AN ABSTRACT OF THE DISSERTATION OF

Daniel C. Donato for the degree of Doctor of Philosophy in Forest Science presented on April 11, 2008.

Title: Forest Vegetation and Fuel Dynamics Following Stand-Replacing Wildfire, Re-Burn, and Postfire Management in the Siskiyou Mountains, Oregon.

Abstract approved:

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Following high-severity fire, forest succession may take alternate pathways depending on the pattern of the fire and any secondary disturbances during early stand development, with lasting consequences for ecosystem function. The objectives of this research were to quantify: (1) early postfire regeneration as influenced by the spatial pattern of a landscape-scale wildfire, and (2) the influence of secondary disturbances during early succession, specifically recurrent high-severity fire and postfire logging.

Four years after the 200,000-hectare Biscuit Fire, patch-scale conifer seedling density was 80% Douglas-fir (*Pseudotsuga menziesii*) and ranged from 127-6494 stems ha^{-1}. Median density (1603 stems ha^{-1}) was ~12 times the prefire overstory density of 134 stems ha^{-1}. Due to the mixed-severity fire mosaic, ~58% of high-severity area was ≤ 200 m from patches of live trees, and ~81% was ≤ 400 m. Median conifer density exceeded 1000 stems ha^{-1} out to 400 m distance before declining rapidly at larger distances.

Following a short-interval (15-year) repeat fire, vegetation communities contained nearly all species found in mature/old-growth stands and after a single fire, indicating high community persistence through two severe fires. The short-interval burn had the highest species richness and plant cover with additions of disturbance-adapted forbs and low shrubs, likely associated with a propagule bank that developed between fires. Sprouting capacity of hardwoods and shrubs was unaltered by recurrent fire, and conifer regeneration density (median 1495 stems ha^{-1}) was similar to single burn stands.

Three to four years after fire, high-intensity logging resulted in a greater proportion (28%) of felled biomass left on site as slash compared to moderate-intensity logging (14%), because tree felling was less selective. However, despite bole removal and slash generation, there was no significant difference in surface woody fuels among logged and unlogged treatments at 17-18 years after fire. Fuel profiles and fire modeling both suggested that regenerating vegetation rather than residual dead wood is the main driver of early seral fire hazard, with low fire potentials 3-4 years postfire and very high potentials at 17-18 years. Postfire logging increased fire potentials within this context due to generation of slash, with differences fading in ~15-20 years.

The results from this research underscore the importance of the mixed-severity context in which stand-replacing fire often occurs, both for providing seed sources within a fire and for highly variable disturbances that interact with succession and plant adaptation.

Forest Vegetation and Fuel Dynamics Following Stand-Replacing Wildfire, Re-Burn, and Postfire Management in the Siskiyou Mountains, Oregon

by
Daniel C. Donato

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APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of the Graduate School

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

Daniel C. Donato, Author

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CONTRIBUTION OF AUTHORS

Joseph B. Fontaine assisted with study design, data collection, and writing of chapters 2-4. Beverly E. Law and J. Boone Kauffman assisted with study design and writing of chapters 2-4. John L. Campbell assisted with study design of chapters 2-4 and writing of chapter 2. W. Douglas Robinson assisted with writing of chapters 2-4.

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Forest Vegetation and Fuel Dynamics Following Stand-Replacing Wildfire, Re-Burn, and Postfire Management in the Siskiyou Mountains, Oregon

by
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PREFACE

From such small beginnings…do mighty trees take their rise.

-Henry David Thoreau

CHAPTER 1: INTRODUCTION

The structure and function of forest ecosystems are regulated by succession, which in turn is driven by disturbances such as wildfire (Cowles 1899, Clements 1916, Tansley 1924, Agee 1993, Perry 1994, Franklin et al. 2002). Fires vary in frequency, severity, extent, and spatial pattern, with different combinations giving rise to unique postfire conditions and successional pathways. High-severity (stand-replacing) fire initiates secondary succession by inflicting mortality to vegetation, consuming organic matter, and triggering tree establishment.

Postfire succession may take multiple pathways depending on variability in biotic and abiotic conditions after fire, the availability of propagules for regeneration, and any additional disturbances during early succession (Tansley 1924, Noble and Slatyer 1980, Gray and Franklin 1997, Paine et al. 1998). These variations in early succession may have important influences on long-term stand development and therefore ecosystem function (e.g., Franklin and Hemstrom 1981). With large severe wildfires increasing in North America under a warming climate (Whitlock et al. 2003, McKenzie et al. 2004, Westerling et al. 2006), understanding postfire ecology is increasingly important to informed forest management. The overall objectives of this research were to address two important gaps in this understanding by quantifying: (1) early postfire regeneration as influenced by the spatial pattern of a landscape-scale wildfire, and (2) the influence of secondary disturbances during early succession, specifically recurrent high-severity fire and postfire logging.

In Douglas-fir forests of the Pacific Northwest U.S., intervals between stand-replacing fires are typically several decades to several centuries (Agee 1993). Studies of natural succession and stand structure in mature to old-growth (>100 year-old) Douglas-fir forests have been extensive (e.g., Ruggiero et al. 1991 and references therein). Using age structure of the dominant tree cohort(s), these studies have inferred a wide variety of stand establishment patterns, from rapid and dense tree regeneration (i.e., within ~10 years of fire) to slow and sparse (occurring over ~50-100 years after fire), with important implications for structural succession (Franklin and Hemstrom 1981, Agee 1991, Tappeiner et al. 1997, Franklin et al. 2002, Poage and Tappeiner 2002, Winter et al. 2002, Larson and Franklin 2005). The mechanisms underlying this variability are poorly understood.

Two of the most commonly speculated mechanisms behind variable establishment patterns involve variation in seed source availability and the occurrence of short-interval repeat fires during early succession (i.e., ‘re-burns’; Franklin and Hemstrom 1981). Seed source limitations may arise due to landscape-scale (~10^4-10^6 ha) wildfires, which are thought to have occurred in region-wide episodes historically in the Pacific Northwest (Weisberg and Swanson 2003). Due to their sheer size, landscape-scale wildfires have the potential to eliminate seed sources over broad areas (Romme et al. 1998). Lack of conifer regeneration due to limited seed source could consequently lead to dramatically altered successional patterns compared to smaller fires. Short-interval repeat fires, by killing existing regeneration, may protract the establishment process (Franklin and Hemstrom 1981, Agee 1993, Poage and Tappeiner 2002). These short-interval fires (a type of 'compound disturbance'; Paine et al. 1998) have been hypothesized to not only reset succession, but also alter long-term trajectories (Gray and Franklin 1997). This hypothesis is supported by limited studies in Mediterranean and boreal regions (Zedler et al. 1983, Delitti et al. 2005, Johnstone 2006, Johnstone and Chapin 2006). Despite the potential importance of landscape-scale and recurrent severe wildfires in driving successional processes, vegetation response to these disturbances has received little study in Pacific Northwest forests.

Early succession may also be influenced by postfire management activities. Postfire logging (i.e., salvage), an increasingly prominent component of forestland management (McIver and Starr 2001), is often aimed at reducing fire behavior/effects in the event of a short-interval repeat fire (e.g., McIver and Starr 2001, USDA 2004). High-severity fire kills most trees on site, generating a pulse of dead wood that may function as a positive feedback mechanism by providing fuel for early seral fires (Agee and Huff 1987). By removing snag boles, postfire logging is presumed to decrease the accumulation of fuels on the ground in the decades following the initial fire. However, early seral fuel profiles (amount, composition, distribution of aboveground biomass) and related fire potentials have not been well quantified. Little empirical information exists on the composition and arrangement of dead wood remaining after fire, particularly as influenced by postfire logging (McIver and Starr 2001, Peterson et al. in press). Moreover, considerable uncertainty exists regarding the relative importance of residual dead vs. regenerating live fuels to fire hazard in young stands, and how this interaction changes over time with and without postfire management (Thompson et al. 2007).

Response to high-severity fire depends on the larger fire pattern in which it occurs. In many forest types, stand-replacement occurs as part of a mixed-severity patchwork (Arno 1976, Morrison and Swanson 1990, Agee 1993, Turner et al. 1994, Chappell and Agee 1996, Fule et al. 2003, Lentile et al. 2005, Hessburg et al. 2007). The mixed-severity fire regime is among the most complex and poorly understood disturbance types (Agee 2005). A mix of surface, torching, and running crown fire behavior within and between fires leads to complex patch structure at multiple scales. Mixed-severity fires contain substantially more edge between live and dead vegetation than either high-severity (stand-replacement) or low-severity (surface) fires (Lentile et al. 2005). The resulting mosaic of burn severities likely influences regeneration via the distribution of seed sources and patch environments (Chappell and Agee 1996). Moreover, highly variable fire intervals and burn severities in these regimes create the potential for recurrent fires in stand-replacement patches (Thompson et al. 2007).

In 2002, the Biscuit Fire burned in a mosaic pattern over 200,000 hectares of mixed-evergreen forest in the Klamath-Siskiyou Mountains of southwest Oregon and northwest California, USA. The Klamath-Siskiyou region, much of which is covered in Douglas-fir dominated forest, comprises the most diverse forest flora of western North America (Whittaker 1960). Along with sharp topographic, climatic, and edaphic gradients, the area is influenced by complex mixed-severity fire regimes (Agee 1991, Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000, USDA 2004). The Biscuit Fire, together with a series of adjacent fires that burned 15 years prior in 1987, presented several unique research opportunities. Being the largest fire on record for Oregon and among the largest in modern U.S. history, regeneration following the Biscuit Fire is of high relevance in an era of increasingly large wildfires. The fire also re-burned the 1987 Silver Fire, itself 38,000 hectares, affording an opportunity to quantify effects of a short-interval repeat fire on early successional pathways. In addition, postfire logging after the Biscuit Fire (USDA 2004) allowed assessment of changes in fuel profiles across varying harvest intensities and environmental settings. Finally, two older fires outside the Biscuit perimeter (1987 Galice Fire and 1987 Longwood Fire) allowed investigation of longer-term fuel dynamics with and without postfire management.

Research Objectives

Chapter 2 addresses the regeneration of conifers and broadleaf vegetation in stand-replacement patches within the Biscuit Fire. We focused on how the spatial pattern of burn severity, through its influence on seed source distribution, interacts with microsite variability to control regeneration abundance in a landscape-scale wildfire. We examined the following research questions:

(1) What are early patterns of density, distribution, and composition of conifers and associated vegetation in stand-replacement portions of a landscape-scale, mixed-severity fire?

(2) In the context of a large burn mosaic, what is the distribution of seed sources relative to stand-replacement areas?

(3) What abiotic and biotic site factors (bottom-up) are most important in predicting initial conifer abundance, and how important are these site factors compared to potential seed supply limitations (top-down)?

Chapter 3 examines the effects of recurrent high-severity fire during early succession, utilizing two overlapping wildfires as a natural experiment on fire interval variation (1987 Silver Fire, re-burned by 2002 Biscuit Fire). The conceptual framework for this research was to assess whether a short-interval severe fire simply resets the successional clock (i.e., a repeat of the response following a single fire) or results in a unique vegetation community and early successional pathway. We tested for unique effects of a short-interval fire (15-yr interval prior to 2002 fire) by comparing resulting vegetation communities to those following a long-interval fire (>100-yr interval prior to 2002 fire). We addressed the following research questions:

(1) Is vegetation response following short-interval fire consistent with a linear (similar to long-interval fire) or nonlinear (different from long-interval fire) model, in terms of initial vegetation cover, diversity, and species composition?

(2) Is regeneration of major structural components—hardwoods, woody shrubs, and conifers—reduced in the short-interval burn relative to the long-interval burn?

(3) To improve predictive capability and potential insights into differing responses across ecosystems, we explored the question: What plant functional traits are positively or negatively associated with the short-interval fire?

Chapter 4 addresses early successional fuel (biomass) dynamics and their implications for potential fire behavior. We quantified changes in the quantity and arrangement of dead wood remaining after high-severity fire with and without postfire logging, and how these dead fuels interact with regenerating live fuel over the first decades following fire. Utilizing the Biscuit Fire as well as two adjacent 17-18 year-old fires (1987 Galice and Longwood Fires), we examined the following research questions:

(1) What is the quantity, composition, and vertical distribution of aboveground biomass following stand-replacement fire, including all material (fine and coarse, live and dead) in both the aerial and surface fuel strata?

(2) What are the immediate effects of postfire logging on these fuel profiles and potential fire behavior, and how do these changes vary by harvest intensity and biophysical setting (high productivity coastal forest type vs. drier inland forest type)?

(3) How do fuel profiles and potential fire behavior change over early succession (17-18 years) with and without postfire logging?

CHAPTER 2: CONIFER REGENERATION IN STAND-REPLACEMENT PORTIONS OF A LANDSCAPE-SCALE MIXED-SEVERITY WILDFIRE

ABSTRACT

The 2002 Biscuit Fire burned over 200,000 hectares of mixed-evergreen forest in the Klamath-Siskiyou Mountains, Oregon (USA), presenting an important opportunity to study vegetation response to a landscape-scale, mixed-severity wildfire. Across a broad range of environmental conditions, we quantified: 1) the abundance, distribution, and composition of regenerating conifers and associated vegetation in stand-replacement patches 2-4 years after fire; 2) the isolation of these areas from potential seed sources (surviving mature trees) in the context of a large mixed-severity mosaic; and 3) the relative importance of seed supply (top-down) and abiotic/biotic site factors (bottom-up) in controlling early regeneration densities. Patch-scale conifer seedling density ranged widely, from 303-4190 stems ha^{-1} two years after fire and 127-6494 stems ha^{-1} four years after fire, but was generally abundant (study-wide mean = 1721 and 1603 stems ha^{-1}, respectively; approximately 12 times the prefire overstory density of 134 stems ha^{-1}). Regeneration was 72-80% Douglas-fir (*Pseudotsuga menziesii*). Combined cover of hardwoods and woody shrubs also ranged widely, with means of 25% and 33% two and four years after fire, respectively.

Despite the size of the fire, the mixed-severity mosaic resulted in ~58% of stand-replacement area being ≤ 200 m from patches of live trees, and ~81% ≤ 400 m. Median regeneration densities declined gradually with distance from these edges, but still

exceeded 1000 stems ha^{-1} out to 400 m distance before declining rapidly at larger distances. Similar densities across most distances were likely due to long-distance seed dispersal events (e.g., wind updrafts) and isolated remnant seed sources scattered throughout stand-replacement patches. The two most important predictors of regeneration density were distance to live trees and soil type, with skeletal coarse-grained igneous soils supporting lower densities (133 stems ha^{-1}) than fine-grained soil types with higher water retention capacity (729-1492 stems ha^{-1}). Other site factors (e.g., topography, broadleaf cover) had little association with conifer regeneration. The mixed-severity fire pattern dramatically influenced the regeneration process by providing seed sources throughout much of the large burn. Coupled with variable soil properties, variation in burn patch size is a key mechanism underlying heterogeneity in regeneration, successional pathway, and forest structure—thus contributing to the globally renowned biodiversity of the Klamath-Siskiyou region.

INTRODUCTION

In many temperate forests, fires generate and maintain ecosystem structure in part by regulating tree establishment (Heinselman 1973, Foster et al. 1998, Turner et al. 1999, Shatford et al. 2007). Patterns of conifer regeneration after stand-replacing wildfire strongly influence future succession, plant community composition, and wildlife habitat. Postfire regeneration has long been of basic interest to ecologists and land managers (e.g., Isaac and Meagher 1936, Franklin and Hemstrom 1981, Turner et al. 1999, Larson and Franklin 2005, Shatford et al. 2007), and recent increases in the occurrence of large wildfires have heightened this interest (see GAO 2006). In particular, considerable uncertainty exists regarding the capacity of forests to regenerate following fires that burn over landscape scales (~10^4-10^6 hectares).

Patterns of conifer regeneration are governed by the interaction between seed availability (top-down) and favorable microsites for germination and survival (bottom-up) (Galipeau et al. 1997, Beach and Halpern 2001, Bonnet et al. 2005). Seed availability for species with wind-dispersed seeds typically follows a negative exponential decline with increasing distance from seed source (Greene and Johnson 2000). For species reliant on regeneration from live-tree seed sources, this dispersal pattern leads to abundant regeneration near burn edges and less in patch interiors (Greene and Johnson 2000, Bonnet et al. 2005). Local site factors, including both abiotic (e.g., topography, soils, precipitation) and biotic (e.g., interspecific competition) conditions, act as a filter between seedfall and successful seedling establishment. For example, soil moisture is a highly important factor for regenerating seedlings (Minore and Laacke 1992). Dry soil conditions or competition from broadleaf vegetation for soil resources may reduce conifer establishment, even if seedfall is abundant (Minore and Laacke 1992, Tappeiner et al. 1992). The relative contribution of top-down vs. bottom-up controls likely varies by forest type, environmental conditions, and the size and patch structure of a fire.

Landscape-scale wildfires have the potential to lack seed sources over much of their area due to their sheer size (Romme et al. 1998). Thus, top-down control via seed availability may be the main limiting factor for regeneration in these burns. Lack of conifer regeneration due to limited seed source could consequently lead to dramatically altered successional patterns compared to smaller fires. Although the occurrence of large fires has increased recently—accounting for much of the area burned in North America (Westerling et al. 2006)—the historically low frequency of extremely large events (e.g., >100,000 ha) has made opportunities for study rare. Most research has been conducted in boreal regions, where large stand-replacing fires have predominated (e.g., Galipeau et al. 1997, Greene et al. 1999). Surprisingly few studies have quantified regeneration following landscape-scale wildfire in temperate North America. To our knowledge, such studies have been conducted following two historic events: the 1933 Tillamook Burn in the Oregon Coast Range (Isaac and Meagher 1936) and the 1988 fires on the Yellowstone Plateau (Turner et al. 1999). Apparently no studies have quantitatively explored the relative importance of top-down vs. bottom-up controls on regeneration in the context of a large (>100,000 ha) temperate wildfire.

An important aspect of many temperate forests is the mixed-severity fire regime (Arno 1976, Morrison and Swanson 1990, Agee 1993, Turner et al. 1994, Chappell and Agee 1996, Fule et al. 2003, Lentile et al. 2005), which is among the most complex and poorly understood disturbance types (Agee 2005). A mix of surface, torching, and running crown fire behavior within and between fires leads to complex patch structure at multiple scales. Mixed-severity fires contain substantially more edge between live and dead vegetation than either high-severity (stand-replacement) or low-severity (surface) fires (Lentile et al. 2005). The resulting mosaic of burn severities likely strongly influences regeneration via the distribution of seed sources and patch environments (Chappell and Agee 1996).

In 2002, the Biscuit Fire burned in a mosaic pattern over 200,000 hectares of mixed-evergreen forest in the Klamath-Siskiyou Mountains, Oregon (USA), presenting an important opportunity to study regeneration following a landscape-scale, mixed-severity wildfire. Across a broad range of environmental conditions, we quantified regeneration of conifers and associated vegetation in stand-replacement patches two to four years after fire. We addressed the following research questions: (1) What are early patterns of density, distribution, and composition of conifers and associated vegetation in stand-replacement portions of a landscape-scale, mixed-severity fire? (2) In the context of a large burn mosaic, what is the distribution of seed sources relative to stand-replacement areas? (3) What abiotic and biotic site factors (bottom-up) are most important in predicting initial conifer abundance, and how important are these site factors compared to potential seed supply limitations (top-down)? In addition to providing basic ecological insight, increased understanding of the factors controlling postfire conifer regeneration will aid land managers allocating limited resources to achieve reforestation objectives following large wildfires.

METHODS

Study area

The Klamath-Siskiyou region is characterized by sharp climatic and topo-edaphic gradients and comprises the most diverse forest flora of western North America (Whittaker 1960). The region is characterized by a Mediterranean-type climate with warm, dry summers (mean max. July temperature: 27 °C) and cool, wet winters (mean min. January temperature: 2 °C). Mean annual precipitation ranges from 140-500 cm over the burn area, less than 15% of which falls from May-September (Daly et al. 2002; prismclimate.org). The area supports a mosaic of plant communities including coniferous forest, serpentine woodlands, and montane shrubs and hardwoods. Species composition is characteristic of the mixed-evergreen and *Abies concolor* zones of southwest Oregon (Franklin and Dyrness 1973), dominated by conifers Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*); evergreen hardwoods tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), and canyon live oak (*Quercus chrysolepis*); and shrubs greenleaf manzanita (*Arctostaphylos patula*) and snowbrush (*Ceanothus velutinus*). Less common but notable conifer species include the endemic weeping spruce (*Picea breweriana*), an Arcto-Tertiary relict restricted to cool, wet sites of low evaporative demand (Waring et al. 1975); and the fire-dependent, relatively short-lived knobcone pine (*Pinus attenuata*), which regenerates from serotinous cones (Agee 1993) and has been in decline in southwest Oregon since the onset of fire suppression around 1940.

Major vegetation types in the Klamath-Siskiyou region (locally referred to as plant association groups) reflect gradients in precipitation and elevation and are often used as a stratification tool for regeneration management (Vagle 1986, Atzet et al. 1992). These vegetation types include low- to mid-elevation dry sites in the eastern portion of the burn (tanoak/oak and Douglas-fir associations, respectively), low- to mid-elevation wetter sites in the western portion of the burn (tanoak associations), and high-elevation sites distributed throughout the burn (white fir associations) (USDA 2004). Other distinct vegetation types occur on ultramafic (serpentine) soils which cover ~23% (45,000 ha) of the burn area; these types have a unique ecology (Whittaker 1960) and are outside the scope of this study.

Fire History

Fire regimes in the Klamath-Siskiyou region are complex, typically described as low- to mixed-severity (Agee 1991, Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000, USDA 2004). Variable fire intervals, extents, and severities within and between fires lead to complex forest age structures and successional pathways, with even-aged overstory cohorts generally attributed to past stand-replacement patches (Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998). Fire intervals range from 5-35 years in drier vegetation types to 50-200 years in higher elevation and wetter types (Agee 1991, Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000, USDA 2004). The frequency of landscape-scale ($>10^4$ ha) fires is not well quantified but such fires are thought to occur historically (Agee 1993). The proportion of a burn area experiencing high severity is known to vary among fire events, vegetation types, and topographic positions, and has been reported as ~10-30% (Taylor and Skinner 1998).

The Biscuit Fire, the largest forest fire on record for the state of Oregon and among the largest in modern United States history, burned for four months between July and November of 2002 over a wide range of vegetation, topography, and weather conditions. Varying degrees of surface, torching, and active crown fire behavior resulted in a complex spatial mosaic of tree mortality and survivorship (Fig. 2-1). Stand-replacement (high-severity) occurred in discrete patches up to ~13,000 hectares in size, with a skewed patch size distribution (median patch sizes were ~100-300 ha depending on scale definition and aggregation) and highly variable patch shapes (U.S. Forest Service GIS data; Fig. 2-1). Total high-severity area of the Biscuit Fire, which at times burned under extreme weather conditions and came after a 60-year period of effective fire suppression, is estimated at 84,000 ha (42% of 200,000-ha burn area) based on remotely sensed vegetation change (USDA 2004).

Sampling design

Scope. We sampled across a representative range of biotic and abiotic conditions within the Biscuit Fire (Table 2-1), with an approach similar to Isaac and Meagher (1936) and Turner et al. (1999). In this study, sampling was carried out in conjunction with a study of postfire management, and the particular patches sampled were identified a priori by the management plan (USDA 2004). These sites captured the major biophysical gradients and conditions within the Biscuit Fire (Table 2-1). Thus, we expect they provide a reasonably representative picture of conifer regeneration in much of the burn area, and most importantly afford analysis of how regeneration varies across these gradients.

Study areas were upland slopes covered in mature to old-growth conifer-dominated forest (see Thornburgh 1982, Agee 1993 for developmental/structural descriptions) that experienced high-severity fire (defined here as ≥90% overstory conifer mortality, top-kill of all understory and surface layer vegetation, and combustion of most ground layer organic matter). We excluded extremely steep rocky areas, riparian zones, and pre-existing plantations and shrub fields. A large portion of the shrub fields were in areas previously burned by the 1987 Silver Fire; see Chapter 3 for conifer regeneration in the Silver-Biscuit overlap area.

Annual climatic variation may be large and thus strongly influence a study's scope of inference. With respect to conifer regeneration, sufficient moisture is necessary for flower development, seed and cone maturity, germination, and early growth/survival. To relate the years we sampled to the long-term climate record, we summarized precipitation patterns using local climate data (Daly et al. 2002; PRISM Group, Oregon St. Univ., prismclimate.org) for the five growing seasons from 2002-2006. This period included the year of cone development for the first postfire seed crop through the latest year we measured regeneration (Fig. 2-2). Precipitation during the period was generally within a characteristic envelope (27 of 30 months were within one standard deviation of 30-year mean), but overall was relatively dry, with 24 of 30 months below average, and no year with >1 wet month except for the spring of 2005 (Fig. 2-2).

Sampling. We sampled regeneration in 11 discrete stand-replacement patches in the Biscuit Fire (identified a priori based on agency management plan; range of patch sizes 15 – 13,000 ha, median 180 ha), surveying 60 plots (1-12 per patch, mean 5.5). Within each burn patch, sample plots were located systematically at 250-m intervals along elevational contours beginning from a random start point. Burn patches were saturated with sample plots given constraints of size, access, and the presence of conditions outside the study scope (Fig. 2-1).

To best assess spatial variability in conifer regeneration, sample plots were surveyed using two complementary approaches. In every plot, conifer seedlings were measured in a central 5-m radius circular subplot. In approximately every fifth sample plot, conifer seedlings were also measured in four 75x0.5-m rectangular subplots radiating from plot center in the subcardinal directions. Plots were chosen to receive additional sampling based solely on their proximity to proposed logging units (as these plots served as controls for an associated study on management effects), and were not systematically different from the rest of the burn patch in terms of stand characteristics (see Chapter 4). The single circular subplot, based on regional regeneration survey protocols (USDI 2003), affords an efficient way to assess frequency (i.e., presence/absence, or stocking) at the burn patch scale via widely dispersed sample plots. The supplementary long rectangular subplots more effectively capture heterogeneity in microsites and obtain a more precise estimate of plot-scale seedling density (Elzinga et al. 1998). We verified that rectangular subplots yield higher precision (mean coefficient of variation 62%) than four circular subplots (mean CV 80%), with highly similar point estimates between the two methods (paired *t*-test: t_{23}=0.728, P=0.47, mean ratio of estimates = 1.07).

Sampling and analysis were focused primarily on 2006 data, four years postfire. These data represented the largest sample size (n=60 plots across 11 sites) and the latest year of measurement and thus stand establishment. A smaller set of plots (n=25 across 11 sites) was measured in 2004, two years postfire; these data were utilized to augment the 2006 data by quantifying early patterns of establishment. Not all 2004 plots were in common with the 2006 sample because postfire logging between sampling years eliminated 14 of 25 from suitability for this study. Thus, in terms of comparability, the two sampling years do not represent an identical population tracked between years, rather they provide a measure of broad-scale temporal regeneration patterns after the fire.

For each seedling encountered we recorded species (per Franklin 1961), height, age by whorl count, and rooting substrate. We also recorded whether each seedling fell within a 3.6 m radius circle inside the larger 5 m radius circle (allowing an estimate of occupancy at smaller scale of 0.004 ha or 1/100 acre). Additionally, we quantified plot-scale spatial pattern (uniform to clumped) via the spatial C-statistic, which is based on nearest-neighbor distances of seedlings and subplot centers (USDI 2003).

Concurrent measurements in each plot (site factors) included percent cover, height, and canopy volume of all hardwoods and woody shrubs by species; percent cover of all forbs and low (suffrutescent) shrubs by species; percent cover of ground substrates (litter, exposed mineral soil, rock >1 cm diameter, woody detritus >1 cm diameter, moss/lichen); and density, diameters (dbh), and species of all fire-killed conifers and hardwoods >10 cm dbh as a measure of prefire stand condition. Environmental parameters recorded for each plot included elevation, slope, aspect, soil parent material (USDA 2004), plant association group (Atzet et al. 1992), and estimated mean annual precipitation (Daly et al. 2002). Aspect was mathematically folded about the SW-NE axis so that SW slopes were assigned the highest (warmest) value and NE slopes the lowest (coolest) value (see Vagle 1986), then combined with slope to create one continuous variable estimating potential annual solar heat load for each plot (McCune and Keon 2002).

Seed source data

Potential seed source availability was assessed for each plot by recording the distance to the nearest contiguous patch of live mature conifers (>25% overstory survival over area >1 ha) using 2003 digital orthoquad aerial photos, geospatial data, and field checking. We also recorded whether the patch was above or below the plot in elevation. Isolated remnant trees and small patches could not be reliably identified with the available data but are an inherent feature of stand-replacement as it is commonly defined (i.e., 70-90% overstory mortality and therefore up to 10-30% survivorship). Therefore, the metric we used is a measure of isolation in a high-severity patch relative to surrounding areas of contiguous live trees (hereafter, ‘live-tree edge’).

We also used Forest Service GIS data to perform a landscape analysis on the isolation of stand-replacement portions of the Biscuit Fire relative to areas of surviving trees, similar to Turner et al. (1994). We identified areas of potential seed source, defined as medium- to large-sized conifer-dominated forest experiencing <75% mortality (i.e., low to moderate fire effects per the fire severity layer). We then estimated the Euclidean distance from each 30-m pixel of high-severity to the nearest edge of the seed source layer. (Note that this is a conservative estimate of seed source since the minimum grain of 30 m excludes isolated individual remnant trees.) Finally, we constructed a cumulative frequency diagram of these distances for the entire high-severity portion of the Biscuit Fire. Ultramafic soil areas and the combined 6% of the burn in California or on BLM land (insufficient spatial data) were excluded.

We extensively ground-truthed the fire severity and seed source layers in the field and with aerial photos and found them to be quite accurate for quantifying coarse-scale pattern. Remotely sensed spatial data over domains as large and complex as the Biscuit landscape will typically contain inaccuracies for fine scale entities such as small, isolated patches of surviving trees. We therefore developed an envelope of estimates, one based on unaltered Forest Service data and a second, more conservative estimate based on adjustments that excluded seed sources <1 ha in size (to eliminate possibility of false positives for small seed sources) and high-severity patches <10 ha in size (to eliminate edge influence of very small patches).

Data analysis

We investigated seed-source vs. site-factor controls on conifer regeneration density using linear mixed effects regression models evaluated within an information theoretic framework (Burnham and Anderson 2002). Analysis was conducted using data collected four years postfire. To account for the lack of spatial independence among plots within each patch, we used hierarchical mixed linear regression models with penalized quasi-likelihood to determine parameter estimates for the influence of each variable on seedling density. These models penalize estimated standard errors for dependence within groups (i.e., patches), making them appropriate for the analysis of clustered, spatially dependent data (see Breslow and Clayton 1993). Groups were allowed to vary randomly and all other variables were treated as fixed effects. Analysis was implemented in R 2.5.1 (R Development Core Team 2007) using the glmmPQL function in the MASS package (Venables and Ripley 2001). Because conifer seedling densities were typically positively skewed, data were $\log_e(x+1)$-transformed to better meet distributional assumptions (Ramsey and Schafer 2002, Larson and Franklin 2005). We also accounted for positive skew by reporting patch-scale seedling densities as median values. Residuals and model fits were checked using residual-vs.-fit diagnostics described by Ramsey and Schafer (2002).

Our approach was to assess the importance of distance to nearest live-tree edge (top-down) relative to 11 site factor (bottom-up) variables. The latter included several factors potentially influencing available germination substrate, water, light and nutrient resources for regenerating seedlings: exposed mineral soil cover %, rock cover %, mean annual precipitation zone, annual solar heat load (proxy for aspect), slope, elevation, hardwood/shrub cover, forb/low-shrub cover, and basal area of standing dead trees, and a fire intensity indicator variable (crown-scorched vs. crown-consumed). We also included an indicator variable for soil originating from coarse-grained igneous parent materials; these soils are typically skeletal (>40% rock fraction), very well-drained, and experience prolonged drought during the growing season (other soils within the study area are typically more loamy and derived from finer-grained metasedimentary and metavolcanic materials) (see USDA Forest Service 2004, nrcs.gov). Because the number of variables was large relative to sample size, we performed the analysis in two steps. First, univariate regression models of seedling density vs. each of the 11 site variables were ranked based on their model weights (weight of evidence supporting a particular model given the data and model set; see Burnham and Anderson 2002). Second, the top six site variables were then tested against the seed source variable using an all subsets approach to give equal consideration to all variables. Models with >5 predictors (+ intercept), or interaction terms, were excluded from analysis due to modest sample size, resulting in a set of 120 candidate models.

Models were evaluated using an information theoretic framework (Burnham and Anderson 2002), in which the relative support in the data for hypotheses (in the form of models) was assessed with Akaike's information criterion (AIC; Akaike 1973). We applied the small sample size correction (AIC_c) to all AIC calculations (Hurvich and Tsai 1989). Conditional parameter estimates and 95% confidence intervals for each predictor were computed for each model. These estimates, coupled with relative importance (RI) values obtained by summing weights (w_i) of the models containing each predictor, were used to rank the importance of the predictors on regeneration density (Burnham and Anderson 2002).

RESULTS

Overall density, distribution, and composition

Across both sample years, conifer regeneration density in individual plots ranged over five orders of magnitude, from 0 to 12,987 stems ha^{-1}. Median density within each burn patch ranged from 303 to 4190 stems ha^{-1} two years after fire and from 127 to 6494 stems ha^{-1} four years after fire (Table 2-2). Averaging these median values across all patches yielded a study-wide mean of 1721 and 1603 stems ha^{-1} in 2004 and 2006, respectively—approximately 12 times the mean prefire overstory density of 134 stems ha^{-1} (Table 2-2).

Regeneration was detected in all sampled patches, and a mean of 90% (range 60-100%) of plots were occupied within patches (Table 2-3). Spatial distribution of seedlings was random rather than regular or clumped (Table 2-3).

Regeneration composition was similar to prefire overstory composition, dominated by Douglas-fir (72-80% in 2004-2006), followed by white fir and sugar pine (2-10%) (Table 2-2). The primary exception to this similarity was knobcone pine, which on average constituted ~14% of regeneration but was rarely detected in the survey of prefire stems (Table 2-2). No weeping spruce seedlings were detected in the three patches in which prefire stems of that species were counted. Other species present at low density/frequency included incense cedar (*Calocedrus decurrens*), ponderosa pine, and Shasta red fir (*Abies magnifica* var. *shastensis*). Most plots contained one to three species of conifer (Table 2-2); a maximum of six were detected in one 5-m radius plot.

By two years postfire, hardwoods + woody shrubs attained mean cover of 25% (range 9-49%), and forbs + low shrubs attained 34% mean cover (range 4-85%) (Table 2-2). Postfire hardwood/shrub cover was dominated by tanoak, canyon live oak, Pacific madrone, and chinquapin, with lesser amounts of snowbrush and manzanita species. By four years postfire, hardwood/shrub cover averaged 33% (range 4-63%), and forb/low shrub cover averaged 48% (range 5-197%).

Grouped by vegetation type. Wetter vegetation types had higher regeneration densities (1146-1401 stems ha^{-1}) and forb/low-shrub cover (42-53%) than drier types (334-700 stems ha^{-1}, 14-19% cover, respectively) (Table 2-4). Douglas-fir seedlings dominated in all four vegetation types. Sugar pine occurred almost exclusively in dry associations and white fir was almost exclusively in high-elevation white fir associations; knobcone pine density was highest in mid- to high-elevation types. White fir associations were distinct in having relatively low cover (21%) and canopy height (61 cm) of hardwoods and shrubs compared to other associations, which had 37-51% cover and 125-155 cm canopy heights. Broadleaf species were taller than conifers in all types (Table 2-4), suggesting their likely canopy dominance during early succession; this differential was greatest in west-side low elevation associations and slightest in high elevation associations.

Regeneration timing and early survival

Regeneration was a continual process, occurring all four years after fire (Fig. 2-3). However, the second year after fire, 2004, was by far the major year of conifer establishment (Fig. 2-3). This pattern was driven by Douglas-fir and white fir, while the serotinous-coned knobcone pine regenerated primarily in the first year. Age structure in the first four years was hump-shaped rather than the J-shape typical of high-turnover populations (Fig. 2-3). Data from plots measured in both sample years indicated a mean survival rate for the main cohort of 67% between postfire years two and four. This relatively low mortality rate, coupled with continued seedling establishment, kept overall densities high (Fig. 2-3, Table 2-2).

Seed source distribution and relations

The complex burn mosaic resulted in potential seed sources distributed throughout most of the burn. The envelope of estimates for isolation of stand-replacement areas indicated that, of the 42 400 hectares of non-serpentine high-severity burn, 46-70% was within 200 m of a green edge, and 71-90% was within 400 m (Figs. 2-4, 2-5). Thus, out of a 200,000-hectare landscape fire, only 13,000-23,000 hectares of non-serpentine area were farther than 200 m from surviving trees, and only 4200-12,000 hectares were at distances exceeding 400 m.

Regeneration density was high across most of the measured range of distance to live-tree edge (62-552 m) (Fig. 2-6). Although the upper bounds of the data showed a negative exponential decline with increasing distance (Fig. 2-6), median densities declined only gradually, remaining above 1000 seedlings ha^{-1} with a threshold at 400 m, beyond which densities were below 300 seedlings ha^{-1} (Fig. 2-6 inset). Of the unoccupied plots, 75% were >400 m from live-tree edge. Elevation differential of the nearest potential seed source was not a major factor (Fig. 2-6). The overall pattern of density vs. distance was driven by Douglas-fir since it constituted most of the seedlings. Only one seedling of the heavier-seeded white fir was detected beyond 220 m distance. Sugar pine and knobcone pine were detected at all distances and did not show strong trends with distance.

Supply side vs. site factor associations

The six site variables selected by analysis step #1 (univariate regressions) were the coarse-grained igneous soil indicator, rock cover, forb/low-shrub cover, hardwood/shrub cover, slope, and standing dead basal area (see Appendix A for full outputs). When these variables were combined with seed source distance in an all subsets analysis, the top-ranked model was (intercept + distance to live-tree edge + coarse grained igneous soil) with a model weight of 0.13 (Table 2-5). The most important predictors by far were distance to live-tree edge (RI=0.95) and the coarse-grained igneous soil indicator (RI=0.88), both of which had negative parameter estimates and were the only variables with 95% CIs that excluded no effect (Table 2-5). Based on 95% CIs within the top models (Table 2-5), each meter of distance to live-tree edge was associated with a reduction in seedling densities of 0.1-1%, and coarse-grained igneous soils had 5-74% of the seedling densities occurring on other soils (Fig. 2-7). Hardwood/shrub cover and rock cover ranked as moderately important (RI=0.47 and 0.40, respectively); both parameters were negative but had confidence intervals that included no effect (Table 2-5). Relatively unimportant correlates with seedling density were (in decreasing order of importance): forb/low-shrub cover, slope, standing dead basal area, mean annual precipitation zone, mineral soil cover, solar heat load index (aspect), elevation, and fire intensity (crown-scorched vs. crown-consumed) (see Appendix A).

DISCUSSION

Early density, distribution, and composition

Despite the large size of the burn, we observed abundant but spatially variable conifer regeneration following the Biscuit Fire (Table 2-2). Thornburgh (1982) suggests that in the Klamath-Siskiyou Mountains, where Douglas-fir establishes immediately after fire it will develop in co-dominant status with resprouting broadleaf vegetation, and where seedling establishment is delayed or sparse, Douglas-fir will develop more slowly until emerging above broadleaf canopies. Given the wide variability in patch size, initial conifer density, and broadleaf cover after the Biscuit Fire (Fig. 2-5, Tables 2-2, 2-4), both pathways will likely operate in different portions of the burn. Thus, the fire created heterogeneity in succession and forest structure that is likely to persist for decades to centuries. This fire-maintained heterogeneity in part underlies the globally significant biodiversity of the Klamath-Siskiyou region (Whittaker 1960).

Comparable regeneration has been reported after other landscape-scale fires. In a Douglas-fir ecosystem in the Oregon Coast Range, Isaac and Meagher (1936) reported 69% of sampled areas had natural conifer densities exceeding 1235 ha^{-1} two years after the 100,000-hectare Tillamook Fire. After the ~400,000-hectare 1988 Yellowstone Fires, Turner et al. (1999) found lodgepole pine densities of 1900 to 10,000 stems ha^{-1} following stand-replacement fire, with high spatial variation in occupancy. Following large fires in mixed-wood boreal forests (6000 – 17,000 ha), Greene and Johnson (1999) reported jack pine and black spruce seedling densities of ~500 to >100,000 stems ha^{-1} depending on prefire conspecific basal area, with higher densities associated with higher basal area. In the latter two regions, cone serotiny in dominant species including lodgepole pine (*Pinus contorta*), jack pine (*Pinus banksiana*), or black spruce (*Picea mariana*) provides rapid in-situ recolonization across large burned areas. Notably, non-serotinous conifers such as white spruce (*Picea glauca*) have also persisted for millennia in boreal regions under a regime of landscape-scale crown fires (Galipeau et al. 1997, Greene and Johnson 2000). By contrast, dry ponderosa pine (*Pinus ponderosa*) forests of the interior U.S. often exhibit sparse regeneration in severe burns except near edges (e.g., Bonnet et al. 2005, Lentile et al. 2005). Heavy seeds and a general adaptation to smaller patch sizes, coupled with compositional changes due to fire exclusion and high-grade logging of large pines (Agee 1993), likely contribute to lower seed availability in large burns in ponderosa pine forests. Thus, regeneration following landscape-scale fire is more expected in wetter forest types with longer fire-return intervals.

Within the Klamath-Siskiyou region, our observations are consistent with reports of conifer regeneration following several smaller wildfires (Roy 1956, Shatford et al. 2007), as well as with several fire history studies reporting regeneration of distinct age cohorts following past high-severity fires (Agee 1991, Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000). Although regional heavy seed crops for Douglas-fir occur only every 3-11 years (Isaac and Dimock 1960), postfire regeneration is not solely tied to this cycle since establishment occurs across years of variable seed crops (Shatford et al. 2007). Conifers of the region possess reproductive and autecological traits well adapted to fires of both high and low severity (e.g., well-dispersed seeds, germination on mineral soil, thick bark, etc.), and are thus well adapted to the mixed-severity fire regime of the region.

Early patterns indicate high temporal continuity in conifer species composition through high-severity fire (Table 2-2). Douglas-fir will likely continue to be the most abundant conifer in most sites. This continuity may simply reflect the relative availability of seed sources for each species at the time of fire, or it may indicate that overstory composition in many mature forests was determined in large part by past fires. One notable change in species composition was the major establishment of knobcone pine, a fire-dependent species which had been in decline in the area since the onset of fire suppression. Due to its rapid early growth and relatively short life span, knobcone pine will be an important component of early and mid-seral communities along with evergreen shrubs.

Regeneration timing and survival

Timing: relevance to seed source. Seeds for postfire conifer regeneration generally come from two potential sources: viable seeds retained in cones of fire-killed trees (i.e., aerial seed bank, Greene et al. 1999, Larson and Franklin 2005), or from residual live trees in and around a burn. These two sources may produce very different age structures because aerial seed banks are only viable for a short time—only one year for Douglas-fir seeds (Isaac and Dimock 1960)—while live trees can produce seed over several postfire years. The peak we observed in Douglas-fir regeneration during the second year (Fig. 2-3) indicates that most areas were seeded by live trees producing seed in 2003, rather than by cones on fire-killed trees which would have produced a peak in the first postfire year. The lack of difference in regeneration density between crown-consumed areas and crown-scorched areas (in which viable cones are more likely to persist) further suggests that aerial seed banks were not a major factor (see Appendix A). We therefore conclude that, in the Biscuit Fire, live trees were the primary conifer seed source.

Early survival. This early cohort is the first in a larger continual dynamic of establishment and mortality over time (Shatford et al. 2007). The lack of a J-shaped age structure (Fig. 2-3) indicates establishment and early survival of a main cohort rather than successive annual pulses of regeneration with high turnover. The 2004 cohort had been present for three growing seasons at the time of 2006 sampling. Mortality of natural seedlings is generally concentrated in the first growing season, leveling off by year three (Cui and Smith 1991, Minore and Laacke 1992, Beach and Halpern 2001, Charron and Greene 2002). Thus, the period of high initial mortality has likely passed. Interestingly, even during the first growing season for the major cohort (2004), seedling survival was high despite below-average precipitation that year (Fig. 2-2). This observation differed from low seedling survival in this region following timber harvests, which has been addressed by years of intensive silvicultural research (see Tappeiner et al. 1992 and references therein). Several reasons could explain high postfire survival. First, postfire environments are likely ideal for seedling establishment and survival given the evolutionary history of local conifers. Examples include exposed mineral soil seedbeds, open light conditions, a period of reduced leaf area of hardwood/shrub species, and beneficial mycorrhizal associations between conifer seedlings and intact belowground structures of resprouting hardwoods (Borchers and Perry 1990). Second, a major structural feature of postfire sites is ‘dead shade’ created by standing snags. Dead structure reduces direct solar insolation and resulting evaporative stress but does not compete for water, and is known to increase conifer seedling survival (Minore 1971, Conard and Radosevich 1982, Minore 1986). Third, while past reforestation research in southwest Oregon has focused on the most difficult sites to regenerate (e.g., hot dry slopes at low elevation), the Biscuit Fire comprises a full range of site conditions including large portions in higher-elevation and mesic areas, which are likely more favorable to regeneration. By this measure, conditions in the Biscuit Fire are broader than the scope of those studies. Fourth, naturally regenerated conifers allocate much of their initial biomass growth belowground, such that at two years of age, seedlings typically have root:shoot length ratios of 5:1 and taproot lengths of 50-100 cm (Stein 1978). These deep roots can access soil layers in which summer moisture deficits are less severe.

Broadleaf vegetation interactions. Over longer time periods in this mixed-evergreen region, interactions between conifers and evergreen broadleaf species will have a major influence on forest development (Atzet et al. 1992, Tappeiner et al. 1992). Broadleaf vegetation can compete strongly with conifers for growing space and water resources over annual to decadal time scales. In some sites, such as tanoak associations with especially rapid broadleaf recovery (Table 2-4), only a portion of the early conifer cohort will eventually emerge to canopy dominance. Coupled with recurrent low-severity fires (Agee 1993), this competition may be an important factor thinning the extremely high regeneration densities toward the low densities characteristic of mature/old-growth forests (Table 2-2).

Interactions between conifers and broadleaf vegetation are not solely competitive in nature. Facilitative interactions through shade provision, nitrogen fixation, and mycorrhizal associations can be important (Borchers and Perry 1990, Dunne and Parker 1999, Gomez-Aparicio et al. 2004), particularly over long time scales (Busse et al. 1996). These effects, and the observation that Douglas-fir in southwest Oregon is capable of growth in just 7% of full sunlight (Emmingham and Waring 1973), may explain observations of high postfire conifer survival and growth in spite of dense broadleaf cover (Shatford et al. 2007). Further study is needed on the ecological roles of hardwoods and shrubs in the region, particularly how any facilitative and competitive interactions influence stand development over time scales measured in fire cycles.

Seed source distribution and relations

By their sheer size, extremely large wildfires may potentially lack seed sources over most of their area (Romme et al. 1998). However, as Isaac and Meagher (1936) stated, “Contrary to the general belief that the Tillamook Burn contained a great many large clear-burned areas devoid of seed trees, relatively few [such areas] were found." Our findings are consistent with this observation (Figs. 2-4, 2-5). Similarly, Turner et al. (1994) concluded that 75% of severely burned areas of the Yellowstone Fires were within 200 m of a live-tree edge. Greene and Johnson (2000) reported average distances of 150 m between burn edges and random points in large burns (5000-13,000 ha). Large fires typically burn over long time periods with variable weather and fuel conditions (Turner et al. 1994), and have greater proportional area of residual live vegetation than small fires (Eberhart and Woodard 1987). In mixed-severity fires, the spatial arrangement of residuals reflects the complex nature of fire behavior and fire effects (Lentile et al. 2005), resulting in highly intermixed patches with highly convoluted edges. Thus, while large fires can include very large burn patches, potential seed sources may be well distributed throughout most of their area. With respect to conifer regeneration, large mixed-severity fires can be described as a collection of smaller stand-replacement patches in a matrix of surviving canopy, rather than vice versa (Lentile et al. 2005).

Regeneration densities are generally expected to decline rapidly with distance to live-tree edge, such that conifer regeneration would be minimal beyond 100-200 m (e.g., Roy 1960, Greene et al. 1999). Our observations on the Biscuit Fire were largely inconsistent with this expectation in that regeneration densities were high out to 400 m from live-tree edges before declining (Fig. 2-6), consistent with several other empirical postfire studies (e.g., Galipeau et al. 1997, Larson and Franklin 2005, Shatford et al. 2007). There are several possible reasons for this pattern. First, negative-exponential seed dispersal models tend to underpredict long-distance seed flights that occur due to (among other things) wind updrafts (McCaughey et al. 1986), which result in a flattening of the dispersal curve at distances of hundreds of meters (Greene and Johnson 1995, Greene et al. 1999, Nathan and Muller-Landau 2000). For example, Isaac (1930) found that 10-50% of Douglas-fir seeds dispersed to 500 m or more over flat ground (depending on release heights of 30-60 m). In complex mountainous terrain with strong temperature fluctuations and vertical air movements such as the Klamath-Siskiyous, updrafts and elevational gradients may be particularly important in increasing dispersal distances. Second, isolated remnant trees embedded throughout high-severity areas very likely serve as local seed sources after fire (Isaac and Meagher 1936, Greene and Johnson 2000). This mechanism is in general difficult to study (Greene and Johnson 2000) and spatial data were not available to quantify this reliably for our analysis. However, we know with certainty that most high-severity areas retained scattered live conifers and that many of our sample plots had live trees that were closer than the nearest contiguous live-tree edge. Third, secondary seed dispersal occurring after initial deposition, especially over snow surfaces, can also be an important mechanism (Thoreau 1861, Matlack 1989, Greene et al. 1999). For Douglas-fir, typically more than half of annual seedfall occurs after October (Reukema 1982) and some is likely deposited onto snow, where it may be re-deposited by strong autumn-winter winds. Fourth, aerial seed banks on fire-killed trees can provide viable seed distributed throughout a high-severity patch (Isaac and Meagher 1936, Greene et al. 1999, Turner et al. 1999, Larson and Franklin 2005). However, in the Biscuit Fire this mechanism was likely only important for the serotinous-coned knobcone pine (see 'Regeneration timing and survival').

Supply side vs. site factor controls

Both seed supply and local site factors were important controls on early regeneration density. Similar to Galipeau et al. (1997), who studied a boreal fire $>10^6$ ha, most predictive ability came from two variables: distance to live-tree edge, and soil parent material (Table 2-5). Median densities in the Biscuit Fire were relatively flat between 0-400 m from live-tree edges, but the seed source predictor was still important since densities declined sharply beyond 400 m and were occasionally very high at short distances (Fig. 2-6). Thus, even though seed sources were well distributed across much of the burn, wide variation in patch size and distance to edge was still a highly important influence on regeneration density (Table 2-5).

Soil parent material (coarse-grained igneous vs. others) ranked much higher in importance than surface cover of exposed mineral soil or rock (Table 2-5). Skeletal coarse-grained igneous soils, which cover ~5% of the burn (USDA 2004), supported much lower regeneration densities than metasedimentary and metamorphic/volcanic soils (Fig. 2-7). We also found that regeneration occurred preferentially on exposed mineral soil (Appendix B), consistent with results from other studies (Greene et al. 1999, Charron and Greene 2002, Bonnet et al. 2005, Larson and Franklin 2005). However, mineral soil seed beds were generally abundant (i.e., not limiting) following fire. Thus, our data suggest that ground surface cover was less important than the water retention capacity of the underlying soil matrix.

Much of the variation in regeneration density is still unexplained by the variables we assessed. For example, the relatively low importance of most abiotic and biotic site factors (e.g., local precipitation regime and interspecific competition) indicates that, if these factors are to be important, the effects have yet to manifest themselves. In addition to uncertainties in predicting seedling densities due to (among other things) the heterogeneous nature of the process, inherent sampling error, and difficulties in quantifying isolated seed sources, several other unmeasured processes may be important. For example, seed/seedling predation by small mammals may affect Douglas-fir regeneration (Isaac and Dimock 1960). In an exploratory analysis, we found a strong negative correlation between deer mouse (*Peromyscus maniculatus*) abundance and seedling density (Spearman r = -0.73, n=6 plots) (Fontaine 2007).

Reconstructive (tree-ring) studies in old-growth Douglas-fir forests have identified a wide range of early establishment patterns, from rapid and dense to slow and sparse (Franklin and Hemstrom 1981, Agee 1991, Tappeiner et al. 1997, Poage and Tappeiner 2002, Winter et al. 2002, Larson and Franklin 2005). Mechanisms behind this variation are poorly understood, usually speculated to be some combination of seed availability, germination conditions, early broadleaf competition, or repeat fires after the initiating disturbance. Regeneration following the Biscuit Fire shows that both the slow and rapid patterns may occur within a single large burn. Areas very distant from live-tree edges (>400 m) or on poor soils (i.e., dry, coarse-textured, etc.) may take a slow pathway due in part to seed source limitations and low germination/juvenile survivorship. Other areas, which may include significant portions of even large burns, are not limited in terms of seed availability or suitable substrate, leading to dense early regeneration. If the latter areas are found to exhibit slow recruitment over time, it could be inferred that later conditions such as interspecific competition or re-burn events, rather than early factors, are driving long-term recruitment rates.

Management implications

After large wildfires, conifer establishment is typically a management goal (e.g., USDA 2004) but often receives limited funding (GAO 2006). Despite the large size of the Biscuit Fire, we observed abundant natural regeneration in most areas, and it is likely that these early cohorts are but the first of several (Shatford et al. 2007). Given limited resources for conifer planting, postfire management may benefit greatly by utilizing natural regeneration where possible. Natural postfire succession, which has operated in the Klamath-Siskiyou region for millennia, may include prolonged periods of dominance by early seral hardwoods and shrubs (Thornburgh 1982, Agee 1993). Utilizing natural regeneration will thus require flexibility regarding spatial variation and the time period over which regeneration and conifer crown emergence occur. Variable stand development patterns likely contribute to the region's renowned floral diversity (Whittaker 1960), and extended periods of broadleaf dominance benefit landscape-scale wildlife diversity (Fontaine 2007). The degree of flexibility clearly depends on management objectives; i.e., prioritization of timber production, wildlife habitat, etc.

Although natural regeneration densities are often high following wildfire in the Klamath-Siskiyou region (Table 2-2, Shatford et al. 2007), artificial reforestation of some areas may still be necessary where different species mixes (e.g., greater abundance of pines) or uniform densities/distributions (e.g., for timber production) are management goals. But with respect to attaining prescribed densities alone, postfire planting may be unnecessary in many areas, and in fact may augment natural regeneration to the point of creating extremely dense young stands. For example, in planted areas of a 17-year-old fire adjacent to the Biscuit Fire, we observed conifer densities of 1082 - 12 628 stems ha^{-1}, with a median density (2308 stems ha^{-1}) nearly double the planted density of ~1200 stems ha^{-1}. Such dense stands resulting from natural + artificial regeneration may stagnate in terms of stand growth and necessitate thinning projects in later years (see Main and Amaranthus 1996).

Mixed-severity fire patterns may result in seed sources distributed throughout much of even very large burns (Figs. 2-4, 2-5). Quantifying the distribution of these potential sources could be an essential tool for prioritizing postfire planting activities. In the Biscuit Fire, natural seedling densities and stocking rates were at or above prescribed levels (250-500 stems ha-1, USDA 2004) across most of the conditions we sampled, made possible by well-distributed seed sources (Figs. 2-4, 2-5, 2-6). Nonetheless, low densities and stocking rates were measured in areas >400 m from live-tree edges or on soils with low water retention capacity. Such areas could be prioritized for planting if deemed appropriate.

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Table 2-1. Sampled range of biophysical characteristics and relation to Biscuit Fire area.

Biophysical characteristic	Sampled range (mean)	Proportion of Biscuit Fire area within sampled range	Source
Mean annual precipitation	178 – 381 cm (287)	93%	PRISM Group, Oregon State University, http://www.prismclimate.org
Soil types	coarse-grained igneous, metasedimentary, metavolcanic	95%	U.S. Forest Service GIS data; USDA 2004; http://www.gis.state.or.us/data/alphalist.html
Plant association group	tanoak moist, tanoak dry, Douglas-fir, white fir	98%	Atzet et al. 1992; USDA 2004
Aspect	All	100%	10-m digital elevation model (DEM)
Slope †	12 – 41° (28)	88%	10-m digital elevation model (DEM)
Elevation ‡	490 – 1368 m (1004)	80%	10-m digital elevation model (DEM)
Distance to contiguous seed source §	≤ 552 m (240)	89%	U.S. Forest Service GIS data; digital orthoquad aerial photos; Fig. 2-4

Note: Statistics exclude areas of ultramafic soil and associated communities, which constitute ~23% (45,000 ha) of the Biscuit Fire area. Also omitted is the 4.7% (9400 ha) of the burn area in California (much of which is ultramafic as well) due to limited data availability. We make no inference to these areas.

† Areas flatter or steeper than sampled range are primarily riparian or ridgetop (flatter), or non-stockable rocky cliffs (steeper).

‡ Nearly all of the unsampled remainder is at 200 – 490 m elevation, primarily along the lower Illinois and Chetco Rivers.

§ Percentage based on stand-replacement portion only to avoid influencing estimate with areas of substantial canopy survival. If all severities are included, estimate is ~96%.

Table 2-2. Patch-scale abundance and composition of conifers and associated vegetation before and 2-4 years after the Biscuit Fire.

Time point	Conifers ha^{-1}	Plot-scale conifer species richness	Conifer composition --% of total density--				Hardwood & shrub abund.	Hardwood/shrub composition --% of total abundance--				% cover forbs & low shrubs †
			Douglas-fir	white fir	sugar pine	knobcone pine		tanoak	madrone	canyon live oak	chinqu-apin	
Pre-fire	134 (64-208)	2.2 (1-3)	82 (29-100)	5.4 (0-17)	10 (0-54)	0 (0-0)	198 (0-540) stems ha^{-1}	31 (0-80)	25 (0-88)	15 (0-79)	26 (0-100)	18 (12-25)
2 yr post-fire (2004)	1721 (303-4190)	2.3 (1-4)	72 (32-100)	3.8 (0-26)	9.2 (0-28)	15 (0-59)	25 (9-49) % cover	36 (18-61)	6.8 (0-28)	22 (0-56)	2.7 (0-14)	34 (4-85)
4 yr post-fire (2006)	1603 (127-6494)	1.7 (1-3)	80 (46-100)	5.7 (0-28)	1.6 (0-17)	13 (0-49)	33 (4-63) % cover	31 (0-68)	6.8 (0.2-44)	13 (0-40	6.3 (0-14)	48 (5-197)

Notes: Data are mean (range) of patch-scale means, except conifer densities which are from patch-scale medians to account for positive skew. Pre-fire densities are for overstory conifers >30 cm dbh and hardwoods >10 cm dbh. Postfire hardwood/shrub abundance is reported in % cover due to highly coppiced postfire resprouts that render stem densities less meaningful. Other conifer species present in minor amounts include ponderosa pine, incense cedar, and red fir. Other hardwood and shrub species present include Oregon myrtlewood, snowbrush, deer brush, and manzanita spp.

† Unburned forb and low-shrub data from Chapter 3.

Table 2-3. Mean ± S.E. (range) spatial pattern and frequency of conifer regeneration four years after stand-replacement in the Biscuit Fire.

# of patches	# of plots within patches	Spatial C statistic †	% patches occupied	% plots occupied within patches	% plots occupied within patches (by trees ≥20 cm ht.)
11	5.5 ± 1.0 (1-12)	0.51 ± 0.03 (0.37-0.62)	100	90 ± 5.1 (60-100)	69 ± 8.6 (29-100)

Notes: Occupancy is defined at minimum density of 250 stems ha^{-1} (see USDI 2003).
† Spatial distribution metric ranging from 0-1 (0= uniform, 0.5= random, 1= highly clumped).

Table 2-4. Conifer regeneration density, composition, and associated vegetation characteristics by vegetation type four years after the Biscuit Fire.

Vegetation Type †	Total conifer seedlings ha^{-1}	% of plots occupied at ≥250 ha^{-1}	Conifer regeneration composition‡				Conifer seedling height (cm)	Shrub/ hardwood cover (%)	Shrub/ hardwood height (cm)	Forb/ low-shrub cover (%)
			% Douglas-fir	% white fir	% sugar pine	% knobcone pine				
White fir associations (high elevation)	1401 (127-12987)	96%	69 (0-100)	11 (0-67)	0 (0-1)	20 (0-100)	18 (8.2-41)	21 (2.5-71)	61 (20-160)	42 (1.5-197)
Douglas-fir associations (mid-elevation, dry)	334 (0-1146)	75%	75 (46-100)	0 (0-0)	2.6 (0-7.7)	23 (0-46)	13 (8.1-17)	46 (36-65)	139 (99-160)	19 (7.0-51)
Tanoak/oak associations (low elevation, dry)	700 (0-2674)	88%	79 (0-100)	0 (0-0)	5.0 (0-38)	14 (0-100)	16 (9.7-40)	51 (32-67)	125 (74-170)	14 (4.5-31)
Tanoak associations (low-mid elevation, wet)	1146 (0-3565)	83%	97 (58-100)	0.4 (0-3.8)	0 (0-0)	3.1 (0-42)	21 (13-47)	37 (0-75)	155 (90-204)	53 (1-101)

Notes: Data are means (range) of plot values, except for total conifer seedlings ha^{-1} which are medians (range) of plot values.

† Vegetation type is based on super plant association groups (see USDA 2004).

‡ Other conifer species present in minor amounts include ponderosa pine, incense cedar, and red fir.

Table 2-5. Top-ranked models and parameter estimates (95% CIs in parentheses) from mixed-effects regression of conifer seedling density as a function of seed source and site variables four years after the Biscuit Fire.

Model diagnostics				Parameter estimates †						
Model rank	AIC_c	ΔAIC_c	Akaike weight (w_i)	Distance to live-tree edge [m] *RI=0.95* ‡	Coarse-grained igneous soil [1/0] *RI=0.88*	Hardwood/ shrub cover [%] *RI=0.47*	Rock cover [%] *RI=0.40*	Forb/ low-shrub cover [%] *RI=0.22*	Slope [degrees] *RI=0.22*	Standing dead basal area [m^2 ha^{-1}] *RI=0.20*
1	179.95	0	0.13	0.994 (0.990, 0.998)	0.182 (0.059, 0.561)	--	--	--	--	--
2	180.39	0.44	0.11	0.994 (0.990, 0.998)	0.223 (0.070, 0.709)	0.985 (0.962, 1.007)	--	--	--	--
3	181.03	1.08	0.08	0.995 (0.991, 0.999)	0.235 (0.075, 0.738)	0.982 (0.960, 1.005)	0.985 (0.963, 1.008)	--	--	--
4	181.12	1.17	0.08	0.995 (0.991, 0.999)	0.185 (0.060, 0.569)	--	0.987 (0.965, 1.010)	--	--	--
5	182.08	2.14	0.05	0.994 (0.990, 0.998)	0.207 (0.061, 0.704)	--	--	--	0.979 (0.909, 1.054)	--
6	182.24	2.29	0.04	0.994 (0.990, 0.998)	0.194 (0.060, 0.631)	--	--	1.004 (0.987, 1.021)	--	--
7	182.45	2.50	0.04	0.994 (0.990, 0.998)	0.178 (0.052, 0.611)	--	--	--	--	0.999 (0.984, 1.015)

Notes: All models with $\Delta AIC_c \leq 2.50$ are shown. All models had structure: $y \sim \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_k x_k$. Other site variables analyzed included: exposed mineral soil cover %, elevation (m), annual precipitation zone (cm yr^{-1}), annual solar heat load index (aspect proxy), and a fire intensity indicator (crown-scorched vs. crown-consumed). These variables were excluded from all subsets analysis by analysis step #1 (site variable elimination step; see text), due to lower importance and weaker effect sizes than variables shown in table (see Appendix 1).

† Multiplicative effect, obtained via backtransformation from analysis of log$_e$(x+1) data. A value of 1 = no effect.

‡ *RI* (relative importance) value provides a measure of strength of association with seedling density (calculated by summing Akaike weights across all models in which a variable appears).

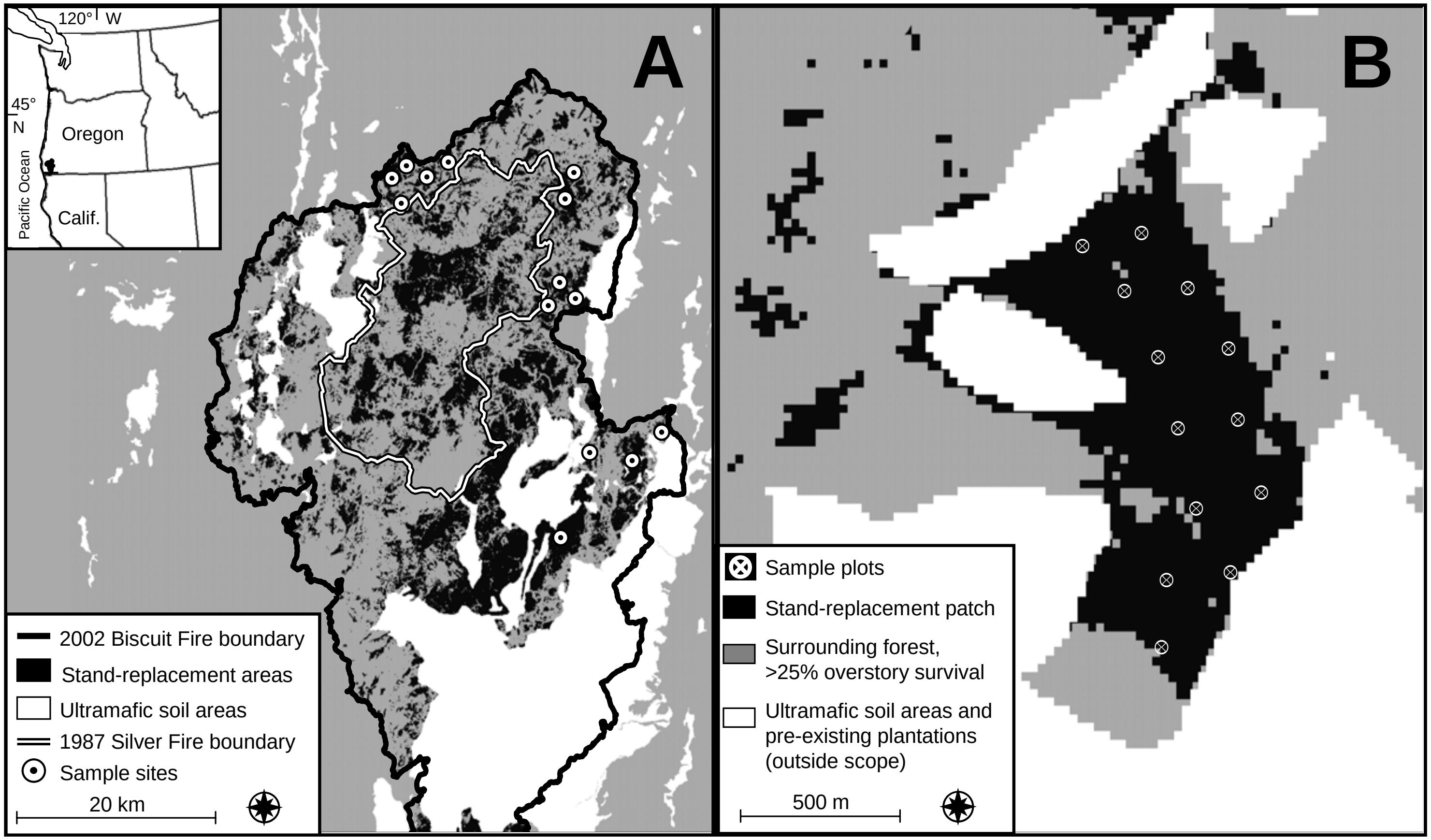


Figure 2-1. Map of study area and sampling design. **(A)** The 2002 Biscuit Fire burned over 200,000 ha of mixed-evergreen forest, imparting a complex mosaic of mortality and survivorship on the landscape. Regeneration was sampled in high-severity patches. Ultramafic soil areas and pre-existing plantations were not examined. For regeneration data in the Silver-Biscuit overlap area, see Chapter 3. **(B)** Example of sampling layout in a typical stand-replacement patch. Plots were spaced at ~250-meter intervals along elevational contours. Spatial data courtesy of Rogue River-Siskiyou National Forest; see USDA (2004).

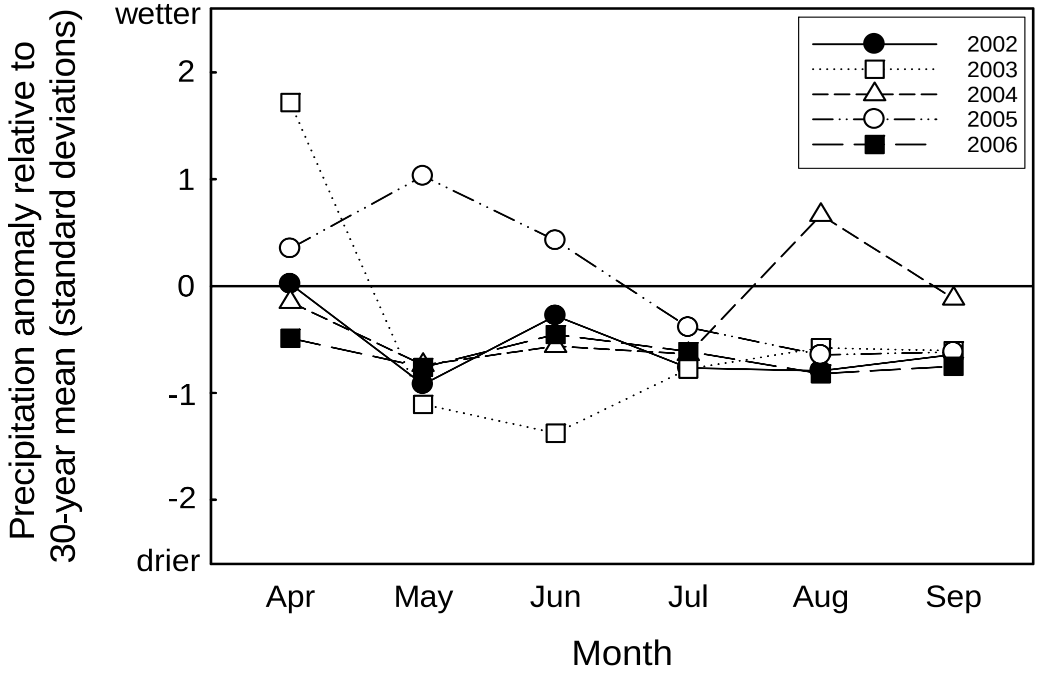


Figure 2-2. Monthly precipitation patterns, in standard deviations (s.d.) above or below the 30-year mean, for the five growing seasons of 2002-2006. 27 of 30 months were within 1 s.d. of the mean (all 30 ≤1.7 s.d.); 24 of 30 months were drier than average. Computations were derived from PRISM climate data (Daly et al. 2002; PRISM Group, Oregon State University, http://www.prismclimate.org, accessed 7 Nov 2006).

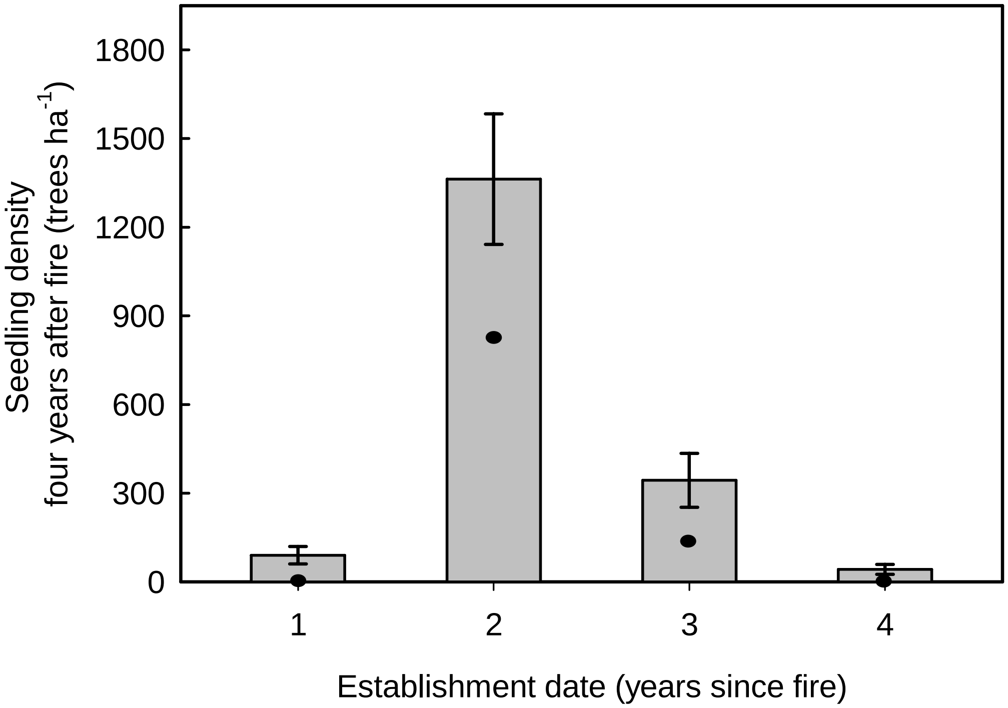


Figure 2-3. Conifer seedling establishment by year after the Biscuit Fire, based on age structure from whorl counts four years post-fire (mean ± S.E.; median indicated by ●). Data represent the net balance of germination and mortality for each cohort as of year four. Patch-scale median cumulative density by year four was 1603 ± 542 stems ha^{-1}.

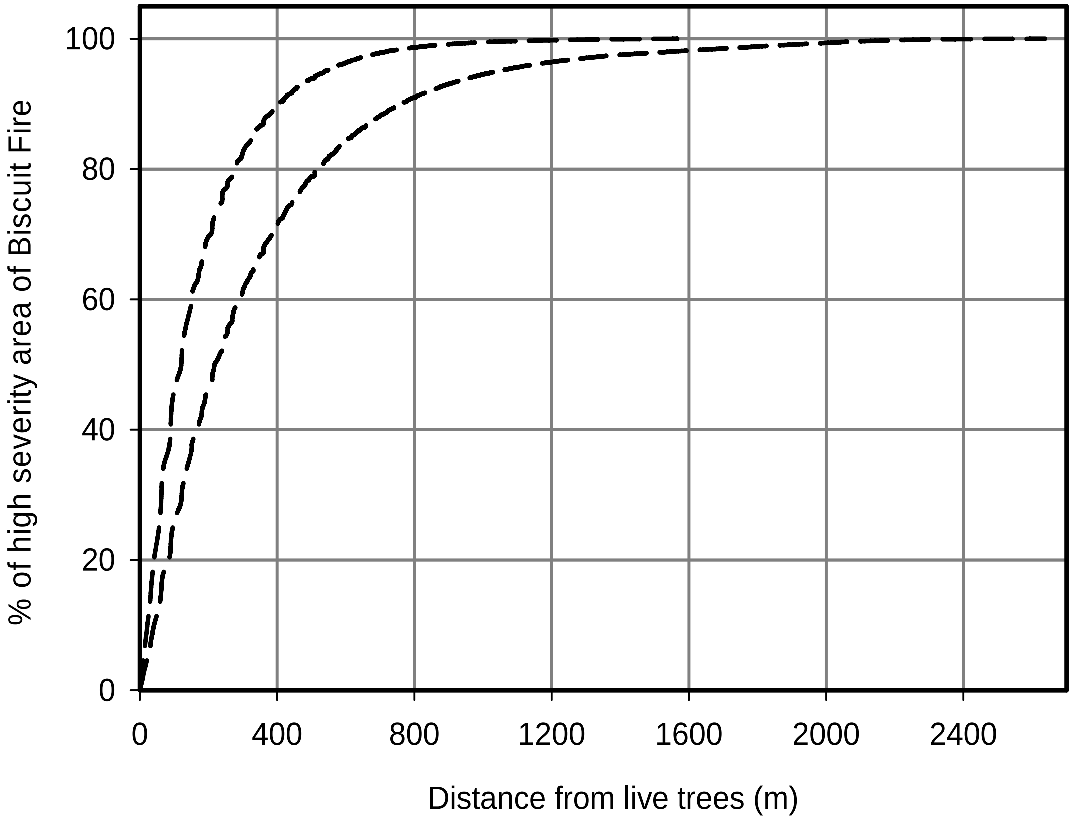


Figure 2-4. Cumulative frequency diagram for distance of Biscuit high-severity area from patches of surviving trees. Envelope of estimates based on U.S. Forest Service data using two different data treatments: Upper curve was derived from unaltered data; lower curve is conservative estimate derived by eliminating very small patches of surviving trees (<1 ha) and of high-severity burn (<10 ha), which eliminated possibility of false positives for small seed sources and edge effects of small burn patches. Ultramafic soil areas were excluded from analysis.

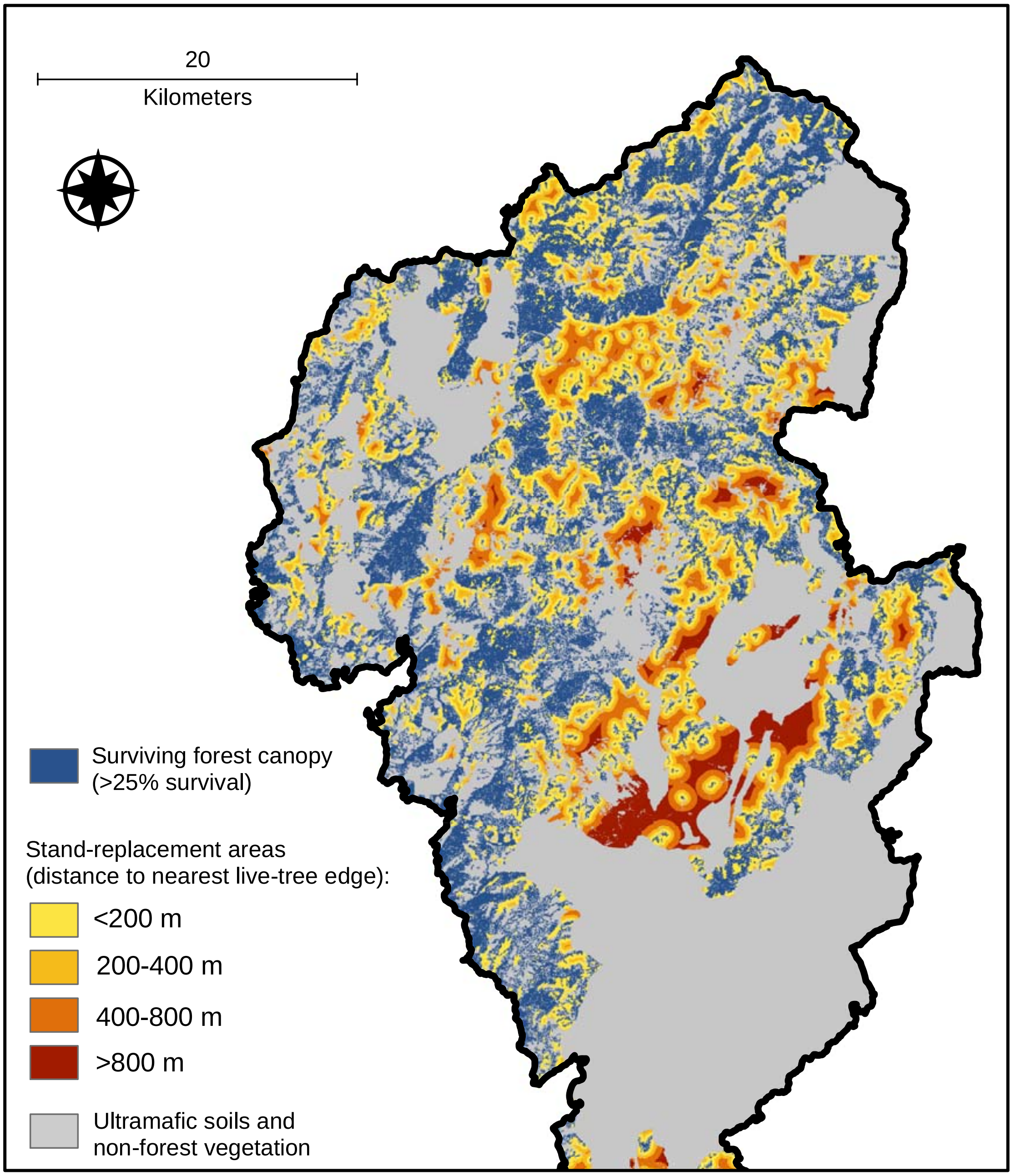
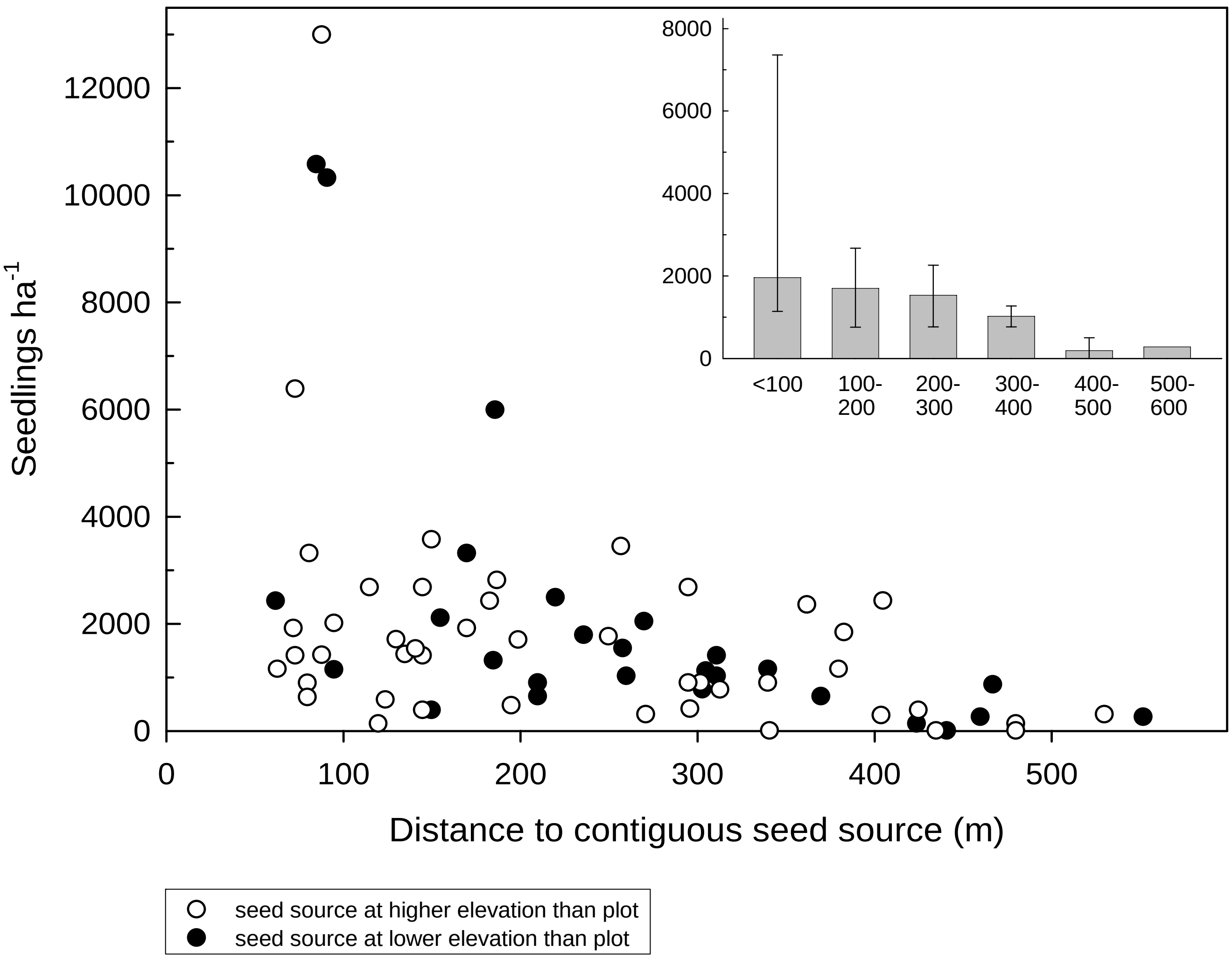


Figure 2-5. Map of Euclidean distance between high-severity areas of the Biscuit Fire and adjacent patches of surviving trees (potential seed source). Ultramafic soils, non-forest vegetation, and areas with insufficient data (small areas in south and northeast corners) were excluded**.** Of high-severity area, ~58% was within 200 m of a live-tree edge, and ~81% was within 400 m.

Figure 2-6. Postfire seedling density as a function of distance to nearest contiguous (≥1 ha) patch of surviving trees, and whether seed source was above or below plot in elevation. Inset shows median and 25th-75th percentile of same data, by 100-m distance class. Distances <50 m were not sampled. Regression analysis after log-transformation (which effectively linearized the relationship) indicated that each meter of distance to live-tree edge was associated with a reduction in seedling densities of 0.1-1% (see Table 2-5 for regression model outputs)..


Seedlings ha^{-1}
0
2000
4000
6000
8000
10000
12000
Distance to contiguous seed source (m)
0
100
200
300
400
500
8000
6000
4000
2000
0
<100
100-200
200-300
300-400
400-500
500-600
○ seed source at higher elevation than plot
● seed source at lower elevation than plot

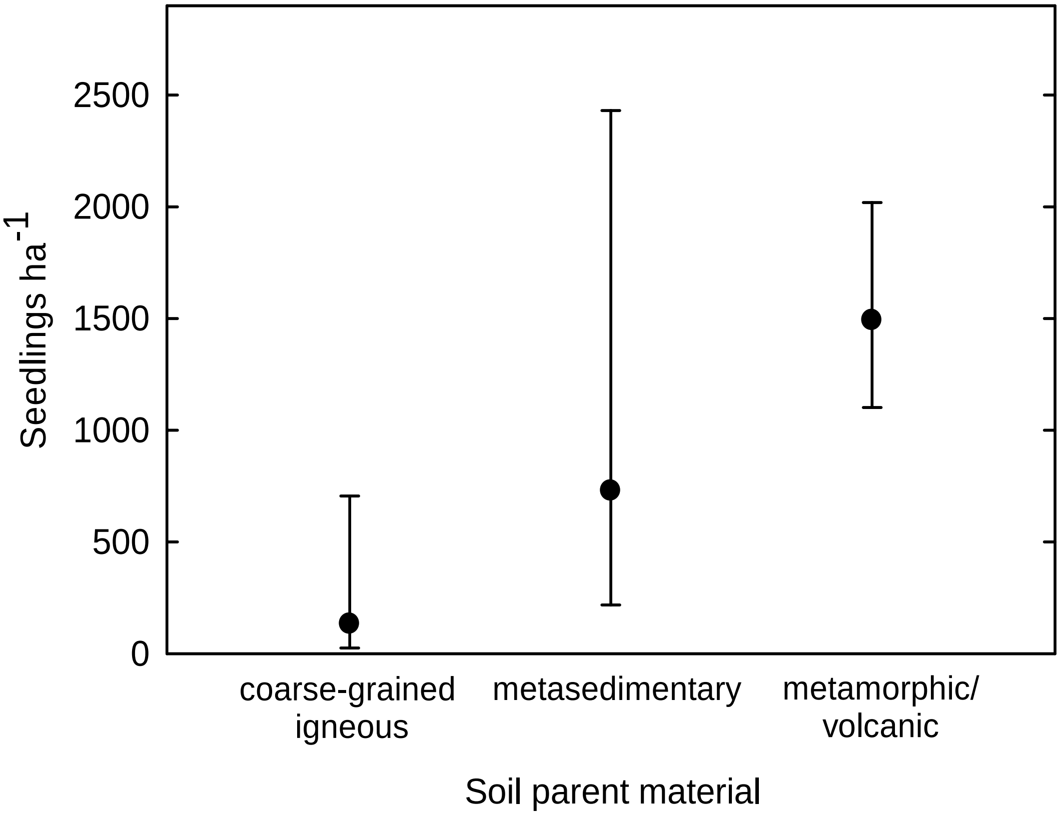


Figure 2-7. Median (95% CI) conifer seedling density in high-severity portions of the Biscuit Fire area by soil parent material, four years after fire (excludes ultramafic soils). Coarse-grained igneous soils had significantly lower seedling densities than other types. Medians and CIs were obtained by back-transformation from $\log_e(x+1)$-transformed data..

CHAPTER 3: VEGETATION RESPONSE TO A SHORT INTERVAL BETWEEN HIGH-SEVERITY WILDFIRES IN A MIXED-EVERGREEN FOREST

ABSTRACT

Variations in disturbance regime strongly influence ecosystem structure and function. A prominent form of such variation is when multiple high-severity wildfires occur in rapid succession (i.e., short-interval severe fires, or ‘re-burns’). These events have been proposed as key mechanisms altering successional rates and pathways.
We utilized a natural experiment afforded by two overlapping wildfires of differing age in the Klamath-Siskiyou Mountains of Oregon, USA. We tested for unique effects of a short-interval fire (15-yr interval prior to 2002 fire) by comparing vegetation communities two years postfire to those following a long-interval fire (>100-yr interval prior to 2002 fire) and in mature/old-growth stands (no high-severity fire in >100-yr). Nearly all species found in mature/old-growth stands were present at similar relative abundance in both the long-interval and short-interval burns, indicating high community persistence through multiple high-severity fires. However, the short-interval burn had the highest species richness and total plant cover with additions of open-adapted forbs and low shrubs, likely associated with a propagule bank of early seral species that developed between fires. Several broadly generalizable plant functional traits, such as long-lived seeds stored in soil, were strongly associated with the short-interval burn. Sprouting capacity of hardwoods and shrubs was unaltered by recurrent fire, but hardwood/shrub

biomass was lower in the short-interval burn because individuals were smaller prior to the second fire. Conifer regeneration densities were high in both the short-interval and long-interval burns (range= 298-6086 and 406-2349 trees ha^{-1}, respectively), reflecting similar availability of seed source and germination substrates.

Short-interval severe fire resulted in distinct early seral assemblages but included key structural species (e.g., conifers, hardwoods), thus contributing to landscape heterogeneity while retaining the potential to develop toward mature forest. Although such events are typically expected to be deleterious to forest flora and development, these results indicate that in systems characterized by highly variable natural disturbances (e.g., mixed severity fire regime), native biota possess functional traits well adapted to recurrent severe fire. Process-oriented ecosystem management incorporating variable natural disturbances, including 'extreme' events such as short-interval severe fires, would likely perpetuate a diversity of habitats and successional pathways on the landscape.

INTRODUCTION

Variations in disturbance frequency, severity, and extent strongly influence ecosystem structure and function (Pickett and White 1985, Agee 2005). For disturbances such as fire, frequency and severity are typically negatively correlated, such that frequent disturbances are of lower severity. However, in many ecosystems high-severity events occasionally occur in rapid succession, resulting in a compound disturbance event (Paine et al. 1998). These compound disturbances may generate ecological responses unique from those following single events spaced at longer intervals, with lasting influences on ecosystem pattern and process (Zedler et al. 1983, Paine et al. 1998, Johnstone and Chapin 2006).

In forests with mixed- and high-severity fire regimes, such as in the Pacific Northwest, USA, intervals between stand-replacing fires are typically several decades to several centuries (Agee 1993). Occasionally, however, these fires are followed closely by recurrent fires during early succession (Morris 1934, Franklin and Hemstrom 1981, Agee 1991, Agee 1993, Gray and Franklin 1997, Thompson et al. 2007). Retrospective (dendrochronological) studies in mature forests of the Pacific Northwest have implicated these repeat fires as potentially important influences on long-term successional trajectories (Franklin and Hemstrom 1981, Agee 1991, Gray and Franklin 1997). In the present study, we report vegetation responses immediately following recurrent high-severity fire to clarify the potential mechanisms underlying such influences.

Short-interval fires (or 're-burns', Brown et al. 2003) occur in early seral vegetation and likely differ in behavior and effects from long-interval fires, which generally occur in mature forests. Young stands carry legacies of recent disturbance such as open microclimates, early seral vegetation, and woody fuels derived from fire-killed trees (Agee and Huff 1987). Since patterns of secondary succession correspond to pre-disturbance condition (Halpern and Franklin 1990), succession following a short-interval (SI) fire would thus likely differ from that following a long-interval (LI) fire both in terms of rate (Franklin and Hemstrom 1981) and trajectory. Response of forest vegetation to short-interval severe fire may be nonlinear (Johnstone and Chapin 2006), meaning that the response differs from that following a single long-interval fire, resulting in altered successional trajectories (Eugenio and Lloret 2006, Johnstone 2006). Alternatively, the response may be linear—i.e., a repeat of the response following a single fire such that the successional clock is merely reset.

Recurrent severe fires might generally be expected to reduce plant cover, diversity, and site productivity (e.g., soil nutrient capital, biomass production) by eliminating fire-sensitive community components (Kutiel 1997), eliminating seed sources or sprouting capacity (Isaac and Meagher 1936, Zedler et al. 1983, Trabaud 1991, Delitti et al. 2005, Eugenio et al. 2006), and continually volatilizing soil nutrients (Brown et al. 2003). However, several studies have reported high resilience or even increases in vegetation cover or diversity following recurrent fires (Beck and Vogl 1972, Delitti et al. 2005, Wittenberg et al. 2007). These observations may be consistent with theoretical predictions of nonlinear effects of disturbance frequency on biotic communities (e.g., Intermediate Disturbance Hypothesis, Connell 1978). Responses likely depend on the fire regime context to which local biota are adapted and the available species pool. Generalities across ecosystems, or mechanisms underlying differences, have remained elusive. One promising tool for identifying generalities and mechanisms is the analysis of plant functional traits, attributes that show a common response to the environment independent of phylogeny (Lavorel and Garnier 2002). Functional traits allow categorical groupings of plant species and evaluation of generalizable hypotheses regarding plant responses to disturbance across ecosystems (Rowe 1983, Lavorel and Garnier 2002).

In this study, we examined the effects of recurrent high-severity disturbance in the Klamath-Siskiyou ecoregion, USA, utilizing two overlapping wildfires as a natural experiment on fire interval variation. This region provides an exceptional opportunity to study responses of vegetation, particularly functional traits, to short-interval fire. First, the region sits at the convergence of northern (more mesic) and southern (more xeric) temperate vegetation zones and comprises the most diverse forest flora of western North America, both in terms of species and physiognomy (Whittaker 1960). As such, plant functional traits are well represented, allowing a broad template of possible responses. Second, a complex fire regime prevails, characterized by frequent but variable fire returns (~5-75 yr) and a mix of severities over time and space (Agee 1991, Agee 1993, Taylor and Skinner 1998, Stuart and Salazar 2000). When stand-replacement occurs, rapid recovery of vegetation cover and fuel continuity, coupled with dry summers and frequent lightning ignitions, create the potential for recurrent high-severity fires over short (~decadal) time scales (Thompson et al. 2007). Thus, short-interval severe fires have likely been a characteristic component of the complex fire regime and a factor structuring vegetation communities of the region (Agee 1991, Agee 1993).

We addressed the following research questions:

1) Is vegetation response following SI fire consistent with a linear (similar to LI fire) or nonlinear (different from LI fire) model, in terms of initial vegetation cover, diversity, and species composition? We hypothesized a nonlinear response, with disturbance-adapted community components increasing, late-seral associated components decreasing, and a decrease in overall diversity and cover due to the effects of two severe fires on soil propagule banks and productivity.

2) Is regeneration of major structural components—hardwoods, woody shrubs, and conifers—reduced in the SI burn relative to the LI burn? For hardwoods and shrubs, a brief fire interval may be shorter than the recovery time of belowground carbohydrate reserves. Also, in a SI burn, combustion of woody fuel accumulations derived from trees killed in the first fire may result in higher soil heat fluxes (Brown et al. 2003) and mortality of belowground meristematic tissues. Based on these expectations and results of previous works in shrub-dominated ecosystems (Trabaud 1991, Delitti et al. 2005), we hypothesized that repeated fires reduce sprouting probability and vigor (biomass). For conifers, retrospective studies in the Douglas-fir region have pointed to sparse or altered regeneration following SI fires (e.g., Agee 1991, Gray and Franklin 1997), but the mechanisms behind this pattern have not been identified (i.e., seed source limitations, unfavorable germination substrates, or subsequent survival). In this study we quantified early conifer establishment to test whether initial establishment conditions (seed source, substrate) limited regeneration in the SI burn.
3) To improve predictive capability and potential insights into differing responses across ecosystems, we explored the question: What plant functional traits are associated with the different fire histories (SI fire, LI fire, mature/old-growth stands with no recent fire)? We focused on broadly applicable traits including regenerative strategy, life form, and dispersal vector. We hypothesized that disturbance-associated traits such as invader regenerative strategy (Rowe 1983) and highly dispersive propagules would be positively associated with the SI fire, while late seral traits would have strongly negative associations with the SI burn.

METHODS

Study Area and Recent Fire History

The study was conducted in the lower Illinois River drainage of the Klamath-Siskiyou Mountains, Southwest Oregon, USA (42°26’ N, 123°54’ W). A mixed-severity fire regime, complex geology, and steep topographic and climatic gradients support a diverse mosaic of plant communities in the region (Whittaker 1960). The climate regime is Mediterranean-type with warm, dry summers and cool, moist winters. Annual precipitation ranges from 150-300 cm over the study area (Daly et al. 2002, www.prismclimate.org), with <15% falling from May-September. Soils were derived from metasedimentary, metavolcanic, and coarse-grained igneous parent materials. Ultramafic (serpentine) substrates (Whittaker 1960) were avoided in this study.

Study sites were in the upper mixed-evergreen zone, where it begins to intergrade with white fir (*Abies concolor*) (Franklin and Dyrness 1973). All sites supported—currently or prior to recent fires—Douglas-fir (*Pseudotsuga menziesii*) dominated mature or old-growth forest (>100 yr old; see Bingham and Sawyer 1991, Agee 1993 for developmental/structural descriptions). Mature/old-growth (M/OG) stands are typically dominated by conifers Douglas-fir, white fir, sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*); evergreen hardwoods tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), Pacific madrone (*Arbutus menziesii*), and chinquapin (*Chrysolepis chrysophylla*); and woody shrubs greenleaf manzanita (*Arctostaphylos patula*), snowbrush (*Ceanothus velutinus*), and Sadler oak (*Quercus* *sadleriana*). Forb and low shrub communities are diverse and spatially heterogeneous (Whittaker 1960).

In 1987, the 38,000-hectare Silver Fire burned with mixed severity, including patches of stand replacement with subsequent establishment of early seral stands. Fifteen years later, in 2002, the 200,000-hectare Biscuit Fire re-burned the entire Silver Fire area, with most early seral stands again experiencing stand replacement (Thompson et al. 2007). In the interim, postfire logging occurred over much of the high-severity portions of the Silver Fire; unlogged stands were left primarily due to remoteness or socio-political factors during the planning effort (USDA 1988) rather than any systematic ecological differences. In this study, sampling of burn stands was restricted to high-severity patches only (defined here as ≥90% overstory mortality, top-kill of all understory and surface layer vegetation, and combustion of most ground layer organic matter).

Our approach was to sample all the unmanaged twice-burned stands we could find that met the above criteria for stand type/age present before the first fire (M/OG conifer-dominated forest), plus an equal number of once-burned and unburned stands well matched in terms of stand type/age, plant association (Atzet et al. 1996), and topoedaphic character. No stands had experienced prior timber harvest. All study areas were assessed for similar ca. 1986 overstory and understory composition/structure via detailed stem surveys, agency data layers, and aerial photographs. The character of all study sites was thus defined by the available twice-burned stands, which had biophysical characteristics common to the area. Study sites were on 35-80% slopes on westerly, northerly and easterly aspects; mid- to upper slope positions; and elevations of 700-1150 m. High-severity burn patches were >100 hectares in size. Patch edges (<80 m) were avoided; distances to adjacent intact forest were <400 m due to complex patch shapes.

This study took advantage of an existing arrangement of two superimposed wildfires (i.e., a natural experiment). Like most natural experiments, detailed prefire data were unavailable, and interspersion of sample groups was not possible (see Fulé et al. 2004, Johnstone 2006). Comparability of sites experiencing different burn histories was maximized to the extent possible (with respect to, e.g., abiotic characteristics, plant associations, and prefire stand type/age) but some pre-existing differences likely existed. Also, because the arrangement of fires was preexisting and not implemented randomly, statistical inference from our results is limited to our study area. We interpret our results in this context. For brevity, in this paper sites of differing recent fire history are referred to as ‘treatments.’

Field Measurements

Field data were collected from late June-August 2004, two growing seasons after the Biscuit Fire. A one-hectare plot was randomly placed in each of 18 stands: six twice-burned (Silver-Biscuit, SI fire), six once-burned (Biscuit only, LI fire), and six unburned (immediately outside the Biscuit Fire perimeter, M/OG with no recent fire). Cover (%) of all hardwoods, shrubs, forbs, and low (suffrutescent) shrubs was quantified in each hectare plot in four non-overlapping, regularly spaced circular subplots (35 m apart; see USDA 2003b for layout) with a minimum area of 20 m^2. To ensure adequate sampling when shrubs occurred at low density, subplots were increased in size to capture ~70 hardwood/shrub individuals across the hectare plot, up to 79 m^2 (one low-density stand had subplots of 314 m^2--no results were significantly changed by excluding this plot so we retained it in analyses). Variable radius was accounted for in all analyses where relevant. Nomenclature followed Hickman (1993); see Appendix C for species list. We also recorded substrate in each subplot as percent cover of mineral soil, rock >1 cm diameter, moss/lichen, woody detritus >1 cm diameter, and litter.

Individual hardwood trees and shrubs were also measured for height, width and breadth of live crown; basal diameter of live stems; number of dead stems tallied by 2-cm diameter classes; and categorized as resprout/seedling/dead. We calculated live biomass of hardwoods and shrubs by entering basal diameter and crown dimensions into species-specific allometric equations (Appendix D). For top-killed portions of hardwoods and shrubs, dead stem basal area was computed based upon stem counts by diameter class. Conifer seedlings were sampled in four 75x0.5 m subplots radiating from plot center in the subcardinal directions. Long narrow subplots were chosen for small seedlings to more effectively capture variability in heterogeneous microsites across each sampled stand, and to obtain more precise estimates of stand-level density than that afforded by circular subplots (Elzinga et al. 1998). Species, rooting substrate, and plot quadrant were recorded for each seedling.

Environmental parameters recorded for each plot included elevation, slope, aspect, soil parent material (USDA 1995), plant association group (Atzet et al. 1996), and estimated mean annual precipitation (Daly et al. 2002). Aspect was mathematically folded about the SW-NE axis so that SW slopes were assigned the highest (warmest) value and NE slopes the lowest (coolest) value, then combined with slope measurements to create one continuous variable estimating potential annual solar heat load in each stand (McCune and Keon 2002). Because slopes were similarly steep throughout the study area (mean ± SD: 59% ± 15%), heat load primarily reflected aspect influence and encompassed most of the topographical variation aside from elevation.

Data Analysis

We used a combination of univariate and multivariate analytical techniques to compare vegetation among treatments (SI burn, LI burn, M/OG). For univariate responses, we computed 95% confidence intervals (CIs) obtained by a *t*-multiplier and standard errors (Ramsey and Schafer 2002). Lack of overlap of CIs with means of other groups was interpreted as strong evidence for differences, while asymmetrical overlap of means (intervals overlap one mean but not the other) was interpreted as suggestive evidence of differences (Ramsey and Schafer 2002). Conifer regeneration was analyzed separately from broadleaf vegetation due to quantification by density rather than cover (density being a more meaningful and commonly used metric for conifer seedlings; e.g., Shatford et al. 2007).

Community composition. To test the hypothesis of no compositional difference between treatments, we used the nonparametric Multi-Response Permutation Procedure (MRPP) using relative Sørensen distance (McCune and Grace 2002). An A-statistic from MRPP provides an estimate of within-group homogeneity in species composition relative to that expected by randomly partitioning the data; a *P*-value estimates the probability of the A-statistic due to chance.

To identify which species drove any community differences among treatments, we conducted Indicator Species Analysis (ISA; Dufrene and Legendre 1997). ISA combines relative frequency and abundance information to assign an indicator value for strength of association between each species and *a priori* groups (treatment) (range 0-100, 0= no association, 100= complete association). An accompanying Monte Carlo randomization with 1000 runs provides a *P*-value for whether the indicator value is stronger than that expected by chance.

Vegetation abundance and diversity. Differences in vegetation cover and diversity among treatments were assessed by comparing 95% CIs. For abundance metrics, hardwood and woody shrub data were grouped due to similar early growth forms (primarily coppiced sprouts). Diversity metrics included alpha richness (mean number of species detected at the hectare-plot scale), gamma richness (total number of species detected in each burn history), and Shannon evenness (index of even species proportions vs. dominance by a few species; range 0-1, 1=perfectly even; Magurran 1988). Both alpha and gamma are positively influenced by area sampled and vegetation abundance (Gotelli and Colwell 2001). Abundance effects were accounted for in part by defining subplot size in accordance with shrub density, which normalizes the number of individuals sampled across plots and reduces the need for rarefaction-based analysis (Gotelli and Colwell 2001), though this does not necessarily account for forb/low-shrub abundance that can also influence richness. Area effects were minimal in this study since area sampled was roughly equivalent for each treatment, and because we found little relationship between subplot size and richness for the scale sampled (R^2=0.21; or 0.01 when outlier with large subplots is excluded).

Hardwood, shrub and conifer responses. For top-killed hardwoods and shrubs, sprout vigor (e.g., biomass) is known to increase with size of the prefire individual (Harrington and Tappeiner 1997). We tested for unique effects of a short-interval fire within the context of this known relationship: if two closely-spaced fires reduce sprouting vigor for shrubs of a given size, then the intercept of this relationship should shift downward. To test for differences in sprouting probability for the 745 individuals present in the plots at the time of the 2002 fire, we used a mixed effects logistic regression model (GLME) for the binary sprouting response as a function of prefire size (basal area), a plot random effect, and treatment as the predictor of interest. To test for differences in sprout mass for the 554 individuals that sprouted, we used a hierarchical linear model (HLM) of aboveground biomass as a function of prefire size, a plot random effect, and treatment as the predictor of interest. Regressions were performed using S-Plus 7.0 software (www.insightful.com) with $\log_e$-transformed data where necessary to better meet model assumptions of linearity/constant variance (Ramsey and Schafer 2002); model fits were assessed with residual-vs.-fit plots. The proportion of seeding, sprouting, and killed individuals were compared among treatments via 95% CIs.

Differences in conifer density among treatments were assessed by comparing 95% CIs. Densities were $\log_e$-transformed to reduce positive skewness and disproportionate influence of extremely high values (Ramsey and Schafer 2002). To evaluate substrate preference of conifers, abundance was also separated by proportion of seedlings on the various substrates and compared to available substrate proportions by treatment. Available substrate proportions were compared between treatments using multivariate analysis of variance (MANOVA; Ramsey and Schafer 2002).

Trait analyses. To quantify associations between plant functional traits and recent fire history, we conducted Indicator Species Analysis and Nonmetric Multidimensional Scaling (NMS) ordination on the abundance of traits in each plot (McCune and Grace 2002). We computed trait abundance by multiplying the species abundance matrix by a binary matrix of traits for each species. Categories of traits included general life form, Raunkiær life form, fire regenerative strategy, general structural/functional attributes, seed dispersal vector, and successional/community association (Table 3-1). NMS and ISA were conducted using PC-ORD software version 5.04 (McCune and Mefford 2006) following data preparation and ordination procedures outlined by McCune and Grace (2002). For NMS, relative Sørensen distance was used as the dissimilarity metric to relativize abundances by sample unit totals, account for variable subplot radius, and allocate proportional influence to small and large distances (McCune and Grace 2002). We used PC-ORD's autopilot mode with random starting configurations and 250 runs of real data, obtaining a two-dimensional solution with final instability <0.0001.

RESULTS

Community abundance, diversity and composition

Total vegetation cover two years after fire was markedly higher in the SI burn (mean 117%, range 55-176%) than in the LI burn (mean 39%, range 27-60). The higher cover in SI burn stands was composed largely of forbs and low shrubs (Fig. 3-1a,b). 95% CIs for differences indicated that, compared to LI burn stands, SI burn stands had higher forb cover by 26-80% and higher cover of low shrubs by 9-54%. Hardwood/shrub cover showed the opposite trend, decreasing with number of recent burns, although confidence intervals overlap substantially among burn histories (Fig. 3-1c). The 95% CI for the difference in hardwood/shrub cover between the SI and LI burn ranged from -22.3 to +10.7%. There were no strong differences in forb, low shrub, or hardwood/shrub cover between the LI burn and M/OG stands (Fig. 3-1a-c). Comparisons between the SI burn and M/OG stands were thus similar to comparisons between the SI and LI burns (Fig. 3-1).

Species richness increased with the number of recent fires and was highest in the SI burn (Table 3-2). This trend was similar when assessed at either the sample-wide (gamma) or plot (alpha) level. Fifty-nine species were detected in the SI burn sample compared to 42 in the LI burn sample, and the SI burn had 4.2-19.8 (95% CI) more species per plot than the LI burn. Some portion of the richness in the SI burn was likely associated with comparatively high forb/low-shrub abundance. There were no strong differences in species richness between the LI burn and M/OG stands (Table 3-2). The higher richness in the SI burn was not dominated by a few species; Shannon evenness was fairly high (0.75, 95% CI 0.67-0.83) and not different from the LI burn (0.73, 95% CI 0.66-0.79).

Species composition differed little between the LI burn and M/OG stands (MRPP: A=0.0095, *P*=0.33), but was strongly different in the SI burn compared to both the LI burn (A=0.13, *P*=0.001) and M/OG stands (A=0.12, *P*=0.002). Consistent with the patterns of increased abundance and diversity, the difference was due primarily to additions or increases in the abundance/frequency of several species in the SI burn, rather than species loss (Table 3-2). Most of the increases were of forb and low stature shrub species. Composition of hardwoods and shrubs showed a decreasing trend with number of recent burns in mean cover of tanoak and canyon live oak, the dominant hardwoods of these plant associations (Table 3-2). Pacific madrone and Sadler oak were mostly absent in the SI burn (Table 3-2). In contrast, greenleaf manzanita occurred in greatest abundance in the SI burn (Table 3-2). The increase in low vegetation components, coupled with reduced cover of major hardwood species, resulted in overall lower-stature communities in the SI burn (Fig. 3-1d).

Indicator Species Analysis results were also consistent with an additive effect of the SI fire (Table 3-2). Only two species, the fire-sensitive forbs rattlesnake plantain (*Goodyera oblongifolia*) and little prince’s pine (*Chimaphila menziesii*), were uniquely associated with M/OG conditions and only one species, Pacific madrone, was strongly associated with the LI fire. In contrast, seven species were strongly associated with the SI fire (Table 3-2). Thus, overall, most species found in M/OG forests occurred with similar abundance/frequency when subject to one or even two high-severity fires, with increases/additions of several disturbance-adapted species in the SI burn.

Hardwood, shrub and conifer responses

Sprouting was the dominant mode of regeneration for hardwoods and woody shrubs in both the SI and LI burn (Fig. 3-2). On average, a greater proportion of prefire individuals were killed by the SI fire (did not sprout), but responses were highly variable (Fig. 3-2). At the individual level, sprouting probability was strongly positively associated with prefire size (GLME: $F_{1,732}=24.9$, $P<0.0001$), and there was no strong shift in this relationship between the SI and LI burns ($F_{1,10}=1.78$, $P=0.21$). Similarly, for individuals that sprouted, sprout biomass was strongly positively associated with prefire size (HLM: $F_{1,540}=338.2$, $P<0.0001$), and there was also no strong shift in this relationship between the SI and LI burns ($F_{1,10}=1.12$, $P=0.32$). However, relative to the LI burn, individuals in the SI burn were smaller at the time of the second fire (mean prefire basal area = 15.3 cm^2 $shrub^{-1}$ in SI burn, 52.2 cm^2 $shrub^{-1}$ in LI burn), which was associated with smaller postfire size (mean sprout mass = 690.7 g $shrub^{-1}$ in SI burn, 1271.8 g $shrub^{-1}$ in LI burn) (Fig. 3-3). This trend was driven largely by canyon live oak, followed by chinquapin, madrone, and greenleaf manzanita (but notably not by tanoak, which had similar prefire basal area between treatments). Thus, individuals of a given size had the same sprouting probability and sprout biomass in both treatments, but plot-averaged biomass was lower in the SI burn since individuals were smaller prior to the second fire.

Conifer establishment roughly spanned an order of magnitude in both burn areas, ranging from 298-6086 ha^{-1} (median 1495 ha^{-1}) in the SI burn and 406-2349 ha^{-1} (median 1002 ha^{-1}) in the LI burn. There was no significant difference in conifer regeneration density between the SI and LI burns (95% CI for SI:LI ratio = 0.4-5.8). Conifer seedling composition in SI burn plots was 99% Douglas-fir with incidental amounts of knobcone pine and sugar pine, whereas LI burn plots contained 66% Douglas-fir, 20% knobcone pine, and 11% sugar pine. Nearly all seedlings became established in 2004, two years postfire, except for knobcone pine (primarily 2003). Seedlings occupied most plot quadrants in both the SI and LI burn (mean of 80% and 93% occupancy, respectively). We detected no strong difference in available substrate proportions between the SI and LI burn (MANOVA $F_{5,6}$=1.45, P =0.33), with mean values of 24-32% mineral soil, 47-56% rock, 10-15% litter, 5-10% wood, and <1% moss/lichen. Substrates utilized by germinating conifers largely reflected the pattern of availability in both the SI and LI fires.

Trait analysis

Trait analysis showed little difference between communities in M/OG stands and the LI burn, while the SI burn differed markedly from the other two treatments (Fig. 3-4a). The ordination of plant functional traits had an R^2 with the original trait distance matrix of 0.98; ranks of scores along ordination Axis 1 (burn axis) show increasing associations of functional traits with the SI burn (Fig. 3-4b). Similar to species patterns, the difference of the SI burn was primarily due to increases in the abundance/frequency of several disturbance-associated traits, rather than reductions in late-seral type traits (Table 3-3). The SI burn was associated with increases in ruderal, small-stature, high turnover community components including native annual forbs, low shrubs and deciduous species (Fig. 3-4, Table 3-3). Obligate seeders, especially species with soil seed banks (evader strategy) or wind-dispersed seeds (invader strategy), responded positively to the SI burn. Sprouters (endurer strategy) exhibited a gradient in response, with those that sprout diffusely from rhizomes better represented in the SI burn than those that sprout from root crowns/burls, which include evergreen hardwoods and shrubs. Fire-sensitive species (avoiders)—of which there were only four in the dataset—were strongly negatively associated with number of recent burns. Nitrogen (N) fixers were most abundant in the SI burn, primarily due to forbs of the Fabacae family (e.g., *Lotus crassifolius, Lupinus spp., Thermopsis macrophyllum*). Species typically associated with late seral forests were located in the middle of the burn axis, reflecting their general presence across all treatments.

Within the trait ordination, number of recent burns had a stronger Pearson correlation coefficient (r=0.87 with Axis 1) than any of the environmental parameters (0.14< |r| <0.36) (Table 3-4) regardless of axis rotation, suggesting that disturbance drove much of the community gradient within this range of environmental conditions. Correlations were generally low between environmental variables and both ordination axes. Categorical variables for plant association and soil type (not shown) were well distributed across axes, suggesting these factors were not major drivers of compositional gradients relative to disturbance history.

DISCUSSION

The early postfire data were most consistent with a nonlinear effect of a short-interval fire relative to a long-interval fire, but in some unexpected ways. The SI burn was rapidly colonized by a unique early seral community with increased rather than reduced diversity, and included the regeneration of major structural species (e.g., conifers, hardwoods), suggesting these stands retained the potential to develop toward mature forest condition.

Community abundance, diversity and composition

The consistent presence of a core assemblage comprising nearly all species found in mature forests suggests high community resistance to one and even two stand-replacing fires. Surprisingly, species were not disproportionately eliminated from the SI burn relative to the LI burn; rather the SI fire resulted in higher species richness and total vegetation cover (Table 3-2; Fig. 3-1). Species additions were largely composed of ruderal or disturbance-adapted flora such as *Rubus spp.* and bracken fern (*Pteridium aquilinum*), the latter also identified by Isaac (1940) as associated with recurrent burning of cutover areas in the Douglas-fir region. Our observation was that repeated fires led to high diversity via the co-existence of competitively superior late seral species (i.e., the core assemblage observed here) with well-dispersed but competitively inferior early seral species, consistent with the Intermediate Disturbance Hypothesis (Connell 1978, Shea et al. 2004). Similar patterns were observed by Delitti et al. (2005) following recurrent fire in a Mediterranean shrub ecosystem in Spain. Although short-interval severe fires are typically considered ‘extreme’ events relative to mean fire return intervals, the repeated disturbance during early succession may behave effectively as an ‘intermediate disturbance’ (Connell 1978).

The mechanisms for increases in early seral species and total richness in the SI burn could be abiotic, such as changes to soil properties that favor such species, or biotic, as in the development of a propagule bank for early seral species during the 15 years between fires (Shea et al. 2004). Changes in substrate heterogeneity due to soil oxidation and intense heat fluxes from log combustion (due to snagfall from first fire; Brown et al. 2003) may have contributed, but we found little support for this abiotic effect in our data. Based on the abundance of seed bank (evader) species in the SI burn (Table 3-3, Fig. 3-4), we infer that increases in early seral species were driven primarily by the biotic mechanism of propagule availability; i.e., the 'storage effect' mechanism of the Intermediate Disturbance Hypothesis as described by Shea et al. (2004). This mechanism represents a positive feedback legacy effect from one fire to the next, whereby the small compositional changes following a single fire (minor increases in early seral species and accumulation of associated seed banks) lead to greater modifications following a second fire (major increases in early seral species).

The addition of disturbance-adapted community components, and associated higher species richness and cover, resulted in unique communities in the SI burn relative to the LI burn and M/OG stands, which did not differ significantly from each other. These results are consistent with nonlinear effects of a SI fire (Johnstone and Chapin

2006); i.e., that SI fires are not merely a temporal reset of succession, rather they produce unique vegetation communities and possibly unique successional pathways on the landscape. Pre-existing variability among treatments could explain the differences we observed, particularly because of the lack of spatial interspersion of treatments. However, a nearly identical core set of species was found in all three treatments which provides supporting evidence that the sample groups were comparable prior to recent disturbance. Moreover, the primary difference observed in the SI burn—addition of disturbance-adapted components—is logically consistent with a fire response.

Hardwood, shrub and conifer responses

Hardwoods and shrub regeneration. Hardwood and shrub individuals of a given size had similar sprouting probability and vigor in the SI and LI burns. A 15-year interval between fires appears sufficient for belowground carbohydrate reserves to support sprouting following top-kill for the species examined in this study. Similarity of sprouting between treatments also suggests there was no difference in heat-related damage to below-ground tissues; thus fire severity was apparently similar across treatments in this respect. Given the history of variable but frequent fires in the Klamath-Siskiyou region (Agee 1993), most broadleaf woody species are likely well adapted to SI fires. Nevertheless, it is possible that a shorter interval fire, or further repeated fires, could reduce the sprouting response relative to what we observed (Delitti et al. 2005).

The relationship between postfire sprouting vigor and prefire size was the same across treatments. Thus, the lower postfire hardwood/shrub cover and biomass in the SI treatment must be due to the smaller size of individuals at the time of the second fire (Fig. 3-3). This may be associated with: a) the conversion by the first fire of large hardwood trees to smaller, multi-stemmed sprouts with lower leaf or basal area; b) a compositional shift toward smaller species that colonized the site over time following the first burn (e.g., greenleaf manzanita) (Table 3-2); or c) pre-existing differences in hardwood/shrub sizes. The conversion by the first fire of tree forms to sprout-shrub forms, and its feedback to re-burn response (smaller subsequent sprouts), is a possible mechanism by which recurrent burning could reduce dominance by hardwoods and shrubs during early succession, creating growing space for other vegetation (Fig. 3-1).

Conifer establishment. Initial postfire conditions were apparently not limiting to conifer establishment in the Silver-Biscuit SI burn. Thus, if differences emerge later between conifer regeneration in the SI vs. LI fires (sensu Gray and Franklin 1997), it could be inferred that latent differences (e.g., competition, herbivory, soil properties) drove the difference. The dense early establishment of conifers likely reflected the presence of nearby seed sources (contiguous patches of surviving trees) and similar germination substrate to that present in the LI burn. Distance to contiguous seed source ranged from 85-300 m for SI burn plots compared to 80-370 m for LI burn plots, a range applicable to 70-90% of the stand-replacement portions of the Biscuit Fire excluding serpentine areas (based on U.S. Forest Service GIS data).

Mixed severity fire typically produces complex patterns of tree mortality on the landscape (Agee 1993, Agee 2005). These patterns result in much of a burned area being close to live-tree seed sources, even in large fires with substantial stand replacement

(Turner et al. 1994). In the Silver-Biscuit SI burn, areas that burned with low severity in the initial fire tended to re-burn with low severity (Thompson et al. 2007), such that the mosaic of available seed sources largely persisted through the second fire. This persistence of the mosaic over certain time scales (Odion et al. 2004) may result in well dispersed seed sources following repeated mixed severity burns. This dynamic differs from observations of sparse regeneration following SI fires in ecosystems dependent on on-site seed rain from serotinous cones, where a brief fire interval can be shorter than the reproductive age of local conifers (Eugenio et al. 2006, Johnstone and Chapin 2006), or in systems largely dependent on off-site seed rain (as in this system) but with seed sources reportedly reduced by the second fire (Isaac and Meagher 1936). Our inference of off-site source in this study is based on nearly all seedlings establishing two years postfire, too late for a dead-tree canopy seed bank source, such as observed by Larson and Franklin (2005).

Trait analysis

Analysis of plant functional traits showed several strong associations with recent fire history, providing support for the use of functional traits in predicting vegetation response to short-interval severe fires (Table 3-3, Fig. 3-4). Some associations were intuitive while others were unanticipated. As we hypothesized, several disturbance-adapted traits and functional types were positively associated with the SI burn. Broadly applicable examples included invader and evader regenerative strategies, ruderal/early seral associates, and wind-dispersed seeds. Low-stature community components such as low shrubs and forbs (mainly hemicryptophytes and therophytes), particularly those with short-lived tissues such as annuals and deciduous species, also responded positively to the SI burn. Delitti et al. (2005) also observed increases in low shrubs and forbs, especially hemicryptophytes, following recurrent fires in a Spanish Mediterranean ecosystem. In contrast, we observed little association of evergreen woody broadleaf vegetation (hardwoods and shrubs, or phanerophytes) with any fire history, although they tended to have lower mass/cover in the SI burn, also similar to Delitti et al. (2005). These observations suggest that plant species not investing resources in long-lived leaves and secondary tissues (wood) may be expected to be relatively dominant immediately following recurrent severe fires. Nitrogen-fixers were highly associated with the SI burn, possibly signifying their competitive advantage due to changes in ecosystem nitrogen associated with repeated fires. Over time, the presence of N-fixers may lend a compensatory mechanism for ecosystem nitrogen (Agee 1993) following repeated intense fires.

Consistent with observations made by Lloret et al. (2005) in a Spanish Mediterranean ecosystem, seeder species were associated with recurrent fires while sprouter species (particularly those that sprout from central root crowns or burls) did not show strong associations with recent fire history (Table 3-3). The exception in our study was that species that sprout from diffuse rhizomatous structures responded positively to the SI fire. Diffuse sprouters may have increased due to a legacy effect associated with the establishment of these species after the first fire, or due to interactions between fire recurrence/severity and soil properties that favor different root forms or sprouting mechanisms (Johnstone 2006).

Surprisingly, very few traits were strongly negatively associated with the SI burn (Table 3-3). Avoiders were the primary negative responders, but the community we studied only included four such species--the forbs and low shrubs rattlesnake plantain, little prince's pine, prince's pine (*Chimaphila umbellata*), and boxwood (*Pachystima myrcinites*). However, most species typically associated with late seral conditions were present with similar relative abundance/frequency in M/OG, LI burn, and SI burn stands. This response, coupled with the low number of avoiders in the study area, likely reflects the fire-adapted nature of Klamath-Siskiyou vegetation communities.

The functional trait patterns we quantified may provide insight into differing responses to recurrent fires among ecosystems. Interactions between fire regime, regenerative types and functional traits of the local biota determine the potential for regeneration. Regions in which negative overall responses have been reported (e.g., Kutiel 1997, Diaz-Delgado et al. 2002) may have greater proportional representation of fire-sensitive or woody species, and a less robust low vegetation community, compared to the Klamath-Siskiyou region. Also, interactions with recent management history are important (Paine et al. 1998) and vary widely by region; our study areas were relatively uninfluenced by recent forest management activities such as timber harvest. Perhaps most importantly, the Silver-Biscuit double burn occurred in a mixed-severity fire regime context, in which local biota are presumably well adapted to wide variations in fire interval and severity.

Implications across time, space and taxa

Ecological communities are rarely in an equilibrium state; rather they are constantly in some state of response to disturbances that vary widely over time and space (Reice 1994, Whitlock et al. 2003). Early responses to SI fire can be viewed in this broader context, with the recognition that initial regeneration processes may be important determinants of eventual successional trajectories (Noble and Slatyer 1980). Studies in other systems have also identified shifts in early vegetation composition and structure following short-interval burns and pointed to potential long-term successional impacts (Delitti et al. 2005, Eugenio and Lloret 2006, Johnstone 2006, Johnstone and Chapin 2006). How long the initial differences observed in the Silver-Biscuit area persist or influence stand development is unknown. If the legacy of the early response persists through time either directly or indirectly, the unique disturbance history may explain some of the Klamath-Siskiyou region's structural and floristic diversity across sites possessing otherwise similar environmental attributes (see Agee 1991, Agee 1993, Odion et al. 2004). Alternatively, if these differences are ephemeral, these patches would only be maintained as part of a shifting landscape mosaic driven by variations in fire pattern and overlap.

The abundance, character, and landscape distribution of short-interval burns have likely varied widely over time. Important factors in this variability may include long-term climatic variability (Whitlock et al. 2003) as well as recent fire exclusion (Agee 1991, Taylor and Skinner 1998). Also, stand-scale variation in fire interval may be important since feedbacks between multiple fires may exhibit threshold behavior, with increased probability of high-severity re-burning over short time scales (Thompson et al. 2007), but decreased probability over longer time scales that allow for canopy closure and large stature trees (Odion et al. 2004). Where positive feedbacks exist, continual short-interval fires could lead to different biotic responses and successional trajectories.

The early uniqueness, abundance, and species richness found in the SI burn indicate that recurrent fire was not deleterious to native flora, including species important to long-term forest development, such as conifers and hardwoods. This response suggests that in landscapes characterized by natural disturbances that vary widely in time, space, and intensity (e.g., mixed severity fire regimes and some high-severity regimes), much of the native biota is well adapted to extreme events such as recurrent severe fire. Concurrent studies in the same area suggest that this premise also extends to avian and small mammal communities of the Klamath-Siskiyou region (Fontaine 2007). In other regions with less variable disturbance regimes (e.g., *Pinus ponderosa* forests of the interior U.S. that historically tended toward frequent low-intensity fires (Agee 1993), local biota may not possess this degree of adaptation. Fire exclusion has likely had stronger effects in such forests and these may interact with responses to SI fire. In the context of the variable-frequency fire regime of the Klamath-Siskiyou region, exactly how fire exclusion has affected response to recent fires is less clear. Further studies of SI severe fires across a range of fire regime contexts are needed to explore this question.

Postfire management activities are often focused, in part, on reducing anticipated adverse effects of repeat high-severity fires (USDA 1988, Brown et al. 2003). For certain objectives, such as the rapid attainment of late-successional condition, recurrent stand-replacement fires are obviously counterproductive in the short term. However, such events may be consistent with objectives that include maintaining or managing in accordance with characteristic landscape disturbance processes and regional vascular plant diversity (see Landres et al. 1999). Given the Klamath-Siskiyou region's characteristic patterns of fire severity, productivity, and ignition source, there is little reason to believe that short-interval severe fires have not been a component of the fire regime historically. Our results indicate that SI burns can contribute to the landscape heterogeneity inherent to mixed-severity fire regimes. In these landscapes, variability in fire frequency, severity, and spatial pattern can be more important than central tendencies (Agee 2005). Process-based disturbance management could include this variation, perpetuating a diversity of conditions across the landscape.

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Table 3-1. Plant traits for which each species was assigned binary (0/1) values for trait analyses.

Trait	Description
General life form	
Forb	little or no wood above ground; aboveground parts of <1 yr duration
Graminoid	monocotyledonous plant of the family Poaceae
Low shrub	low-stature shrubs, generally with little secondary growth
Hardwood/shrub	broadleaf woody species, often multi-stemmed, hardwoods can be trees
Raunkiær life form	
Phanerophyte	perennating tissue >25 cm above soil surface (trees, large woody shrubs)
Chamaephyte	perennating tissue within ~25 cm of soil surface (typically low shrubs)
Hemicryptophyte	perennating tissue at the soil surface (forbs and trailing shrubs)
Therophyte	perennating tissue contained in seed (annual forbs)
Geophyte	perennating tissue below the soil surface (rhizomatous perennials)
Fire regenerative strategy	
Avoider	fire-sensitive, no fire adaptation; usually shade-tolerant, late-successional
Invader	highly dispersive, pioneering fugitives with short-lived disseminules
Evader	long-lived propagules stored in soil or canopy that germinate after fire
Endurer	ability to sprout from above- or belowground structures when top-killed
General structure and function	
Rhizomes	having underground, often elongate, more or less horizontal stems
Fibrous root	root system composed of many roots similar in length and thickness
Tap root	main, tapered root that generally grows straight down into soil
Obligate Seeder	incapable of sprouting after top-kill; relies solely on regeneration by seed
Sprout-root crown	sprouting occurs primarily from root crown (surface)
Sprout-root deep	sprouting occurs primarily from central belowground burl or lignotuber
Sprout-diffuse	sprouting occurs from >1 location, generally from spreading rhizomes
Nitrogen fixer	associations with microbes that fix atmospheric nitrogen to usable forms
Deciduous	leaves not persistent >1 yr
Evergreen	leaves persistent >1 yr
Annual	completing life cycle within one year or growing season
Perennial	living more than two years or growing seasons
Seed dispersal vector	
Wind dispersed	seeds primarily dispersed by wind
Animal dispersed	seeds primarily dispersed by animals
Successional/community association	
Early seral assoc.	most associated with early seral forest; shade intolerant
Late seral assoc.	most associated with late seral forest; shade tolerant
All seral assoc.	typically found in both early and late seral forests
Non-native	not native to Pacific Northwest region
Ruderal	grows best in disturbed sites, usually short-lived, little community affinity

Notes: Sources were Raunkiær (1934), Rowe (1983), Agee (1993), Hickman (1993), www.plants.usda.gov, fs.fed.us/database/feis. Conifer seedlings were analyzed separately due to quantification by density rather than cover.

Table 3-2. Indicator values, diversity statistics, and mean abundance for eight of the most common hardwoods/shrubs, low shrubs, and forbs by recent burn history.

Species	Indicator value† —group	Mature/ old-growth [M/OG]		Long-interval fire [LI]		Short-interval fire [SI]	
		% cover $\overline{x}$ (S.E.)	% freq.	% cover $\overline{x}$ (S.E.)	% freq.	% cover $\overline{x}$ (S.E.)	% freq.
Forbs							
Chimaphila menziesii	**85.7 – M/OG**	0.5 (0.2)	100	0.0 (0.0)	0	0.1 (0.1)	17
Goodyera oblongifolia	**66.7 – M/OG**	0.3 (0.2)	67	0.0 (0.0)	0	0.0 (0.0)	0
Achlys triphylla	44.7 – SI	1.1 (0.7)	50	0.3 (0.1)	67	2.7 (1.4)	67
Graminoid species	**88.2 – SI**	0.1 (0.1)	17	0.0 (0.0)	0	0.6 (0.3)	100
Lotus crassifolius	64.7 – SI	0.0 (0.0)	0	0.3 (0.3)	17	9.5 (6.7)	67
Pteridium aquilinum	**95.4 – SI**	0.0 (0.0)	17	0.9 (0.6)	50	18.7 (9.8)	100
Trientalis latifolia	**93.3 – SI**	0.0 (0.0)	0	0.2 (0.1)	67	2.0 (1.0)	100
Vancouveria hexandra	**66.3 – SI**	0.0 (0.0)	0	0.0 (0.0)	17	4.3 (2.3)	67
Low shrubs							
Polystichum munitum	21.0 – M/OG	0.7 (0.6)	33	0.0 (0.0)	17	0.4 (0.2)	50
Berberis nervosa	44.1 – SI	4.2 (1.5)	100	3.6 (1.1)	100	6.1 (2.0)	100
Rosa gymnocarpa	55.9 – SI	0.7 (0.3)	67	1.2 (0.4)	83	2.3 (0.5)	100
Rubus ursinus	**97.5 – SI**	0.0 (0.0)	17	0.5 (0.3)	50	19.0 (7.8)	100
Rubus leucodermis	**65.0 – SI**	0.0 (0.0)	0	0.0 (0.0)	17	0.8 (0.4)	67
Symphoricarpus mollis	**94.4 – SI**	0.1 (0.1)	17	0.1 (0.0)	33	3.2 (1.2)	100
Whipplea modesta	20.0 – SI	0.5 (0.2)	50	0.4 (0.2)	67	1.3 (1.1)	33
Xerophyllum tenax	36.2 – SI	1.9 (1.9)	50	0.4 (0.4)	17	2.7 (1.1)	67
Hardwoods and woody shrubs							
Lithocarpus densiflorus	39.6 – M/OG	13.6 (4.4)	83	8.4 (2.1)	100	6.6 (2.5)	100
Quercus chrysolepis	34.3 – M/OG	11.0 (4.2)	67	6.9 (2.0)	100	3.5 (3.1)	50
Quercus sadleriana	25.4 – M/OG	9.1 (8.6)	33	2.8 (2.2)	33	0.0 (0.0)	0
Arbutus menziesii	**75.3 – LI**	0.2 (0.2)	17	4.7 (1.3)	83	0.3 (0.2)	33
Ceanothus velutinus	12.5 – LI	0.0 (0.0)	0	0.4 (0.2)	50	1.1 (1.1)	17
Garrya species	18.5 – LI	1.7 (1.7)	17	2.4 (2.3)	33	0.2 (0.2)	33
Arctostaphylos patula	46.8 – SI	1.8 (1.3)	33	0.7 (0.6)	50	5.8 (3.1)	67
Chrysolepis chrysophylla	23.5 – SI	0.8 (0.8)	17	1.3 (1.3)	17	1.9 (1.4)	50
Mean # of species detected in ha plot (95% CI)		14.0 (9.1 – 18.9)		19.2 (11.5 – 26.8)		31.2 (26.5 – 35.8)	
Total # of species detected in sample		39		42		59	
# of significant indicator species		2		1		7	

† Metric combining relative abundance and frequency for most strongly associated group (burn history) (Dufrene and Legendre 1997). Range 0-100, 100=always and only occurs in given group. Values are bolded for strong (≥65) affinities, which have *P*≤0.01 by randomization test.

Table 3-3. Results of indicator analysis of plant traits by recent burn history.

Trait category	Trait	Indicator value†	Group of maximum association
General life form	Graminoid	**95.7**	**SI**
	Forb	**88.9**	**SI**
	Low shrub	**66.7**	**SI**
	Hardwood/shrub	43.8	M/OG
Raunkiær life form	Hemicryptophyte	**88.0**	**SI**
	Therophyte	**87.0**	**SI**
	Geophyte	61.6	SI
	Chamaephyte	60.3	SI
	Phanerophyte	40.7	M/OG
Fire regenerative strategy	Evader	**90.3**	**SI**
	Invader	**78.9**	**SI**
	Avoider	**77.4**	**M/OG**
	Endurer	52.7	SI
General structure and function	Nitrogen fixer	**96.3**	**SI**
	Obligate seeder	**92.0**	**SI**
	Annual	**87.0**	**SI**
	Deciduous	**81.4**	**SI**
	Rhizomes	**71.7**	**SI**
	Sprout diffuse	**69.8**	**SI**
	Perennial	54.9	SI
	Sprout-root crown	54.0	SI
	Fibrous Root	45.9	LI
	Evergreen	41.6	M/OG
	Tap root	36.6	SI
	Sprout-root deep	34.6	SI
Dispersal vector	Wind dispersed	**83.8**	**SI**
	Animal dispersed	45.4	SI
Successional/ community association	Ruderal	**96.0**	**SI**
	Early seral assoc.	**92.4**	**SI**
	Late seral assoc.	64.3	SI
	Non-native	45.8	SI
	All seral assoc.	40.6	M/OG

Notes: See Tables 3-1 and 3-2 for definitions.

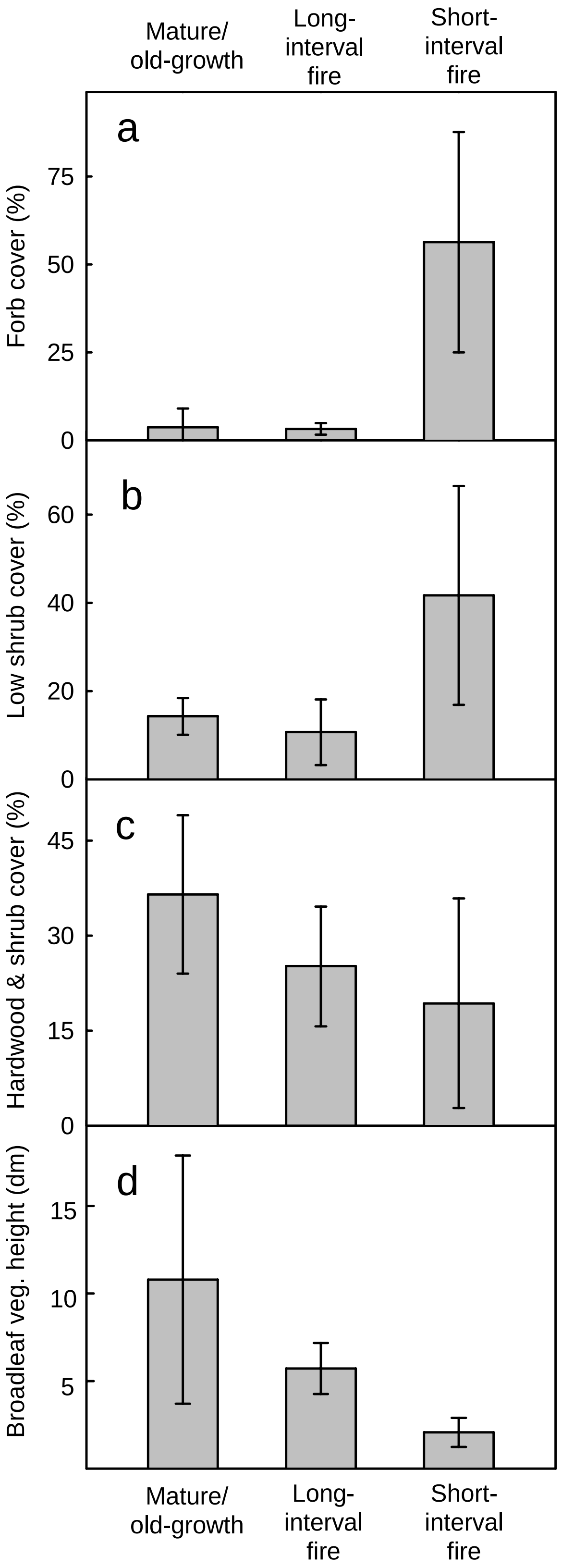
† Metric combining relative abundance and frequency for most strongly associated group (# of recent burns) (Indicator Species Analysis; Dufrene and Legendre 1997). Range 0-100, 100=always and only occurs in given group. Values are bolded for strong (≥65) affinities, which have significance level $P \leq 0.01$ by randomization test.

Table 3-4. Total variance explained (R^2) and Pearson correlation coefficients (r) with continuous environmental variables for axes of NMS ordination of plots in functional trait space.

Variable	Axis 1	Axis 2
Total variance explained (R^2)	0.87	0.11
Number of recent burns	0.86	0.04
Elevation	0.22	0.20
Estimated annual precipitation	-0.19	-0.14
Estimated annual solar heat load †	-0.36	-0.35

† Proxy for aspect (McCune and Keon 2002).

Figure 3-1. Mean (±95% CI): (a) forb cover, (b) low shrub cover, (c) hardwood/shrub cover, and (d) broadleaf vegetation height, for mature/old growth stands, long-interval burn stands, and short-interval burn stands (0, 1, and 2 recent burns, respectively). Heights were calculated as a weighted average based on cover x height of each species.


Mature/
old-growth
Long-
interval
fire
Short-
interval
fire
a
Forb cover (%)
0
25
50
75
b
Low shrub cover (%)
0
20
40
60
c
Hardwood & shrub cover (%)
0
15
30
45
d
Broadleaf veg. height (dm)
5
10
15
Mature/
old-growth
Long-
interval
fire
Short-
interval
fire

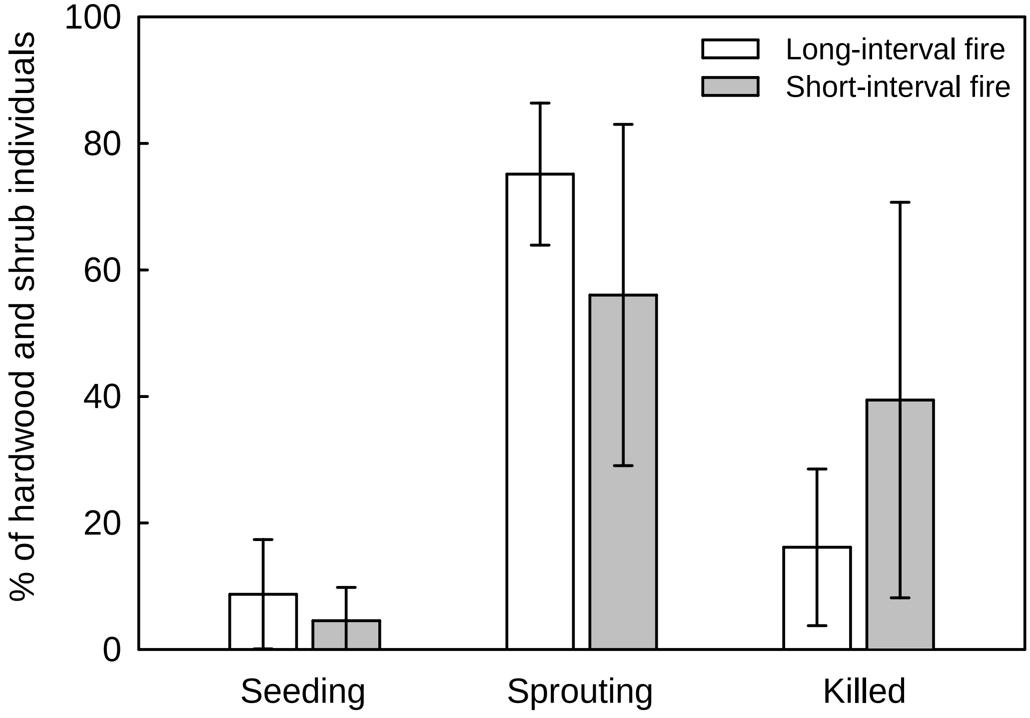


Figure 3-2. Hardwood and shrub reproductive modes by percent of individuals in each plot (mean ±95% CI). No strong shift in dominant regenerative mode in the SI burn was apparent; sprouting dominates over seeding in both treatments. There is suggestive evidence of higher mortality of prefire individuals in SI burn plots; however, variability was high.

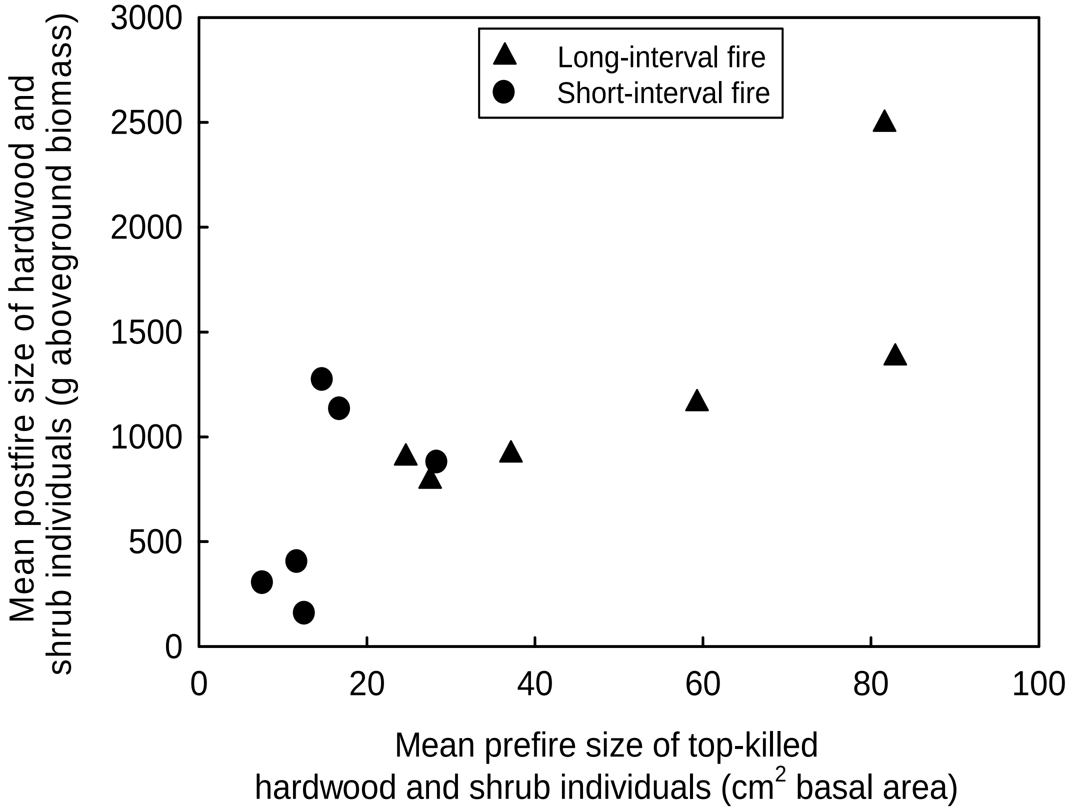


Figure 3-3. Mean postfire biomass of hardwoods and shrubs as a function of mean prefire size of hardwoods and shrubs. Data are shown aggregated by plot for clearer visual display of trend; regression analysis was performed on 554 individual shrubs, with plot as a random effect. There was no strong evidence for differences between burn histories in the relationship between pre- and postfire size (HLM: $F_{1,10}$=1.12, *P*=0.32), but individuals were smaller prior to the short-interval fire which was associated with smaller postfire size (HLM: $F_{1,540}$=338.2, *P*<0.0001).

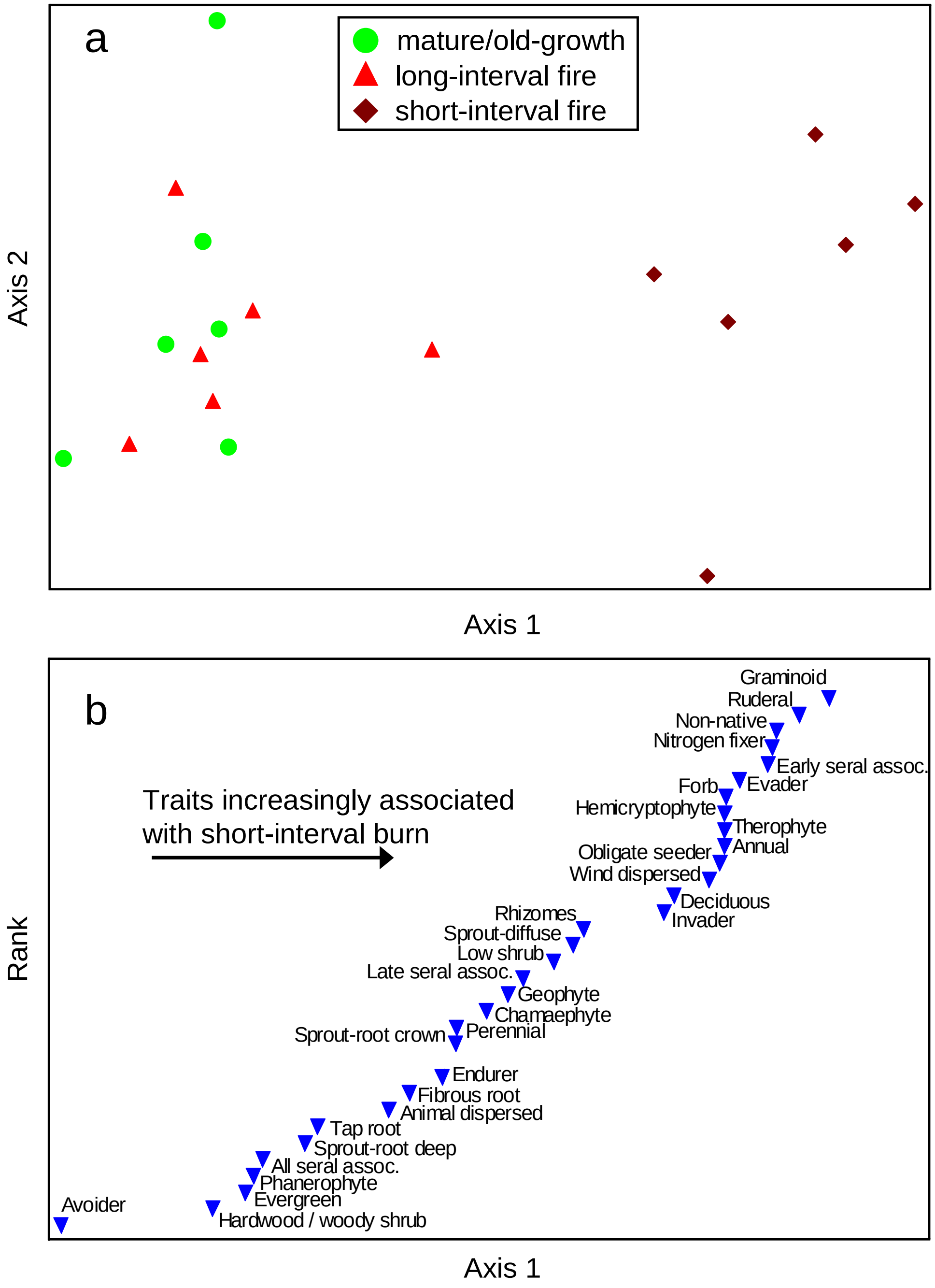


Figure 3-4. (a) Ordination of plots in plant functional trait space. Larger distances between points represent larger differences in trait abundance; SI burn plots separate strongly from other treatments. See Table 3-4 for correlations of environmental variables with ordination axes. (b) Ranks of plant functional traits along Axis 1. Attributes to right are increasingly associated with (but not exclusive to) the SI burn. The 'Non-native' point is due to minor occurrences of *Cirsium spp.* or *Senecio sylvaticus* (<1% cover in four plots).

CHAPTER 4: FUEL MASS AND DISTRIBUTION FOLLOWING STAND-REPLACEMENT FIRE AND POSTFIRE LOGGING IN A MIXED-EVERGREEN FOREST

ABSTRACT

Postfire fuel dynamics are a major land management concern in light of recent increases in wildfire activity. Management objectives often include reducing the potential for severe re-burns by removing fire-killed trees that may eventually fuel subsequent fires. We quantified fuel mass and structure 3-4 and 17-18 years after stand-replacing fire in mixed-evergreen Douglas-fir (*Pseudotsuga menziesii*) forests in southwest Oregon, USA. We assessed effects of three postfire logging intensities (unlogged [*U*], moderate-intensity [*M*], high-intensity [*H*]) across two climatically distinct areas (mesic coastal, drier interior). Only ~17% of aboveground biomass was consumed by high-severity fire, primarily surface fuels (forest floor, fine wood). Residual biomass was mostly standing snags, and was 1.6 times higher in mesic stands (709.1 Mg ha^{-1}) than drier stands (434.9 Mg ha^{-1}). Three to four years after fire, high-intensity logging resulted in a greater proportion (28%) of felled biomass left on site as slash compared to moderate-intensity logging (14%), because tree felling was less selective. Mean surface woody fuel loads after logging (Mg ha^{-1}) were *U*: 11.4-27.1, *M*: 57.8-84.8, *H*: 98.5-192.4, with the higher means in mesic stands.

It is generally hypothesized that without logging, surface fuel loads will reach very high levels 15-30 years after fire as snags fall; however, we found no significant difference in surface woody fuels among logged and unlogged treatments at 17-18 years

after fire (61.8 vs. 72.9 Mg ha^{-1}, respectively). Snags in unlogged stands apparently decayed rapidly rather than accumulate on the surface, leaving large-diameter broken-topped boles. Because such snags stand the longest, surface fuels derived from residual snags had largely peaked by 18 years in unlogged stands. Fuel profiles and fire modeling both suggested that regenerating vegetation rather than residual dead wood is the main driver of early seral fire hazard, with low fire potentials 3-4 years postfire and very high potentials at 17-18 years. Postfire logging increased fire potentials within this context due to generation of slash, but treatment differences became negligible by ~15-20 years (with slash treatment). Based on these data, postfire logging is not consistent with objectives for reducing early fire hazard in this forest type.

INTRODUCTION

In many forest types, fire is the predominant disturbance regulating stand structure and the generation of dead wood (Harmon et al. 1986, Spies et al. 1988). Stand-replacement fire, in which most or all aboveground biomass is killed, generates a pulse of dead wood (Agee and Huff 1987, Campbell et al. 2007) which in turn affects many ecosystem properties including carbon cycling, wildlife habitat, and the re-development of fuel profiles (amount, composition, distribution of aboveground biomass) (Brown et al. 2003). As fire-killed trees fall, they may function as a positive feedback mechanism by providing fuel for subsequent fires, or 're-burns' (Brown et al. 2003). Postfire logging (i.e., salvage), an increasingly prominent component of forestland management (McIver and Starr 2001), is often aimed at reducing fuel loads and thus fire behavior/effects in the event of a re-burn (e.g., McIver and Starr 2001, USDA 2004). However, little empirical information exists on the quantity, composition, and arrangement of residual postfire wood, particularly how these characteristics are influenced by postfire logging (McIver and Starr 2001, Peterson et al. in press).

Only a small portion of biomass is consumed in wildfires, even when vegetation mortality approaches 100% (Agee 1993, Campbell et al. 2007). The remainder, composed almost entirely of dead wood (Fahnestock and Agee 1983), is carried into the next stand as residual biomass. Dead wood is dynamic over forest succession, in many forest types exhibiting a characteristic U-shaped temporal pattern of accumulation (Agee and Huff 1987, Spies et al. 1988, Bormann and Likens 1994). This pattern is a consequence of disturbance-generated dead wood in young stands, decay of that material over time, followed by recruitment of new dead wood in mature/old-growth stands (Spies et al. 1988). These long-term dynamics have been studied extensively, focused primarily on larger material (i.e., tree boles and logs). Far less is known regarding the dynamics of fine materials (e.g., branches, twigs, bark), which presumably operate over shorter time scales due to faster decay and fragmentation rates (Harmon et al. 1986), influencing important processes such as nutrient cycling and potential fire behavior.

In many forest types, fire hazard may be relatively high during early postfire succession (Agee and Huff 1987, Thompson et al. 2007). This phenomenon is thought to be due to some combination of live and dead fuel contributions (McIver and Ottmar 2007, Thompson et al. 2007). Although unavailable to the previous fire, residual wood mass eventually desiccates, decays, fragments and drops from the aerial layer (standing mid- and overstory) to the surface layer (down/understory), in which most wildfires propagate (Pyne et al. 1996). Further decay of this material eventually removes it from the fuel profile. Regenerating early seral vegetation is typically low-stature and spatially continuous, thus capable of supporting rapid fire spread and susceptible to fire mortality (Weatherspoon and Skinner 1995, Stephens and Moghaddas 2005, McIver and Ottmar 2007). Considerable uncertainty exists regarding the relative importance of residual dead vs. regenerating live fuels to fire hazard in young stands, and how this interaction changes over time (Thompson et al. 2007).

Postfire logging objectives typically include reducing the intensity and severity of subsequent fires by removing residual dead mass (McIver and Starr 2001, Brown et al. 2003). However, the few relevant studies of postdisturbance logging have reported either no effects on, or increases in, the severity of subsequent fires despite removal of large woody fuels (Hansen 1983, Kulakowski and Veblen 2007, Thompson et al. 2007). Timber harvest in general is well known to increase surface fine woody fuel loads by transferring nonmerchantable branches and tree tops to the ground (Snell and Brown 1980). Exactly how this premise extends to postfire logging is less clear due to potential consumption of fine canopy fuels during the fire (McIver and Starr 2001). Recent studies indicate that surface fine fuel loads are indeed elevated following postfire logging, and models suggest these elevated loads may persist for ~20 years (Donato et al. 2006a, McIver and Ottmar 2007). On the other hand, coarse woody fuels are expected to accumulate less on the surface over the intermediate term (~10-50 yr) if boles are removed, which could decrease potential fire effects such as soil heating (McIver and

Ottmar 2007). Postfire woody fuel accumulation and decay rates—either fine or coarse—have not been well quantified empirically. Re-burn behavior may also be influenced by alterations to live fuels, such as conifer planting (Thompson et al. 2007). Thus far, retrospective studies of postdisturbance management have involved multiple confounded treatments affecting both live and dead fuels (e.g., logging, slash burning, conifer planting), thus lacking the ability to identify causal mechanisms. Data are needed quantifying the specific effects of individual treatments (McIver and Starr 2001, Donato et al. 2006b).

Although postfire logging is known to remove large-diameter wood and transfer fine materials to the surface (Donato et al. 2006a, McIver and Ottmar 2007), the specific quantity and composition of remaining fuels may vary widely by logging method and biophysical setting (Donato et al. 2006b). Knowledge of this variation is essential to informed postfire decision making (Peterson et al. in press).

In this study, we investigated biomass dynamics in high-severity (stand-replacement) portions of the 2002 Biscuit Fire, a large mixed-severity wildfire in southwest Oregon, USA. Our objectives were to: (1) quantify aboveground biomass quantity, composition, and vertical distribution following stand-replacement fire, including all material (fine and coarse, live and dead) in both the aerial and surface fuel strata; (2) quantify immediate changes in these profiles resulting from postfire logging, and how these changes vary by harvest intensity and biophysical setting (high productivity coastal forest type vs. drier inland forest type); (3) investigate longer-term (17-18 year) dynamics by comparing fuel profiles between logged and unlogged stands in two 1987 wildfires adjacent to the Biscuit Fire; and (4) assess potential fire behavior and effects for all treatments using common fire models.

METHODS

Study area

The study was conducted in the Siskiyou Mountains of southwest Oregon, USA (Fig. 4-1), within the mixed-evergreen and *Abies concolor* zones described by Franklin and Dyrness (1973). The region is characterized by a Mediterranean-type climate with warm, dry summers (mean max. July temperature: 27 °C) and cool, wet winters (mean min. January temperature: 2 °C). Mean annual precipitation ranges from 140-500 cm over the burn area, < 15% of which falls from May-September (Daly et al. 2002; prismclimate.org). Forests are dominated by conifers Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*); evergreen hardwoods tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), and canyon live oak (*Quercus chrysolepis*); and shrubs greenleaf manzanita (*Arctostaphylos patula*) and snowbrush (*Ceanothus velutinus*). Fire regimes are complex, described as low- to mixed-severity with return intervals ranging from 5-35 years in drier plant associations to 50- >100 years in higher elevation and wetter associations (Agee 1991, Agee 1993, Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000, USDA 2004). Stand-replacement fire effects (≥90% overstory mortality) typically occur in variably-sized patches as part of a complex burn mosaic.

All sample areas were mature to old-growth (MOG) Douglas-fir-dominated forest currently or prior to stand-replacement fire (see Thornburgh 1982, Agee 1993 for developmental/structural descriptions). Study areas were on steep slopes (generally >20°) between ~600-1300 m elevation, at mid-slope positions on a full range of aspects. Soils were derived from metasedimentary, metavolcanic, and coarse-grained igneous parent materials (USDA 2004). We excluded conditions generally excluded from postfire logging: extremely steep rocky areas, riparian zones, ultramafic soils (see Whittaker 1960), areas burned with low or moderate severity (USDA 2004), and pre-existing plantations and shrub fields.

The Siskiyou region is renowned for floristic diversity due in part to sharp topoedaphic and climatic gradients (Whittaker 1960). Among the most important gradients are west-to-east trends in moisture and productivity. Western portions of the area (Fig. 4-1) receive greater maritime influence, experience less severe summer moisture deficits, and have longer fire return intervals than inland sites to the east (Daly et al. 2002, USDA 2004). As such, mesic western areas tend to support higher basal area and aboveground biomass than drier eastern areas.

Study fires

The Biscuit Fire burned with mixed severity over 200,000 ha of the Siskiyou Mountains in July-November, 2002, making it the largest contiguous wildfire on record for Oregon. Relative proportions of low, mixed, and high severity (as assessed by vegetation change) were ~30%, 27%, and 43%, respectively (USDA 2004). The fire perimeter encompassed a broad range of biophysical conditions and spanned both western and eastern plant associations (Fig. 4-1). Following the fire, the Rogue River-Siskiyou National Forest implemented postfire logging in limited areas of the burn. In addition to recouping economic value, primary stated objectives of postfire logging included reducing fire hazards associated with residual wood (USDA 2004).

Postfire logging was conducted largely during the fall-spring of 2004-2005 (2-3 yr postfire) with some additional logging during the winter-summer of 2005-2006 (3-4 yr postfire). Logging occurred in stand-replacement patches ranging from ~4 to over 1000 ha. Harvest units (spatially distinct logging parcels within timber sales) ranged from 1-70 ha in size (mean= 8 ha). Harvest method consisted of hand felling and either helicopter or cable yarding; logs were limbed and bucked on site, generating slash in place. Slash treatment, where conducted (<30% of sampled stands as of late 2006), occurred after field data were collected; thus all post-logging data presented here from the Biscuit Fire reflect effects of tree harvest only and not any subsequent stand treatments. Slash treatments were planned if down wood levels exceeded prescriptions, which varied between 24 and 106 Mg ha^{-1} depending on plant association (USDA 2004). Harvest prescriptions called for retention of 3-29 large (>41 cm) snags per hectare, and variable retention of smaller (<41 cm) snags depending on merchantability (USDA 2004). Spatial arrangement of snag retention varied, ranging from clumped at edges of logging units, resembling a small clearcut, to dispersed across logging units. Retained snags were often clustered in riparian buffers around streams running through logging units (USDA 2004).

The 8700-ha Galice Fire and the 4000-ha Longwood Fire both occurred in September of 1987. Both fires were mixed severity and occurred in similar plant associations, elevation zones, and terrain as the eastern Biscuit region (the eastern Biscuit perimeter is within 15 km of both older fires) (Fig. 4-1). Sampled postfire treatments consisted of logging 1-2 years postfire with retention of 7-12 snags ha^{-1}. Harvest method consisted of hand felling and cable yarding; logs were limbed and bucked on site, generating slash in place. Postlogging treatments consisted of pile or broadcast burning of slash, planting with 1076-1328 conifer seedlings ha^{-1}, and manual release treatments (shrub/hardwood cutting) 5-12 years postfire. Notwithstanding the standard limitations of chronosequence-type studies—e.g., spatial segregation of treatments, substitution of space for time (Agee and Huff 1987, Spies et al. 1988)—these data provide insight into general successional trends in fuel profiles and lend temporal context to the early profiles measured in the Biscuit Fire.

Data collection

Biscuit Fire (3-4 year postfire data). We sampled all large Biscuit Fire timber sales completed by late 2005, with one exception in the extreme western portion of the fire due to access logistics. We sampled 26 stands in the eastern portion of the fire and 12 in the western portion (68% east, 32% west), corresponding to the distribution of Biscuit postfire logging (67% east, 33% west by area). Study areas were identified a priori from Forest Service spatial data layers on proposed sale boundaries, burn severity, and prefire forest cover/type. We interspersed treatment and control stands by sampling unlogged areas in and around each sampled sale. Sampled mature/old-growth stands were also distributed over a broad area corresponding to the distribution of sampled burn stands (Fig. 4-1). Study plots (no more than one per harvest unit) were located randomly within harvest units and adjacent unlogged areas. Pre-treatment measurements occurred in the summer of 2004; post-treatment measurements (including re-measurement of control stands) occurred in the summers of 2005 and 2006, within 3-9 months of logging.

We categorized Biscuit Fire stands into three levels of treatment intensity: unlogged (U), logged at moderate intensity (M), and logged at high intensity (H). Moderate-intensity harvest units were helicopter-yarded with 25-75% basal area cut at the hectare scale (mean 46% ±5.5 SE); high-intensity harvest included a mix of cable and helicopter yarding with >75% basal area cut at the hectare scale (mean 89% ±3.5 SE). The 26 eastern stands consisted of eight U stands, seven M stands, six H stands, as well as five unburned mature/old-growth stands. The 12 western stands included three each of the four treatments.

Galice/Longwood Fires (17-18 year postfire data). Five stands experiencing high-severity fire and postfire logging were sampled in the Galice Fire in 2004, 17 years postfire. No unlogged high-severity burn could be located in the Galice Fire, but four such stands were identified and sampled in the Longwood Fire in 2005, 18 years postfire. In both fires, we sampled all stands we could find meeting the study criteria for prefire forest type and fire severity (mature to old-growth Douglas-fir-dominated forest experiencing high-severity fire)—i.e., an all-inclusive rather than random sample. These stands were in similar plant associations and terrain as the eastern Biscuit region, and include U and H* (high-intensity logging + slash burn + conifer planting) treatments only.

Plot Measurements. We sampled each stand with a one-hectare plot, the layout of which was based on regional forest inventory protocols (USDA 2003b). All aboveground biomass pools were measured, partitioned by fuel stratum (sensu Pyne et al. 1996). Aerial biomass was defined as standing over- and mid-story components (live and dead trees >10 cm dbh). Surface biomass was defined as standing understory components (live and dead small trees, shrubs, forbs, grasses), down woody detritus, stumps, and forest floor organic material. Aerial and standing surface biomass were each measured in four regularly-spaced circular subplots ranging from 2-m radius for the surface stratum to 17-m radius for the aerial stratum (surface and aerial subplots were concentric) (see USDA 2003b). For each tree we recorded species, diameter at breast height (dbh), total height, decay class (per Cline et al. 1980), and percent of bole surface area affected by surface (bark) and deep (wood) charring. For understory hardwoods, shrubs, forbs and grasses we recorded percent cover by species. Hardwoods and woody shrubs were further measured on an individual basis for live crown dimensions (l, w, h), basal diameter of live stems, and height and count of dead stems by 2-cm basal diameter class. Forest floor mass (litter and duff) was quantified by collecting eight systematically located cores of 5.6-cm diameter down to the mineral soil surface in each of the four subplots (32 samples per plot), separating litter and duff components, drying samples to constant mass, and calculating dry mass of each per hectare.

Down woody detritus was sampled with four 75-m planar intercept transects (Brown 1974, Harmon and Sexton 1996) radiating from plot center in subcardinal directions. Starting from the distal end of each transect, fine woody detritus (FWD; <7.62 cm) was tallied by fuel timelag class (Agee 1993): 1-hour fuels (<0.62 cm diameter) were sampled from 0-5 m, 10-hour fuels (0.62-2.54 cm) from 0-15 m, and 100-hour fuels (2.54-7.62 cm) from 0-25 m. Total sample lengths per plot were thus 20 m, 60 m, and 100 m for 1 hr, 10 hr, and 100 hr fuels respectively. We also recorded whether each FWD piece was charred. For coarse woody detritus (CWD; >7.62 cm), both 1000-hour (7.62-20.32 cm) and >1000-hour (>20.32 cm) fuels were sampled over all 75 transect meters (300 m total in plot). For each CWD piece we recorded diameter, species, decay class, and the presence of deep (wood) char.

Biomass computations. We computed bole mass for the 6390 individual tree records using species- and region-specific allometric equations relating stem diameter to volume and species-specific wood density (Walters et al. 1985, Means et al. 1994, Van Tuyl et al. 2005). Masses of tree foliage, bark, branch, and unmerchantable tops were estimated directly from species-specific allometric equations (Means et al. 1994). Merchantable mass was defined as sound conifer bole wood >20 cm diameter (USDA 2004). All biomass components were adjusted for individual-specific metrics of bark/bole charring, top breakage, and decay class status (Harmon and Sexton 1996, Appendix E, F); as well as plot-specific ocular estimates of foliage and branch consumption (sensu USDA 2003a). Due to confounding of fire effects with definitions of decay class 1-2 characteristics (e.g. fine branch loss, bark-loosening; Cline et al. 1980), recently fire-killed trees were assigned mean decay class 1-2 inputs. For the 9160 surface-layer hardwood/shrub records, biomass was calculated via allometric equations derived empirically from tissue harvests made in the Biscuit area relating basal diameter and crown dimensions to wood and foliage mass (Appendix D). Mass of forbs and low shrubs was estimated from regional equations relating cover to mass per area (Means et al. 1994). We computed mass of down woody detritus from line intercept data using standard geometric scaling and species- and decay class-specific wood density values (Brown 1974, Harmon and Sexton 1996). Down wood (~34,000 pieces) was corrected on an individual piece basis for mass loss due to charring (Appendix F).

Data Analysis

Fire effects. Mature/old-growth stands were compared to three-year postfire stands to quantify apparent fire effects on aboveground biomass pools. We present means and 95% confidence intervals (CIs) by biomass category to evaluate magnitude of differences rather than obtain test-statistics. Data for fire effects assessment were pooled across western and eastern stands because exploratory two-way analysis of variance (ANOVA; Ramsey and Schafer 2002) showed that effects did not differ strongly by forest type ($P>0.05$ for all burn*forest type interaction terms).

Early postfire logging effects (Biscuit Fire). To assess how postfire logging effects varied by logging intensity and biophysical setting 3-4 years after fire, we analyzed responses as a function of the three treatment levels (U, M, H); forest type (mesic, drier); and a treatment*forest type interaction term in a two-way ANOVA. The forest type term allowed biomass levels to vary between mesic vs. drier stands, while the interaction term tested whether treatment effects varied by forest type. All analyses were conducted using S-Plus 7.0 software (www.insight.com). Responses analyzed were live and dead total biomass by stratum as well as fine (1-100 hr timelag) and coarse (>1000 hr timelag) down woody fuels. Test statistics for basal area and snag densities are also presented to illustrate treatment magnitude and variability.

Analysis of forest type and treatment differences was focused on post-treatment comparisons (n= 30 burn stands [U= 11, M= 10, H= 9]). Because treatments were not implemented randomly (per the agency management plan), we also present results of a two-way ANOVA for the subset of stands for which we were able to collect before-after data (n= 19 [U= 8, M= 7, H= 4]) to assess whether strong differences among treatments existed prior to logging and whether the pre-post change was greater in treated stands than in controls. For all analyses, model residuals were evaluated via residual-vs.-fit plots using standard diagnostics described by Ramsey and Schafer (2002). Residuals from analysis of basal area and snag densities were generally funnel-shaped; these data were $\log_e$-transformed to improve homoscedasticity. Biomass quantities were not transformed because the data were symmetrically distributed, showed no consistent pattern in residual spread, and because our research objectives were to quantify absolute amounts rather than proportional changes. Specific treatment comparisons were afforded by computing 95% CIs for each treatment within each forest type; lack of overlap of CIs with means of other groups was interpreted as strong evidence for differences (Ramsey and Schafer 2002). For the relatively few variables having high variance around low means, we used zero-truncation of confidence intervals to exclude biologically impossible negative biomass values (Cowen and Ellison 2006).

17-18 year-old fires. Evaluation of older burns was a two-sample comparison of unlogged and logged treatments. Data were symmetrically distributed but substantial heteroscedasticity in variance was present. We thus employed a Welch-modified *t*-test, which does not require constant variance (Ramsey and Schafer 2002), coupled with presentation of 95% confidence intervals. All biomass categories are presented for reference; statistical tests were only performed for a priori questions addressing grand totals, live and dead totals by stratum, and surface woody fuels by timelag class.

Fire modeling. We assessed potential fire behavior and effects under 50th and 90th-percentile weather conditions using BehavePlus 3.0 (Andrews et al. 2005) and CONSUME 3.0 (Prichard et al. 2006) fire modeling software. We constructed a custom fuel model for each treatment from field-measured data (sensu Agee and Lolley 2006). For derived parameters such as packing ratios and surface area-to-volume ratios, we consulted the closest standard fuel models (3-4 yr postfire: model 11 [light logging slash], 17-18 yr postfire: model 4 [chaparral], mature/oldgrowth: model 10 [timber with litter and understory]) (see Andrews et al. 2005). Fuelbed depth was based on both live and dead surface components, and litter mass was included as 1 hr fuel for all treatments (Andrews et al. 2005, Prichard et al. 2006). The applicability of custom fuel models to postfire settings is not well tested (Passovoy and Fulé 2006), and absolute magnitudes of outputs likely vary from actual fire behavior. Although this limitation is widely recognized for many post-fuel-treatment situations, model exercises are still useful for comparing relative differences among treatments (Agee and Lolley 2006). Weather inputs and fuel moistures were obtained from USDA (2004), which in turn was based on local remote weather station data. Comparisons among treatments were highly similar between weather conditions; we present 90th-percentile outputs for simplicity and highest relevance. See Appendix G for model inputs.

RESULTS

Mature/old-growth biomass profiles

Total aboveground biomass in MOG stands ranged from 230-1049 Mg ha^{-1}, with a mean of 615.5 Mg ha^{-1}. Most aboveground biomass consisted of standing live trees in the aerial stratum (Table 4-1). Dead wood mass averaged 21.4 Mg ha^{-1} for aerial standing snags and 24.9 Mg ha^{-1} for surface material. Mean total live:dead ratio was 85:15 by mass.

Fire Effects

Most aboveground biomass persisted through high-severity fire. Summed across all biomass pools, mean residual dead mass after fire was 514.8 Mg ha^{-1} (83% of the 615.5 Mg ha^{-1} in MOG), with a confidence interval broadly overlapping that of MOG stands (Table 4-1).

The primary effect of high-severity fire, in addition to converting live biomass to dead (mean postfire live:dead ratio = 1:99), was to consume the forest floor as well as fine live and dead fuels in the surface layer. Mean forest floor mass was 1.1 Mg ha^{-1}

(95%CI: 0.5-1.7) after fire, 96% lower than the 27.2 Mg ha^{-1} (95%CI: 20.6-33.8) in MOG stands (Table 4-1). Mean FWD mass was also lower in postfire stands by 58-73% for all fuel timelag classes (Table 4-1). For CWD, mean 1000 hr fuel loads in postfire stands were 47% of that in MOG, while >1000 hr fuels were similar (Table 4-1). Fire also apparently consumed or felled standing surface biomass (small trees and shrubs), since standing dead surface mass was 3.7 Mg ha^{-1} (95%CI: 2.0-5.4) after fire compared to 6.7 Mg ha^{-1} (95%CI: 3.2-10.1) of standing surface mass in MOG. All live surface biomass in postfire stands (Table 4-1) was composed of regenerating hardwoods, shrubs, forbs, and conifers, which by three years postfire had obtained similar mass (combined) to MOG live surface mass.

Consumption of aerial biomass was minimal: the 95% confidence interval for postfire dead aerial mass was 352-628 Mg ha^{-1}, broadly similar to total aerial mass in MOG stands (315-801 Mg ha^{-1}) (see Table 4-1, Fig. 4-2). Foliage consumption approached 100%, but most aerial wood consumption was of twigs (needle-bearing and immediately adjacent branchlets), which compose a small fraction of total aerial mass, rather than larger branches (Table 4-2). Bole consumption was negligible, as most stems experienced bark charring only. Wood charring affected only 7.1% (±1.0 SE) of bole surface area.

Surface fuels became more patchy following fire. Variability in CWD mass at the hectare scale (as measured by the coefficient of variation [CV%] among transects within a plot) increased from a mean CV% of 72 (±5.6 SE) in MOG stands to 110.9 (±11.5 SE) in postfire stands. FWD variability increased from a mean CV% of 28.1 (±7.7 SE) in

MOG stands to 57.4 (±10.6 SE) in postfire stands. Mean cover of litter and woody detritus were lower in postfire stands at 16.3% (±4.1 SE) and 6.3% (±1.3 SE) respectively, compared to 62.0% (±6.9 SE) and 14.5% (±4.7 SE) in MOG. Mean cover of bare ground (mineral soil + rock) was 63.1% (±4.5 SE) in postfire stands, versus 12.6% (±5.8 SE) in MOG.

Forest type differences in postfire biomass. Following fire, mesic stands had higher residual dead biomass (mean 709.1 Mg ha^{-1}, 95%CI: 555-864) than drier stands (mean 434.9 Mg ha^{-1}, 95%CI: 340-530). Most of this difference was in the aerial stratum (680.9 Mg ha^{-1} in mesic vs. 418.6 Mg ha^{-1} in drier), associated with larger mean snag diameter (44.9 vs. 36.5 cm) and standing dead basal area (94.3 vs. 68.1 m^2 ha^{-1}). Postfire dead basal area was dominated by conifers in both types, composed of (mean) 83% Douglas-fir, 3% incense cedar, and 3% white fir in mesic stands, and 65% Douglas-fir, 21% sugar pine, and 6% white fir in drier stands. Hardwoods constituted a mean of 11% of total basal area in mesic stands (mainly tanoak) and 4% in drier stands (mainly Pacific madrone).

Early postfire logging effects

Pre-treatment and pre-post change comparisons. Prior to logging, we detected no strong pre-existing differences among treatments in terms of basal area, stem densities, fine and coarse woody fuels, or live and dead biomass (Table 4-3). Change magnitudes (post-treatment value minus pre-treatment value) were significantly greater in logged vs. unlogged stands for all variables except live biomass and density of small snags (Table 4-3). Nearly all variables showed significantly larger changes with increasing harvest intensity (Table 4-3). In unlogged stands, 95% confidence intervals for all variables but live biomass (which increased) included zero change between years.

Post-treatment comparison. Postfire logging reduced standing dead basal area and large snag densities to a greater degree in mesic stands than in drier stands (Table 4-4). Aerial dead biomass, including boles and branches, decreased monotonically with increasing harvest intensity in both forest types (Fig. 4-2, Tables 4-4, 4-5). Relative to unlogged stands, mean aerial dead mass in mesic stands was reduced by 428 Mg ha^{-1} in M stands and 660 Mg ha^{-1} in H stands, and in drier stands by 306 Mg ha^{-1} and 376 Mg ha^{-1}, respectively. Conversely, surface dead biomass increased monotonically with increasing harvest intensity in both forest types, with treatment effects greater in mesic stands (Fig. 4-2, Table 4-4). Logging in mesic stands increased mean surface dead mass relative to unlogged stands by 74 Mg ha^{-1} and 195 Mg ha^{-1} for M and H stands respectively, while increases in drier stands were 53 Mg ha^{-1} and 102 Mg ha^{-1} for M and H stands respectively (Table 4-4).

Total dead mass was higher for all treatments in mesic stands relative to the drier stands (Table 4-4). Treatment effects on total dead mass reflected the net balance of changes in aerial (decrease) and surface (increase) components. Moderate-intensity logging substantially reduced total dead mass, from 709.1 Mg ha^{-1} in U stands to 355.2 Mg ha^{-1} in M stands in mesic stands, and from 434.9 Mg ha^{-1} in U stands to 181.9 Mg ha^{-1} in M stands in drier stands (Table 4-4). However, total dead mass after high-intensity logging did not differ strongly from moderate-intensity logged stands, with confidence intervals overlapping broadly, particularly in drier stands (Table 4-4). Thus, relative to moderate-intensity logged stands, a greater proportion of felled biomass was transferred to the surface (rather than removed) by high-intensity logging.

Both fine and coarse surface woody fuel loads increased following moderate- and high-intensity logging (Fig. 4-2, Table 4-4). This increase applied to all fuel timelag classes (Table 4-5). Relative to drier stands, logging in mesic stands resulted in greater increases in both fine and coarse surface fuels, and absolute levels were higher in mesic stands for all treatments (Fig. 4-2, Table 4-4). Using basal area cut as a continuous measure of harvest intensity (Fig. 4-3), each m^2 ha^{-1} of basal area cut was associated with an increase of 0.10 Mg ha^{-1} of surface FWD (95%CI: 0.04-0.15) and 0.73 Mg ha^{-1} of surface CWD (95%CI: 0.39-1.06). At both moderate and high-intensity treatment levels, surface fuel loads generally exceeded those in MOG stands, except for 1 hr fuels (Table 4-1, Table 4-5). Overall, >1000 hr fuels dominated surface mass (Table 4-5).

Surface woody fuel loads became more spatially homogeneous following logging, due mainly to coarse fuels. Within-stand variability (CV%) in CWD mass differed strongly by treatment (two-way ANOVA $P<0.0001$), decreasing from 110.9 (±11.5 SE) in U stands to 59.7 (±8.6 SE) in M stands and 37.0 (±5.5 SE) in H stands. FWD spatial variability was lowest in H stands (CV% = 41 ±4.8, compared to 64.7 ±8.4 in M stands and 57.4 ±10.6 in U stands), but overall treatment differences were not statistically significant ($P=0.270$). Surface cover of woody detritus differed strongly by treatment ($P<0.0001$), increasing from 6.3% (±1.3 SE) in unlogged stands to 21.2% in M stands and 33.3% (±4.6 SE) in H stands (compared to 14.5% in MOG). Litter cover did not differ by treatment (*P*=0.668), with 16.3% (±4.1 SE) cover in U stands, 15.7% (±3.4 SE) in M stands, and 17.4% (±3.0 SE) in H stands (compared to 62.0% in MOG). There were no significant east-west differences in CV% or ground cover (*P*>0.53).

In unlogged burn stands, a substantial fraction of surface fuels were deeply charred, particularly for larger timelag classes (Table 4-6). The aerial wood biomass transferred to the surface by postfire logging was less charred, resulting in a decrease in the fraction of deeply charred surface fuels following logging (Table 4-6). Regenerating live biomass was significantly lower after high-intensity logging than in other treatments (Table 4-4). This pattern apparently was associated with weak treatment effects coupled with weak pre-existing differences (see Table 4-3, Appendix H).

17-18 year-old fires

Stand structure and fuel profiles in unmanaged stands. Comparison of 18-year-old unmanaged stands to 3-year-old stands indicated that most dead basal area remained standing 18 years after fire, with primarily small snags having fallen (Table 4-7). 18-year stands were otherwise similar to 3-year stands in terms of basal area, snag density, and species composition (dominated by Douglas-fir [65-83%] and sugar pine [12-21%] in both samples) (Table 4-7).

Despite the persistence of most standing basal area, mean aerial dead biomass in 18-year stands was 65% (272 Mg ha^{-1}) lower than in 3-year stands due to stem breakage, aerial decay, and natural falling of fine materials (Tables 4-5, 4-8). The majority of standing snags had progressed to decay class three by 18 years, and most were broken-topped, resulting in mean snag height of 10.0 m (95%CI: 6.2-13.8), compared to 17.7 m (95%CI: 14.9-20.4) in 3-year stands. Most aerial branch mass had fallen or decayed by 18 years postfire (Fig. 4-4).

A portion of the loss in aerial mass by 18 years postfire was mirrored by increases in surface dead mass, presumably due to snag fall/fragmentation. Surface masses of all woody fuel size classes, except 1 hr fuels, were substantially elevated in 18-year stands relative to 3-year stands (Table 5, 7). Nevertheless, the total increase in surface mass from 3-year stands to 18-year stands (66.1 Mg ha^{-1}) was relatively small compared to the total reduction in aerial mass (-272 Mg ha^{-1}), indicating that snag fall/fragmentation had not resulted in extremely large surface accumulations. Overall, mean total dead biomass in 18-year stands, including all standing and down material (224.0 Mg ha^{-1}), was only 52% of that in 3-year stands (434.9 Mg ha^{-1}) (Table 5, 7).

Comparison of managed and unmanaged stands. Unmanaged and managed 17-18 year-old stands were similar in terms of forest type, elevation, topography, soils, and precipitation zone (Table 4-8). There were few differences in fuel profiles between managed and unmanaged stands 17-18 years after fire. Only aerial dead biomass differed strongly, with 6.6 Mg ha^{-1} (95%CI: 1.8-10.2) in managed stands compared to 146.8 Mg ha^{-1} (95%CI: 99.1-191) in unmanaged stands (Fig. 4-4, Table 4-9). However, there was no apparent effect of management on surface dead biomass pools: means and confidence intervals were similar for all woody fuel timelag classes (Fig. 4-4, Table 4-9). In 17-year-old logged stands, mean surface masses of 10 hr, 100 hr, and >1000 hr woody fuels were 36-47% lower than immediately following high-intensity logging in the eastern Biscuit

Fire, while other timelag classes were similar (Tables 4-5, 4-9). In both logged and unlogged stands, mean surface masses of >1000 hr fuels 17-18 years after fire (36.7-44.7 Mg ha^{-1}) did not exceed that immediately following logging in the eastern Biscuit Fire (46.7-69.1 Mg ha^{-1}) (Tables 4-5, 4-9).

Within-stand variability in surface woody fuel loads was also similar between treatments in older stands. For FWD, mean CV% was 37.1 (±12.9 SE) in unmanaged stands and 33.5 (±9.0 SE) in managed stands (*P*=0.830 by Welch *t*-test). For CWD, mean CV% was 51.3 (±10.6 SE) in unmanaged stands and 57.5 (±13.4 SE) in managed stands (*P*=0.769). Mean surface cover of woody detritus was 32.9 (±2.9 SE) in managed stands, compared to 25.3 (±2.2 SE) in unmanaged stands (*P*=0.084).

Although live biomass did not differ significantly between treatments (*P*=0.263, Table 4-9), and total vegetation cover was similarly high in both managed and unmanaged stands (109% ±9.6 SE and 92% ±11 SE, respectively), conifer planting in managed sites altered live fuel composition (Fig. 4-5). Of live woody biomass in the surface stratum, a mean of 44.3% (95%CI: 4.8-83.9) was composed of conifers in managed stands, compared to 4.4% (95%CI: 3.0-5.7) in unmanaged stands (*P*=0.049 by Welch *t*-test; Fig. 4-5).

Potential fire behavior

Model outputs for potential fire behavior suggested that recently burned stands had substantially reduced fire potentials compared to MOG stands (Fig. 4-6). Postfire logging increased modeled rate of spread, flame length, and heat release from both fine and coarse fuels in 3-4 year-old stands (Fig. 4-6). Most fire potentials were similar across the two forest types, with two exceptions: M stands showed higher fire potentials in mesic stands than in drier stands, and potential soil heating was much higher in mesic stands (Fig. 4-6). Fire behavior potentials in treated 3-4 year-old stands remained below that of MOG stands (Fig. 6a-b), while potential soil heating was much higher in treated stands than in MOG (Fig. 4-6c).

In 17-18 year-old stands, potentials for behavior of the flaming front were higher than in any other condition, with similar to slightly higher potentials in managed stands (Fig. 4-6a-b). Predicted soil heating was also relatively high in 17-18 year-old stands, and was similar between managed and unmanaged stands (Fig. 4-6c). In neither managed nor unmanaged 17-18 year-old stands did soil heating appreciably exceed that immediately following high-intensity logging in drier stands, or any logging treatment in mesic stands (Fig. 4-6c). In both treatments in 17-18 year-old stands, mortality of regenerating trees in the event of a re-burn was projected at 100%.

DISCUSSION

Mature/old-growth biomass profiles

Mean total dead wood biomass in MOG stands (46.3 Mg ha^{-1}) was low relative to other western Oregon Douglas-fir forests (46-136 Mg ha^{-1}, Spies et al. 1988). Forest Service inventory data (USDA 2003b) also show relatively low dead biomass levels in the Siskiyou region, typically <50 Mg ha^{-1} for MOG (Campbell et al. 2007, Hudiburg et al. in press). This difference cannot be explained by lower productivity, live biomass, or mortality rates (Hudiburg et al. in press), and is therefore likely associated with faster wood decomposition or consumption rates. Decomposition may be relatively fast in the Siskiyou region because of sufficient moisture and warm temperatures, but with fewer prolonged periods of moisture saturation which can limit log decomposition (Wright et al. 2002). Historically frequent surface fires also may have consumed much of the down woody material (Skinner 2002). However, surface fires have not played a significant role for >60 years (onset of fire suppression), and environmental factors (e.g., moisture regime) have been found to influence CWD levels more than variations in fire frequency alone (Wright et al. 2002). Thus, evidence from MOG stands suggests fairly rapid wood decay in this region.

Fire Effects

Our estimate of total biomass consumption in high-severity fire (17%) agrees well with that of Fahnestock and Agee (1983), who estimated ~16% consumption from high-severity fires in western Washington Douglas-fir forests. Campbell et al. (2007), using a different approach from ours based on before-after data, estimated ~23% consumption of aboveground biomass in high-severity portions of the Biscuit Fire (primarily fine materials and forest floor). This estimate also agrees well with ours given that it comprised all prefire stand types including small-stature stands composed mainly of fire-available fine/surface fuels.

Despite most of our study stands having experienced active crown fire behavior, nearly all biomass consumption was in the surface stratum, while only foliage and a portion of fine twigs were consumed in the aerial stratum (Tables 4-1, 4-2). Because the vast majority of residual postfire biomass is in the aerial stratum (Table 4-1; Fahnestock and Agee 1983, Campbell et al. 2007), early woody fuel succession will depend primarily on rates of aerial decay, fragmentation, and falling of standing snags.

Low continuity and amount of surface/ground fuels following fire suggest that repeat fires are unlikely to spread rapidly or have major ecological impacts in the first several years after fire. However, recovery of live vegetation is rapid in the Siskiyou region, with live surface mass three years after fire already equaling prefire live surface mass (Table 4-1); thus, the window of reduced, discontinuous surface biomass will likely close within 5-10 years.

Early postfire logging effects

Merchantability of residual biomass. We estimate that 60.9% (±3.1 SE) of residual biomass in postfire stands was composed of merchantable-sized (>20 cm diameter) conifer bole wood, before accounting for any defect or postfire decay. The remaining 39.1% was composed of down material, prefire snags, shrub necromass, small conifers, hardwoods, branches and tops. If standard background levels of timber harvest defect/breakage are considered (conservatively 10%, Snell and Brown 1980), this estimate increases to ~45%, (or 194-336 Mg ha^{-1} depending on drier vs. mesic forest type), and greater still if any unique aspects of fire-killed trees factor in (e.g., postfire decay or greater breakage-upon-felling than live trees). Thus, management of any fire hazard associated with residual wood would need to emphasize these materials, since they may constitute as much as half of all biomass and are composed of more fire-available material (e.g., fine fuels and fragmented/rotted coarse fuels).

Treatment effects by biophysical setting and intensity. Following logging, mesic high-biomass stands experienced larger basal area reductions and larger increases in surface fuel loads than drier stands (Fig. 4-2, Table 4-4). This pattern follows from the strong relationship between basal area cut and postlogging surface fuel loads (Fig. 4-3), a relationship that likely extends across forest types. For example, in ponderosa pine (*Pinus ponderosa*) stands with relatively low basal area (15-19 m^2 ha^{-1}), McIver and Ottmar (2007) reported elevated postlogging fuel loads, but at a fraction of that in the Siskiyous at just 14-17 Mg ha^{-1}. The ratio of basal area cut to surface fuel increase reported by McIver and Ottmar (2007) corresponds well to that in Figure 4-3.

Relative to moderate-intensity logging, a greater proportion of felled biomass was transferred to the surface (rather than removed) by high-intensity logging. In moderate-intensity logged stands, ~14% of aerial biomass reductions were transferred to the surface, with the remainder removed from the site, while in high-intensity logged stands, ~28% of aerial biomass reductions were transferred to the surface (point estimates vary slightly by forest type and whether post-data or change values are used, but the pattern does not). In general, moderate-intensity logging on the Biscuit Fire resulted when only trees deemed merchantable were felled, while high-intensity logging resulted when nearly all trees (aside from prescribed retention) were felled regardless of condition, with logs then yarded if merchantable. Thus, high-intensity treatment, less selective in the felling process (particularly with cable yarding), resulted in proportionally more dead material left after harvest. This observation suggests that where postfire logging is conducted, moderate-intensity treatment may be a more deliberate approach to postfire wood management, more likely to result in down wood levels within prescribed ranges, versus high-intensity treatment in which resulting levels become more dependent on timber decay status (see also Rickards 1989).

The time period between fire and logging is likely a factor in the resulting amount of surface fuels because of wood decay. In this region, cull levels associated with postfire decay are expected to increase to ~10-20% of merchantable volume, mostly affecting smaller trees, by 2-3 years after fire (Lowell and Cahill 1996). Although this decay probably affected postlogging slash levels in Biscuit sites, our data suggest this was not a major driver since a) no fine fuels were merchantable in any case, and b) nearly all coarse fuel increases could be accounted for by nonmerchantable species, prefire decay status, tree tops/branches, and standard defect/breakage rates associated with mature/old-growth timber harvest (Snell and Brown 1980). Snag decay varied widely in the Biscuit Fire, with trees in some units in near perfect condition four years after fire, and in others heavily checked/decayed within 2 years (J. Lehmann, RSNF, pers. comm.). Our dataset did not include sufficient variation in time since fire, at least in replicated fashion, to assess its effect.

Brown et al. (2003) described optimum ranges of postfire down woody detritus in fire-prone forests, given the management need to balance fire hazard with the many other ecological functions of woody detritus (e.g., habitat, moisture retention, soil productivity, etc.) The optimum range most applicable to the Biscuit area is 23-68 Mg ha^{-1} of CWD, given fine fuel loadings <11 Mg ha^{-1}. Surface CWD loads following moderate-intensity logging in drier stands were within this range, and slightly higher in mesic stands (Fig. 4-2). High-intensity logging generated surface fuel loads well above these levels, particularly in mesic stands (Fig. 4-2). Mesic plant associations, being more productive and having longer fire return intervals, are likely characterized by higher natural ranges of CWD loading; thus, optimum ranges may be higher in mesic stands. Nevertheless, these data suggest that moderate-intensity postfire logging may result in acceptable surface fuel loads, while high-intensity logging may require additional or alternative treatments to mitigate short-term fire hazard.

Contribution of postlogging fuels to fire hazard. Model outputs suggested that the primary driver of early seral fire hazard was time since fire, and that slash generated by postfire logging resulted in elevated fire potentials within this context (Fig. 4-6). The applicability of fire models such as BehavePlus to postfire settings is not well established (Passovoy and Fulé 2006), and the actualization of these increased potentials is yet unknown. Nevertheless, customization of fuel models with empirical data appeared to yield reasonable results in that fire potentials were generally low in 3-4 year-old stands since most fine surface fuels had been consumed, and that logging slash increased fire potentials, other factors being equal (Fig. 4-6).

Slash fuels will decay over time; however, studies in both young and mature stands have reported increased fire severity associated with untreated slash from logging and fuel-reduction treatments (Weatherspoon and Skinner 1995, Stephens 1998, Raymond and Peterson 2005, Stephens and Moghaddas 2005). We found that, in addition to increasing surface fuel mass, logging resulted in more homogeneous fuel distribution, which was otherwise quite patchy following fire. In high-intensity logged stands, percent cover of wood was higher, and stand-scale variation in CWD mass lower, than in MOG stands that likely have not experienced fire for >60 years. Variation in fuel continuity is poorly addressed in common fire models; thus the fire behavior differences we observed could be lessened if fire is incapable of spreading in very young stands, or amplified if postlogging fuels are more likely to meet a threshold for sustained fire spread.

Slash treatment considerations. Knowledge of logging-generated fuel loads, specifically mechanistic relationships that may apply across forest types (Fig. 4-3), should provide insight into when slash treatments may be warranted given different harvest intensities and settings. Fuel data following tree felling, without subsequent treatment, are also relevant when slash is left on site (e.g., McIver and Ottmar 2007, and much of the Biscuit Fire). The necessity of slash treatment varies according to fire regime and the balance of several wood-related management objectives (USDA 2004).

Slash treatments (e.g., broadcast burning) have been well studied following live-tree harvest where the forest floor organic layer is still present (e.g., Hobbs et al. 1992), but in postfire settings the efficacy of such treatments has not been studied, nor have any unique effects of introducing a second fire to recently severely burned soils. With respect to the latter question, it is possible that broadcast burning of the substantial postlogging coarse fuel loads—which were higher immediately after logging than in any other stand type—could result in similar or even larger soil effects to those of a natural re-burn (Fig. 4-6c). Impacts may be larger still where slash occurs in “jackpot” accumulations (Brown et al. 2003). However, broadcast burning can be conducted under milder conditions than most wildfires, which could lessen this impact. Further research, including before-after monitoring, is needed on the efficacy and effects of various slash treatments in postfire settings.

17-18 year-old fires

In the absence of postfire management, it is generally expected that woody fuels will accumulate on the surface in large quantities as residual aerial biomass collapses, resulting in high fire hazard compared to logged stands (McIver and Starr 2001 and references therein). Although this pattern has not been quantified empirically (McIver and Starr 2001), we anticipated data from 17-18 year-old stands would support this hypothesis. We did observe some surface accumulation from snag fall/fragmentation. However, surface loads of all fuel size classes, as well as projected fire behavior and effects, were similar between managed and unmanaged stands 17-18 years after fire (Figs. 4-4, 4-6). Moreover, mean CWD loads in both treatments were within the acceptable ranges for fire prone forests described by Brown et al. (2003). Passovoy and Fulé (2006) reached similar conclusions in a ponderosa pine forest, noting that CWD accumulated in a broad temporal plateau rather than a sharp spike, and that unmanaged fuel loads did not exceed acceptable ranges over a 27-year postfire chronosequence.

The lack of superabundant surface fuels in unlogged stands was likely due in part to aerial decay (decomposition of standing wood), which can contribute substantially to overall decay rates in Douglas-fir forests (Sollins 1982). We observed stem breakage well above ground level and the presence of fungal conks all along the boles of snags, indicating significant mineralization of standing wood (M.E. Harmon, pers. comm.). At 18 years postfire in unmanaged stands, less than 25% of the apparent reduction in aerial biomass could be accounted for by increased surface mass. Roughly half of residual dead biomass (or 211 Mg ha^{-1}) had apparently decomposed completely—leaving large-diameter, broken-topped, few-branched snags as the main residual wood legacy in unlogged stands and the only biomass difference between treatments (Fig. 4-4, Table 4-7). Because such snags have the longest standing half-life (Morrison and Raphael 1993, Everett et al. 1999), coupled with the negative-exponential nature of wood decay (Harmon et al. 1986), there will likely be comparatively few inputs from aerial material beyond ~20 years, particularly of 1-1000 hr fuels.

As in any chronosequence, changes observed over a sere are part real, part accounting technique and part site variability (Agee and Huff 1987). The apparent 48% biomass reduction we observed in unmanaged stands seems large, but two lines of evidence suggest the pattern is real. First, snag densities, basal area, and tree species composition were all comparable between 3-year and 18-year stands (Table 4-7), with the only difference being slightly less basal area in older stands due to lower density of small snags—an ecologically sensible pattern given that small snags are known to decay and fall early (Morrison and Raphael 1993, Lowell and Cahill 1996). Even without comparing the two time points, simple reconstruction of standing biomass from existing basal area in 18-year stands indicates biomass loss of ~37% (which excludes all losses from complete falling of snags). Second, the difference in total dead mass between 3-year and 18-year stands yields a single-exponential decay constant (Harmon et al. 1986) of k=0.040, which is within reason compared to other studies in Douglas-fir forests. Reported values are typically ~0.030 (e.g., Sollins 1982, Spies et al. 1988), but these include coarse materials only, while our dataset also includes fine materials which typically decay faster (Harmon et al. 1986). An expected overall k can be calculated from our data using k_{CWD}= 0.030 and k_{FWD}= 0.090 (sensu McIver and Ottmar 2007), weighted by the relative abundance of each in 3-year-old stands. This approach yields an expected k=0.036. Rapid decay rates in the Siskiyou region could explain the remaining difference between our rate and this value. Notably, Agee and Huff (1987) also reported ~50% (600 Mg ha^{-1}) lower wood biomass 19 years postfire relative to 3-year-old stands in Douglas-fir forests of the Olympic Peninsula.

Given our observation that fuel mass was largely similar between managed and unmanaged older stands, the question remains of why fire severity was greater in managed stands where the Biscuit Fire re-burned the 15-year-old Silver Fire (Thompson et al. 2007). The 17-18 year-old stands we sampled should serve as good proxies for post-Silver stands prior to re-burning because they comprised similar plant associations, terrain, postfire treatments, age, and postfire climatic conditions. The only two measurable differences we observed in managed versus unmanaged stands were a lack of standing snags, and that live surface biomass was composed of nearly half conifers due in part to planting (Fig. 4-5). Standing snags seem unlikely to reduce fire behavior unless dead shade appreciably increases fuel moisture or snags reduce surface wind speeds (these potential influences have not been tested). More likely, the live fuel contributions of young conifers versus broadleaf vegetation were the key difference, due either to increased stem densities or altered fuel properties associated with conifer planting. Relevant studies comparing fuel properties of different types of early seral vegetation are lacking, but Perry (1994) hypothesized that hardwoods in the Siskiyou region reduce fire effects in young stands via increased spatial heterogeneity and foliar moisture content. It is possible that the fine foliage of conifer crowns is more conducive to fire spread than broadleaf vegetation. Perhaps more importantly, planting records from the Galice and Silver Fires indicate 3x3-m spacing of planted trees (data on file at RSNF, Wild Rivers RD). Though there was likely variation around this target, this spacing may homogenize the fuelbed compared to the patchy distribution of intermixed hardwoods, conifers, and gaps in naturally regenerated stands. Early seral stands tend to experience high mortality when burned (Thompson et al. 2007), and these effects may be more homogeneous if dense, uniform conifer planting makes the fuelbed more homogeneous.

In all modeled fire scenarios, fire was predicted to kill 100% of emergent trees via torching behavior and critical scorch heights. This observation agrees well with at least one other study, that residual dead fuels—managed or unmanaged—may be less important to early fire susceptibility than live fuelbed components (McIver and Ottmar 2007). Studies in Rocky Mountain forests have also suggested that changes in live structure associated with previous disturbances may be more important to subsequent fire behavior than residual dead material (e.g., Lynch et al. 2006). Moreover, in dry ponderosa pine forests natural fuel loads from fire-killed trees remained within optimum levels (11-45 Mg ha^{-1}, Brown et al. 2003) over a 27-year chronosequence (Passovoy and

Fulé 2006) and over a 50-year projection based on empirical data (McIver and Ottmar 2007). Thus, while there are examples of prior disturbances increasing fire severity through generation of dead material (e.g., Stocks 1987), in many cases changes in live fuel structure are the dominant driver of fire hazard in young stands. This pattern is especially relevant in forest types with quickly regenerating vegetation such as re-sprouting shrubs and hardwoods, such as the Siskiyou region (Hobbs et al. 1992).

Synthesis of early fuel profile development

Data from this study suggest a model of early fire hazard succession following stand-replacement fire composed of three stages. For the initial ~5 years, fire potentials (e.g., rate of spread, flame length, tree mortality probability) are very low due to lack of a continuous forest floor and low levels of live and dead surface fuels (Table 4-1, Fig. 4-6). In the second stage (~5-30 yr), fire potentials increase markedly, driven primarily by the development of a continuous surface layer of live vegetation, associated forest floor accumulation, and small mean tree size. Fire potentials peak at ~15-30 years and may be higher than in any other successional stage (Fig. 4-6). Relative to live fuels, residual wood from the prefire stand contributes only marginally to surface fire potentials because of rapid decay of all but the largest material (Tables 4-5, 4-9). By ~20 years, inputs from standing snags have largely diminished since most remaining material is large-diameter material with long standing half-life (Table 4-9). In the third stage (~30-50 yr), the development of larger live tree sizes and canopy stratification reduce the potential for stand-replacement fire effects.

Data from both 3-4 year-old and 17-18 year-old stands were not consistent with the hypothesis that postfire logging reduces surface fuel loads and fire potentials (Figs. 4-2, 4-4, 4-6). Postfire logging slash appeared to increase potential fire behavior parameters and potential soil heating (Fig. 4-6), with the discrepancy varying according to logging intensity, slash treatment, or live fuel alterations, and diminishing over time as slash fuels decay. For example, following high-intensity logging with slash treatment, the discrepancy disappeared by ~15-20 years (Table 4-9), perhaps later if left untreated. Overall, trends in fire hazard during early succession are driven primarily by changes in live structure associated with time since fire, with or without management of postfire residual wood (Fig. 4-6).

Primary Uncertainties

Several issues for future research emerge from this study. Among the most important is increasing the temporal resolution and duration of measurements. Our data suggest that additional fuel inputs from aerial material will decrease substantially by ~20 years postfire, but this deserves further empirical investigation. If inputs are larger than expected, potential soil heating in a future fire could be significantly higher where more standing biomass has been retained. Increased temporal resolution over the first 20 years would provide critical insight into rates of aerial vs. surface decay and the role of snag fragmentation. Although there is evidence for rapid wood decomposition in the Siskiyou region, local decay rates have not been well quantified, and variation in these rates has several important ecological consequences (Harmon et al. 1986). Of particular interest is the transition of large wood from sound to rotten, which likely increases its combustibility (Brown et al. 2003), and the degree to which charred wood—which composed a large fraction of surface fuels after fire but not after postfire logging (Table 4-6)—has unique fuel properties or decay rates. Finally, spatial variability in residual fuels is poorly understood; for example, small pockets of accumulated snagfall in 18-year-old unmanaged stands may vary widely from the stand-level means we quantified.

Another important uncertainty is the role of standing snags in fire behavior. Surface fuels are the primary carrier of wildfire and contribute the most to soil heat flux and regeneration mortality (Pyne et al. 1996), but there are anecdotal observations of standing snags also contributing to fire behavior via spotting of embers (e.g., Kemp 1967). To our knowledge, such effects have not been reported quantitatively. Snags can experience bole charring during wildfires (Donato and Fontaine, unpubl. data); whether such combustion significantly affects overall fire behavior remains a question for future studies. Oregon's 1933 Tillamook Burn, which re-burned three times at six-year intervals, is a commonly cited example of the fire contribution of snags since fires ceased to occur following extensive snag removal (Kemp 1967). However, the case of the Tillamook Burn is complicated by the fact that all three re-burns were started by postfire logging operations, and that the re-burns were a mix of both logged and unlogged areas (Kemp 1967, Peterson et al. in press). Fuel conditions in these areas were not well quantified at the time, making it difficult to infer the effects of snags—or snag felling—on fire behavior.

Patterns of early fuel succession and management effects will vary among forest types and disturbance modes. Among the most important differences are site-specific variations in standing biomass, decay rates, and productivity (Fig. 4-2). Relative to other fire-prone forests, the Siskiyou region is likely in the upper range for all three variables, which has major consequences for both live and dead postfire fuel dynamics. For example, aerial decay is likely far slower in colder, drier interior forest types (M.E. Harmon, pers. comm.), potentially increasing the amount of dead material reaching the surface. Insect outbreaks and windthrow disturbances differ from fire in that they do not consume surface fuels and, in the case of wind, result in immediate felling of standing biomass. Thus, the patterns we observed may be in part unique to succession following fire. Finally, secondary disturbances during early succession could play a large role. The occurrence of extreme wind events, for example, could accelerate the transfer of aerial biomass to the surface in large pulses, resulting in deviations from what we observed. Repeat fires may also consume or fell residual wood, potentially affecting woody detritus levels for decades to centuries (Spies et al. 1988). The effects of successive interacting disturbances on biomass dynamics have received little study to date.

Live vegetation structure appears to be a dominant driver of fire hazard in early seral forests of this region, and alterations to this fuel component may underlie the higher re-burn severity observed in managed vegetation (Figs. 4-4, 4-5; Thompson et al. 2007). Live vegetation structure may be altered by direct and indirect effects of logging (Stuart et al. 1993), or by subsequent treatments such as tree planting. Differing fuel properties among types of early seral vegetation have not been well described. Other uncertainties include the effects of clumped vs. dispersed snag retention on future fuel distribution (Brown et al. 2003), the landscape context of logged units with respect to fire spread, and the applicability of common fire models to severely burned stands.

Management Implications

Management of postfire residual wood is typically concerned with avoiding surface fuel loads deemed to be excessive with respect to fire hazard (Brown et al. 2003). Considering the many ecological functions of CWD, optimum levels should be assessed in a broad context, with particular consideration of the local fire regime (Brown et al. 2004). Pulses of dead wood represent the main biotic legacy carried into the new stand and are a characteristic feature of mixed- and high-severity fire regimes (Spies et al. 1988, Skinner 2002). Within the context of natural variation in the amount and function of woody detritus, the ecological basis for reducing postfire fuels is most pertinent to low-severity fire regimes, rather than mixed- and high-severity regimes.

In the mixed evergreen forest types we studied, management of postfire residual wood does not seem warranted from the perspective of fire hazard, for two main reasons. First, natural accumulations of fine and coarse fuels derived from fire-killed trees were within commonly acceptable ranges both three and 18 years after fire. Stand structure at 18 years indicated that most fine material had fallen and/or decayed, leaving large-diameter broken-topped boles as the primary dead wood legacy. As such, inputs to the surface will likely be comparatively minor after ~20 years, with surface accumulations of 1-1000 hr fuels having already peaked or reached a plateau (see also Passovoy and Fulé

2006). Second, empirical data from 3-4 years and 17-18 years postfire did not support the hypothesis that postfire logging reduces fine and coarse surface fuel loads or potential fire behavior (Figs. 4-2, 4-4, 4-6). Management of any fire hazard associated with residual dead wood may need to focus on nonmerchantable material since it composed ~40% of residual biomass, remains on site after logging, and is likely the more fire-available component (fine branches, etc.). More importantly, live vegetation structure associated with time since fire was the main driver of fire susceptibility in young stands, with slash from postfire logging increasing fire potentials within this context (Fig. 4-6; see also McIver and Ottmar 2007). Whether or not stands were logged, mortality of regenerating trees in the event of a repeat burn was projected at 100%.

The high fire hazard inherent to early seral forests in this region presents a difficult management challenge. In most cases, commonly employed fuel treatments in young stands have been found to make little difference in reducing the potential for stand-replacement fire (Roloff et al. 2005, Stephens and Moghaddas 2005, McIver and Ottmar 2007, Thompson et al. 2007, but see Weatherspoon and Skinner 1995). Inherent structural features of regenerating vegetation (high stem density, continuous low canopy, small thin-barked trees, etc.) result in high fire-susceptibility in young stands. Where reduction of early fire hazard is a goal, potentially effective treatments may include reducing connectivity of live fuels at landscape scales via, for example, shaded fuel breaks (Agee et al. 2000). Also, maintaining a diversity of vegetation structure and composition within and between stands may result in more heterogeneous fire effects. Conifer planting, if dense and uniform, may contribute to increased average fire severity

(Thompson et al. 2007); however, the risk tradeoffs between this influence and any long-term effects of more rapid canopy development have not been well evaluated.

There are several reasons to consider postfire logging and/or re-planting of burned areas, including (depending on management objectives) the generation of timber revenue, establishing a future timber crop, increasing worker safety, etc. Postfire timber harvest is first and foremost an economic undertaking (Peterson et al. in press) that can be incorporated into the broader context of ecosystem management. This approach will likely be most effective when postfire management objectives are clearly articulated in anticipation of large fires rather than addressed as emergencies (Peterson et al. in press), and are broadly consistent with prefire management objectives for a given area. Where postfire logging interfaces with ecological objectives such as habitat and fire potential, moderate-intensity treatment appears to be a more deliberate approach to postfire dead wood management: typically only merchantable trees were felled, a higher percentage of felled biomass was removed (reducing the need for follow-up treatments), and more of the remaining material was left as standing habitat rather than felled and left due to decay status. Where postfire logging is prescribed, an effective approach may be to conduct logging relatively quickly following fire, enabling selective removal of merchantable wood in small- to medium-diameter boles (prior to decay) while retaining the largest stems of high longevity and ecological importance. Whole-tree yarding may also be an option where minimizing logging slash is an objective. Finally, designing postfire management projects as controlled, replicated experiments will be essential to further understanding of the tradeoffs involved with various management approaches.

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Table 4-1. Mean (95% CI) aboveground biomass pools in mature/old-growth sites and 3 years after stand-replacement wildfire (Mg ha^{-1}).

Biomass Category	Mature/old-growth		Postfire	
<u>DEAD MASS</u>				
Aerial stratum				
Branch	1.4	(0.2 - 2.6)	69.0	(49.5 - 88.4)
Bole	20.0	(5.8 - 34.2)	421.1	(288 - 555)
Total Aerial Dead	21.4	(6.1 - 36.6)	490.1	(352 - 628)
Surface stratum				
Bole + branch	2.4	(0.0 - 5.5)	3.7	(2.0 - 5.4)
Stumps	0.0	(0.0 - 0.0)	0.2	(0.0 - 0.4)
1 hr fuels	1.1	(0.9 - 1.4)	0.3	(0.1 - 0.4)
10 hr fuels	1.9	(1.1 - 2.7)	0.8	(0.5 - 1.1)
100 hr fuels	3.8	(2.9 - 4.6)	1.1	(0.7 - 1.6)
1000 hr fuels	3.0	(1.7 - 4.2)	1.6	(0.7 - 2.5)
>1000 hr fuels	12.8	(5.0 - 20.5)	11.9	(0.0 - 24.2)
Forest floor (L+D)	27.2	(20.6 - 33.8)	1.1	(0.5 - 1.7)
Total Surface Dead	52.1	(43.2 - 61.1)	19.6	(6.1 - 33.0)
<u>LIVE MASS</u>				
Aerial stratum				
Foliage	15.9	(10.2 - 21.6)	0.0	(0.0 - 0.0)
Branch	54.3	(22.9 - 85.7)	0.0	(0.0 - 0.0)
Bole	466.6	(248 - 685)	0.0	(0.0 - 0.0)
Total Aerial Live	536.8	(294 - 780)	0.0	(0.0 - 0.0)
Surface stratum				
Foliage	1.0	(0.2 - 1.7)	1.4	(0.9 - 1.9)
Bole + branch	3.3	(1.4 - 5.1)	2.2	(1.4 - 3.1)
Forbs/low shrubs	1.2	(0.0 - 2.5)	1.4	(0.6 - 2.3)
Total Surface Live	5.4	(2.9 - 7.9)	5.1	(3.6 - 6.5)
Grand Total Dead	73.5	(55.9 - 91.2)	509.7	(363 - 656)
Grand Total Live	542.2	(300 - 784)	5.1	(3.7 - 6.5)
Grand Total Biomass	615.5	(376 - 855)	514.8	(368 - 661)

Notes: Bole masses include bark.
n= 8 MOG stands and 11 burned stands.

Table 4-2. Mean (SE) estimated consumption of aerial wood mass during stand-replacement fire.

Aerial biomass category	% consumed	% killed but present
Twigs	32.2 (3.8)	67.8 (3.8)
Large branches	7.7 (1.7)	91.9 (1.3)
Bole wood	<1	~100

Notes: Aerial stratum = trees >10 cm dbh. Twigs defined as needle-bearing and immediately adjacent branchlets; large branches are remainder of non-stem wood. Negligible bole wood consumption based on Campbell et al. (2007) and references therein.

Table 4-3. Assessment of pre-treatment similarity and pre-post change for the subset of stands with before-after data (n=19), via two-way ANOVA.

Stand characteristic	Pre-treatment				Pre-Post Change				
	Comparison†	$F_{2,13}$	P	M-D ‡ diff.	Comparison† (magnitude of change)	Direction of change in treated stands	$F_{2,13}$	P	M-D ‡ diff./ inter.
Standing dead basal area	U ≈ M ≈ H	1.81	0.203	y	U < M < H	(-)	20.0	0.0001	y
Snags ha^{-1} [>30 cm dbh]	U ≈ M ≈ H	3.24	0.072	n	U < M < H	(-)	110.3	<0.0001	n
Snags ha^{-1} [10-30 cm dbh]	U ≈ M ≈ H	3.19	0.077	n	U < M ≈ H	(-)	7.00	0.009	y
Snags ha^{-1} [<10 cm dbh]	U ≈ M ≈ H	2.96	0.087	n	U ≈ M ≈ H	na	0.29	0.754	n
Dead biomass total	U ≈ M ≈ H	1.63	0.233	y	U < M < H	(-)	10.4	0.0020	y
Dead biomass aerial	U ≈ M ≈ H	1.93	0.184	y	U < M < H	(-)	13.9	0.0006	y
Dead biomass surface	U ≈ M ≈ H	0.56	0.587	y	U < M < H	(+)	41.4	<0.0001	n
Fine woody detritus [<7.62 cm]	U ≈ M ≈ H	0.16	0.851	n	U < M < H	(+)	52.7	<0.0001	y
Coarse woody detritus [>7.62 cm]	U ≈ M ≈ H	0.55	0.590	y	U ≈ M < H	(+)	36.4	<0.0001	y
Live biomass total	U ≈ M ≈ H	1.30	0.306	n	U ≈ M ≈ H	na	2.97	0.087	n
Live biomass aerial §	U ≈ M ≈ H	na	na	n	U ≈ M ≈ H	0	na	na	n
Live biomass surface	U ≈ M ≈ H	1.30	0.306	n	U ≈ M ≈ H	na	2.97	0.087	n

Notes: U= burned, unlogged, M= burned, moderate-intensity logged, H= burned, high-intensity logged.

† Results of Fisher's *F*-protected LSD comparisons with α set at 0.05 to aid interpretation (Ramsey and Schafer 2002).

‡ *F*-statistics and *P*-values are shown for treatment effect only; for variables with significant mesic-dry (M-D) differences/interactions, mesic stands had higher absolute amounts or stronger treatment effects for pre-post change. See Appendix H for side/interaction terms and means and 95% CIs by treatment.

§ Live biomass aerial = 0 in all plots.

Table 4-4. Post-treatment comparison (point estimate, 95% CI) of unlogged (U), moderate-intensity logged (M), and high-intensity logged (H) burn stands.

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (*P*)		
	U	M	H	U	M	H	Trt † (df=2,24)	FType† (df=1,24)	Trt*Ftype (df=2,24)
Standing dead basal area (m^2 ha^{-1})	94.3 (41.8-213)	41.5 (18.4-93.6)	2.5 (1.1-5.7)	68.1 (41.4-112)	23.7 (13.9-40.3)	9.7 (5.4-17.1)	<0.0001	0.586	0.019
Snags ha^{-1} [>30 cm dbh]	136.7 (50.8-368)	55.7 (20.7-150)	2.5 (0.9-6.7)	165.3 (90.1-303)	72.5 (37.9-139)	29.4 (14.6-59.3)	<0.0001	0.007	0.015
Snags ha^{-1} [10-30 cm dbh]	210.9 (69.5-640)	303.0 (99.8-918)	2.8 (0.9-8.5)	237.2 (120-468)	148.8 (71.9-308)	45.9 (20.9-101)	<0.0001	0.060	0.002
Snags ha^{-1} [<10 cm dbh]	124.1 (20.9-736)	334.4 (56.4-1981)	10.2 (1.7-60.7)	716.9 (241-2132)	622.0 (194-1994)	39.0 (11.1-137)	0.0005	0.049	0.733
Dead biomass total (Mg ha^{-1})	709.1 (555-864)	355.2 (201-510)	243.9 (89.5-398)	434.9 (340-530)	181.9 (80.8-283)	161.1 (51.9-270)	<0.0001	0.002	0.336
Dead biomass aerial (Mg ha^{-1})	680.9 (537-825)	253.3 (109-398)	21.2 (0.0-166)	418.6 (330-507)	112.5 (18.0-207)	43.0 (0.0-145)	<0.0001	0.015	0.076
Dead biomass surface (Mg ha^{-1})	28.1 (0.0-63.1)	101.9 (66.9-137)	222.7 (188-258)	16.4 (0.0-37.8)	69.5 (46.6-92.4)	118.2 (93.4-141)	<0.0001	0.0003	0.010
Fine woody detritus (Mg ha^{-1}) [<7.62 cm]	1.4 (0.0-5.1)	12.8 (9.1-16.5)	19.0 (15.3-22.7)	2.5 (0.2-4.8)	5.7 (3.3-8.1)	15.6 (13.0-18.2)	<0.0001	0.019	0.041
Coarse woody detritus (Mg ha^{-1}) [>7.62 cm]	25.6 (0.0-56.8)	72.0 (40.8-103)	173.4 (142-205)	8.9 (0.0-28.0)	52.1 (31.7-72.5)	82.9 (60.8-105)	<0.0001	0.0005	0.013
Live biomass total (Mg ha^{-1})	5.6 (3.4-7.8)	7.3 (5.1-9.5)	1.6 (0.0-3.8)	4.9 (3.5-6.3)	4.9 (3.4-6.4)	2.8 (1.2-4.4)	0.0008	0.385	0.170
Live biomass aerial (Mg ha^{-1})	0	0	0	0	0	0	na	na	na
Live biomass surface (Mg ha^{-1})	5.6 (3.4-7.8)	7.3 (5.1-9.5)	1.6 (0.0-3.8)	4.9 (3.5-6.3)	4.9 (3.4-6.4)	2.8 (1.2-4.4)	0.0008	0.385	0.170

95% CIs were derived from two-way ANOVA outputs. See table 4-5 for standard errors and individual biomass components.
n= 8, 7, 6 for U, M, H in drier stands; 3 each for U, M, H in mesic. † Trt= treatment (U,M,H), Ftype= forest type (mesic, drier).

Table 4-5. Mean (SE) aboveground biomass pools by category (Mg ha^{-1}) three years after stand-replacement wildfire, subject to three postfire treatments: unlogged (U), moderate-intensity logged (M), and high-intensity logged (H).

Biomass Category	Mesic stands			Drier stands		
	U	M	H	U	M	H
DEAD MASS						
Aerial stratum						
Branch	49.4 (11.1)	11.4 (7.4)	0.0 (0.0)	76.3 (10.4)	20.6 (6.0)	5.4 (1.8)
Bole	631.5 (130)	241.9 (84.8)	21.2 (16.8)	342.2 (44.6)	91.8 (18.5)	37.6 (14.3)
Total Dead Aerial	680.9 (139)	253.3 (92.1)	21.2 (16.8)	418.6 (52.3)	112.5 (23.1)	43.0 (16.1)
Surface stratum						
Bole + branch	0.9 (0.4)	3.8 (1.7)	0.4 (0.3)	4.7 (0.7)	3.3 (1.0)	0.5 (0.3)
Stumps	0.2 (0.2)	13.3 (4.2)	29.9 (7.5)	0.2 (0.1)	8.4 (1.9)	19.2 (1.9)
1 hr fuels	0.2 (0.0)	0.6 (0.2)	0.8 (0.1)	0.3 (0.1)	0.4 (0.1)	0.6 (0.2)
10 hr fuels	0.6 (0.2)	2.6 (0.5)	3.6 (0.1)	0.9 (0.1)	1.5 (0.2)	4.1 (0.6)
100 hr fuels	0.6 (0.4)	9.7 (0.8)	14.6 (0.9)	1.3 (0.2)	3.8 (0.6)	10.9 (2.0)
1000 hr fuels	2.8 (1.2)	13.1 (4.1)	15.6 (3.6)	1.1 (0.2)	5.4 (1.1)	13.8 (2.0)
>1000 hr fuels	22.9 (21.2)	58.9 (13.4)	157.8 (8.8)	7.8 (1.8)	46.7 (13.4)	69.1 (9.3)
Total Dead Surface	28.1 (23.6)	101.9 (24.2)	222.7 (16.7)	16.4 (2.6)	69.5 (14.0)	118.2 (10.9)
LIVE MASS						
Aerial stratum						
Total Live Aerial	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Surface stratum						
Foliage	1.0 (0.2)	2.5 (0.4)	0.2 (0.1)	1.6 (0.3)	1.7 (0.4)	0.6 (0.1)
Bole + branch	1.8 (0.2)	3.6 (0.5)	0.4 (0.2)	2.4 (0.5)	2.9 (0.5)	0.9 (0.1)
Forbs/low shrubs	2.9 (0.9)	1.2 (0.2)	1.0 (0.4)	0.9 (0.2)	0.3 (0.1)	1.3 (0.3)
Total Live Surface	5.6 (1.3)	7.3 (0.7)	1.6 (0.3)	4.9 (0.8)	4.9 (0.8)	2.8 (0.4)
Grand Total Dead	709.1 (161)	355.2 (90.1)	243.9 (22.1)	434.9 (53.0)	181.9 (26.7)	161.1 (17.9)
Grand Total Live	5.6 (1.3)	7.3 (0.7)	1.6 (0.3)	4.9 (0.8)	4.9 (0.8)	2.8 (0.4)
Grand Total Biomass	714.8 (160)	362.4 (90.4)	245.5 (22.0)	439.8 (53.0)	186.8 (26.9)	163.9 (17.8)

n= 8, 7, 6 for U, M, H in drier stands; and 3 each for U, M, H in mesic stands.

Table 4-6. Mean (SE) char status of surface woody fuels three years after stand-replacement wildfire, with and without postfire logging.

Fuel timelag class (diameter)		% of surface mass composed of deeply charred pieces	
		Burn only	Burn-logged
1 hr	(<0.6 cm)	4.1 (1.7)	0.5 (0.1)
10 hr	(0.6-2.5 cm)	10.6 (3.1)	2.3 (0.8)
100 hr	(2.5-7.6 cm)	39.5 (7.5)	7.2 (1.7)
1000 hr	(7.6-20.3 cm)	67.8 (9.1)	17.4 (2.5)
>1000 hr	(>20.3 cm)	74.3 (9.7)	16.8 (3.5)

Table 4-7. Median (95%CI) basal area and snag densities in unmanaged 3-year-old and 18-year-old stands.

Stand age (yr)	Snag basal area (m^2 ha^{-1})	Snag density [>30 cm dbh] (tr ha^{-1})	Snag density [10-30 cm dbh] (tr ha^{-1})
3	68.1 (41.4-112)	165.3 (90.1-303)	237.2 (120-468)
18	56.7 (53.1-60.5)	179.4 (86.8-371)	144.4 (113-184)

Table 4-8. Mean (SE) site characteristics for 17-18-year-old stands. Unmanaged and managed stands were similar other than management history.

Characteristic	Burn only		Burn + salvage/plant	
Elevation (m)	862.2	(123)	877.8	(49.3)
Slope (degrees)	23.3	(8.1)	28.6	(3.1)
Solar heat load index (aspect proxy)	2.3	(0.2)	1.9	(0.1)
Mean annual precipitation (cm)	168.3	(3.2)	177.8	(16.6)

Table 4-9. Mean (95% CI) aboveground biomass pools 17-18 years after stand-replacement wildfire, with and without postfire logging (Mg ha^{-1}).

Biomass Category	Burn only 18 yr	Burn-logged/planted 17 yr	Welch *t*-test *P*
DEAD MASS			
Aerial stratum			
Branch	11.4 (2.0 - 20.8)	0.2 (0.0 - 0.5)	---
Bole	138.2 (78.9 - 197)	6.4 (2.1 - 10.7)	---
Total Dead Aerial	149.6 (84.4 - 215)	6.6 (2.2 - 11.1)	0.006
Surface stratum			
Bole + branch	0.7 (0.0 - 2.5)	2.8 (0.0 - 8.1)	---
Stumps	0.8 (0.0 - 1.8)	7.8 (3.4 - 12.2)	---
1 hr fuels	0.4 (0.0 - 1.0)	0.6 (0.2 - 1.0)	0.485
10 hr fuels	2.8 (0.0 - 6.3)	2.6 (0.0 - 5.3)	0.873
100 hr fuels	9.3 (0.0 - 23.7)	7.0 (4.1 - 9.9)	0.577
1000 hr fuels	15.7 (11.1 - 20.4)	14.9 (11.3 - 18.6)	0.702
>1000 hr fuels	44.7 (11.4 - 78.1)	36.7 (0.7 - 72.8)	0.647
Forest floor (L+D)	15.9 (0.0 - 41.0)	25.0 (2.6 - 47.5)	---
Total Dead Surface	82.5 (23.7 - 141)	103.2 (47.6 - 159)	0.317
LIVE MASS			
Aerial stratum			
Foliage	0.3 (0.0 - 0.6)	1.0 (0.3 - 1.7)	---
Branch	0.03 (0.0 - 0.1)	5.8 (0.0 - 19.6)	---
Bole	2.1 (0.0 - 5.6)	14.2 (0.0 - 28.6)	---
Total Live Aerial	2.4 (0.0 - 6.1)	21.0 (0.0 - 48.8)	0.138
Surface stratum			
Foliage	3.7 (0.0 - 9.1)	2.5 (0.5 - 4.5)	---
Bole + branch	10.3 (2.0 - 18.6)	10.7 (3.5 - 17.8)	---
Forbs/low shrubs	0.3 (0.0 - 1.2)	1.3 (0.4 - 2.1)	---
Total Live Surface	14.4 (1.7 - 27.1)	14.4 (5.5 - 23.3)	0.995
Grand Total Dead	224.0 (168 - 280)	108.9 (53.4 - 164)	0.017
Grand Total Live	16.5 (7.2 - 25.8)	35.6 (0.0 - 79.8)	0.263
Grand Total Biomass	240.6 (181 - 301)	144.6 (90.5 - 199)	0.025

Notes: All aboveground biomass is partitioned by category for reference; statistical tests were only performed for a priori questions regarding grand totals, live and dead totals by stratum, and surface woody fuels. For one stand in each treatment, only aerial, 1000 h, and >1000 h fuels could be measured due to stand treatments outside study scope affecting other pools just prior to sampling.

n= 4 burn-only stands and 5 burn-logged/planted stands.

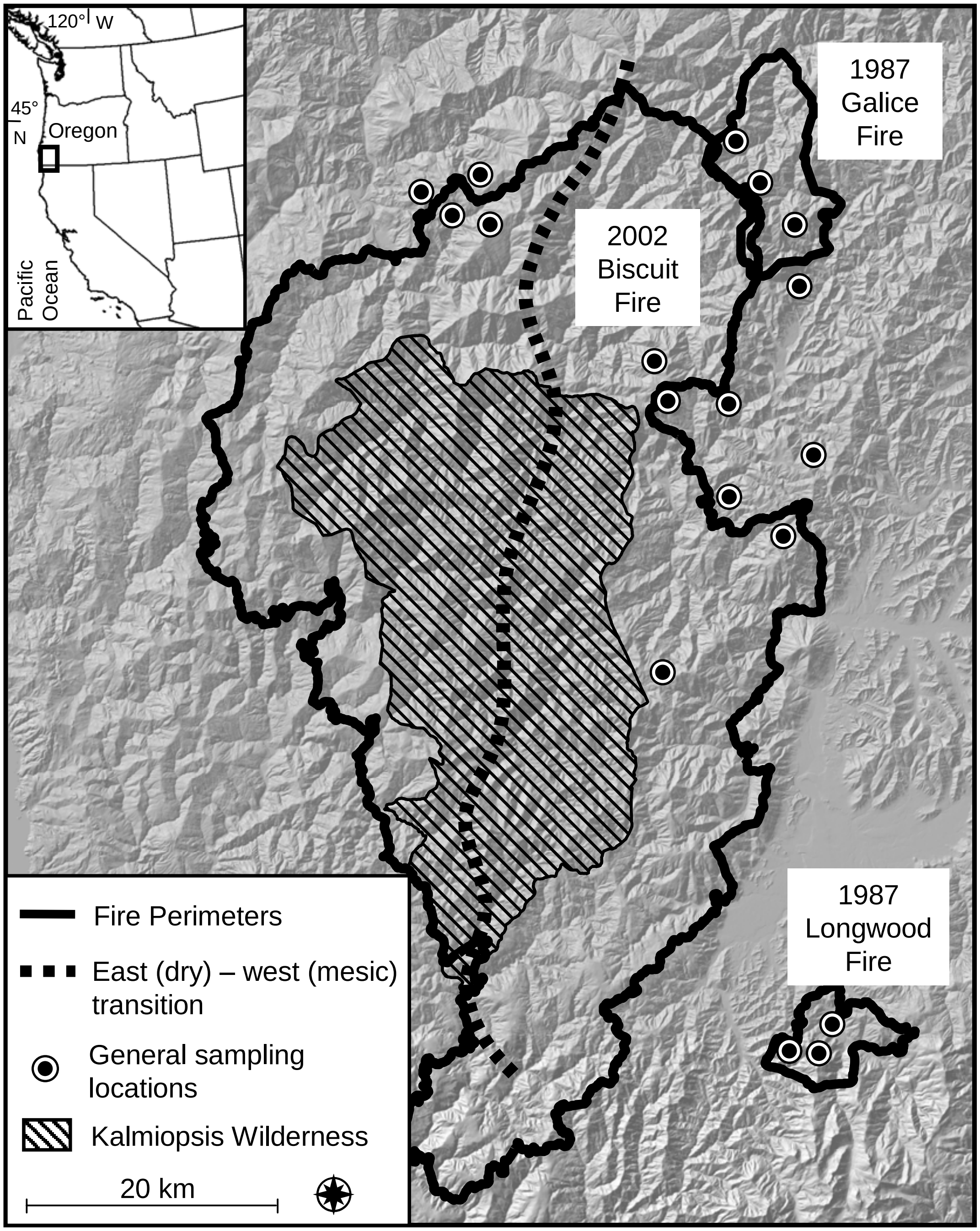

Figure 4-1. Study area and sampling locations for quantification of fire and postfire logging effects. Dots correspond to postfire timber sales and adjacent unburned areas in which sample stands were located (total n= 47 stands: 30 in Biscuit Fire, 5 in Galice Fire, 4 in Longwood Fire, and 8 unburned mature/old-growth stands). Dashed line approximating transition between mesic westerly plant associations and drier easterly plant associations adapted from USDA (2004). Spatial data courtesy of Rogue River-Siskiyou National Forest.

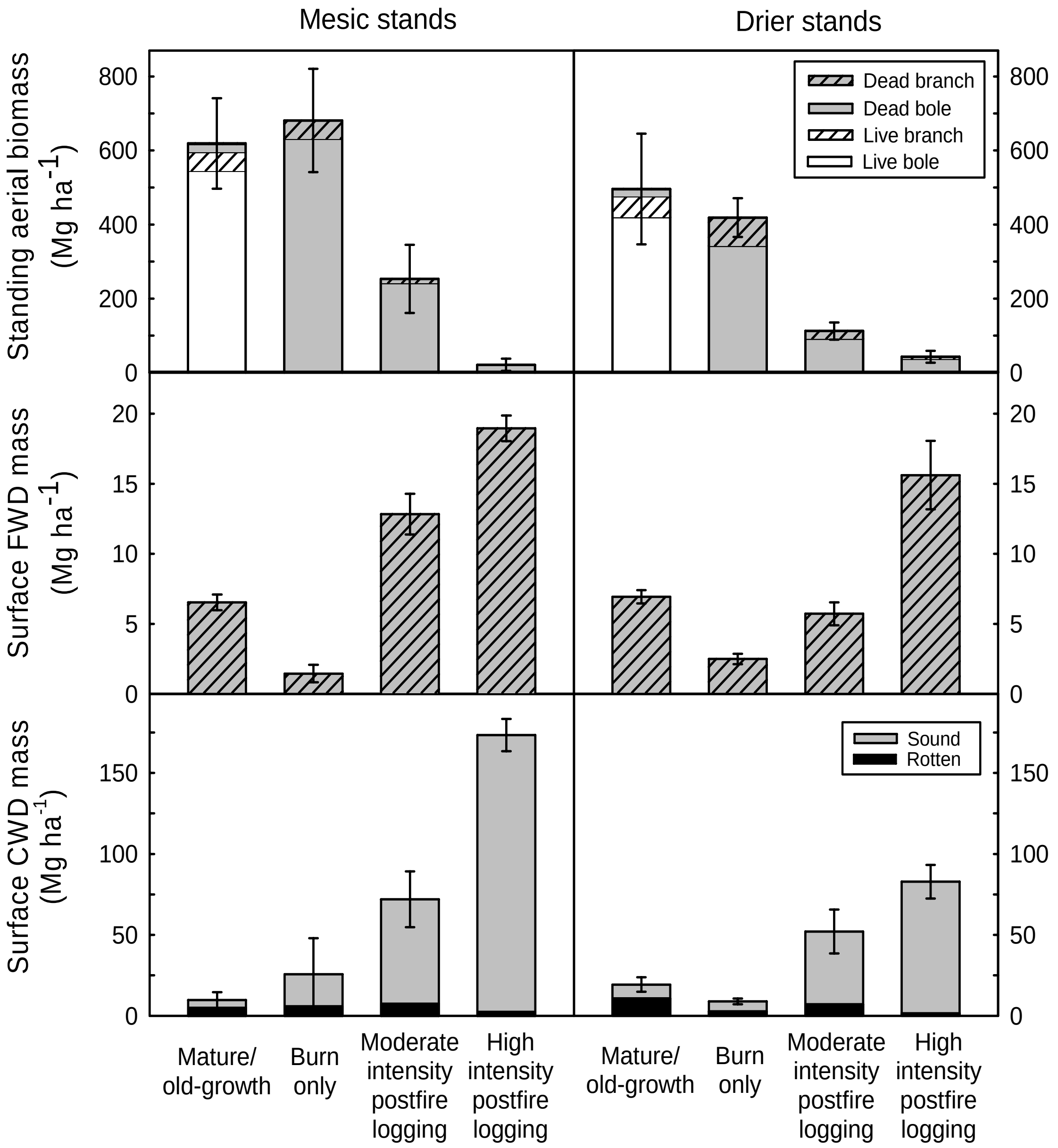

Figure 4-2. Mean (± SE) aerial and surface down wood biomass in mature/old-growth stands and following stand-replacement fire and postfire logging. See Table 4-4 for statistical comparisons.

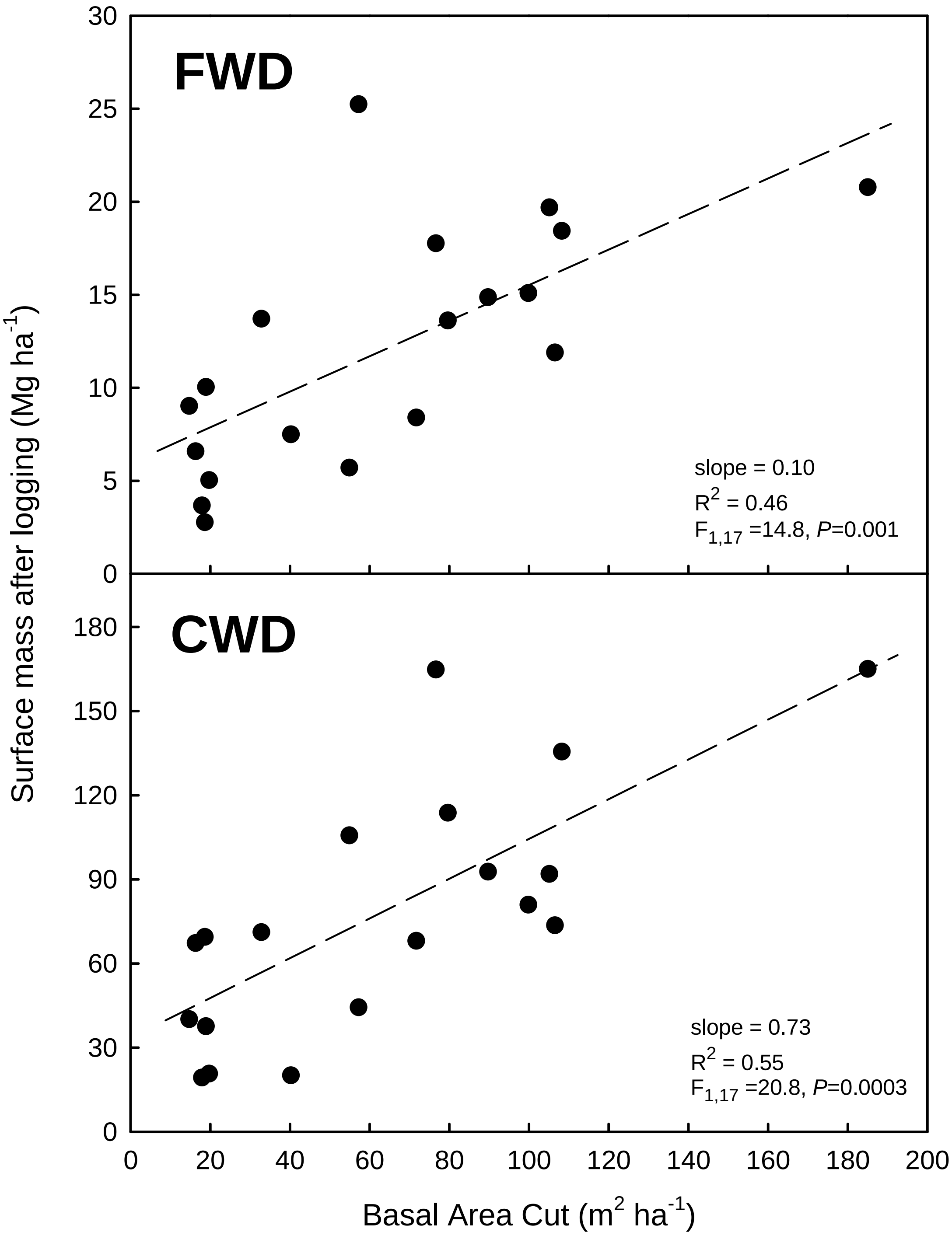

Figure 4-3. Surface down wood biomass after postfire logging as a function of absolute basal area cut.

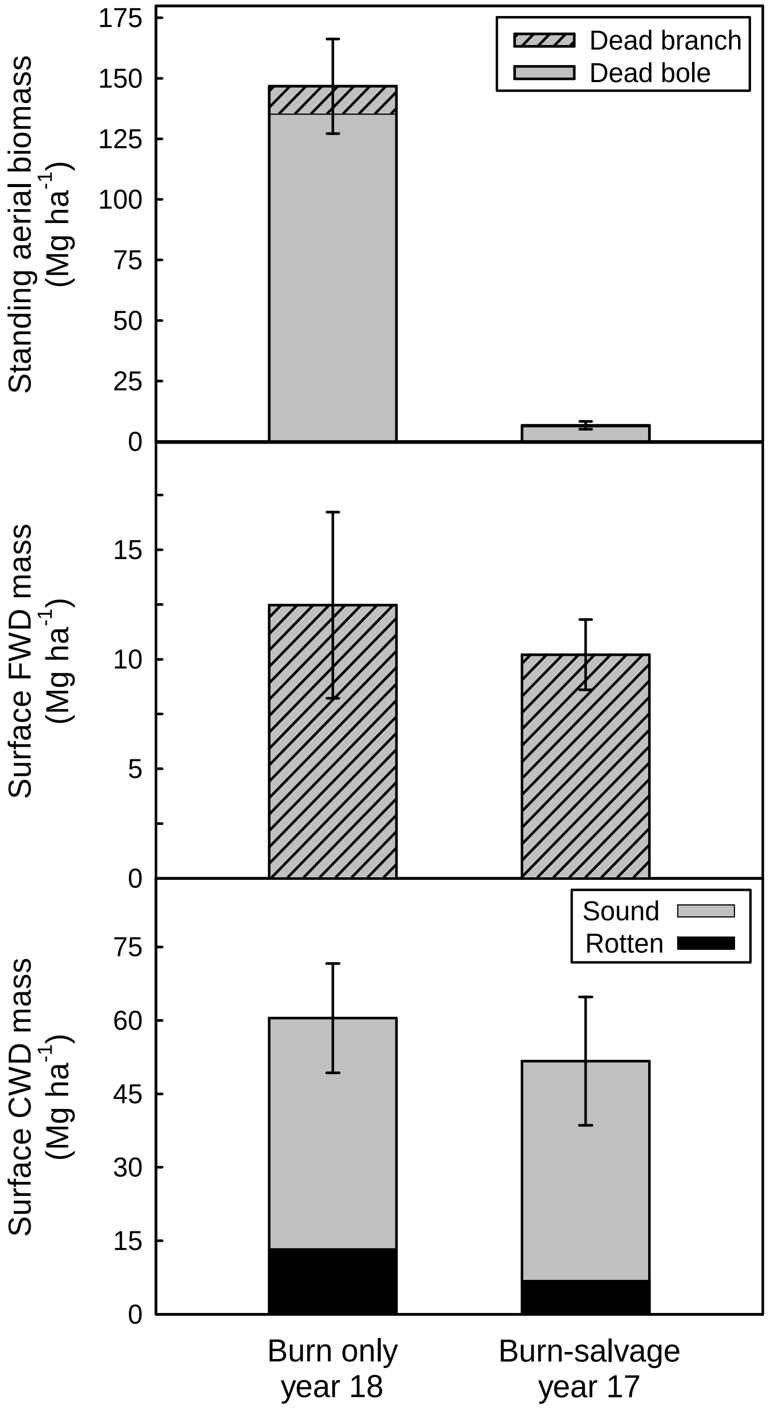

Figure 4-4. Mean (± SE) aerial and surface dead wood biomass in 17-18 year-old burns, with and without postfire logging. These sites are biogeographically most comparable to the eastern portion of the Biscuit Fire (see Fig. 4-2).

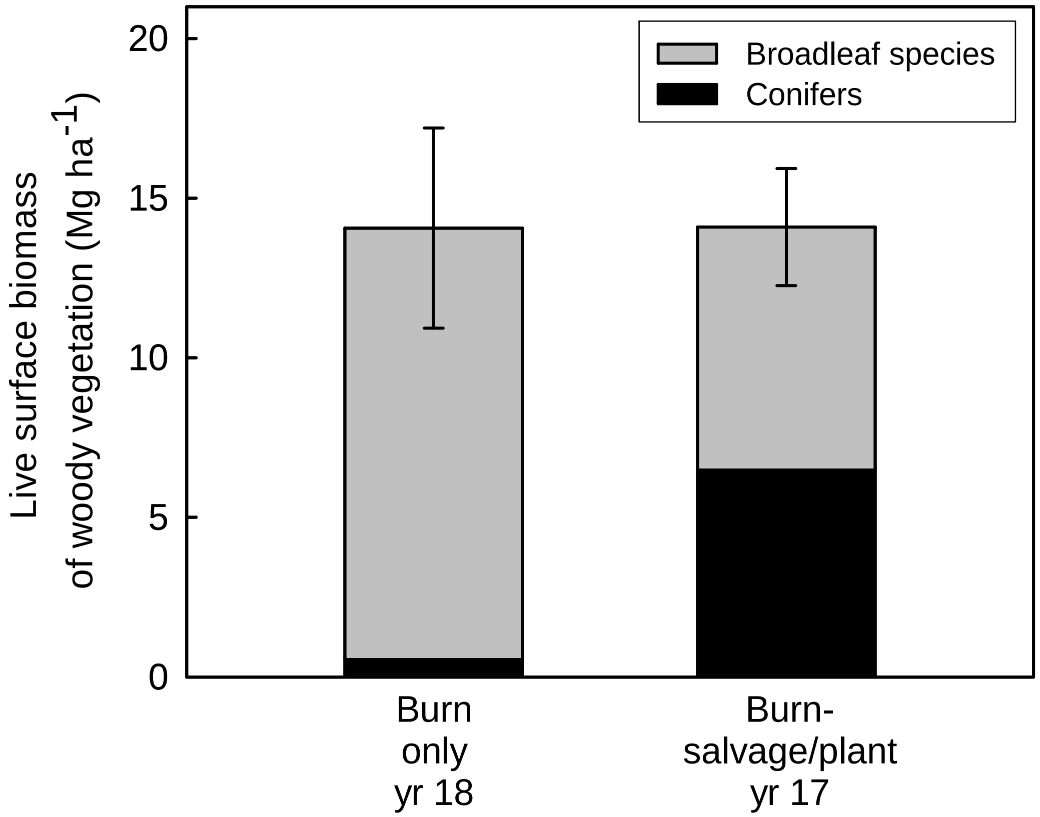

Figure 4-5. Mean (± SE) live surface biomass of woody vegetation in 17-18 year-old burns, with and without postfire logging and planting.

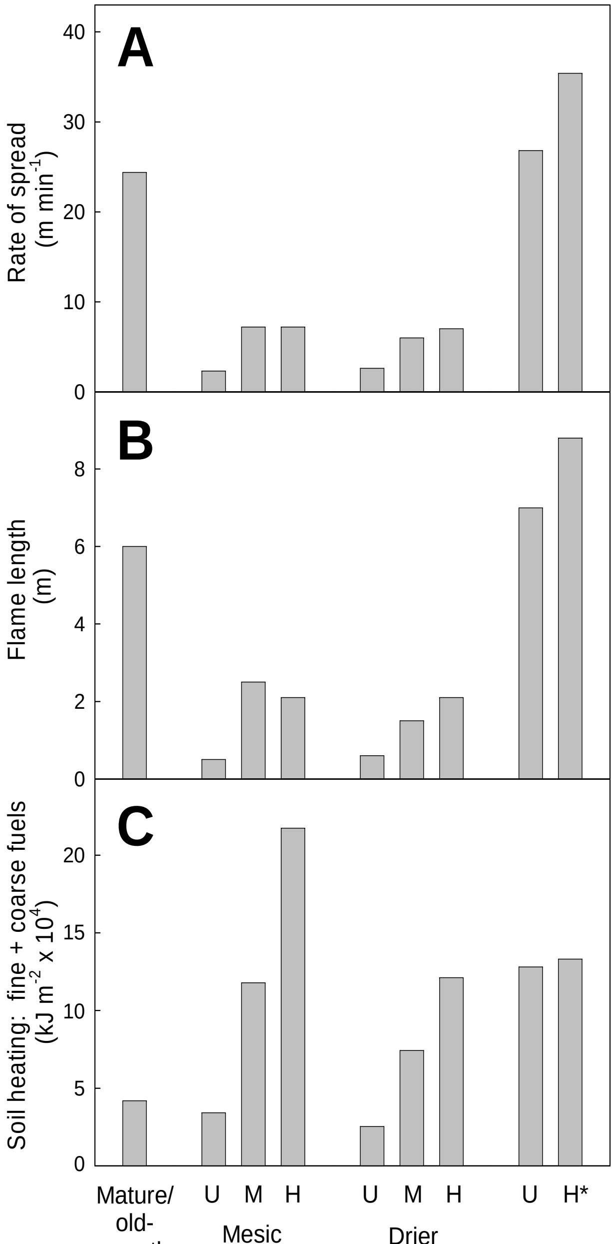

Figure 4-6. Fire behavior model outputs (BehavePlus and CONSUME) for projected rate of spread (A), flame length (B), and soil heating from all combustion phases including consumption of coarse fuels (C), under 90th-percentile weather conditions (USDA 2004). Model outputs indicated 100% mortality of regenerating trees for all postfire treatments. U= unlogged, M= moderate-intensity logged, H= high-intensity logged, H*= high-intensity logged + slash treatment + conifer planting.

CHAPTER 5: CONCLUSIONS

The objectives of this research were to investigate how early vegetation and fuel dynamics following high-severity wildfire are influenced by the mixed-severity fire pattern in which regeneration occurs (Chapter 2), and by the occurrence of secondary disturbances during early succession, specifically recurrent fire (Chapter 3) and postfire logging (Chapter 4).

Early regeneration patterns in a landscape-scale mixed-severity fire

The objective of the first study was to quantify how the spatial pattern of burn severity, through its influence on seed source distribution, interacts with microsite variability to control regeneration following a landscape-scale wildfire. We found that, despite the large size of the Biscuit Fire, the mixed-severity mosaic resulted in well-distributed seed sources throughout most of the burn. This seed availability led to variable but generally abundant regeneration in stand-replacement areas. The patchy nature of the fire meant that, from the perspective of conifer regeneration, the mixed-severity burn was more appropriately viewed as a collection of smaller stand-replacement patches in a matrix of surviving canopy, rather than one large fire with scattered surviving trees.

Soil parent material was also highly important to regeneration, with dry, coarse-grained igneous soils supporting lower regeneration density than soils derived from metasedimentary and metavolcanic materials. Other site factors (e.g., topography, broadleaf cover) had little association with early conifer regeneration.

Variation in burn patch size—which determines how distant stand-replacement areas are from seed source edges—was a dominant control on early postfire regeneration. This variation is therefore a key mechanism underlying heterogeneity in stand establishment, successional pathway, and forest structure—thus contributing to the globally renowned biodiversity of the Klamath-Siskiyou region.

After large wildfires, conifer establishment is typically a management goal but often receives limited funding. Given these limited resources, postfire management may benefit greatly by utilizing natural regeneration where possible. This approach would be aided substantially by quantifying the distribution of potential seed sources, as in this study. Natural postfire succession, which has operated in the Klamath-Siskiyou region for millennia, may include prolonged periods of dominance by early seral hardwoods and shrubs. Utilizing natural regeneration will thus require flexibility regarding spatial variation and the time period over which regeneration and crown emergence occur, recognizing that this variation contributes to the region's unique diversity. The degree of flexibility clearly depends on specific management objectives.

Vegetation response to a short-interval repeat fire

The objective of the second study was to assess whether a short-interval severe fire during early succession resulted in a unique vegetation community and initial successional pathway (relative to a single long-interval fire). We found that vegetation following the short-interval fire differed from that in the long-interval fire, but in some unexpected ways. The short-interval burn was rapidly colonized by a unique early seral community with increased rather than reduced plant cover and diversity. This pattern was due to additions or increases in disturbance-adapted species, likely associated with a propagule bank that developed between fires. The short-interval burn community still included major structural species such as hardwoods and conifers, suggesting that the short-interval burn retained the potential to develop toward mature forest condition. Further research will be necessary to determine whether potential longer-term influences of recurrent fire (e.g., differences in soil productivity, woody detritus quantities, or interspecific competition) will manifest in stand development.

Although short-interval severe fires are typically expected to be deleterious to forest flora and development, these results indicate that in systems characterized by highly variable natural disturbances (e.g., mixed-severity fire regime), native biota are well adapted to recurrent severe fire. Process-oriented ecosystem management incorporating variable natural disturbances, including 'extreme' events such as recurrent severe fires, would likely perpetuate a diversity of habitats and successional pathways on the landscape.

Early successional fuel dynamics with and without postfire logging

The objective of the third study was to quantify changes in fuel mass and distribution after high-severity fire with and without postfire logging, and how dead fuels interact with regenerating live fuels over the first decades following fire. We found that, three to four years after fire, high-intensity logging resulted in a greater proportion of felled biomass left on site as slash compared to moderate-intensity logging, because tree felling was less selective. Mean surface woody fuel loads after logging increased in a predictable way with the amount of basal area cut. Logged stands had higher ground cover of wood and lower variation in surface mass, suggesting increased homogenization of otherwise patchy postfire fuels.

It is generally hypothesized that in the absence of postfire logging, surface fuel loads will reach very high levels 15-30 years after fire as snags fall; however, we found no significant difference in surface woody fuels among logged and unlogged treatments at 17-18 years after fire. Snags in unlogged stands apparently decayed rapidly rather than accumulate on the surface, leaving large-diameter broken-topped boles as the main dead wood legacy. Because such snags stand the longest, surface fuels derived from residual snags had largely peaked by 18 years in unlogged stands.

Fuel profiles and fire modeling both suggested that regenerating vegetation rather than residual dead wood is the main driver of early seral fire hazard, with low fire potentials 3-4 years postfire and very high potentials at 17-18 years. Postfire logging increased fire potentials within this context due to generation of slash, but treatment differences became negligible by ~15-20 years (with slash treatment). Whether or not stands were logged, model outputs projected 100% mortality of regenerating trees in the event of a repeat burn. Based on these data, postfire logging does not appear to be consistent with objectives for reducing early fire hazard in the mixed-evergreen forest type we studied. Where reduction of early fire hazard is a goal, potentially effective treatment alternatives may include reducing connectivity of live fuels at landscape scales via, for example, shaded fuel breaks.

Primary uncertainties that would benefit from further research include how snag decay and fall rates vary by region and disturbance type (e.g., insects, fire, wind), potential fire behavior contributions of standing snags, and how different types of early seral vegetation contribute to fire potentials.

Implications for forest development

The objective of this research was to quantify early postfire processes widely thought to be important influences on long-term forest succession: variation in seed source availability, and the occurrence of secondary disturbances. Results from these studies underscore the importance of the mixed-severity context in which stand-replacing fire often occurs.

Within a fire, the mixed-severity pattern can dramatically influence the regeneration process by providing propagules for regeneration throughout much of even very large burns. This observation suggests that variation in the timing of stand establishment in the Douglas-fir region may be driven in large part by the spatial pattern of fire severity (and thus seed source). Other influences, such as interspecific competition, may become important later in stand development; however, such influences likely act upon a template of existing variation determined by variation in fire pattern.

Over broad time scales in a complex mixed-severity fire regime, native biota have been subject to highly variable disturbance frequencies, severities, and extents. Included in these variable disturbances are positive feedback mechanisms, wherein stand-replacing fire increases the likelihood of recurrent events (due to high fire hazard in early seral stands). This process has likely operated as long as high-severity fires have affected these forests (i.e., millennia). As such, native biota are well adapted to ‘extreme’ events such as recurrent severe fire. The robust vegetation response to the short-interval fire was congruent with this expectation.

Fire regimes, including the full range of behavior and effects characteristic to an area—not just the central tendency (e.g., mean return interval)—are widely recognized as essential to the maintenance of forest ecosystems. This notion underscores the importance of evaluating ecological response to wildfire, as well as associated management activities, within the context of the fire regime in a given area.

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APPENDICES

APPENDIX A. UNIVARIATE REGRESSIONS—SEEDLING ANALYSIS.

Table A-1. Model ranks and parameter estimates from mixed-effects regression of conifer seedling densities as a function of each of 11 site variables four years after the Biscuit Fire (analysis step #1). For step #2, the six top variables here were combined with distance to live-tree edge in an all subsets regression analysis (see text).

Model rank	Variable	AIC	ΔAIC	Akaike weight (w_i)	Parameter estimate † (95% CI)
1	Coarse-grained igneous soil [1/0]	187.63	0	0.69	0.085 (0.028, 0.259)
2	Rock cover [%]	190.80	3.17	0.14	0.971 (0.947, 0.996)
3	Forb/low-shrub cover [%]	193.93	6.30	0.03	1.017 (0.996, 1.038)
4	Hardwood/shrub cover [%]	194.10	6.47	0.03	0.977 (0.948, 1.007)
5	Intercept only	194.11	6.48	0.03	na
6	Slope [degrees]	195.01	7.38	0.02	0.947 (0.862, 1.040)
7	Standing dead basal area [m^2 ha^{-1}]	195.12	7.49	0.02	1.010 (0.993, 1.026)
8	Mean annual precipitation [cm]	195.30	7.67	0.01	0.981 (0.946, 1.018)
9	Soil cover [%]	196.17	8.53	0.01	1.010 (0.970, 1.050)
10	Annual solar heat load [index]	196.27	8.64	0.01	0.742 (0.130, 4.22)
11	Elevation [m]	196.32	8.69	0.01	0.999 (0.996, 1.003)
12	Crown-scorched vs. consumed [1/0]	196.40	8.76	0.01	0.967 (0.209, 4.483)

Notes: All models had structure: $y \sim \beta_0 + \beta_1 x$, except intercept only model ($y \sim \beta_0$).

† Multiplicative effect, obtained via backtransformation from analysis of $\log_e(x+1)$ data. A value of 1 = no effect.

APPENDIX B. SUBSTRATE UTILIZATION BY SEEDLINGS.

For substrate associations, we used a chi-square analysis on expected vs. observed seedling counts on litter, exposed mineral soil, and rock >1 cm diameter. Seedlings rarely occurred on other substrates. Expected values were based on % cover of each substrate class in a plot times the total number of seedlings in that plot. Plots with more than one expected value <5, or with any expected value of zero, were excluded from analysis; this resulted in 13 plots analyzed for 2004 and 15 for 2006. Expected values were then compared with observed seedling numbers on each substrate to generate observed minus expected values to compare to a chi-square distribution.

The chi-square analysis of substrate utilization was highly significant in both 2004 ($\chi^2_{24}=215.5$, $P<0.0001$) and 2006 ($\chi^2_{28}=519.3$, $P<0.0001$), driven largely by differences in utilization of rock and soil. Seedlings were found on rock less than expected by chance (availability) both years, suggesting low germination and early survival rates on rocky substrates. In contrast, seedlings were on soil substrates more than expected by chance both years, suggesting high germination and early survival rates on exposed mineral soil. Nevertheless, as concluded in the multi-model regression framework, soil cover % was unimportant as a plot-scale predictor of regeneration density, likely because exposed mineral soil substrates were abundant in an absolute sense after high-severity fire, and therefore not limiting.

APPENDIX C. SPECIES LIST.

Table C-1. Species list

Scientific name	Common name
<u>TREES</u>	
Abies concolor	white fir
Abies magnifica	Shasta red fir
Acer circinatum	vine maple
Acer glabrum	Rocky Mountain maple
Acer macrophyllum	bigleaf maple
Alnus rubra	red alder
Arbutus menziesii	Pacific madrone
Calocedrus decurrens	incense cedar
Chrysolepis chrysophylla	giant chinquapin
Chamaecyparis lawsoniana	Port Orford cedar
Corylus cornuta	California hazel
Cornus nutallii	Pacific dogwood
Lithocarpus densiflorus	tanoak
Picea breweri	weeping spruce
Pinus attenuata	knobcone pine
Pinus contorta	lodgepole pine
Pinus jeffreyi	Jeffrey pine
Pinus lambertiana	sugar pine
Pinus ponderosa	ponderosa pine
Pseudotsuga menziesii	Douglas-fir
Quercus chrysolepis	canyon live oak
Quercus kelloggii	California black oak
Taxus brevifolia	Pacific yew
Thuja plicata	western redcedar
Tsuga heterophylla	western hemlock
Umbellularia californica	Oregon myrtlewood
<u>LARGE WOODY SHRUBS</u>	
Alnus sitchensis	Sitka alder
Amelanchier alnifolia	western serviceberry
Arctostaphylos columbiana	hairy manzanita
Arctostaphylos hispidula	Howell's manzanita
Arctostaphylos patula	greenleaf manzanita
Arctostaphylos viscida	whiteleaf manzanita
Ceanothus integerrimus	deerbrush
Ceanothus thyrsiflorus	blue blossom
Ceanothus velutinus	snowbrush

Eriodictyon californicum	yerba santa
Garrya buxifolia	wavy-leafed silk tassel
Garrya elliptica	elliptical silk tassel
Garry fremontii	silk tassel
Holodiscus discolor	creambush oceanspray
Kalmiopsis leachiana	kalmiopsis
Quercus sadleriana	Sadler oak
Quercus vaccinifolia	huckleberry oak
Rhamnus purshiana	cascara
Rhododendron macrophyllum	Pacific rhododendron
Rhododendron occidentale	western azalea
Sambucus racemosa	blue elderberry
Vaccinium ovatum	evergreen huckleberry
Vaccinium parvifolium	red huckleberry

LOW SHRUBS

Arctostaphylos nevadensis	pinemat manzanita
Arctostaphylos uva-ursi	kinnikinnick
Blechnum spicant	deer fern
Ceanothus cordulatus	mountain whitethorn
Ceanothus cuneatus	buckbrush
Ceanothus prostratus	mahala mat
Ceanothus pumilus	dwarf ceanothus
Chimaphila menziesii	little prince's pine
Chimaphila umbellata	pipsissewa
Cornus canadensis	bunchberry
Crataegus douglasii	Douglas' hawthorne
Gaultheria shallon	salal
Juniperus communis	common juniper
Linnaea borealis	twinflower
Lonicera ciliosa	orange honeysuckle
Lonicera hispidula	hairy honeysuckle
Mahonia nervosa	dwarf Oregon grape
Mahonia piperiana	tall Oregon grape
Mahonia pumila	pygmy Oregon grape
Pachystima myrcinites	Oregon boxwood
Polystichum munitum	sword fern
Rhamnus californica	California coffeeberry
Ribes roezlii	Sierra gooseberry
Ribes sangiuneum	red currant
Rosa gymnocarpa	baldhip rose
Rubus leucodermis	black cap raspberry
Rubus nivalis	snow dwarf bramble
Rubus parviflorus	thimbleberry

Rubus ursinus	trailing blackberry
Symphoricarpus albus	common snowberry
Symphoricarpus mollis	trailing snowberry
Toxicodendron diversilobum	poison oak
Vaccinium membranaceum	thinleaf huckleberry
Vaccinium scoparium	grouse huckleberry
Whipplea modesta	whipplevine
Xerophyllum tenax	beargrass

FORBS AND GRASSES

Achillea millefolium	common yarrow
Achlys triphylla	vanilla leaf
Adenocaulon bicolor	pathfinder
Anaphalis margaritacea	pearly everlasting
Antennaria suffrutescens	shrubby everlasting
Apocynum androsaemifolium	dogbane
Apocynum cannabinum	common dogbane
Apocynum pumilum	mountain dogbane
Aquilegia formosa	Sitka columbine
Arnica cernua	nodding arnica
Asarum hartwegii	wild ginger
Astragulus species	milkvetch
Athyrium filix-femina	lady fern
Boschniakia strobilacea	California ground cone
Calypso bulbosa	fairy slipper
Calochortus elegans	elegant mariposa lily
Calochortus tolmei	pussy ears
Carex species	sedges
Castilleja miniata	common paintbrush
Castilleja species	paintbrush
Cirsium arvense	Canada thistle
Claytonia perfoliata	miner's lettuce
Clintonia uniflora	queen's cup
Collinsia rattanii	sticky blue-eyed mary
Collomia tinctoria	prickly collomia
Convulvulus arvense	morning glory
Corallorhiza maculata	spotted coralroot
Corallorhiza striata	striped coralroot
Delphinium sonnei	Sonne's larkspur
Dicentra formosa	Pacific bleeding heart
Disporum hookeri	Hooker's fairybells
Epilobium angustifolium	fireweed
Epilobium bracteosum	willowherb
Epilobium ciliatum	purple-leaved willowherb

Epilobium miniatum	small-flowered willowherb
Equisetum arvense	horsetail
Fragaria vesca	woods strawberry
Gallium amiguum	obscure bedstraw
Gallium triflorum	fragrant bedstraw
Goodyera oblongifolia	rattlesnake plantain
Hypericum perforatum	St. John's wort
Iliamna latibracteata	California globemallow
Iris chrysophylla	slender-tubed iris
Juncus species	rushes
Lilium bolanderi	Bolander's lily
Lilium columbianum	tiger lily
Lilium washingtonianum	Washington lily
Lotus crassifolius	deer vetch
Lupinus albifrons	white-leaved lupine
Lupinus bicolor	bi-colored lupine
Maianthemum racemosa	false Solomon's seal
Maianthemum stellata	star-flowered false Solomon's seal
Mimulus species	monkey flower
Montia parvifolia	small-leaved montia
Oxalis oregana	wood sorel
Penstemon angustifolium	penstemon
Penstemon parvulus	small azure penstemon
Phacelia hastata	silverleaf phacelia
Poaceae species	grasses
Pterospora andromedea	pinedrop
Pteridium aquilinum	bracken fern
Pyrola dentata	wintergreen
Pyrola picta	white-veined wintergreen
Sedum oreganum	Oregon stonecrop
Senecio sylvaticus	wood groundsel
Taraxacum officinale	dandelion
Thermopsis macrophyllum	false lupine
Trientalis latifolia	western starflower
Trillium ovatum	white trillium
Vancouveria hexandra	inside-out flower
Vancouveria planipetala	redwood ivy
Veratrum viride	false hellebore
Vicia americana	American vetch
Viola species	violas

Nomenclature based on Hickman (1993).

APPENDIX D. HARDWOOD AND SHRUB MASS ALLOMETRY

Allometric equations for live aboveground biomass of hardwoods and shrubs were generated from samples collected during this study. We derived allometry specifically for postfire resprouts of eight different species of the Klamath-Siskiyou region. Seventy-six individuals from representative size ranges were measured, harvested, oven dried at 70 °C until constant weight was achieved, then weighed by component (stem, branch, foliage). Species-specific regression lines were fit using SigmaPlot® ver. 8 software to obtain equations relating diameter and/or canopy volume metrics to live aboveground biomass of each component. Volume measurements and associated equations were used when very coppiced individuals made measurement of individual stems impractical. For species encountered in plots but not harvested, a general equation obtained from the composite of all species, or general equations for facultative vs. obligate shrub forms, were used. Diameter-mass equations took the form:

(Eqn. D-1) $m = dba^{a}e^{b}$

where m = mass, dba = basal diameter, and a & b are species- and component-specific constants (Table D-1). Canopy volume-mass equations took the form:

(Eqn. D-2) $m = a(1-e^{-b(v)})$

where m = mass, v = canopy volume (height x breadth x width), and a & b are species- and component-specific constants (Table D-2).

Dead shrub stem mass was obtained by an equation approximating a tapered cylinder, $0.8*\pi r2h$, using the mid-point of the basal area diameter class to obtain r (mid-point-diameter/2) for each dead stem. Dead stem lengths (h) were obtained from field-measured dead stem heights using the relationship shown in Figure D-1.

Table D-1. Allometric equations based on basal diameter (Equation D1)

Species	Total aboveground biomass		Stem mass		Foliage mass	
	a	b	a	b	a	b
Lithocarpus densiflorus	2.161	4.250	2.387	3.593	1.776	3.495
Quercus chrysolepis	1.591	3.868	1.817	3.363	1.289	2.904
Arbutus menziesii	1.952	4.486	2.228	3.874	1.343	3.673
Chrysolepis chrysophylla	2.158	4.006	2.293	3.536	1.848	3.011
Obligate shrubs†	2.045	3.855	2.213	3.586	1.779	2.307
Facultative shrubs combined	2.112	4.173	2.325	3.577	1.710	3.320
All species combined	2.174	4.084	2.293	3.606	1.982	2.970

† Obligate shrubs include *Ceanothus integerrimus, C. velutinus, Acer circinatum, Vaccinium parvifolium.*

Table D-2. Allometric equations based on crown volume (Equation D2)

Species	Total aboveground biomass		Stem mass		Foliage mass	
	a	b	a	b	a	b
Lithocarpus densiflorus	10071	0.0001	5723.1	0.0001	4155.5	0.0001
Quercus chrysolepis	6989.5	0.0015	3881.7	0.0014	2629.0	0.0015
Arbutus menziesii	14233	0.0001	9097.5	0.0001	4616.6	0.0001
Chrysolepis chrysophylla	2374.0	0.0012	1490.1	0.0011	880.4	0.0012
Obligate shrubs	5232.3	0.0002	4417.4	0.0002	853.1	0.0002
Facultative shrubs combined	9185.9	0.0001	6657.9	0.0001	2155.6	0.0006
All species combined	8863.1	0.0001	6497.7	0.0001	2203.4	0.0002

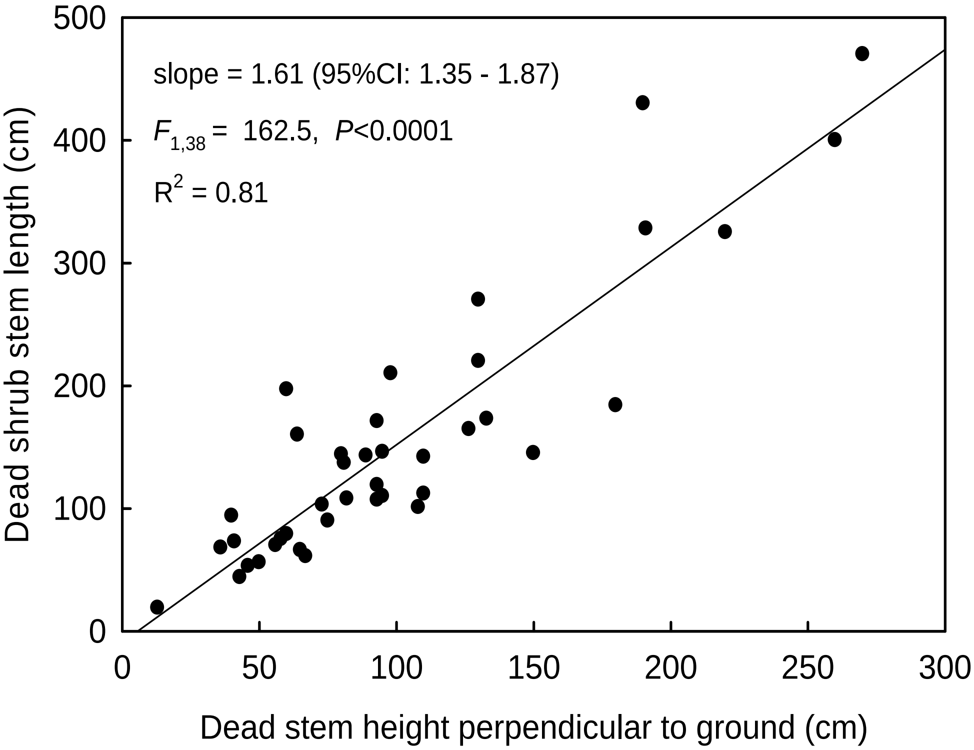

Figure D-1. Regression used to obtain dead stem lengths from field-measured dead stem heights. Data were obtained by measuring the nearest shrub to plot center in 40 stands.

APPENDIX E. DECAY INPUTS FOR TREE MASS COMPUTATIONS.

Adjustments to tree mass components for decay status (e.g., wood density) were largely obtained from Harmon and Sexton (1996). For broken-topped trees, stem volume was computed using an equation for a tapered cylinder, $0.8*\pi r^2 h$, and branch and bark masses were reduced proportional to amount of crown lost to breakage. Additional adjustments for branches and bark were adapted from several sources as shown in Table E-1.

Table E-1. Decay class adjustments to tree branch and bark computations.

Characteristic	Decay class				
	1	2	3	4	5
Ratio of branch volume to original volume	1.00	0.80	0.40	0.00	0.00
Ratio of branch density to original density	1.00	0.78	0.67	0.38	0.37
Ratio of bark mass to original mass	1.00	1.00	0.20	0.00	0.00

Estimates adapted from Cline et al. 1980, Harmon and Sexton 1996, van Tuyl et al. 2005.

APPENDIX F. FUEL CHAR COMPUTATIONS.

Accurately quantifying woody detritus (WD, fuel) levels following wildland fire is an essential component of fire research and management. An important, but largely overlooked, aspect of postfire fuel quantification is that often a substantial portion of these fuels has been charred to some degree. Woody material charred but not consumed during a fire has lost significant mass (Czimczik et al. 2002, Dietenberger 2002). If this loss is not taken into account, standard calculations based on field-measured diameters can result in significant overestimation of fuel mass for certain timelag classes. Moreover, recent evidence indicates that char has important implications for ecosystem productivity and global climate (Lehmann et al. 2003, DeLuca and Aplet 2008). In this appendix I present simple estimates of the overestimation bias, char formation levels, and report easily incorporated adjustments to standard fuel measurements to correct for mass loss due to charring.

Generation of char. Char, the thermally altered residue remaining after incomplete combustion of vegetation matter (Baldock and Smernik 2002), is a variable but unique biogeochemical material formed by the smoldering and glowing phases of combustion (Goldberg 1985, Pyne et al. 1996). The formation of char can be simultaneous with, sequential to, or independent of distillation-based flaming combustion of wildland fuels. Charring often affects material to some depth below its surface before combustion extinction occurs depending on moisture and oxygen conditions in a fuel particle's interior (see Costa and Sandberg 2004). This process of char production results in a blackened rind on the surface of woody detritus (Tinker and Knight 2000).

Overestimation bias and char formation. Planar intercept transects, the most widely used WD sampling method, allow computation of fuel volume and mass using diameter as the only morphometric measurement (Brown 1974, Harmon and Sexton 1996). Sampling error aside, this method is likely effective in accounting for the portion of WD completely consumed by fire: if the wood is not there, it is not measured, and the reduced/low diameters will reflect any complete combustion. However, in general the technique does not account for the material charred but remaining as a rind on the WD (Fig. F-1). Calculations of fuel mass based on field-measured diameters assume the density of char layers to be unaltered, when in reality they have lost most of their mass (Di Blasi et al. 2001, Czimczik et al. 2002, Dietenberger 2002). This bias can result in substantial overestimation of postfire fuel mass for all but the largest timelag classes.

Although few data exist on the magnitude of this overestimation bias, some constraints can be estimated based on a survey of the literature on wood combustion, which we augmented with field data. Studies have consistently arrived at estimates of ~60-80% mass loss on charring for temperatures typical of wildland fires (e.g., Di Blasi et al. 2001, Czimczik et al. 2002, Dietenberger 2002), with little dependence on heating rate, initial density, burn duration, or wind speed. Estimates of depth of char are not as well established. In a laboratory setting, char depth has been observed to increase with burn duration for Douglas-fir (*Pseudotsuga menziesii*), red oak (*Quercus rubra*), redwood (*Sequoia sempervirens*), and maple (*Acer* spp.), with values ranging from 0.1-33 mm for times up to 25 minutes, and up to 50 mm for burn times of 75 minutes (Spearpoint and Quintiere 2000). For wildland fires, the limited available field data suggest that char depths are fairly consistent and most often well below these values. Tinker and Knight (2000) found charcoal thickness to be fairly consistent on WD in a high severity wildfire, with no strong relationship with decay class.

To provide some initial field numbers on depth, we opportunistically collected char depth data from WD in three large wildfires in Oregon: the 2002 Biscuit, 2002 Eyerly, and 2003 B&B Complex fires, representing a range of forest types including mesic Mediterranean Douglas-fir/sclerophyll, interior ponderosa pine (*Pinus ponderosa*), and high Cascades mixed conifer, respectively (Franklin and Dyrness 1973). Char depths fell within a fairly narrow range (1-17 mm, mean=6.4 mm, S.D.=3.7 mm, n=56 pieces) despite variable substrates (standing, down, bark, wood, decay classes 1-4, and low- to high-severity burns) and different visual appearances of depth. Down WD charred to greater depths (8.2 mm) than standing WD (5.7 mm) (two-sample pooled variance *t*-test: $t_{54}=2.41$, $P=0.02$). Given relatively consistent depths, the proportion of a given particle affected by char therefore depended largely on its size (Fig. F-1).

The firm estimates of mass loss on charring (~70%) and relatively narrow constraints on char depth across a range of conditions (typically <15 mm, mean 5.7 mm and 8.2 mm for standing and down WD, respectively) allow an assessment of overestimation bias for WD inventories. We used a straightforward computational approach similar to that described by Tinker and Knight (2000), in which standard WD volume calculations (Brown 1974, Harmon and Sexton 1996) are made for the outer cylinder including the charred rind, then for an inner uncharred cylinder whose diameter depends on char depth. The difference represents the charred volume. Volume of the uncharred core (vol_{core}) is converted to mass using wood density (ρ_{wood}) and, for the charred exterior (vol_{rind}), wood density with 70% mass loss:

(Eqn. F-1) $\text{Total fragment mass} = vol_{core} * \rho_{wood} + vol_{rind} * \rho_{wood} * (1-0.7)$

where volumes are in units of cm^3 and densities in g cm^{-3} (units are not critical but must be consistent). This corrected mass can be compared to standard mass computations, which are based on conversion of whole-piece volume to mass using a single wood density value. Percent overestimation bias is calculated by the difference between the corrected mass estimate ($mass_{corr}$) and the standard mass estimate ($mass_{std}$), divided by the corrected estimate and scaled to percentage:

(Eqn. F-2) $\text{Overestimation bias} = 100 * (mass_{std} - mass_{corr}) / mass_{corr}$

Using the relevant example of wood char on down WD, a central value of 8.2 mm char depth (with empirically based assumption of uniformity across size classes) produces illustrative estimates of bias (Table F-1, Fig. F-2). Overestimation is substantial for smaller fuel classes, rapidly tapering off with piece diameter (Fig. F-2). The bias is non-trivial for all but the largest size classes. For example, if char rind is not accounted for, 10-hr fuels (0.6-2.5 cm) are overestimated by more than a factor of 3 (233%), 100-hr fuels (2.5-7.6 cm) by 78%, and even 1000-hr (7.6-20.3 cm) fuels by 12-37% depending on exact size (Table F-1, Fig. F-2). Charred 1-hr fuels (<0.6 cm) may be less relevant to fuel inventories because they could be missed, or dismissed, as litter rather than wood. Also, for the largest pieces (>50 cm) the bias of less than 5% is relatively unimportant for mass estimates; the error associated with thick bark may well surpass that associated with char. However, char on these large pieces contributes most to black C formation on an individual fragment basis (Fig. F-3).

When char is most and least relevant. Quantifying char may be most relevant when research objectives include postfire wildlife response and habitat selection by WD-associated species; for modeling and projecting postfire WD decay rates and distribution over time; when fire-induced changes in C cycling are of interest; following multiple fires closely spaced in time (re-burns, repeated entry prescribed burns, or post-fire salvage slash treatments) such that WD derived from the mortality of woody stems in one fire experiences decay, bark sloughing, and/or subsequent burning; and when the most accurate estimates of postfire fuel mass are sought—particularly when fuels will be reported separately by timelag class (rather than a single number for total fuel load), and there are significant amounts of fine fuels and/or char on wood rather than bark. Quantifying char may be unimportant when fuel loads will only be reported by volume, when mass will only be reported with a single number for total load (a number mainly governed by large particles for which overestimation bias is minimal), or when char is primarily on bark, which will slough off in a relatively short time. Nonetheless, even when char is exclusively on bark it could contribute substantially to overall black C formation at stand and landscape scales.

*Correcting and reporting mass estimates for charred woody detritus. A*lthough WD mass estimates typically have low precision at all but the most intensive sampling efforts (Harmon and Sexton 1996), correcting for mass loss on charring can still increase accuracy since the error in not doing so is unidirectional (systematic positive bias). A computational approach is outlined here that can be adapted to a given fire or forest type. Because the quantifications of char depth and overestimation bias described above should be considered exploratory, the first component is to obtain site-specific char depths and their potential relationship to meaningful gradients within the context of a study's objectives. This task requires minimal time and effort, and takes only a blade and a ruler with mm graduations to identify the generally abrupt boundary between charred and virgin wood. Representative measurements can be taken either as part of normal plot sampling or conducted separately, the latter of which takes less than one field day for a typical fire area.

During collection of WD data, char can be recorded as a simple presence/absence tally for each piece since there tends to be a relatively narrow range of char depth. Depending on research objectives, a distinction can be made for bark vs. wood char. Like decay status (Brown 1974), the determination of char presence is assessed at the transect line only (regardless of the rest of the piece), and in the case of partial charring, is based on the dominant character of the piece at the transect.

Once WD data are collected and representative char depths are known, a simple computational adjustment incorporates mass loss for charred pieces. The method arrives at the same adjustment as the inner-core/outer-shell method used by Tinker and Knight (2000) and for the bias estimates above, but differs in that it can be easily routed through standard equations for volume and/or mass per unit area. The standard equation for scaling coarse WD fragment diameters to volume per unit area, which would still be applied to all uncharred fragments, is:

$$\text{(Eqn. F-3)} \qquad Vol = 9.869 * \sum (d^2/8L)$$

where *Vol* is the volume per unit area ($m^3\ m^{-2}$), *d* is the piece diameter (m), and *L* is the transect length (m) (Harmon and Sexton 1996). Volume is converted to mass using species- and decay class-specific wood densities. For charred fragments, *d* can be substituted with an adjusted diameter (d_{adj}) based on the depth of char. This value is equivalent to the diameter of the uncharred core plus 30% of the charred rind:

$$\text{(Eqn. F-4)} \qquad d_{adj} = d - (2 * depth_{char} * 0.7)$$

where $depth_{char}$ is in the same units as *d*. Equation F-4 incorporates a proxy for 70% mass loss for the charred rind, and a factor of two since the equation is based on diameter rather than radius. An adjusted volume equation results, (Eqn. F-5) $\mathrm{Vol}_{adj} = 9.869 * \sum ([d - (2 * \mathrm{depth}_{char} * 0.7)]^2/8L)$.

from which mass is calculated in the normal fashion using standard wood densities. This adjustment can also be applied to the quadratic mean diameters used for fine WD calculations (Harmon and Sexton 1996), with the recognition that for the smallest classes (1-hr and 10-hr), char will likely extend to the core, in which case a simple mass reduction of 70% can be applied.

Black C formation can be calculated on a per area basis by scaling each piece tallied on a transect (in similar manner to standard volume-mass calculations) by computing charred volume and multiplying by wood density, proportion of mass remaining, and final C concentration:

(Eqn. F-6) $\mathrm{Vol} - (9.869 * [d - (2 * \mathrm{depth}_{char})]^2 / 8L) * \rho_{wood} * (1-0.7) * 0.75$

where 0.75 is the final C concentration assuming heating to 300-400 °C (Baldock and Smernik 2002, Czimczik et al. 2002, Branca and Di Blasi 2003).

These calculations assume approximately uniform charring over the length and circumference of a WD fragment. Certainly there is substantial variation around this under field conditions. This variation is mostly an issue for large fuels with greater surface area, while smaller fuels tend to char rather uniformly. Tinker and Knight (2000) noted that most pieces were either nearly completely charred or not charred at all following wildfire, which is consistent with our observations. Where the char status of a piece at the transect is not representative of the piece as a whole, probabilistic symmetry about this error as it is scaled from many data points should result in unbiased stand/plot-level estimates. Another consideration is that the above calculations assume consistent char depth in wood regardless of fragment diameter, based on our field measurements.

Lastly, the calculations outlined here are tailored to down WD surveys. When quantifying total black C in a stand following a fire, char on standing live and dead trees would need to be included. This would require recording/computing surface area of char on boles (separated by bark vs. wood), then scaling to black C mass using factors for char depth, bark/wood density, mass loss on charring, and C concentration, as in Equation F-6—an approach similar in principle to that of Campbell et al. (2007).

Summary of recording, computing, and reporting charred WD

1) Obtain representative sample of char depths for a given study area. Appropriate sample size depends on any gradients or distinctions of interest (e.g., standing vs. down, bark vs. wood, fire severity, etc.), but should be >30.
2) Record presence/absence of char for each WD fragment encountered during surveys.
3) Modify diameters to reflect char effects, then calculate mass in normal manner.
4) Report total mass for each timelag class; consider separation by charred/uncharred depending on research or management objectives.

Table F-1. Overestimation bias and black carbon formation for various WD particle sizes.

	timelag class (hr)	representative diameter (cm)	Fractional mass loss due to charring	over-estimation of mass (%) (Eqn. F-2)	Black C mass (kg ha^{-1})
Fine WD	1	0.31	0.70	233	0.5
	10	1.37	0.70	233	8.8
	100	4.22	0.44	78	51.1
Coarse WD	1000	12	0.18	22	61.1
	>1000	50	0.05	4.7	268.6
	>1000	100	0.02	2.3	541.8

Notes: Black C calculations incorporate 0.45 g/cm3 as representative wood density for conifer-dominated forest (Harmon and Sexton 1996), and scale up one piece to mass per hectare using Equation F-6 with transect lengths of 30 m for fine WD and 75 m for coarse WD.

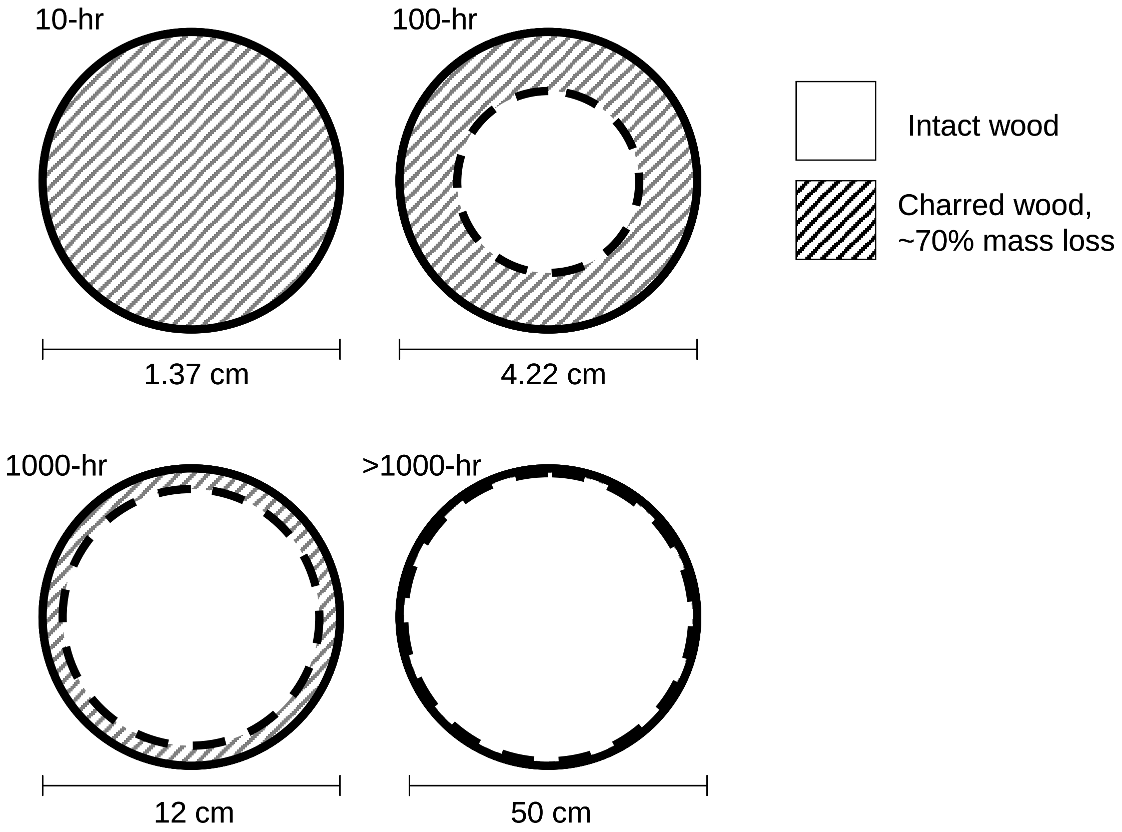

Figure F-1. Idealized cross-sectional views of charred woody detritus. Example uses 8.2 mm as typical char depth for downed material, based on field-measured depths. Volume of charred shell relative to overall fragment volume is substantial for small pieces (e.g., 1-hr, 10-hr, 100-hr and 1000-hr fuels). Char volume is much less relatively important for large pieces, but the absolute amount of char created increases linearly with fragment diameter, such that larger pieces are more important in creation of recalcitrant carbon (black C). Diameters for 1, 10 and 100-hr fuels are "average quadratic mean diameters" from Harmon and Sexton (1996); others are chosen to represent a range.

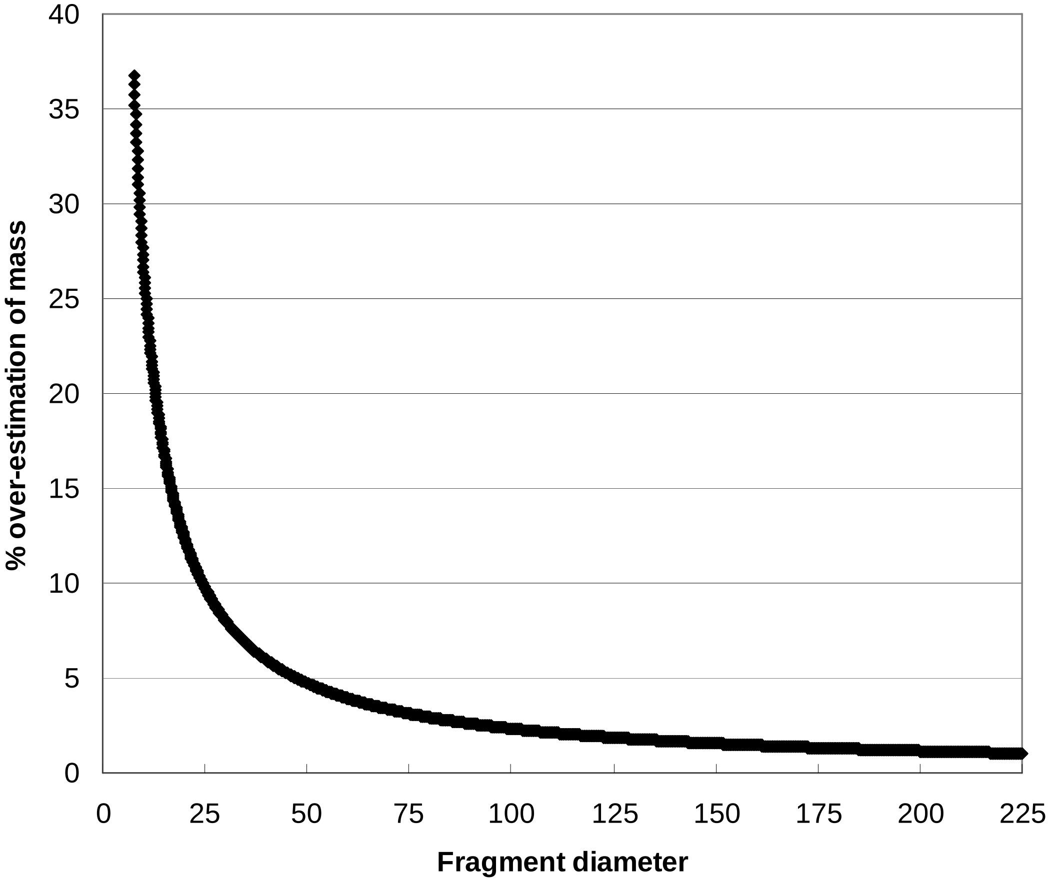

Figure F-2. Estimated positive bias in WD mass computations, expressed on a percentage basis, when wood charring is present but not taken into account. In this example, typical values of char depth (8.2 mm) and mass loss on charring (70%) are used, with empirically based assumption of uniformity of wood char depth across diameter classes. Shape of curve reflects the relationship between total cross-sectional area, which varies with the square of fragment radius (πr^2), and a rind of fixed width, which increases linearly with radius ($2\pi r$).

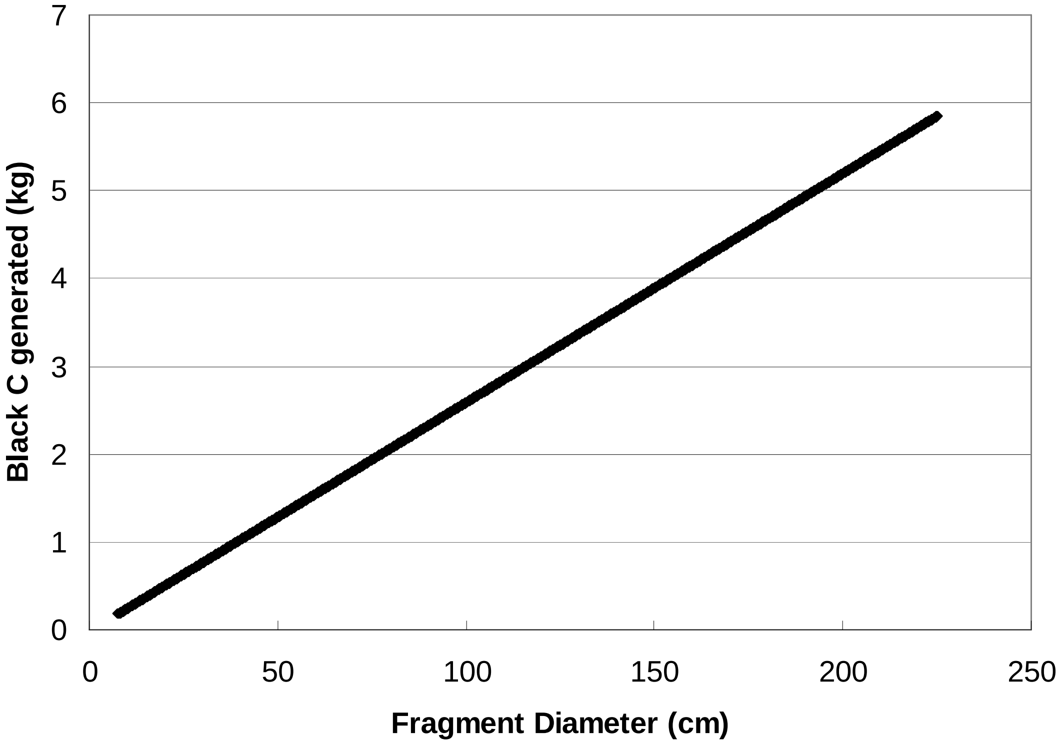

Figure F-3. Black carbon generated by wood charring for fragments of 1-meter length. Amount scales linearly to diameter since size of charred rind depends on circumference of fragment.

APPENDIX G. FIRE MODELING INPUTS.

For both BehavePlus and CONSUME model runs, all fuel loading and stand structure data were based on empirical measurements (see Tables 4-1 through 4-7 in text), and SA:volume and packing ratios were based on fuel models 11, 4, and 10 for 3-4 year-old, 17-18 year-old, and mature/old-growth stands, respectively. Weather inputs (see Table G-1) were adapted from USDA (2004), incorporating wind adjustment factors of 0.5 for open postfire stands and 0.25 for mature/old-growth stands. Moisture of extinction was set at 20%. Static model settings were used for all runs in BehavePlus (Andrews et al. 2005). Duff depths were obtained by conversion factors relating mass to depth in Prichard et al. (2006).

Table G-1. Weather, fuel moisture, and terrain inputs for fire modeling exercise.

Variable	50th percentile weather	90th percentile weather
1 h moisture %	5.8	3.2
10 h moisture %	7.2	4.6
100 h moisture %	13.3	8.9
1000 h moisture %	14	12
Duff moisture %	60	50
Live Herb moisture %	100	70
Live Wood moisture %	102	75.5
MidFlame Wind Speed (k hr^{-1})	11	13
Slope Steepness (%)	55	55

APPENDIX H. BEFORE-AFTER ANOVA OUTPUTS.

Means, 95% confidence intervals, and two-way ANOVA outputs from assessment of pre-treatment similarity and pre-post change for subset of plots with before-after data are presented in Tables H-1 and H-2.

Table H-1. Means, 95% CIs (in parentheses), and two-way ANOVA test-statistics for pre-treatment comparisons for the subset of stands with before-after data (n=19).

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (*P*)		
	U	M	H	U	M	H	Trt (df=2,13)	Side (df=1,13)	Trt*Side (df=2,13)
Standing dead basal area (m^2 ha^{-1})	104.8 (67.0-164)	88.4 (56.5-138)	146.3 (84.6-253)	54.8 (38.7-77.5)	54.0 (36.6-79.5)	75.8 (43.8-131)	0.203	0.004	0.901
Snags ha^{-1} [>30 cm dbh]	152.1 (99.3-233)	114.3 (74.6-175)	172.1 (102-290)	124.2 (89.2-173)	142.8 (98.7-207)	270.7 (161-457)	0.072	0.360	0.287
Snags ha^{-1} [10-30 cm dbh]	194.2 (89.9-420)	428.4 (198-926)	43.5 (11.5-165)	242.9 (103-681)	246.8 (127-481)	265.0 (146-481)	0.077	0.161	0.061
Snags ha^{-1} [<10 cm dbh]	489.0 (131-1820)	1272 (342-4731)	194.8 (66.9-974)	1276 (461-3530)	1298 (416-4049)	340.2 (68.0-1701)	0.087	0.335	0.707
Dead biomass total (Mg ha^{-1})	859.1 (540-1178)	913.8 (595-1232)	1303 (984-1622)	397.6 (202-593)	308.9 (100-518)	459.2 (234-685)	0.233	0.0002	0.501
Dead biomass aerial (Mg ha^{-1})	816.8 (511-1123)	839.7 (533-1146)	1251 (945-1557)	364.0 (176-552)	282.2 (81.7-483)	444.0 (227-661)	0.184	0.0002	0.523
Dead biomass surface (Mg ha^{-1})	42.3 (6.9-77.7)	74.1 (38.7-110)	51.5 (16.1-86.9)	33.7 (12.0-55.4)	26.6 (3.4-49.8)	15.2 (0.0-40.3)	0.587	0.043	0.439
Fine woody detritus (Mg ha^{-1})	1.2 (0.1-2.3)	2.0 (0.9-3.1)	2.0 (0.9-3.1)	1.9 (1.2-2.6)	1.3 (0.6-2.0)	1.7 (0.9-2.5)	0.852	0.818	0.293
Coarse woody detritus (Mg ha^{-1})	35.1 (3.3-66.9)	60.3 (28.5-92.1)	47.1 (15.3-78.9)	18.4 (0.0-37.9)	17.1 (0.0-37.9)	1.7 (0.0-24.2)	0.590	0.014	0.542
Live biomass total (Mg ha^{-1})	4.3 (1.6-7.0)	5.3 (2.6-8.0)	3.1 (0.4-5.8)	4.2 (2.5-5.9)	3.8 (2.0-5.6)	1.8 (0.0-3.7)	0.306	0.356	0.806
Live biomass surface (Mg ha^{-1})	4.3 (1.6-7.0)	5.3 (2.6-8.0)	3.1 (0.4-5.8)	4.2 (2.5-5.9)	3.8 (2.0-5.6)	1.8 (0.0-3.7)	0.306	0.356	0.806

See text for treatment descriptions. 95% CIs derived from two-way ANOVA outputs.
n= 5, 4, 2 for U, M, H on east side; and 3, 3, 2 for U, M, H on west side.

Table H-2. Means, 95% confidence limits (in parentheses), and two-way ANOVA test-statistics for pre-post change comparisons for the subset of stands with before-after data (n=19).

Stand characteristic	Mesic stands			Drier stands			Two-way ANOVA result (*P*)		
	U	M	H	U	M	H	Trt (df=2,13)	Side (df=1,13)	Trt*Side (df=2,13)
Standing dead basal area (m^2 ha^{-1})	-9.7 (-42.8, 23.4)	-50.1 (-83.2, -17.0)	-154.0 (-195, -113)	3.9 (-21.8, 29.6)	-23.0 (-51.7, 5.7)	-60.0 (-101, -19)	0.0001	0.004	0.077
Snags ha^{-1} [>30 cm dbh]	-16.5 (-40.7, 7.7)	-49.3 (-73.5, -25.1)	-175.1 (-205, -145)	5.0 (-13.8, 23.8)	-45.1 (-66.1, -24.1)	-189.9 (-220, -160)	<0.0001	0.704	0.342
Snags ha^{-1} [10-30 cm dbh]	24.4 (-42.2, 91.0)	-129.8 (-196, -63.2)	-21.8 (-103, 59.8)	21.9 (-29.7, 73.5)	24.5 (-33.2, 82.2)	-161.8 (-243, -80.2)	0.009	0.883	0.002
Snags ha^{-1} [<10 cm dbh]	-254.7 (-1518, 1009)	-1224 (-2488, 40)	-596.9 (-2145, 951)	-443.6 (-1422, 535)	-263.1 (-1357, 831)	-266.4 (-1814, 1281)	0.754	0.468	0.576
Dead biomass total (Mg ha^{-1})	-150.0 (-417, 117)	-558.6 (-825, -292)	-1072.3 (-1399, -746)	12.3 (-194, 219)	-123.3 (-354, 108)	-261.7 (-588, 64.6)	0.0020	0.0006	0.083
Dead biomass aerial (Mg ha^{-1})	-135.9 (-425, 153.5)	-586.4 (-876, -297)	-1246.4 (-1601, -892)	27.5 (-197, 252)	-148.6 (-399, 102)	-374.3 (-729, -19.8)	0.0006	0.0008	0.082
Dead biomass surface (Mg ha^{-1})	-14.1 (-49.3, 21.1)	27.8 (-7.4, 63.0)	174.1 (131, 217)	-15.2 (-42.5, 12.1)	25.3 (-5.2, 55.8)	112.6 (69.5, 156)	<0.0001	0.137	0.212
Fine woody detritus (Mg ha^{-1})	0.3 (-2.4, 2.9)	10.8 (8.2, 13.4)	17.6 (14.4, 20.8)	0.3 (-1.7, 2.4)	3.4 (1.2, 5.7)	9.3 (6.1, 12.5)	<0.0001	0.0002	0.007
Coarse woody detritus (Mg ha^{-1})	-9.5 (-37.8, 18.9)	11.7 (-16.6, 40.0)	124.5 (89.8, 159)	-7.9 (-29.8, 14.0)	17.3 (-7.2, 41.8)	93.5 (58.8, 128)	<0.0001	0.484	0.426
Live biomass total (Mg ha^{-1})	1.4 (-0.3, 3.0)	2.0 (0.3, 3.6)	-1.3 (-3.3, 0.8)	1.9 (0.6, 3.2)	1.5 (0.1, 2.9)	1.0 (-1.0, 3.0)	0.087	0.261	0.297
Live biomass surface (Mg ha^{-1})	1.4 (-0.3, 3.0)	2.0 (0.3, 3.6)	-1.3 (-3.3, 0.8)	1.9 (0.6, 3.2)	1.5 (0.1, 2.9)	1.0 (-1.0, 3.0)	0.087	0.261	0.297

See text for treatment descriptions. 95% CIs derived from two-way ANOVA output.
n= 5, 4, 2 for U, M, H in drier stands; and 3, 3, 2 for U, M, H in mesic stands.

APPENDIX I. TEMPORAL MODEL FOR POSTFIRE WOODY FUEL

To explore the relative contribution to postfire wood dynamics of aerial decomposition, fall rate, and surface decomposition, a simple spreadsheet model was constructed and compared to empirical stand data. A standard single-exponential decay rate was applied separately to standing and down material, of the form

(Eqn. I-1) $Y_t = Y_o e^{-kt}$

(see Harmon et al. 1986 for description of terms). This equation was also applied to a fall/fragmentation rate for the transfer of woody material from standing to surface pools.

The model was initialized with empirical data on standing and down biomass from immediately postfire (using the eastern Biscuit Fire since these are most comparable in a chronosequence with 18-year stands). Then, each year after fire:

- a portion of standing biomass is mineralized according to a specified aerial decomposition rate,
- a portion falls to the surface layer according to a specified fall/fragmentation rate,
- a portion of surface down wood is mineralized at a specified decomposition rate.

The decomposition and fall rates can then be adjusted to explore the sensitivity of fuel quantity and distribution to each of these parameters. The unmanaged scenario, in which all snags are left, can also be compared to logged scenarios. For simplicity, we restricted the logged scenario to high-intensity treatment which felled ~90% of snag basal area and resulted in slash levels just exceeding 100 Mg ha^{-1} (see Chapter 4).

The rates can also be varied to explore which combination(s) of rates produce outputs consistent with empirical fuel data from 3-year and 17-18-year stands (Fig. I-1). We found that the combination of rates resulting in outputs most consistent with empirical data (which indicated reduction of aerial biomass to ~150 Mg ha^{-1} by 18 yr, surface fuel accumulations of ~65-85 Mg ha^{-1} by ~18 year, and no substantial difference in surface fuels between managed and unmanaged stands at ~18 yr) were an aerial decomposition rate of 0.040, a fall rate of 0.027, and a surface decomposition rate of 0.035 (Fig. I-1). These decomposition rates are rapid but within reason for this region (M.E. Harmon, pers. comm.). The fall rate is fairly slow (M.E. Harmon, pers. comm.). Note that for the outputs to match the data, it appears necessary that the aerial decomposition rate exceeds the surface rate. It is worth emphasizing that this is an exploratory exercise, not conclusive. Wood decomposition and fall rates have not been well quantified in this region, and stochastic events such as windstorms are not considered. Nevertheless, this exercise, as well as FIA data from this region (see Chapter 4, Hudiburg et al. in press), suggest relatively rapid decomposition in the Siskiyou Mountains.

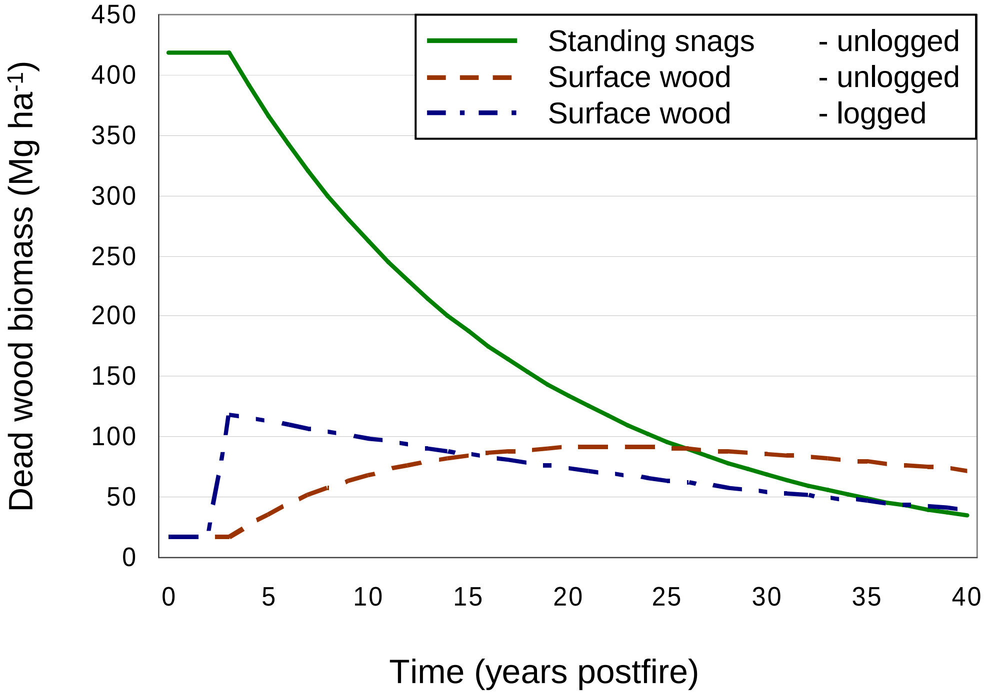

Figure I-1. Modeled residual dead wood mass as a function of time since fire, using decay rates of 0.040 and 0.035 for standing and down material, respectively, and a fall rate of 0.027. The 'surface wood – logged' curve is based on ~90% basal area cut and resulting generation of slash based on empirical postlogging measurements. These curves represent one possible dynamic based on these rates and on assumption of steady rates (i.e., stochastic events are not considered). In this example, quantities of standing and surface wood at 3 years and 18 years match empirical field-measured quantities.