it is unclear how quickly these fuel levels recover and whether fuel accumulation trajectories differ based on burn severity.

In an effort to understand the effect of burn severity on dead fuels in a mixed-evergreen forest type over time, I looked at data from the northeast section of the Biscuit Fire six years after the fire. In 2002, the Biscuit Fire burned over 200,000 ha in a mosaic of burn severities in the Klamath-Siskiyou Mountains of southwest Oregon and northern California. It also completely encompassed the 40,000 ha burned by the 1987 Silver Fire, which also burned in a mosaic of burn severities. The confluence of these two disturbances, their size, and the variation in burn severity provide a unique opportunity to study fire effects for this fire regime. My questions were: 1) Are fuel quantities correlated with burn severity six years after the Biscuit Fire? 2) What biotic, abiotic, and climatic factors are most useful in predicting current fuel quantities? 3) Is there an underlying correlational structure or relationship among the different fuel classes? 4) Do fuel quantities differ as function of fire history (no fire disturbance for an extended period, burned once 6 years ago, and burned twice within the last 21 years)? The first question addresses the relationship of fire severity to fuel accumulation, while the second looks at other potential explanatory variables for fuel quantities. In the third question I seek to understand the multivariate relationships within the set of fuel classes to determine if fuel in one size class might be predicted from fuel in other size classes. Fuel correlational structure (or lack thereof) will also provide insight into what fuel classes may

have similar processes and patterns of accumulation and decomposition. Finally, I am interested in whether dead fuels differ based on fire frequency. Prior to the Biscuit Fire, fuel quantities in unburned areas may have differed from areas that burned in the Silver Fire. They may have been lower due to the relatively recent fire disturbance. However, in a highly productive ecosystem like this one, it is possible that dead fuels may have returned to or surpassed pre-fire levels in the 15-years between the Biscuit and Silver fires. Potentially different starting conditions might lead to different post-fire conditions in areas that experienced multiple fire disturbances. The answers to these questions will provide insight into fuel dynamics across the full spectrum of burn severities, and provide a baseline for comparison over time.

METHODS

Study area

In 2002, fires from five ignitions in the Siskiyou National forest between July 13th and 15th converged in the following weeks to create the Biscuit Fire complex (GAO 2004). The fire was declared controlled on November 8, 2002 but was not declared extinguished until December 31, 2002. In total 202,328 hectares burned, 94% of which were on the Rogue-Siskiyou National Forest in southwestern Oregon, 4% on the Six Rivers National Forest in Northern California, and 2% on Bureau of Land Management land. Additionally, 72,000 hectares of the Kalmiopsis Wilderness burned (USDA Forest Service 2004). The landscape burned in a mosaic of different burn severities: 17% of the area experienced 0-5% crown mortality, 14% experienced 5-35% crown mortality, 23% experienced 35-65% crown mortality, 27% experienced 65-95% crown mortality, and 19% experienced greater than 95% crown mortality (Thompson 2008). Only10% of the landscape experienced complete crown

mortality. Tree damage also varied based on conifer diameter and understory composition; conifer mortality was negatively correlated with tree size and positively correlated with understory shrub cover (Thompson and Spies 2009). Surface effects of the fire were extensive and variable: the fire consumed 70-100% of the litter layer and 40-100% of the duff layer within the fire boundary (Campbell et al. 2007). The Biscuit Fire completely encompassed the 40,000 ha burned in the 1987 Silver Fire, which also burned with a mosaic of fire severities (Atzet et al. 1988, USDA Forest Service 1988). Post-fire salvage logging took place on approximately 1850 ha of the Biscuit Fire (<1%), and at least 800 ha of the Silver Fire (~2%), but those areas were excluded from this study (USDA Forest Service 1988, USDA Forest Service 2004).

The Biscuit Fire occurred in the geologically and floristically diverse Klamath Province, which has a rugged topography and a steep climatic gradient (Whittaker 1960). This diversity is likely due in part to its geological history and the orientation of the mountain ranges. The Siskiyous form a high-elevation east-west land bridge between the north-south Coast and Cascade ranges, allowing movement of species along a marine to inland gradient (Agee 1998).

The climate is predominantly Mediterranean, though it is modified by marine influences up to 80km inland (Whittaker 1960, Atzet and Martin 1992). Average annual precipitation is 240 cm/year, only 8% of which falls from June through September. Average minimum temperature in December is 1.4˚C and average maximum July temperature is 27.4˚C (Daly et al. 2002). The Klamath Province is subject to both cold storms from northern latitudes and tropical storms from southern latitudes (Atzet and Wheeler 1982).

The study area is in the “mixed evergreen” forest zone, with a typical overstory of evergreen needle-leaved trees and an understory of sclerophyllous broadleaf vegetation. This forest type is dominated by Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Lithocarpus densiflorus*) but may also include conifers such as sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and incense-cedar (*Calocedrus decurrens*), and hardwoods such as Pacific madrone (*Arbutus menziesii*) and giant chinquapin (*Chrysolepis chrysophylla*). Huckleberry oak (*Quercus vaccinifolia*) and manzanita (*Arctostaphylos* spp.) are often present in the shrub layer (Franklin and Dyrness 1988). The short-lived and strictly serotinous knobcone pine (*Pinus attenuata*), may be found on sites that experienced recent crown fires (Franklin and Dyrness 1988, Atzet and Martin 1992). Productivity in this area is high relative to most fire-prone forested areas of the Pacific Northwest (Waring et al. 2006).

This study also includes sites on serpentine soils. These soils, derived from ultramafic rock, support a unique plant community with a wide variety of endemic species. Non-endemic species growing on serpentine soils tend to have a stunted or depauperate appearance (Franklin and Dyrness 1988), due to high concentrations of Mg, Ni, and Cr in the soil (White 1971). Tree cover is sparse, and is generally dominated by a mixture of conifers including Jeffrey pine (*Pinus jeffreyi*). Understory plant communities include open grassy areas, or a patchwork of shrubs and herbaceous cover depending on elevation, moisture, and seral stage (Franklin and Dyrness 1988).

The fire regime in the Klamath-Siskiyous of southwest Oregon is complex and not well understood. Estimated mean fire return intervals range from 10-50 years, and in general fire frequency increases from west to east and with increasing elevation (Atzet and Wheeler 1982, Agee 1991, Atzet and Martin 1992, Agee 1993). Lightning strikes are common in this

region and provide ample sources of ignition for almost any location (Atzet and Wheeler 1982, Agee 1993). Although the Biscuit Fire was the largest in the state's recorded history (GAO 2004), the Klamath Siskiyous of southwest Oregon have a history of large fires: 72,400 hectares burned in 1917, 61,500 hectares burned in 1918, and 20,500 hectares burned in 1938 (Cooper 1939, Atzet et al. 1988, USDA Forest Service 1988). Fire was also likely used by Native Americans to foster the growth of early seral species used for food and as forage for desired animal species. In some areas fires may have been set as often as annually (Lewis 1989). Though fire suppression efforts have decreased the frequency of fire disturbance in this area in the latter half of the 20th century, there are historical precedents for fire-free periods of a century or more over the past two millennia (Colombaroli and Gavin 2010).

The historical fire regime for this area is classified as "mixed severity" (Agee 1993), but historical proportions of low, medium and high severity fire, as well as their spatial configurations and extents, are unknown. Studies in the northern California range of the Klamath-Siskiyous show that the majority of fires were low- to moderate-severity (Taylor and Skinner 1998, 2003). However, it is not known how applicable this fire regime is to the Klamath-Siskiyou Mountains in Oregon, due to differences in climate, topography and vegetation. It is also unclear how changes in fuel amounts due to fire suppression have affected the fire regime in this region, and how to best address the impacts of fire exclusion (Brown et al. 2004, Noss et al. 2006). Fire suppression may change future stand dynamics and structure. Understory vegetation may have been lower due to more frequent fires prior to fire suppression in the 1920s. Less understory vegetation may have lead to lower tree densities and higher diameter growth rates. In the Siskiyou Mountains, diameter growth of 50 year old trees was higher in old-growth stands (>250 year-old) than young stands (<100 year-old)

(Sensenig 2002). However, long periods of fire absence do not necessarily correlate with higher proportions of high-severity fire (Odion et al. 2004, Odion et al. 2010), and in areas that burned in both the Biscuit and Silver Fires, areas that burned at high severity tended to reburn at high severity (Thompson et al. 2007), implying that long-term fuel buildup is not necessarily the primary factor in predicting high-severity fire.

Site selection

Study sites were chosen using a stratified random sample based on three strata: burn severity, elevation (above or below 914 m), and parent material (ultramafic or non-ultramafic.) Study sites were confined to the northeast section of the Biscuit Fire, where LiDAR imagery had been collected for a companion study.

Seventy-eight sites were sampled: 13 unburned, 21 low-severity, 13 moderate-severity, 18 high-severity, and 13 extreme-severity (Figure 2.1). Unburned measurements were collected outside the Biscuit Fire boundary. Nine ultramafic sites were selected based on the USDA Soil Survey Geographic (SSURGO) database (USDA 2008); however, field observation and orthophotos showed that one of these sites was not ultramafic, so it was reclassified as non-ultramafic during data analysis. Fifteen of the selected sites also burned in the 1987 Silver Fire.

I used the differenced Normalized Burn Ratio (dNBR) as my measure of fire severity (Thompson 2008). This metric uses Landsat TM/ETM+ data to calculate the pre- to post-fire difference of near-infrared (band 4) and mid-infrared (band 7) reflectance ratios. Band 4 corresponds to leaf area and plant productivity, and band 7 changes based on soil reflectance and moisture content (Lutes et al. 2006). This method provides a quick and relatively accurate

way of measuring burn severity in the forest canopy layer (Miller and Yool 2002, Brewer et al. 2005).

Only areas greater than 50 m and less than 500 m from a road were considered for sampling. The 50 m distance was intended to limit human influence (such as the harvesting of roadside "hazard trees"). The 500 m limit was a compromise between site accessibility and full coverage of the sample area. Without this constraint the steep and challenging terrain may have significantly lowered the potential sample size due to the time and effort required to access a site. To create potential sample locations, the dNBR value from each 30 m pixel was assigned to one of five severity classes: unburned, low (0-35% canopy mortality), moderate (35-65% canopy mortality), high (65-95% canopy mortality), and extreme (95-100% canopy mortality) (Thompson 2008). The dNBR raster was smoothed using ArcGIS FOCALMEAN with an 80 m (2 ha) radius; each pixel was assigned a classification if 75% or more of the surrounding pixels were in a given class (ESRI 2010) . The 75% threshold was a tradeoff between burn severity purity in a patch, and having enough uniform patches from which to choose sites. The resulting "patches" of burn severity were exported as shape files and potential sites were located in the centroid of each polygon. Some sites were discarded due to steep slope (>90%), or the presence of landslides or cliffs. Near the end of the sampling season one north-facing site and five west-facing sites were selected to increase representation of those aspects.

Data collection

Field measurements were conducted during the summer of 2008. Each site consisted of three 0.1 ha plots (Figure 2.2). Plots were located using a Garmin 60CX GPS in combination with LiDAR images, aerial photos, and on-the-ground surveying. On each plot,

large woody debris (LWD) was sampled via the line intercept method (Brown 1974) on three 17.84 m slope-corrected transects. Large woody debris included branches, logs, uprooted stumps, dead trees on the ground or leaning more than 45 degrees from vertical that were at least 7.62 cm in diameter and 1 m long. Species or species type (conifer or hardwood), diameter at point of intersection and decay class (1-5) (Maser et al. 1979, Sollins 1982) were recorded for each piece of woody debris.

Fine woody debris (FWD, woody material 0.64-7.62 cm in diameter) was sampled along four 2.52 m transects along the LWD transect lines as described in Brown (1974) (Figure 2.2). These transects were not slope-corrected in the field. Tallies of 10-hour (0.64-2.54 cm diameter) and 100-hour (2.54-7.62 cm diameter) fuels were made using the line intercept method and a go/no go gauge (Brown 1974, Avery and Burkhart 2002). One hour fuels (<0.64 cm diameter) were not tallied separately in this study, but were collected as part of the litter samples.

Litter and duff were sampled at four locations per plot (12 per site) within a 20 cm diameter PVC ring: just beyond 2.5 m along transect 1, and just before the 12.5 m mark along transects 1, 2, and 3 (Figure 2.2). Litter is the top layer of the forest floor comprised of debris that has not been affected by decomposition (organic-fibric layer, Oi). In this study litter included 1-hour fuels (twigs <0.64 cm), needles and leaves, small chunks of rotted wood, detached bark, dead moss, dead lichens, dead herbaceous stems, and flower parts. Duff is comprised of organic material that lies beneath the litter and above the soil (organic-hemic layer, Oe). At each of the four locations, a representative depth of litter and duff was measured to the nearest 0.1 cm. All litter, duff, and 1-hour fuels were then collected in a single paper bag for all four locations within a plot. A total of three bags, one per plot, were collected for

each site. These bags were brought back to the lab where the samples were oven-dried at 68-70° C for a minimum of 48 hours and then weighed.

In each plot all trees and snags ≥50 cm DBH (diameter at breast height, 1.37m) were measured within a 17.84 m horizontal radius (0.1 ha), all trees and snags 15-50 cm DBH were measured within a 12.61 m horizontal radius (0.05 ha), and all live and dead saplings 5-15 cm DBH were measured within the four 2.52 m (slope distance, 0.002 ha) microplots. Species or species type was recorded for all live trees and snags when possible. Decay class (1-5) (Cline et al. 1980), was recorded for snags, as well as well as whether the Biscuit Fire was the cause of death.

Data preparation

Ten fuel classes were considered for analysis (Table 2.1). Litter and duff depth measurements were averaged to the site level based on the average depth of all twelve sample locations. Dry weight for the combined samples of litter and duff was converted to metric tons per hectare, and averaged to the site level. The four 2.52 m plot transects for 10- and 100-hour fuels were slope-corrected, then tallies for fine fuels and LWD for each plot were converted to biomass (tons/ha) as detailed in Marshall et al. (2003). All 10-hour, 100-hour and LWD biomass were calculated at the plot level, and then averaged for the three plots to determine the site average. Large woody debris was separated into three categories by diameter: small (7.62 cm - 30 cm), medium (30 cm - 60 cm) and large (>60 cm). LWD was separated into these categories because different size classes have different frequency distributions within a forest, vary between forest types and have different decay rates (Spies et al. 1988). A few sites were missing litter depths, a litter sample, or transect data from one of the microplots. In these cases values were calculated from the other data collected for that site.

Fifteen explanatory variables and four interaction terms were considered for data analysis (Table 2.2). In addition to fire severity, these variables were selected to represent abiotic, biotic, and climatic influences on site productivity. Sites with higher productivity may be more likely to have higher rates of fuel input, and larger quantities of fuel overall. Elevation, slope, aspect, and dNBR values were extracted for the three plots as referenced by their GPS locations; values were then averaged to generate a site value. Elevation, slope, and aspect were generated from a digital elevation model (DEM). Aspect was converted to values between zero and two as per Beers (1966), where 0.0 corresponds to southwest slopes and 2.0 corresponds to northeast slopes. The original dNBR continuous values were used for data analysis, rather than the five classes used to ensure sites spanned a range of burn severities.

In addition to the abiotic variables listed above, two scales of topographic position index (TPI) were generated for analysis. Fine-scale TPI compared plot elevation to the average elevation of an annulus 150-300 m from the plot; coarse-scale TPI compared plot elevation to the average elevation of an annulus 850-1000 m from the plot. TPI values for each plot were then averaged to the site level.

Biotic variables included pre-fire live tree basal area, hardwood basal area, and percent hardwood basal area. These variables were calculated using field measurements. Pre-fire live tree basal area (m^2/ha) was estimated using the basal area of live trees and trees classified as killed by the Biscuit Fire. Due to fire consumption, post-fire bark loss, and snag fall, this calculation is almost certainly an underestimate of pre-fire basal area, but it is the best estimate available in the absence of pre-fire measurements. Before calculating basal area for trees and snags 5-15 cm in diameter, the slope radius of each 2.5 m radius microplot was

converted to horizontal distance based on the average slope of the three plot transects (Figure 2.2).

Three climatic indices were considered: average maximum August temperature, average minimum December temperature, and average precipitation. These values represent averages from 1971-2000 and were chosen to characterize long-term heat, cold, and moisture stress experienced at each site. All climate data were downloaded from the PRISM website (http://www.prism.oregonstate.edu/, (Daly et al. 2002)). Values were extracted to GPS plot locations, and then averaged to the site level.

Two categorical variables were used to determine what effects, if any, fire return interval had on fuel quantities. Sites outside the Biscuit Fire boundary were denoted as "isUnburned." These sites were assumed to have had no fire disturbances for an extended period of time. Sites that burned in both the Biscuit and Silver fires (15 year return interval) were classified as short-interval (SI) sites ("isSilver" in analyses). All other sites burned in the Biscuit Fire, but not the Silver Fire. These sites were considered long-interval sites (LI), and were assumed to have no fire disturbance for an extended period prior to the Biscuit Fire.

Data analysis

Relationships of litter depth, combined depth of litter and duff, 10-hour fuels, 100-hour fuels, forest floor biomass (litter/duff/1-hour fuels), total LWD, and LWD 7.62-30 cm, to dNBR and other potential explanatory variables were analyzed using multiple linear regression (Table 2.1). All fuel variables except 10-hour fuels were log-transformed to improve linear relationships. The value one was added to all LWD values before log-transformation because LWD was absent on a single site (lowest nonzero value: 0.62 tons/ha). Models including all potential variables were checked for influential points, normality, and

equal variance, and in all cases met the assumptions for linear regression. Models were selected via stepwise selection using the Akaike information criterion (AIC) criterion (Burnham and Anderson 2002). Models within two AIC units of the "best" model were also considered. Final models were chosen based on model parsimony and ecological significance of the potential parameters. Partial R^2 values were calculated for all variables in each of the final models. Correlation between potential explanatory variables was usually low (Pearson's r < 0.4 in most cases), and highly correlated explanatory variables (r = 0.60-0.88) were not used concurrently in any models. Multiple linear regression analysis was conducted using R software's stats package (R Development Core Team 2010). The variance inflation factor (VIF) was checked using the "HH" package (Heiberger 2008), and partial R^2 values were calculated using the "Design" package (Harrell 2007).

Due to their absence on many sites, the presence/absence of duff, LWD 30-60 cm, and LWD >60 cm in relation to dNBR and other explanatory variables were analyzed using logistic regression (Table 2.1). Values were converted to presence/absence and models were again selected via stepwise selection using AIC criterion. Models within two AIC units of the "best" model were also considered. Final models were chosen based on model parsimony and ecological significance of the potential parameters. Logistic regression analysis was conducted using R software's stats package (R Development Core Team 2010). Pseudo R^2 values were calculated as described in Nagelkerke (1991).

In addition to the relationships of each fuel type to explanatory variables, potential relationships between all fuel types and explanatory variables were analyzed using nonmetric multidimensional scaling (NMS) (Mather 1976) using PC-ORD 6 (McCune and Mefford 2010). This analysis looks at the overall structure and relationships of all fuel types, then the

relationships of potential explanatory variables can be explored in the context of fuel structure. Unlike principal components analysis (PCA) or canonical correspondence analysis (CCA), which reduce the dimensionality of a data set by maximizing variance explained on each axis, NMS attempts to find the best arrangement of *n* entities on *k* axes by minimizing stress. "Stress" is a measure of the departure from monotonicity of distance measures between entities in the original data set (with a dimensionality equal to the number of attributes in the data matrix) to the distance between entities as arranged on *k* axes. NMS avoids the assumption of linear relationships between variables, and ameliorates the "zero-truncation" problem, where species absence at a given environmental gradient gives no knowledge as to how unfavorable that environment is for that species. Unlike most other ordination techniques, the composition of each axis may differ based on the total number of axes in the final ordination. Additionally, axes may not be orthogonal to each other, though in practice they are usually close (McCune and Grace 2002).

As the difference between the largest and smallest nonzero value in for each fuel class was often greater than an order of magnitude, data were log transformed prior to performing the NMS ordination. Due to the presence of zeros in the data, a small number was added to each fuel component before transforming (1 for all fuel classes except duff depth, where 0.01 was used). This value varied based on the minimum nonzero value for each fuel class, and was calculated as per the methods outlined in McCune and Grace (2002). After data transformation distributions of the fuel variable types were relatively symmetric. Coefficient of variation was low for plots (32.9%) and fuel types (33.7%). These values imply that relativization would have a small effect on the qualitative outcome of the analysis, so fuels were not relativized for further analysis. Potential outliers were identified via a Bray-Curtis

ordination using Euclidean and Sørensen distance measures (Bray and Curtis 1957). Outliers generally exhibited little influence on fuel gradients. No outliers were removed from the data set for the final statistical analyses. NMS was run using Sørensen distance. Calculations were made for a maximum of 6 axes, 500 maximum iterations, 250 runs with real data, and a random starting configuration.

A multi-response permutation procedure (MRPP) (Biondini et al. 1988) was used to test whether fuel composition varied based on soil type (ultramafic or non-ultramafic), and fire history. MRPP analysis comparing differences in fuel composition based on soil type were conducted on the LI sites (unburned sites and SI sites were excluded).Three MRPP fire-history comparisons were conducted: SI sites to LI sites (sites that burned in both the Biscuit and Silver fires to Biscuit-only sites), SI sites to unburned sites, and LI sites to unburned sites. The MRPP analyses were performed twice, once including all fuel types, and once excluding litter depth, duff depth, and forest floor biomass (biomass of litter, duff and 1-hour fuels). The latter MRPP analyses were conducted to determine if compositional differences between burned and unburned sites were due to fuels other than litter and duff. Ultramafic sites were excluded from the burn history analyses, as no data were collected on SI sites with ultramafic soils. MRPP analysis was conducted using Sørensen distances in PC-ORD 6 (McCune and Mefford 2010).

RESULTS

Effects of burn severity, biotic, abiotic, and climatic variables on fuel quantities

Litter and duff characteristics were strongly related to burn severity six years after the Biscuit Fire, and unburned sites generally had higher quantities of litter and duff than burned sites (Figure 2.3). These findings were corroborated by the multiple linear regression results

for litter depth, combined litter and duff depth, and forest floor biomass, which all showed strong influences of dNBR (Table 2.3). Litter depth, and forest floor depth and biomass were also positively correlated with the proportion of hardwoods, and negatively correlated with ultramafic soils. Unburned and low-severity sites had an overlapping range of dNBR values (Figure 2.3), but for a given value of dNBR unburned sites tended to have a higher amount of litter and duff than burned sites. Logistic regression analysis of duff presence/absence also showed a strong correlation with burn severity, as well as the proportion of hardwood trees (Table 2.4). As the proportion of hardwoods increased, the likelihood of duff presence decreased (Figure 2.4). Variation in litter and duff quantities explained by the models was high (R^2 = 0.42-0.63 for linear regression models, pseudo-R^2 = 0.51 for duff logistic regression model.)

dNBR did not enter the regression models for woody fuels in the smaller size classes (10-hour and 100-hour fuels). Pre-fire live-tree basal area and average maximum August temperature accounted for most of the explained variance of 10-hour fuels, while soil type (ultramafic or non-ultramafic) accounted for most of the explained variance of 100-hour fuels, though the predictive power of the latter model was low (Table 2.3). Burn severity entered into the regression models for overall LWD quantities and LWD in the 7.62-30 cm size class but was a minor component. Overall, variance explained by the regression models was much lower for woody fuels than for litter and duff (Table 2.3). Coarse-scale topographic position was part of the model of LWD in the larger size classes, though predictive power for these models was low (Table 2.4). Full lists of the models considered for final analysis are presented in Appendix I and II.

Correlation and structure of dead fuels and relationships to dNBR, biotic, abiotic, and climatic variables

A three dimensional solution was chosen for the NMS ordination of dead fuels (Figure 2.5). The three axes corresponded to fuel size. Axis 2 showed the highest correlations with litter, duff, and 10-hour fuels; axis 3 showed the highest correlations with the larger size classes of LWD (LWD 30-60 cm and LWD >60 cm); and axis 1 showed the highest correlations with medium-sized fuels (100-hour fuels and LWD7.62-30 cm) (Table 2.5). The final solution was chosen based on an NMS scree plot, which showed a decline in slope after three axes. Final stress of the best 3-dimensional solution was 10.16 after 80 iterations with a final instability < 0.00001 ($p = 0.004$ that a similar final stress could be obtained by chance from a Monte Carlo simulation with 250 runs.)

Of the environmental variables investigated, dNBR showed the highest correlation with any of the axes (axis 2: $R^2 = 0.50$), and it is negatively correlated with litter, duff and 10-hour fuels (Figure 2.5). Total pre-fire live basal area had a weak positive correlation with axis 2 ($R^2 = 0.18$), and coarse-scale topographic position had a weak positive correlation with axis 3 (TPI850-1K $R^2 = 0.12$) (Table 2.6).

MRPP showed a significant difference in fuel composition between ultramafic and non-ultramafic soils ($p = 0.0038$, Table 2.7). The chance corrected within group agreement statistic was moderate ($A= 0.037$).

Burn history effects on fuel quantities and composition

There is no evidence of a difference in dead fuel quantities between short-interval and long-interval sites. The “isSilver” factor variable did not enter any of the regression fuel models (Table 2.3, Table 2.4). Additionally, MRPP analysis of overall dead fuel composition showed no evidence of difference in fuel composition SI and LI sites ($p = 0.60$, $A = -0.0036$,

Table 2.7). Both SI and LI sites showed significant differences in fuel composition from unburned sites, however, after excluding litter depth, duff depth, and forest floor biomass there was no evidence of difference between burned and unburned sites (Table 2.7).

DISCUSSION

Six years after the Biscuit Fire, fuel quantities often showed a relationship to burn severity. However, these relationships varied by fuel type. Litter and duff quantities were lowest on high- and extreme-severity sites, while LWD quantities were generally highest on high- and extreme-severity sites, and 10- and 100-hour fuels showed no relationship to burn severity. Additionally, the biotic, abiotic, and climatic factors that best predicted fuel quantities varied by fuel type. The different responses to burn severity, and the different explanatory variables associated with small, medium, and large fuel types imply that different processes govern their creation and decay.

Effects of burn severity, biotic, abiotic, and climatic variables on fuel quantities

Litter and duff

Unburned sites had higher litter depth, combined litter and duff depth, and litter/duff/1-hour fuel biomass than low-severity burn sites. On burned sites, litter and duff amounts were highest on low-severity sites, and lowest on high- and extreme-severity sites. These findings are consistent with other studies of post-fire fuel-dynamics of a similar time frame, though those studies took place in less-productive ecosystems than the Klamath-Siskiyous. Studies in the ponderosa pine forests of South Dakota and the ponderosa pine, incense cedar, and white fir forests of Yosemite National Park found that 5-6 years post fire, litter and duff were still below pre-fire levels but had recovered a high proportion of mass in low-severity areas (van Wagtendonk and Sydoriak 1987, Keifer et al. 2006, Keyser et al.

2008). As dNBR is highly correlated with crown mortality and vegetation damage (Lutes et al. 2006, Thompson 2008) this result may seem intuitive—the more living trees that remain in an area, the more needles and leaves there are to contribute to litter and duff. However, differences in litter and duff quantities may be partially due to conditions created by the fire disturbance itself. Immediate post-fire litter inputs may also be high in low- or moderate-severity areas due to needle-fall from heat-damaged but unscorched crowns. Additionally, litter and duff experience higher proportions of combustion in high-severity areas (van Wagtendonk and Sydoriak 1987, Keifer et al. 2006, Campbell et al. 2007, Keyser et al. 2008), so low-severity areas may have had higher amounts of litter and duff immediately post-fire. Using permanent plot data from before and after the Biscuit Fire, Campbell et al. (2007) estimated that low-severity sites averaged 70% consumption of litter (including 1-hour fuels) and 44% consumption of duff immediately post-fire as compared to 100% litter consumption and 99% duff consumption on high-severity sites. Despite lower canopy mortality and ground fuel consumption, the moderate- and high-severity areas were not devoid of vegetation that could contribute to litter and duff accumulation. Shrubs and top-killed hardwood trees sprouted prolifically and grew quickly. Based on additional data collected during this study, average shrub cover was 34% on high-severity sites and 40% on extreme-severity sites. Pacific madrone sprouts had grown up to 39 cm in diameter in some high-severity areas. Tanoak, Sadler oak, canyon live oak, deer brush (*Ceanothus integerrimus*), snowbrush (*Ceanothus velutinus*) and many other species could contribute to litter and duff levels. However, despite their rapid colonization of some areas, shrubs and hardwoods did not seem to compensate for overstory tree losses and higher forest floor consumption by fire.

The two other explanatory variables commonly selected for the litter and duff models were soil type (ultramafic or non-ultramafic) and percent hardwood. Predictably, the amount of litter and duff was consistently lower on ultramafic sites. Ultramafic areas are characterized by unique plant communities, and tend to have an open canopy with fewer trees and shrubs (Whittaker 1960, Franklin and Dyrness 1988). Fewer trees and shrubs result in less leaf and needle input for litter and duff. The relationship of hardwood trees to litter and duff quantities was more complicated. Proportion of hardwood trees in a stand was positively correlated with litter depth and biomass, though it was not a dominant factor. Field observations are consistent this result. Litter was often particularly plentiful beneath sprouting Pacific madrone trees, and was also plentiful near resprouting huckleberry oak (*Quercus vaccinifolia*), and canyon live oak (*Quercus chrysolepis*). Conversely, probability of duff presence was negatively correlated with hardwoods. Despite a high input of litter, litter material from hardwood sources does not seem to contribute to duff at the same rate as conifer sources. Hardwoods such as Pacific madrone have faster litter decay rates than conifer species such as Douglas-fir and ponderosa pine (Harmon et al. 1990, Valachovic et al. 2004), so litter in hardwood-dominated areas may decay too quickly to contribute to a deep duff layer.

Small-diameter woody fuels

Final models for 10- and 100-hour fuels did not include dNBR. Instead selected explanatory variables included climate (precipitation or mean maximum August temperature), slope, and soil type. 10-hour fuels were also correlated with pre-fire basal area. As I do not have data from immediately after the fire, it is unclear whether these fuels were consumed equally in areas of different burn severities; however, Campbell et al. (2007) found that consumption of these fuels on the forest floor is similar regardless of dNBR-based burn

severity (mean consumption 62-78% for 10-hour fuels and 62-79% for 100-hour fuels), and that consumption of twigs and branches was low in tree canopies, even in high-severity areas. Another Biscuit Fire study that classified burn severity using plot-data rather than remote-sensing data, found poor relationships between ground-based indices of fire severity (loss of soil organic matter and bole char) with canopy-based indices of severity (crown scorch and tree mortality) (Halofsky and Hibbs 2009). The decoupling of ground-based FWD consumption with dNBR and crown mortality, and a lack of evidence that FWD was related to dNBR 6 years post-fire, imply that FWD inputs in low-severity areas (through self-pruning, mortality, etc.) may have similar rates to branch input from decaying snags in high-severity areas, though this relationship may change in the future.

Large woody debris

In both LWD 7.62-30 cm and total LWD amounts dNBR was positively correlated with LWD, indicating higher amounts of LWD biomass on sites with higher burn severity. This is consistent with expectations from other studies looking at large woody debris (Passovoy and Fule 2006, Keyser et al. 2008). Past studies have found that fire does not consume a large percentage of LWD, fire-killed trees, or snags, even at high severities (Campbell et al. 2007, Donato 2008, Donato et al. 2009a, Meigs et al. 2009). However, a pulse of LWD is expected 5-20 years post-fire, due to snag fall (Parsons 1978, Harmon et al. 1986, Biondini et al. 1988, Spies et al. 1988, Russell et al. 2006). Observations at the Biscuit Fire sites showed evidence of fire-killed fallen snags, and snapped boles of fire-killed trees. Higher amounts of LWD in decay class 2 in high- and extreme- burn severity areas may indicate the initial stages of a pulse in LWD. Large numbers of standing snags in the high- and extreme-severity areas will continue to be a source of LWD for at least the immediate future.

Prior studies in similar areas indicate that LWD quantities in high-severity areas continue to increase at least 15-20 years post fire (Donato 2008), though overall biomass of snags also decreases over time due to aerial decomposition (decomposition of snags and standing dead wood) (Sollins 1982, Donato 2008). Note that the higher quantities of LWD in higher fire severity classes do not reflect increases in all decay classes. Biomass of decay class 2 LWD increases as burn severity increases, but LWD biomass in decay classes 3, 4, and 5 are all highest on unburned sites).

Coarse-scale topographic position had a strong influence on the presence or absence of LWD in the larger size classes. The relationship is negative, indicating ridges tend to have a lower probability of LWD, and may serve as a LWD source for valleys where the probability of LWD presence is higher. It is also possible that valleys are more likely to have large-diameter trees. A comparison of pre-fire basal area to large-scale topographic position found higher amounts of basal area in valleys for trees >60 cm DBH ($F_{(1,76)}$=14.79, p=0.0002) but no relationship with topographic position for trees 30-60 cm DBH ($F_{(1,76)}$=0.2728, p= 0.603), Kennedy and Spies (2007) found similar topographic relationships in the Coast Range, where riparian areas had a disproportionally high amount of logs compared to the overall landscape, and areas of high topographic position appeared to serve as sources of logs for areas of low topographic position. However, it is also important to note that in the current study the correlations were low, indicating that other factors may be important to predict the presence or absence of LWD.

Multivariate analysis of fuel classes

The three axes in the NMS ordination corresponded to fuel diameter: small (including litter and duff), medium, and large. The alignment of fuels to different axes based on size class

implies that different processes generate fuels of different size classes. This finding is consistent with the regression analyses above, which found similar predictors for fuel amounts of similar size classes, but different predictors for different sets of size classes. Similar to the linear regression analysis, dNBR was highly correlated with litter and duff. 10-hour fuels were also represented on the litter/duff axis, but 10-hour fuels were also correlated to a lesser extent with the "medium diameter" fuels axis indicating that burn severity may play a part in the amount of 10-hour fuels six years after the Biscuit Fire, but that other processes that operate on larger fuel classes also have an impact. The other two moderately correlated explanatory variables, pre-fire basal area and coarse-scale topographic position, were also consistent with relationships seen in the regression analyses.

Though 1-hour fuels (woody fuels <0.64 cm) were not sampled in this study, other studies have shown they recover quickly after a fire, potentially within the time frame of this study (van Wagtendonk and Sydoriak 1987, Keifer et al. 2006, Keyser et al. 2008). Biomass of fuels at one size class tend to be correlated with adjacent size classes (USDA Forest Service 1988, Fule and Covington 1994). I conducted a small separate study of 1-hour fuels in 2009 and found that 1-hour and 10-/100-hour fuels were moderately correlated ($R^2 = 0.39$ based on a linear model including 10- and 100-hour fuels, $p < 0.0001$, $N = 46$). I also found that 1-hour fuels and forest floor biomass were correlated ($R^2 = 0.35$ based on a linear model regressing mass of 1-hour fuels against combined mass of litter, duff, and 1-hour fuels, $p < 0.0001$, $N = 46$). Based on the correlations between 1-hour fuels with litter/duff and 10- and 100-hour fuels, I would expect an ordination including 1-hour fuels to align with the "small" and "medium" fuel axes, similar to 10-hour fuels.

Fuel responses to fire on ultramafic soils

The MRPP analysis showed a significant difference in overall fuel composition between ultramafic and non-ultramafic sites that burned in the Biscuit Fire. This is consistent with the multiple linear regression findings, which showed fuel quantities were lower on ultramafic soils. The differences in vegetation and productivity of ultramafic sites make these findings unsurprising; however I am unaware of any studies that compare overall fuel composition in adjacent forested ultramafic/non-ultramafic sites. It is also worth noting that lower overall fuel amounts in ultramafic areas did not correspond to low overall crown mortality. Thompson and Spies (2009) found median crown damage in the Biscuit Fire was 92% for trees on ultramafic soils, as compared to a median crown damage of 59% on non-ultramafic sites.

Fuels and fire history

There was no evidence that dead fuel quantities or composition differed between SI burn sites and LI burn sites. Six years post fire, both LI and SI sites both showed differences in overall fuel composition from unburned sites, though those differences disappeared when litter and duff quantities were not considered. It is important to note that these differences (and their lack, when litter and duff were removed from the analysis) represent overall fuel composition regardless of burn severity. Burn severity does appear to play a role in LWD fuel quantities (Table 2.3, Figure 2.6), but the MRPP analysis suggests that overall within-burn dead-fuel variability does not differ from variability of unburned areas, aside from differences in litter and duff quantities.

Fuels succession and fire behavior

This study is a snapshot of dead fuels at a single point in time. The most important predictor values for dead fuels 6-years after a fire in a mixed-severity mixed-evergreen forest will almost certainly differ from the most important factors immediately post fire, and will probably differ from the most important factors one or two decades post fire. The relationships of fuels to fire severity may also change. For example, though 10- and 100-hour fuels show no relationship to burn severity 6 years post fire, future quantities of these fuels may be higher in high- and extreme-severity areas due to snag decay or mortality of the shrub layer as trees overtop it. Quantities of LWD will likely remain highest on high- and extreme-severity sites for decades, as snag density is also highest in these areas. In an analysis of high-severity burns in a similar area Donato (2008) found that woody fuels greater than 7.62 cm in diameter seem to peak 15-20 years after a fire. However, the decay class distribution of LWD differs between unburned and burned sites, which may affect future LWD distributions, especially when compared to sites with different disturbance processes (e.g. windthrow, insects or pathogens) or different fire disturbance regimes. Temporal dynamics of dead fuels are poorly understood and vary based on forest type, disturbance regime and spatial scale. Long-term studies are needed to investigate how fuels also vary over time in the moderate- and low- severity areas to determine how dead fuel levels differ over longer-term time frames.

Though outside the scope of this study, it is also important to consider the role of live fuels in fire behavior. Thompson et al. (2007) found that areas that burned with high severity in the 1987 Silver Fire tended to burn with high severity 15 years later in the Biscuit Fire, particularly in areas with young vegetation (shrub patches and plantations), possibly due to homogenous and highly contiguous live fuels. Areas that burned with high severity tended to

have more small trees and fewer large trees (Azuma et al. 2004, Campbell et al. 2007). Field measurements in this study also found the highest amounts of pre-fire live basal area in the larger size classes on low-severity sites (Figure 2.7). Shrubs may quickly colonize high-severity areas (Donato 2008), shrub mass has been positively correlated with burn severity (Meigs et al. 2009), and may continue to increase for decades (Dunn 2010). Additionally, areas that have experienced long periods since fire disturbance in mixed-severity forest regimes may be less likely to experience high-severity fire, despite a longer time for potential fuel buildup (Odion et al. 2004). Factors that contribute to lower fire severity in these areas may include understory vegetation composition (Chapter 3), and cooler, moister understory conditions (Countryman 1955). In order to better understand future fire behavior at landscape scales, the dynamics of both live and dead fuels must be considered in the context of all burn severities.

CONCLUSIONS

Six years after the Biscuit Fire, descriptive statistics and linear regression models showed the biomass and depth of litter and duff was lower on burned sites than unburned sites, and lowest on high-severity sites. This relationship was reversed for large-diameter woody fuels, where quantities were highest in high- and extreme-severity areas, though there was no evidence that quantities differed between low-severity and unburned sites. Unlike litter/duff and LWD, 10- and 100-hour fuels showed no relationship with burn severity. The different relationships between litter/duff, 10- and 100-hour fuels, and LWD with fire severity imply that the creation and decomposition of different fuel classes are governed by different processes. Linear regression models support this idea as different biotic, abiotic, and climatic variables were selected for different size fuel class models. The NMS ordination also

demonstrates the different structures and relationships of dead fuels. Just as the linear regression analysis revealed three different associations with burn severity based on fuel size, the three axes in the final NMS solution align with three size classes of dead fuels: small, medium, and large.

There was no evidence of a difference in fuel quantities or overall fuel composition between sites that burned only in the Biscuit Fire and sites that also burned 15 years earlier in the Silver Fire. Overall fuel composition did differ between burned sites and unburned sites, but this difference disappeared if litter and duff quantities were not considered. Though linear regression models indicated large woody debris quantities were associated with burn severity, when all fire severities were considered the overall composition of 10-, 100-hour fuels and LWD did not differ between burned sites (both short-interval and long-interval) and unburned sites.

The Klamath-Siskiyou Mountains are a highly productive area, where a quick return to pre-fire fuel conditions might be expected. Though fire severity influenced many fuel types six years after the Biscuit Fire, these differences may disappear, decrease or have other relationships to burn severity fifteen years post-fire (the time between the Biscuit and Silver Fires), and may change further in subsequent decades. Future studies on fuels succession in areas with mixed-severity fire regimes should include all severities, to determine how future fuel trajectories differ based on the initial disturbance severity.

LITERATURE CITED

Agee, J. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72**:24-34.

Agee, J. K. 1991. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. Northwest Science **65**:188-199.

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.

Agee, J. K. and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management **211**:83-96.

Atzet, T. and D. Wheeler. 1982. Historical and ecological perspectives on fire activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests. USDA Forest Service, Pacific Northwest Region Publication R-6, Portland, OR, p. 19.

Atzet, T. A. and R. Martin. 1992. Natural disturbance regimes in the Klamath province. Pages 40-48 *in* Proceedings of the Symposium on Biodiversity of Northwestern California. Portland OR, USDA Forest Service, Pacific Northwest Region.

Atzet, T. A., D. Wheeler, and R. Gripp. 1988. Fire and forestry in southwest Oregon: Importance of fire. Oregon State University Extension Service, FIR Report, Winter 1988, Medford, Oregon, USA, pp. 4-7.

Avery, T. E. and H. E. Burkhart. 2002. Forest Measurements. 5th edition. McGraw-Hill, New York, NY.

Azuma, D. L., J. Donnegan, and D. Gedney. 2004. Southwest Oregon Biscuit Fire: An analysis of forest resources and fire severity. Portland, OR, p. 32.

Beers, T. 1966. Notes and observations: Aspect transformation in site productivity research. Journal of Forestry **64**:691-692.

Biondini, M., P. Mielke, and K. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Plant Ecology **75**:161-168.

Bray, J. and J. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs **27**:325-349.

Brewer, C. K., J. C. Winne, R. L. Redmond, D. W. Opitz, and M. V. Mangrich. 2005. Classifying and mapping wildfire severity: A comparison of methods. Photogrammetric Engineering and Remote Sensing **71**:1311-1320.

Brown, J. 1974. Handbook for inventorying downed woody material. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-16, Ogden, UT, p. 24.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: Principles in the context of place. Conservation Biology **18**:903-912.

Burnham, K. P. and D. R. Anderson 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research-Biogeosciences **112**:G04014.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management **44**:773-786.

Colombaroli, D. and D. G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. Proceedings of the National Academy of Sciences of the United States of America **107**:18909-18914.

Cooper, L. J. 1939. A history of the Siskiyou National Forest. Unpublished report on file with the Siskiyou National Forest, Grants Pass, Oregon.

Countryman, C. M. 1955. Old-growth conversion also converts fireclimate. U.S. Forest Service Fire Control Notes **17**:15-19.

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research **22**:99-113.

Donato, D., J. Campbell, J. Fontaine, and B. Law. 2009a. Quantifying char in postfire woody detritus inventories. Fire Ecology **5**:104-115.

Donato, D. C. 2008. Forest vegetation and fuel dynamics following stand-replacing wildfire, re-burn, and postfire management in the Siskiyou Mountains, Oregon. Dissertation. Oregon State University, Corvallis, OR.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science **311**:352-352.

Dunn, C. J. 2010. Coarse woody detritus dynamics, variable decay rates and their contribution to wildland fuel succession following high-severity fire disturbance in dry-mixed conifer forests of Oregon's eastern Cascades. Master's thesis. Oregon State University, Corvallis, OR.

ESRI (Environmental Systems Resource Institute). 2010. ArcMap 9.3.1. Redlands, California. Available:

Franklin, J. F. and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Fule, P. Z. and W. W. Covington. 1994. Double sampling increases the efficiency of forest floor inventories for Arizona ponderosa pine forests. International Journal of Wildland Fire **4**:3-10.

GAO. 2004. Biscuit Fire: Analysis of fire response, resource availability, and personnel certification standards. United States General Accounting Office, GAO-04-426, Washington, DC.

Halofsky, J. E. and D. E. Hibbs. 2009. Relationships among indices of fire severity in riparian zones. International Journal of Wildland Fire **18**:584-593.

Harmon, M. E., G. A. Baker, G. Spycher, and S. E. Greene. 1990. Leaf-litter decomposition in the *Picea-Tsuga* forests of Olympic National Park, Washington, USA. Forest Ecology and Management **31**:55-66.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133-302.

Harrell, F. E., Jr. 2007. Design: Design Package. R package version 2.1-1. Available: http://biostat.mc.vanderbilt.edu/s/Design, http://biostat.mc.vanderbilt.edu/rms

Heiberger, R. M. 2008. HH: Statistical analysis and data display: Heiberger and Holland. R package version 2.1-12. Available: http://CRAN.R-project.org/package=HH

Keane, R. E., J. K. Agee, P. Fule, J. E. Keeley, C. Key, S. G. Kitchen, R. Miller, and L. A. Schulte. 2008. Ecological effects of large fires on US landscapes: benefit or catastrophe? International Journal of Wildland Fire **17**:696-712.

Keifer, M., J. W. van Wagtendonk, and M. Buhler. 2006. Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the central and southern Sierra Nevada, CA (USA). Fire Ecology **2**:53-72.

Kennedy, R. S. H. and T. A. Spies. 2007. An assessment of dead wood patterns and their relationships with biophysical characteristics in two landscapes with different disturbance histories in coastal Oregon, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **37**:940-956.

Keyser, T. L., L. B. Lentile, F. W. Smith, and W. D. Shepperd. 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. Forest Science **54**:328-338.

Lewis, H. T. 1989. Reconstructing Patterns of Indian Burning in Southwestern Oregon. Pages 80-84 *in* Living with the land: The Indians of southwest Oregon. The proceedings of the 1989 Symposium on the Prehistory of Southwest Oregon. Southern Oregon Historical Society, Medford, OR.

Lutes, D. C., R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi. 2006. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-164-CD, Ogden, UT, p. 400.

Marshall, P. L., G. Davis, and S. W. Taylor. 2003. Using Line Intersect Sampling for Coarse Woody Debris: Practitioners Questions Addressed. BC Ministry of Forests, Research Section, Coast Forest Region, Nanaimo, BC.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78-95 *in* Wildlife Habitats in Managed Forests the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. J. W. Thomas, editor. USDA Forest Service.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons, New York, NY.

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2010. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.243 beta. MjM Software, Gleneden Beach, Oregon, U.S.A.

Meigs, G. W., D. C. Donato, J. L. Campbell, J. G. Martin, and B. E. Law. 2009. Forest fire impacts on carbon uptake, storage, and emission: The role of burn severity in the eastern Cascades, Oregon. Ecosystems **12**:1246-1267.

Miller, J. D. and S. R. Yool. 2002. Mapping forest post-fire canopy consumption in several overstory types using multi-temporal Landsat TM and ETM data. Remote Sensing of Environment **82**:481-496.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**:691-692.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment **4**:481-487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology **18**:927-936.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology **98**:96-105.

Parsons, D. J. 1978. Fire and fuel accumulation in a giant sequoia forest. Journal of Forestry **76**:104-105.

Passovoy, A. D. and P. Z. Fule. 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management **223**:237-246.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org

Russell, R. E., V. A. Saab, J. G. Dudley, and J. J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management **232**:179-187.

Sensenig, T. S. 2002. Development, fire history and current and past growth, of old-growth and young-growth forest stands in the Cascade, Siskiyou and mid-coast mountains of southwestern Oregon. Dissertation. Oregon State University, Corvallis, OR.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **12**:18-28.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology **69**:1689-1702.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology **20**:351-362.

Taylor, A. H. and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111**:285-301.

Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications **13**:704-719.

Thompson, J. R. 2008. Patterns of crown damage within a large wildfire in the Klamath-Siskiyou bioregion. Dissertation. Oregon State University, Corvallis, OR.

Thompson, J. R. and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management **258**:1684-1694.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America **104**:10743-10748.

USDA. 2008. Soil Survey Geographic (SSURGO) Database for Oregon and California.

USDA Forest Service. 1988. Silver Fire recovery project, final environmental impact statement. Pacific Northwest Region, USDA Forest Service, Grants Pass, OR.

USDA Forest Service. 2004. Biscuit Fire recovery project, final environmental impact statement. Medford, OR.

Valachovic, Y. S., B. A. Caldwell, K. Cromack, and R. P. Griffiths. 2004. Leaf litter chemistry controls on decomposition of Pacific Northwest trees and woody shrubs. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **34**:2131-2147.

van Wagtendonk, J. W. and C. A. Sydoriak. 1987. Fuel accumulation rates after prescribed fires in Yosemite National Park. Pages 101–105 *in* Ninth Conference on Fire and Forest Meteorology. American Meteorological Society, San Diego, CA.

Waring, R. H., K. S. Milner, W. M. Jolly, L. Phillips, and D. McWethy. 2006. Assessment of site index and forest growth capacity across the Pacific and Inland Northwest USA with a MODIS satellite-derived vegetation index. Forest Ecology and Management **228**:285-291.

White, C. 1971. Vegetation, soil chemistry correlations in serpentine ecosystems. Dissertation. University of Oregon, Dept. of Biology, Eugene, OR.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30**:279-338.

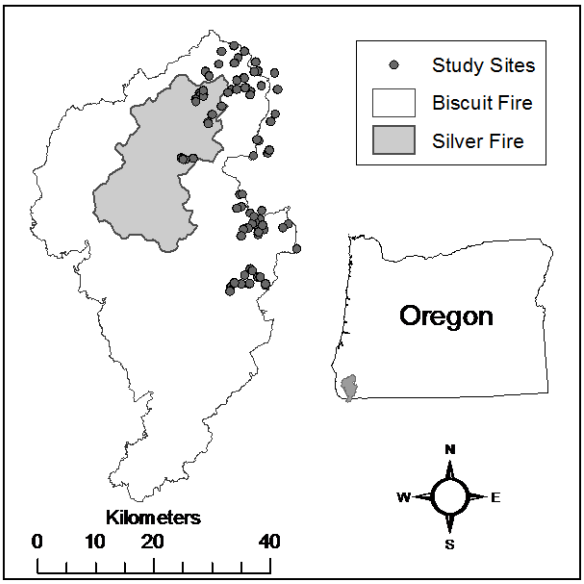


Figure 2.1: Biscuit Fire, Silver Fire and study site locations in Southwestern Oregon.

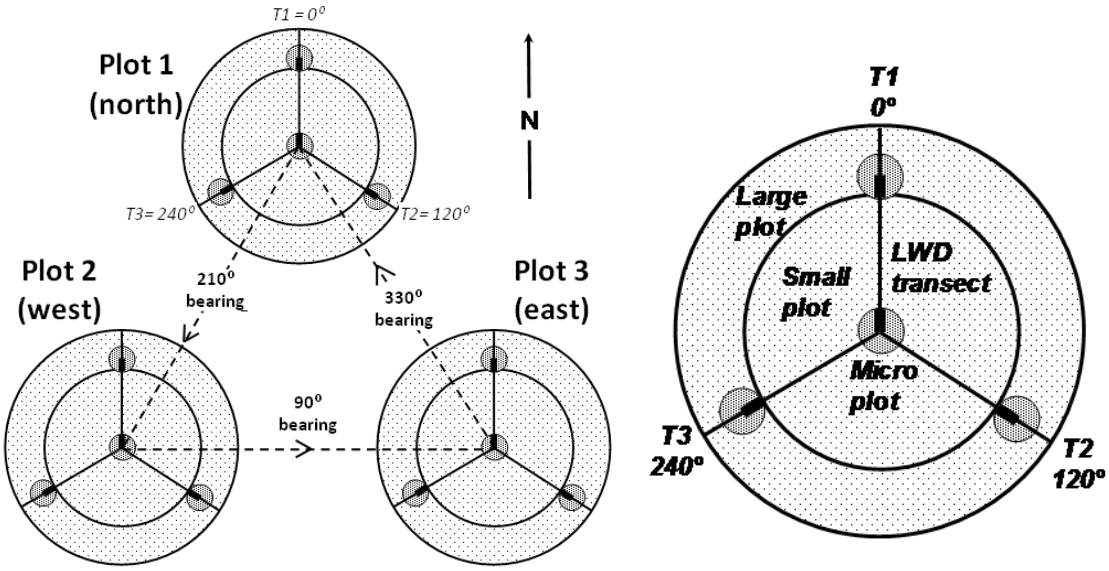


Figure 2.2: Sample plot layout at sites: (left) arrangement of the plot triad within a site, (right) plot detail showing location of 2.52 m radius microplots and transects. Large plot and LWD transects are 17.84 m horizontal distance, small plot is 12.61 m horizontal distance, 2.52 m transects are the thick, short lines within the microplot circles. Horizontal distance between plot centers is 50 m.

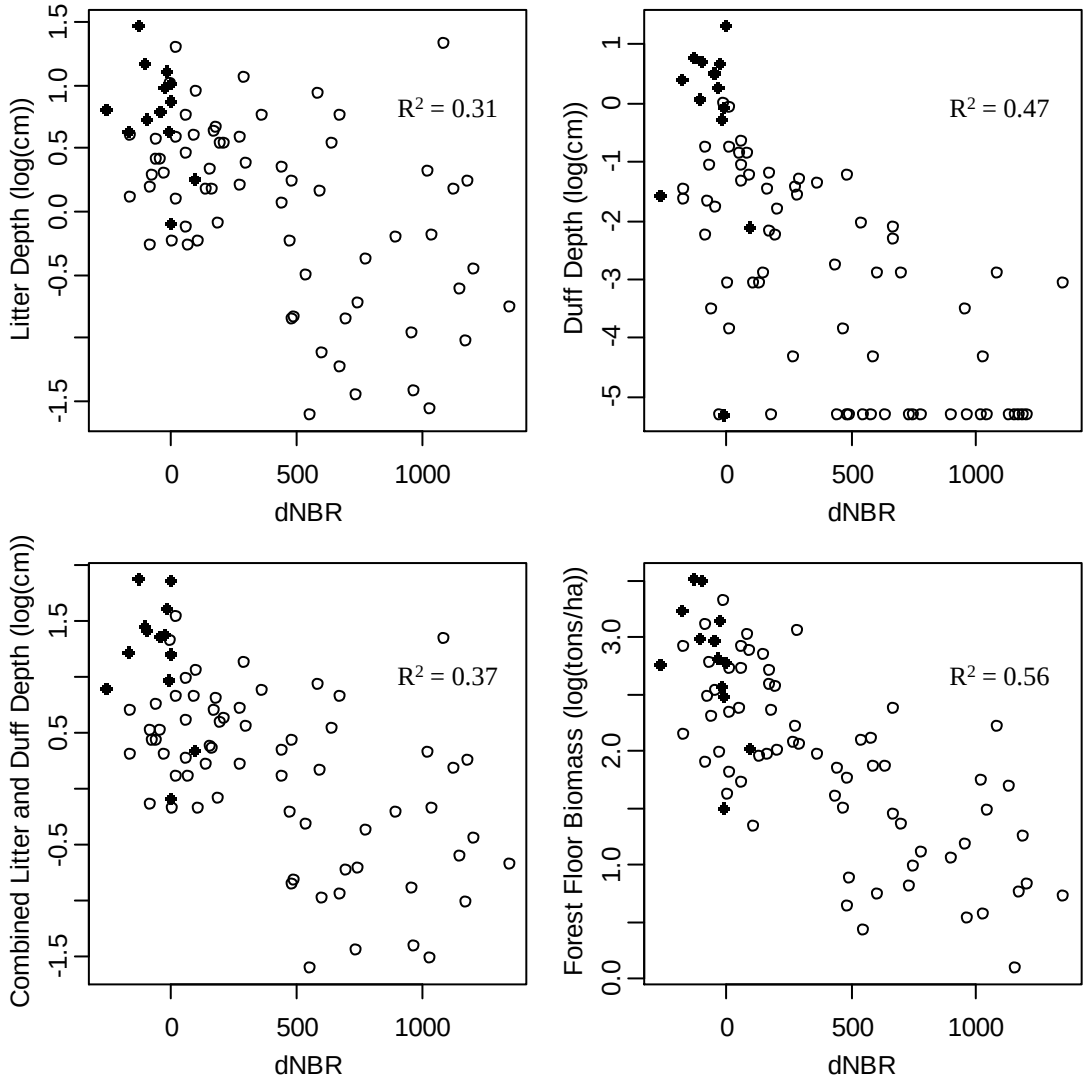
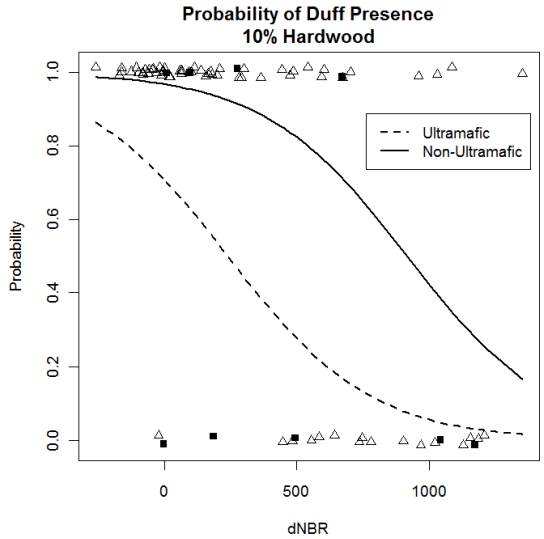
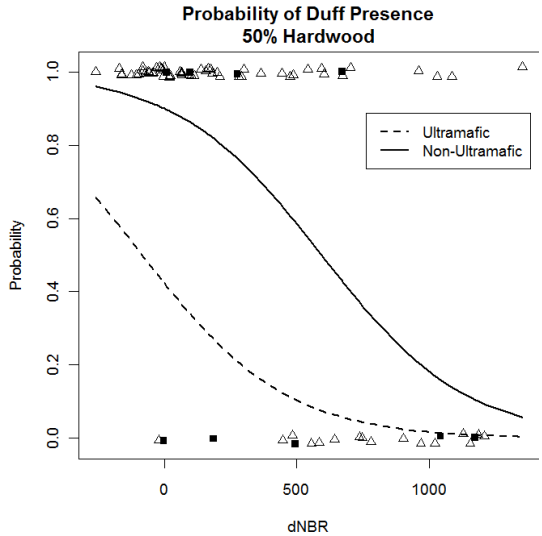


Figure 2.3: Scatterplots for fuel classes that show a strong correlation with dNBR. Forest floor biomass includes litter, duff and 1-hour fuels. Closed circles denote sites not burned in the Biscuit Fire. Higher dNBR values denote higher burn severity.





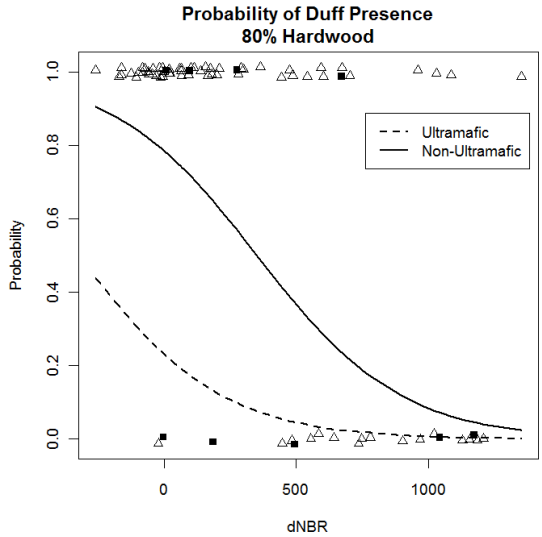


Figure 2.4: Probability of duff presence as a function of burn severity. Note that the probability of duff presence drops off more quickly as hardwoods make up a higher proportion of the site. Black squares denote ultramafic sites, white triangles denote non-ultramafic sites. Site symbols are jittered for better visibility.

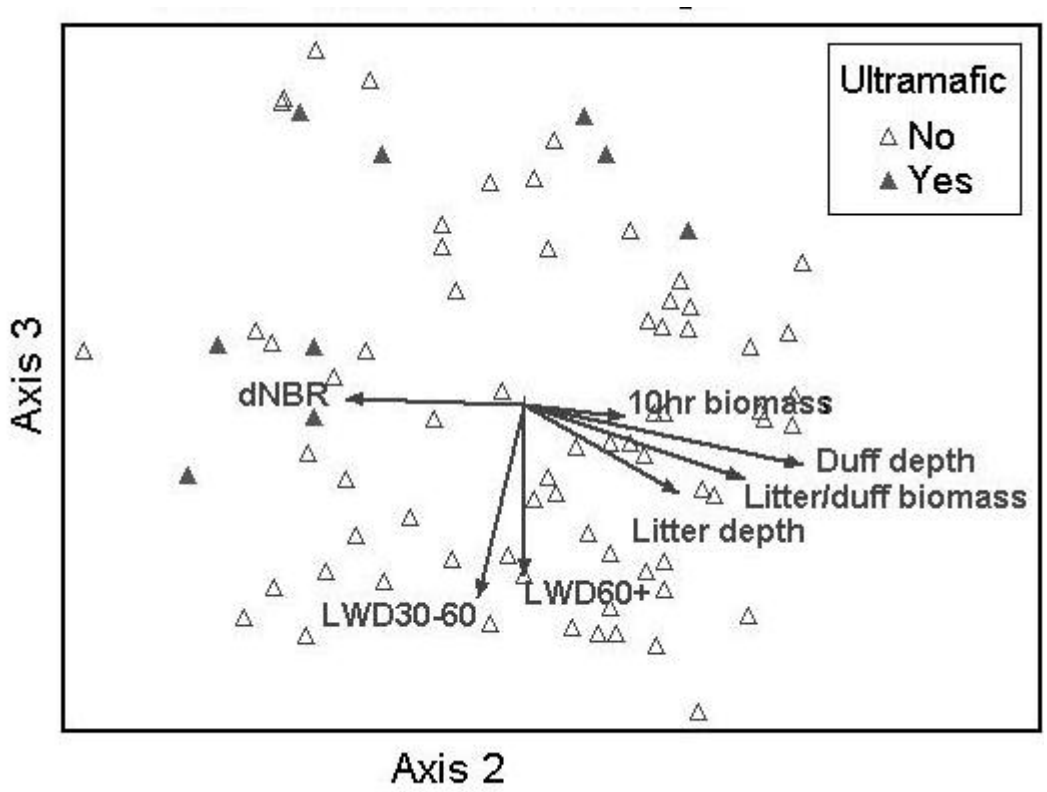


Figure 2.5: Joint plot of NMS fuels ordination. Axes 2 and 3 represent 83% of the variance in fuels. Triangles represent plots in fuels space. Correlations less than 0.2 are not shown. dNBR was the only environmental variable with a correlation greater than 0.2, see Table 2.6 for the full list of environmental variable correlations.

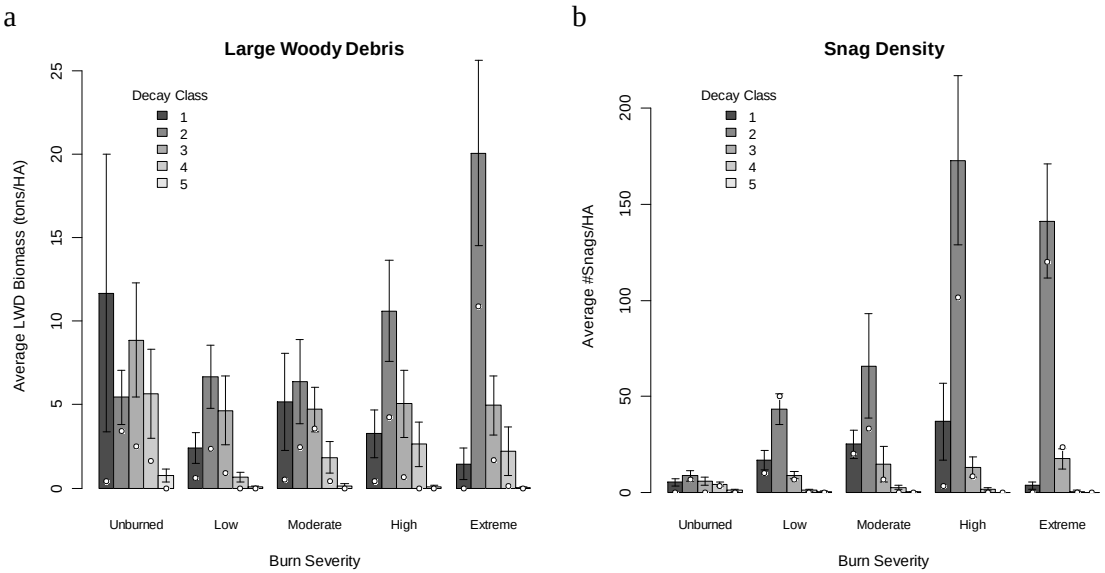


Figure 2.6: Distribution of LWD (a) and large snags (b) based on burn severity and decay classes. Burn severity is based on dNBR values, and represents an estimate of crown mortality, low: 0-35% (n = 21), moderate: 35-65% (n = 13), high: 65-95% (n = 18), extreme >95% (n = 13). Unburned measurements were collected outside the Biscuit Fire boundary (n = 13). LWD consists of logs >7.62 cm in diameter, snags are ≥15 cm DBH. Error bars denote 1 standard error, white dots denote median values. Mean value for severity class 1 LWD on unburned sites is skewed by a single site that had four unusually large logs (diameters 64 cm, 64 cm, 78 cm, 83 cm). This site may have recently experienced a windthrow event. Average biomass for decay class 1 LWD without that site was 3.8 tons/HA.

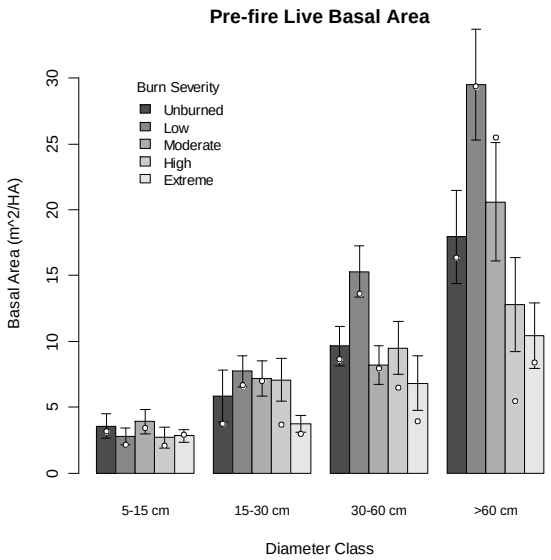


Figure 2.7: Pre-fire live-tree basal area by size class. Sites that experienced lower fire severity had higher basal area in the largest size classes. See Figure 2.6 for details on burn severity classes.

Table 2.1: Summary of fuel quantities and analysis techniques by class. MLR: Multiple linear regression, LR: logistic regression. Total forest floor depth and total LWD were not used in the NMS analysis.

Variable	Nonzero Sites	Mean	Median	Range	Std. Dev	Analysis Method
Litter depth (cm)	78	1.5	1.3	0.2 - 4.3	0.90	MLR
Duff depth (cm)	57	0.3	0.1	0 - 3.7	0.62	LR
Forest floor depth (Litter+duff, cm)	78	1.8	1.4	0.2 - 6.5	1.37	MLR
Forest floor biomass (litter/duff/1-hr fuels, tons/ha)	78	10.11	7.70	1.11 - 33.57	7.52	MLR
10-hr fuels (tons/ha)	78	2.99	2.71	0.67 - 6.63	1.27	MLR
100-hr fuels (tons/ha)	78	4.92	4.39	0.42 - 13.58	2.75	MLR
LWD 7.62-30 cm (tons/ha)	77	7.62	4.96	0 - 49.49	8.94	MLR
LWD 30-60 cm (tons/ha)	46	7.18	2.73	0 - 48.21	10.18	LR
LWD >60 cm (tons/ha)	25	7.33	0	0 - 124.85	16.68	LR
Total LWD (tons/ha)	77	22.12	13.81	0 - 153.59	24.11	MLR

Table 2.2: Potential explanatory variables used in stepwise model selection.

Variable	Description
dNBR	dNBR values
beersxform	Aspect cosine-transformed to be between 0 and 2 (Beers 1966)
elevation	Elevation (m)
slope_pct	Slope (percent)
TPI150_300	Fine topographic position index (annulus 150 m-300 m)
TPI850_1K	Coarse topographic position index (annulus 850 m-1km)
total_BA	Pre-fire live tree basal area as calculated from plot data
total_BA_HW	Total pre-fire live hardwood basal area, as calculated from plot data
pct_HW	Percent pre-fire hardwood basal area, as calculated from plot data
PPT71TO00[1]	Average precipitation 1971-2000
DECMN71_00[1]	Average minimum December temperature 1971-2000
AUGMX71_00[1]	Average maximum August temperature 1971-2000
isUltramafic	Ultramafic soils (yes or no)
isSilver	Site was also burned in the Silver Fire burn (yes or no)
isUnburned	Site was outside Biscuit Fire perimeter (yes or no)

Potential interaction terms: dNBR*isUltramafic, dNBR*isSilver, dNBR*Total_BA, dNBR*beersxform,

[1]Climate information downloaded from http://www.prism.oregonstate.edu/ (Daly et al. 2002).

Table 2.3: Best models from stepwise selection of multiple linear regression of dead fuel classes based on burn severity, biotic, abiotic, and climatic variables. ΔAIC represents the difference between the final model AIC value and the intercept-only model AIC value.

Fuel Variable	Variable	Partial R^2	Regression Equation	Std. Error	Model adjusted-R^2	ΔAIC
Litter depth: ln(cm)	dNBR	0.18	0.26 - 0.00081(dNBR)	0.00017	0.42	38.84
	pct_HW	0.060	+ 0.79(pct_HW)	0.28		
	isUnburned	0.038	+ 0.42(isUnburned)	0.19		
	isUltramafic	0.028	- 0.40(isUltramafic)	0.20		
Combined litter and duff depth: ln(cm)	dNBR	0.18	0.40 - 0.00092(dNBR)	0.00017	0.52	53.35
	pct_HW	0.050	+ 0.82(pct_HW)	0.29		
	isUnburned	0.077	+ 0.67(isUnburned)	0.19		
	isUltramafic	0.036	- 0.50(isUltramafic)	0.21		
Combined litter and duff biomass (includes 1-hr fuels): ln(tons/ha)	dNBR	0.38	5.44 – 0.0013(dNBR)	0.00015	0.63	73.68
	pct_HW	0.044	+ 0.79 (pct_HW)	0.26		
	AUGMX71_00	0.045	- 0.0010(AUGMX71_00)	0.00034		
	slope_pct	0.017	- 0.0069(slope_pct)	0.0037		
	isUnburned	0.015	+ 0.30(isUnburned)	0.17		
10-hour fuels biomass: (tons/ha)	Total_BA	0.13	9.08 + 0.025(Total_BA)	0.0062	0.34	28.69
	AUGMX71_00	0.10	- 0.0023(AUGMX71_00)	0.00067		
	slope_pct	0.030	- 0.014(slope_pct)	0.0076		
	isUltramafic	0.019	- 0.60(isUltramafic)	0.41		
100-hour fuels biomass: ln(tons/ha)	isUltramafic	0.10	2.09 - 0.63(isUltramafic)	0.21	0.10	6.63
	PPT71TO00	0.043	- 2.92e-06(PPT71TO00)	1.52e-06		

(continued)

(Table 2.3 continued)

Fuel Variable	Variable	Partial R^2	Regression Equation	Std. Error	Model adjusted-R^2	ΔAIC
LWD 7.62-30 cm: ln(tons/ha)	slope_pct	0.071	2.13 - 0.014(slope_pct)	0.0055	0.12	7.01
	beersxform	0.050	+ 0.26(beersxform)	0.12		
	dNBR	0.035	+ 0.00035(dNBR)	0.00020		
Total LWD: ln(tons/ha)	Elevation	0.14	13.88 - 0.0034(Elevation)	0.00091	0.20	13.95
	beersxform	0.088	+ 0.45(beersxform)	0.15		
	AUGMX71_00	0.082	- 0.0032(AUGMX71_00)	0.0011		
	dNBR	0.038	+ 0.00049(dNBR)	0.00025		

Table 2.4: Best models for stepwise selection of logistic regression. ΔAIC represents the difference between the final model AIC value and the intercept-only model AIC value.

Fuel Variable	Regression Equation	Pseudo R^2	ΔAIC
Duff	logit(p) = 3.68 -0.0037(dNBR) -2.50(isUltramafic) - 2.98(pct_HW) Std. error: dNBR (0.00091), isUltramafic (1.02), pct_HW (1.36)	0.51	27.64
LWD 30-60 cm	logit(p) = 0.54 - 0.0052 (TPI850_1K) Std. error: TPI850_1K (0.0025)	0.08	2.67
LWD >60 cm	logit(p) = -2.21 - 0.0079(TPI850_1K) + 0.032 (slope_pct) Std. error: TPI850_1K (0.0029), slope_pct (0.018)	0.21	8.47

Table 2.5: Fuel correlation scores with NMS ordination of fuel classes. Axis 1 accounts for 9% of the total variance, axis 2 44%, and axis 3 39% (total variance, 91%). All axes were orthogonal or nearly orthogonal: axis 1 vs. 2, 100%; 1 vs. 3, 99.1%; axis 2 vs. axis 3, 98.0%.

Axis:	1			2			3		
	r	R^2	tau	r	R^2	tau	r	R^2	tau
Litter depth (cm)	0.11	0.01	0.09	0.66	0.43	0.50	-0.50	0.25	-0.31
Duff depth (cm)	0.02	0	-0.01	0.88	0.77	0.71	-0.41	0.17	-0.28
Biomass litter/duff/1-hr fuels	0.10	0.01	0.07	0.79	0.62	0.58	-0.45	0.21	-0.29
Biomass 10-hr fuels	0.40	0.16	0.30	0.53	0.28	0.33	-0.18	0.03	-0.07
Biomass 100-hr fuels	0.42	0.18	0.28	0.14	0.02	0.10	-0.33	0.11	-0.21
Biomass LWD 7.62-30 cm	0.67	0.45	0.50	-0.20	0.04	-0.14	-0.20	0.04	-0.13
Biomass LWD 30-60 cm	0.17	0.03	0.07	-0.36	0.13	-0.27	-0.73	0.53	-0.57
Biomass LWD >60 cm	-0.62	0.38	-0.50	0.05	0.00	0.01	-0.69	0.47	-0.56

Table 2.6: Environmental variable correlations with NMS ordination of fuel classes. See Table 2.2 for explanations of variable names.

Axis:	1			2			3		
	r	R^2	tau	r	R^2	tau	r	R^2	tau
dNBR	-0.004	0	-0.054	-0.704	0.495	-0.466	0.139	0.019	0.126
beersxform	0.057	0.003	-0.001	0.192	0.037	0.141	-0.248	0.062	-0.179
elevation	0.115	0.013	0.087	0.235	0.055	0.164	0.191	0.036	0.152
slope_pct	-0.313	0.098	-0.224	-0.127	0.016	-0.04	-0.025	0.001	-0.011
total_BA	0.102	0.01	0.077	0.42	0.177	0.259	-0.286	0.082	-0.16
total_BA_HW	0.064	0.004	0.007	0.127	0.016	0.063	-0.128	0.016	-0.195
pct_HW	0.03	0.001	-0.013	-0.036	0.001	-0.005	-0.166	0.028	-0.192
TPI150_300	0.046	0.002	0.059	0.053	0.003	0.063	0.253	0.064	0.179
TPI850_1K	0.16	0.026	0.107	-0.038	0.001	0.008	0.352	0.124	0.245
PPT71TO00	-0.072	0.005	-0.059	-0.143	0.02	-0.092	0.226	0.051	0.141
DECMN71_00	-0.08	0.006	-0.06	-0.019	0	-0.01	-0.025	0.001	-0.032
AUGMX71_00	-0.138	0.019	-0.116	-0.189	0.036	-0.11	-0.017	0	-0.037

Table 2.7: MRPP comparisons of fuel composition based on soil type and fire history. "A" is the chance-corrected within-group agreement statistic, a measure of within-group similarity ranging from 0 to 1.

	A	p-value
Soil Type LI only (Biscuit Fire):		
Ultramafic vs non-ultramafic	0.037	0.0038
Fire history, all fuel types:		
SI vs. LI	-0.0036	0.60
SI vs. Unburned	0.14	< 0.0001
LI vs. Unburned	0.066	< 0.0001
Fire History, no litter depth, duff depth, or forest floor biomass:		
SI vs. LI	-0.0026	0.50
SI vs. Unburned	-0.0016	0.41
LI vs. Unburned	-0.0036	0.54

APPENDICES

Appendix A: Linear regression models considered.

Final models are marked with a star. Final models were selected based on explanatory power, parsimony, and ecological significance of the selected variables. ΔAIC represents the difference in AIC values between the stated model and the null (naive) model.

Fuel type/models considered:	ΔAIC	Adj R-sq
Litter depth: ln(cm)		
dNBR	26.70	0.299
dNBR + pct_HW	34.68	0.375
dNBR + pct_HW + isUnburned	36.91	0.400
* dNBR + pct_HW + isUnburned + isUltramafic	38.84	0.421
dNBR + pct_HW + isUnburned + isUltramafic + AUGMX71_00	39.15	0.430
Combined litter and duff depth: ln(cm)		
dNBR	33.56	0.358
dNBR + pct_HW	41.29	0.426
dNBR + pct_HW + isUnburned	49.39	0.489
* dNBR + pct_HW + isUnburned + isUltramafic	53.35	0.520
dNBR + pct_HW + isUnburned + isUltramafic + AUGMX71_00	53.68	0.527
Combined litter and duff biomass (includes 1-hr fuels): ln(tons/ha)		
dNBR	62.19	0.555
dNBR + pct_HW	64.26	0.572
dNBR + pct_HW + AUGMX71_00	70.73	0.611
dNBR + pct_HW + AUGMX71_00 + slope_pct	72.26	0.623
* dNBR + pct_HW + AUGMX71_00 + slope_pct + isUnburned	73.68	0.634
dNBR + pct_HW + AUGMX71_00 + slope_pct + isUnburned + isUltramafic	73.94	0.640
10-hour fuels biomass: (tons/ha)		
Total_BA	17.42	0.210
Total_BA + AUGMX71_00	27.20	0.312
Total_BA + AUGMX71_00 + slope_pct	28.40	0.331
* Total_BA + AUGMX71_00 + slope_pct + isUltramafic	28.69	0.341
Total_BA + AUGMX71_00 + slope_pct + isUltramafic + PPT71TO00	29.65	0.357
100-hour fuels biomass: ln(tons/ha)		

isUltramafic	4.91	0.073
* isUltramafic + PPT71TO00	6.63	0.104
isUltramafic + PPT71TO00 + slope_pct	6.79	0.117
LWD 7.62-30 cm: ln(tons/ha)		
slope_pct	4.56	0.069
slope_pct + beersxform	5.82	0.095
* slope_pct + beersxform + dNBR	7.01	0.119
slope_pct + beersxform + dNBR + TPI150_300	7.12	0.131
Total LWD: ln(tons/ha)		
TPI150_300	5.66	0.082
TPI150_300 + beersxform	6.84	0.106
TPI150_300 + beersxform + dNBR	8.93	0.141
TPI150_300 + beersxform + dNBR + PPT71TO00	9.94	0.162
TPI150_300 + beersxform + dNBR + PPT71TO00 + isUltramafic	10.55	0.178
TPI150_300 + beersxform + dNBR + PPT71TO00 + isUltramafic + dNBR:isUltramafic	10.56	0.188
TPI150_300 + beersxform + dNBR + PPT71TO00 + isUltramafic + Elevation + dNBR:isUltramafic	10.69	0.198
TPI150_300 + beersxform + dNBR + PPT71TO00 + isUltramafic + Elevation + AUGMX71_00 + dNBR:isUltramafic	12.04	0.221
beersxform + dNBR + PPT71TO00 + isUltramafic + Elevation + AUGMX71_00 + dNBR:isUltramafic	12.78	0.220
beersxform + dNBR + PPT71TO00 + isUltramafic + Elevation + AUGMX71_00	13.48	0.218
beersxform + dNBR + isUltramafic + Elevation + AUGMX71_00	13.52	0.209
* beersxform + dNBR + Elevation + AUGMX71_00	13.95	0.204

Appendix B: Logistic regression models considered

Final models are marked with a star. Final models were selected based on explanatory power, parsimony, and ecological significance of the selected variables. ΔAIC represents the difference in AIC values between the stated model and the null (naive) model. Note, "isUltramafic" was not considered as a potential variable for LWD >60 cm, as LWD was not present on any ultramafic sites in that size class. Some ultramafic sites had LWD close to that size class (54-58 cm)

Fuel type/models considered:	ΔAIC	Pseudo R-sq
Duff		
dNBR	22.77	0.395
dNBR + isUltramafic	24.6	0.446
* dNBR + isUltramafic + pct_HW	27.64	0.509
dNBR + isUltramafic + pct_HW + isSilver	28.21	0.54
LWD 30-60 cm		
* TPI850_1K	2.67	0.078
TPI850_1K + Total_BA_HW	3.08	0.117
LWD >60 cm		
TPI850_1K	7.05	0.153
* TPI850_1K + slope_pct	8.47	0.207
TPI850_1K + slope_pct + beersxform	8.49	0.237

CHAPTER 3: ASSOCIATION OF TREE REGENERATION AND UNDERSTORY VEGETATION WITH FIRE SEVERITY FOLLOWING A MIXED-SEVERITY WILDFIRE IN THE KLAMATH-SISKIYOU MOUNTAINS OF SOUTHWEST OREGON

ABSTRACT

The mixed-evergreen forests of the Klamath Siskyous have a long history of large, mixed-severity fires, but factors influencing post-fire vegetation succession are poorly understood. Most work in this region has concentrated on the impacts of high-severity fire, ignoring ecological effects of low- and moderate-severity areas, which may account for over half the landscape affected by fire disturbance. In an effort to understand vegetation response to different fire severities, I examined the abundance and composition of tree seedlings, shrubs, and ground cover six years after the 2002 Biscuit Fire, a large, mixed-severity fire that occurred in the Klamath-Siskiyou Mountains of southwestern Oregon and northern California. This fire also completely encompassed the area burned by the 1987 Silver Fire, which also burned in a mosaic of burn severities. My research was guided by three questions: 1) how does seedling density vary in relation to fire severity? 2) Do ground cover and shrub composition differ in relation to burn severity and geology? 3) Do live fuel quantities differ in relation to burn severity? I used the differenced Normalized Burn Ratio (dNBR), which compares pre- and post-fire Landsat imagery, as my measure of burn severity. Seedling and understory vegetation data were collected on 78 plots, that spanned the full range of burn severities as well as unburned areas just outside the Biscuit Fire boundary.

Generally density for tree seedlings <0.5 m was highest on low-severity sites and lowest on high-severity sites. For seedlings 0.5-1.37 m the relationship was reversed, with the highest seedling densities in high-severity areas. Seedling relationships to burn severity and other explanatory factors varied by species and seedling height. Average seedling densities

were above the minimum acceptable stocking levels of 333 trees per hectare (135 seedlings/acre) that was goal of federal managers following the fire.

Shrub species richness and diversity did not vary with burn severity; however, shrub species and ground cover composition did differ with burn severity six years after the Biscuit Fire. The relationship of understory cover composition with burn severity aligned with species life history traits; fire-adapted, nitrogen-fixing species were more prevalent on high- and extreme-severity sites while species associated with low-severity fire or old-growth forests were more prevalent on low-severity or unburned sites. I found no evidence of difference in total graminoid or forb cover based on fire severity, but shrub quantities were lower on low-severity sites than on unburned, high-, extreme-severity sites.

INTRODUCTION

The mixed-evergreen forests of the Klamath Siskyous have a long history of large, mixed-severity fires (Agee 1993, Taylor and Skinner 1998, 2003). Despite this history, the factors governing fire severity and the ecological effects across all levels of fire severities remain poorly understood. Most work in this region has concentrated solely on the impacts of high-severity fire, ignoring ecological effects of low- and moderate-severity areas (Donato et al. 2006, Shatford et al. 2007, Donato et al. 2009b, Donato et al. 2009c). Though concern about high severity areas is understandable, it is not possible to evaluate ecological responses and future fire behavior of the entire fire mosaic without knowledge of conditions in low- and moderate-severity patches. In the 2002 Biscuit Fire, 54% of the more than 200,000 hectares that burned experienced less than 65% crown mortality. Low- and moderate-severity fires may have limited impact on canopy trees, but the effects on understory vegetation, dead surface fuels, and soils may be substantial. Additionally, ignoring the fire effects on over half the

landscape precludes understanding how areas of different burn severity interact and impact future succession and fire effects. In an effort to understand the effects of burn severity on forest succession I examined the abundance and composition of tree seedlings, shrubs, and ground cover six years after the Biscuit Fire. My research was guided by three major questions.

1) How does seedling density vary in relation to fire severity?

Studies quantifying regeneration in the mixed-evergreen forests of the Klamath-Siskiyous have concentrated on the high-severity areas of fires (Shatford et al. 2007, Donato et al. 2009b). Seedling establishment continues at least one to two decades after high-severity fire (Shatford et al. 2007). Within the Biscuit Fire boundary conifer regeneration was high up to 400 m from a contiguous seed source, a distance threshold met by 80% of high-severity areas (Donato et al. 2009b). Studies that looked at seedling responses to different burn severities found different relationships based on life history traits, fire regime, and seedling size (e.g. Chappell and Agee 1996, Larson and Franklin 2005, Lentile et al. 2005, Keyser et al. 2008), though no such studies have been conducted within the Biscuit Fire boundary until now. In addition to understanding if seedling density relates to fire severity six years post-fire, I also wished to determine 1) if seedling density varies by species, 2) if species density varies by size class, and 3) what other biotic and abiotic factors are most effective at predicting seedling density. Answers to these questions will provide a framework for understanding and predicting future forest succession across a landscape.

2) Does ground cover and shrub composition differ in relation to burn severity and geology?

Donato et al. (2009c) looked at species diversity on high-severity portions of the Biscuit Fire where there had been a long interval since a prior burn (>100 years before the Biscuit Fire), and compared species diversity to sites that had burned 15 years earlier in the 1997 Silver Fire (short interval burn), and also to undisturbed old-growth forests in adjacent areas (no high severity fires in >100 years). They found that total vegetation cover was highest in short-interval (SI) burn areas, that species richness was higher in the SI burn than on the long-interval (LI) or old-growth sites, and that though there were no significant differences between the LI and old-growth sites, both were significantly different from the composition of the SI sites. This study will consider four questions regarding ground cover and shrub composition across the full range of fire severities in the Biscuit Fire: 1) Do shrub species richness and diversity differ with burn severity? 2) Do shrub composition and ground cover type differ with burn severity? 3) Do shrub composition and ground cover type vary between SI sites, LI sites, and unburned sites? 4) Do shrub composition and ground cover differ between sites on ultramafic and non-ultramafic soils after a fire disturbance? The first two questions will tease apart potential differences between species richness/diversity metrics and composition differences based on burn severity. The third question addresses potential impacts of multiple fire disturbances in a short time frame on community composition. Unlike the Donato study, this question answers whether composition differs across the entire affected area, rather than just high severity areas, and will provide a better understanding of the overall impact of multiple fire disturbances in a mixed-severity fire regime. The fourth question investigates whether ultramafic sites retain (or return to) their unique plant communities six years after a fire disturbance, or if fire eliminates differences in plant composition between

areas with different soil types. (Ultramafic sites were not considered in the Donato et al. (2009c) study.)

3) Do live understory fuel quantities differ in relation to burn severity?

Fire spread models consider two classes of live fuels: herbaceous and woody. Herbaceous fuels include annual grasses, perennial grasses, and forbs. Woody fuels include deciduous and evergreen shrubs and small trees up to 1.83 m high (Albini 1976, Anderson 1982, Rothermel 1983, Scott and Burgan 2005). The relationship of live fuels to fire severity is poorly understood (Burgan 1979, Jolly 2007, Weise and Wotton 2010). Live fuels may have a dampening effect on fire when moisture content is high, but may ignite due to drought or desiccation from fire, rapidly and drastically increasing fire severity (Burgan 1979, Weise et al. 2005). Several studies have pointed to live fuels as an important contributing factor for high-severity fires. Odion et al. (2004) found that areas that had not burned in 60 or more years experienced lower proportions of high-severity fire than areas that had burned more recently. They hypothesized the reason these areas burned at lower severities was due to lower shrub quantities and less flammable shrub species growing under closed canopies. Thompson et al. (2007) found areas that burned at high severity in the 1987 Silver Fire were more likely to reburn at high severity in the 2002 Biscuit Fire. They found that the high severity areas tended to have high shrub cover, or dense regenerating conifer plantations. Both of these studies based their conclusions on remotely-sensed data. I tested for differences in graminoid cover, forb cover, and shrub quantities in relation to burn severity using plot data, which allowed me to directly test for differences in live fuel quantities and composition. Higher quantities of live fuels could be a potential explanatory variable for future burn severity.

METHODS

Study area

In 2002, fires from five ignitions in the Siskiyou National forest between July 13th and 15th converged in the following weeks to create the Biscuit Fire complex (GAO 2004). The fire was declared controlled on November 8, 2002 but was not declared extinguished until December 31, 2002. In total 202,328 hectares burned, 94% of which were on the Rogue-Siskiyou National Forest in southwestern Oregon, 4% on the Six Rivers National Forest in Northern California, and 2% on Bureau of Land Management land. Additionally, 72,000 hectares of the Kalmiopsis Wilderness burned (USDA Forest Service 2004). The landscape burned in a mosaic of different burn severities: 17% of the area experienced 0-5% crown mortality, 14% experienced 5-35% crown mortality, 23% experienced 35-65% crown mortality, 27% experienced 65-95% crown mortality, and 19% experienced greater than 95% crown mortality (Thompson 2008). Only 10% of the landscape experienced complete crown mortality. Tree damage also varied based on conifer diameter and understory composition; conifer mortality was negatively correlated with tree size and positively correlated with understory shrub cover (Thompson and Spies 2009). Surface effects of the fire were extensive and variable: the fire consumed 70-100% of the litter layer and 40-100% of the duff layer within the fire boundary (Campbell et al. 2007). The Biscuit Fire completely encompassed the 40,000 hectares burned in the 1987 Silver Fire, which also burned with a mosaic of fire severities (Atzet et al. 1988, USDA Forest Service 1988). Post-fire salvage logging took place on approximately 1850 ha of the Biscuit Fire (<1%), and at least 800 ha of the Silver Fire (~2%), but those areas were excluded from this study (USDA Forest Service 1988, USDA Forest Service 2004).

The Biscuit Fire area is geologically and floristically diverse, with a rugged topography and a steep climatic gradient (Whittaker 1960). This diversity is likely due in part to its geologic history and the orientation of the mountain ranges. The Siskiyous form a high-elevation east-west land bridge between the north-south Coast and Cascade ranges, allowing movement of species along a marine to inland gradient (Agee 1998).

The climate is predominantly Mediterranean, though it is modified by marine influences up to 80km inland (Whittaker 1960, Atzet and Martin 1992). Average annual precipitation is 240 cm/year, only 8% of which falls from June through September. Average minimum temperature in December is 1.4˚C and average maximum July temperature is 27.4˚C (Daly et al. 2002). The Klamath Province is subject to both cold storms from northern latitudes and tropical storms from southern latitudes (Atzet and Wheeler 1982).

The study area is in the "mixed evergreen" forest zone, with a typical overstory of evergreen needle-leaved trees and an understory of sclerophyllous broadleaf vegetation. This forest type is dominated by Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Lithocarpus densiflorus*) but may also include conifers such as sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and incense-cedar (*Calocedrus decurrens*), and hardwoods such as Pacific madrone (*Arbutus menziesii*) and giant chinquapin (*Chrysolepis chrysophylla*). Huckleberry oak (*Quercus vaccinifolia*) and manzanita (*Arctostaphylos* spp.)are often present in the shrub layer (Franklin and Dyrness 1988). The short-lived and strictly serotinous knobcone pine (*Pinus attenuata*), may be found on sites that experienced recent crown fires (Franklin and Dyrness 1988, Atzet and Martin 1992).

This study also includes sites on serpentine soils. These soils, derived from ultramafic rock, support a unique plant community with a wide variety of endemic species. Non-endemic

species growing on serpentine soils tend to have a stunted or depauperate appearance (Franklin and Dyrness 1988) due to high concentrations of Mg, Ni, and Cr in the soil (White 1971).. Tree cover is sparse, and is generally dominated by a mixture of conifers including Jeffrey pine (*Pinus jeffreyi*). Understory plant communities include open grassy areas, or a patchwork of shrubs and herbaceous cover depending on elevation, moisture, and seral stage (Franklin and Dyrness 1988).

The fire regime in the Klamath-Siskiyous of southwest Oregon is complex and not well understood. Estimated mean fire return intervals range from 10-50 years, and in general fire frequency increases from west to east and with increasing elevation (Atzet and Wheeler 1982, Atzet and Martin 1992, Agee 1993). Lightning strikes are common in this region and provide ample sources of ignition for almost any location (Atzet and Wheeler 1982, Agee 1993). Though the Biscuit Fire was the largest in the state's recorded history (GAO 2004), the Klamath Siskiyous of southwest Oregon have a history of large fires: 72,400 hectares burned in 1917, 61,500 hectares burned in 1918, and 20,500 hectares burned in 1938 (Cooper 1939, Atzet et al. 1988, USDA Forest Service 1988). Prior to Fire was also likely used by Native Americans to foster the growth of early seral species used for food and as forage for desired animal species. In some areas fires may have been set as often as annually (Lewis 1989). Though fire suppression efforts have decreased the frequency of fire disturbance in this area in the latter half of the 20th century, there are historical precedents for fire-free periods of a century or more over the past two millennia (Colombaroli and Gavin 2010).

The historical fire regime for this area is classified as "mixed severity" (Agee 1993), but historical proportions of low, medium and high severity burns, as well as their spatial configurations and extents, are unknown. Studies in the northern California range of the

Klamath-Siskiyous show that the majority of fires were low- to moderate-severity (Taylor and Skinner 1998, 2003). However, it is unclear how applicable this fire regime is to the Klamath-Siskiyou Mountains in Oregon, due to differences in climate, topography and vegetation. It is also unclear how changes in fuel amounts due to fire suppression have affected the fire regime in this region, and how to best address the impacts of fire exclusion (Brown et al. 2004, Noss et al. 2006). Fire suppression may change future stand dynamics and structure. Understory vegetation may have been lower due to more frequent fires prior to fire suppression in the 1920s. Less understory vegetation may have lead to lower tree densities and higher diameter growth rates. In the Siskiyou Mountains, diameter growth of 50 year old trees was higher in old-growth stands (>250 year-old) than young stands (<100 year-old) (Sensenig 2002). However, long periods of fire absence do not necessarily correlate with higher proportions of high-severity fire (Odion et al. 2004, Odion et al. 2010), and in areas that burned in both the Biscuit and Silver Fires, areas that burned at high severity tended to reburn at high severity (Thompson et al. 2007), implying that long-term fuel buildup is not necessarily the primary factor in predicting high-severity fire.

Site selection

Study sites were chosen using a stratified random sample based on three strata: burn severity, elevation (above or below 914 m), and parent material (ultramafic or non-ultramafic.) Study sites were confined to the northeast section of the Biscuit Fire, where LiDAR imagery had been collected.

I used the differenced Normalized Burn Ratio (dNBR) as my measure of fire severity (Thompson 2008). This metric uses Landsat TM/ETM+ data to calculate the pre- to post-fire difference of near-infrared (band 4) and mid-infrared (band 7) reflectance ratios. Band 4

corresponds to leaf area and plant productivity, and band 7 changes based on soil reflectance and moisture content (Lutes et al. 2006). This method provides a quick and relatively accurate way of measuring burn severity in the forest canopy layer (Miller and Yool 2002, Brewer et al. 2005).

Seventy-eight sites were sampled: 13 unburned, 21 low-severity, 13 moderate-severity, 18 high-severity, and 13 extreme-severity (Figure 3.1). Nine ultramafic were selected based on the USDA Soil Survey Geographic (SSURGO) database (USDA 2008), however field observation and orthophotos showed that one of these sites was not ultramafic, so it was reclassified as non-ultramafic during data analysis. Fifteen of the selected sites also burned in the 1987 Silver Fire.

Only areas greater than 50 m and less than 500 m from a road were considered for sampling. The 50 m distance was intended to limit human influence (such as the harvesting of roadside “hazard trees”). The 500 m limit was a compromise between site accessibility and full coverage of the sample area. Without this constraint the steep and challenging terrain may have significantly lowered the potential sample size due to the time and effort required to access a site. To create potential sample locations, the dNBR value from each 30 m pixel was assigned to one of five severity classes: unburned, low (0-35% canopy mortality), moderate (35-65% canopy mortality), high (65-95% canopy mortality), and extreme (95-100% canopy mortality) (Thompson 2008). The dNBR raster was smoothed using ArcGIS FOCALMEAN with an 80 m (2 ha) radius; each pixel was assigned a classification if 75% or more of the surrounding pixels were in a given class (ESRI 2010). The 75% threshold was a tradeoff between burn severity purity in a patch, and having enough uniform patches from which to choose sites. The resulting “patches” of burn severity were exported as shape files and

potential sites were located in the centroid of each polygon. Some sites were discarded due to steep slope (>90%), or the presence of landslides or cliffs. Near the end of the season one north-facing site and five west-facing sites were selected to increase representation of those aspects.

Data collection

Field measurements were conducted during the summer of 2008. Each site consisted of three 0.1 ha plots (Figure 3.2). Plots were located using a Garmin 60CX GPS in combination with LiDAR images, aerial photos, and on-the-ground surveying. In each plot seedlings and ground cover were measured within four 2.5 m microplots, for a total of 12 microplots per site (Figure 3.2). Species and height class (short: <0.5 m or tall: 0.5-1.37 m) were collected for each seedling, and percent ground cover was collected for soil, rock, moss, graminoids, forbs, and bracken fern (*Pteridium aquilinum*). Bracken fern was considered separately due to its potential to dominate the understory community and a variety of ecological effects including allelopathy (Gliessman and Muller 1978), competition for tree regeneration (Dolling 1999, Royo and Carson 2006), and fuel for fire (Isaac 1940, Hall et al. 2003).

Percent cover, species, and maximum height were collected for all woody shrubs, though for the first two weeks (7 sites) 70% of maximum height was recorded for each species. Percent ground cover was estimated for each type/species separately, so total ground cover could potentially exceed 100%. In practice total ground cover was usually less than 100%, due to the presence of non-recorded cover types such as leaf-litter.

In each plot all trees and snags greater than 50 cm DBH (diameter at breast height, 1.37m) were measured within a 17.84 m horizontal radius (0.1 ha), all trees and snags 15-50

cm dbh were measured within a 12.61 m horizontal radius (0.05 ha), and all saplings 5-15 cm dbh were measured within the four 2.52 m (slope distance) microplots. Species were recorded for all live trees and snags when possible. Decay class and whether the Biscuit Fire was the cause of death for snags was recorded.

Data analysis

Seedling density

Seedling counts were aggregated for the entire site, then density was calculated using the total area sampled (Table 3.1, Table 3.2). Before calculating micoplot areas, the radius of each 2.5 m-radius (0.002 ha) microplot was adjusted based on the average slope of the three plot transects because they were not slope-corrected in the field. Seedling densities were calculated by life form (conifer/hardwood, seedling/sprout), and also by species. Tree regeneration was analyzed in three ways. First, site seedling densities were compared to the minimum seedling density objective of 333 seedlings/ha (135 seedlings/acre) 3-5 years post-fire as outlined in the Biscuit Fire Environmental Impact Statement (EIS) (USDA Forest Service 2004). Conifer seedlings <1.37 m high were considered, excluding seedlings designated as "seedling of the year." Knobcone pine (*Pinus attenuata*) seedlings were also excluded from this analysis, as they were not a species considered for reforestation efforts. Second, I calculated "stocking" for each site as the proportion of the twelve 0.002 ha (~0.005acre) microplots that contained at least one seedling, excluding knobcone pine and seedlings of the year. Stocking estimates the aggregation of conifer regeneration, as opposed to overall seedling density (USDI 2003). A site was considered 100% stocked if all twelve microplots contained at least one seedling. Minimum nonzero stocking was 8.3%. Third, I looked at whether variation seedling density could be modeled using burn severity, biotic,

abiotic and climatic factors. This analysis was performed for species occurring on at least 12 sites (>15%), as well as overall conifer and hardwood density. Seedlings and sprouts <0.5 m and 0.5-1.37 m were analyzed separately.

A total of 16 explanatory variables were considered for the seedling density analysis (Table 3.4). Elevation, slope, and aspect values were extracted to the three plots as based on their GPS locations and digital elevation models (DEM); values were then averaged to generate a site value. Aspect was cosine-transformed as described by Beers (1966), where zero corresponds to southwest slopes and two corresponds to northeast slopes. Continuous dNBR values were used for data analysis.

Three climatic indices were considered: average maximum August temperature, average minimum December temperature, and average yearly precipitation. These values represent potential heat-, cold- and drought-stress for the 2003-2007 growing seasons. All climate data were downloaded from the PRISM website (http://www.prism.oregonstate.edu/, (Daly et al. 2002)). Values were extracted to GPS plot locations, and then averaged to the site level.

To estimate seed availability, I calculated distance to clumps of live trees at least one hectare in size that encountered less than 65% crown mortality as estimated by dNBR. Shape files created by dNBR classification were compared to 0.5 m resolution digital orthophotos from 2005 (State of Oregon 2007) and LiDAR data (where available), and were edited as necessary. Once the potential seed-source areas were created, a raster containing distances to nearest live tree edge was created using the ArcGIS 9.3 Euclidean distance function (ESRI 2010). Raster distance values were extracted to each GPS plot location, and then averaged to the site level. Note that these calculations generally underestimated distance to nearest seed

source, as single or small clumps of surviving trees were often present even in extreme-severity areas.

Post-fire live basal area (LBA) and snag basal area were calculated using field measurements. Pre-fire hardwood basal area was estimated using the basal area of live trees and trees classified as killed by the Biscuit Fire. Ground cover percentages for exposed mineral soil, shrubs and bracken fern were calculated from field measurements and averaged to the site level. For the seedling density analysis, total cover of all shrub species was combined with bracken fern cover. For the other understory vegetation analyses individual shrub species and bracken fern were considered separately.

The relationship of seedling density to fire severity and other independent variables was analyzed using nonparametric multiplicative regression (NPMR) (McCune 2006) in HyperNiche 2.07 (McCune and Mefford 2009). NPMR seeks relationships between a response variable and one or more predictor variables. Unlike some analysis techniques which assume a given relationship between response and predictor variables (for example a linear response in linear regression) no prior relationships are assumed before analysis. NPMR also explicitly accounts for interactions between predictor variables which are inherent in ecological data. Relationships between the response and predictor variables are estimated using a multiplicative smoothing function and leave-one-out cross-validation to prevent overfitting.

The NPMR analysis was conducted using a Gaussian weighting function and a local mean model with a minimum average neighborhood size of 3.9 (5% of 78 sites). Model selection was conducted using a stepwise selection process regressing the predictors against seedling density, and model fit was evaluated using a cross-validated R^2 value. The cross R-squared value (xR^2) differs from a traditional R^2 value in that as the fit for each data point is

evaluated, that data point is excluded from the estimation of the overall fitted predictor values. Weak models may have a negative xR^2 value (Antoine and McCune 2004). Rather than coefficients, NPMR returns "tolerances", a measure of the standard deviations of the Gaussian kernels of the predictor variables. The effects of the predictor variables were assessed using McCune's (2009) Sensitivity 1 metric. This metric scales the change in the response variable to the change in the predictor variable. For example, a sensitivity value of 1.0 indicates that a 10% change in the predictor variable will result in a 10% change in the response variable. Final model significance was calculated using a randomization test with 200 data runs.

Analyses were conducted on both log-transformed and untransformed seedling densities. For each species/seedling type models with the highest xR^2 values were retained for final analysis. In cases where sites contained zero seedlings, 10 was added to all values before log-transforming as per the methods outlined in McCune and Grace (2002). This value was within the same order of magnitude of a single seedling found at a site. (A single seedling represented approximately 40 seedlings/ha.)

Shrub species diversity and understory cover composition

I investigated the effects of fire severity on shrub species diversity using four different diversity metrics: richness - total number of species found; evenness - H/ln(richness), where H represents Shannon's diversity index; Shannon's diversity index ($-\sum(p_i*\ln(p_i))$), and Simpson's diversity index ($1-\sum(p_i*p_i)$) where p_i is the relative abundance of each species, or the total abundance of species "i" divided by total abundance of all species. Percent cover data for all shrub species including rare species were considered for diversity analysis, though species that could only be identified to the genus level were not considered. PC-ORD 6 (McCune and Mefford 2010), was used to generate diversity metrics for each site. The

continuous dNBR values were binned into five burn severity classes using equations developed by Thompson (2008). The classes were: unburned (13 sites), low (0-35% canopy mortality, 21 sites), moderate (35-65% canopy mortality, 13 sites), high (65-95% canopy mortality, 18 sites), and extreme (95-100% canopy mortality, 13 sites). Potential differences for each diversity metric based on burn severity categories were analyzed using ANOVA, using the R stats package (R Development Core Team 2010).

The relationship of understory composition and ground cover to burn severity and other continuous environmental factors was analyzed using nonmetric multidimensional scaling (NMS) (Mather 1976) using PC-ORD 6 (McCune and Mefford 2010). NMS is a non-parametric ordination technique that attempts to find the best arrangement of *n* entities on *k* axes by minimizing stress. "Stress" is a measure of the departure from monotonicity of distance measures between entities in the original data set (with a dimensionality equal to the number of attributes in the data matrix) to the distance between entities as arranged on *k* axes. NMS avoids the assumption of linear relationships between variables, and ameliorates the "zero-truncation" problem, where species absence at a given environmental gradient gives no knowledge as to how unfavorable that environment is for that species. Unlike most other ordination techniques that minimize dimensionality by maximizing variance explained on each subsequent axis, the composition of each axis may differ based on the total number of axes in the final ordination. Additionally, axes may not be orthogonal to each other, though in practice they are usually close (McCune and Grace 2002).

In addition to shrub species, six general ground cover types: soil, rock, moss, graminoids, forbs and bracken fern, were included in the NMS analysis because they can be an important part of the biophysical structure of a site. Percent cover for the ground cover types

and all shrub species was averaged to the site level. Shrub species that were found on fewer than four sites (5% of all sites) were dropped from consideration, as were all shrub species that could only be identified to the genus level. A total of 39 shrub species plus the 6 ground cover types were analyzed in the NMS ordination. Average skewness for plots was 4.1; average skewness for species was 4.7. The coefficient of variation was 42.3% for sites and 189.5% for species. Despite high skewness and coefficient of variation for species, the data were not transformed or relativized. Log-transformation had little effect on the values, and relativization may hide important relationships. Though common or high-cover species may exact a high amount of influence on the ordination results, they also potentially have high influence on species current and future species composition. In order to better understand these influences data was not relativized or transformed.

Nine environmental variables were also investigated for correlations with the ordination axes. These variables were dNBR, aspect, elevation, percent slope, average precipitation, average maximum August temperature, average minimum December temperature, post-fire LBA, and total snag basal area. These environmental variables were the same as those used in the seedling analyses (Table 3.4). The NMS ordination was run using Sørensen distance. Calculations were made for a maximum of 6 axes, 500 maximum iterations, 250 runs with real data, and a random starting configuration.

After conducting the NMS ordination, I selected six shrub species for further analysis: deerbrush (*Ceanothus integerrimus*), snowbrush (*Ceanothus velutinus*), tanoak (*Lithocarpus densiflorus*), dwarf Oregon-grape (*Mahonia nervosa*), Pacific rhododendron (*Rhododendron macrophyllum*), and red huckleberry (*Vaccinium parvifolium*). These species all had high correlations with the NMS axis most highly correlated with dNBR and post-fire LBA. I used

the same variables used in the tree seedling analysis, excluding soil cover, distance to nearest contiguous seed source, pre-fire hardwood basal area, and snag basal area, as I considered these parameters to be less relevant to shrub establishment than tree establishment. Percent shrub cover was also excluded from the analysis, as it encapsulated the variables being analyzed.

I also conducted an MRPP analysis (Biondini et al. 1988) to determine if community composition varied as a function of soil type (ultramafic and non-ultramafic) and fire history. MRPP analyses comparing differences in fuel composition based on soil type were conducted on the LI sites (unburned sites and SI sites were excluded).Three MRPP fire-history comparisons were conducted: SI sites to LI sites (sites that burned in both the Biscuit and Silver fires to Biscuit-only sites), SI sites to unburned sites, and LI sites to unburned sites Ultramafic sites were excluded from the burn history analyses, as no data were collected on SI sites with ultramafic soils. MRPP is a nonparametric method that tests the null hypothesis of "no difference" between two or more a priori groups by summing the mean weighted within-group distances for each group (*delta*), and then estimating the likelihood of a delta that small or smaller based on random assignments to groups. It is well-suited to ecological data sets because it does not require multivariate normality or equal variances, two assumptions rarely met by ecological data. MRPP reports two statistics: a p-value indicating how likely it is that an observed difference is due to chance, and the chance-corrected within group agreement statistic (*A*). The agreement statistic describes within-group homogeneity, and ranges from 0 to 1 where 0 indicates the agreement expected by chance, and 1 indicates perfect agreement (all items within a group are identical). A value of 0.3 would be very high in community

ecology and values less than 0.1 are very common (McCune and Grace 2002). MRPP analysis was conducted using Sørensen distances in PC-ORD 6 (McCune and Mefford 2010).

Live understory fuels

Analysis of variance/analysis of covariance (ANCOVA/ANCOVA) analyses were used to test whether live fuels varied with burn severity. The Rothermal-based fire spread models consider two classes of live fuels: herbaceous and woody. Herbaceous fuels include annual grasses, perennial grasses, and forbs. Woody fuels include deciduous and evergreen shrubs and small trees up to 1.83 m high (Albini 1976, Anderson 1982, Rothermel 1983, Scott and Burgan 2005). Generally live fuels are quantified based on biomass, volume and area (eg. fuel loading: biomass to unit area ratio, density: biomass to volume ratio, packing ratio: fuel volume to fuel bed volume ratio) (Countryman and Philpot 1970). The data collection protocol in this study emphasized rapid plot-level measurement techniques (i.e. crown cover by species) to maximize the number of sites that could be sampled in this diverse and challenging landscape. Consequently, vegetation measures were not detailed enough to derive standard volume and biomass metrics for live fuels. Percent cover was used as a measure of shrub, forb and graminoid abundance. In an effort to characterize total shrub crown volume, a volume metric was calculated based on estimates of crown height (see below). Percent cover for graminoids and forbs was averaged over the twelve microplots to give a site-level estimate of ground cover. To estimate shrub volume, first the shrub area of each species was calculated by multiplying percent cover by corrected microplot area (see description in seedling density section). Shrub volume was generated by multiplying area by 70% of maximum height for that species on that microplot. The 30% reduction in height was used to prevent total volume from being artificially inflated by using maximum heights, which were usually higher than the

representative height for a species at that location. Total shrub volume (m^3) was summed for all shrub species on all microplots, and then volume/ha was estimated by dividing total shrub value by total microplot area in hectares (m^3/ha). Eight of the 936 microplots were missing shrub heights. When the species was present elsewhere on the site, missing shrub height data was estimated by averaging shrub heights for that species on the other site microplots. In two instances a species was found only on a single miroplot within a site. In these cases height was estimated using average values of the site most similar to the focal site based on burn severity, elevation, and location.

ANOVA/ANCOVA analyses were used to explicitly compare vegetation in unburned sites to to vegetation on sites with different burn severities. Due to overlap in dNBR values between unburned and low-severity sites, analyses using continuous burn severity values would have made comparisons between unburned and burned sites difficult. The continuous dNBR values were binned into five severity classes using equations developed by Thompson (Thompson 2008). The classes were: unburned (13 sites), low (0-35% canopy mortality, 21 sites), moderate (35-65% canopy mortality, 13 sites), high (65-95% canopy mortality, 18 sites), and extreme (95-100% canopy mortality, 13 sites). Elevation and aspect were considered as potential covariates, though only one covariate was considered at a time due to limited degrees of freedom. If neither covariate was significant in the ANCOVA analysis, data was analyzed using analysis of variance (ANOVA).

In order to improve normality and equal variance, data were log-transformed prior to analysis, then checked using residual plots. Before transformation 0.001 was added to all graminoid values, as the minimum nonzero value was 0.0083. The minimum nonzero value was so small because “trace” cover values were encoded as “0.1”. Soil and other live fuel

types contained no zero values. Maximum cover was 20% for soil and forbs, and 40% for graminoids. ANOVA/ANCOVA analyses were conducted using the car (Fox and Weisberg 2010) and stats packages in R (R Development Core Team 2010).

RESULTS

Seedling density

In general, density of short seedlings (<0.5 m high) was highest in low-severity burn areas (Figure 3.3a). Conversely, tall seedlings (0.5-1.37 m) were most abundant in the high-severity burn areas (Figure 3.3b). Though some of the high seedling densities were due to sprouting hardwoods or knobcone pine (*Pinus attenuata*), a fast-growing early-seral species, this pattern holds true for other species as well. Conifer regeneration in the taller size classes was particularly low in the low-severity areas, even when compared to unburned or moderate-severity areas. The majority of sites had conifer seedling densities above minimums outlined in the Biscuit EIS for 3-5 years post fire (Table 3.3). Stocking percentages varied based on burn severity, with highest stocking percentages on low-severity sites, followed by high-severity sites (Figure 3.4, Table 3.3). Stocking was lowest on unburned sites, though stocking guides are generally intended for sites with high canopy removal or morality, not undisturbed sties. All sites contained at least one conifer seedling (minimum stocking 8.3%).

The relationship of dNBR with seedling density was not perfectly reflected in the NPMR seedling analysis; dNBR was only selected as a predictor for knobcone pine seedlings <0.5 m. However, post-fire live basal area (LBA), which is closely related to dNBR, was selected as a predictor for many of the models (Table 3.5, Table 3.6). Post-fire LBA and dNBR are correlated (Pearson product-moment correlation coefficient $r = -0.75$, $R^2 = 0.56$, Figure 3.5).

Other variables commonly included in the seedling density models were average maximum August temperature from 2002-2007, and elevation. Selected predictor values and their relationships to seedling density varied by species and height class. For example, the two most sensitive variables selected for short conifer seedlings were post-fire LBA and average yearly precipitation, but for tall conifer seedlings the most sensitive variables selected were average maximum August temperature and slope (Table 3.5, Table 3.6). Post-fire LBA was also selected as a predictor variable for conifer seedlings in the tall height class, but the relationship between LBA and seedling density differed. Seedling density was positively correlated with post-fire LBA for short seedlings, but seedling density was negatively correlated with post-fire LBA for tall seedlings (Figure 3.6a, Figure 3.7b). Short knobcone pine seedlings were positively correlated with higher burn severity as measured by dNBR (Figure 3.6b); tall knobcone seedlings were correlated with areas of low post-fire LBA, another potential indicator of high crown mortality (Figure 3.7c). Short Douglas-fir seedlings were highest in areas with high post-fire LBA, and low average August maximum temperatures (Figure 3.6c). The only model found significant after a randomization test for tall Douglas-fir seedlings was a single-variable model. Tall Douglas-fir seedling density was positively correlated with increasing shrub cover (Figure 3.7d). The two other conifer species with significant models were white fir and ponderosa pine. The environmental variables selected for these models are consistent with the environmental conditions associated with these species. White fir seedling density was highest in higher elevation areas with cooler average August maximum temperatures, and ponderosa pine seedling density was highest in areas with lower average yearly precipitation (Figure 3.6d, f). Interestingly, no models for

sugar pine (*Pinus lambertiana*) were found significant after a randomization test, despite widespread establishment of this species (short seedlings: 51 sites, tall seedlings: 19 sites).

The final model for hardwood seedlings of all species <0.5 m selected elevation, post-fire LBA, and average yearly post-fire precipitation (Table 3.5). Hardwood seedling density generally increased with higher LBA (Figure 3.8a). Elevation and slope were the two most sensitive variables selected for the short Pacific madrone seedling model, followed by live post-fire LBA (Table 3.5). Pacific madrone seedling density showed a pronounced hump-shaped curve along the elevation gradient (Figure 3.8b), which is consistent with its known elevation range in this region (455-1435 m) (Reeves 2007). Pacific madrone seedling density is also higher in areas with higher post-fire LBA (Figure 3.8c). Despite relatively widespread establishment (N > 16), no significant models were found for total hardwood or Pacific madrone seedlings at the $p = 0.05$ level. Similarly, hardwood sprouts were commonly found on study sites for both size classes, the only statistically significant model was found for total tall hardwood sprouts. Hardwood sprout density was highest in low elevation areas with high pre-fire hardwood basal area (Figure 3.8d).

Shrub species diversity and understory cover composition

There was little evidence of differences in shrub species diversity of sites based on burn severity. Species richness showed a possible difference between burn severities ($F_{(4,73)} = 2.74$, $p = 0.035$), but post-hoc comparisons of all burn severities (10 comparisons total including unburned sites) using the Tukey HSD test 95% family-wise confidence interval showed no differences at the $p = 0.05$ level. All other ANOVA analyses of species diversity showed no evidence of differences (evenness: ($F_{(4,73)} = 0.68$, $p = 0.61$), Shannon's diversity index: ($F_{(4,73)} = 1.29$, $p = 0.28$), Simpson's diversity index: ($F_{(4,73)} = 1.10$, $p = 0.36$).

Though diversity metrics for shrub species showed no significant differences based on burn severity, the NMS ordination of shrub and understory cover composition showed evidence that burn severity (for both dNBR and post-fire live basal area measures) was correlated with differences in shrub composition and ground cover. In the final solution chosen for the NMS ordination, dNBR burn severity was correlated with the third axis, and post-fire LBA was correlated with axes 2 and 3 (Table 3.7). Aspect was the environmental variable most highly correlated with the first axis. The three-dimensional solution was selected based on an NMS scree plot which showed a decline in slope after three axes.

Environmental niches and life history traits for species and ground cover classes were consistent with environmental variables associated with each axis (Table 3.8, Figure 3.9a). For example, species associated with the third axis (dominant environmental factors dNBR and post-fire LBA), include deerbrush (*Ceanothus integerrimus*) and snowbrush (*Ceanothus velutinus*), both early successional species. Deerbrush is also negatively correlated with axis 2, where post-fire LBA, elevation, and average maximum August temperature are the dominant environmental factors, which is consistent with its life history traits as a lower-elevation, post-fire colonizing shrub. Shade-tolerant species such as Dwarf Oregon-grape (*Mahonia nervosa*), tanoak (*Lithocarpus densiflorus*), and salal (*Gaultheria shallon*) were negatively correlated with the first axis, while plants associated with warmer, drier areas like graminoids had negative correlations. This is consistent with the Beers-transformed aspect, the environmental variable most highly correlated with this axis.

The *Ceanothus* species had the highest cover on high-severity sites, while Pacific rhododendron and red huckleberry were more common on low-severity and unburned sites. Tanoak and Dwarf Oregon-grape did not seem to have strong relationships to dNBR (Figure

3.10). NPMR analysis of shrub cover selected dNBR as an explanatory variable for the *Ceanothus* species, and showed high cover for *Ceanothus* for high dNBR values. Percent cover of the other species was generally highest for northwest aspects and low average August maximum temperatures. Average yearly precipitation was also selected for the red huckleberry and Pacific rhododendron models (Table 3.9, Figure 3.11).

There was no evidence that understory cover composition differed between SI and LI burn sites ($p = 0.19$, $A = 0.0035$). However, there was a significant difference in understory cover composition between SI sites and unburned sites ($p = 0.0001$, $A = 0.056$) as well as LI sites and unburned sites ($p = 0.0065$, $A = 0.017$). The chance corrected within group agreement statistic (A) was moderate for all groups with statistically significant differences. MRPP also showed a significant difference in understory vegetation and cover composition between ultramafic and non-ultramafic soils on LI sites ($p = 0.0005$, $A = 0.030$) (Figure 3.9b).

Ground cover and live fuels

The proportion of ground covered by forbs, graminoids and soil were generally low (<10%, Figure 3.12). Graminoid cover was investigated using ANCOVA, as elevation was significantly related to percent graminoid cover (Table 3.10). However, ANCOVA analysis showed no evidence of differences in graminoid cover based on burn severity after controlling for the effect of elevation. Neither elevation nor aspect were significantly related to percent forb cover, percent soil cover, or shrub volume ($F_{(1,72)} < 3.97$, $p > 0.05$ in all cases), so ANOVA was used for all other ground cover analyses. There was also no evidence of differences in percent forb cover based on burn severity (Table 3.10).

Shrub volume differed significantly among the burn severity classes (Table 3.10). Post-hoc comparisons of all burn severities indicated low-severity sites had lower shrub crown

volume than unburned, high-, or extreme-severity sites (Table 3.11). Percent soil cover also varied based on burn severity (Table 3.10). Unburned sites had less exposed mineral soil than medium-, high-, and extreme-severity sites, and low-severity sites had less exposed mineral soil than extreme-severity sites (Table 3.11).

DISCUSSION

Seedling density

Seedling density varied with burn severity six years after the Biscuit Fire, though the relationship varied by size class. Descriptive statistics binning burn severity as defined by dNBR show that generally seedling density in the short height class is highest in low severity areas, but seedling density in the tall height class is highest in high- and extreme-severity areas (Figure 3.3). Additionally, seedling density differed between unburned and low-severity areas, and this difference varied by height class. Seedling density in the short height class was greater on low-severity sites than unburned sites, but seedling density in the tall height class was lower on low-severity sites than unburned sites. Though dNBR burn severity was not one of the most commonly selected environmental variables for short or tall seedlings in the NPMR analysis, post-fire LBA burn severity was commonly selected in the models for short and tall seedlings.

There are several complicating factors in comparing dNBR burn severity with post-fire LBA burn severity. First, dNBR is a measure of changes in both foliage and soil reflectance, not simply a change in live basal area (Lutes et al. 2006), so the specific ecological implications of different dNBR values are uncertain. Second, changes in dNBR values cannot distinguish between changes in tree canopy reflectance and changes in shrub canopy reflectance, so areas with low pre-fire basal area may have high dNBR values due to

high shrub mortality but low tree mortality. Third, dNBR is a remotely sensed burn severity metric; there may be registration errors between the dNBR value and ground coordinates, and there may be variation within the smallest discernable unit (a 30 m x 30 m pixel). Additionally, dNBR values reflect burn severity immediately after the fire, while post-fire LBA measurements were taken 6 years post-fire, and thus reflect any delayed post-fire tree morality (eg. Agee 2003, Lentile et al. 2005). Despite these limitations, there is a high correlation between dNBR and post-fire LBA, so both may be considered measures of crown mortality.

Other studies have found associations between seedling density and burn severity. Chappell and Agee (1996) found that overall seedling density was highest on low-severity sites and lowest on high severity sites in the Shasta red fir (*Abies magnifica* var. *shastensis*) forests of Crater Lake National Park in southern Oregon 8-12 years post-fire. However, they also found the proportion of seedlings >15 cm tall increased with increased fire severity. In the ponderosa pine forests of Black Hills South Dakota, seedling densities were highest in low- and moderate-severity burn areas, and were lowest in areas that experienced high tree mortality 2, 3 and 5 years post-fire (Lentile et al. 2005, Keyser et al. 2008). Lentile et al. (2005) found no seedlings in high-severity areas >30 m from a live-tree edge two years post-fire. Larson and Franklin (2005) found that densities for Douglas-fir seedlings >5 cm tall were highest in high-severity areas, though they attributed the high density to the persistence of an aerial seed bank, an unusual occurrence for burned Douglas-fir forests. Pausas et al. (2003) found no clear relationship between fire severity and seedling density in the Aleppo pine (*Pinus halepensis*) woodlands of the eastern Iberian Peninsula. The lack of a consistent pattern in the relationship of seedling density to burn severity may be due to differences in species life

histories and reproduction strategies. Ponderosa pine have heavy seeds with relatively small wings, so dispersal distances are short (1-1.5 times tree height), and seedlings establish only in areas with low basal area (<14 m^2/ha) (Shepperd and Battaglia 2002). Therefore ponderosa pine seedling densities would be limited by proximity to seed sources and areas with low basal area. In the Pausas et al. (2003) study, there were few areas where crown damage was low regardless of burn severity classification. Because Aleppo pine is serotinous, the high proportion of areas with heat or fire in the tree crown may account for the lack of difference in seedling density. The different relationships Chapell and Agee (1996) found between tall and short shasta red fir seedlings may be due to tradeoffs between optimal conditions for germination and growth. Shasta red fir is shade-tolerant and partial shade is best for seedling establishment, but it grows best in full sunlight (Laacke 1990). It is possible that seedlings that survived initially harsher conditions might later be in a location with better resources for additional growth.

Differences in seedling establishment based on different life history strategies were also seen in this study. The obligate serotinous knobcone pine (*Pinus attenuata*) may only reproduce through seeds from an in situ aerial seed bank (Howard 1992b) and may regenerate primarily the first year after fire (Donato et al. 2009b). As expected, seedling density for knobcone pine was highest in high severity burn areas, regardless of size class. Conversely, while Douglas-fir (*Pseudotsuga menziesii*) may also reproduce from an aerial seed bank, seeds may also disperse from surviving trees to distances of 400 m or more (Isaac 1930, Shatford et al. 2007, Donato et al. 2009b), and may be heavily influenced by post-fire mast years which tend to occur every 2 to 7 years (Reukema 1982, Hermann and Lavender 1990). Because most areas of the Biscuit Fire (>80%) were within 400 m of a seed source (Donato et al. 2009b), it

is not surprising that Douglas-fir seedlings were present on most sites. Regeneration was rarely seed limited, regardless of burn severity.

It is unlikely that the differences in seedling density in this study are due to a lack of exposed mineral soil for seedlings immediately post-fire, as there were high rates of litter and duff consumption regardless of burn severity (Campbell et al. 2007). There is also evidence that exposed mineral soil is not necessary for conifer seedling establishment the Pacific Northwest (Gray and Spies 1996). Based on counts of current year seedlings, germination continued to be high on low-severity sites, which had the highest quantities of litter and duff six years after the Biscuit Fire (Chapter 1). Additionally, exposed mineral soil was highest on high- and extreme-severity sites, but these sites had relatively low densities of small seedlings.

A complication of using dNBR or post-fire LBA as an explanatory factor is that live trees may serve as seed sources, but may also compete with seedlings for light, water and nutrient resources. These competing factors may explain some of the differences in seedling densities between size classes. Low-severity sites may possess ample seed sources, but seeds that germinate may not have sufficient resources to survive and thrive. Conversely, conditions may be better for seeding growth and long-term survival on high-severity sites, but seedling density may be lower due to several factors including lower rates of seedling establishment, higher rates of first year mortality, or longer distances to seed sources.

There are several examples of differences between conditions ideal for germination or initial establishment and conditions ideal for growth. In the transition hardwoods-white pine-hemlock forest type of Massachusetts, George and Bazzaz (1999) found that red maple (*Acer rubrum*) seedlings showed no pattern in establishment based on presence or absence of a dense fern understory, but seedlings that established under dense fern cover had reduced

survivorship. Battaglia et al. (2000) found that the factors influencing seed emergence of sweetgum (*Liquidambar styraciflua*) and swamp chestnut oak (*Quercus michauxii*) were different than the factors influencing seedling mortality and height growth, and that the important factors varied by species. However, a decoupling between early seedling establishment and future growth is not universal. In the great lakes region of Wisconsin and Michigan, Rooney et al. (2002) found that seedling densities in taller size classes for northern white cedar (*Thuja occidentalis*) were more likely to be found in areas that also had high seedling density in the lower size classes.

The relationship of Douglas-fir seedlings to burn severity may be an example of how different factors govern early seedling establishment and later growth. Douglas-fir seedlings in the taller size class were higher on unburned, high- and extreme-severity sites, and lowest on low-severity sites. Douglas-fir is a moderately shade-tolerant species especially in the seedling stage (Hermann and Lavender 1990), and tall Douglas-fir seedlings were present on unburned sites. Therefore the absence of taller seedlings on low-severity sites implies that they were probably consumed or killed by the fire. Despite high densities of short Douglas-fir seedlings on low-severity sites, these seedlings were less likely to attain the heights seen of seedlings on higher severity sites. Presence of taller Douglas-fir seedlings in the understory may be due to canopy gaps from overstory tree mortality that later closed (Gray and Spies 1996). Seedling densities and site conditions within the Biscuit Fire boundary may continue to change for decade or more. Studies have shown that seedlings continue to establish 10-15 years or longer after a fire (Shatford et al. 2007, Donato et al. 2009b), but the long-term survival of these seedlings will depend on specific site conditions that will change over time.

There was generally a positive association between increased shrub cover and seedling density for all conifer species combined and Douglas-fir seedlings in the taller size classes (Figure 3.7b, d). Other studies have found correlations between shrub cover and seedling density or growth. Irvine et al. (2009) found that generally, overtopping vegetation had little effect on the growth of Douglas-fir seedlings, though in dry or low-elevation sites there was a positive association between overtopping shrub vegetation and seedling growth. However, Newton and Cole (2008) found that planted Douglas-fir seedlings had higher height, DBH, and volume growth when there were lower densities of competing Pacific madrone and whiteleaf manzanita over multiple decades. Lower growth rates may be due to differences in water competition and utilization, as the two hardwood species have deeper root systems and can utilize narrower fissures in bedrock than Douglas-fir (Zwieniecki and Newton 1995). Shatford et al. (2007) found positive associations between shrub cover and seedling density for Douglas-fir forest types, but negative correlations for the white fir series. Interestingly, this study also found a negative association between shrub cover and white fir seedling density (Figure 3.6e). It is unclear whether positive associations between shrubs and seedlings result in enhanced seedling survival, for example via the production of shade for seedlings (Berkowitz et al. 1995) or nitrogen fixation (Howard 1997), or whether the shrubs and tree seedlings are responding to the same factors (lack of competition for moisture/light, exposed mineral soil, mitigation of seed dormancy via heat or scarrification). Competition for water and other resources still exist between shrub and tree seedlings, though the intensity of competition may vary based on site productivity.

For some species, no statistically significant NPMR models were found. Sugar pine (*Pinus lambertiana*), which was widely distributed was one such case. Sugar pine is present

throughout most of the Klamath-Siskiyous, on western slopes of the Cascade and Sierra Nevada ranges, and in pockets of the southern Oregon and California Coast ranges. Despite its ubiquity, pure sugar pine stands are rare; usually sugar pine trees are found singly or in small groups. Sugar pine has large seeds, do not wind-disperse far from their source trees (Kinloch and Scheuner 1990) and are a favorite food of small mammals, which also contribute to dispersal through seed caching (Kinloch and Scheuner 1990, Vander Wall 2003). A study on natural regeneration of sugar pine and other conifer species found high germinations rates and high rates of survival after 1 and 5 years (Fowells and Stark 1965). The lack of a narrow habitat niche, short dispersal distances, and high predation and secondary dispersal by small mammals may explain why environmental variables selected for final NPMR models performed no better than a randomly selected set of environmental variables.

No statistically significant models were found for Pacific madrone (*Arbutus menziesii*) or total hardwood seedlings in the tall height class, despite being relatively common on study sites. Though germination for Pacific madrone seeds may be high (Tappeiner et al. 1986), seedling mortality is extremely high due to mold, slugs, and drought (McDonald 1978, Tappeiner et al. 1986, Reeves 2007). NPMR analysis did find a statistically significant model for short Pacific madrone seedlings, but the factors related to Pacific madrone seedling growth and survival may differ from those that govern germination and initial establishment, and may not have been considered in this analysis.

Understory cover composition and shrub species diversity

The NMS ordination of shrub species and other cover types showed that crown mortality influenced species composition six years post-fire; dNBR and post-fire LBA were highly correlated with one or more axes. Fire-associated nitrogen-fixing *Ceanothus* species

were positively correlated with higher burn severity. dNBR was also selected as an explanatory variable in the NMPR analysis of these two species. Deerbrush is usually known as a lower-elevation and post-fire colonizing shrub in Oregon, and both deerbrush and snowbrush seeds require exposure to heat or some other scarification process in order to germinate (Howard 1997, Anderson 2001). Pacific rhododendron (*Rhododendron macrophyllum*), a species usually associated with unburned areas or low-severity fire (Crane 1990), was negatively correlated with burn severity. Elevation, aspect, and maximum August temperature also were highly correlated with shrub species and ground cover distributions. Though dNBR was not selected as an explanatory variable in the NPMR analysis for species that were correlated with low burn severity, the other selected variables were consistent with those found in the NMS analysis. The ordination of different species based on burn severity underscores the importance of looking at plant composition in addition to diversity metrics when assessing differences between different area classifications.

I found no evidence of difference in species and ground cover composition between SI sites and LI sites; however, both SI and LI sites had a different species composition than unburned sites. These results differ from those found by Donato et al. (2009c), who found significant differences in species composition between SI sites and LI sites, as well as SI sites and nearby unburned stands, but no differences between LI sites and unburned stands. Donato et al. (2009c) also found species richness was highest in SI areas. These discrepancies may be due to the fact that Donato et al. included forb species in their analysis, which would allow for a greater range of species diversity. Additionally, Donato et al. (2009c) only considered high-severity areas of the Biscuit Fire, rather than the full range of burn severities as considered in this study. As seen in the NMS ordination, shrub species and ground cover composition vary

with burn severity. I would expect species composition to be more similar within high-severity sites, than within an area that encompasses all burn severities. These differences may help explain the different results in these two studies.

Different groups of species flourish in different environments, as evidenced by the significant difference in plant composition between ultramafic and non-ultramafic soils. Though these differences are not surprising given past studies (Whittaker 1960, White 1971), it shows that a fire disturbance did not eliminate differences in species composition between the two soil types. Few studies look at difference in species composition to fire disturbance between serpentine and non-serpentine soils, but they seem to show different responses to fire based on soil type. Safford and Harrison (2004) found that species overlap between serpentine and non-serpentine soils in a California chaparral system increased from 25% to 66% after a fire. They also found that species richness increased on both soil types after the fire. However, though non-serpentine areas had greater increases in species richness post-fire, they also had higher quantities of non-native species both pre- and post-fire. Fire also increased exotic and total species richness more on non-serpentine soils in a California grassland system (Harrison et al. 2003), but native species richness increased more on serpentine sites. Harrison et al. (2003) found changes in species richness to be short-lived; they returned to pre-fire levels 2 years post-fire. Ample opportunity exists for further research on vegetation responses to fire in serpentine areas of the Klamath-Siskiyou ecoregion.

Live understory fuels

Though there was no evidence of difference in total graminoid or forb cover based on fire severity, shrub crown volume was positively correlated with fire severity. This study did not collect the data necessary to generate the metrics used in fire spread equations such as

biomass and fuel volume, but it strongly suggests that live fuel quantities are lower on low-severity areas 6 years post-fire than on high-severity and unburned areas. In order to understand or predict future fire behavior and severity in this area, it is imperative to understand the role of live fuels and how they change over time based on prior burn severity.

The findings in this study are consistent with other studies investigating shrub responses to fire in Oregon mixed-severity fire regimes. Meigs et al. (2009) found that shrub biomass was higher in high-severity areas than low-severity areas in the ponderosa pine and mixed-conifer forests east of the Oregon Cascade Mountains 4-5 years post-fire. Also in the mixed-conifer forests of the eastern Oregon Cascades, Dunn (2010) found that shrub biomass appears to increase for at least 24 years in areas that experienced high-severity fire. Though both these studies took place in lower productivity regions of Oregon, they suggest that live fuel responses vary based on burn severity, and that these changes may persist for extended time periods.

The effect of live fuels on fire behavior is poorly understood (Burgan 1979, Jolly 2007, Weise and Wotton 2010), and there has recently been renewed interest in understanding the role of live fuels in fire behavior (Jolly 2007, Weise and Wotton 2010). Live fuels may have a dampening effect on fire spread when moisture content is high, however if live fuel content is low due to dry conditions or desiccation from fire live fuels may ignite, rapidly increasing fire intensity (as measured by energy output) and severity (as measured by ecological impact) in a threshold-type effect (Burgan 1979, Weise et al. 2005). Additionally, live fuel moisture content fluctuates widely throughout the year in Mediterranean climates with little summer precipitation so impacts of live fuels to fire severity will vary throughout the fire season (eg. Agee et al. 2002).

The burn history of the Biscuit fire attests to the importance of understory vegetation on fire severity. In 2002, when the Biscuit Fire burned across the entire area burned in the 1987 Silver Fire, areas that burned at high severity tended to reburn at high severity, and areas that burned at low severity tended to reburn at low severity (Thompson et al. 2007). It is unclear why this pattern occurred, though areas that had been salvage logged and then replanted tended to burn at the highest severity (Thompson et al. 2007), as did unmanaged areas with highly contiguous regenerating understory vegetation including both trees and shrubs (Thompson et al. 2007, Thompson and Spies 2010), implying that live fuels are a key factor in predicting fire severity. These studies were based on remotely-sensed data including aerial photographs and dNBR (Landsat) data; there were no pre-fire measurements of shrubs or other live fuels to directly compare to fire severity. This study was conducted six years post-fire, as compared to the fifteen year interval between the Biscuit and Silver fires. It is difficult to predict what may happen to shrub quantities and composition in the next decade. A chronosequence study in the dry-mixed conifer forests of Oregon's eastern Cascades, found that shrub biomass increased for at least 25 years in high-severity fire areas (Dunn 2010). However, seedlings may also overtop and shade out the shrub layer in that decade, which would lower live fuel quantities but increase quantities of small-diameter dead fuels. Other studies also suggest that live fuels are an important factor in predicting future fire severity. Odion et al. (2004) found that areas that had not burned for a half-century or more were less likely to burn at high severity than areas that had burned more recently. They speculated that closed canopy conditions resulted in lower quantities of shrubs and trees in the understory, and that the remaining shrubs and trees were less fire prone than their early-seral counterparts. In turn, lower live fuel quantities as well as cooler, moisture conditions in the understory may

have resulted in lower incidences of crown fires. Fuel profiles and modeling by Donato (2008) suggested that vegetation rather than dead fuels was the primary predictor of future fire severity one to two decades post-fire, though that study only considered high-severity burns in the Klamath-Siskiyous. My study lends further credence to the hypothesis that live vegetation is a major contributing factor in burn severity. Six years post-fire, shrub vegetation volumes were lower in low-severity sites than unburned, high-, and extreme-severity sites. The lower amount of understory vegetation in low-severity sites is consistent with the finding that there was a high spatial correlation of burn severities between the areas burned in the Silver Fire that later burned in the Biscuit Fire (Thompson et al. 2007). It also corroborates the finding that shrub quantities were low on low on low-severity sites and high on high-severity sites, based on remote-sensing data (Thompson and Spies 2010). Though I found no evidence that shrub volumes differed between unburned areas and high- or extreme-severity areas as predicted by Odion et al. (2004), shrub composition did vary based on burn severity and between burned and unburned areas. The presence or quantities different chemical compounds in different shrub species can cause differences in volatility and fire intensity (Green 1982, Rundel 1982), so differences in fuel composition may result in different fire effects despite similarities in overall quantity. Additionally, microclimate in closed-canopy low-severity or unburned areas may differ from high- or moderate-severity areas in terms of humidity, ground temperature, moisture content, and windspeed, all of which may influence fire severity and spread (Countryman 1955). Six years after the Biscuit Fire, litter and duff depth and biomass continued to be lower on high- and extreme-severity sites than on low severity sites, and fuels 0.64-7.62 cm in diameter had no relationship to fire (Chapter 2), suggesting that the buildup of dead fuels may not be the primary factor influencing fire severity in that time frame.

Understanding the dynamics of shrubs and other understory vegetation in addition to dead fuels is crucial towards understanding future fire effects and behavior.

MANAGEMENT IMPLICATIONS

Despite concerns about lack of regeneration in high-severity portions of the Biscuit Fire (Sessions et al. 2004, USDA Forest Service 2004) average seedling densities were above the minimum acceptable stocking levels of 333 trees per hectare (135 seedlings/acre) for all fire severities (Table 3.3). Though regeneration was sometimes clumped rather than evenly distributed, most sites had stocking rates above 50%, regardless of burn severity (Figure 3.4). As shrub cover was highest on high- and extreme-severity sites, many if not most of these seedlings may not be "free to grow", however removing shrub competition would require some kind of mechanical or chemical intervention regardless of whether seedlings were natural or planted. Additionally, prior studies have shown that tree regeneration continues for decades after a fire (Shatford et al. 2007). Therefore there is little evidence showing that planting seedlings is necessary to restore this area to a forested condition some time in the future. However, different management goals such as creating well-stocked evenly-spaced plantations for efficient timber production, or accelerating the creation of old-growth structural characteristics may require active management.

Long-term impacts of fire severity on tree regeneration and succession are unclear. It is possible that the high densities of short conifer seedlings in the understory of low-severity areas will serve as a "seedling bank" for future cohorts, which may be released by canopy gaps from single-tree mortality. However, these seedlings may be ephemeral, quickly replaced by the ample seed sources in low-severity areas. A third possibility is that the high short seedling density in low-severity areas will lead to a dense understory of trees. I did not

see any evidence of this scenario in unburned areas, but unburned sites also lacked the pulse of regeneration seen in low-severity areas. Though shade tolerance declines with age for many tree species, in some low-severity areas the overstory may be open enough to support a second, lower story. Conversely, higher-severity areas tended to have higher densities of tall seedlings than low-severity areas. These areas may be more amenable to long-term seedling survival and growth. Unfortunately this study protocol did not collect seedling ages, so it is impossible to determine whether most tall seedlings established immediately after the fire or if they continued to establish and grow quickly after the fire. Similarly, there is no way to determine if short seedlings in low-severity areas are young, or just slow-growing due to light, moisture and nutrient competition. Future studies directly measuring seedling age and long-term survival are critical to fully understand succession in a mixed-severity fire regime.

The presence of numerous taller seedlings on high-severity sites indicate that most high-severity areas have the potential to return to forested conditions without human intervention. Additionally, old-growth stands may have established with tree densities as low as 60-120 trees/ha (Tappeiner et al. 1997, Sensenig 2002), rather than the 333 trees/ha required in the Biscuit FEIS (USDA Forest Service 2004), indicating that minimum required seedling densities may be too high if old-growth characteristics are desired. Though seedlings appear to be well-distributed regardless of burn severity, a quick return to a closed-canopy in all areas is not necessarily an ecological imperative. Between 1944 and 1985 Skinner (1995) found that the average size of forest openings decreased in the Klamath Mountains of Northern California. Average distance to the nearest forest opening also increased. Forest openings and early seral habitat provide important resources to a variety of species, and are also an important component to landscape diversity. The creation and potential persistence of

open and early-seral habitat represents a return of a habitat type that was in decline due to years of fire suppression.

It is unclear what impact vegetation control efforts might have on understory shrub quantities and future fire effects. Studies in less productive fire-prone forest systems have found that prescribed fire and/or mechanical treatments may initially decrease shrub cover or quantities (Kauffman and Martin 1990, Metlen et al. 2004), but shrub stem densities may increase from vegetative propagation as quickly as one year post-fire (Kauffman and Martin 1990), and total shrub cover may radically increase from pre-fire conditions within a few years (Kane et al. 2010). Quantities of non-sprouting chaparral species such as whiteleaf manzanita (*Arctostaphylos manzanita*) may be low after mechanical treatments (Perchemlides et al. 2008), but seeds can remain viable for decades (Howard 1992a) meaning quantities may increase after a fire disturbance. The Klamath-Siskiyou ecoregion has a higher productivity than the sites of these studies, and a high number of species that sprout or germinate in response to fire. An effort to lower future fire severity through vegetation control would almost certainly be a costly and time-intensive undertaking, due to the large areas that would require treatment and the frequency with which treatments would need to reoccur.

CONCLUSIONS

Six years after the Biscuit Fire, tree regeneration, understory composition, and live fuel quantities all varied in relation to fire severity. Most studies looking at regeneration and fuels in the mixed-evergreen forests of the Klamath-Siskiyous have concentrated solely on the high-severity portions of these fires. Though these areas are of high concern due to interest in successional pathways as well as potential economic returns of salvage logging, looking only at these areas ignores the majority of the affected area in ecosystems with mixed-severity fire

regimes. In order to understand the mechanics of a complex system like the mixed-evergreen forests of the Klamath-Siskiyous, it is necessary to look at the full range of disturbed areas and investigate how all respond to a disturbance, not just ~20% of the area that represents the highest impact on tree survival.

Seedling response to fire severity varied by size class and species. In general, densities of short seedlings were highest in low-severity areas and lowest on high- and extreme-severity areas. This trend was reversed for tall seedlings. It is unclear whether seedlings in the two size classes also represented different age classes. The high number of short seedlings in low-severity areas might be seedlings that established immediately after the Biscuit Fire, but grow slowly due to resource competition from established overstory trees. They may also be ephemeral; short seedlings in low-severity areas die after a short time but are quickly replaced due to plentiful seed sources. Similarly, it is unclear whether tall seedlings in high-severity areas are those that established immediately post-fire, or if they are younger seedlings that established in the years following the fire. Seedlings may continue to establish one to two decades after a fire disturbance (Shatford et al. 2007), so seedlings in high-severity areas may represent different establishment times regardless of height.

Better understanding of understory vegetation response to fire, especially for shrub species, is critical to understanding future species composition and fire behavior, Shrub crown volume in low-severity areas was significantly lower than shrub crown volume in both unburned and high-/extreme-severity areas. Understory fuel quantities may be responsible for the high degree of fidelity in fire severity between the Biscuit and Silver fires, where high-severity areas tended to reburn at high severity, and low severity areas tended to reburn at low severity (Thompson et al. 2007). Conventional wisdom holds that high-severity fires are due

to the buildup of dead fuels. However, recent studies suggest the factors leading to high-severity fire are more complex (e.g. Thompson et al. 2007). Only by looking at the full range of fire severities, and how they differ, can we better understand the mechanics governing fire severity. Understanding the processes governing fire severity will help to make better and more effective management decisions to manage future fire disturbances, as well and protect public health and welfare from their impact. Future studies investigating how regeneration, diversity, and live fuels change over time will also be important in understanding ecological processes and predicting potential future impacts of large, mixed-severity fires.

LITERATURE CITED

Agee, J. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72**:24-34.

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.

Agee, J. K. 2003. Monitoring postfire tree mortality in mixed-conifer forests of Crater Lake, Oregon, USA. Natural Areas Journal **23**:114-120.

Agee, J. K., C. S. Wright, N. Williamson, and M. H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management **167**:57-66.

Albini, F. A. 1976. Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-30, Ogden, UT, p. 92.

Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-122, Ogden, Utah, p. 22.

Anderson, M. D. 2001. *Ceanothus velutinus*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/ceavel/all.html [2011, March 8].

Antoine, M. E. and B. McCune. 2004. Contrasting fundamental and realized ecological niches with epiphytic lichen transplants in an old-growth Pseudotsuga forest. Bryologist **107**:163-172.

Atzet, T. and D. Wheeler. 1982. Historical and ecological perspectives on fire activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests. USDA Forest Service, Pacific Northwest Region Publication R-6, Portland, OR, p. 19.

Atzet, T. A. and R. Martin. 1992. Natural disturbance regimes in the Klamath province. Pages 40-48 *in* Proceedings of the Symposium on Biodiversity of Northwestern California. Portland OR, USDA Forest Service, Pacific Northwest Region.

Atzet, T. A., D. Wheeler, and R. Gripp. 1988. Fire and forestry in southwest Oregon: Importance of fire. Oregon State University Extension Service, FIR Report, Winter 1988, Medford, Oregon, USA, pp. 4-7.

Battaglia, L. L., S. A. Fore, and R. R. Sharitz. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. Journal of Ecology **88**:1041-1050.

Beers, T. 1966. Notes and observations: Aspect transformation in site productivity research. Journal of Forestry **64**:691-692.

Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology **76**:1156-1168.

Biondini, M., P. Mielke, and K. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Plant Ecology **75**:161-168.

Brewer, C. K., J. C. Winne, R. L. Redmond, D. W. Opitz, and M. V. Mangrich. 2005. Classifying and mapping wildfire severity: A comparison of methods. Photogrammetric Engineering and Remote Sensing **71**:1311-1320.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: Principles in the context of place. Conservation Biology **18**:903-912.

Burgan, R. E. 1979. Estimating live fuel moisture for the 1978 National Fire-Danger Rating System. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-226, Ogden, Utah, p. 17.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research-Biogeosciences **112**:G04014.

Chappell, C. B. and J. K. Agee. 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades, Oregon. Ecological Applications **6**:628-640.

Colombaroli, D. and D. G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. Proceedings of the National Academy of Sciences of the United States of America **107**:18909-18914.

Cooper, L. J. 1939. A history of the Siskiyou National Forest. Unpublished report on file with the Siskiyou National Forest, Grants Pass, Oregon.

Countryman, C. M. 1955. Old-growth conversion also converts fireclimate. U.S. Forest Service Fire Control Notes **17**:15-19.

Countryman, C. M. and C. W. Philpot. 1970. Physical characteristics of chamise as a wildland fuel. USDA Forest Service, Pacific Southwest Forest & Range Experiment Station, Research Paper PSW-RP-66, Berkeley, CA, p. 16.

Crane, M. F. 1990. *Rhododendron macrophyllum*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/rhomac/all.html [2011, March 8].

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research **22**:99-113.

Dolling, A. 1999. The vegetative spread of *Pteridium aquilinum* in a hemiboreal forest - invasion or revegetation? Forest Ecology and Management **124**:177-184.

Donato, D. C. 2008. Forest vegetation and fuel dynamics following stand-replacing wildfire, re-burn, and postfire management in the Siskiyou Mountains, Oregon. Dissertation. Oregon State University, Corvallis, OR.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science **311**:352-352.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009b. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **39**:823-838.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009c. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology **97**:142-154.

Dunn, C. J. 2010. Coarse woody detritus dynamics, variable decay rates and their contribution to wildland fuel succession following high-severity fire disturbance in dry-mixed conifer forests of Oregon's eastern Cascades. Master's thesis. Oregon State University, Corvallis, OR.

ESRI (Environmental Systems Resource Institute). 2010. ArcMap 9.3.1. Redlands, California. Available:

Fowells, H. A. and N. B. Stark. 1965. Natural regeneration in relation to environment in the mixed conifer forest type of California. USDA Forest Service, Pacific Southwest Forest & Range Experiment Station, Research Paper PSW-RP-24, Berkeley, CA, p. 14.

Fox, J. and S. Weisberg. 2010. car: Companion to Applied Regression. R package version 2.0-2. Available: http://CRAN.R-project.org/package=car

Franklin, J. F. and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

GAO. 2004. Biscuit Fire: Analysis of fire response, resource availability, and personnel certification standards. United States General Accounting Office, GAO-04-426, Washington, DC.

George, L. O. and F. A. Bazzaz. 1999. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. Ecology **80**:833-845.

Gliessman, S. R. and C. H. Muller. 1978. Allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. Journal of Chemical Ecology **4**:337-362.

Gray, A. N. and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology **84**:635-645.

Green, L. R. 1982. Prescribed burning in the California mediterranean ecosystem. Pages 464-471 *in* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, June 22-26. USDA Forest Service General Technical Report PSW-058, San Diego, CA.

Hall, W. L., H. R. Zuuring, C. C. Hardy, and R. H. Wakimoto. 2003. Applying logistic regression to determine regeneration risk to stand replacement fire on the Kootenai National Forest, Montana. Western Journal of Applied Forestry **18**:155-162.

Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology **17**:837-845.

Hermann, R. K. and D. P. Lavender. 1990. *Pseudotsuga menziesii* - Douglas-fir. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Howard, J. L. 1992a. *Arctostaphylos viscida*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/arcvis/all.html [2011, April 13].

Howard, J. L. 1992b. *Pinus attenuata*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/pinatt/all.html [2011, March 2].

Howard, J. L. 1997. *Ceanothus integerrimus*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/ceaint/all.html [2011, March 3].

Irvine, D. R., D. E. Hibbs, and J. P. A. Shafford. 2009. The Relative Importance of Biotic and Abiotic Controls on Young Conifer Growth after Fire in the Klamath-Siskiyou Region. Northwest Science **83**:334-347.

Isaac, L. A. 1930. Seed flight in the Douglas-fir region. Journal of Forestry **24**:492-499.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas Fir region with special reference to fire. Journal of Forestry **38**:716-721.

Jolly, W. M. 2007. Sensitivity of a surface fire spread model and associated fire behaviour fuel models to changes in live fuel moisture. International Journal of Wildland Fire **16**:503-509.

Kane, J. M., J. M. Varner, E. E. Knapp, and R. F. Powers. 2010. Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. Applied Vegetation Science **13**:207-220.

Kauffman, J. B. and R. E. Martin. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra-Nevada mixed conifer ecosystems. Forest Science **36**:748-764.

Keyser, T. L., L. B. Lentile, F. W. Smith, and W. D. Shepperd. 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. Forest Science **54**:328-338.

Kinloch, B. B., Jr. and W. H. Scheuner. 1990. *Pinus lambertiana* Dougl. - Sugar Pine. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Laacke, R. J. 1990. *Abies magnifica* A. Murr. - California Red Fir. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Larson, A. J. and J. F. Franklin. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management **218**:25-36.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:2875-2885.

Lewis, H. T. 1989. Reconstructing Patterns of Indian Burning in Southwestern Oregon. Pages 80-84 *in* Living with the land: The Indians of southwest Oregon. The proceedings of the 1989 Symposium on the Prehistory of Southwest Oregon. Southern Oregon Historical Society, Medford, OR.

Lutes, D. C., R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi. 2006. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-164-CD, Ogden, UT, p. 400.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons, New York, NY.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. Journal of Vegetation Science **17**:819-830.

McCune, B. 2009. Nonparametric multiplicative regression for habitat modeling. http://www.pcord.com/NPMRintro.pdf

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2009. HyperNiche. Nonparametric Multiplicative Habitat Modeling. Version 2.07. MjM Software, Gleneden Beach, Oregon, U.S.A.

McCune, B. and M. J. Mefford. 2010. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.243 beta. MjM Software, Gleneden Beach, Oregon, U.S.A.

McDonald, P. M. 1978. Silviculture-ecology of three native California hardwoods on high sites in north central California. Dissertation. Oregon State University, Corvallis, OR.

Meigs, G. W., D. C. Donato, J. L. Campbell, J. G. Martin, and B. E. Law. 2009. Forest fire impacts on carbon uptake, storage, and emission: The role of burn severity in the eastern Cascades, Oregon. Ecosystems **12**:1246-1267.

Metlen, K. L., C. E. Fiedler, and A. Youngblood. 2004. Understory response to fuel reduction treatments in the blue mountains of northeastern oregon. Northwest Science **78**:175-185.

Miller, J. D. and S. R. Yool. 2002. Mapping forest post-fire canopy consumption in several overstory types using multi-temporal Landsat TM and ETM data. Remote Sensing of Environment **82**:481-496.

Newton, M. and E. C. Cole. 2008. Twenty-six-year response of ponderosa pine and Douglas-fir plantations to woody competitor density in treated stands of madrone and whiteleaf manzanita. Forest Ecology and Management **256**:410-420.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment **4**:481-487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology **18**:927-936.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology **98**:96-105.

Pausas, J. G., N. Ouadah, A. Ferran, T. Gimeno, and R. Vallejo. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. Plant Ecology **169**:205-213.

Perchemlides, K. A., P. S. Muir, and P. E. Hosten. 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in southwestern Oregon. Rangeland Ecology & Management **61**:98-109.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org

Reeves, S. L. 2007. *Arbutus menziesii*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/arbmen/all.html [2011, March 3].

Reukema, D. L. 1982. Seedfall in a young-growth Douglas-fir stand: 1950-1978. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **12**:249-254.

Rooney, T. P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. Forest Ecology and Management **163**:119-130.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-143, Ogden, UT, p. 161.

Royo, A. A. and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:1345-1362.

Rundel, P. W. 1982. Successional dynamics of chamise chaparral: The interface of basic research and management. Pages 86-90 *in* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, June 22-26. USDA Forest Service General Technical Report PSW-058, San Diego, CA.

Safford, H. D. and S. Harrison. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. Ecology **85**:539-548.

Scott, J. H. and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-153, Fort Collins, CO, p. 72.

Sensenig, T. S. 2002. Development, fire history and current and past growth, of old-growth and young-growth forest stands in the Cascade, Siskiyou and mid-coast mountains of southwestern Oregon. Dissertation. Oregon State University, Corvallis, OR.

Sessions, J., P. Bettinger, R. Buckman, M. Newton, and A. J. Hamann. 2004. Hastening the return of complex forests following fire: The consequences of delay. Journal of Forestry **102**:38-45.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry **105**:139-146.

Shepperd, W. D. and M. A. Battaglia. 2002. Ecology, silviculture, and management of Black Hills ponderosa pine. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-97, Fort Collins, CO, p. 112.

Skinner, C. N. 1995. Change in spatial characteristics of forest openings in the Klamath mountains of northwestern California, USA. Landscape Ecology **10**:219-228.

State of Oregon. 2007. 2005 Digital Orthophotos [computer file]. Available from Oregon Imagery Explorer. Oregon Department of Administrative Services Geospatial Enterprise Office (DAS-GEO), Salem, OR. http://oregonexplorer.info/imagery [May 10, 2011].

Tappeiner, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **27**:638-648.

Tappeiner, J. C., P. M. McDonald, and T. F. Hughes. 1986. Survival of tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) seedlings in forests of southwestern Oregon. New Forests **1**:43-55.

Taylor, A. H. and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111**:285-301.

Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications **13**:704-719.

Thompson, J. R. 2008. Patterns of crown damage within a large wildfire in the Klamath-Siskiyou bioregion. Dissertation. Oregon State University, Corvallis, OR.

Thompson, J. R. and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management **258**:1684-1694.

Thompson, J. R. and T. A. Spies. 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. Landscape Ecology **25**:775-789.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America **104**:10743-10748.

USDA. 2008. Soil Survey Geographic (SSURGO) Database for Oregon and California.

USDA Forest Service. 1988. Silver Fire recovery project, final environmental impact statement. Pacific Northwest Region, USDA Forest Service, Grants Pass, OR.

USDA Forest Service. 2004. Biscuit Fire recovery project, final environmental impact statement. Medford, OR.

USDI. 2003. Regeneration stocking surveys handbook. U.S. Bureau of Land Management, Oregon State Office, H-5705-1, Rel. 5-249, Portland, OR.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. Oikos **100**:25-34.

Weise, D. R. and B. M. Wotton. 2010. Wildland-urban interface fire behaviour and fire modelling in live fuels. International Journal of Wildland Fire **19**:149-152.

Weise, D. R., X. Y. Zhou, L. L. Sun, and S. Mahalingam. 2005. Fire spread in chaparral - ‘go or no-go?’. International Journal of Wildland Fire **14**:99-106.

White, C. 1971. Vegetation, soil chemistry correlations in serpentine ecosystems. Dissertation. University of Oregon, Dept. of Biology, Eugene, OR.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30**:279-338.

Zwieniecki, M. A. and M. Newton. 1995. Roots growing in rock fissures - Their morphological adaptation. Plant and Soil **172**:181-187.

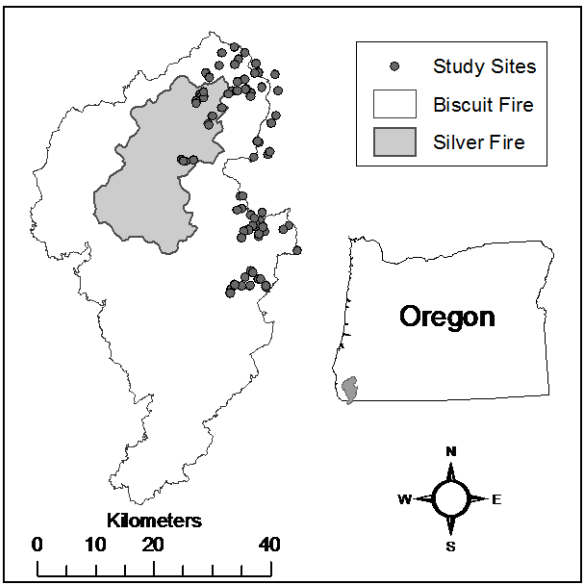


Figure 3.1: Biscuit Fire, Silver Fire and study site locations in Southwestern Oregon.

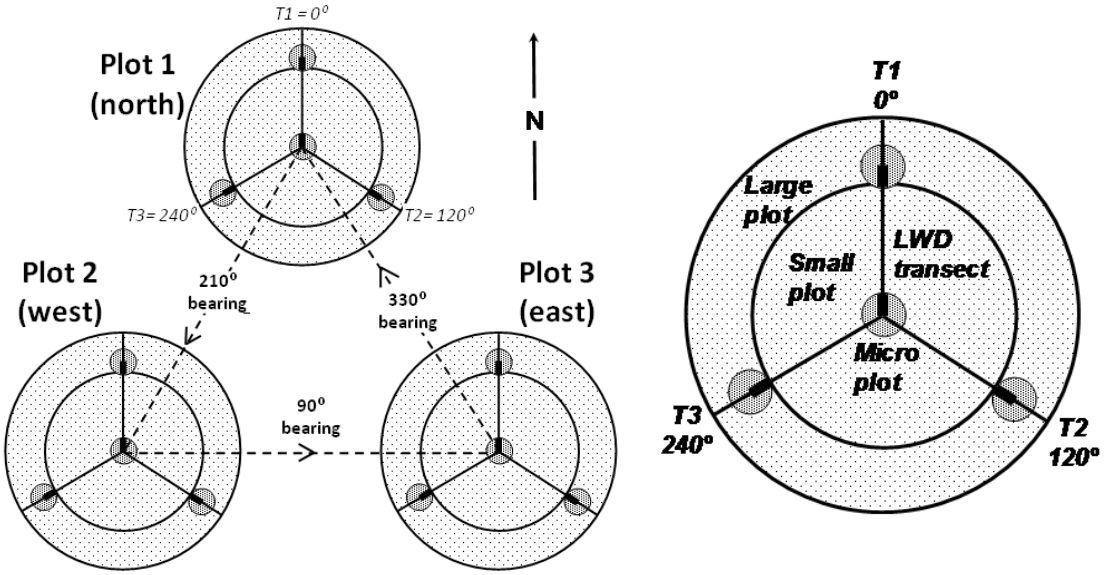
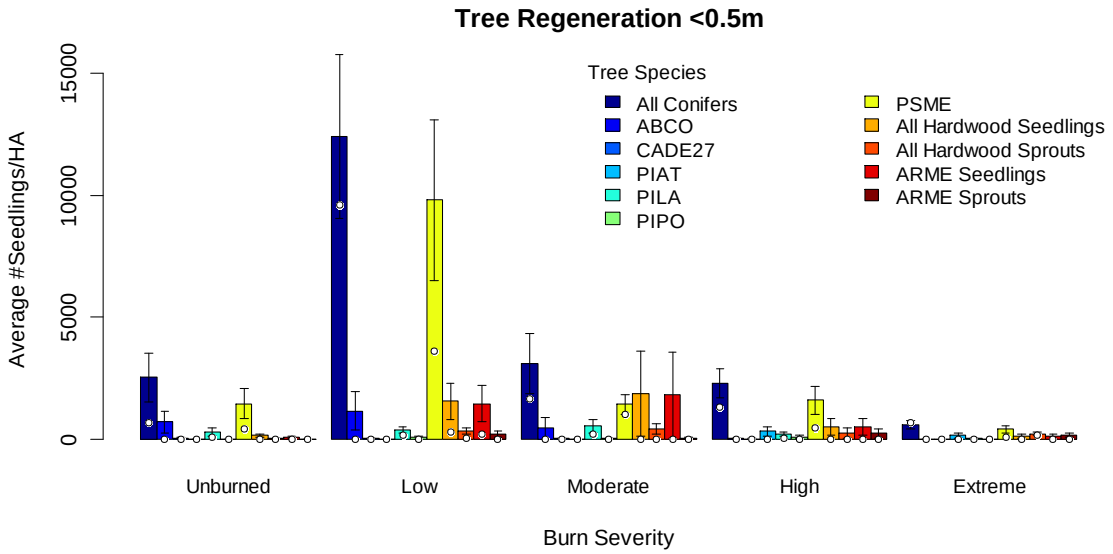


Figure 3.2: Sample plot layout at sites: (left) arrangement of the plot triad within a site, (right) plot detail showing location of 2.52 m radius microplots and transects. Large plot and LWD transects are 17.84 m horizontal distance, small plot is 12.61 m horizontal distance, 2.52 m transects are the thick, short lines within the microplot circles. Horizontal distance between plot centers is 50 m.

a



b

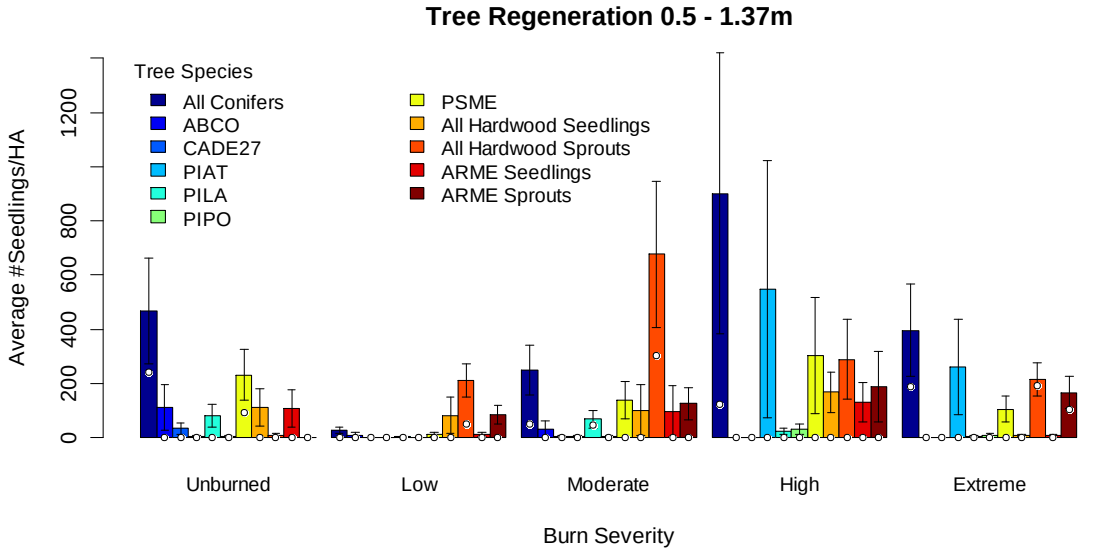


Figure 3.3: Seedling density (no./ha) based on burn severity for most common tree species less than 0.5 m (a), and 0.5-1.37 m (b). Burn severity is based on dNBR values, and represents an estimate of crown mortality, low: 0-35% (n = 21), moderate: 35-65% (n = 13), high: 65-95% (n = 18), extreme >95% (n = 13). Unburned measurements were collected outside the Biscuit Fire boundary (n =13). Bars denote means, error bars denote one standard error, white dots denote median values. Note scale differences on Y-axis. See Table 3.1 and Table 3.2 for species code descriptions.

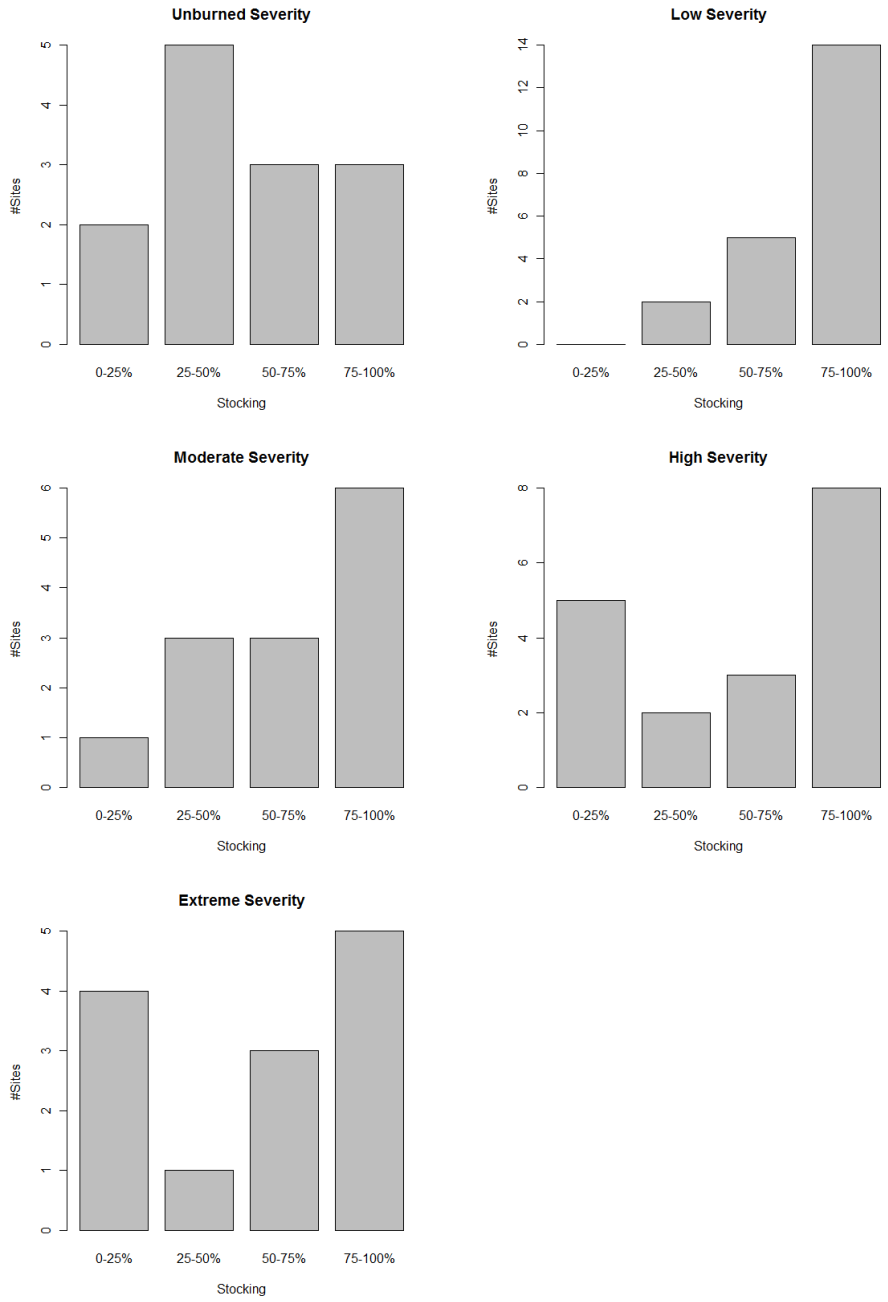


Figure 3.4: Distribution of the proportion of the 12 0.002 ha plots stocked with at least one seedling by burn severity. Note scale differences on Y-axes. See Figure 3.3 for details on burn severity classes.

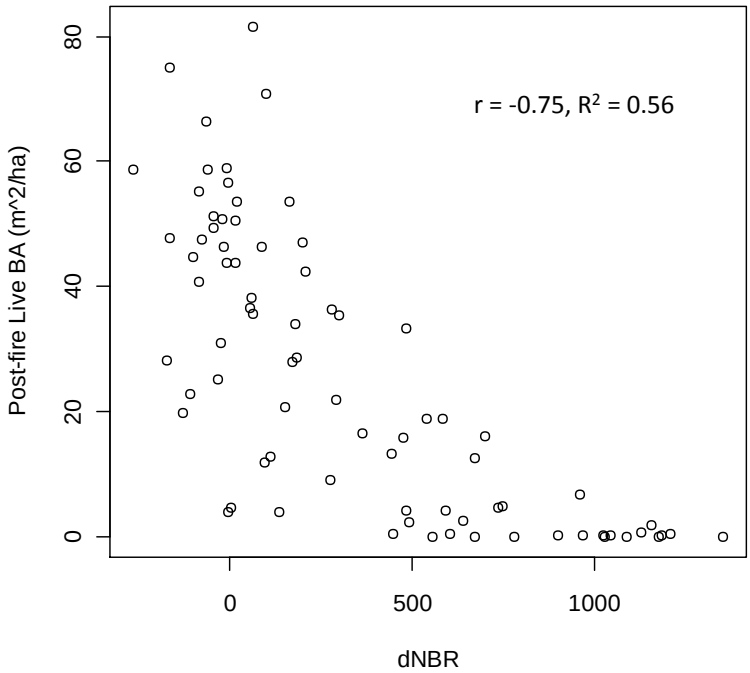


Figure 3.5: Scatterplot of dNBR values to post-fire LBA. Basal area values are based on plot measurements 6 years post-fire.

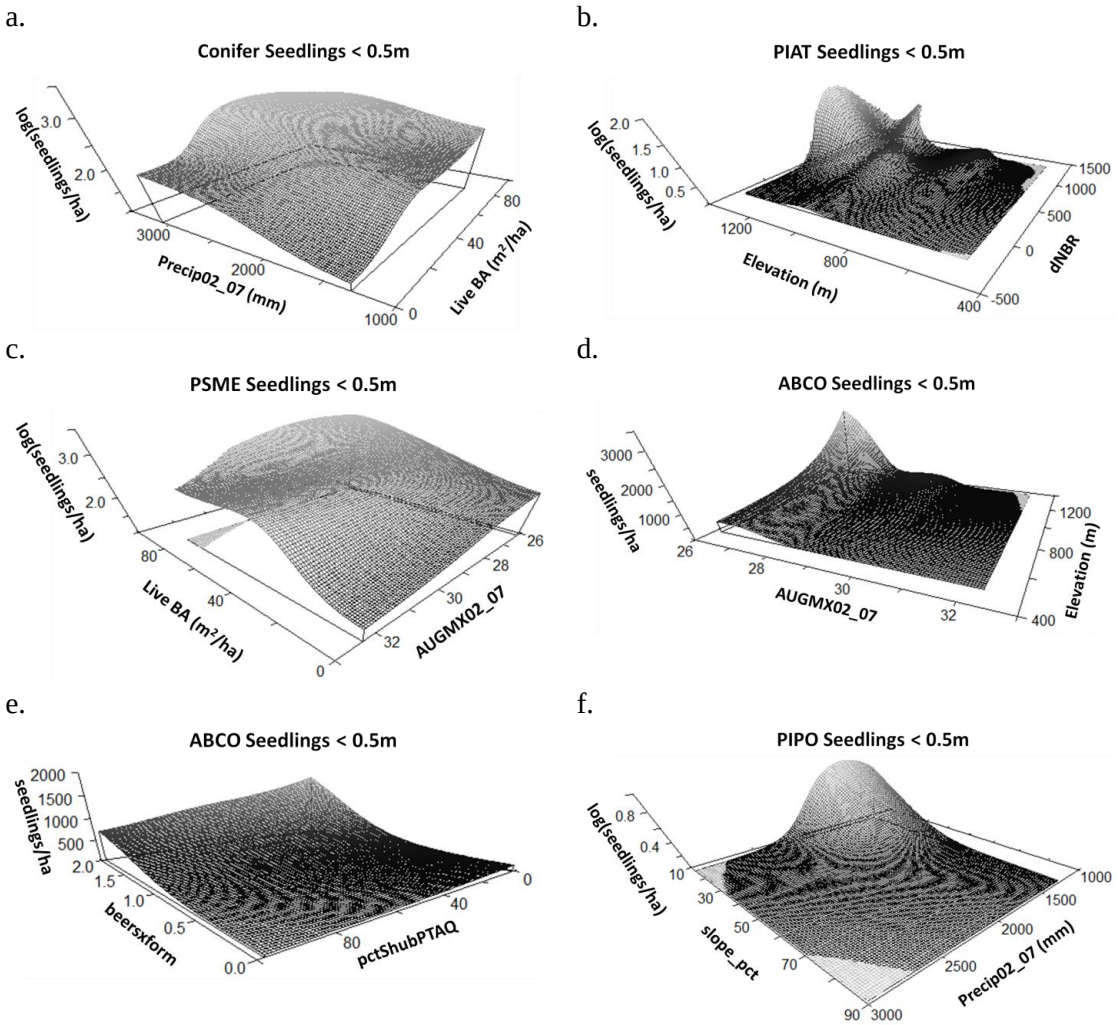


Figure 3.6: Relationship of short (<0.5 m) conifer seedling density to the two most sensitive explanatory variables based on NPMR model selection. The second ABCO graph (e) displays relationships to environmental variables that have been explored in other studies. See Table 3.1 for species code descriptions.

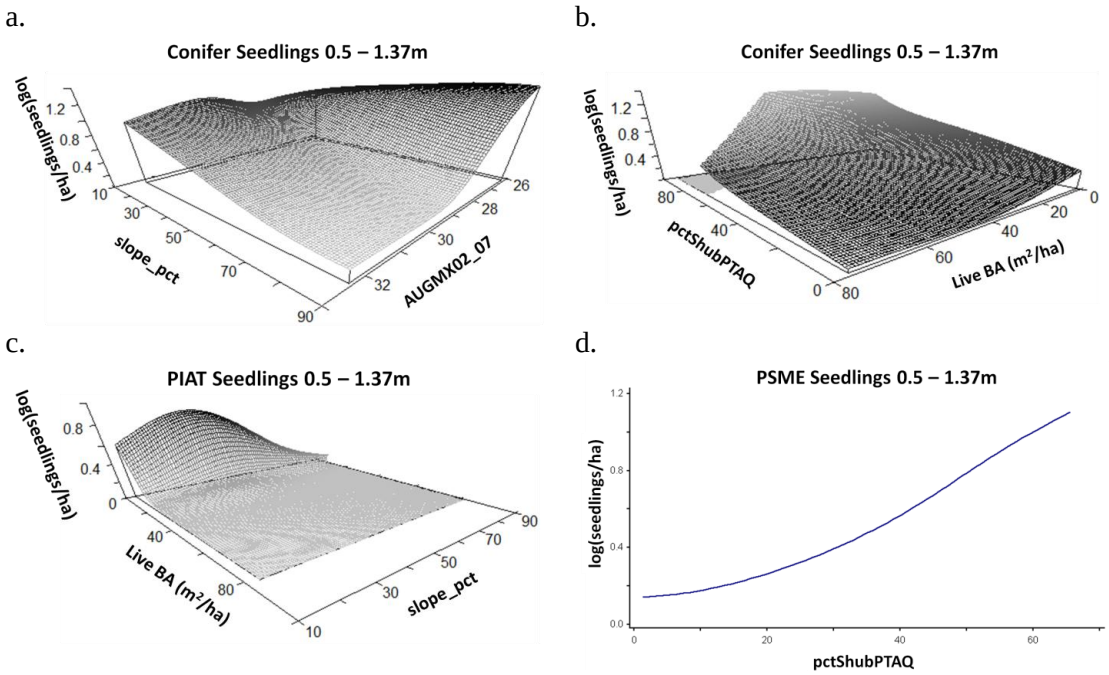


Figure 3.7: Relationship of tall (0.5-1.37 m) conifer seedling density to explanatory variables based on NPMR model selection. The first graph for each species denotes the two most sensitive model parameters. The second conifer graph (b) shows seedling density relationships to shrub cover and post-fire live basal area (details in text). PSME graph is two-dimensional because the only statistically significant model contained a single parameter. See Table 3.1 for descriptions of species codes.

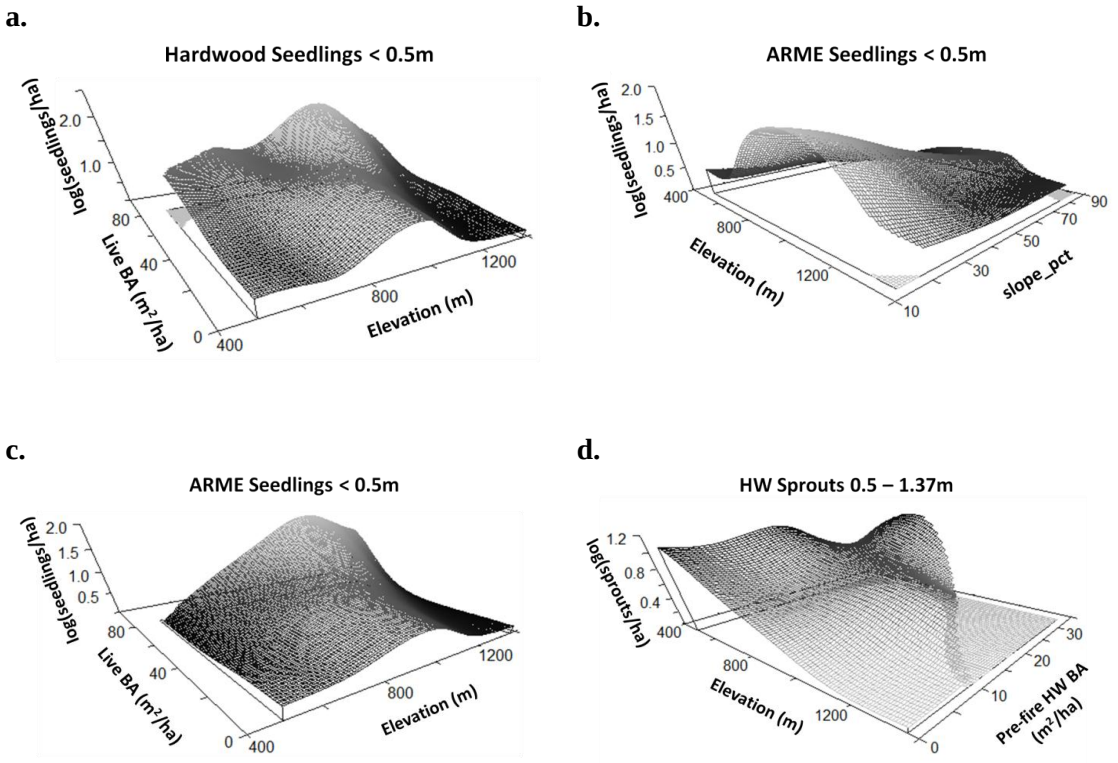


Figure 3.8: Relationship of hardwood seedling density (both short and tall height classes) to explanatory variables based on NPMR model selection. The first graph for each species denotes the two most sensitive model parameters. The second ARME graph (c) shows seedling density relationships to shrub cover and post-fire live basal area (details in text). See Table 3.2 for descriptions of species codes.

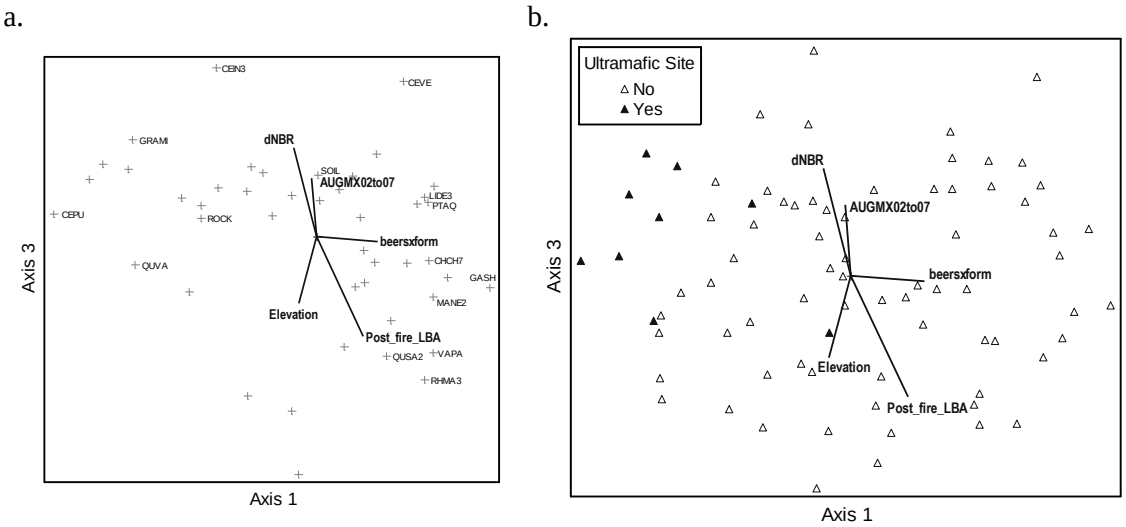


Figure 3.9: NMS ordinations of shrub species and ground cover categories: (a) species in site space, (b) sites in species space. Joint plot overlay shows environmental variables with high correlations to axis 1 or axis 3 (R^2 value > 0.1). Note how ultramafic sites are clustered in "b". Species labeled in "a" are those with an R^2 > 0.1 to at least one axis. See Table 3.8 for species code descriptions.

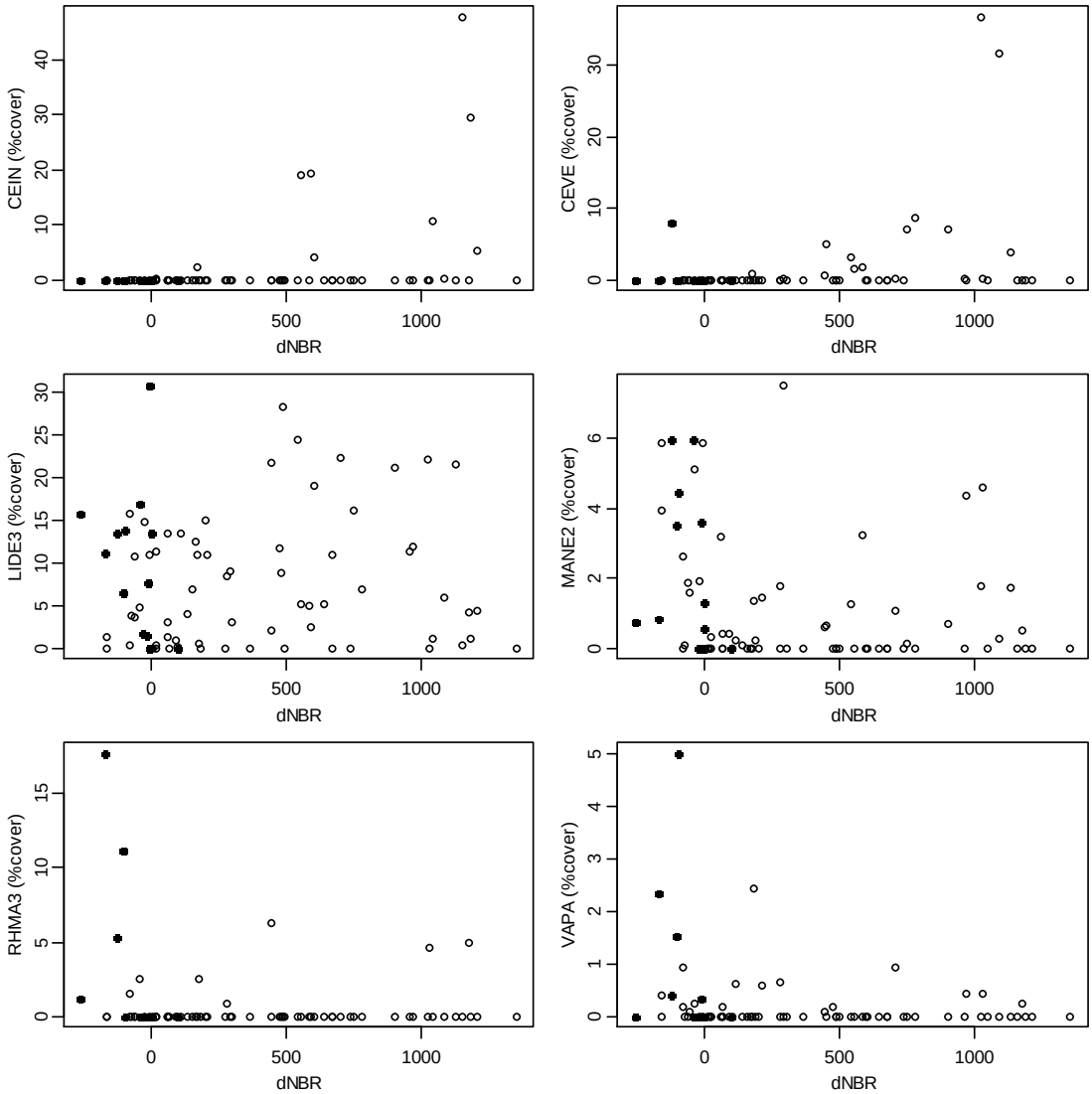


Figure 3.10: Relationship of percent ground cover to dNBR for six species highly associated with burn severity based on final NMS ordination solution. Open circles represent burned areas, closed circles represent unburned areas. See Table 3.8 for species code descriptions.

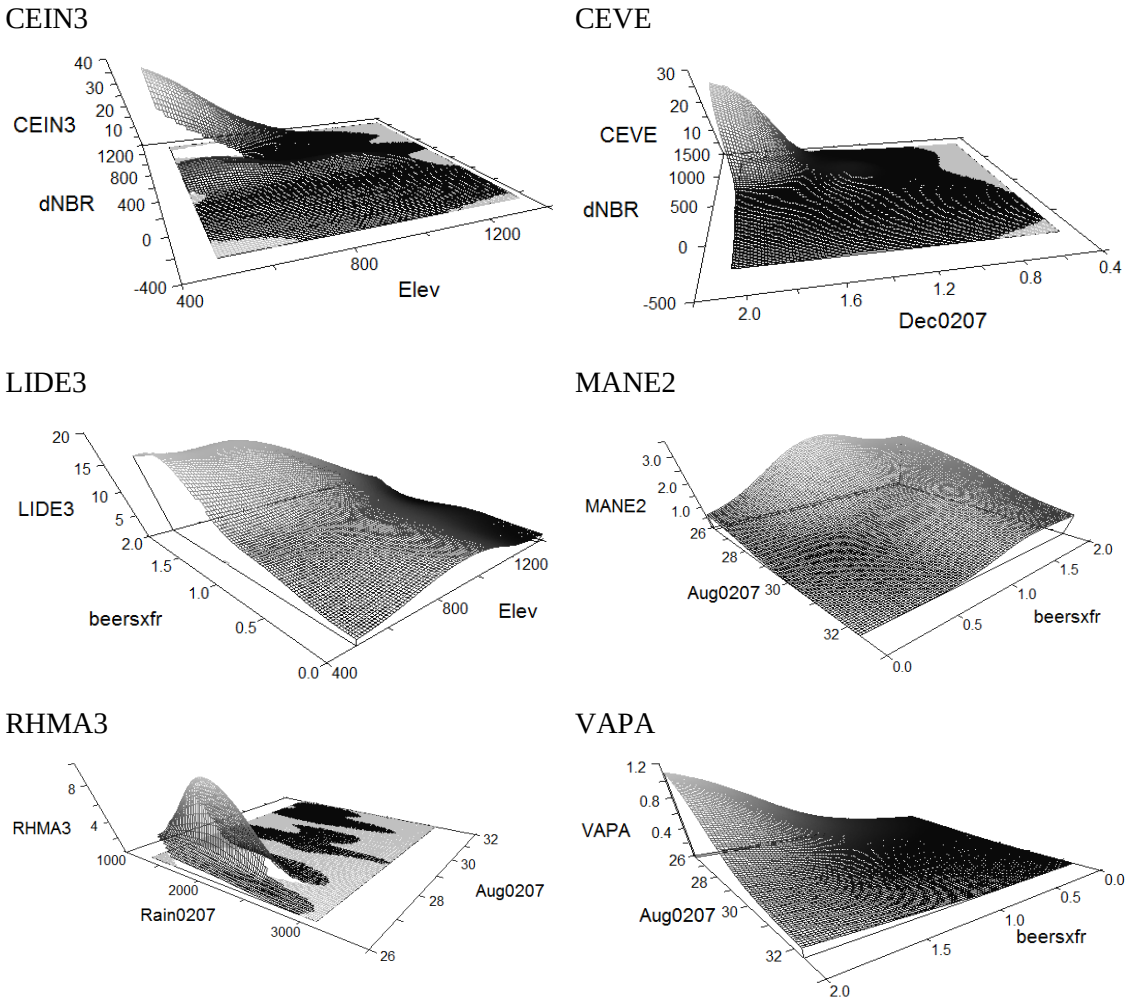


Figure 3.11: Relationship of percent cover to explanatory variables based on NPMR model selection for shrub species that have high correlations with burn severity. All figures display the two most sensitive variables selected, except VAPA which displays 2nd and 3rd most sensitive variables.

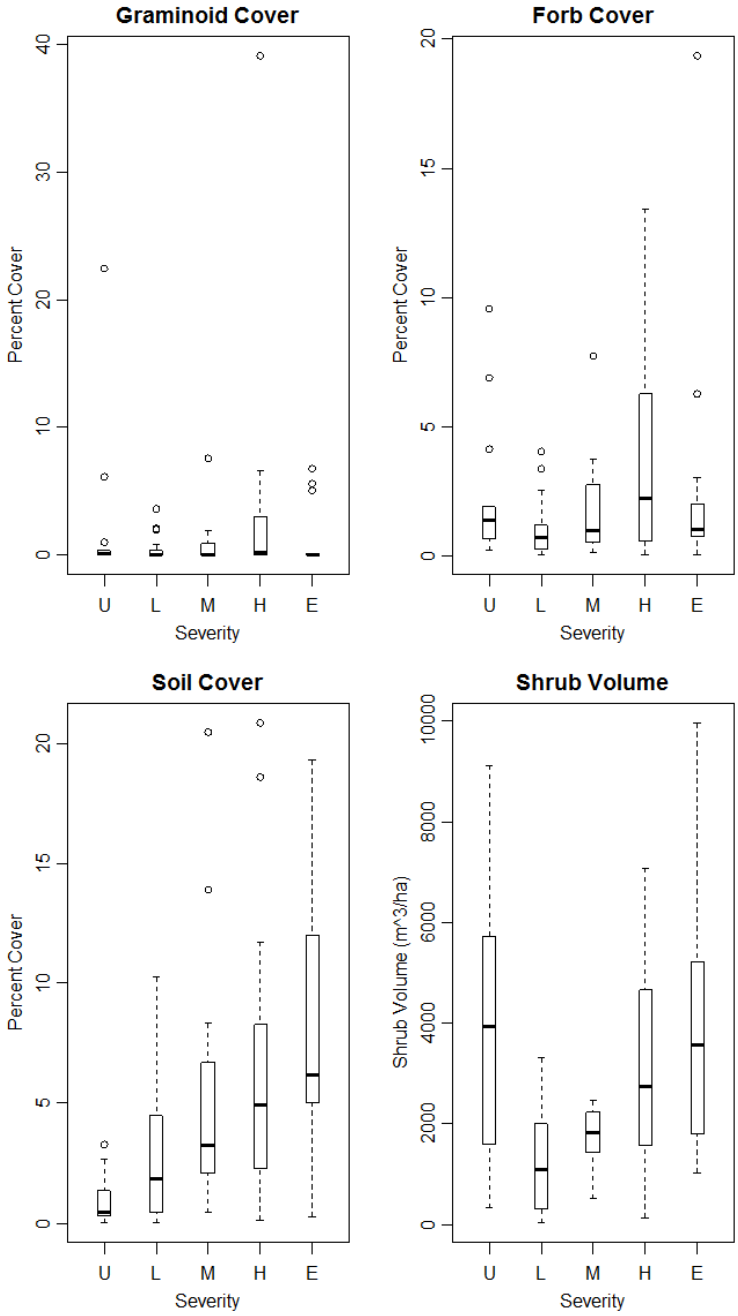


Figure 3.12: Distribution of graminoid cover, forb cover, soil cover and shrub crown volume by burn severity. U: unburned, L: low-severity, M: moderate-severity, H: high-severity, E: extreme severity. Dark bars represent medians, whiskers represent 1.5 times the interquartile range (IQR). Data were log-transformed prior to analysis.

Table 3.1: Conifer seedling density (no./ha) in different fire severity and height classes. Conifer represents all conifers, regardless of species. Burn severities correspond to crown mortality as estimated by dNBR values: low: 0-35% (n = 21), moderate: 35-65% (n = 13), high: 65-95% (n = 18), extreme >95% (n = 13). Unburned measurements were collected outside the Biscuit Fire boundary (n = 13). Species codes: ABCO - white fir (*Abies concolor*), CADE27 - incense cedar (*Calocedrus decurrens*), PIAT - knobcone pine (*Pinus attenuata*), PILA - sugar pine (*Pinus lambertiana*), PIPO - ponderosa pine (*Pinus ponderosa*), PSME - Douglas-fir (*Pseudotsuga menziesii*).

	Unburned			Low			Moderate			High			Extreme		
Species	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max
Seedlings <0.5 m															
Conifer	92	2538 (687)	9891	100	12408 (9632)	68333	100	3108 (1645)	15906	100	2304 (1313)	8834	100	594 (674)	1683
ABCO	31	714 (0)	5250	33	1162 (0)	16042	8	450 (0)	5852	6	27 (0)	490	0	0 (0)	0
CADE27	31	52 (0)	300	19	29 (0)	326	15	21 (0)	174	11	20 (0)	302	8	3 (0)	45
PIAT	0	0 (0)	0	5	4 (0)	87	8	7 (0)	90	39	318 (0)	2867	23	154 (0)	1002
PILA	77	292 (90)	624	67	367 (184)	2310	92	532 (192)	3680	67	217 (50)	1088	23	22 (0)	148
PIPO	0	0 (0)	0	10	71 (0)	1447	31	37 (0)	216	17	100 (0)	1235	7	3 (0)	45
PSME	92	1457 (403)	6098	95	9811 (3629)	67812	92	1441 (1025)	4370	83	1595 (461)	8834	92	404 (90)	1534

(continued)

(Table 3.1 continued)

Species	Unburned			Low			Moderate			High			Extreme		
	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max
Seedlings 0.5 - 1.37 m															
Conifer	69	467 (240)	2550	29	27 (0)	238	62	250 (48)	915	61	901 (124)	8692	69	396 (188)	2186
ABCO	30	110 (0)	1100	5	9 (0)	191	8	31 (0)	400	0	0 (0)	0	0	0 (0)	0
CADE27	30	33 (0)	283	0	0 (0)	0	8	3 (0)	43	0	0 (0)	0	0	0 (0)	0
PIAT	7	4 (0)	46	0	0 (0)	0	8	3 (0)	45	33	546 (0)	8602	31	259 (0)	2186
PILA	46	80 (0)	503	5	2 (0)	51	54	67 (45)	414	22	22 (0)	178	8	4 (0)	47
PIPO	8	4 (0)	47	0	0 (0)	0	8	4 (0)	48	16	30 (0)	309	8	7 (0)	90
PSME	53	231 (94)	1100	14	11 (0)	100	46	138 (0)	819	44	303 (0)	3755	39	105 (0)	523

Table 3.2: Hardwood seedling density(no./ha) in different fire severity and height classes. Seedlings denoted by "sd", sprouts denoted by "sr". Burn severities correspond to crown mortality as estimated by dNBR values: low: 0-35% (n = 21), moderate: 35-65% (n = 13), high: 65-95% (n = 18), extreme >95% (n = 13). Unburned measurements were collected outside the Biscuit Fire boundary (n =13). Species codes: HW - includes Pacific dogwood (*Cornus nuttallii*), Bigleaf maple (*Acer macrophyllum*), Califorina black oak (*Quercus kellogii*), red alder (*Alnus rubra*), ARME - Pacific madrone (*Arbutus menziesii*). The following species were considered shrubs rather than hardwood regeneration: golden chinquapin (*Chrysolepis chrysophylla*), tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), Oregon white oak (*Quercus garryana*), huckleberry oak (*Quercus vacciniifolia*), and Califorina bay laurel (*Umbellularia californica*).

	Unburned			Low			Moderate			High			Extreme		
Species	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max	% Sites	Mean (Med.)	Max
Seedlings <0.5 m															
HW (sd)	46	150 (0)	461	81	1558 (305)	14950	46	1870 (0)	22892	44	508 (0)	5948	39	113 (0)	1046
HW (sr)	8	24 (0)	315	52	330 (46)	2678	46	439 (0)	2440	39	270 (0)	3818	54	222 (183)	816
ARME (sd)	31	86 (0)	461	62	1451 (191)	14950	31	1808 (0)	22805	39	500 (0)	5948	31	110 (0)	1046
ARME (sr)	0	0 (0)	0	38	218 (0)	2678	15	40 (0)	482	28	234 (0)	3818	46	166 (0)	816
Seedlings 0.5 - 1.37 m															
HW (sd)	39	110 (0)	868	19	81 (0)	1413	23	101 (0)	1219	44	168 (0)	1222	15	7 (0)	48
HW (sr)	8	7 (0)	90	57	211 (51)	926	62	677 (303)	2581	39	288 (0)	2353	69	215 (193)	720
ARME (sd)	31	106 (0)	868	10	11 (0)	190	15	97 (0)	1219	33	130 (0)	1222	15	7 (0)	48
ARME (sr)	0	0 (0)	0	38	85 (0)	552	39	125 (0)	626	28	187 (0)	2353	62	165 (103)	720

Table 3.3: Proportion of sites with seedling densities meeting Biscuit EIS minimums at the 3-5 year mark (USDA Forest Service 2004).

Burn Severity	% Sites >333 trees/ha
Unburned	85%
Low	100%
Moderate	100%
High	83%
Extreme	69%

Table 3.4: Potential explanatory variables used in seedling density analysis.

Variable	Description
dNBR	dNBR values
beersxform	Aspect cosine-transformed to be between 0 and 2 (Beers 1966)
elevation	Elevation (m)
slope_pct	Slope (percent)
isUltramafic	Ultramafic soil (yes or no)
isUnburned	Site was outside the Biscuit Fire Boundary (yes or no)
isSilver	Site was also burned in the Silver Fire burn (yes or no)
PPT02to07[1]	Average precipitation 2002-2007 (mm)
DECMN02to07[1]	Average minimum December temperature 2002-2007 (°C)
AUGMX02to07[1]	Average maximum August temperature 2002-2007 (°C)
dist_to_Live_Tree_Edge	Distance (m) to nearest cluster of trees at least 1 ha in size, that experienced <65% crown mortality.
preFire_HW_BA	Pre-fire live hardwood basal area as calculated from plot data (m^2/ha)
post_fire_LBA	Post-fire live tree basal area as calculated from plot data (m^2/ha)
snagBA	Post-fire snag basal area as calculated from plot data (m^2/ha)
pctSOIL	Percent visible mineral soil as calculated from plot data
pctShrubPTAQ	Combined coverage of all shrubs and bracken fern, as calculated from plot data

[1]Climate information downloaded from http://www.prism.oregonstate.edu/ (Daly et al. 2002). Cell size 4km x 4km.

Table 3.5: Sensitivity/tolerance of explanatory variables for best models predicting short (<0.5 m) seedling density based on NPMR variable selection. Only statistically significant models are shown. All seedling densities were log-transformed except ABCO. "Conifer" denotes all conifers, regardless of species and regardless of whether they were common enough to be analyzed as a separate species. See Table 3.1 and Table 3.2 for species codes. "Seed" denotes that the species group reproduced via seeds rather than via vegetative propagation. No sensitivity or tolerance metrics can be calculated for categorical variables; models that include a categorical variable contain "NA" in the appropriate column. PIPO seedling density was lower on unburned sites. PSME seedling density was lower on ultramafic sites.

# Sites	Species	xR^2/ (p-val.)	#Var	Explanatory Variables: Sensitivity/(Tolerance)											
				Ultra.	Un-burned	Aspect	Precip (2002 - 2007)	AugMax (2002 - 2007)	% Shrub	dNBR	Elev.	% Slope	% Soil	Post-fire LBA	Pre-Fire HW BA
Seedlings <0.5 m															
77	Conifer	0.473	4	-	-	0.13	0.25	0.17	-	-	-	-	-	0.35	-
		(0.005)				(0.72)	(339.9)	(1.60)						11.41	
13	ABCO	0.466	4	-	-	0.070	-	0.11	0.053	-	0.079	-	-	-	-
		(0.020)				(0.46)		(0.62)	(26.52)		(229.1)				
12	PIAT	0.309	2	-	-	-	-	-	-	0.34	0.60	-	-	-	-
		(0.045)								(209.9)	(61.7)				
10	PIPO	0.691	4	-	NA	0.11	0.20	-	-	-	-	0.12	-	-	-
		(0.005)				(0.32)	(25045)					(13.0)			
71	PSME	0.582	4	NA	-	-	-	0.12	-	-	-	-	-	0.34	0.058
		(0.005)						(1.72)						(12.2)	(12.9)
44	HW	0.250	3	-	-	-	0.21	-	-	-	0.84	-	-	0.37	-
	(seed)	(0.025)					(46513)				(79.3)			(17.9)	
32	ARME	0.343	4	-	-	-	-	0.093	-	-	0.62	0.48	-	0.25	-
	(seed)	(0.025)						(2.59)			(114.5)	(12.2)		(17.9)	

Table 3.6: Sensitivity/tolerance of explanatory variables for best models for predicting tall (0.5-1.37 m) seedling and sapling density based on NPMR variable selection. Only statistically significant models are shown. All seedling densities were log-transformed before analysis. No sensitivity or tolerance metrics can be calculated for categorical variables; models that include a categorical variable contain "NA" the appropriate column. Hardwood sprout densities were higher on burned sites.

				Explanatory Variables: Sensitivity/(Tolerance)											
# Sites	Species	xR^2/ (p-val.)	#Var	Ultra.	Un-burned	Aspect	Precip (2002 - 2007)	AugMax (2002 - 2007)	% Shrub	dNBR	Elev.	% Slope	% Soil	Post-fire LBA	Pre-Fire HW BA
Seedlings 0.5 - 1.37 m															
43	Conifer	0.415	5	-	-	-	-	0.34	0.29	-	-	0.32	0.11	0.23	-
		(0.005)						(0.99)	(21.4)			(15.2)	(6.0)	(21.2)	
12	PIAT	0.445	3	-	-	-	-	-	-	-	0.23	0.27	-	0.53	-
		(0.040)									(211.4)	(12.2)		(5.7)	
29	PSME	0.182	1	-	-	-	-	-	1.64	-	-	-	-	-	-
		(0.025)							(11.2)						
37	HW	0.270	3	-	NA	-	-	-	-	-	0.57	-	-	-	0.527
	(sprout)	(0.010)									(141.0)				(5.27)

Table 3.7: Environmental variable correlations with NMS ordination of shrub species and ground cover types. Axis 1 accounts for 35% of the total variance, axis 2: 27%, and axis 3: 16% (total variance: 78%). All axes are 100% orthogonal to each other.

Axis:	1			2			3		
	r	R^2	tau	r	R^2	tau	r	R^2	tau
dNBR	-0.263	0.069	-0.199	0.112	0.012	0.07	0.522	0.272	0.365
beersxform	0.43	0.185	0.276	0.264	0.07	0.166	-0.118	0.014	-0.11
elevation	-0.232	0.054	-0.163	0.323	0.104	0.256	-0.453	0.206	-0.308
slope_pct	-0.257	0.066	-0.171	-0.109	0.012	-0.079	-0.026	0.001	-0.034
PPT02to07	-0.098	0.01	-0.051	0.242	0.058	0.157	-0.109	0.012	-0.08
DECMN02to07	0.154	0.024	0.115	0.149	0.022	0.071	-0.041	0.002	-0.049
AUGMX02to07	-0.121	0.015	-0.133	-0.391	0.153	-0.243	0.423	0.179	0.277
post_fire_LBA	0.381	0.145	0.261	-0.354	0.125	-0.21	-0.553	0.306	-0.379
SnagBA	-0.017	0	-0.009	-0.001	0	-0.005	0.309	0.095	0.164

Table 3.8: Site occupancy, max % cover, mean % cover, and species/ground cover scores for NMS ordination of shrub species and ground cover types. Only species with an NMS R^2 value greater than 0.1 are listed. Mean % cover calculations exclude sites where species was not present.

Code	Species Name/Cover Type	# Sites	Max Cover	Mean Cover	NMS Scores: r	R^2	tau
Axis 1:							
CEPU	*Ceanothus pumilus*	8	4.0%	1.3%	-0.351	0.123	-0.403
CHCH7	*Chrysolepis chrysophylla*	46	15.2%	2.5%	0.343	0.118	0.311
GASH	*Gaultheria shallon*	28	49.1%	7.5%	0.428	0.183	0.438
GRAMI	Graminoids	59	39.1%	2.3%	-0.365	0.133	-0.170
LIDE3	*Lithocarpus densiflorus*	66	30.8%	9.4%	0.671	0.450	0.535
MANE2	*Mahonia nervosa*	46	7.5%	2.0%	0.455	0.207	0.417
PTAQ	*Pteridium aquilinum*	43	8.3%	1.9%	0.348	0.121	0.362
QUVA	*Quercus vacciniifolia*	30	19.0%	5.1%	-0.511	0.261	-0.466
ROCK	Rock	77	58.3%	13.0%	-0.671	0.450	-0.617
Axis 2:							
CEIN3	*Ceanothus integerrimus*	14	47.8%	10.0%	-0.384	0.147	-0.305
CHCH7	*Chrysolepis chrysophylla*	46	15.2%	2.5%	0.422	0.178	0.432
QUSA2	*Quercus sadleriana*	21	20.0%	7.0%	0.397	0.157	0.432
ROCK	Rock	77	58.3%	13.0%	0.355	0.126	0.204
Axis 3:							
CEIN3	*Ceanothus integerrimus*	14	47.8%	10.0%	0.368	0.135	0.267
CEVE	*Ceanothus velutinus*	29	36.7%	4.0%	0.353	0.125	0.286
LIDE3	*Lithocarpus densiflorus*	66	30.8%	9.4%	0.351	0.123	0.217
MANE2	*Mahonia nervosa*	46	7.5%	2.0%	-0.330	0.109	-0.244
QUSA2	*Quercus sadleriana*	21	20.0%	7.0%	-0.454	0.206	-0.342
RHMA3	*Rhododendron macrophyllum*	11	17.7%	5.3%	-0.351	0.123	-0.358
SOIL	Soil	78	20.9%	4.6%	0.477	0.227	0.360
VAPA	*Vaccinium parvifolium*	21	5.0%	0.9%	-0.328	0.107	-0.333

Table 3.9: Sensitivity/tolerance of explanatory variables for best models for predicting percent cover of shrub species that have high correlations with burn severity.

# Sites	Species	xR^2/ (p-val.)	# Var	Explanatory Variables: Sensitivity/(Tolerance)						
				dNBR	beersxfr	Elevation	pctSlope	Rain0207	Aug0207	Dec0207
14	CEIN3	0.49/ 0.040	2	0.37 (80.7)	-	0.19 (123.3)	-	-	-	-
29	CEVE	0.60/ 0.034	3	0.24 (177.6)	-	-	0.046 (20.6)	-	-	0.15
66	LIDE3	0.29/ 0.005	2	-	0.53 (0.28)	0.65 (140.0)	-	-	-	-
46	MANE2	0.25/ 0.010	2	-	0.53 (0.36)	-	-	-	0.50 (1.05)	-
11	RHMA3	0.43/ 0.020	2	-	-	-	-	0.19 (268.3)	1.24 (0.18)	-
21	VAPA	0.47/ 0.010	4	-	0.16 (0.46)	-	0.30 (9.14)	0.079 (554.6)	0.14 (1.48)	-

Table 3.10: ANOVA/ANCOVA results for differences in live fuels and soil cover based on fire severity. Fire severity classes included unburned, low, moderate, high, and extreme.

Cover Type	Covariate	Model Result
Graminoids	Elevation $F(1,72) = 9.44$, $p = 0.030$	$F_{(4,72)} = 0.668$, $p = 0.616$
Forbs	None	$F_{(4,73)} = 1.760$, $p = 0.146$
Shrub Crown Volume	None	$F_{(4,73)} = 1054.2$, $p < 0.0001$
Soil	None	$F_{(4,73)} = 8.021$, $p < 0.0001$

Table 3.11: Significant differences in shrub crown volume and soil cover by burn severity. Significant differences based on post-hoc comparisons of all burn severities (10 comparisons total) using the Tukey HSD test 95% family-wise confidence interval. Results have been back-transformed from logged data. Differences represent multiplicative differences in median values for each cover type. For example, median shrub volumes are 3.1 times higher on high severity burn sites than low severity burn sites. Upper and lower bounds represent 95% adjusted confidence intervals.

Burn Severities	Difference	Lower bound	Upper bound	p-adjusted
Shrub Crown Volume				
Unburned-Low	4.2	1.7	10.2	0.0002
High-Low	3.1	1.4	7.0	0.0015
Extreme-Low	4.3	1.8	10.5	0.0001
Percent Soil Cover				
Medium-Unburned	6.7	1.6	28.1	0.0034
High-Unburned	7.5	2.0	28.5	0.0006
Extreme-Unburned	11.6	2.8	48.6	< 0.0001
Extreme-Low	4.6	1.3	16.5	0.013

CHAPTER 4: CONCLUSIONS

In this thesis I examined what associations dead fuels and understory vegetation had with fire severity six years after the Biscuit Fire. I found that most fuels and understory vegetation varied with burn severity, though these relationships differed by fuel type, vegetation species, and other factors. This study represents a snapshot of a single point in time. The relationships of fuels and vegetation to fire severity probably differed immediately after the fire, and will almost certainly change over time. Nonetheless, the findings in this study provide a baseline for comparison with future vegetation and forest succession, changes in dead fuel quantities, and their potential impacts on future fire disturbances. These findings also show why it is important to consider the full range of fire severities when looking at the impact of a mixed-severity fire disturbance.

DEAD FUELS

Six years after the Biscuit Fire, the biomass and depth of litter and duff was lower on burned sites than unburned sites, and lowest on high-severity sites. This relationship was reversed for large-diameter woody fuels, where quantities were highest in high- and extreme-severity areas, though there was no evidence that quantities differed between low-severity and unburned sites. Unlike litter/duff and LWD, 10- and 100-hour fuels showed no relationship with burn severity. The different relationships between litter/duff, 10- and 100-hour fuels, and LWD imply that the creation and decomposition of different fuel classes are governed by different processes. The linear regression models support this idea as different biotic, abiotic, and climatic variables were selected for different size fuel class models. The NMS ordination also demonstrates the different structures and relationships of dead fuels. Just as the linear regression analysis revealed three different associations with burn severity based on fuel size,

the three axes in the final NMS solution align with three size classes of dead fuels: small, medium, and large.

There was no evidence of a difference in fuel quantities or overall fuel composition between sites that burned only in the Biscuit Fire and sites that also burned 15 years earlier in the Silver Fire. Overall fuel composition did differ between burned sites and unburned sites, but this difference disappeared if litter and duff quantities were not considered. Though linear regression models indicated large woody debris quantities were associated with burn severity, when all fire severities were considered the overall composition of 10-, 100-hour fuels and LWD did not differ between burned sites (both short-interval and long-interval) and unburned sites.

Fuel composition did differ based on soil type for sites burned in the Biscuit Fire. Fuel quantities were lower on ultramafic sites than non-ultramafic sites. However, lower dead fuel quantities do not necessarily relate to lower burn severities. A prior study found median crown damage was much higher on ultramafic sites than non ultramafic (92% vs. 59%) after the Biscuit Fire (Thompson and Spies 2009).

UNDERSTORY VEGETATION

Seedling response to fire severity varied by size class and species, though seedling densities were almost always higher than the minimums detailed in the Biscuit Fire EIS (USDA Forest Service 2004). In general, densities of short seedlings were highest in low-severity areas and lowest on high- and extreme-severity areas. This trend was reversed for tall seedlings. It is unclear whether seedlings in the two size classes also represented different age classes. The high number of short seedlings in low-severity areas might be seedlings that established immediately after the Biscuit Fire, but grow slowly due to resource competition

from established overstory trees. They may also be ephemeral; short seedlings in low-severity areas die after a short time but are quickly replaced due to plentiful seed sources and suitable seed beds. Similarly, it is unclear whether tall seedlings in high-severity areas are those that established immediately post-fire, or if they are younger seedlings that flourished in high-severity conditions. Seedlings may continue to establish one to two decades after a fire disturbance (Shatford et al. 2007), so seedlings in high-severity areas may represent different establishment times regardless of height.

Shrub species richness and diversity did not vary with burn severity; but shrub species and ground cover type composition did differ with burn severity six years after the Biscuit Fire. Understory cover composition with burn severity aligned with species life history traits; fire-adapted, nitrogen-fixing species were more prevalent on high- and extreme-severity sites while species associated with low-severity fire or old-growth forests were more prevalent on low-severity or unburned sites. I found no evidence of difference in total graminoid or forb cover based on fire severity, but shrub quantities were lower on low-severity sites than on unburned, high-, or extreme-severity sites. The differences in shrub quantity and composition by burn severity underscore the importance of live fuel quantities and dynamics in addition to dead fuels, when considering factors on future fire severity.

It is important to consider the impacts of both dead fuels and vegetation on future fire severity. In this study, quantities of fuels that I would expect to be most associated with fire spread (litter, duff, and small-diameter woody fuels) were not highest on high- and extreme-severity sites. Nonetheless, areas that burned at high severity in the 1987 Silver Fire tended to reburn with high severity in the 2002 Biscuit Fire (Thompson et al. 2007). It is possible that the relationships between these fuels and fire severity were different 15 years post-fire

compared to the relationships I found 6 years after the Biscuit Fire, perhaps due to snag decay. However, live fuels may also have contributed to high fire severity in reburned areas. Live fuels may have a dampening effect on fire, but may also ignite and contribute to fire spread and increased fire severity (Burgan 1979, Weise et al. 2005). Live fuels may also contribute to dead fuel quantities. If live fuels are overtopped by tree seedlings in the high-severity areas, and die due to resource competition, they may contribute huge quantities of small-diameter woody fuels that can influence fire spread and severity. Future dynamics of dead fuels cannot be fully understood without considering the vegetation context, and how it may change over time.

FUTURE IMPLICATIONS AND RESEARCH

The use of stepwise selection (or any other model selection technique without a limited set of a priori models) entails the risk of finding relationships where none exist, or missing important relationships. As this study investigates a natural experiment, I cannot infer causal relationships between burn severity and fuels or vegetation. Despite these limitations, exploratory studies create a framework for discussion and future investigations which may then use other analysis techniques and allow the creation of a priori hypotheses for further testing.

Six years after the Biscuit Fire, vegetation and dead fuels show relationships to fire severity. Prior studies that focused on high-severity areas overlook these relationships, and ignore a large proportion of the landscape affected by fire disturbance. In order to understand the mechanics of a complex system like the mixed-evergreen forests of the Klamath-Siskiyous, it is necessary to look at the full range of disturbed areas and investigate how all respond to a disturbance, not just ~20% of the area that represents the highest impact on tree

survival. The relationship of fire severity to fuels and vegetation may disappear, decrease or change in subsequent decades. Shrub species quantity and composition, especially in high- and extreme severity areas, may change if seedlings continue to grow and overtop the shrub layer. Shrub mortality could also contribute to an increase in small-diameter dead fuels. Current seedling densities meet or exceed target densities as described in the Biscuit EIS, though it is unclear whether these seedlings are ephemeral or if they will survive in the long term. Longevity of seedlings may also vary based on factors specific to the area of establishment, including burn severity.

Future studies should investigate how regeneration, diversity, and live and dead fuels change over time, and should do so over the full range of burn severities in a mixed-severity fire regime. Ideally, my study sites would be remeasured in the future, so that they could be compared to these baseline measurements. Understanding how fuels and vegetation change, and how those changes relate to initial fire disturbance severity, will be important in understanding ecological processes and predicting potential future impacts of large, mixed-severity fires.

LITERATURE CITED

Burgan, R. E. 1979. Estimating live fuel moisture for the 1978 National Fire-Danger Rating System. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-226, Ogden, Utah, p. 17.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry 105:139-146.

Thompson, J. R. and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management 258:1684-1694.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America 104:10743-10748.

USDA Forest Service. 2004. Biscuit Fire recovery project, final environmental impact statement. Medford, OR.

Weise, D. R., X. Y. Zhou, L. L. Sun, and S. Mahalingam. 2005. Fire spread in chaparral - ‘go or no-go?’. International Journal of Wildland Fire 14:99-106.

BIBLIOGRAPHY

Agee, J. 1998. The landscape ecology of western forest fire regimes. Northwest Science **72**:24-34.

Agee, J. K. 1991. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. Northwest Science **65**:188-199.

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.

Agee, J. K. 2003. Monitoring postfire tree mortality in mixed-conifer forests of Crater Lake, Oregon, USA. Natural Areas Journal **23**:114-120.

Agee, J. K. and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management **211**:83-96.

Agee, J. K., C. S. Wright, N. Williamson, and M. H. Huff. 2002. Foliar moisture content of Pacific Northwest vegetation and its relation to wildland fire behavior. Forest Ecology and Management **167**:57-66.

Albini, F. A. 1976. Estimating wildfire behavior and effects. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-GTR-30, Ogden, UT, p. 92.

Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-122, Ogden, Utah, p. 22.

Anderson, M. D. 2001. *Ceanothus velutinus*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/ceavel/all.html [2011, March 8].

Antoine, M. E. and B. McCune. 2004. Contrasting fundamental and realized ecological niches with epiphytic lichen transplants in an old-growth Pseudotsuga forest. Bryologist **107**:163-172.

Atzet, T. and D. Wheeler. 1982. Historical and ecological perspectives on fire activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests. USDA Forest Service, Pacific Northwest Region Publication R-6, Portland, OR, p. 19.

Atzet, T. A. and R. Martin. 1992. Natural disturbance regimes in the Klamath province. Pages 40-48 *in* Proceedings of the Symposium on Biodiversity of Northwestern California. Portland OR, USDA Forest Service, Pacific Northwest Region.

Atzet, T. A., D. Wheeler, and R. Gripp. 1988. Fire and forestry in southwest Oregon: Importance of fire. Oregon State University Extension Service, FIR Report, Winter 1988, Medford, Oregon, USA, pp. 4-7.

Avery, T. E. and H. E. Burkhart. 2002. Forest Measurements. 5th edition. McGraw-Hill, New York, NY.

Azuma, D. L., J. Donnegan, and D. Gedney. 2004. Southwest Oregon Biscuit Fire: An analysis of forest resources and fire severity. Portland, OR, p. 32.

Battaglia, L. L., S. A. Fore, and R. R. Sharitz. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. Journal of Ecology **88**:1041-1050.

Beers, T. 1966. Notes and observations: Aspect transformation in site productivity research. Journal of Forestry **64**:691-692.

Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology **76**:1156-1168.

Biondini, M., P. Mielke, and K. Berry. 1988. Data-dependent permutation techniques for the analysis of ecological data. Plant Ecology **75**:161-168.

Bray, J. and J. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs **27**:325-349.

Brewer, C. K., J. C. Winne, R. L. Redmond, D. W. Opitz, and M. V. Mangrich. 2005. Classifying and mapping wildfire severity: A comparison of methods. Photogrammetric Engineering and Remote Sensing **71**:1311-1320.

Brown, J. 1974. Handbook for inventorying downed woody material. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-16, Ogden, UT, p. 24.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: Principles in the context of place. Conservation Biology **18**:903-912.

Burgan, R. E. 1979. Estimating live fuel moisture for the 1978 National Fire-Danger Rating System. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-226, Ogden, Utah, p. 17.

Burnham, K. P. and D. R. Anderson 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research-Biogeosciences **112**:G04014.

Chappell, C. B. and J. K. Agee. 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades, Oregon. Ecological Applications **6**:628-640.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management **44**:773-786.

Colombaroli, D. and D. G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. Proceedings of the National Academy of Sciences of the United States of America **107**:18909-18914.

Cooper, L. J. 1939. A history of the Siskiyou National Forest. Unpublished report on file with the Siskiyou National Forest, Grants Pass, Oregon.

Countryman, C. M. 1955. Old-growth conversion also converts fireclimate. U.S. Forest Service Fire Control Notes **17**:15-19.

Countryman, C. M. and C. W. Philpot. 1970. Physical characteristics of chamise as a wildland fuel. USDA Forest Service, Pacific Southwest Forest & Range Experiment Station, Research Paper PSW-RP-66, Berkeley, CA, p. 16.

Crane, M. F. 1990. *Rhododendron macrophyllum*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/rhomac/all.html [2011, March 8].

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research **22**:99-113.

Dolling, A. 1999. The vegetative spread of *Pteridium aquilinum* in a hemiboreal forest - invasion or revegetation? Forest Ecology and Management **124**:177-184.

Donato, D., J. Campbell, J. Fontaine, and B. Law. 2009a. Quantifying char in postfire woody detritus inventories. Fire Ecology **5**:104-115.

Donato, D. C. 2008. Forest vegetation and fuel dynamics following stand-replacing wildfire, re-burn, and postfire management in the Siskiyou Mountains, Oregon. Dissertation. Oregon State University, Corvallis, OR.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science **311**:352-352.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009b. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **39**:823-838.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009c. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology **97**:142-154.

Dunn, C. J. 2010. Coarse woody detritus dynamics, variable decay rates and their contribution to wildland fuel succession following high-severity fire disturbance in dry-mixed conifer forests of Oregon's eastern Cascades. Master's thesis. Oregon State University, Corvallis, OR.

ESRI (Environmental Systems Resource Institute). 2010. ArcMap 9.3.1. Redlands, California. Available:

Fowells, H. A. and N. B. Stark. 1965. Natural regeneration in relation to environment in the mixed conifer forest type of California. USDA Forest Service, Pacific Southwest Forest & Range Experiment Station, Research Paper PSW-RP-24, Berkeley, CA, p. 14.

Fox, J. and S. Weisberg. 2010. car: Companion to Applied Regression. R package version 2.0-2. Available: http://CRAN.R-project.org/package=car

Franklin, J. F. and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Fule, P. Z. and W. W. Covington. 1994. Double sampling increases the efficiency of forest floor inventories for Arizona ponderosa pine forests. International Journal of Wildland Fire **4**:3-10.

GAO. 2004. Biscuit Fire: Analysis of fire response, resource availability, and personnel certification standards. United States General Accounting Office, GAO-04-426, Washington, DC.

George, L. O. and F. A. Bazzaz. 1999. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. Ecology **80**:833-845.

Gliessman, S. R. and C. H. Muller. 1978. Allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. Journal of Chemical Ecology **4**:337-362.

Gray, A. N. and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology **84**:635-645.

Green, L. R. 1982. Prescribed burning in the California mediterranean ecosystem. Pages 464-471 *in* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, June 22-26. USDA Forest Service General Technical Report PSW-058, San Diego, CA.

Hall, W. L., H. R. Zuuring, C. C. Hardy, and R. H. Wakimoto. 2003. Applying logistic regression to determine regeneration risk to stand replacement fire on the Kootenai National Forest, Montana. Western Journal of Applied Forestry **18**:155-162.

Halofsky, J. E. and D. E. Hibbs. 2009. Relationships among indices of fire severity in riparian zones. International Journal of Wildland Fire **18**:584-593.

Harmon, M. E., G. A. Baker, G. Spycher, and S. E. Greene. 1990. Leaf-litter decomposition in the *Picea-Tsuga* forests of Olympic National Park, Washington, USA. Forest Ecology and Management **31**:55-66.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133-302.

Harrell, F. E., Jr. 2007. Design: Design Package. R package version 2.1-1. Available: http://biostat.mc.vanderbilt.edu/s/Design, http://biostat.mc.vanderbilt.edu/rms

Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology **17**:837-845.

Heiberger, R. M. 2008. HH: Statistical analysis and data display: Heiberger and Holland. R package version 2.1-12. Available: http://CRAN.R-project.org/package=HH

Hermann, R. K. and D. P. Lavender. 1990. *Pseudotsuga menziesii* - Douglas-fir. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Howard, J. L. 1992a. *Arctostaphylos viscida*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/arcvis/all.html [2011, April 13].

Howard, J. L. 1992b. *Pinus attenuata*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/pinatt/all.html [2011, March 2].

Howard, J. L. 1997. *Ceanothus integerrimus*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory

(Producer). Available: http://www.fs.fed.us/database/feis/plants/shrub/ceaint/all.html [2011, March 3].

Irvine, D. R., D. E. Hibbs, and J. P. A. Shafford. 2009. The Relative Importance of Biotic and Abiotic Controls on Young Conifer Growth after Fire in the Klamath-Siskiyou Region. Northwest Science **83**:334-347.

Isaac, L. A. 1930. Seed flight in the Douglas-fir region. Journal of Forestry **24**:492-499.

Isaac, L. A. 1940. Vegetative succession following logging in the Douglas Fir region with special reference to fire. Journal of Forestry **38**:716-721.

Jolly, W. M. 2007. Sensitivity of a surface fire spread model and associated fire behaviour fuel models to changes in live fuel moisture. International Journal of Wildland Fire **16**:503-509.

Kane, J. M., J. M. Varner, E. E. Knapp, and R. F. Powers. 2010. Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. Applied Vegetation Science **13**:207-220.

Kauffman, J. B. and R. E. Martin. 1990. Sprouting shrub response to different seasons and fuel consumption levels of prescribed fire in Sierra-Nevada mixed conifer ecosystems. Forest Science **36**:748-764.

Keane, R. E., J. K. Agee, P. Fule, J. E. Keeley, C. Key, S. G. Kitchen, R. Miller, and L. A. Schulte. 2008. Ecological effects of large fires on US landscapes: benefit or catastrophe? International Journal of Wildland Fire **17**:696-712.

Keifer, M., J. W. van Wagtendonk, and M. Buhler. 2006. Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the central and southern Sierra Nevada, CA (USA). Fire Ecology **2**:53-72.

Kennedy, R. S. H. and T. A. Spies. 2007. An assessment of dead wood patterns and their relationships with biophysical characteristics in two landscapes with different disturbance histories in coastal Oregon, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **37**:940-956.

Keyser, T. L., L. B. Lentile, F. W. Smith, and W. D. Shepperd. 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. Forest Science **54**:328-338.

Kinloch, B. B., Jr. and W. H. Scheuner. 1990. *Pinus lambertiana* Dougl. - Sugar Pine. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Laacke, R. J. 1990. *Abies magnifica* A. Murr. - California Red Fir. *in* Agriculture Handbook 654, Silvics of North America: 1. Conifers. R. M. Burns and B. H. Honkala, (tech. coords.). U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Larson, A. J. and J. F. Franklin. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management **218**:25-36.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:2875-2885.

Lewis, H. T. 1989. Reconstructing Patterns of Indian Burning in Southwestern Oregon. Pages 80-84 *in* Living with the land: The Indians of southwest Oregon. The proceedings of the 1989 Symposium on the Prehistory of Southwest Oregon. Southern Oregon Historical Society, Medford, OR.

Lutes, D. C., R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, S. Sutherland, and L. J. Gangi. 2006. FIREMON: Fire Effects Monitoring and Inventory System. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-164-CD, Ogden, UT, p. 400.

Marshall, P. L., G. Davis, and S. W. Taylor. 2003. Using Line Intersect Sampling for Coarse Woody Debris: Practitioners Questions Addressed. BC Ministry of Forests, Research Section, Coast Forest Region, Nanaimo, BC.

Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78-95 *in* Wildlife Habitats in Managed Forests the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553. J. W. Thomas, editor. USDA Forest Service.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons, New York, NY.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. Journal of Vegetation Science **17**:819-830.

McCune, B. 2009. Nonparametric multiplicative regression for habitat modeling. http://www.pcord.com/NPMRintro.pdf

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2009. HyperNiche. Nonparametric Multiplicative Habitat Modeling. Version 2.07. MjM Software, Gleneden Beach, Oregon, U.S.A.

McCune, B. and M. J. Mefford. 2010. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.243 beta. MjM Software, Gleneden Beach, Oregon, U.S.A.

McDonald, P. M. 1978. Silviculture-ecology of three native California hardwoods on high sites in north central California. Dissertation. Oregon State University, Corvallis, OR.

Meigs, G. W., D. C. Donato, J. L. Campbell, J. G. Martin, and B. E. Law. 2009. Forest fire impacts on carbon uptake, storage, and emission: The role of burn severity in the eastern Cascades, Oregon. Ecosystems **12**:1246-1267.

Metlen, K. L., C. E. Fiedler, and A. Youngblood. 2004. Understory response to fuel reduction treatments in the blue mountains of northeastern oregon. Northwest Science **78**:175-185.

Miller, J. D. and S. R. Yool. 2002. Mapping forest post-fire canopy consumption in several overstory types using multi-temporal Landsat TM and ETM data. Remote Sensing of Environment **82**:481-496.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika **78**:691-692.

Newton, M. and E. C. Cole. 2008. Twenty-six-year response of ponderosa pine and Douglas-fir plantations to woody competitor density in treated stands of madrone and whiteleaf manzanita. Forest Ecology and Management **256**:410-420.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment **4**:481-487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology **18**:927-936.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology **98**:96-105.

Parsons, D. J. 1978. Fire and fuel accumulation in a giant sequoia forest. Journal of Forestry **76**:104-105.

Passovoy, A. D. and P. Z. Fule. 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management **223**:237-246.

Pausas, J. G., N. Ouadah, A. Ferran, T. Gimeno, and R. Vallejo. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. Plant Ecology **169**:205-213.

Perchemlides, K. A., P. S. Muir, and P. E. Hosten. 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in southwestern Oregon. Rangeland Ecology & Management **61**:98-109.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: http://www.R-project.org

Reeves, S. L. 2007. *Arbutus menziesii*. Fire Effects Information System, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/plants/tree/arbmen/all.html [2011, March 3].

Reukema, D. L. 1982. Seedfall in a young-growth Douglas-fir stand: 1950-1978. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **12**:249-254.

Rooney, T. P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. Forest Ecology and Management **163**:119-130.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-143, Ogden, UT, p. 161.

Royo, A. A. and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **36**:1345-1362.

Rundel, P. W. 1982. Successional dynamics of chamise chaparral: The interface of basic research and management. Pages 86-90 *in* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, June 22-26. USDA Forest Service General Technical Report PSW-058, San Diego, CA.

Russell, R. E., V. A. Saab, J. G. Dudley, and J. J. Rotella. 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management **232**:179-187.

Safford, H. D. and S. Harrison. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. Ecology **85**:539-548.

Scott, J. H. and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-153, Fort Collins, CO, p. 72.

Sensenig, T. S. 2002. Development, fire history and current and past growth, of old-growth and young-growth forest stands in the Cascade, Siskiyou and mid-coast mountains of southwestern Oregon. Dissertation. Oregon State University, Corvallis, OR.

Sessions, J., P. Bettinger, R. Buckman, M. Newton, and A. J. Hamann. 2004. Hastening the return of complex forests following fire: The consequences of delay. Journal of Forestry **102**:38-45.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry **105**:139-146.

Shepperd, W. D. and M. A. Battaglia. 2002. Ecology, silviculture, and management of Black Hills ponderosa pine. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-97, Fort Collins, CO, p. 112.

Skinner, C. N. 1995. Change in spatial characteristics of forest openings in the Klamath mountains of northwestern California, USA. Landscape Ecology **10**:219-228.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **12**:18-28.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology **69**:1689-1702.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology **20**:351-362.

State of Oregon. 2007. 2005 Digital Orthophotos [computer file]. Available from Oregon Imagery Explorer. Oregon Department of Administrative Services Geospatial Enterprise Office (DAS-GEO), Salem, OR. http://oregonexplorer.info/imagery [May 10, 2011].

Tappeiner, J. C., D. Huffman, D. Marshall, T. A. Spies, and J. D. Bailey. 1997. Density, ages, and growth rates in old-growth and young-growth forests in coastal Oregon. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **27**:638-648.

Tappeiner, J. C., P. M. McDonald, and T. F. Hughes. 1986. Survival of tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) seedlings in forests of southwestern Oregon. New Forests **1**:43-55.

Taylor, A. H. and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management **111**:285-301.

Taylor, A. H. and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecological Applications **13**:704-719.

Thompson, J. R. 2008. Patterns of crown damage within a large wildfire in the Klamath-Siskiyou bioregion. Dissertation. Oregon State University, Corvallis, OR.

Thompson, J. R. and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management **258**:1684-1694.

Thompson, J. R. and T. A. Spies. 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. Landscape Ecology **25**:775-789.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences of the United States of America **104**:10743-10748.

USDA. 2008. Soil Survey Geographic (SSURGO) Database for Oregon and California.

USDA Forest Service. 1988. Silver Fire recovery project, final environmental impact statement. Pacific Northwest Region, USDA Forest Service, Grants Pass, OR.

USDA Forest Service. 2004. Biscuit Fire recovery project, final environmental impact statement. Medford, OR.

USDI. 2003. Regeneration stocking surveys handbook. U.S. Bureau of Land Management, Oregon State Office, H-5705-1, Rel. 5-249, Portland, OR.

Valachovic, Y. S., B. A. Caldwell, K. Cromack, and R. P. Griffiths. 2004. Leaf litter chemistry controls on decomposition of Pacific Northwest trees and woody shrubs. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **34**:2131-2147.

van Wagtendonk, J. W. and C. A. Sydoriak. 1987. Fuel accumulation rates after prescribed fires in Yosemite National Park. Pages 101–105 *in* Ninth Conference on Fire and Forest Meteorology. American Meteorological Society, San Diego, CA.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. Oikos **100**:25-34.

Waring, R. H., K. S. Milner, W. M. Jolly, L. Phillips, and D. McWethy. 2006. Assessment of site index and forest growth capacity across the Pacific and Inland Northwest USA with a MODIS satellite-derived vegetation index. Forest Ecology and Management **228**:285-291.

Weise, D. R. and B. M. Wotton. 2010. Wildland-urban interface fire behaviour and fire modelling in live fuels. International Journal of Wildland Fire **19**:149-152.

Weise, D. R., X. Y. Zhou, L. L. Sun, and S. Mahalingam. 2005. Fire spread in chaparral - ‘go or no-go?’. International Journal of Wildland Fire **14**:99-106.

White, C. 1971. Vegetation, soil chemistry correlations in serpentine ecosystems. Dissertation. University of Oregon, Dept. of Biology, Eugene, OR.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30**:279-338.

Zwieniecki, M. A. and M. Newton. 1995. Roots growing in rock fissures - Their morphological adaptation. Plant and Soil **172**:181-187.