AN ABSTRACT OF THE DISSERTATION OF

Lori J. Kayes for the degree of Doctor of Philosophy in Forest Science presented on December 12, 2008.

Title: Early-Successional Vegetation Dynamics and Microsite Preferences following Post-fire Forest Restoration in Southwestern Oregon

Abstract approved:

Klaus J. Puettmann Paul D. Anderson

Reforestation-based restoration of severely burnt plantations is one of the primary management activities following wildfire on U.S. federal lands. Restoration effects on early-seral plant and cryptogam communities have not been documented. The objectives of this study were, in severely burnt plantations two to four years post-fire, to examine the: (1) temporal patterns of succession within and among structural layers and influence of site conditions on these patterns, (2) effects of restoration treatments on composition and succession of early-seral vegetation, including terrestrial cryptogams, on moderate and harsh aspects, and (3) the role of microsites and bryophytes in germination and establishment of vascular plants.

Structural layers established rapidly after wildfire in plantations following an initial floristics model of succession. Succession within and among structural layers occurred simultaneously but at different rates and with different drivers. Successional starting points differed based on fire severity, site history, species life history traits, topography and pre-disturbance plant community. Multiple successional trajectories were evident in severely burnt plantations based on varying initial species compositions.

Restoration treatments, characterized by conifer planting and removal of woody shrubs, altered plant community composition and succession. Cover of bryophytes and shrubs initially decreased in areas with vegetation removal compared to areas without vegetation removal but bryophyte cover recovered over time. Exotic and annual herb cover increased with vegetation removal on harsh aspects by year four post-fire compared to areas without vegetation removal. Effects of vegetation removal on trait group cover were more pronounced on harsh aspects for groups with mostly herbs and on moderate aspects for groups with mostly shrubs and bryophyte communities.

Microsites were heterogeneous following wildfire and restoration. Early-seral bryophytes preferentially occupy microsites with undisturbed soil and lower litter and overstory cover. Growth, but not germination, of early-seral vascular plants was lower on burnt bryophyte seedbeds than other seedbeds. Growth and germination of some conifers were higher on unburnt bryophyte seedbeds than other seedbeds.

Results suggest that restoration activities shortly after fire had minimal effects on early vegetation cover, but altered early-seral vegetation composition and successional trajectories. Furthermore, early-seral bryophytes played a critical role in succession and establishment of other vegetation.

Early-Successional Vegetation Dynamics and Microsite Preferences following Post-fire Forest Restoration in Southwestern Oregon

by
Lori J. Kayes

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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.

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Lori J. Kayes, Author

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CONTRIBUTION OF AUTHORS

Paul Anderson and Klaus Puettmann assisted in the study design, implementation, analysis, writing, and interpretation of Chapters 2, 3 and 4.

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DEDICATION

To Chase, this thesis is as much his as mine. And to Maxwell, for being the best baby in the world and letting me write while watching him grow.

Early-Successional Vegetation Dynamics and Microsite Preferences following Post-fire Forest Restoration in Southwestern Oregon

CHAPTER 1 - INTRODUCTION

Disturbances, which range in periodicity and severity, cause major changes in ecosystem structure and function. Periodic fire characterizes the majority of the ecosystems in the Pacific Northwest and is one of the dominant natural processes shaping vegetation heterogeneity of forests. In the last 100 years, the wide array of historic fire regimes has been altered by fire suppression and forest management activities. The resulting accumulation of fuels may contribute to an increased occurrence of large-scale, high-severity fires (Agee and Skinner 2005; Jain and Graham 2007). Although high-severity fires may be natural in some areas, frequent mixed-severity fires are typical of the Klamath Mountains and have been an integral process in the development of late-seral forests of that region (Taylor and Skinner 1998). Due to management practices, a significant proportion of western forests are currently in plantation forests. Plantation forests are typically dense with few conifer species resulting in high fuel loads and an associated high fire severity during wildfires (Odion et al. 2004; Thompson et al. 2007). Recovery of burnt plantations concerns managers, scientists, and the general public due to the areal extent and severity of recent fires.

Hastening the development of late-successional forest characteristics has been of interest in the Pacific Northwest for some time and drove the implementation of the Northwest Forest Plan (FEMAT 1993; USDA 1994). A large body of research has been directed towards using silviculture treatments to enhance development of late-seral vegetation characteristics (e.g. Cissel et al. 1999; Garman et al. 2003; Davis and Puettmann 2009). Many species depend on late-seral habitat and quantity of this habitat is currently in decline in the Pacific Northwest due to replacement by plantation or early-seral forests (Bolsinger and Waddell 1993; DellaSala and Strittholt 2000). When large wildfires occur in areas set aside to provide late-seral characteristics, such as Late Successional Reserves (LSRs: FEMAT 1993; USDA 1994) and wilderness areas, the management priority for these areas is often the maintenance or development of late-seral characteristics. Many LSRs have large acreage of plantation forests within their boundaries. These areas are prime targets for reforestation-based restoration following wildfire.

Post-fire restoration aimed at regeneration of conifers and specific structural goals following high-severity wildfire in plantations must address challenges including: (1) competition from sprouting vegetation, (2) lack of conifer seed sources due to high severity fire (but see Keeton and Franklin 2005) and (3) harsh regeneration sites (Walstad et al. 1987; Hobbs et al. 1992). Conifer establishment and canopy closure are steps in the development of late successional forest and a common focus of restoration in early successional stages. Difficulty in establishing conifers following timber harvest and fire is well documented in southwestern Oregon (Hobbs et al. 1992). Many hardwood shrubs and trees in this region sprout vigorously or produce abundant seedlings from a fire stimulated seedbank following disturbance. Competition from these species and other vegetation can severely limit growth and survival of natural or planted conifer seedlings (Hobbs et al. 1992; but see Lopez-Ortiz 2007). Additionally, southwestern Oregon has extreme environmental gradients, including differences in aspect that contribute to differing plant community compositions (Whittaker 1960) and conifer establishment potentials (Hobbs et al. 1992; USDI 2003), with some aspects being particularly difficult for conifer regeneration.

In addition to causing conifer mortality, high severity fire resets succession of native plant communities to an early-successional state. Although there has been a long-term focus on late-successional forest development, more recent concerns have arisen over the status and functions of early-seral vegetation. Early-seral vegetation plays a key ecological role and is a major source of diversity following fire in mixed conifer forests. Concern over forest restoration in early-seral states stems from the propensity of early-seral environments to become overrun by non-native and invasive species, which can alter ecosystem function and eliminate native species (D'Antonio and Vitousek 1992). Plantation susceptibility to post-fire invasion may be relatively high due to low species diversity prior to burning (Schoonmaker and McKee 1988). Additionally, roles of early-seral species in secondary succession are not well understood. Documented functions of early-seral species include erosion control (Beyers 2004), replenishment of soil organic matter, nitrogen fixation (Chapin et al. 1994), provision of wildlife habitat (Saab et al. 2005) and facilitation of late-seral species germination and growth (Chapin et al. 1994). Furthermore, interactions among and influences of early-seral species, such as competition or facilitation, may be vital to ecosystem function and recovery following wildfire and may vary at different scales.

Chapter two addressed vegetation establishment and successional dynamics in burnt plantations. A large body of research exists on successional processes in unmanaged forests but the effects of disturbance and resulting successional processes in managed landscapes result from an interaction of natural disturbances and pre- and post disturbance management activities (Penman et al. 2008). Plantation management resulting in landscape variation in fire severity and vegetation communities can alter post-fire successional dynamics relative to unmanaged landscapes (Weatherspoon and Skinner 1995; Thompson et al. 2007). Chapter two focused on conditions with little or no restoration activity to gain a picture of vegetation establishment in severely burnt plantations in the absence of management activities. The main objective addressed in chapter two was to improve our understanding of vegetation succession two to four years following wildfire in severely burnt plantations in southwestern Oregon. Specific objectives were to: (1) describe general temporal patterns of species richness and cover; (2) examine the relative importance of relay versus initial floristics (sensu Egler 1954) in defining patterns of succession within and among structural layers; and (3) discern the influence of stand scale (e.g. 0.2 to 5 ha) site conditions on these patterns.

Chapter three addressed the effects of post-fire restoration treatments on early-seral vegetation. To facilitate a return to conifer-dominated and/or late-successional forest following fire, artificial regeneration (tree planting) and vegetation control of sprouting species are typically implemented. In addition to traditional forest management, artificial regeneration may also be used to facilitate restoration of late-seral conditions through accelerating conifer reestablishment that can create overstory stand structure typically found in late successional forests. However, typical high conifer densities associated with plantations are not conducive to the development of understory structure that is associated with late-successional forests (Bailey and Tappeiner 1998). When restoration to late-successional forest is the management goal, mixed species plantings that incorporate the range of native conifers that existed in unmanaged forests are used in an attempt to restore the natural diversity of forests. Single-entry manual control of shrubs has been demonstrated to be ineffective at limiting shrub growth for any length of time due to sprouting capacity of most shrubs in southwestern Oregon (Hobbs et al. 1992). However, restrictions on herbicide use on federal land coupled with the desire to ensure conifer establishment, make manual shrub control the predominant method of vegetation control on federal land. Using manual shrub control for enhancing conifer survival and early growth may provide enough advantage for conifers to gain dominance over sprouting shrubs (Wagner 2000). However, poor documentation exists for the effects of mixed species plantings or vegetation control on natural vegetation, successional processes and species interactions, particularly at early-seral stages. The objective of this study was to evaluate effects of restoration treatments on early-seral vegetation composition and succession in severely burnt plantations two to four years following wildfire. Specifically, the effects of vegetation removal and conifer planting on temporal dynamics of plant communities, structural layers, terrestrial cryptogams, and trait groups on two different site qualities, reflected by roughly eastern (moderate) and western (harsh) aspects were examined.

Chapter four addressed the relationships between early-seral bryophytes and germination and growth of conifer and early-seral vascular plants to determine effects of species interactions and microsite conditions on vegetation structure and composition. In the presence of a seed supply, microsites (i.e. micro-habitats immediately surrounding a seedling sensu Helms 1998) can determine site suitability for germination and establishment of different species and thus influence succession. During secondary succession, biotic factors interact with abiotic factors to determine microsite suitability. Early-seral bryophytes are the dominant vegetation layer immediately following fire and thus can impact microsite quality. Fire legacies and management activities following fire can also alter microsite conditions. The objectives of chapter four were to: (1) describe the distribution and characteristics of microsites following fire and restoration activities (e.g. vegetation removal and conifer planting), (2) determine if early-seral bryophytes preferentially inhabit specific microsites, (3) describe distinctive microsite characteristics of early-seral bryophyte habitat if such microsites exist and (4) compare germination and establishment of early-seral vascular plants and conifers between bryophyte and bare soil seedbeds. Examination of these objectives was accomplished at a fine scale (e.g. < 2 m^2), through a multi-faceted approach that included an observational study, a controlled greenhouse experiment and a field seeding trial in an attempt to separate effects of bryophyte from the effects of microsites that bryophyte inhabit on germination and establishment of vascular plants.

This study is part of a larger project, the Timbered Rock Reforestation, Stand Development and Fuels Study, which will determine if there are combinations of silviculture treatments that can maintain and develop late-seral vegetation characteristics from stand initiation. The study will continue through canopy closure and stem exclusion stages of development, allowing an evaluation of how planned elements of late-seral forests are initiated and maintained.

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CHAPTER 2 – VEGETATION SUCCESSION WITHIN AND AMONG STRUCTURAL LAYERS FOLLOWING WILDFIRE IN MANAGED FORESTS

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ABSTRACT

Question: How does early vegetation develop following severe wildfire in managed forests?

Location: Southwestern Oregon, USA

Methods: In severely burnt plantations, dynamics of (1) shrub, herbaceous and cryptogam richness and (2) cover; and (3) topographic, overstory and site influences were characterized on two contrasting aspects two to four years post fire. Analysis of variance was used to examine change in structural layer richness and cover over time. Nonmetric multidimensional scaling, multi-response permutation procedure and indicator species analysis were used to evaluate changes in community composition over time.

Results: Vegetation established rapidly following wildfire in burnt plantations following an initial floristics model of succession. Succession occurred simultaneously within and among structural layers following wildfire but at different rates and with different drivers. Stochastic (fire severity and site history) and deterministic (species life history traits, topography and pre-disturbance plant community) factors determined starting points of succession. Multiple successional trajectories were evident in early succession.

Conclusions: Mixed conifer forests are resilient to interacting effects of natural and human-caused disturbances. Predicting the development of vegetation communities following disturbances requires an understanding of the various successional components, such as succession among and within structural layers. Succession among and within structural layers can follow different trajectories, occur at different rates and are affected by multiple interacting factors.

Keywords: Succession, initial floristics, relay floristics, fire severity, plant community, early-seral, managed forests, cryptogams, bryophytes, aspect

Nomenclature: USDA (2007).

Abbreviations: BA = basal area; dbh = diameter at breast height; ha = hectare; ISA = indicator species analysis; MRPP = multi-response permutation procedure; NMS = nonmetric multidimensional scaling; tph = trees per hectare

INTRODUCTION

Disturbance is a major driver in structuring vegetation heterogeneity and plant communities (Heinselman 1981; Pickett and White 1985; Naveh 1994). Many ecosystems are resilient to natural disturbances and recover rapidly with abundant early-seral and residual vegetation (Agee 1993; Naveh 1994; DeBano et al. 1998). Succession, directional change in vegetation over time, is reinitiated by catastrophic disturbances and varies among ecosystems and disturbance events. Due to many potential drivers and influences of stochastic events, multiple trajectories of succession are possible following disturbance (Connell and Slayter 1977; Franklin and Hemstrom 1981; Noble and Slatyer 1981; Naveh 1994). Documentation of vegetation dynamics within the first five years of disturbance can provide insights into long-term successional trajectories, particularly in an initial floristics scenario (Egler 1954).

While significant ecological research has focused on successional dynamics in unmanaged forests, the effects of disturbance in managed landscapes are derived from an interaction of natural disturbances and management activities (Penman et al. 2008). For example, in southwest Oregon, large portions of the forested landscape have been harvested and reforested into dense conifer plantations. This type of management alters fire severity due to its creation of high fuel loads, low branches and continuous fuel arrangement compared to uncut or partially cut forests (Weatherspoon and Skinner 1995; Thompson et al. 2007) and has been hypothesized to increase susceptibility to fire (Franklin and Hemstrom 1981). In addition to altered fuels, dense overstory cover associated with plantations in the stem exclusion phase (e.g. Oliver and Larson 1996) may lead to reductions in understory abundance and diversity (Schoonmaker and McKee 1988; Halpern 1989; Spies 1991; Naveh 1994; Bailey et al. 1998). Plantation management resulting in landscape variation in fire severity and vegetation communities can alter post-fire successional dynamics relative to natural forests (Stuart et al. 1993; Weatherspoon and Skinner 1995; Thompson et al. 2007).

Forest succession is generally associated with changes in forest structure with progressively larger plants dominating over time. Succession has typically been described as having four stages of structural layer (i.e. vegetation strata occupying different vertical positions in the forest) dominance in forested ecosystems worldwide: (1) bryoid layer, (2) herb, (3) shrub and (4) tree (Cremer and Mount 1965; Dyrness 1973; Chapin et al. 1994; Tatoni and Roche 1994; Trabaud 1994). Secondary succession, i.e. where legacies of the previous community survive, generally follows a model of initial floristics (Egler 1954) in which most species are present in early-seral stages and subsequent successional dynamics are defined by changes in the abundances of different species (Foster 1985; Halpern 1989; Naveh 1994; Debussche et al. 1996). Under an initial floristics model in southwestern Oregon, high diversity across all structural layers would be expected early in succession with changes in structural layer dominance over time. In contrast, primary succession, i.e. on a barren landscape, often follows a relay floristics model (Egler 1954) characterized by vegetation cohorts replacing one another over time due to the creation of more hospitable habitat and changes in propagule availability (Chapin et al. 1994; Titus and del Moral 1998; Chapin et al. 2002). Under the relay floristics model in southwestern Oregon, increasing diversity in upper structural layers and decreasing diversity in lower structural layers would be expected to precede changes in structural layer dominance. Due to an assumed depauperate pre-fire herbaceous community and high fire severity that potentially killed locally abundant sprouting shrubs, it was hypothesized that, within severely burnt plantations, vegetation development would demonstrate a relay floristics model of succession occurring among structural layers.

In addition to succession among structural layers, succession within structural layers occurs simultaneously. Overstory succession is well documented in many ecosystems (Heinselman 1981; Uhl et al. 1981; Foster 1985) and differences in herbaceous and shrub vegetation have been documented in forest developmental stages (Spies 1991; Trabaud 1994). Successional development of the bryoid layer has also been observed following fire (Cremer and Mount 1965; DeGrandpre et al. 1993; de las Heras et al. 1994). It was hypothesized that simultaneous succession among and within structural layers would occur with transitions in dominance from ruderal to stress-tolerating species within each structural layer (sensu Grime 2001).

Differences in environmental conditions associated with aspect contribute to differing plant community compositions in Mediterranean ecosystems (Whittaker 1960; Kadmon and Harari-Kremer 1999; Guo 2001) and to variation in fire intensities and severities (Beaty and Taylor 2001; Mermoz et al. 2005). Given similar pre-fire conditions and management histories, it was hypothesized that plantations on a given aspect in the stem exclusion phase (e.g. Oliver and Larson 1996) would have similar plant communities and successional patterns following fire but plant communities and successional patterns would differ on contrasting aspects.

The main objective of this study was to improve understanding of vegetation succession two to four years following wildfire in severely burnt plantations in southwestern Oregon. Specific objectives were to: (1) describe general temporal patterns of species richness and cover; (2) examine the relative importance of relay versus initial floristics in defining patterns of succession within and among structural layers; and (3) to discern the influence of site conditions on these patterns.

METHODS

Study Area

The Timbered Rock fire occurred within the Western Cascades physiographic province, near the intersection of the Klamath and Cascade Mountains, in mixed conifer forest primarily within the *Abies concolor* and mixed conifer forest zones (Franklin and Dyrness 1973). Southwestern Oregon has a mixed severity fire regime with fires burning every 5 to 75 years (Agee 1993). Warm, dry summers and mild, wet winters characterize the regional climate. Within the study area, 89 - 152 cm of annual precipitation falls primarily between October and May. Average summer high temperatures range from 24° C to 30° C, with daily highs reaching over 38° C. Average winter high temperatures range from 8° C to 12° C and low temperatures range from -1° C to -2° C (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?orpros for Prospect, OR).

The 2002 wildfire burnt with varying intensity and severity 11,000 hectares (ha) between July 13th to August 9th. Approximately 40% of the burned area was occupied by *P. menziesii* plantations less than 35 years of age. The study was conducted within five *P. menziesii* plantations (blocks) in three different watersheds that originated 15 to 40 years prior to fire with an average of 283 *P. menziesii* trees per hectare (tph). Prior to fire, plantations included a significant hardwood component (combined average 500 tph) comprised of *Arbutus menziesii*, *Acer macrophyllum*, *Quercus chrysolepis* and *Chrysolepis chrysophylla* and low densities (combined average 45 tph) of other conifers including *Abies concolor*, *Pinus ponderosa*, *Pinus lambertiana*, and *Calocedrus decurrens.* Study area topography is steep (slopes >20%) with volcanic bedrocks and elevations between 800 m and 1000 m.

Study Design

Within the Timbered Rock fire perimeter, blocks were selected one year post fire for moderate to high fire severity (based on Bureau of Land Management fire severity maps derived from Landsat 7 satellite imagery of burned areas), sufficient plantation size for study implementation and lack of other planned restoration activities (USDI 2003). Full descriptions of blocks are given in Table 2.A1 (App. 2.A). Within each block in the second year after the fire, four experimental plots were established on one generally uniform aspect (large sub-block) and two experimental plots were established on a contrasting aspect (small sub-block). Plots were square with a slope corrected treatment area of 0.25 ha and an internal sampling area of 0.2 ha. Treatments were randomly assigned to experimental plots within each sub-block. Treatments on the large sub-block included: Control - unplanted without vegetation removal; Low-density NVR - planted at 470 tph without vegetation removal; High-density NVR - planted at 1075 tph without vegetation removal; and High-density VR - planted at 1075 tph with vegetation removal. Treatments repeated on the small sub-block included: High-density NVR and High-density VR. Contrasting sub-block aspects were designated as relatively “harsh” and “moderate” based on azimuth; harsh aspects ranged from 220^{o} to 360^{o} and moderate aspects ranged from 44^{o} to 160^{o}. Due to the influence of high summer temperatures and drought, aspect has been demonstrated to be a suitable criterion for characterizing site challenge to conifer regeneration in southwestern Oregon (Hobbs et al. 1992). Aspect assignment of the sub-blocks was constrained by available area. Therefore, one block had the large sub-block on the moderate aspect whereas the other four blocks had the large sub-block on the harsh aspect.

Plots were planted with 40% *P. menziesii* and 20% each of *P. lambertiana*, *P. ponderosa* and *C. decurrens*. Vegetation removal consisted of manual cutting of tall vegetation focused on woody shrub stems in years two through four post-fire over the entire treatment plot and scraping away all vegetation to mineral soil (scalping) in an approximate 0.75 m radius around planted conifer seedlings in year three post-fire. A single work crew implemented conifer planting and vegetation removal. One High-density NVR plot on the harsh aspect was accidentally scalped.

Data Collection

Within each plot, slope (%), aspect (º, corrected for declination) and basal area (BA: m^2/ha) of live and dead standing trees (> 5 cm diameter at breast height (dbh)) by species were measured. Aspect was converted to a heat load index (McCune and Grace 2002, pg. 24). Percent dead BA has been demonstrated to be a good measure of fire severity (Halofsky 2007) and was used here as such with low severity having lower percentage of BA mortality. Additional data were retrieved from United States Department of Interior, Bureau of Land Management records (plantation age at time of burn) or derived from Geographical Information System layers (watershed, elevation and distance from plot center to nearest edge of unburnt forest ($\geq$ 0.16 ha) and downhill stream (1^{st} to 4^{th} order)).

Vascular plant percent cover data were collected three summers, years two through four post-fire, by a four to seven person crew with one crew member providing consistency across all years. Within each plot, four permanently marked 0.01 ha square quads (randomly dispersed with the restriction that each fit within one quadrant of the 0.2 ha sample plot) were used to measure tall ($\geq$1.3 m) shrubs and small hardwood trees ($\leq$ 5 cm dbh), collectively referred to as tall shrubs. Tall shrub percent cover for individual shrubs was measured as the canopy area (width x length: cm^2) per quad area (cm^2) * 100, summed by species over the quad. Total tall shrub cover/quad was calculated as the sum of all individual tall shrub covers minus visually estimated overlap between neighboring tall shrubs. All other vascular plant species, including shrubs and hardwood trees < 1.3 m (low shrubs), were measured by ocular estimation of percent cover to the nearest one percent in four 3 m x3 m (0.009 ha) square subplots, one at each quad corner (a total of 16 subplots/plot). Total percent cover (maximum cover =100%) was estimated for low shrubs, forbs, ferns, grasses and combined herbaceous species in subplots. Natural germinants of tree species were counted in a 1 m x10 m transect on the upslope side of each quad and converted to seedling density/ha.

Non-vascular plant cover data were collected in the summers in years three and four post fire in a 0.5 m x10 m strip transect on the upslope side of each quad in 20 contiguous 0.5 m x 0.5 m subplots by one observer. Percent cover by class (adapted from Forest Inventory Analysis lichen protocol (McCune et al. 1997)) was estimated for individual species (except fungi) and bryophytes, liverworts, lichens and fungi across taxa. Approximately log-scaled cover classes were coded as follows: (1) <3 individuals present, (2) 4 -10 individuals present, (3) > 10 individuals but < 25% cover, (4) 26-50% cover, (5) 51-80% cover, and (6) 81-100% cover. On this scale, the average value approximates average log (abundance) and is not transformable to an arithmetic scale. Vascular plants and cryptogams were determined to the species level when possible, otherwise to the genus level or rough life form group. Fungi were not identified. Due to the difficulty of identifying extremely small or immature samples, several species were lumped into species groups for the final analysis (App. 2.A, Table 2.A2).

To examine correlations between species traits and community patterns, trait groups were defined based on USDA (2006; 2007), Hickman (1993), Spies (1991) and Wang and Kemball (2005). Categories of trait groups for vascular plants included disturbance response (invaders – highly dispersive pioneer species; avoiders – late successional, slow colonizing species; evaders – seed-banking species; or endurers - sprouting species) as defined by Rowe (1983); growth form (annual forbs, perennial forbs, annual graminoids, perennial graminoids, ferns, sub-shrubs, evergreen shrubs, deciduous shrubs or conifers); seral stage (early or late); weediness (not weedy, weedy native or weedy exotic); origin (native or exotic) and nitrogen fixing capacity (nitrogen fixer). For bryophytes, trait group categories, including disturbance response (invading or residual) and longevity (short or long-lived) were identified based on Lawton (1971), Vitt (1988) and personal experience. See Appendix B for full list of species and traits. For this study's purposes, a trait group was a set of species that have similar biological characteristics, occupy comparable niches in ecosystems and respond in similar way to environmental factors. "Trait" group was used rather than "functional" group because the specific ecosystem functions of trait groups are currently broad or unknown.

Data Analysis

Analysis of variance (ANOVA) of cover and richness of different structural layers, indicator species analysis (ISA), multi-response permutation procedure (MRPP) and correlations of species and traits from nonmetric multidimensional scaling (NMS) were used to examine the general patterns of species richness and cover and succession among and within structural layers in burnt plantations on contrasting aspects. Correlations of environmental factors with NMS gradients and MRPP were used to examine the factors related to gradients in species composition and the effects of site conditions in influencing successional patterns. For all analysis, data were aggregated at the plot level and tall shrubs and low shrubs of the same species were analyzed separately.

Mixed model ANOVA for a randomized complete block was performed using PROC MIXED, SAS v. 9.1 with block as a random effect and each plot as a replicate observational unit repeated across years. Aspect was modeled as a split-plot factor due to restriction of plot location. The model was fitted individually for 14 response variables: cover and richness of all herbaceous species, forbs, ferns, graminoids and bryophytes; total vascular plant and shrub richness; and tall shrub and low shrub cover. Cover and richness of lichens, liverworts and fungi were not examined due to few observations. Due to the study layout, data were partitioned into two sets for analysis. First, a two-way factorial by year including High-density

NVR and High-density VR treatments from large and small sub-blocks was used to look at the effects of aspect on successional patterns while controlling for planting density with vegetation removal (NVR/VR), aspect (harsh/moderate) and year (three years for vascular plants and two years for cryptogams) as explanatory variables. Within the two-way factorial, results were reported for treatments without vegetation removal only using multiple comparisons. Second, due to a lack of interaction between aspect and year (except for low shrubs) and a lack of effect of planted conifers on vegetation (data not shown), all treatments without vegetation removal on both aspects were used to examine successional patterns following fire with aspect (harsh/moderate) and year (three years for vascular plants and two years for cryptogams) as explanatory variables. To determine the most appropriate repeated measures covariance structure for each response variable, the models were fitted with eight different covariance structures (compound symmetry, unstructured order 1-3, autoregressive order 1 and toeplitz order 1-3). If the model assumptions were met, the covariance structure with the lowest corrected Akaike's Information Criterion (AICc) value was selected as the most appropriate, unless covariance structures had ΔAICc < 2, then the covariance structure with the least number of parameters was selected.

The assumptions that errors were normally distributed and variation among replicates was the same for all treatments at one point in time but may vary between time periods were assessed for all models and covariance structures using PROC UNIVARIATE and plots of residual versus predicted and residual versus normal percentile. If assumptions were not met, they were reassessed after log transformation of the response variable and, if still not met, the covariance structure was not considered. Log transformed variables (graminoid and fern cover) were backtransformed prior to reporting results. For all models and selected covariance structures, residuals were symmetric and assumptions of normality and constant variance of residuals were adequately met. Removal of blocks with accidentally scalped plots and treatments on opposing aspects did not alter the results so blocks were retained with the exception of the scalped plot (High-density NVR on harsh aspect) from year three and four, which was removed from analysis due to this plot altering the results. To investigate differences between years and aspects, multiple comparisons were adjusted with the Tukey Honestly Significant Difference (1949) adjustment for pairwise comparisons of all treatment means.

To examine successional trajectories and the role of site conditions in influencing community patterns, multivariate analysis on data from treatments without vegetation removal was done using PC-ORD 5.1 (McCune and Mefford 2005). Vascular plants and cryptogams were analyzed separately because there were no year two crytogam data, the cover measures were continuous for vascular plants in contrast to categorical for cryptogams, and to allow comparisons between groups, which have been demonstrated to respond differently to gradients and follow different successional patterns (McCune and Antos 1981). Sørenson distance was used in the data analysis, unless specified, because it works well for community data even with high beta diversity (McCune and Grace 2002).

NMS was used to examine plant community composition and multivariate relationships within treatments, while avoiding assumptions of linearity among community variables (McCune and Grace 2002). NMS was performed using the PC-ORD autopilot mode on the "slow-and-thorough" setting with random starting configurations, a maximum of 500 iterations and 250 runs of real data. The coefficient of determination (R^2) is the proportion of variance in Sørenson distance from the original matrix that was represented by Euclidean distance in the ordination. Joint plots were used to represent the linear correlations between ordination scores and environmental variables (slope, heat load index, % dead BA, % live BA, harvest year, distance to unburnt forest, distance to stream and elevation); richness and cover of structural layers; and trait groups. Indicators for years, aspects, blocks and watersheds were overlain on the ordination to examine differences in groups. To examine change in plant communities over time, remeasured plots were connected by successional vectors. The relative length and direction of successional change for each plot were examined using the same ordination by translating the tail of each successional vector to the origin (McCune and Grace 2002; McCune and Mefford 2005).

MRPP (Mielke 1984), a non-parametric method for testing group differences, was used to compare watersheds, blocks, aspects and year for both communities. MRPP generates an A statistic, the chance-corrected within-group agreement indicative of within group homogeneity, and the probability of the observed differences being greater than differences due to chance. Blocked MRPP (MRBP) with Euclidean distance, which requires balanced data, was used to compare aspects in individual years. Plots were median aligned to zero within blocks to focus on the within block differences. ISA (Dufrêne and Legendre 1973) was used to determine which species were characteristic of specific blocks, aspects and years. The resulting indicator value (IV) was compared to results from 1000 randomizations of data using a Monte Carlo test.

For multivariate analysis, species cover per plot was relativized by species maximum in order to standardize for different measures of cover and large variation in magnitudes of cover between different species. Species that occurred in less than 5% of the plots (63 vascular and 20 cryptogam species) were deleted to reduce the noise in the data set. In the vascular plant community, two treatments (one Control and one Low-density NVR) were labeled as outliers based on outlier analysis using Sørenson distance but their removal did not result in significant improvement and thus outliers were retained.

RESULTS

Two hundred twenty-two taxa were observed across all treatments, including five conifers, 33 woody shrubs and hardwood trees, 134 herbaceous species (six ferns, 20 graminoids and 108 forbs) and 50 non-vascular taxa (35 bryophytes, eight liverworts and six lichens). Thirty-two vascular plants were exotic species (two shrubs, four graminoids and 26 forbs).

Three axis solutions best represented the structure of the vascular plant community (final stress = 16.49, final instability = 0.00, number of iterations=163) and cryptogam community (final stress = 13.75, final instability = 0.00, number of iterations=101) in NMS (Fig. 2.1). For both communities, a Monte Carlo test using 250 runs of randomized data indicated that the final stress was less than expected by chance ($p=0.004$ for all axes). The vascular plant ordination was not rotated because fire severity (indicated by % live basal area) was already aligned with axis 1 but the cryptogam community was rotated to maximize fire severity (e.g. % live basal area) on axis 1 for comparison. Gradients in species composition were related most strongly to (1) heat load index, (2) time since fire and (3) fire severity for the vascular plant community and (1) fire severity, (2) heat load index and (3) time since fire for the cryptogam community, in order from most to least variation explained.

Succession among Structural Layers

Succession among structural layers followed a pattern of dominance shifting from low to progressively taller structural layers (Fig. 2. 2 and 2.3). Vegetation cover increased over time quickly following wildfire in all structural layers. The average total species richness per plot peaked in the third year post-fire due largely to increases in forb and graminoid richness per plot and declined in year four due to decreased forb species richness per plot (Fig. 2.2a). High bryophyte cover occurred under the herbaceous layer throughout the study (Fig. 2.3) even though bryophyte cover decreased in the fourth year. Bryophyte richness per plot increased from the third to the fourth year (Fig. 2.2a). Average cover of forbs and the herbaceous layer increased from the second to the third year and dropped off in the fourth year following fire (Fig. 2.2b). Average cover of tall shrubs, low shrubs and graminoids increased over the three years with the largest increase in low shrub cover from year two to three and in tall shrub and graminoid cover from year three to four. Average low shrub cover had surpassed herb cover by the fourth year on moderate aspects and combined tall and low shrub cover (non-accounting for tall/low shrub overlap) was higher than herb cover on harsh aspects. No change over time in shrub richness per plot was evident. Shrub cover was directly related to pre-fire shrub and hardwood tree cover due to post-fire regeneration mode of sprouting (30 species) or soil seed banking (3 species) for all shrubs. No invading shrub species (dependent on seed dispersal for colonization) were documented.

Succession within Structural Layers

Plant community composition changed over time for both cryptogams and vascular plants (Fig. 2.1). For both communities, composition differed by year based on MRPP but with small within group homogeneity (Table 2.1). Succession within the herbaceous layer from early seral to later successional species was occurring by the fourth year as evidence by NMS correlations and indicator species analysis (Table 2.2). For the vascular plant community, indicators for year two were early-seral species that decreased through time, *Collomia heterophylla* and *Montia diffusa*. Traits associated with early-seral environments (invaders, annuals and herbaceous species) were indicators for year three. Enduring herbs, low shrubs and graminoids were correlated with year four (Fig. 2.A1, App. 2.A) and traits (perennial forbs, graminoids and shrubs) and species (*Iris chrysophylla, Ceanothus integerrimus* and *Whipplea modesta*) associated with later-seral environments were indicators for year four (Table 2.2 and 2.3). Succession was also occurring within the cryptogam layer, based on short-lived invading species (*Didymodon vinealis* and *Funaria hygrometrica*) that were indicator species for year three (Table 2.2). Meanwhile, longer-lived colonizers, *Bryum capillare* (also a year four indicator species), *Bryum argenteum* and *Ceratodon purpureus* were correlated with longer time since fire. Several previously unobserved bryophyte species associated with older forest floors (Vitt et al. 1988) occurred in the fourth year with very low cover, including *Hypnum subimponens*, *Eurhynchium oreganum* and *Leucolepis acanthoneuron*.

Successional trajectories (directional shift) of vascular plant communities were similar in all plots over time except for those dominated by *Ceanothus integerrimus* (Fig. 2.4). The divergent vascular plant trajectories occurred where cover of *C. integerrimus* was the highest (49 and 88% cover). The magnitude of successional change was larger from year two to year three and from year two to year four than from year 3 to year 4 for the vascular plant communities (Fig. 2.1). While most cryptogam communities were moving in the same general direction (correlated with year) over time, several divergent cryptogam trajectories occurred, more than for vascular plant communities (Fig. 2.4).

Role of Site Conditions

Site conditions were important in influencing plant community composition within burnt plantations for the vascular plant community but were less important for the cryptogam community (Fig. 2.1) as indicated by larger differences among blocks than within blocks and among watersheds than within watersheds regardless of time since fire. Differences among blocks and watersheds were corroborated by MRPP. The highest within group homogeneities were for block (Table 2.1: vascular: A=0.14, cryptogam: A=0.15). ISA also detected many indicator species for blocks (Table 2.4, App. C). Differences in communities from different blocks resulted from plant community responses to variability in fire severity and topography, aspects and species life history traits.

Vascular plant community composition in areas with relatively low fire severity (indicated by % live BA) was correlated with high elevation and plantation age at time of burn and in areas with higher fire severities was correlated with high total basal area and steeper slopes (Fig. 2.1). Cryptogam community composition in areas with high fire severity was also correlated with steeper slopes (Fig. 2.A1, App. 2.A). Sprouting residual species (including *Acer circinatum*, *Rubus leucodermis*, *Mahonia nervosa* and *Polystichum munitum*) dominated higher severity sites while invading species (*Collomia heterophylla*) dominated lower severity sites. In the cryptogam community, lower fire severity was correlated with liverwort, lichen and fungi cover (Fig. 2.A1, App. 2.A) and several bryophyte species/groups (*Aulacomnium androgynum*, *Fissidens* sp., *Homalothecium* group and *Weissia* group).

Aspect and heat load index influenced plant community composition although not as strongly as expected. Moderate aspects grouped near the upper end of the axis correlated with heat load index even though the correlations were weak (Fig. 2.1: vascular: R=-0.374 with axis 2, cryptogam: R=-0.223 with axis 3). Correlations with heat load index were stronger for individual years (data not shown). Both harsh and moderate aspects in block WBEC grouped with the moderate aspects of other blocks and this block had a number of traits that differ from the other blocks including younger stand age at time of burn, more moderate slopes and higher elevation (Table 2.A1, App. 2.A). Differences in plant community composition due to aspect were not discernable based on MRPP except for the cryptogam community in year four (Table 2.1). In the vascular plant community, evergreen shrub and hardwood tree cover (Fig. 2.A1, App. 2.A) and harsh aspect indicator species (*Chimaphila umbellata*) were associated with higher heat load, while deciduous shrub and hardwood tree, forb, herbaceous and low and tall shrub cover (Fig. 2.A1, App. 2.A), moderate aspect indicator species (*A. macrophyllum, Agoseris* sp., and *Rubus ursinus*) and indicator traits (early-seral and evader species) were correlated with low heat load (Table 2.2 and 2.3). In the cryptogam community, bryophyte, lichen and liverwort cover, and that of *Polytrichum juniperinum*, *Aulacomnium androgynum* and *Didymodon vinealis*, as well as evergreen shrubs and hardwood trees were correlated with higher heat load, while tall shrub richness increased with low heat load.

All structural layers and trait groups had slightly lower average cover on harsh aspects than on moderate aspects (Fig. 2.2b and 2.3) but differences were statistically significant at the $p < 0.05$ level only for average low shrub cover (8.9% less (95% CI: 1.6 %, 16.2%) cover on harsh aspects than on moderate aspects in the second year, 13.7 % less (95% CI: 2.0%, 25.5%) in the third year and 13.2% less (95% CI: 1.9%, 24.5%) in the fourth year). No differences occurred in species richness per plot on contrasting aspects (Fig. 2. 2a). Based on ISA, seven trait groups were indicators for moderate aspects, while there were no indicators for harsh aspects (Table 2.3 and 2.4). On harsh aspects, all life forms were apparently less abundant.

DISCUSSION

The data support the initial floristic model of succession (Egler 1954) among structural layers evidenced by fairly constant species richness per plot in upper structural layers coupled with a shift in the dominance of structural layers over time. Fire-responding cryptogams begin as the dominant structural layer in early succession, particularly in severely burned areas (Issac 1940; Dyrness 1973; Wang and Kemball 2005) because they can occupy mineral soil as soon as moisture becomes available and reproduce over the winter (Shaw and Goffinet 2000) giving them a competitive advantage over herbaceous species. Typically, sprouting residual and invading herbaceous species become the primary cover within one to two growing seasons following disturbance (Uhl et al. 1981; Naveh 1994; Tatoni and Roche 1994) due to species disturbance adaptations, rapid colonization of invading species and rapid growth (DeBano et al. 1998). Woody shrubs are slower to recover than herbaceous species due to the time needed to grow woody tissue. However, in Mediterranean ecosystems, abundance of sprouting shrubs can decrease the time needed to reach shrub dominance (Arianoutsou-Faraggitaki 1984; Trabaud 1994; Ojeda et al. 1996). As found in burnt plantations, other studies have found that areas with high hardwood tree or shrub abundance prior to the fire proceed rapidly to shrub and hardwood tree dominance after the fire (Naveh 1994; Ojeda et al. 1996; Ghermandi et al. 2004). Early succession among structural layers in burnt plantations of southwestern Oregon fits the model outlined above based on the rapidly shifting dominance (1-3 years) from cryptogam to herbaceous to shrub structural layers. Succession among structural layers appears to be driven by growth and colonization rates which constrain the rate at which different structural layers are able to occupy sites.

Grime's (2001) model of succession suggests that early-seral species within each structural layer are replaced with slower growing, more competitive species associated with increased competition beneath the canopy, as also demonstrated in this study. Succession within structural layers is driven by differential species resistance or resilience to fire, regeneration mode, growth rates and site adaptations rather than those traits of structural layers as a whole. Succession within different structural layers occurred at different rates as previously documented (McCune and Antos 1981; Penman et al. 2008) and appeared to be slower than among structural layers. Late-seral cryptogam colonization and growth rates, dictated by asexual reproduction and lateral spread (Shaw and Goffinet 2000), slow the transition from early-seral to later seral cryptogams. The slow transition and lack of late-seral cryptogams early in succession may indicate of relay floristics acting within the cryptogam layer (DeGrandpre et al. 1993). However, facilitating effects of early-seral vegetation, such as increasing nutrient availability, were not tested to determine if relay floristics were occurring. Unlike the cryptogamic layer, transition between ruderal and stress-tolerating species in the herbaceous layer occurs rapidly due to the short-lived nature of ruderal species and rapid cover established by perennial species, which are often stress-tolerating. Many herbaceous species associated with year two in this study were invasive annuals (Grime's ruderal species) that gain dominance rapidly following disturbance due to their reproductive strategy (i.e. many small, wind dispersed seeds) and requirements for establishment (i.e. germination in mineral soil and lack of canopy) (Issac 1940; Chapin et al. 1994; Trabaud 1994; Ghermandi et al. 2004). Such ruderal species have been demonstrated to peak within the first two years post disturbance and then decline (West and Chilcote 1968; Halpern 1989). As observed in this study, subsequent vegetative growth of native perennial and graminoid species (Grime's competitive or stress-tolerating species) associated with later seral forests may increase or stabilize herbaceous cover after the decline of ruderal species (Halpern 1989; Tatoni and Roche 1994; Debussche et al. 1996; Ojeda et al. 1996). In contrast to the cryptogamic layer, sprouting of residual vegetation in the herb and shrub layers coupled with invasion by ruderal species contributes to the presence of early and late-seral species simultaneously and initial floristics model seems more applicable within these layers.

Other successional theories focus on the impact and heterogeneity of disturbance as drivers of succession (Gleason 1926; Pickett and White 1985). Geographic location, an indicator of the importance of stand history and abiotic factors, was found to be the best predictor of vascular plant community differences following fire in Yellowstone National Park (Turner et al. 1997), the Mediterranean Canary Islands (Arevalo et al. 2001) and following forest management activities in the Pacific Northwest (Bailey et al. 1998; Fahey and Puettmann 2007). Successional starting points of plant community composition following fire in burnt plantations were site dependent with differing responses of structural layers to fire and environmental factors as documented in other studies (McCune and Antos 1981; Penman et al. 2008). Both deterministic (pre-disturbance plant community, life history characteristics and topography) and stochastic (disturbance severity and site history) factors influenced successional starting points of plant community composition.

Fire severity (indicated by % live basal area) strongly influenced differences in plant community composition as in other studies for the Cascades (Halpern 1989; Chappell and Agee 1996), the Mediterranean (Arevalo et al. 2001) and the boreal forest (Purdon et al. 2004; Wang and Kemball 2005). Variability in fire severity occurs in most wildfires and is an important source of heterogeneity for plant communities (Turner et al. 1997). Fire severity was closely tied to topographic factors that can also influence community composition including slope (Weatherspoon and Skinner 1995; Turner et al. 1997; Halofsky 2007) and elevation (Wang and Kemball 2005). Fire severity may control succession within structural layers by determining survival of residual/late-seral species (Uhl et al. 1981; Turner et al. 1999; Bonet and Pausas 2004; Wang and Kemball 2005). Succession among structural layers would not necessarily be affected by fire severity except perhaps for the rate of transition between structural layers.

Species composition and life history traits can drive plant community composition and successional trajectories among and within structural layers (Connell and Slayter 1977; Cattelino et al. 1979; Noble and Slatyer 1981; Thornburgh 1982). Some species exhibit inhibitory effects on other vegetation that can potentially alter successional trajectories, including *Ceanothus integerrimus* (Heisey and Delwiche 1983) and sclerophyllous vegetation (Mallik 2003). As hypothesized by Thornburgh (1982) and documented in the current study, multiple successional pathways in xeric mixed-conifer forests were based on initial dominance of certain species or groups of species. Differences in plant community composition on contrasting aspects and changes in successional trajectories were linked to shrub and hardwood tree composition as previously documented (DeGrandpre and Bergeron 1997; Ghermandi et al. 2004; Purdon et al. 2004). Differences in aspect may be confounded by the influence of disturbance early in succession and may become stronger over time (Callaway and Walker 1997; Kadmon and Harari-Kremer 1999). Lower stature, denser branches and decreased light under evergreen shrubs and hardwood trees (Purdon et al. 2004) contribute to decreases in herbaceous and cryptogam vegetation. Slower growth of evergreen species may decrease the cover of the shrub layer initially compared to deciduous species. Dominance by evergreen shrubs could slow succession within structural layers and result in the persistence of a bryophyte-herbaceous co-dominance as demonstrated in other ecosystems following severe disturbance (Cremer and Mount 1965; Esposito et al. 1999; Wang and Kemball 2005). Altered successional trajectories due to species composition appear to occur within structural layers but may have long-term effects on succession among structural layers as well.

Attempts to develop a unified theory of succession have been hampered by the variability and complexity of successional processes (Clements 1916; Gleason 1926; Egler 1954; Odum 1969; Shafi and Yarranton 1973; Whittaker 1975; Pickett et al. 1987). While many factors contribute to recovery following disturbance in burnt plantations, burnt plantations appear to be resilient to disturbance exhibiting rapid establishment of primarily native residual vegetation and successional progression. In this system, succession among structural layers follows the initial floristics model, while succession within structural layers is more difficult to define by floristics theory and may vary by structural layer. While this study was able to examine short-term patterns in diversity and cover and determine influence of environmental factors on plantation succession following wildfire, it is a very short window into the full succession of these communities. Long-term research on the effects of wildfire on managed landscapes is needed. It is difficult to say at this point if strong differences among sites will be sustained and the long-term effects of fire severity and heat load on succession in burnt plantations are unknown.

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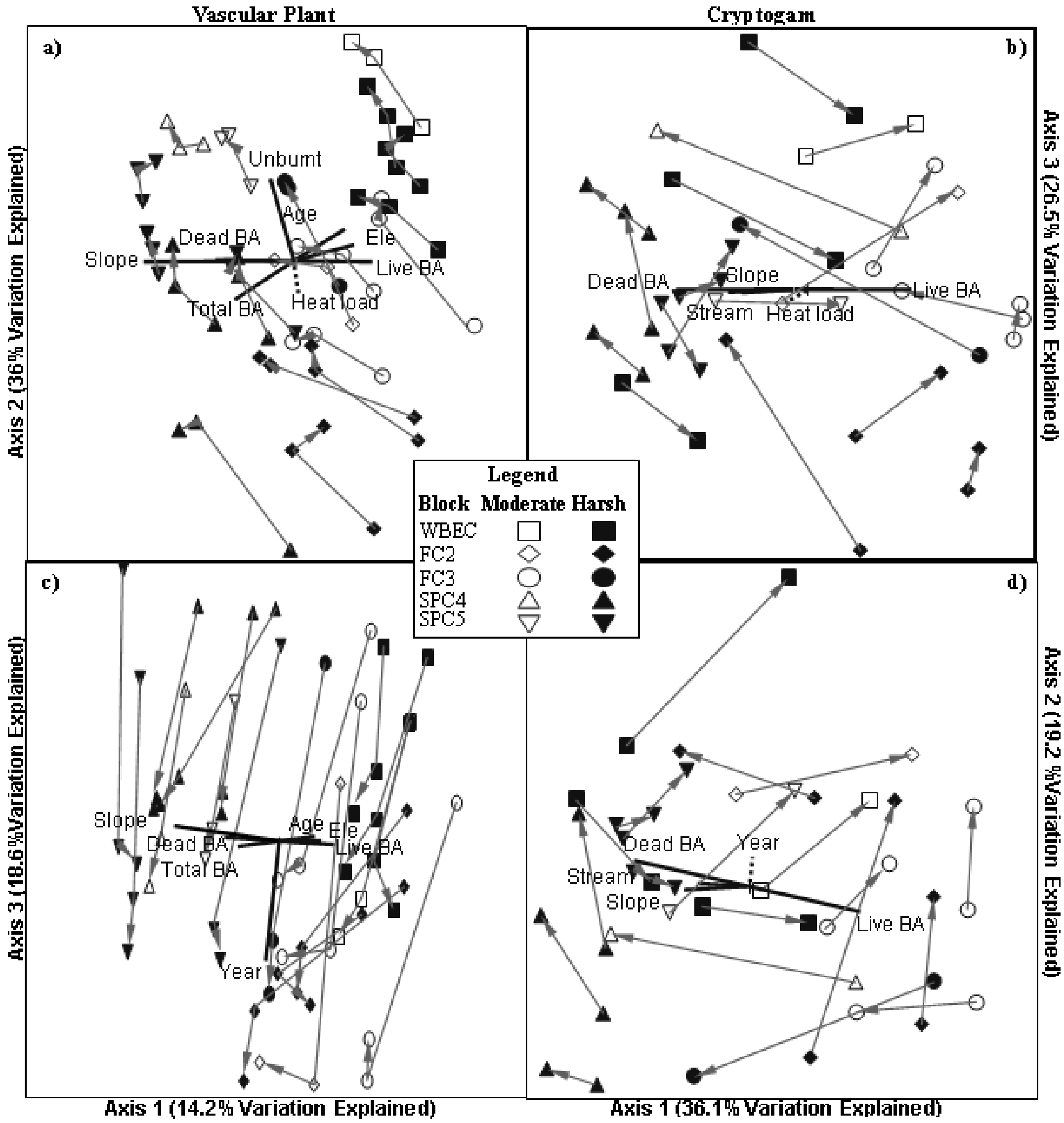
Figure 2.1. Three-dimensional NMS ordinations of vascular plant (a and c: R^2=69% for all three axes) and cryptogam (b and d: R^2=81.8% for all three axes) communities for treatments without vegetation removal. Point represent plots, with each plot represented three times (vascular plants or two times (cryptogams) corresponding to years of sampling. Successional arrows (grey) connect the same plot through years and environmental variable joint plots overlain. Angles and length of joint plot lines (black) represents the direction and strength of relationships with environmental variables (Dead BA =% dead BA, Live BA = % live BA, Yr = time since fire, Ele = elevation, Age = plantation age at time of burn, Stream = distance to Stream and Unburnt = distance to unburnt forest). Cryptogam community axes were rigidly rotated to align % live BA with axis 1. All joint plot correlations have $R^2 \geq 0.2$ except dashed lines are $R^2 > 0.08$.


Vascular Plant
Cryptogam
a)
b)
c)
d)
Unburnt
Age
Ele
Live BA
Slope
Dead BA
Total BA
Heat load
Stream
Year
Axis 2 (36% Variation Explained)
Axis 3 (26.5% Variation Explained)
Axis 3 (18.6%Variation Explained)
Axis 2 (19.2 %Variation Explained)
Axis 1 (14.2% Variation Explained)
Axis 1 (36.1% Variation Explained)
Legend
Block Moderate Harsh
WBEC
FC2
FC3
SPC4
SPC5

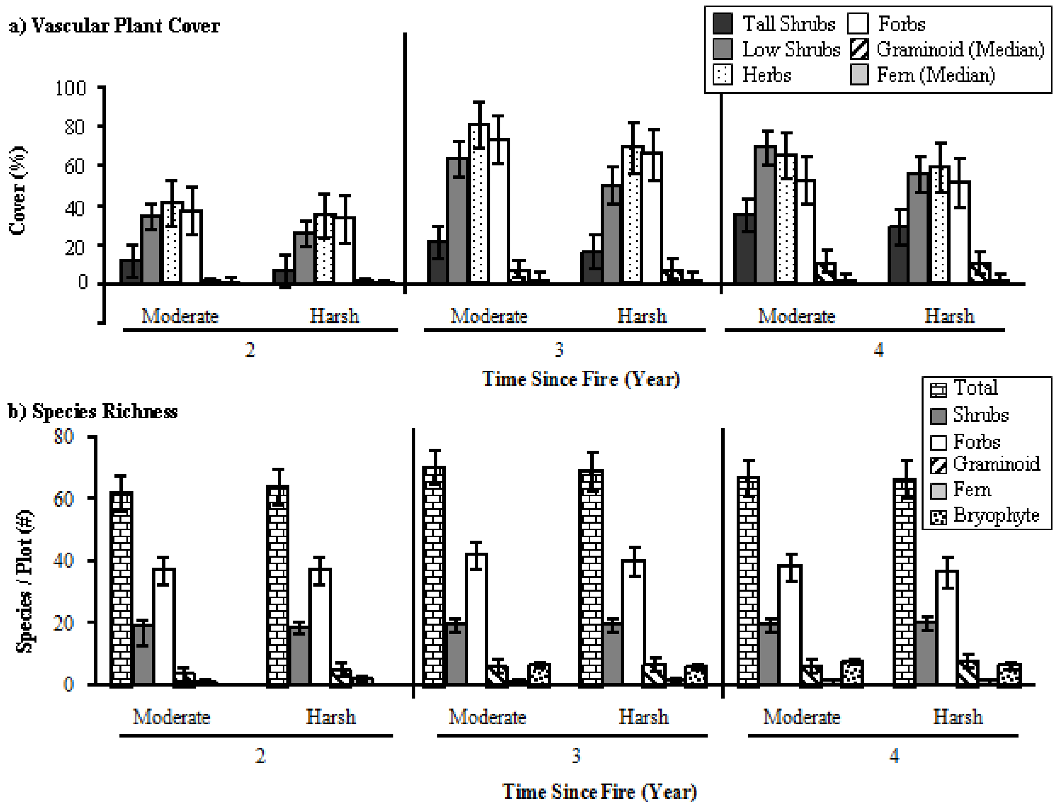


Figure 2.2. Average species richness per plot (a) and vascular plant percent cover (b) by time since fire on harsh and moderate aspects in treatments without vegetation removal for different life form groups. Values are means and 95% confidence intervals. Bryophytes were not measured in year two. Moderate = moderate aspect and Harsh = harsh aspect.

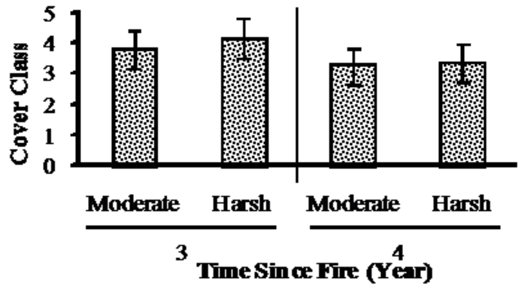


Figure 2.3. Bryophyte cover class by time since fire on harsh and moderate aspects in treatments without vegetation removal. Values are means and 95% confidence intervals. Cover classes are: (1) <3 individuals present, (2) 4 -10 individuals present, (3) > 10 individuals but < 25% cover, (4) 26-50% cover, (5) 51-80% cover, and (6) 81-100% cover. Moderate = moderate aspect and Harsh = harsh aspect.

Table 2.1. MRPP/MRBP results for differences in vascular plant and cryptogam communities between aspects, years, watersheds, and blocks for treatments without vegetation removal. All differences were considered individually without regard to other groups. Due to the need for balanced groups, MRBP analysis included only high-density treatments without vegetation removal on two aspects for the second (vascular), third (cryptogam) and fourth year post fire. Relatively strong A-statistics are in bold.

	Vascular Plants		**Cryptogam**	
Individual Factors (MRPP)				
	A	**P**	**A**	**P**
Aspects	0.011	0.002	0.04	0.00
Year	0.03	0.000	0.02	0.01
Watershed	0.09	0.000	**0.1**	0.00
Block	**0.14**	0.000	**0.15**	0.00
Blocked Factors (MRBP)				
	A	**P**	**A**	**P**
Aspect in Year 2(3)	0.013	0.200	0.06	0.10
Aspect in Year 4	-0.0002	0.515	0.08	0.03

Table 2.2. Indicator species for aspects and years in treatments without vegetation removal and trait group designations for indicator and non-indicator species mentioned in the text. All indicator species had $p \leq 0.05$. Higher indicator value (IV) mean that the species was more restricted to that particular group. *indicates cryptogams. Trait groups are designated by letters: EN = endurer, EV = evader, I = invader, R = residual, AV = avoider, a = annual forb, p = perennial forb, f = forb, pg = perennial graminoid, fe = perennial fern, b = bryophyte, d = deciduous shrub, eg = evergreen shrub, ss = sub-shrub, e = early-seral, l = late-seral, sl=short-lived, ll = long-lived n = native, ex=exotic, Wn = weedy native, Wex = weedy exotic and nf = nitrogen fixer.

Aspect			**Year Post Fire**		
Harsh	**Trait Groups**	**IV**	**Two**	**Trait Groups**	**IV**
Luzula comosa	EN, pg, n	87.2	*Collomia heterophylla*	I, a, n	89
Asyneuma prenanthoides	EN/EV, p, n	83.6	*Montia diffusa*	I, a, Wn	56.6
Arnica latifolia	EN, p, n, e/l	66.7	**Three**		**IV**
Xerophyllum tenax	EN, p, n, e/l	64.7	*Nemophila parviflora*	I/EV, a, n	77.5
Chimaphylla umbellata	AV, ss/p, n, l	40	*Fragaria vesca*	EN, p, n, e	76.6
Moderate		**IV**	*Senecio sylvaticus*	I, a, Wex, e	71.2
Madia madioides	I, a, n	92.9	*Didymodon vinealis**	I, b, ll	65.4
Agoseris sp.	EV, f, ex	84.4	*Lactuca serriola*	I, a, Wex	63.8
Galium triflorum	EV/EN, p, n, e/l	80.9	*Asyneuma prenanthoides*	EN/EV, p, n	60
Fissidens sp.*	I, b, sl	77.7	*Funaria hygrometrica**	I, b, sl	54.3
Epilobium ciliatum	I, p, Wn	76.2	*Epilobium ciliatum*	I, p, Wn	53
Cirsium vulgare	I, a, Wex, e	73.6	*Crepis capillaris*	I, a, Wex, e	50.7
Weissia group*	I, b, sl	72.4	*Epilobium minutum*	I,a,Wn	47.1
Rubus ursinus	I/EN/EV,d/ss,n ,e	68.6	*Euchiton japonicum*	I, a, Wex	45.1
Corylus cornuta var. *californica* - tall	EN, d, n, e/ l	65.7	*Stephanomeria virgata*	I, a, n	45.1
Homalothecium group*	R, b, ll	64.9	*Erechtites minima*	I/EV, p, n	44.5
Acer macrophyllum - tall	EN, d, n	60	*Poa* sp.	g	31.2
FUNGI*	N/A	52.6	*Galium aparine*	I, a Wn	85.1
Achyls triphylla	EN, p, n, l	47.3	**Four**		**IV**
Lotus micranthus	I, a, Wex, nf	39.9	*Bryum capillare* group*	I, b, sl	80.7
Non-Indictor Species			*Ceanothus integerrimus*	EV, d, n, nf, e	71.4
Acer circinatum	EN, d, n, e/l	NA	*Festuca occidentalis*	I/EN, pg, Wn, e/l	64.8
Mahonia nervosa	EN, eg/ss, n, l	NA	*Elymus glaucus*	EN, pg, n, e	55.9

Table 2.2 (Continued)

			Year Post Fire		
Non-Indicator Species	**Trait Groups**	**IV**	**Four**	**Trait Groups**	**IV**
Polystichum munitum	I/EN, fe, n, e/l	NA	*Cirsium vulgare*	I, a, Wex, e	54
*Aulacomnium androgynum**	I, b, ll	NA	*Iris chrysophylla*	EN, p, n	52.7
*Bryum argenteum**	I, b, ll	NA	*Deschampsia elongata*	EN, pg, n, e/l	50.7
*Ceratodon purpureus**	I, b, sl	NA	*Whipplea modesta*	EN, ss/p, n,	48.9
*Eurhynchium oreganum**	R, b, ll	NA	*Ceanothus sanguineus*	EV, d, n, e, nf	41.8
*Hypnum subimponens**	R, b, ll	NA	*Rubus leucodermis* – tall	I/EN/EV, d, n, e	34.7
*Leucolepis acanthoneuron**	R, b, ll	NA	*Trisetum canescens*	EN/EV, pg, n, e	25.3
*Polytrichum juniperinum**	R, b, ll	NA	*Leptobryum pyriforme**	I, b, sl	25.2

Table 2.3. Vascular plants indicator traits for aspects and years in treatments without vegetation removal. All indicator traits had $p \leq 0.05$. Higher indicator values (IV) mean that the trait is more restricted to that particular group. A trait can be an indicator for more than one group.

Aspect		**Year Post Fire**	
Moderate	**IV**	**Three**	**IV**
Exotic	69.1	Annual Forbs	50.5
Conifer	65	Herb	46.1
Weedy	64.3	Weedy Native	45.9
Invaders	59.3	Weedy	43.9
Deciduous Shrubs	58.7	Invaders	43.6
Early	57.3	Native	41.4
		Four	**IV**
		Nitrogen Fixers	54.2
		Graminoids	50.3
		Deciduous Shrubs	46.1
		Shrub	45.6
		Sub-shrub	45.1
		Early	44.7
		Late	43.6
		Evader	43.2
		Endurer	42.5
		Perennial Forbs	41.7

Table 2.4. Number of indicator species with p $\leq$ 0.05 by block, aspect and year in treatments without vegetation removal. Numbers indicate total number of species or traits that were indicators/group.Vasc.= vascular, WBEC, FC2, FC3, SPC4 and SPC5 are block codes.

Group	Vasc. Plants	Cryptogam	Total Species	Traits
FC2	13	1	14	2
FC3	16	4	20	3
WBEC	21	0	21	1
SP4	6	0	6	0
SP5	16	1	17	0
Harsh	5	0	5	0
Moderate	10	4	14	6
Year 2	2	.	2	0
Year 3	11	2	13	6
Year 4	9	2	11	10

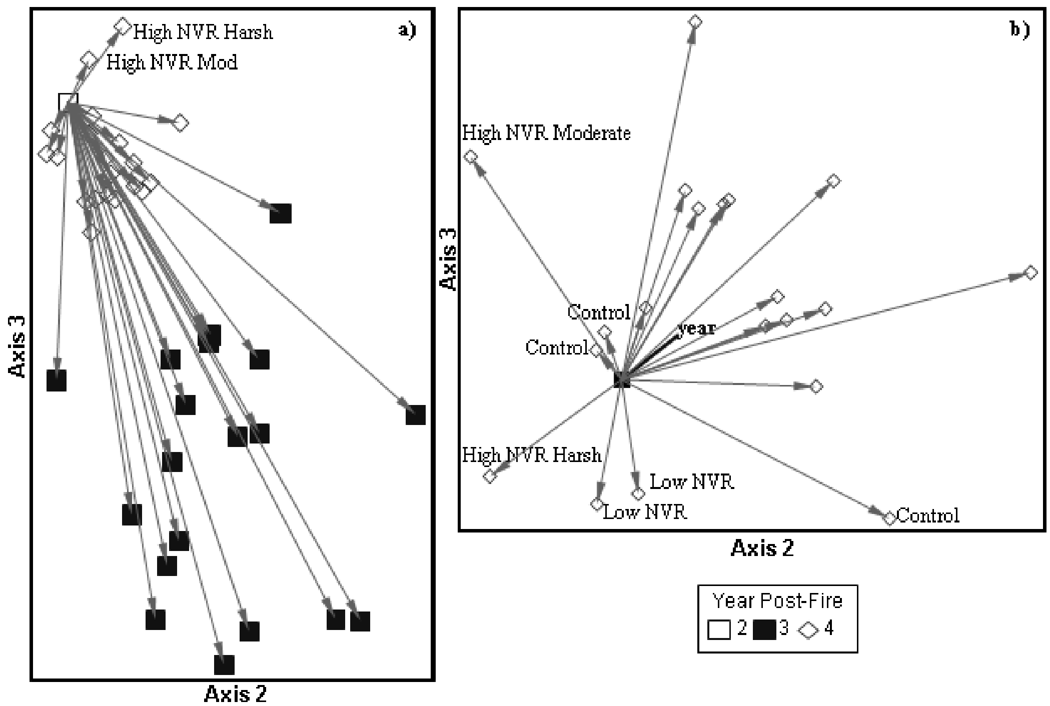


Figure 2.4. Relative length and direction of successional trajectories over time of (a) vascular plant community for three years and (b) cryptogam community for two years in treatments without vegetation removal; from NMS ordinations shown in Fig. 2.1. Origin represents the year two centroid for changes from year two to three and the year three centroid for changes from year three to four. Grey arrows indicate direction and rate of change between years and black line is correlated environmental variable ($R^2 \geq 0.2$). Plots with trajectories that diverge from the majority of plots are labeled.

ELECTRONIC APPENDIX 2.A.

Table 2.A1. Characteristics of blocks used in randomized complete block design. *Prior to fire, all blocks consisted of planted *Pseudotsuga menziesii* except FC2 which consisted of planted *Pseudotsuga menziesii* and *Pinus ponderosa*. Abbreviations are as follows: SS = Strait-Shippa Extremely Gravelly Loams, SS1 = 30-60% slopes, SS2 = 35-70% slopes, FG = Freezener-Geppert Complex, 35-60% slopes, SVC = Silicic Vent Complexes UTS = Undifferentiated Tuffaceous Sedimentary, Moderate Aspect = 44 to 160^{o}, Harsh Aspect = 220 to 360^{o}, PCT = Pre-commercial thin or removal of non-merchantable trees, MB = manual brush or chainsaw cutting of shrubs and hardwood trees and Herb = herbicide applied.

Block	**W. Branch Elk Creek**	**Flat Creek 2**	**Flat Creek 3**	**Sugar Pine Creek 4**	**Sugar Pine Creek 5**
Code	WBEC	FC2	FC3	SPC4	SPC5
Soil	SS1	SS2 / FG	SS1	SS2	SS2
Geology	SVC	SVC / UTS	SVC	UTS	UTS
Slope (%)	24-32	22-36	25-35	36-40	37-42
Elevation (m)	939-1000	865-915	800-840	845-895	815-855
Harsh Azimuth (°)	260-292	270-312	220-230	282-320	314-360
Moderate Azimuth (°)	108-110	160	90-150	62-68	44-55
Dead Basal Area (%)	54 - 84	49-100	55-75	91-100	99-100
Total Basal Area (m^2/ha)	6-10	14-30	12-21	13-23	14-26
Harvest Year	1985	1965	1965	1965/1967	1965
Harvest System	Overstory Removal	Clearcut	Clearcut	Overstory Removal/ Shelterwood	Shelterwood
Plantation Origin*	1985	1972	1965	1972	1967
Vegetation Control	PCT, MB, Herb	PCT	PCT, MB	PCT, MB	PCT, MB, Herb

Table 2.A2. Cryptogam species combined into groups for data analysis.

Group	**Species**
Weissia group	*Timmiella crassinervis*
	Weissia controversa
Homalothecium group	*Brachythecium velutinum*
	Claopodium whippleanum
	Homalothecium fulgescens
	Isothecium myosuroides
Bryum capillare group	*Pohlia longibracteata*
	Bryum capillare

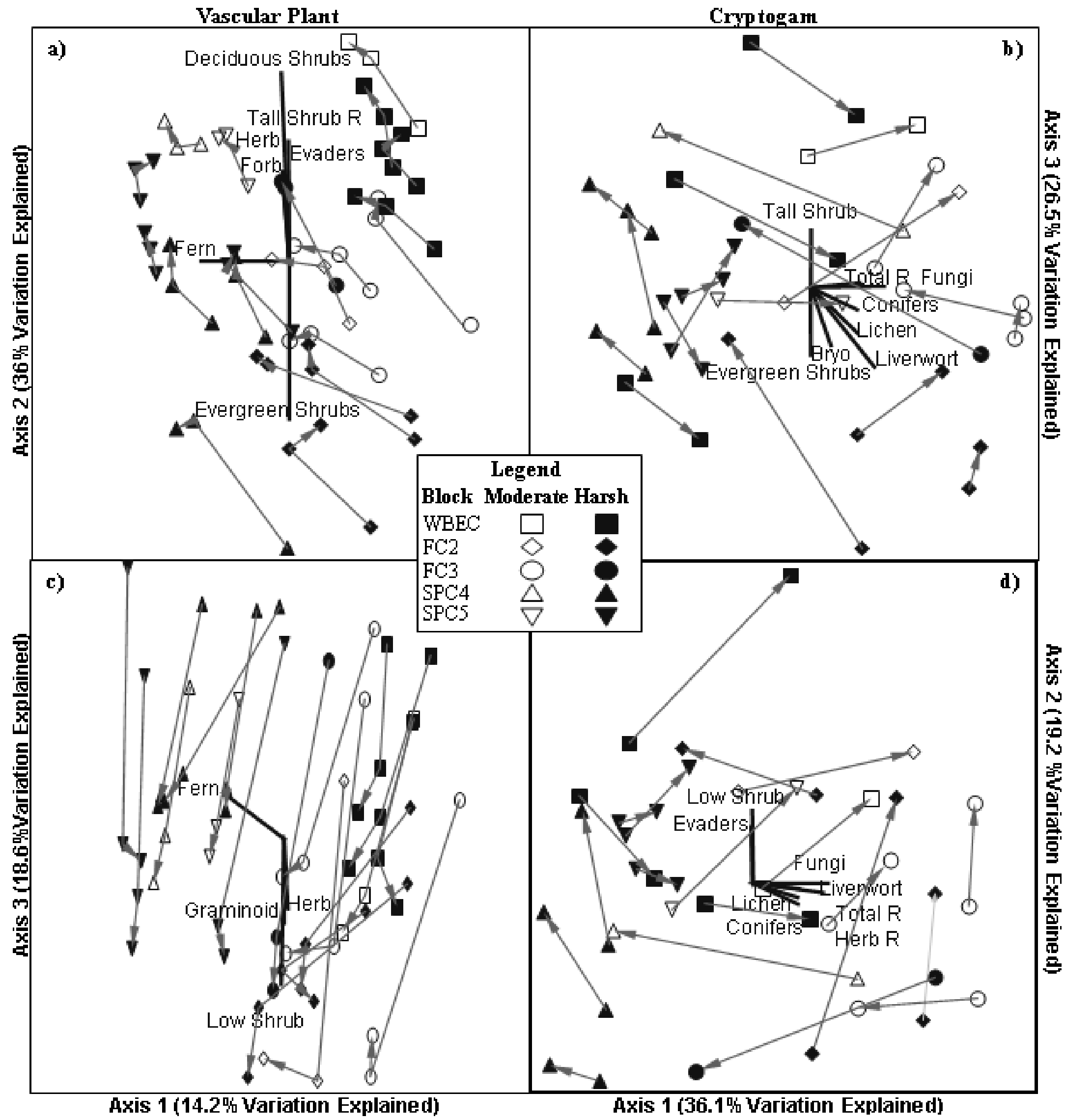


Figure 2.A1. Three-dimensional NMS ordinations shown in Fig. 2.1 of vascular plant (a and c) and cryptogam (b and d) communities in treatments without vegetation removal.Successional arrows connect the same plot through years and trait group joint plots overlain. Angles and length of joint plot lines represents the direction and strength of relationships with trait cover and richness (R) variables (Bryo = bryophyte). Cryptogam community axes were rigidly rotated to align % live BA with axis 1. All correlations have $R^2 \geq 0.2$.

CHAPTER 3 – VEGETATION AND PLANT COMMUNITY RESPONSE TO REFORESTATION-BASED RESTORATION FOLLOWING HIGH SEVERITY FIRE IN PLANTATION FORESTS

ABSTRACT

Post-fire restoration goals, especially for federal lands in the western United States, have changed in recent years to include forest regeneration, maintenance of biodiversity, and retention or accelerated development of late-seral habitat characteristics. Lack of seed sources, competition from other vegetation, and abiotic conditions can limit conifer reestablishment in burnt plantations leading to restoration using mixed species planting coupled with vegetation control. The presence of early-seral vegetation, particularly cryptogams (i.e. spore producing plants), coincides with the most active period of management intervention in post-fire restoration and is a good indicator of change due to restoration activities. The objective of this study was to evaluate the effects of restoration activities on early-seral vegetation, including terrestrial cryptogams, and successional patterns in severely burnt plantations on moderate and harsh aspects in mixed conifer forests of southwestern Oregon. Conifer seedlings were planted as a four-species mixture or a monoculture at different densities with and without vegetation removal on contrasting aspects in severely burnt plantations. These restoration treatments, particularly vegetation removal, influenced plant communities and successional trajectories. Initially bryophyte and shrub cover were lower where vegetation was removed compared to areas without vegetation removal. Reestablishment of bryophyte cover in areas with vegetation removal was evident by the fourth year after fire, but shrub cover remained decreased due to direct manipulation by vegetation removal. In general, cover of exotic species was very low. However, by the end of the study on harsh aspects only, exotic and annual herb cover was higher in areas with vegetation removal compared to those without vegetation removal. Differences in cover between areas with and without vegetation removal were greater on harsh aspects for trait groups with mostly herb species and on moderate

aspects for bryophytes and trait groups with primarily shrub species. Repeated manual vegetation removal was effective at suppressing tall shrubs with minimal effects on other vegetation components.

INTRODUCTION

Early-seral vegetation plays a key ecological role following fire. Early-seral species perform a variety of ecosystem functions vital to recovery from disturbance and to plant community dynamics and succession. Functions of early-seral vegetation include erosion control (Foster 1985; Agee 1993; Beyers 2004), replenishment of soil organic matter (Chapin et al. 1994), nitrogen fixation (Chapin et al. 1994; Busse et al. 1996; de las Heras and Herranz 1996), provision of wildlife habitat (Agee 1993; Saab et al. 2005; Cannon 2007) and facilitation of late-seral species germination and growth (During and van Tooren 1990; Chapin et al. 1994). Additionally, early-seral vegetation is a major source of floristic diversity (Halpern 1988; Schoonmaker and McKee 1988), coincides with the most active period of management intervention in post-fire restoration, and is a good indicator of ecosystem health and environmental change due to forest management activities (Haeussler et al. 2007).

Early-seral vegetation is comprised of species that vigorously sprout following disturbance, grow from fire stimulated seed/spore banks, or invade with wind- or animal-dispersed seeds/spores (Cremer and Mount 1965; Hobbs and Wearstler 1985; Schoonmaker and McKee 1988; Halpern 1989). In areas with high abundance of shrubs prior to fire, shrubs tend to regain cover rapidly due to vigorous sprouting and rapid growth (Hobbs et al. 1992; Agee 1993). The resulting shrub community is often thought to prevent or slow the establishment of other vegetation including conifers (Monleon et al. 1999), although this is not always the case (Lopez-Ortiz 2007).

Terrestrial cryptogams (i.e. spore producing plants), particularly bryophytes, are a critical component of early-seral vegetation (Cremer and Mount 1965; Wang and Kemball 2005), but taxonomic complexity often excludes cryptogams from vegetation studies (Frego 2007). Cryptogams are sensitive to forest management activities (Newmaster and Bell 2002; Fenton et al. 2003; Newmaster et al. 2007) and may be good indicators of forest integrity, i.e. capacity of a forest to maintain a community of organisms similar to undisturbed forests in that region (Frego 2007). Cryptogams and vascular plants often respond differently to disturbance and environmental factors (McCune and Antos 1981; Penman et al. 2008). Documentation of vascular plant and cryptogams can lead to increased insights into vegetation responses following disturbance and restoration activities.

Post-fire restoration goals, especially for federal forest lands in the western United States, have changed in recent years from a focus on rapid conifer regeneration to also include maintenance of species and structural diversity and retention or accelerated development of late-seral habitat characteristics (Curtis et al. 1998). Burnt plantations are a prime location for reforestation-based restoration because plantations have specific management objectives, successful prior plantation establishment, altered pre-fire overstory composition with few species and young trees that may not be significant seed sources, and often burn with high fire severity (Weatherspoon and Skinner 1995; Odion et al. 2004; Thompson et al. 2007). Some of the challenges to restoration aimed at specific forest composition and structural goals following high-severity wildfire in plantations include competition from sprouting and other vegetation, lack of conifer seed sources due to high severity fire, and harsh regeneration sites (Walstad et al. 1987; Hobbs et al. 1992). To meet these challenges on federal lands, reforestation and control of competing vegetation are the primary restoration activities undertaken following wildfire to reestablish forest vegetation and reinitiate development toward late-successional conditions. Through direct manipulation and indirect effects, restoration activities and management intervention have the potential to alter early-seral vegetation and the ecosystem functions that it provides. However, permanent extirpation of non-conifer species is not a desired result of restoration practices (Walstad and Kuch 1987; Newmaster et al. 2007).

The objective of this study was to evaluate effects of restoration treatments on early-seral vegetation composition and succession in severely burnt plantations two to four years following wildfire. Specifically examined were the effects of vegetation removal and conifer planting on temporal dynamics of plant communities, structural layers, terrestrial cryptogams, and trait groups on two contrasting classes of site quality, defined approximately by eastern (moderate) and western (harsh) aspects. Sites on western aspects are more likely to have higher insolation and temperatures that limit the growth and establishment of some species, including conifers, than eastern aspects (Hobbs et al. 1992). We developed three hypotheses to address these objectives. (1) A shift in dominant structural layers and trait groups would occur due to restoration treatments with vegetation removal relative to those with conifer planting only, resulting in altered plant community composition. Specifically, invading, early-seral, cryptogam, and annual herbaceous species would increase and shrubs, hardwood trees, and late-seral species would decrease when vegetation was removed. (2) Initial removal of vegetation would have limited effects on structural layer and trait group cover due to low cover of taller structural layers immediately following wildfire, but differences in plant communities, structural layers and trait groups between areas with and without vegetation removal would become more pronounced over time. (3) Differences in structural layers, trait groups, and plant community composition between areas with and without vegetation removal would be more pronounced on harsh aspects than moderate aspects.

METHODS

Study Site

The Timbered Rock fire occurred within the Western Cascades physiographic province, near the intersection of the Klamath and Cascade Mountains, in mixed conifer forest primarily within the *Abies concolor* and mixed conifer forest zones (Franklin and Dyrness 1973). Southwestern Oregon has a mixed severity fire regime with fires burning every 5 to 75 years (Sensenig 2002). The climate is generally characterized by mild, wet winters and warm, dry summers. Topography is often steep (slopes >25%) with volcanic bedrocks and elevations between 800 m and 1000 m.

The wildfire burnt with varying intensity and severity 11,000 hectares (ha) between July 13th and August 9th, 2002. Approximately 40% of the burned area was occupied by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) plantations less than 35 years old. The study was conducted within five Douglas-fir plantations (blocks) that originated 15 to 40 years prior to fire with an average of 280 Douglas-fir trees per hectare (tph). In addition to Douglas-fir, plantations had components of *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir), *Pinus ponderosa* (ponderosa pine), *Pinus lambertiana* (sugar pine), and *Calocedrus decurrens* (incense cedar), and abundant hardwoods: including *Arbutus menziesii* (madrone), *Acer macrophyllum* (big-leaf maple), *Cornus nuttallii* (Pacific dogwood), *Quercus chrysolepis* (canyon live oak), and *Chrysolepis chrysophylla* (golden chinquapin) with a combined average density of 500 tph. See chapter 2 for full block descriptions.

Research Design

Five blocks were selected one year post-fire for moderate to high fire severity (based on Bureau of Land Management fire severity maps derived from Landsat 7 satellite imagery of burned areas), sufficient size for study implementation, and lack of other planned restoration activities (USDI 2003). Within each block, five treatment plots and a control plot were established on one generally uniform aspect (large sub-block) and two treatment plots were established on a contrasting aspect (small sub-block) two years post-fire. Treatment plots were square with a slope corrected treatment area of 0.25 ha and an internal sampling area of 0.2 ha. Treatments were randomly assigned to treatment plots within each sub-block. Treatments on the large sub-block (referred to as restoration treatments) included: Control - unplanted without vegetation removal; Low-density NVR – mixed species planted at 470 tph without vegetation removal; High-density NVR – mixed species planted at 1075 tph without vegetation removal; Low-density VR – mixed species planted at 470 tph with vegetation removal; High-density VR – mixed species planted at 1075 tph with vegetation removal; and Monoculture – Douglas-fir planted at 1075 tph with vegetation removal. Treatments repeated on the small sub-block included: High-density NVR and High-density VR.

Mixed species were comprised of 40% Douglas-fir and 20% each of sugar pine, ponderosa pine, and incense cedar seedlings. Vegetation removal consisted of manual cutting of tall vegetation focused on woody shrub stems in the summers of years two through four post-fire over the entire treatment plot. In addition, all vegetation was scraped (scalped) down to mineral soil in an approximate 0.75 m radius around planted conifer seedlings in year three post-fire. Scalping resulted in between 0 - 22% average cover of scalped area in the third year and less than 8% cover of scalped area by the fourth year post-fire within a given treatment. The same work crew implemented all aspects of the vegetation removal and conifer planting. One high-density NVR treatment on a harsh aspect was accidentally scalped.

Contrasting sub-blocks were designated as relatively “harsh” and “moderate” based on azimuth. Harsh aspects ranged from 220^{o} to 360^{o} and moderate aspects ranged from 44^{o} to 160^{o} to reflect solar radiation and temperature patterns. During the summer, steep west-facing slopes receive as much or more solar radiation as south-facing slopes with the maximum radiation shifted to hottest time of the day (i.e. afternoon). In contrast, east-facing slopes receive maximum radiation early in the morning when it is cooler (Gates 1972). Aspect is a major cause of differences in plant community composition (Whittaker 1960; Small and McCarthy 2002; Lopez-Ortiz 2007) and fire regimes (Taylor and Skinner 1998). Furthermore, due to the influence of high summer temperatures and drought, aspect is as a suitable criterion for characterizing potential conifer seedling mortality in southwestern Oregon (Hobbs et al. 1992; USDI 2003). Assignment of the small and large sub-blocks was constrained by available area. Therefore, one block had the large sub-block on the moderate aspect whereas the other four blocks had the large sub-block on the harsh aspect.

Data Collection

Vascular plant percent cover data were collected three summers, years two through four post-fire, by a four to seven person crew with one crew member providing consistency across all years. Within each treatment plot, four permanently marked 0.01 ha measurement plots or quads (randomly dispersed with the restriction that each fit within one quadrant of the sampling area), were used to measure shrubs ($\geq$ 1.3 m) and re-sprouting hardwood trees (< 5 cm dbh), collectively referred to as tall shrubs. Tall shrub percent cover for individual shrubs was measured as the canopy area (width x length: cm^2) per quad area (cm^2) * 100, summed by species over the quad. Total tall shrub percent cover per quad was calculated as the sum of all individual tall shrub percent covers minus visually estimated overlap between neighboring tall shrubs. Percent cover of all other vascular plants, including shrubs < 1.3 m tall (low shrubs), was estimated by species to the nearest one percent in four 3 m x 3 m (0.009 ha) subplots, one at each quad corner (16 subplots/treatment plot/block). Percent cover of low shrubs, forbs, ferns, grasses, and all herbaceous species combined, excluding species overlap (i.e. maximum cover =100%), was estimated in each subplot. Natural germinants of tree species were measured using a density count in a 1 m x10 m transect on the upslope side of each quad and converted to seedling density/ha for inclusion in multivariate analyses. To examine changes in species composition, trait groups including fire response (invader – highly dispersive pioneer species; avoider – late successional, slow colonizers; evader – seedbanking species; or endurer - sprouting species) as defined by Rowe (1983); growth form (annual herb, perennial herb, graminoid, fern, sub-shrub – low-lying woody species, deciduous shrub or evergreen shrub); successional status (early or late); nitrogen fixing capacity (fixer); and origin (exotic or native), were defined based on Hickman (1993), Wang and Kemball (2005), USDA (2006; 2007), and Spies (1991). For bryophytes, trait group categories, including disturbance response (invading or residual) and longevity (short- or long-lived) were identified based on Lawton (1971), Vitt (1988) and personal experience. See Table 3.4 for partial list and Appendix B for full list of species and traits. For this study's purposes, a trait group was a set of species with similar biological characteristics, occupy comparable niches in ecosystems and respond in similar way to environmental factors. "Trait" group was used rather than "functional" group because the specific ecosystem functions of trait groups are currently broad or unknown.

Terrestrial cryptogam cover was estimated using cover classes adapted from Forest Inventory Analysis lichen protocol (McCune et al. 1997) for individual species and bryophytes, liverworts, lichens, and fungi across taxa in the third and fourth summer post-fire in a 0.5 m x10 m transect across the upslope side of each quad in 20 contiguous subplots (0.5 m x 0.5 m) by one observer. Cover classes were coded as follows: (1) < 3 individuals present, (2) 4 to 10 individuals present, (3) > 10 individuals but < 25% cover, (4) 25-50% cover, (5) 50-80% cover and (6) 80-100% cover. Since individual cryptogam species may have limited cover with dispersed individuals, including the abundance count at a fine scale weights species with small populations more heavily and simplifies quantifying dispersed populations. On this scale, the average value approximates average log (abundance) and is not transformable to an arithmetic scale. Plant nomenclature follows USDA (2007). Vascular plants and cryptogams were determined to the species level when possible, otherwise to the genus level or life form group. Fungi were not identified. Due to the difficulty of identifying of extremely small or immature samples, several species were lumped into species groups for the final analysis (*Weissia controversa* includes *Timmiella crassinervis*; *Homalothecium* includes *Brachythecium velutinum*, *Claopodium whippleanum, Homalothecium fulgescens*, and *Isothecium myosuroides*; *Bryum capillare* includes *Pohlia longibracteata*).

Data Analysis

A combination of univariate and multivariate analyses were used to test hypotheses in order to examine interaction effects and causes of change in community composition. For all analyses, data were aggregated to the treatment plot level. Tall shrubs and low shrubs of the same species were analyzed separately. Influence of treatments on plant community composition and successional trajectory were examined using nonmetric multi-dimensional scaling (NMS: Kruskal 1964; McCune and Mefford 2005), multi-response permutation procedure (MRPP), and indicator species analysis (ISA). NMS, MRPP and ISA were performed using PC-ORD 5.1 (McCune and Mefford 2005). For multivariate analyses, three communities (vascular plant, cryptogam, and full (combined vascular plant and cryptogam)) were analyzed separately due to a lack of year two cryptogam data, continuous cover measures for vascular plants versus categorical abundance measures for cryptogams, and to allow comparisons between groups. Full community response was the primary interest so other results are reported only when differences from the full community occurred or for year two vascular plant data. Additionally, a trait composition community was tested for group difference in MRPP to examine multivariate trait response to treatments. Sørenson distance works well for community data with high beta diversity (McCune and Grace 2002) and was used for multivariate analysis unless specified. Before analysis, species and trait cover per treatment plot were relativized by species maximum to standardize for different measures of cover and large variation in magnitudes of cover between different species. Species that occurred in less than 5% of treatment plots over the study period (63 vascular plants and 20 cryptogams) were deleted to reduce dataset noise (McCune and Grace 2002).

NMS was performed on all three communities using PC-ORD (McCune and Mefford 2005) autopilot “slow-and-thorough” setting with random starting configurations, 500 maximum iterations, and 250 runs of real data. Joint plots were used to represent the linear correlations between ordination scores and cover variables or a vegetation removal indicator. Indicators for restoration treatments on large sub-block, vegetation removal including the monoculture/no vegetation removal including control across both aspects, and vegetation removal/no vegetation removal by aspect were overlain on the ordination to examine differences between treatments. Vector overlays connecting each treatment to the control treatment within each block were used to examine change due to treatment. To examine relative length and direction of change in communities for each treatment over time, remeasured treatments were connected by successional vectors and the tail of each successional vector was translated to the origin (McCune and Grace 2002; McCune and Mefford 2005). Two treatments (one Control and one high-density VR) from year two were labeled as outliers in the vascular plant community. Outlier removal did not improve the ordination and therefore outliers were retained.

MRPP, a non-parametric technique testing differences between predefined groups, (Mielke and Berry 2001; McCune and Grace 2002) was used to test for multivariate differences between groups (vegetation removal including monoculture treatments versus no vegetation removal including control treatments across both aspects) in different years. Comparisons between groups were made for individual years including the first (year two for vascular plant and trait communities, and year three for full and cryptogam communities) and the last (year four for all communities) year of treatment. MRPP generates an A statistic, the chance-corrected within-group agreement indicative of within group homogeneity and does not require balanced data. Due to the blocked design, differences between groups (restoration treatments on large sub-block; planting only versus control on large sub-block; vegetation removal versus no vegetation removal across both aspects; vegetation removal versus no vegetation removal on moderate aspects; and vegetation removal versus no vegetation removal on harsh aspects) in individual years (see above) were tested with blocked MRPP (MRBP) and Euclidean distances. Euclidean distance was used due to incompatibility of MRBP and Sørenson distance and median alignment. MRBP requires balanced data so the block containing the plot that was accidentally scalped was removed (but see App. E, Table E1). Treatments were median aligned to zero within blocks to focus on the within block differences and rank transformed.

Characterization of species driving community composition was performed by treatment groups using ISA (Dufrêne and Legendre 1973). Treatment groups consisted of vegetation removal versus no vegetation removal on two aspects. Resulting indicator values were compared to 1000 randomization of data using a Monte Carlo test.

Effects of restoration treatments in the large sub-block on structural layer and trait group cover over time were evaluated using a mixed model analysis of variance (ANOVA) applied to the randomized complete block design using PROC MIXED SAS v. 9.1. Treatment was a fixed effect and block was a random effect. Treatment plots served as the subject for repeated measurements (two years for bryophytes and three years for vascular plants). Mixed-models were fitted individually for four structural layer response variables (cover of herbs, bryophytes, low and tall shrubs) and 15 trait response variables (cover of invaders, evaders, endurers, deciduous and evergreen shrubs, perennial and annual herbs, graminoids, ferns, sub-shrubs, late- and early-seral species, nitrogen fixers, exotics, and natives). Eight covariance structures (compound symmetry, unstructured order 1-3, autoregressive order 1, and toeplitz order 1-3) were considered in determining the most appropriate repeated measures covariance structure for each response variable. If the model assumptions were met, the covariance structure with the lowest corrected Akaike's Information Criterion (AICc) value was selected as the most appropriate, unless covariance structures had ΔAICc < 2, then the covariance structure with the least parameters was selected.

Models assume normal error distribution and constant variance among treatments in a given year. Assumptions were assessed for all models and covariance structures using PROC UNIVARIATE and plots of residual versus predicted and residual versus normal percentile. If assumptions were not met, they were reassessed after log transformation of the response variable and, if still not met, the covariance structure was not considered in model selection. Log transformed variables (graminoid, fern, annual herb, and exotic cover) were back-transformed prior to reporting results. For all models and selected covariance structures, residuals were symmetric and assumptions of normality and constant variance of residuals were adequately met. Removal of blocks with accidentally scalped plot and treatments on opposing aspects did not alter the results so blocks were retained with the exception of the scalped plot (High-density NVR on harsh aspect) from year three and four, which was removed from all analysis due to this plot altering the results. Contrasts were used to examine differences between vegetation removal and no vegetation removal treatments (low- and high-density NVR treatments versus low- and high–density mixed species VR treatments) and the control and no vegetation removal treatments (low- and high-density NVR treatments versus control treatments) in individual years.

Influence of aspect on differences between areas with and without vegetation removal was assessed using high-density NVR and VR treatments on contrasting aspects. The same statistical analysis as described above was used except that the explanatory variables were vegetation removal (vegetation removal or vegetation retention), year (two years for bryophytes and three years for vascular plants), and aspect (harsh or moderate) modeled as a split plot factor due to restriction of treatment plot location. Contrasts were used to examine differences between vegetation removal and no vegetation removal on moderate aspects and on harsh aspects. When interactions with time occurred, multiple pairwise comparisons with Tukey adjustment were used to examine differences in areas with and without vegetation removal on different aspects in individual years.

Statistical significance was defined at $p < 0.05$ for all analyses. However, ANOVA p-values should be viewed with caution due to the analysis of many different response variables that increases the probability of type I errors. Trait group analyses, in particular, should be viewed as exploratory analyses rather than hypothesis testing. P-values are presented to give an indication of the effect size. Discrepancies between multivariate and univariate results would indicate if type I errors have occurred.

RESULTS

Restoration Treatments

Response to restoration treatments varied by composition of structural layers and trait groups. In general, the effect of restoration treatments on cover of structural layers and trait groups with many shrub species (including tall and deciduous shrubs, evaders, early- and late-seral species, and nitrogen fixers) over time based on the significance of the treatment x year interactions (Tables 3.1 and 3.2). Cover of herb, graminoid, and native species differed among restoration treatments but with similar change over time in all treatments based on significance of treatment and year but not treatment x year (Tables 3.1 and 3.2).

Structural layer and trait group cover differed due to vegetation removal but not due to conifer planting, regardless of planting density (Tables 3.1 and 3.2). No structural layer or trait group cover differed detectibly between treatments without vegetation removal (i.e. conifers planted only) and control treatments. Cover of tall shrub, low shrub, and bryophyte structural layers, ferns and most trait groups with many shrub species (i.e. evaders, natives, nitrogen-fixers, deciduous shrubs, and early and late-seral species) differed between areas with and without vegetation removal in some years (Tables 3.1 and 3.2). Differences in trait group composition were not detectible by MRPP among restoration treatments or between control and planting only treatments (Table 3.3).

The full plant community composition differed due to restoration treatments as detected by NMS (Fig. 3.1) and was expected due to direct vegetation manipulation. However, different treatments within the same block were more similar in community composition than were the same treatments in different blocks. Furthermore, while generally differences in full plant community composition were greater between areas with vegetation removal and the control than between areas without vegetation removal and the control, the direction of change from the control varied for treatments in different blocks (Fig. 3.1). When the vascular plant community ordination was rotated by vegetation removal status, areas with vegetation removal in all but one block (SPC4) fell at one end of the axis and those without vegetation removal generally fell on the opposite end of the axis (Fig. 3.2A). Annual herbaceous species were positively correlated plant community composition of areas with vegetation removal. Bryophytes, tall shrubs and nitrogen-fixing species were positively correlated with plant community composition of areas without vegetation removal. Block SPC4 had extremely low vegetation cover and its community composition was more similar to areas with vegetation removal, regardless of vegetation removal status. Three axis NMS solutions (Figs. 3.1 and 3.2) best represented the structure of the full community (final stress = 17.23, 137 iterations, R^2 = 69.8%); vascular plant community (final stress = 18.11, 149 iterations, R^2 = 67.1%); and cryptogam community (final stress = 16.73, 301 iterations, R^2 = 75.9%). For all communities, final instability was 0 and a Monte Carlo test indicated the final stress was less than expected by chance (p=0.004 for all axes). By the end of the study period, MRPP confirmed differences among restoration treatments with low within group homogeneity for the full and vascular plant communities and between areas with and without vegetation removal for all communities with some relatively high within group homogeneities (Table 3.3). However, no differences in plant community composition occurred in between planting only treatments and the control.

Vegetation Removal over Time

Vegetation removal decreased cover of low shrubs, tall shrubs and bryophytes initially, but had no effect on herbs (Fig. 3.3). Low shrub and bryophyte cover did not differ in areas with and without vegetation removal by year four post-fire, but tall shrubs continued to have lower cover in areas with vegetation removal over time (Table 3.1, Fig. 3.3).

Differences in cover of trait groups between areas with and without vegetation removal varied in timing, magnitude and direction (Figs. 3.4 and 3.5). For most trait groups, the differences in cover between areas with and without vegetation removal were more pronounced with time since first treatment, confirmed by MRPP with differences in trait group composition in year four (Table 3.3). Trait groups with many shrub species were directly manipulated by vegetation removal resulting in the absence of tall shrubs, and therefore, reduced cover in areas with vegetation removal with varying significance (Tables 3.1 and 3.2). In contrast, cover of tall shrubs and associated trait groups increased over time where no vegetation removal occurred. Differences in cover of evaders, natives, early- and late-seral species, nitrogen-fixers and deciduous shrubs between areas with and without vegetation removal were more pronounced over time (Table 3.2, Fig. 3.5). Differences in trait group cover between areas with and without vegetation removal varied some in year three, probably due to the effects of scalping in this year. Differences in fern cover were more distinct between areas with and without vegetation removal in the first year of treatment. Fern cover in areas with vegetation removal recovered over time.

In the vascular plant community, successional trajectories were altered in areas with vegetation removal by year four compared to areas without vegetation removal (Fig. 3.2B). Changes in community composition from year two to year three were similar in direction and magnitude for all plots, regardless of vegetation removal status. Trajectories in areas without vegetation removal continued in the same direction as year three plots and were positively associated with forb and herbaceous cover and scalped area. Differences in plant community composition between areas with and without vegetation removal were corroborated by MRPP, with relatively strong within group homogeneity by the end of the study period for vascular plant and full communities and initially for cryptogams (Table 3.3). Differences in community composition between areas with and without vegetation removal were minor but statistically significant initially for vascular plant communities (Table 3.3). No difference in the cryptogam community composition in areas with and without vegetation removal was evident by year four (Table 3.3).

Vegetation Removal on Contrasting Aspects

Structural layers responded similarly to vegetation removal on contrasting aspects except for low shrubs (Table 3.1). Low shrub cover was 16% lower (95% CI:

-6%, -26%) when vegetation was removed on moderate aspects compared to areas without vegetation removal, but did not differ on harsh aspects (Table 3.1).

The majority of trait groups (endurers, evaders, late-seral, sub-shrubs, perennials, graminoids, ferns, nitrogen fixers, and deciduous and evergreen shrubs) showed no difference in response to vegetation removal on contrasting aspects, demonstrated by the lack of interaction between vegetation removal and aspect (Table 3.2). However, trait group composition while initially different between areas with and without vegetation removal on both aspects, showed no difference on harsh aspects by year four based on MRPP (Table 3.3). Differences in cover of trait groups with primarily herbaceous species were more pronounced between areas with and without vegetation removal on harsh aspects than on moderate aspects (Table 3.2). Exotic species cover differed across aspects over time ($F_{2, 38}$=3.9, p=0.03). Exotic cover did not differ between areas with and without vegetation removal on either aspect initially (Table 3.2). However, cover was 2.3 times (95% CI = 1.1, 5.0) higher where vegetation was removed by the end of the study period on harsh aspects compared to areas without vegetation removal. Annual herbaceous cover was 1.5 times (95% CI: 1.0, 2.4) higher in areas with vegetation removal than areas without vegetation removal on harsh aspects but did not differ on moderate aspects (Table 3.2). Invader cover decreased 27% (95% CI: -7, -47%) in areas with vegetation removal compared to areas without vegetation removal on moderate aspects, but showed little different on harsh aspects (Table 3.2). Many species (between 36 and 95%) overlap in annual, exotic and invader trait groups (App, B). Differences in cover of native and early-seral cover between areas with and without vegetation removal were greater on moderate aspects (average difference = -51% and -45% respectively) than harsh aspects (average difference = -30% and 19% respectively).

Cryptogam community composition differed in areas with and without vegetation removal more dramatically on moderate aspects than on harsh aspects as demonstrated by NMS (Fig. 3.2B) and MRBP (Table 3.3). On the other hand, community composition was similar in areas with and without vegetation removal on both aspects for the full community. Vegetation removal lead to a unique array of indicator species compared to no vegetation removal, with indicators varying by aspect (Table 3.4). Lack of vegetation removal on moderate aspects resulted in more invading bryophytes (e.g. *Fissidens* sp.), enduring hardwood trees (e.g. *Corylus cornuta*, *Arbutus menziesii*, and *Acer macrophyllum*) and exotic forbs (e.g. *Cirsium vulgare*). Lack of vegetation removal on harsh aspects resulted in more residual bryophytes (e.g. *Polytrichum juniperinum*), enduring native herbs (e.g. *Luzula comosa, Asyneuma prenanthoides* and *Lonicera hispidula*), enduring hardwood trees (e.g. *Cornus nuttallii*) and evading shrubs (e.g. *Ceanothus sanguineus*: Table 3.4). Vegetation removal on moderate aspects was indicated by an enduring deciduous hardwood tree (*Acer macrophyllum*), while on harsh aspects, an evergreen evading shrub and enduring hardwood tree (e.g. *Arctostaphylos patula* and *Chrysolepis chrysophylla*) were indicator species.

DISCUSSION

Early successional flora was resilient to changes due to restoration activities as demonstrated by similar within-block community composition in burnt plantations. Mixed conifer forests are adapted to frequent disturbance and recover quickly (Stuart et al. 1993; Taylor and Skinner 1998). In the absence of vegetation manipulation, initial post-fire community composition was quite variable among plantations and reflected site differences at a stand scale (Kayes et al. in review) possibly contributing to a lack of consistent response to restoration activities. Site conditions appeared to affect responses to vegetation removal, with more pronounced effects on harsh aspects (i.e. xeric sites) for trait groups with primarily herbaceous species but stronger effects on moderate aspects (i.e. mesic sites) for shrubs and cryptogams. Differing site conditions also influence vegetation recovery whether from mechanical site preparation (Haeussler et al. 1999) or wildfire (Turner et al. 1997). For example, long-term vegetation effects of mechanical site preparation differed based on site moisture status, resulting in dominance of herbaceous species at moist sites and woody species at drier sites (Haeussler et al. 1999). In contrast, the results of the current study indicate that vegetation removal may homogenize sites by shifting community composition and vegetation cover on moderate aspects towards that of harsh aspects by increasing herbaceous components on harsh aspects and decreasing shrub components on moderate aspects. Higher cover of vegetation (including bryophytes), more rapid progression to shrub dominance, and more profound initial effects of vegetation removal on moderate aspects (Kayes, et al. in review) may indicate that removing vegetation on these aspects may be more beneficial for enhancing conifer growth than on harsh aspects. Alternatively, because vegetation removal increases conifer survival and establishment on xeric sites (Hobbs et al. 1992; Tesch et al. 1992), focusing restoration on harsh aspects would be prudent due to limited effects on other species groups. In removing vegetation repeatedly on harsh aspects, exotic species would need to be monitored due to potential increased population sizes, particularly in areas with resident populations of these species (Davis and Puettmann 2009).

The primary changes due to initial application of woody overstory removal were decreases in the tall shrub and bryoid layers. Similar patterns of decreased bryophyte cover with woody overstory removal were observed in several forest types and attributed to direct removal and desiccation (Bell and Newmaster 1998; Fenton et al. 2003; Davis and Puettmann 2009). However, bryophyte cover recovered over time due to the prevalence of invading, disturbance-tolerant bryophytes as found in other studies following site preparation (Haeussler et al. 1999; Newmaster et al. 2007). Cryptogams, shrubs and hardwood trees have important ecological roles that may be diminished due to decreased initial cover with vegetation removal. Tall shrubs provide shade, browsing protection and stabilize temperature variation (Walstad et al. 1987); increase net primary productivity and contribute to nutrient cycling especially on xeric sites (Zatvitkovski and Newton 1968; Yarie 1980; Walstad et al. 1987); and create structural continuity to the canopy that is important habitat for wildlife (Carey 1996; Hagar et al. 1996; Fontaine 2007) and epiphytes (Rosso et al. 2000). Cryptogams decrease erosion (Foster 1985), moderate soil surface temperatures (Richardson 1958), maintain soil moisture (Jack 1935; Richardson 1958), increase infiltration (Brotherson and Rushforth 1983) and contribute to organic matter and nutrient accumulation following disturbance (Yarie 1980; de las Heras and Herranz 1996; Shaw and Goffinet 2000).

Increased resource availability (Blumenthal 2005) due to the removal of woody stems allowed increases in exotic and annual herb cover with vegetation removal on harsh aspects. Similar increases in exotic species cover have been documented in the boreal forest due to vegetation removal (Haeussler et al. 1999; Haeussler et al. 2004) and following thinning and/or burning (Bailey et al. 1998; Griffis et al. 2001; Thysell and Carey 2001; Dodson and Fielder 2006). Exotic species pose a threat to native plant diversity, can alter ecosystem functions (D'Antonio and Vitousek 1992) and can be very difficult to eradicate. However, exotic cover was very low throughout the study and did not appear to be a threat to native vegetation at the present time. Once established, many annual and exotic species are aggressive competitors with conifers and other native vegetation. Competition from herbaceous vegetation has been demonstrated to be more limiting to conifer growth than shrubs (Newton 1982; Newton and Preest 1988; Pabst et al. 1990; Monleon et al. 1999). Therefore, conifer growth may be limited by the increased cover of annual herbs on harsh aspects following vegetation removal, especially since scalping was ineffective at reducing herbaceous cover.

It is impossible to determine at this time if successional trajectories with and without vegetation removal will continue to diverge or converge in the future. Lack of root removal should allow for the recovery of vegetation and plant communities from restoration activities over time, as seen in other studies (Haeussler et al. 2004). However, altered shrub compositions and increases in exotic species on harsh aspects may result in a longer time period of altered trajectories for early-successional forests (D'Antonio and Vitousek 1992; Pausas 1999; Keeley and Fotheringham 2004). Increased disturbance frequency, such as restoration activities following fire, has been shown to shift dominant vegetation from evading to enduring shrubs (Pausas 1999) or to exotic grasses and forbs (Pausas 1999; Keeley and Fotheringham 2004). The current study documented a decrease in evading species in areas with vegetation removal coupled with constant cover of enduring species over time, indicating that such a shift in trait group dominance may be possible. Of additional concern is that several evading shrubs are important nitrogen fixers (e.g. *Ceanothus* sp.). Reduction of these species could result in reduced community nitrogen fixation (Busse et al. 1996). Although, reduction of *Ceanothus* sp. would not necessarily effect community nitrogen levels at sites that are not severely nitrogen deficient, such as the western Cascades (Zatvitkovski and Newton 1968; but see Binkley et al. 1982). *Ceanothus* sp. do not respond consistently to forest management, with higher cover in managed areas in some studies (Halpern 1988; Huffman and Moore 2004; Lopez-Ortiz 2007) and lower cover in other areas compared to unmanaged areas (Stuart et al. 1993). Differences in *Ceanothus* sp. response to management may be related to amount of ground disturbance since *Ceanothus* seeds require mechanical or heat scarification prior to germination. In this study, no differences in nitrogen-fixing species cover occurred due to restoration activities or vegetation removal making concerns over community nitrogen unwarranted at this time. However, the potential lack of ability of evading shrubs to recover from vegetation removal could result in long-term differences in community nitrogen in areas where *Ceanothus* had been removed. Regardless of altered trajectories or a shift in dominance from evading to enduring shrub, conifers can survive under abundant shrub layers (Lopez-Ortiz 2007; Shatford et al. 2007) and will likely become the dominant canopy layer over the long-term.

Manual shrub removal enhances conifer seedling growth in southwestern Oregon (Conard and Radosevich 1982; McDonald and Fiddler 1986; Pabst et al. 1990; Hobbs et al. 1992; Tesch et al. 1992) and was documented here as effective at suppressing tall shrubs early in succession. Ecological benefits of manual shrub removal are potentially limited by abundant shrub sprouting (Hobbs and Wearstler 1985; Tesch et al. 1992). Additionally, many sprouting species have deep rooting systems (Hobbs and Wearstler 1985) and continue to compete with conifers for soil moisture following manual shrub removal (Zatvitkovski et al. 1969; Conard and Radosevich 1982; Radosevich 1984; Pabst et al. 1990). If rapid conifer growth is not of concern, intensive shrub removal may not be necessary because conifer survival can be high under abundant shrub cover (Lopez-Ortiz 2007; Shatford et al. 2007) and is not affected by single-entry manual vegetation removal (Tesch et al. 1992). However, if conifer growth and establishment is a concern, repeated manual vegetation removal may reduce shrub cover long enough to shift the competitive advantage to conifers (McDonald and Fiddler 1986; Wagner and Radosevich 1998).

Thorough minimizing the intensity of vegetation removal (i.e. manual removal < herbicide removal) native plant communities can be maintained during restoration activities, in the absence of exotic species. The transition to a conifer dominated system will alter the current plant communities in areas with conifer planting. Long-term effects of vegetation removal on exotic species should be monitored to prevent further establishment, particularly in the presence of noxious weeds (e.g. *Bromus tectorum* and *Cirsium* sp. found in the current study). Long-term effects of manual vegetation removal in the absence of salvage logging on structure and plant communities are unknown, but the short-term nature of the removal leaves the potential for many native species to recover over time.

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Table 3.1. ANOVA results, treatment means (% cover except for bryophytes where treatments mean is cover class) and contrast p-values of structural group percent cover. Results are for five restoration treatments and one control in the large sub-block. Numerator d.f. for treatment = 5, year = 2 (bryophyte: year = 1) and treatment x year = 10 (bryophyte: treatment x year = 5). Denominator d.f. = 66 (bryophyte = 42). ^ Results are for high-density mixed species plantings with and without vegetation removal in large and small sub-blocks. There were no aspect x year x vegetation removal interactions. Numerator d.f. for VR x aspect =1, denominator d.f. = 38(bryophyte = 22). Significant p-values ($\leq$ 0.05) are in bold. Mod = moderate aspect, Har = harsh aspect, NVR = no vegetation removal, VR = vegetation removal.

	Tall Shrubs		**Low Shrubs**		**Herbs**		**Bryophytes**	
ANOVA Results	F	P	F	p	F	p	F	P
Treatment	8.5	**<0.0001**	1.51	0.20	2.5	**0.043**	1.5	0.21
Year	44.0	**<0.0001**	194.6	**<0.0001**	131.5	**<0.0001**	13.1	**0.0008**
Treatment x Year	9.5	**<0.0001**	1.09	0.39	0.47	0.9	2.1	0.079
Treatment Means								
Year	**Two**	**Four**	**Two**	**Four**	**Two**	**Four**	**Three**	**Four**
Control	9	26	22	50	28	53	4	3
Low-density NVR	8	22	22	47	33	60	4	4
High-density NVR	6	22	27	62	37	63	4	3
Low-density VR	.	.	21	56	43	74	4	3
High-density VR	.	.	18	47	29	63	3	3
Monoculture	.	.	21	49	33	64	4	4
Contrast p-values								
Year	**Two**	**Four**	**Two**	**Four**	**Two**	**Four**	**Three**	**Four**
NVR vs. control	0.55	0.55	0.40	0.52	0.34	0.25	0.36	0.83
NVR vs. VR	**0.03**	**<0.0001**	**0.01**	0.56	0.84	0.19	**0.007**	0.27
ANOVA Results	F	p	F	p	F	p	F	p
VR x Aspect^	0.24	0.63	6.16	**0.02**	0.25	0.62	0.23	0.64
Aspect Contrast p-values								
Aspect	Mod	Har	Mod	Har	Mod	Har	Mod	Har
NVR vs. VR^	**<0.0001**	**0.0002**	**<0.0001**	0.44	0.71	0.81	**0.0008**	**0.03**

Table 3.2. ANOVA results, treatment means or medians (% cover) and contrast p-values of vascular plant trait group percent cover. Results are for five restoration treatments and one control in the large sub-block. Numerator d.f. for treatment = 5, year = 2 (bryophyte: year = 1) and treatment x year = 10 (bryophyte: treatment x year = 5). Denominator d.f. = 66 (bryophyte = 42). ^ Results are for high-density mixed species plantings with and without vegetation removal in large and small sub-blocks. There were no aspect x year x vegetation removal interactions. Numerator d.f. for VR x aspect =1, denominator d.f. = 38(bryophyte = 22). Significant p-values (≤ 0.05) are in bold. Yr = year, Mono = Monoculture, Mod = moderate aspect, Har = harsh aspect, NVR = no vegetation removal and VR = vegetation removal. [a] Group log-transformed before analysis, reported values are back-transformed.

Table 3.2.

	Disturbance Response						Origin				Seral Stage					
	Endurer		Evader		Invader		Natives		Exotics[a]		Late[a]		Early		N- Fixers	
ANOVA	F	p	F	p	F	P	F	p	F	p	F	p	F	p	F	p
Treatment	1.04	0.4	2.24	0.06	1.83	0.12	4.81	**< 0.0001**	0.21	0.96	0.77	0.57	2.19	0.07	2.67	**0.03**
Year	195.2	**< 0.0001**	121.5	**< 0.0001**	128	**< 0.0001**	245.2	**< 0.0001**	93.6	**< 0.0001**	67.8	**< 0.0001**	118	**< 0.0001**	46.4	**< 0.0001**
Treatment x Year	4.24	**< 0.0001**	3.16	**0.002**	0.94	0.5	1.11	0.37	0.75	0.68	4.01	**< 0.0001**	5.78	**< 0.0001**	2.94	**0.004**
Treatment Means																
Year	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**
Control	40	103	16	55	31	68	55	146	1	5	15	43	30	91	5	29
Low NVR	35	102	13	47	34	65	59	145	1	4	16	48	26	85	4	25
High NVR	43	101	22	73	31	62	67	159	1	3	15	43	34	111	11	47
Low VR	42	107	17	43	41	78	61	141	1	4	11	35	34	86	4	16
High VR	29	74	12	37	25	64	44	111	1	5	10	28	22	69	4	17
Mono.	35	93	15	40	32	65	50	123	1	3	12	30	29	69	4	14
Contrast p-values																
Year	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**
NVR vs. control	0.88	0.92	0.62	0.57	0.81	0.64	0.22	0.63	0.86	0.6	0.86	0.79	0.91	0.51	0.16	0.39
NVR vs. VR	0.5	0.35	0.31	**0.01**	0.91	0.31	**0.05**	**0.02**	0.91	0.62	**0.02**	**0.02**	0.65	**0.03**	**0.03**	**0.005**
ANOVA	F	p	F	p	F	P	F	p	F	p	F	p	F	p	F	p
VR x Aspect^	0.37	0.55	3.73	0.06	7.4	**0.01**	5.72	**0.02**	1.55	0.22	0.08	0.77	18.1	**0.0001**	0.05	0.82
Aspect Contrast p-values																
Aspect	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har
NVR vs. VR^	**0.008**	0.06	**0.01**	**0.02**	**0.0008**	0.76	**< 0.0001**	**< 0.0001**	0.61	0.22	**0.03**	0.07	**< 0.0001**	**< 0.0001**	0.24	0.40

Table 3.2 (Continued).

	Growth Form													
	Deciduous		**Evergreen**		**Sub-shrub**		**Annual**[a]		**Perennial**		**Graminoid**[a]		**Fern**[a]	
ANOVA Results	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Treatment	2.24	0.06	1.35	0.26	0.91	0.48	0.6	0.7	1.25	0.3	3.75	**0.005**	1.57	0.18
Year	123	**<0.0001**	46.5	**<0.0001**	110.2	**<0.0001**	68.8	**<0.0001**	57.8	**<0.0001**	66.8	**<0.0001**	23.8	**<0.0001**
Treatment x Yr	4.28	**<0.0001**	1.42	0.19	1.94	**0.06**	0.46	0.91	1.53	0.15	0.42	0.93	0.72	0.7
Treatment Means														
Year	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**
Control	18	63	11	24	12	40	9	14	16	44	0.3	7	1	1
Low NVR	18	58	8	20	12	39	9	21	14	43	0.7	11	1	3
High NVR	24	78	8	19	18	48	12	19	21	47	1	11	0.4	0.7
Low VR	15	46	4	11	15	47	13	24	28	58	1	12	3	5
High VR	11	40	5	12	11	36	13	30	15	33	1	16	2	2
Mono.	14	39	5	14	16	49	10	18	21	51	0.2	8	1	2
Contrast p-values														
Year	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**	**2**	**4**
NVR vs. control	0.53	0.65	0.23	0.43	0.43	0.7	0.76	0.36	0.64	0.92	0.12	0.21	0.8	0.74
NVR vs. VR	**0.02**	**0.01**	0.06	0.07	0.5	0.84	0.43	0.31	0.32	0.93	0.92	0.42	**0.04**	0.13
ANOVA Results	F	p	F	p	F	p	F	p	F	p	F	p	F	p
VR x Aspect^	3.36	0.07	0.37	0.54	0.38	0.54	3.12	0.09	0.31	0.58	0.02	0.88	0.07	0.80
Aspect Contrast p-values														
Aspect	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har	Mod	Har
NVR vs. VR^	**<0.0001**	**0.009**	0.08	0.36	**0.04**	0.23	0.75	**0.009**	0.57	0.19	0.17	0.22	0.65	0.26

Table 3.3. A-statistics and p-values for differences in plant community and trait composition among all restoration treatments and between planting only versus control treatments large subblock and vegetation removal (VR) versus no vegetation removal (NVR) on two aspects (harsh and moderate) from MRBP/MRPP. Block with accidentally scalped NVR plot was excluded from year three and four analyses. All differences were considered individually without regard to other groups. *Analyzed with MRPP, included control and monoculture treatments on both aspects. Due to the need for balanced groups in MRBP, partial datasets were used for blocked factors as follows: restoration treatments included five restoration treatments and one control treatment in large sub-block, NVR/VR by aspect included high-density treatments with and without vegetation removal on two aspects, NVR/VR (harsh) and (moderate) included high-density treatments with and with vegetation removal on one aspect. Significant p-values (≤ 0.05) and relatively strong A-statistics (> 0.1) are in bold.

Community		**Vascular Plant Year Two**		**Full Year Three**		**Cryptogam Year Three**		**Trait Year Two**	
Factors	**Group (#)**	**A**	**p**	**A**	**p**	**A**	**p**	**A**	**p**
Restoration Treatments	6	-0.10	0.98	0.001	0.43	0.03	0.06	-0.03	0.76
Control/ Planting only	3	-0.02	0.99	-0.01	0.92	-0.02	0.83	-0.06	0.95
NVR/VR*	2	0.048	**0.013**	0.09	**0.002**	0.09	**0.000**	0.02	0.09
NVR/VR by aspect	4	-0.007	0.51	0.02	**0.007**	**0.10**	**0.003**	**0.20**	**0.006**
NVR/VR (harsh)	2	-0.01	0.69	0.02	**0.04**	0.09	**0.04**	**0.13**	**0.04**
NVR/VR (moderate)	2	0.02	0.10	0.05	**0.03**	**0.17**	**0.04**	**0.44**	**0.02**
Community		**Vascular Plant Year Four**		**Full Year Four**		**Cryptogam Year Four**		**Trait Year Four**	
Factors	**Group (#)**	**A**	**p**	**A**	**p**	**A**	**p**	**A**	**p**
Restoration Treatments	6	0.02	**0.05**	0.01	**0.05**	0.01	0.25	-0.03	0.64
Control/ Planting only	3	-0.02	0.94	-0.02	0.95	-0.009	0.59	-0.08	0.90
NVR/VR*	2	**0.13**	**0.000**	**0.13**	**0.0007**	0.03	0.08	**0.10**	**0.003**
NVR/VR by aspect	4	0.03	**0.02**	0.03	**0.01**	0.05	**0.02**	**0.25**	**0.01**
NVR/VR (harsh)	2	0.04	**0.03**	0.03	**0.03**	-0.02	0.72	0.08	0.26
NVR/VR (moderate)	2	0.04	**0.04**	0.05	**0.03**	**0.14**	**0.03**	**0.43**	**0.04**

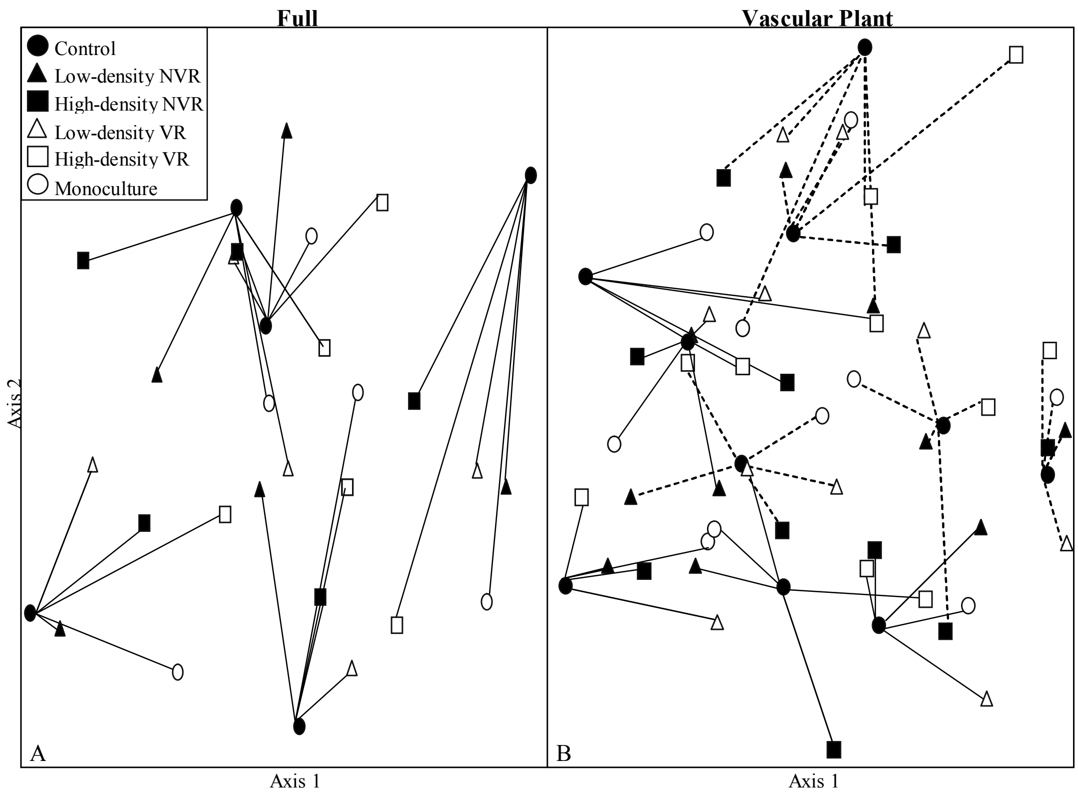

Figure 3.1. Three-dimensional NMS ordination of A) full vascular plant and cryptogam community in year four and B) vascular plant only community in year two (dashed lines) and year four (solid lines) with lines indicating change in restoration treatments from the control treatments within large sub-blocks (small sub-block treatments are not shown). NVR = no vegetation removal, VR = vegetation removal, High-density = mixed species planting at 1075 tph, Low-density = mixed species planting at 470 tph, monoculture = Douglas-fir monoculture at 1075 tph with vegetation removal.

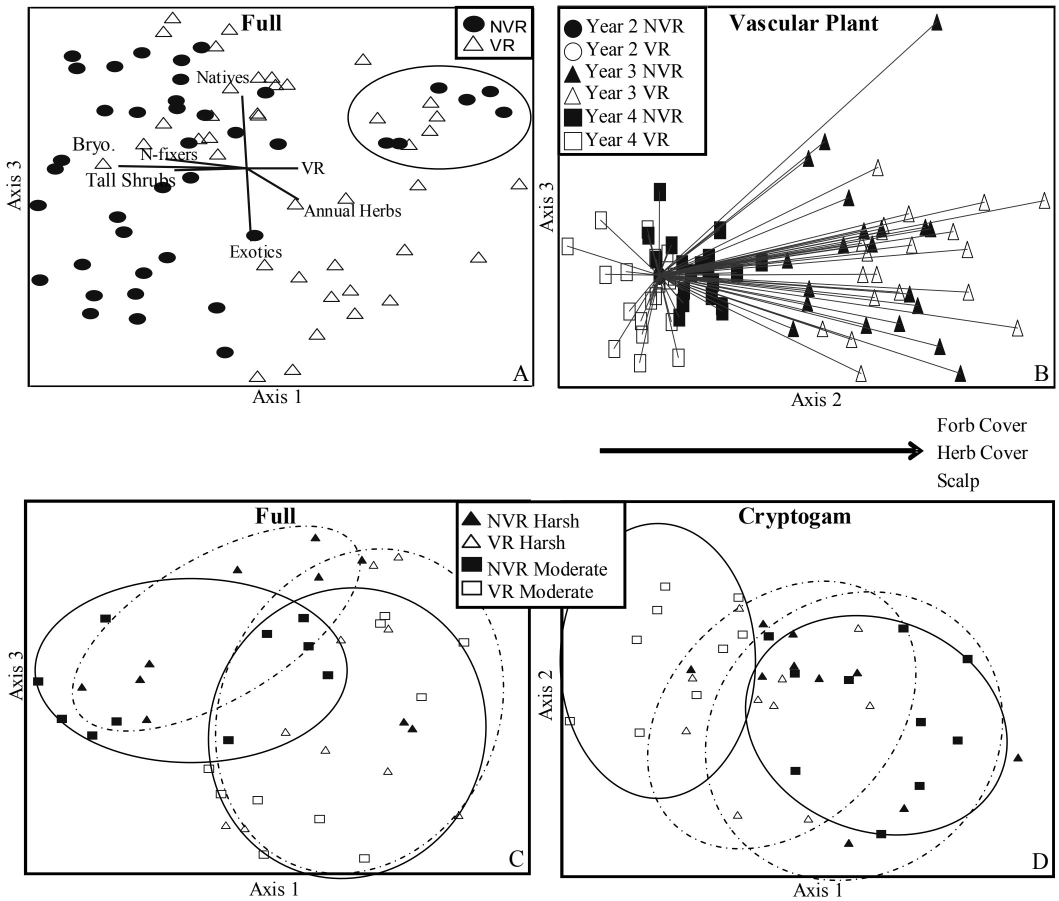

Figure 3.2. Full vascular plant and cryptogam community NMS ordination. (A) Coded for and rigidly rotated by vegetation removal status (VR = vegetation removal, NVR = no vegetation removal). Black lines are joint plots or correlations of trait groups ($R^2 \geq 1.80$). Lines represents stregnth of correlation, longer lines having stronger correlation. Circled block had low overall vegetation cover. (B) Relative length and direction of successional trajectories over time for vascular plant community NMS ordination shown in Fig. 3.1 coded for vegetation removal status by year. The centroid or origin represents the year two for changes from year two to three and is rescaled to represent year three for changes from year three to four. Dark grey indicate direction and magnitude of change between years and black arrow below ordination indicates direction of correlated cover variables ($R^2 \geq 0.2$). (C) Axis 1 and 3 of full community NMS ordination shown in Fig. 3.1 and (D) cryptogam community NMS ordination coded for vegetation removal status on contrasting aspects (moderate and harsh). Dashed circles are harsh aspects and solid circles are moderate aspects.

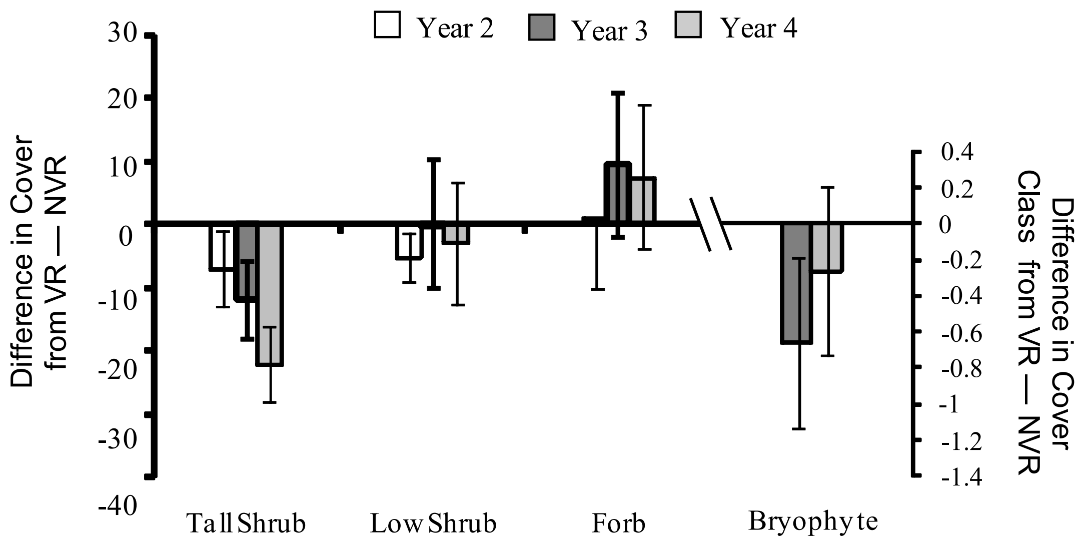

Figure 3.3. Average difference in percent cover (left axis) and bryophyte cover class (right axis) of structural layers in vegetation removal versus no vegetation removal treatments over time. Numbers are average difference between vegetation removal and no vegetation removal and 95% CIs. Differences with CIs that do not encompass zero were significantly different from zero at $p < 0.05$. NVR = mixed species planting without vegetation removal and VR = mixed species planting with vegetation removal.

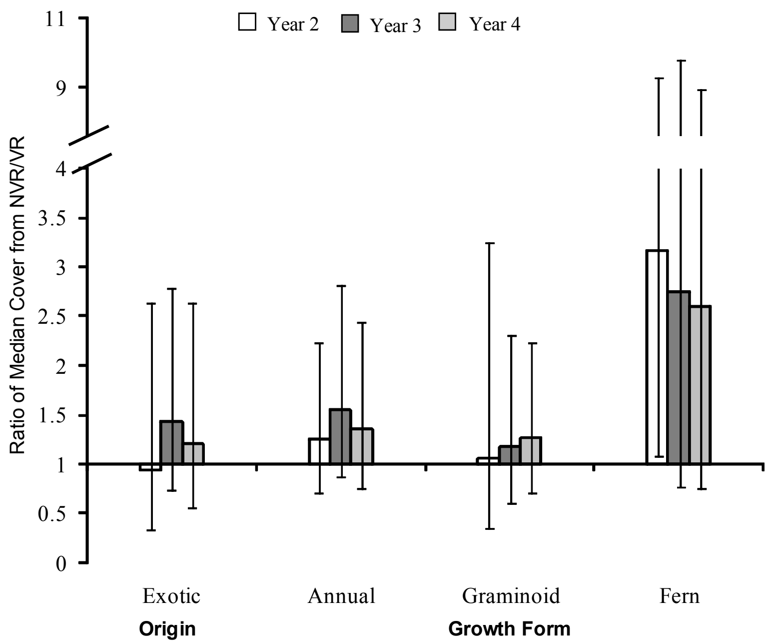

Figure 3.4. Ratio of median percent cover of vegetation removal to no vegetation removal treatments for log transformed trait group cover over time. Numbers represent ratio of medians and 95% CI. Ratios with CIs that do not encompass one were significantly different from zero at $p < 0.05$. NVR = mixed species planting without vegetation removal and VR = mixed species planting with vegetation removal.

Figure 3.5. Differences in average percent cover between vegetation removal and no vegetation removal treatments over time for different trait groups including seral stage, nitrogen fixing capacity, origin, fire response, and growth form for traits whose cover was not log transformed. Numbers are average difference and 95% CI. Differences in CIs that do not encompass zero were significantly different from zero at $p < 0.05$. Evgreen shrub = evergreen shrubs, Decid. shrub= deciduous shrubs, NVR = mixed species planting without vegetation removal and VR = mixed species planting with vegetation removal.

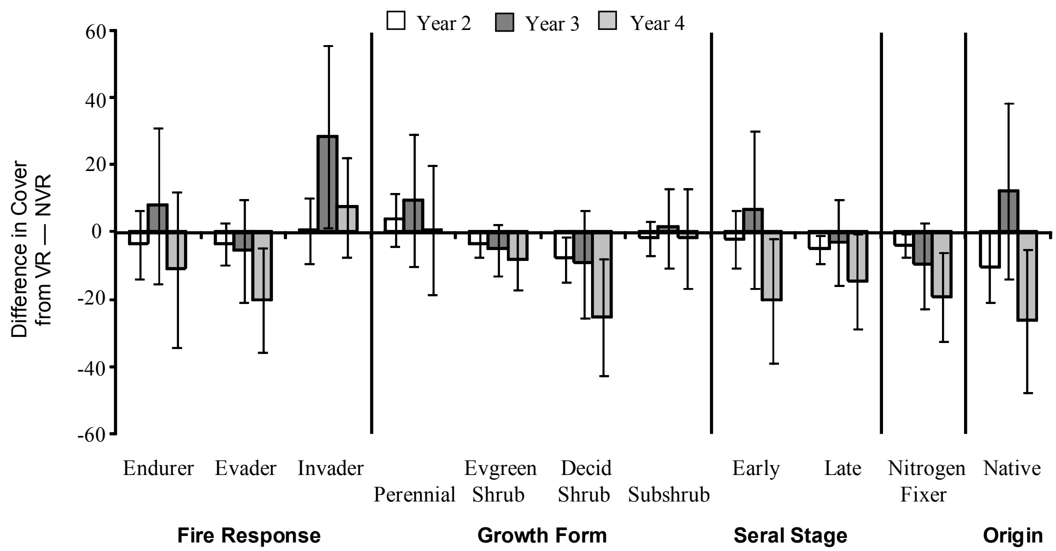

Table 3.4. Indicator species and their trait group designations for vegetation removal (VR) and no vegetation removal (NVR) on contrasting aspects. Indicator values (IV) with Monte Carlo significance greater than $p < 0.05$ are shown. [t]Tall shrub only. [s]Seedlings of a given species. Trait group of species are designated by letters: En = endurer, Ev = evader, I = invader, R = residual, a = annual herb, p = perennial herb, g = graminoid, b = bryophyte, ss = sub-shrub, eg = evergreen shrub, d = deciduous shrub, e = early-seral, l = late-seral, n = native, ex = exotic and nf = nitrogen fixer. Blank indicates undefined status.

		Species	Fire Response	Growth Form	N-Fix	Seral Stage	Origin	IV
Harsh	**NVR**	*Luzula comosa*	En	g			n	70.0
		Cornus nuttallii [t]	En	d		e/l	n	53.3
		Vicia americana	I/Ev	P	nf	e/l	n	52.4
		Lathyrus polyphyllus	I/Ev	P	nf		n	52.2
		Asyneuma prenanthoides	Ev/En	p			n	51.8
		Holodiscus discolor[t]	Ev/En	d		e/l	n	43.0
		Polytrichum juniperinum	R	b			n	40.6
		Ceanothus sanguineus [t]	Ev	d	nf	e	n	30.5
	VR	*Cornus nuttallii*	En	d		e/l	n	59.0
		Arctostaphylos patula	I/Ev	eg		e	n	42.3
		Chrysolepis chrysophylla	En	eg		e/l	n	37.1
Moderate	**NVR**	*Fissidens* sp.	I	b		e	n	79.5
		Corylus cornuta[t]	En	d		e/l	n	61.1
		Rubus leucodermis [t]	I/En/Ev	d		e	n	59.5
		Acer macrophyllum [st]	I/En	d			n	50.7
		Cirsium vulgare	I	a		e	ex	49.1
		Arbutus menziesii [t]	I/En	eg		e	n	42.4
		Rubus ursinus	I/En/Ev	d/ss		e	n	42.4
		Weissia controversa	I	b			n	41.3
		Ribes cruentum	I/En/Ev	d			n	34.3
	VR	*Acer macrophyllum*	En	d			n	61.8

CHAPTER 4 – POST-FIRE MICROSITES AND EFFECTS OF BRYOPHYTES ON GERMINATION AND ESTABLISHMENT OF CONIFERS AND EARLY-SERAL SPECIES

ABSTRACT

In early post-fire succession, bryophytes are often the dominant vegetation layer. Early-seral bryophyte distributions following fire are patchy. Little is known about habitat requirements of early-seral bryophytes or their influence on germination and establishment of vascular plants. In the presence of seed or spore sources, microsite conditions can affect distributions of bryophytes, conifers and early-seral vegetation. The objectives of this study were to examine the distribution and characteristics of microsites following post-fire restoration, habitat requirements for establishment of post-fire bryophytes, and to compare germination and establishment of vascular plants between bryophyte and bare soil seedbeds. An observational study and two seeding trials (one each in a greenhouse and the field) were utilized to address these objectives. Post-fire microsites were heterogeneous, partially due to the existence of pre-fire legacies, including downed wood, snags, and sprouting vegetation. Post-fire bryophytes occupied specific microsites that generally occurred on undisturbed soil with low to moderate litter and overstory cover. Impacts of bryophyte seedbeds on germination and growth of vascular plants differed by bryophyte type, vascular plant species, and interactions with slope, predators, and other environmental factors. In a greenhouse study, germination of early-seral vascular plants or conifers was not affected by burnt bryophyte seedbeds, but *Pinus ponderosa* germination was higher in unburnt bryophytes compared to other seedbeds. *Ceanothus sanguineus* and *Chamerion angustifolium* had reduced growth in burnt bryophyte seedbeds compared to other seedbeds while conifers did not. *Pseudotsuga menziesii, Abies concolor* and *Pinus ponderosa* had higher shoot biomass in unburnt bryophyte seedbeds than other seedbeds. Competitive interactions appeared to occur between early-seral bryophytes and vascular plants but not between late-seral bryophytes and vascular plants. Fundamental differences

exist between early-seral and late-seral bryophytes that could cause this discrepancy including dominant bryophyte lifeforms, mat density, and mat depth Contrary to the greenhouse results, higher *Chamerion angustifolium* germination and *Ceanothus sanguineus* establishment occurred in burnt bryophyte seedbeds than other seedbeds in the field, indicating facilitation due to early-seral bryophyte physical and microsite characteristics, or their interactions. Restoration treatments have the potential to alter successional patterns following fire due to alteration of microsite characteristics, which impact early-seral bryophyte distributions and germination and establishment of vascular plants.

INTRODUCTION

Biological and physical characteristics of habitat immediately surrounding a seedling, labeled microsites (Whittaker and Levin 1977), affect germination and establishment of species in the presence of propagules (Beatty 1984; Fowler 1988; DeLong et al. 1997; Gray and Spies 1997; Elmarsdottir et al. 2003; Bonnet et al. 2005). Habitat suitability at a fine scale can result in microsites overriding larger scale environmental conditions in terms of their influence on plant establishment and growth (Gray and Spies 1997; Beatty 2003). Microsites can be particularly important for species establishment in early successional environments (Gomez-Aparicio 2008). Disturbances, such as fire or forest harvest, increase microsite heterogeneity through variation in disturbance severity (Turner et al. 1994) and legacy components, such as downed wood, sprouting shrubs, or tree uprooting (George et al. 2003). Fire can also homogenize forest microsites by decreasing or eliminating microsites associated with decayed wood, pleurocarpous bryophyte cover, deep duff and closed canopies. Interactions of abiotic and biotic factors control microsite availability and quality during secondary succession due to the recovery of vegetation that alters environmental conditions.

Bryophytes are the dominant vegetation layer immediately following fire in many regions (Cremer and Mount 1965; Eversman and Horton 2004; Wang and Kemball 2005; Kayes et al. in review). Post-fire bryophyte distributions are patchy, at millimeter to meter scales. Due to patchiness, post-fire bryophytes have the potential to increase microsite heterogeneity and influence vascular plant distributions. Presence of bryophytes can enhance (Minore et al. 1984; Keizer et al. 1985; Belnap et al. 2001; Dovčiak et al. 2003; Elmarsdottir et al. 2003; Bonnet et al. 2005) or inhibit (Keizer et al. 1985; van Tooren 1990; Zamfir 2000; Otsus and Zobel 2004) germination and/or survival of vascular plants. Effects of bryophytes on germination and establishment vary by bryophyte and vascular plants studied. Specifically, post-fire bryophytes effects on microsite suitability for germination and establishment and their contributions to microsite variability have not been documented.

Mixed-conifer forest, the dominant forest type in southwestern Oregon, burns with an average fire return interval of 5 to 75 years (Sensenig 2002). Following fire in mixed-conifer forests, conifers regenerate by seed and have specific microsite requirements for germination and survival, ranging from mineral soil substrate to presence of mycorrhizal fungi (Christy and Mack 1984; Harmon and Franklin 1989; Burns and Honkala 1990; Gray and Spies 1997). On the other hand, many early-seral vascular plants, such as *Ceanothus sanguineus* Pursh, *Chamerion angustifolium* (L.) Holub, and *Vicia americana* Muhl. ex Willd., are able to germinate and establish in a wide variety of microsites in mixed-conifer forests (Hickey and Leege 1970; USDA 2006). Presence of a large variety of conifer and other species and the frequent fire regime make southwestern Oregon an ideal place to study post-fire seedling regeneration and microsite interactions. Additionally, mixed-conifer forests are often managed for timber production. To meet these management objectives, reforestation coupled with vegetation removal is often implemented to restore conifer forests following fire. Restoration activities have the potential to alter microsite conditions through soil disturbance and removal of legacy components, such as sprouting shrubs (Hobbs et al. 1992; Haeussler et al. 1999; Current manuscript, Ch. 3). Interactions among microsites, post-fire bryophytes and regenerating vascular plants are poorly understood. Understanding these interactions, as well as, the ecology of seed germination, seedling emergence, and establishment of early-seral vascular plants and conifers is critical for explaining ecosystem recovery patterns following fire and will help develop management strategies that efficiently achieve management goals in mixed-conifer forests.

The objectives of this study were to: (1) describe the distribution and characteristics of microsites following fire and restoration activities (e.g. vegetation removal and conifer planting), (2) determine if early-seral bryophytes preferentially inhabit specific microsites, (3) describe distinctive microsite characteristics of early-seral bryophyte habitat if such microsites exist and (4) compare germination and establishment of early-seral vascular plants and conifers between bryophyte and bare soil seedbeds.

METHODS

Study Site

The Timbered Rock fire occurred within the Western Cascades physiographic province, near the intersection of the Klamath and Cascade Mountains, in mixed conifer forest primarily within the *Abies concolor* and mixed conifer forest zones (Franklin and Dyrness 1973). The climate is generally characterized by mild, wet winters and warm, dry summers. Topography is often steep (slopes >20%) with volcanic bedrocks and elevations between 800 m and 1000 m. The 2002 wildfire burnt with varying intensity and severity over 11,000 hectares (ha) between July 13th and August 9th. Approximately 40% of the burned area was occupied by *Pseudotsuga menziesii* (Mirb.) Franco plantations < 35 years of age. In addition to *P. menziesii*, plantations had components of *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., *Pinus ponderosa* C. Lawson, *Pinus lambertiana* Douglas, *Calocedrus decurrens* (Torr.) Florin, and a significant hardwood component with a combined average density of 500 hardwood trees per ha (tph).

In 2004 (two years post-fire), the Timbered Rock Reforestation, Stand Development, and Fuels (Timbered Rock) Study was implemented in five burnt plantations (blocks) to study the effects of mixed species conifer planting, vegetation removal, and site quality (in eight treatment combinations) on conifer development, plant communities and fuels. See Ch. 2 for full block descriptions (Ch. 2, Table 2.A1) and Ch. 3 for full treatment descriptions. Vegetation removal was applied to half of the restoration treatments (four out of eight treatments in each block) and consisted of manual cutting of tall vegetation focused on woody shrubs in years two through four post-fire over the entire treatment plot and scraping away all vegetation to mineral soil (scalping) in an approximate 0.75 m radius around planted conifer seedlings in year three post-fire. The same work crew applied all components of vegetation removal treatments. One plot without vegetation removal was accidentally scalped.

Experiment Overview

Three experiments, described below, were utilized to meet the objectives. First, a randomized block design within the Timbered Rock Study was used to examine microsites following wildfire and restoration activities combined and determine if early-seral bryophytes inhabit specific microsites. Second, a greenhouse seeding experiment was used to examine the effects of different seedbeds on germination and growth. Third, a field seeding trial was used to further examine effects of different seedbeds, as well as to separate microsite effects from bryophyte effects, on germination and establishment. Early-seral vascular plants (*C. sanguineus, C. angustifolium,* and *V. americana*) were selected to represent different life history traits (i.e. shrub, herb, nitrogen-fixing) and reproductive strategies (fire-stimulated, wind-dispersed) of early-seral vascular plants. Dominant conifers (*P. ponderosa, P. lambertiana, P. menziesii, C. decurrens,* and *A. concolor*) were selected due to interest in conifer regeneration and the importance of conifers in forest recovery. Population inferences are limited to the mixed-conifer forests of southwestern Oregon from which the seeds and soil were collected.

Experimental Design and Data Collection

Microsite Variation and Bryophyte Habitat

To describe microsites following fire and restoration treatments combined and to determine if early-seral bryophytes inhabit specific microsites, microsite plots were examined within the Timbered Rock study in areas with and without vegetation removal. Four permanent subplots (10 m x 10 m "quads") were established to measure vegetation and fuels within each of eight treatments (four each with and without vegetation removal) in five blocks. Within each quad, 3 m x 3 m subplots were delineated in each corner for measuring vegetation variables. Coordinates of one microsite center from the uphill and left corner of each subplot were selected using a random number table to examine proportions of all potential microsites. New coordinates were selected for five microsites (less than 1% of all microsites) that fell on a large log or stump that had not yet begun to decompose (i.e. germination was not probable), slightly biasing the microsite distribution results. Microsites were temporarily delineated using a cross section of a PVC pipe with 15 cm diameter interior (considered the "plant's eye view" sensu Collins and Good 1987). All microsites (640 total) were measured by a seven person crew between June and August 2005, three years post-fire.

Microsite characteristics observed included general site description, substrate, litter composition, micro-topography, micro-topographic height (perpendicular to the micro-slope), and litter composition categories (Table 4.1), and number of seedlings, litter and duff depth, micro-slope, micro-aspect, canopy cover, and percent cover of total ground cover (combined cover of all other cover groups except for vascular plants or 1-bare ground), small woody debris (< 2.54 cm diameter), large woody debris (> 2.55 cm diameter), vascular plants (below 10 cm height), bryophytes, lichens (ground-dwelling only), litter, fungi, and other. For categorical data, more than one category was assigned when applicable (Table 4.1). Micro-slope (%, slope of the microsite along the aspect) and micro-aspect (degrees, aspect within the microsite) were measured with a compass and compass clinometer. Litter (to duff or mineral soil) and duff depth (bottom of litter layer to mineral soil) were measured to the nearest mm at one point within the microsite, chosen to reflect the average depth. Percent cover of different variables was measured by ocular estimation in each microsite. Percent canopy cover in microsites was estimated using a convex densiometer at 10 cm above the surface, i.e. at seedling level. If present, number of *C. angustifolium*, *P. menziesii*, *V. americana*, *C. sanguineus* and *A. concolor* seedlings were counted in each microsite. *Pinus ponderosa, P. lambertiana* and *C. decurrens* seedlings were not present in any microsite.

Seedbed Effects on Germination and Establishment

Seed Collection and Testing. Ceanothus sanguineus, C. angustifolium, and *V. americana* seeds were collected from six sites around the Timbered Rock fire near the end of the growing season (August) when seeds had matured but not dispersed. Seed were cleaned and stored at room temperature (~21° C) until the experiment started (2 - 4 months). Medford District Bureau of Land Management (BLM) provided seeds of five conifers (*A. concolor, C. decurrens, P. lambertiana, P. ponderosa,* and *P. menziesii*). Seeds of each conifer species were collected within the seed zone for that species that encompassed the Timbered Rock fire. BLM seed had been in cold (0° C) storage for less than five years. Fifty to a hundred seeds of each species were tested for germination viability either in potting soil (conifers) or on moist blotter paper (early-seral species) in a 20°C germination chamber prior to seeding (Table 4.2). The germination chamber was illuminated for eight hours per day and seeds were germinated until no more seeds appeared to be viable (1 – 3 months).

Greenhouse Study. To compare germination and growth of early-seral vascular plants and conifers in different seedbeds under controlled conditions a greenhouse experiment was utilized. Soil samples of three different seedbeds with intact surface layer were collected in 10 cm diameter x 10 cm deep PVC pipes (pots) from a site within the Timbered Rock three years post-fire. “Burnt bryophyte” seedbeds were burned (evidenced by blackened soil and tree boles) with > 75% bryophyte cover; "burnt bare soil" seedbeds were burned with < 10% early-seral bryophyte cover; and "unburnt bryophyte" seedbeds was unburnt with 100% bryophyte/lichen cover. Burnt bryophyte seedbeds were dominated by early-seral bryophytes, *Funaria hygrometrica* Hedw. and *Ceratodon purpureus* (Hedw.) Brid. Unburnt bryophyte seedbeds were dominated by *Eurhynchium oreganum* (Sull.) A. Jaeger with a small lichen (*Peltigera membranacea* (Ach.) Nyl.) component and assumed to represent later-seral species. All bryophyte cover was scraped away from the surface of burnt bare soil seedbeds prior to seed sowing. However, early-seral bryophytes are common greenhouse weeds that are very difficult to eradicate and by the end of the experiment several of the burnt bare soil seedbed pots had significant early-seral bryophyte cover (20 - 70%, one pot having 95% cover). Inferences were still possible because at the end of the experiment, cover of early-seral bryophytes was generally higher (≥ 95%) in burnt bryophyte seedbeds than burnt bare soil seedbeds.

Pots were systematically numbered within each of the three different seedbeds and randomly assigned (using a random number table) a species to allow inference to the effects of seedbeds. Conifer and *C. sanguineus* seeds were wet/cold (5°C) stratified for the recommended length of time for each species (Table 4.2: Baskin and Baskin 1998). *C. sanguineus* seeds were scarified for five minutes in boiling water prior to stratification to break dormancy. Many *C. sanguineus* seeds molded during stratification. Moldy seeds were removed and remaining seeds sprayed with a mild Captan fungicide solution three times over 35 days. Five replicate pots per seedbed were sown between January 10 and 12, 2006 for all eight species (Table 4.2) resulting in a total of 15 pots per species (120 total pots). Due to loss of moldy seeds and variation in seed size (from 1 to 15 mm), different numbers of seeds were sown for each species. Available seeds per species were either evenly distributed between pots or a maximum of 30 large (> 5 mm) or 100 small (<5 mm) seeds were sown, resulting in minimum of 13 seeds sown/pot (Table 4.2).

In the greenhouse, pots were exposed to supplementary light (high-pressure sodium and mercury halide lamps) 16 hrs per day, watered daily, and kept between 21°C and 15.5°C (day and night respectively). Trays (containing 8 - 9 pots of one seedbed with a mixture of species) were rotated on the bench bi-weekly. The number of seeds germinated was recorded every 1 - 3 days for 30 days. A seed was considered germinated when the radical emerged. Natural emergent vascular plants were removed from pots without disturbing the upper seedbed layer. After 30 days (February 14), seedlings were thinned to one per pot, selecting for a medium-sized seedling towards the pot center. Seeds that germinated after this date were recorded and removed. Germination success was calculated as the percent of sown seeds that germinated. After thinning, seedling heights were measured weekly, to calculate initial growth rate. *Chamerion angustifolium* started to flower at three months (April 17) so all plants of *C. angustifolium* were harvested at that time. Other seedlings were harvested after six months (June 6). After harvesting, roots were cleaned and separated from shoots at the soil line. Presence of root nodules from nitrogen-fixing bacteria was recorded for *C. sanguineus* and *V. americana.* Shoots and roots were oven-dried (at 65°C for 15 hours) and weighed to the nearest one hundredth of a gram.

Field Seeding Study. Further comparison of germination and establishment of early-seral vascular plants and conifers in different seedbeds was undertaken in the field seeding study. Using the same eight species as in the greenhouse study, field seeding trials were implemented in three slope positions (summit, mid-slope, and toeslope), with two replicates per slope position on west to northwest aspects. Three 15 cm diameter seedbed/species combination split plots were implemented in November 2005 at each slope position: (1) “bare soil” = < 10% bryophyte cover, (2) “bryophyte” = >75% bryophyte cover, and (3) “scalped” = entire upper surface layer removed (>75% bryophyte cover prior to removal). Seedbeds were selected within 10 m of each other and, when possible, within the same contiguous area of ground cover. There were two replicates of three slope positions, eight species (Table 4.2) and three seedbeds for a total of 144 split plots.

Prior to seeding, all microsite characteristics were recorded as previously described and aboveground vascular plants were pulled out in all split plots. A handheld hoe was used to remove all ground cover (including bryophytes) in scalped seedbed split plots. *C. sanguineus* seeds were heat scarified for 5 minutes prior to seeding; no other pre-treatment was applied to seeds. Seeds of each species were randomly assigned to and sown (scattered) in separate permanently marked seedbed split plots to avoid competition among germinants of different species. Number of seeds sown varied for each species due to seed availability (Table 4.2). Either available seeds were evenly divided between split plots, or 50 large and 100 small seeds were sown per seedbed split plot. Seedbed split plots were visited in April, June, and August of 2006 and in June 2007. At each visit, germinants were counted and split plots were examined for evidence of remaining seeds, seed predation, and down slope dislocation of seeds.

Statistical Analysis

<u>Microsite Distribution and Characteristics</u>

To describe microsites following combined following fire and restoration treatments, indicator variables were created for categorical descriptions of general site, litter composition, micro-topography, micro-topography height, and substrate, and species presence/absence, vegetation removal present/absent and bryophyte cover ≥ 75% (bryophyte microsite) or < 75% (non-bryophyte microsite). The bryophyte cover cutoff (75%) was chosen arbitrarily to represent high bryophyte establishment success. To examine differences in microsite characteristics in areas with and without vegetation removal, multi-response permutation procedure (MRPP: Mielke 1984) was used in PC-Ord 5.1 (McCune and Mefford 2005). MRPP is a non-parametric method testing for testing group differences that generates an A statistic, the chance-corrected within-group agreement indicative of within group homogeneity, and the probability of the observed differences being greater than differences due to chance. All values for a given parameter were divided by its maximum characteristic value for the entire study to adjust for different scales.

To determine which microsite characteristics differed in areas with and without vegetation control, chi-square tests of independence in individual blocks were used for categorical data in SAS. Since more than one category was assigned for site description and substrate when applicable, comparisons were made between counts of each category within these microsite characteristics. Due to lack of normal distribution, Wilcoxon rank sum tests for continuous data were used in individual blocks in SAS. Chi-square test of independence was used to examine presence/absence of *C. sanguineus, P. menziesii* and *C. angustifolium* germinants in bryophyte microsites and non-bryophyte microsites in all blocks combined due to few germinants of these species. Although there were only two bryophyte microsites in one block, its removal did not alter the results and therefore it was retained in the analysis.

Bryophyte Habitat

In order to determine if bryophytes inhabit specific microsites, MRPP (Mielke 1984) was used. Characteristics of microsites with versus without bryophytes present and with versus without bryophyte cover $\geq$ 75% in different blocks were compared. Microsite characteristics present in less than 10% of microsites and bryophyte cover were removed to reduce the noise in the dataset. The resulting data set included micro-topography; micro-topographic height; micro-aspect (translated to heat load index: McCune and Grace 2002); micro-slope; loose rock, undisturbed and disturbed bare soil; litter composition; litter and duff depth; and cover of total ground, litter, small woody debris, large woody debris and vascular plants, site within 1 m of coarse woody debris (CWD) or dead tree or stump, exposed site and canopy cover. All values for a given parameter were divided by its maximum characteristic value for the entire study to adjust for different scales.

To describe the characteristics of early-seral bryophyte microsites, regression tree analysis (RTA) was used. Using RTA, the relationships between the microsite characteristics and log transformed bryophyte cover for individual blocks were examined. Vegetation removal was not accounted for in RTA due to overlapping distributions of all microsite characteristics in vegetation removal and no vegetation removal microsites. RTA is a non-parametric technique that uses recursive partitioning to divide the data into subsets with increasing homogeneity of response (Breiman et al. 1984; McCune and Grace 2002), resulting in a regression tree representing a set of rules for predicting the response based on predictor variables. RTA was performed in SPLUS v. 6.0 using the tree function. This method overfits the data and creates the largest tree possible for the given settings (i.e. 5 minimum observations before split, minimum node size =10, minimum node deviance = 0.01). The RTA algorithm used by SPLUS is as follows: (1) rank transform continuous variables; (2) iteratively partition the data between all possible combinations of values for categorical variables and between each of two non-overlapping sets in ranked continuous; (3) estimate within-partition heterogeneity or deviance (log-likelihood estimator based on the empirical distribution of samples into groups along each branch of the tree); (4) implement binary split of the data based on maximum decrease in deviance; (5) Recursively repeat steps 2-5 until either terminal nodes are at minimum group size or homogeneous. Regression trees were pruned using a 10-fold cross-validation and selecting for the tree with the smallest estimated error rate (Breiman et al. 1984; De' ath and Fabricius 2000).

Seedbed Effects on Germination and Establishment

Greenhouse Study. Two-factor analysis of variance (ANOVA) was used to examine differences among seedbeds for different species. The response variables were germination success (%), dry shoot biomass (g), dry root biomass (g), dry root:shoot ratio, and growth rate (cm/wk) measured as final height minus initial height at thinning/ weeks measured. The numbers of seedlings available for observation differed among species due to differences in number of seeds sown, germination success and mortality (Appendix F). Data for *C. decurrens*, were excluded from the analysis due to very low germination (four seeds). The model is based on assumptions of equal variance among treatments and normally distributed residuals. Compliance with the model assumption of normality was evaluated using SAS PROC UNIVARIATE and compliance with the assumption of homogeneity of variance was evaluated using plots of predicted versus residual values and residuals versus normal percentiles before the interpretation of the parameter estimates and model results. Assumptions of normality and constant variance were not met for growth rate, root:shoot ratio, root weight or shoot weight so variables were log transformed. After the log transformation, the assumptions were met for log (shoot weight). Log (growth rate) had a *P. menziesii* seedling outlier in the burnt bryophyte seedbed, which had the lowest growth rate of seedlings for this species. Log (root weight) and log (root:shoot ratio) had two outliers: *C. sanguineus* in burnt bryophyte seedbed and *A. concolor* in unburnt bryophyte seedbed. The data was run with and without the outliers. Log (growth rate) outlier significantly influenced results by decreasing the making the interaction term insignificant, but other outliers did not. After the deletion of this seedling the assumptions were met for log (growth rate). Log (root weight) and log (root:shoot ratio) models included outliers since ANOVA is robust to outliers and results were not altered by inclusion.

Field Seeding Study. Seeding data were summarized as number and percent of seeds germinated, and number of seedlings that survived one and two years in each seedbed type and slope position. Percent germination and survival were summarized without *C. angustifolium*, due to 100% mortality *C. angustifolium* germinants. No statistical comparison was attempted due to low germination and survival of all species.

RESULTS

Microsite Distribution and Characteristics

After the wildfire and restoration treatments (including areas with and without vegetation removal), microsites with a wide range of characteristics were found in the study sites. Flat or irregular microsites were more common than concave or convex microsites (Table 4.3). Lower micro-topographic heights were more common than high micro-topographic heights. Micro-slopes were steep (median: 30% $\pm$ 0.54 SE) and heat load index high (median: 0.60 $\pm$ 0.01 SE). Undisturbed bare soil, loose rock, and disturbed bare soil were the most common microsite substrates (Table 4.3). All other microsite substrates were present but rare, each accounting for less than 2% of microsites. Exposed sites, sites within 1 m of a stump/tree and sites within 1 m of CWD were the most common site characteristics, with other site characteristics occurring in less than 10% of microsites.

Total ground cover within microsites was high (median: 65% $\pm$ 1.3 SE) and primarily composed of litter (median: 35% cover $\pm$ 1.3 SE). Litter composition was predominantly leaf and needle combined, or leaf-only; needle-only accounted for 5% of microsites and less than 2% of microsites had no litter (Table 4.3). Litter depth (median: 8 mm $\pm$ 0.51 SE) was greater than duff depth (median: 0 mm $\pm$ 0.09 SE).

Bryophyte cover was low (median: 5% $\pm$ 1.1 SE) within microsites and microsites with very high cover of bryophytes ($\geq$ 75%) were rare (n=66: Table 4.4). Vascular plant cover at seedling level (median: 40% $\pm$ 1.3 SE) was greater than bryophyte cover but less than total ground cover (which did not include vascular plant cover). Canopy cover at seedling level was very high (median: 96.1% $\pm$ 0.42 SE). *Chamerion angustifolium, C. sanguineus*, *P. menziesii* and *V. americana* seedlings were uncommon in microsites. *Abies concolor* was not found in any microsite.

Microsites in areas with vegetation removal were different from those without vegetation removal based on MRPP (Table 4.5). Vegetation removal resulted in more open canopies and increased soil disturbance, duff depth, and litter cover compared to microsites without vegetation removal (Tables 4.4 and 4.6). Additionally, fewer microsites were under tall shrubs when vegetation was removed. However, the range of variation of specific microsite characteristics where vegetation had been removed was very similar to areas with intact vegetation.

Bryophyte Habitat

Early-seral bryophytes appear to have specific microsite requirements for establishment, based on differences between bryophyte and non-bryophyte microsites from MRPP in all blocks (Table 4.5). Within group homogeneities were small when looking at bryophyte presence versus absence but larger when looking at bryophyte cover $\geq 75\%$ versus $< 75\%$. Characteristics of bryophyte habitat varied among blocks. In general, bryophyte cover was higher when other ground cover (litter, small and large woody debris) was lower, overstory cover (vascular plant and canopy cover) was lower and substrate was undisturbed bare soil based on RTA (Fig. 4.1). Pruned regression trees had between four and seven terminal nodes in different blocks. Microsite characteristics were unable to explain variation in bryophyte cover in block SPC4, which had extremely low bryophyte cover.

Seedbed Effects on Germination

Greenhouse Study. Bryophyte seedbeds had no effect on germination of early-seral vascular plants or conifers except *P. ponderosa*, which had higher germination in unburnt bryophyte seedbeds than other seedbeds (Fig. 4.2). Germination success is not directly comparable among species due to differences in seed viability (Table 4.2). Therefore, results are reported only for differences in seedbeds within species.

Field Seeding Study. Total germination was very low in the field seeding study. In all sites combined, only 196 of 6118 seeds sown germinated (Table 4.7). One hundred fifty-eight *C. angustifolium*, 16 *C. decurrens*, ten *A. concolor*, six *C. sanguineus*, four *P. ponderosa*, and two *P. menziesii* seeds germinated. Bryophyte seedbeds and summits had the most germinated seeds, but the majority of germination for species other than *C. angustifolium* occurred in scalped seedbeds and toeslopes.

Seedbed Effects on Establishment

During the microsite survey, *C. sanguineus* was found more commonly in microsites with ≥ 75% bryophyte cover (Table 4.5) than expected by chance. No other species demonstrated a difference between bryophyte and non-bryophyte microsites.

Greenhouse Study. Impact of bryophytes on plant establishment varied across growth metrics and seedbeds for different species (Fig. 4.3). Growth rate and shoot biomass varied by species in different seedbeds as indicated by the significance of the species x seedbed interactions (growth rate: $F_{12, 79}$=2.57, p=0.0063; shoot biomass: $F_{12, 73}$=3.05, p=0.002: Fig. 4.3). Seedling root:shoot ratio varied by species ($F_{6, 73}$=11.34, p<0.0001), but not by seedbed ($F_{2, 73}$=2.62, p=0.08) or seedbed x species ($F_{12, 73}$=1.77, p=0.07). Root biomass of seedlings varied by seedbed ($F_{2, 73}$=5.81, p=0.005), and species ($F_{6, 73}$=8.92, p<0.0001), with no interaction ($F_{12, 73}$=1.12, p=0.36). Median root biomass of seedlings in burnt bryophyte seedbeds was lower than in burnt bare soil and unburnt bryophyte seedbeds (Fig. 4.3), but no difference occurred between burnt bare soil and unburnt bryophyte seedbeds.

Growth of early-seral vascular plants, *C. angustifolium* and *C. sanguineus,* was lower in burnt bryophyte seedbeds than other seedbeds, evidenced by lower median root biomass, shoot biomass and growth rate of seedlings (Fig. 4.3). *V. americana*, on the other hand, exhibited no response to seedbeds. Root nodulation response followed that of biomass. *C. sanguineus* root nodulation occurred in burnt bare soil and unburnt bryophyte seedbeds (66% and 40% of seedlings respectively), but not in burnt bryophyte seedbeds. *V. americana* root nodulation occurred in all seedbeds (78% of burnt bare soil, 50% of burnt bryophyte and 75% of unburnt bryophyte seedlings).

While conifers exhibited varied responses to seedbeds, growth of conifers appeared to be higher in unburnt bryophyte seedbeds than in burnt seedbeds.

Differences in germination carried over into the establishment phase of *P. ponderosa* (Fig. 4.3) with seedlings in unburnt bryophyte seedbeds having higher growth rate and shoot biomass than seedlings in burnt bryophyte seedbeds. *Abies concolor* seedlings had lower shoot biomass and higher root:shoot ratio in both burnt seedbeds than unburnt bryophyte seedbeds. *Pseudotsuga menziesii* had lower shoot biomass in burnt bryophyte seedbeds than in unburnt bryophyte seedbeds.

Field Seeding Study. Seedling survival was generally low for all species in the field seeding trials (Table 4.8). Eighteen seedlings (eight *Calocedrus decurrens,* four *Ceanothus sanguineus,* and two each of *Abies concolor*, *Pinus ponderosa* and *Pseudotsuga menziesii*) survived the first year. Bryophyte seedbeds and summits had the highest first year survival (Table 4.8). Six seedlings (four *Calocedrus decurrens* and two *Pinus ponderosa*) survived the second year (Table 4.8).

DISCUSSION

Microsite Distribution and Characteristics

Post-fire microsites were heterogeneous, and vegetation removal had limited effects on microsite distributions. Legacy components, including snags, CWD, and sprouting shrubs, contributed to microsite diversity by altering canopy cover and increasing protection (Minore 1986; Gray and Spies 1997; Maher et al. 2005). Fire contributed to micro-topographic variation by creating rootwad mounds and root burn out holes which influence litter build-up (DeLong et al. 1997; Beatty 2003; Lusk and Kelly 2003) and soil properties, such as pH, moisture and nutrient availability (Beatty 2003). Although a few dominant microsite characteristics emerged, the full array of anticipated microsites was encountered. In this study, most microsites seemed suitable as habitat for vascular plants (although microsites entirely on stumps or CWD were not measured) and all microsites were suitable habitat for some bryophyte species. Studies have documented the importance of seedbed or soil moisture (Tappeiner and Helms 1971; Hobbs et al. 1992; Caccia and Ballaré 1998; Bai et al. 2000; Cornett et al. 2000; Noe and Zedler 2000), litter (DeLong et al. 1997;

Caccia and Ballaré 1998; Bai et al. 2000), temperature (Caccia and Ballaré 1998; Noe and Zedler 2000) and shade (Maher et al. 2005) in determining the suitability of microsites for germination and establishment of plants. Although not all were measured directly, these factors were incorporated in microsite classifications based on proxy variables identified from published literature.

Bryophyte Habitat

Early-seral bryophytes are often assumed to be generalists (i.e. species able to establish in a wide variety of conditions) and their distributions related to dispersal and colonization rather than environmental factors (e.g. Mills and Macdonald 2005). However, this study demonstrated that while early-seral bryophytes occurred in a wide variety of microsites, cover of early-seral bryophytes was higher when litter and canopy cover were lower and on undisturbed mineral soil substrate. Substrate appeared as the first predictor in three out of four blocks, an indication of its importance in determining bryophyte habitat. Substrate specificity is well known in bryophytes and early-seral bryophytes are restricted to mineral soil substrates as documented (Lawton 1971). Bryophyte colonization of other substrates may take years due to spore limitation following fire and time required for establishment of later-seral bryophytes (Shaw and Goffinet 2000; Cutler et al. 2008; Kayes et al. in review). However, initial establishment may require rough surfaces to trap spores (Cutler et al. 2008), but the three-year post fire delay in sampling precluded evaluation of initial establishment conditions. In light of this study, it was surprising that early-seral bryophytes did not establish on disturbed mineral soil as well. Litter and canopy cover have been documented as affecting terrestrial bryophyte distributions in other studies as well (Sedia and Ehrenfeld 2003; Jones and del Moral 2005; Mills and Macdonald 2005). A study of primary succession demonstrated similar results for some bryophyte species (*Hypnum* Hedw. sp.), while another bryophyte species (*Rhytidiopsis robusta* (Hook.) Broth.) was positively associated with litter (Jones and del Moral 2005). Litter cover could inhibit bryophyte establishment either by physically blocking access to soil substrates or by altering soil chemistry as demonstrated in New England forest pits (Beatty 2003). Canopy cover reflects the importance of light and associated environmental and resource conditions in determining terrestrial bryophyte habitat suitability. These results support those in pitch pine forests, where bryophyte dominance is related to light conditions (Sedia and Ehrenfeld 2003).

Seedbed Effects on Germination and Establishment

Life cycle stages of species, i.e. germination and establishment, responded differently to seedbeds. Similarly, habitat requirements have been documented as differing between life cycle stages (Keizer et al. 1985; Schupp 1995; George and Bazzaz 1999). As occurred in this study, requirements for establishment are generally more restrictive than those for germination (Turnbull et al. 2000). In general, seedbed effects on germination did not seem to account for species distributions as demonstrated by other studies (Noe and Zedler 2000; Otsus and Zobel 2004), except for *P. ponderosa*. However, growth and establishment of early-seral vascular plants and conifers in different seedbeds varied by bryophyte type. This supports the results of other studies that have documented variation in establishment based on type of bryophyte for other species (St. Hilaire and Leopold 1995; Hörnberg et al. 1997).

Interactions of germination and moisture were not measured and may account for lack of differences in germination between seedbeds. Contrary to our findings, previous studies have shown that many conifer species and *C. angustifolium* require bare mineral soil for germination (Burns and Honkala 1990; Hobbs et al. 1992; Bai et al. 2000; USDA 2006). In other studies, decreased germination in bryophyte seedbeds has been attributed to decreased soil moisture (Keizer et al. 1985; Zamfir 2000; Otsus and Zobel 2004). In dry conditions, which are more likely to occur in field studies, bryophytes may compete with seeds for water (Zamfir 2000; Serpe et al. 2006), which may explain the discrepancy in results of the greenhouse and field studies. Soil moisture content is thought to be higher under bryophytes than in bare soil in wet conditions, as occurred in the greenhouse. *Pinus ponderosa* germination is sensitive to low soil moisture (Burns and Honkala 1990) and increased moisture in unburnt bryophyte seedbeds may support greater germination. Decreased germination under bryophytes has also been attributed to decreased radiant flux or red/far-red ratio (Keizer et al. 1985; van Tooren 1990). However, conifers used in this study do not require light to germinate (Baskin and Baskin 1998) and have increased germination in intermediate shade (Strothmann 1972; Hobbs et al. 1992; Caccia and Ballaré 1998; Bonnet et al. 2005). Therefore, light conditions are unlikely affect germination of these species. Based on germination requirements and timing (i.e. fall or spring when moisture is less limiting (Burns and Honkala 1990)), bryophytes appear to be suitable seedbeds for germination of early-seral vascular plants and conifers in mixed-conifer forests.

In general, late-seral bryophytes were suitable seedbeds for conifer establishment but early-seral bryophytes did not appear to be suitable seedbeds for establishment. Fundamental differences exist between early- and late-seral bryophytes, including thickness and structure, which may account for different seedbed effects on growth of vascular plants. Burnt bryophyte seedbeds had primarily early-seral acrocarpous bryophytes with long seta that form dense mats and exhibit seasonal growth patterns (Lawton 1971; Shaw and Goffinet 2000). Competitive interactions between early-seral bryophytes and vascular plants have been previously documented (Keizer et al. 1985; Jeschke and Kiehl 2008) and appear to be a likely mechanism for decreased establishment in early-seral bryophyte seedbeds. Unburnt bryophyte seedbeds were composed of loosely packed pleurocarpous bryophytes and cyanolichens. Similar to current findings, pleurocarpous bryophytes have been documented as positively affecting establishment of conifers on downed wood (Liao et al. 2003), in wetlands (St. Hilaire and Leopold 1995), and forests (Collins and Good 1987; Dovčiak et al. 2003). Contrary to findings of these and the current study, Harmon and Franklin (1989) observed that pleurocarpous bryophytes decreased survival of conifers on the forest floor in the Pacific Northwest. The difference in results may be due to interacting competitive effects of the bryophyte layer, understory vegetation, and canopy cover in closed canopy forests (Gray and Spies 1997; Bonnet et al. 2005). In the absence of canopy cover, beneficial effects of unburnt bryophytes including increased soil moisture (Keizer et al. 1985; Dovčiak et al. 2003), higher soil temperature during cool seasons (Harper and Pendleton 1993), shading (DeLach and Kimmerer 2002), and/or enhanced nutrient availability (Harper and Pendleton 1993; Chapin et al. 1994; Purvis 2000; Hart et al. 2005) may outweigh competitive effects. Enhanced nutrient availability was most likely the cause of increased growth of conifers in unburnt bryophyte seedbeds in the greenhouse because other factors were controlled in the greenhouse at levels deemed to be not limiting.

This study was unable to separate bryophyte effects on germination and establishment from microsite effects due to the failure of the field seeding trial. Lack of germination in the field seeding study could be due to seed predation or competition from established vegetation arising from a delay in seeding until several years following the fire (Charron and Greene 2002). Some evidence was found for increased germination of *C. angustifolium* and establishment of *C. sanguineus* in bryophyte seedbeds in the field. Similarly, facilitation by the bryophyte layer has been attributed to seed trapping (Harper et al. 1965; van Tooren 1990; Jumpponen et al. 1999; Elmarsdottir et al. 2003; Sedia and Ehrenfeld 2003) and concealment from predators (Parker 2001) that would not be evident in a greenhouse experiment. The importance of the bryophyte layer in seed trapping may vary by seed size (Zamfir 2000; Lusk and Kelly 2003; Otsus and Zobel 2004). Small seeds are more susceptible to movement, and thus more likely to be trapped (Gray 2005; Jones and del Moral 2005). Seed trapping may account for increased germination of *C. angustifolium*, which had the smallest seeds by several orders of magnitude, in bryophyte seedbeds in the field seeding study. Research on the effects of bryophytes on soil moisture, soil erosion, and soil chemistry would help clarify mechanisms behind bryophyte effects on germination and establishment of vascular plants. Examination of other species and types of seedbeds would lead to better understanding of post-fire successional processes and community development, since habitat requirements vary by species.

Spatial and temporal variability occur in microsites in secondary succession. Scale of measurement may affect microsite heterogeneity due to spatial variation in plant communities, canopy conditions, and topography that occurs across spatial scales (Schupp 1995; Bonnet et al. 2005; Mills and Macdonald 2005; Cutler et al. 2008; Samonil et al. 2008). However, environmental variation may affect regeneration only at the fine scale (Bonnet et al. 2005) and therefore, the current study measured microsite characteristics at a small scale. Additionally, continuous microsite measurement along gradients of interest rather than discrete microsite plots used in the current study would increase understanding of species tolerances. Microsite suitability and habitat requirements change over time (Jones and del Moral 2005) and the role of microsites is altered due to changes in species resource use (Whittaker 1993). Post-fire microsites change over time and variation may exist in their effects on germination and establishment due to changing vegetation, woody debris, and litter conditions. Canopy cover and litter cover will increase as tall shrub cover increases in areas without vegetation removal (Kayes et al. in review) and result in a decrease of early-seral bryophytes. The resulting shift in bryophyte species from early-seral to late-seral species, as seen in Kayes et al. (in review), could increase the number of microsites suitable for conifer establishment. Areas without shrub cover are more likely retain microsite characteristics similar to current conditions, at least in the short run. Microsites are also likely to change due to snag dynamics. As more snags fall, woody debris will have more of an impact on microsite distributions by eliminating microsites in the open, increasing debris piles, and increasing woody substrates. As wood decomposes, woody substrate microsites are likely to become important for germination and establishment of vascular plants (Harmon and Franklin 1989; Gray and Spies 1997; Beach and Halpern 2001; Dovčiak et al. 2003). Examination of change in microsite characteristics over time would allow insights into the establishment of late-successional species and communities.

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Table 4.1. Categories used to classify microsites for site description, substrate, micro-topography, micro-topographic height and litter composition. For site description and substrate, more than one category was assigned to microsites when applicable. Micro-topography height class was measured with a ruler perpendicular to the aspect.Irregular microtopography were those that did not fit any other category. CWD = coarse woody debris.

Characteristic	Categories
Site Description	Exposed, Within 1m of CWD, Within 1m dead tree/stump, Beneath tall ($\geq$ 1.3m height) shrub, Beneath short (<1.3 m height) shrub, Beneath slash pile, In rootwad pit, In burnt root/hole, On rootwad mound
Substrate	Bedrock, Loose Rock, Undisturbed Bare Ground, Disturbed Bare Ground, Ash, Duff, Mixture
Micro-topography	Convex, concave, irregular, flat
Micro-topographic Height	$\leq$ 5 cm, 5.1 -20 cm, $\geq$ 20.1 cm
Litter Composition	Needle, Leaf, Needle/Leaf, Other, None

Table 4.2. Number of seeds sown per bryophyte cover split plot, viability (%), and stratification for greenhouse sowing by species. *Two plots had 14 seeds sown. Cold/moist stratification was at 5°C. ^Seeds were scarified for five minutes in boiling water prior to stratification.

Species	**Field (Seeds)**	**Greenhouse (Seeds)**	**Stratification (days)**	**Viability (%)**
Pseudotsuga menziesii	50	30	31	59
Abies concolor	50	30	31	25
Pinus lambertiana	15*	15	90	100
Pinus ponderosa	30	30	31	89
Calocedrus decurrens	50	30	31	8
Vicia americana	15	15	-	2
Ceanothus sanguineus	30	13	90^	19
Chamerion angustifolium	100	100	-	86

Table 4.3. Distribution of microsite characteristics in relation to vegetation control and block. Percentage of all, no vegetation removal (NVR) and vegetation removal (VR) microsites with the most common categorical microsite characteristics and p-values from chi-square test of counts between VR and NVR microsites by block. P-values with significance of $p \leq 0.05$ are in bold. MT = micro-topography, CWD = coarse woody debris, Stump/Tree = $\leq$ 1m distance of a stump or tree, Exposed = indicates lack of other applicable site description, tall shrub = $\geq$ 1.3 m tall, short shrub = < 1.3 m tall. WBEC, FC2, FC3, SPC4, SPC5 are block codes.

Table 4.3.

	Block	ALL	WBEC			FC2			FC3			SPC4			SPC5		
	Vegetation Removal		NVR	VR		NVR	VR		NVR	VR		NVR	VR		NVR	VR	
	Microsite Traits	%	%	%	p	%	%	p	%	%	p	%	%	p	%	%	p
Micro-topography	**Concave**	16.1	18.8	7.8	0.12	12.5	6.3	0.52	14.1	20.3	0.59	15.6	25	0.24	18.8	21.9	0.66
	Convex	7.03	1.6	7.8		7.8	4.7		6.2	7.8		10.9	3.1		10.9	9.4	
	Flat	38.8	50.0	50.0		35.9	42.2		45.3	34.4		35.9	35.9		25	32.8	
	Irregular	38.1	29.7	34.4		43.8	46.9		34.4	37.5		37.5	35.9		45.3	35.9	
MT Height	**<5 cm**	46.1	56.3	56.3	0.78	64.1	46.9	0.11	59.4	46.9	0.32	32.8	31.3	0.54	37.5	29.7	0.49
	5-12 cm	42.2	37.5	34.4		32.8	45.3		34.4	42.2		50.0	43.8		50.0	51.6	
	>12 cm	11.7	6.3	9.4		3.1	7.8		6.3	10.9		17.2	25		12.5	18.8	
Substrate	**Loose Rock**	29.1	6.3	3.1	0.4	43.8	17.2	**0.001**	20.3	14.1	0.34	75	57.8	**0.04**	42.2	10.9	**<0.0001**
	Disturbed Bare Soil	13.9	9.4	23.4	**0.03**	9.4	10.9	0.76	3.1	17.2	**0.009**	4.69	20.3	**0.008**	4.7	35.9	**<0.0001**
	Undisturbed Bare Soil	78.9	95.3	79.7	**0.008**	75	78.1	0.67	98.4	79.7	**0.0007**	71.9	56.3	0.07	89.1	65.6	**0.002**
	Bedrock	2	3.13	3.13	NA	0	0	NA	0	0	NA	1.56	3.13	NA	7.81	1.56	NA
	Duff	1.1	0	1.56	NA	6.25	0	NA	3.13	0	NA	0	0	NA	0	0	NA
	Mixture	1.7	0	0	NA	7.81	0	NA	3.13	4.69	NA	1.56	0	NA	0	0	NA
	Ash	0.3	0	1.56	NA	0	0	NA	0	0	NA	0	0	NA	1.56	0	NA
	Root	0.8	0	0	NA	1.56	0	NA	0	3.13	NA	1.56	0	NA	0	1.56	NA
Litter Composition	**None**	1.4	0.0	0.0	0.21	1.6	0.0	0.77	0.0	0.0	0.13	1.6	3.1	0.77	3.3	3.1	0.59
	Leaf only	40.2	34.4	1.6		28.1	31.3		15.6	29.7		37.5	29.7		71.9	78.1	
	Needle only	5.0	3.1	45.3		10.9	10.9		6.3	3.1		3.1	3.1		6.3	3.1	
	Leaf and Needle	53.1	62.5	53.1		59.4	57.8		78.1	67.2		57.8	64.1		15.6	15.6	
	Other/Pine Cone	0.3	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		3.1	0.0	

Table 4.3 (Continued)

	Block	ALL	WBEC			FC2			FC3			SPC4			SPC5		
	Vegetation Removal		NVR	VR		NVR	VR		NVR	VR		NVR	VR		NVR	VR	
	Microsite Traits	%	%	%	p	%	%	**p**	%	%	**p**	%	%	**p**	%	%	**p**
Site Description	**Exposed**	35.6	26.5	50	**0.006**	45.3	31.3	0.1	37.5	31.3	0.45	23.4	31.3	0.32	39.1	40.6	0.85
	≤ 1 m CWD	22	23.4	26.6	0.68	10.9	29.7	**0.008**	23.4	21.9	0.83	26.6	31.3	0.56	15.6	10.9	0.43
	Under Short Shrub	3.1	7.8	1.6	0.09	4.7	4.7	NA	3.1	1.6	NA	4.7	0.0	NA	3.1	0.0	NA
	Under Tall Shrub	9.5	20.3	0.0	**<0.0001**	20.3	9.4	0.08	9.4	6.3	0.5	10.9	1.6	**0.02**	17.2	0.0	**0.0005**
	Stump/Tree	38.8	28.1	23.4	0.54	18.8	48.4	**0.0004**	45.3	40.6	0.6	57.8	39.1	**0.03**	34.4	51.6	**0.05**
	Under Slash	1.3	0	3.13	NA	1.56	1.56	NA	0	1.56	NA	0	1.56	NA	1.56	1.56	NA
	In Rootwad Pit	0.6	1.56	0	NA	0	0	NA	0	1.56	NA	1.56	0	NA	1.56	0	NA
	On Rootwad Mound	1.4	3.13	3.13	NA	1.56	1.56	NA	0	3.13	NA	0	0	NA	0	1.56	NA
	In Hole	0.9	0	0	NA	4.69	0	NA	1.56	1.56	NA	1.56	0	NA	0	0	NA

Table 4.4. Species occurrence for all sites and for those sites with bryophyte cover ≥ 75% or < 75%. Percentages of microsites (all and ≥ 75% bryophyte cover) with presence of *Ceanothus sanguineus*, *Chamerion angustifolium, Pseudotsuga menziesii*, or *Vicia americana* and p-values from chi-square for differences in species counts between microsites with and without bryophyte cover ≥ 75%. Percentage of all microsites with bryophyte cover < 75% or ≥ 75% (all microsites only). P-values with significance of p ≤ 0.05 are in bold.

	All Sites	**Bryophyte Cover ≥ 75%**	
n	640	66	
Species	%	%	p
Chamerion angustifolium	7.2	10.9	0.10
Pseudotsuga menziesii	1.9	1.5	0.82
Ceanothus sanguineus	3.9	9.1	**0.02**
Vicia americana	0.8	1.5	0.47
Bryophyte cover < 75%	89.7		
Bryophyte cover ≥ 75%	10.3		

Table 4.5. MRPP results for differences in microsites characteristics between treatments with and without vegetation removal, bryophytes present and bryophyte cover ≥ 75% for individual blocks. Numbers of microsites with and without bryophytes present and with and without ≥ 75% bryophyte cover. WBEC, FC2, FC3, SPC4, SPC5 are block codes.*Not including plot that was accidentally scalped.

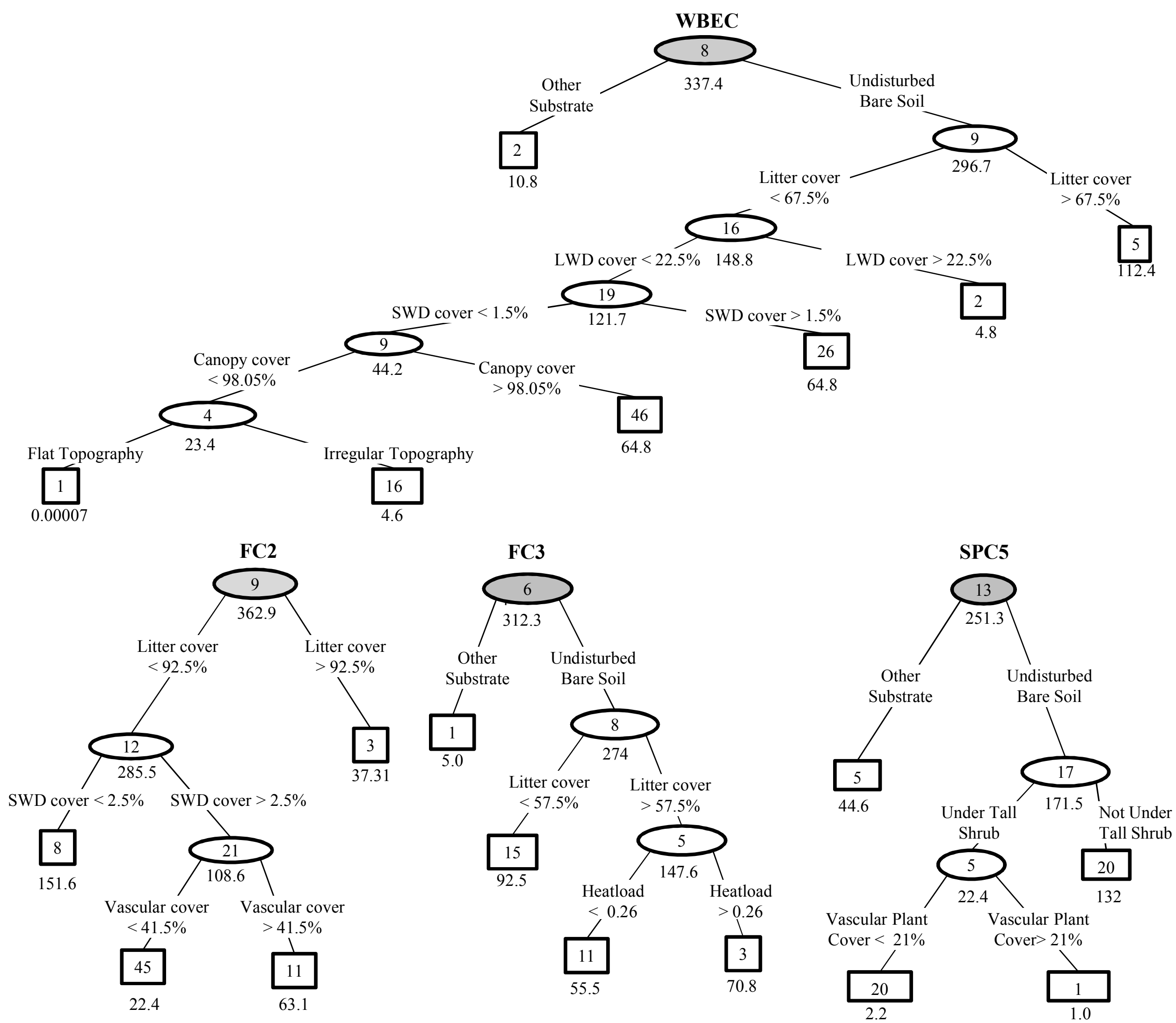
	NVR vs. VR		Bryophyte Presence vs. Absence				Bryophyte Cover ≥ 75% vs. < 75%			
	MRPP		Present	Absent	MRPP		≥75% Cover	< 75% Cover	MRPP	
Block	A	p	n	n	A	p	n	n	A	p
WBEC	0.02	**0.0001**	93	35	0.02	**0.0005**	11	117	0.05	**0.0000**
FC2*	0.04	**0.000**	97	31	0.02	**7E-05**	21	107	0.09	**0.0000**
FC3	0.01	**0.010**	93	35	0.01	**0.003**	16	112	0.07	**0.0005**
SPC4	0.02	**0.006**	75	53	0.01	**0.01**	2	126	0.03	**0.0004**
SPC5	0.05	**0.000**	114	14	0.02	**0.002**	16	112	0.08	**0.0000**

Table 4.6. Differences in continuous microsite characteristics between vegetation removal (VR) and no vegetation removal (NVR) microsites based on Wilcoxon rank sum tests by block. Values are median and standard error. Ground cover = combined cover of all variables except vascular plant and canopy cover, SWD = small woody debris, LWD = large woody debris. *indicates significant difference at $p \leq 0.05$ between NVR and VR for variable in that block. WBEC, FC2, FC3, SPC4, SPC5 are block codes.

Block	**WBEC**		**FC2**		**FC3**		**SPC4**		**SPC5**	
Treatment	**NVR**	**VR**	**NVR**	**VR**	**NVR**	**VR**	**NVR**	**VR**	**NVR**	**VR**
Canopy Cover (%)	96.2 (± 1.3)	86.7 * (± 2.0)	97.6 (± 0.7)	94.2 * (± 0.98)	99.0 (± 0.6)	98.2 (± 0.8)	96.9 (± 1.3)	92.9 * (± 1.6)	97.7 (± 1.1)	95.3 * (± 1.3)
Vascular Cover (%)	50 (± 4.3)	47.5 (± 4.4)	36.5 (± 3.7)	50 (± 4.5)	37.5 (± 4.1)	42.5 (± 3.7)	25 (± 3.9)	35 (± 3.9)	30 (± 4.2)	45 (± 4.0)
Ground Cover (%)	95 (± 3.6)	80 * (± 4.0)	84 (± 3.5)	80 (± 4.2)	75 (± 3.9)	88.5 (± 3.7)	30.5 (± 3.6)	42.5 (± 4.0)	42.5 (± 3.4)	41.5 (± 4.2)
Bryophyte Cover (%)	10 (± 3.8)	5 (± 3.0)	20 (± 4.0)	6.5 (± 3.9)	7 (± 2.8)	3.5 (± 4.1)	1 (± 1.6)	2 (± 1.9)	15 (± 2.8)	15 (± 4.1)
Litter Cover (%)	52.5 (± 4.5)	50 (± 4.1)	35 (± 4.3)	50 * (± 4.0)	65 (± 4.2)	65 (± 4.0)	16.5 (± 3.3)	30 (± 3.9)	10 (± 2.5)	17.5 (± 3.0)
SWD Cover (%)	5 (± 4.5)	5 (± 1.1)	2 (± 0.78)	2 (± 0.91)	4.5 (± 0.86)	3.5 (± 2.0)	2 (± 0.69)	3 (± 1.3)	3 (± 1.7)	2 (± 1.0)
LWD Cover (%)	0 (± 2.2)	0 (± 1.3)	0 (± 0.83)	0 (± 0.61)	0 (± 0.76)	0 (± 1.1)	0 (± 1.1)	0 (± 1.4)	0 (± 1.5)	0 * (± 1.0)
Micro-slope (%)	28.0 (± 12.6)	27 (± 1.8)	25 (± 1.5)	30 * (± 1.5)	23.5 (± 1.6)	30 * (± 1.7)	36 (± 1.8)	39 (± 1.6)	36 (± 1.6)	36 (± 1.9)
Heat Load Index	0.81 (± 0.04)	0.79 (± 0.04)	0.59 (± 0.04)	0.66 (± 0.03)	0.43 (± 0.04)	0.35 (± 0.04)	0.71 (± 0.04)	0.65 (± 0.04)	0.51 (± 0.04)	0.34 (± 0.04)
Litter Depth (mm)	12.5 (± 1.8)	10 (± 1.7)	8 (± 1.3)	8.5 * (± 2.1)	10 (± 1.2)	10.5 (± 2.0)	6 (± 0.86)	7 (± 1.6)	7 (± 1.3)	7 (± 1.5)
Duff Depth (mm)	0 (± 0.26)	0 (± 0.31)	0 (± 0.43)	0 (± 0.40)	0 (± 0.39)	0 * (± 0.21)	0 (± 0.19)	0 (± 0.18)	0 (± 0)	0 (± 0.04)

Figure 4.1. Pruned microsite characteristic regression trees for bryophyte cover by block. Block SPC4 was excluded due to inability of microsite characteristics to explain variation in bryophyte cover. Numbers in boxes (terminal nodes) and circles (branch nodes) are median bryophyte cover for node back-transformed and number below is deviance for that node. Length of the line indicates the relative decrease in deviance for a given split. SWD=small woody debris ≤ 2.54 cm, LWD = woody debris > 2.54 cm. Root nodes are colored gray and labeled above with block code. WBEC, FC2, FC3 and SPC5 are block codes.

Figure 4.1.


WBEC
8
337.4
Other Substrate
Undisturbed Bare Soil
2
10.8
9
296.7
Litter cover < 67.5%
Litter cover > 67.5%
5
112.4
16
148.8
LWD cover < 22.5%
LWD cover > 22.5%
2
4.8
19
121.7
SWD cover < 1.5%
SWD cover > 1.5%
26
64.8
9
44.2
Canopy cover < 98.05%
Canopy cover > 98.05%
46
64.8
4
23.4
Flat Topography
Irregular Topography
1
0.00007
16
4.6
FC2
9
362.9
Litter cover < 92.5%
Litter cover > 92.5%
3
37.31
12
285.5
SWD cover < 2.5%
SWD cover > 2.5%
8
151.6
21
108.6
Vascular cover < 41.5%
Vascular cover > 41.5%
45
22.4
11
63.1
FC3
6
312.3
Other Substrate
Undisturbed Bare Soil
1
5.0
8
274
Litter cover < 57.5%
Litter cover > 57.5%
15
92.5
5
147.6
Heatload < 0.26
Heatload > 0.26
11
55.5
3
70.8
SPC5
13
251.3
Other Substrate
Undisturbed Bare Soil
5
44.6
17
171.5
Under Tall Shrub
Not Under Tall Shrub
20
132
5
22.4
Vascular Plant Cover < 21%
Vascular Plant Cover> 21%
20
2.2
1
1.0

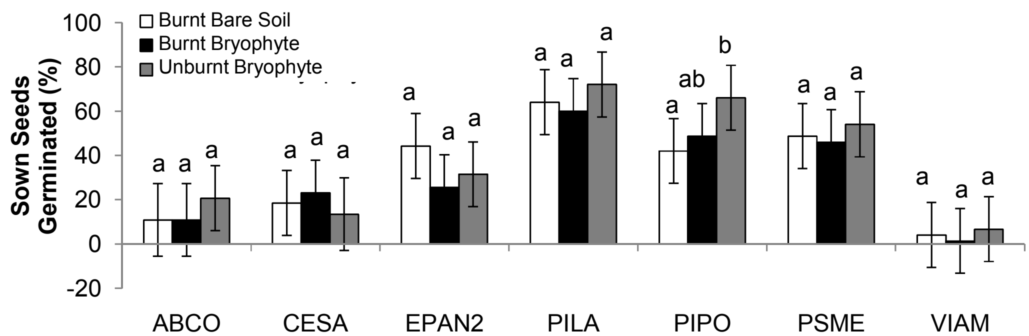


Figure 4.2. Germination success of seven species in three seedbeds from greenhouse experiment. Values are means and 95% confidence intervals. Treatments with different letters differed for that species. Species codes are ABCO = *Abies concolor*, CESA = *Ceanothus sanguineus*, CHANA2 = *Chamerion angustifolium*, PILA = *Pinus lambertiana*, PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii* and VIAM = *Vicia americana.*

Table 4.7. Germination of seeds sown in the field seeding study. See Table 4.2 for number of seeds sown. CHANA2 = *Chamerion angustifolium*. All values are numbers of seeds unless stated as percentages. All germinants other than CHANA2 germinants were conifers.

Germination of all Species					
Slope Position	Bryophyte Seedbeds	Bare Soil Seedbeds	Scalped Seedbeds	Total Germinants	% Total Germination
Summit	54	15	19	88	44.9
Mid-slope	17	17	11	45	23.0
Toeslope	32	9	22	63	32.1
Total Germinants	103	41	52	196	
% Total Germination	52.5	20.9	26.5		
Germination excluding CHANA2					
Slope Position	Bryophyte Seedbeds	Bare Soil Seedbeds	Scalped Seedbeds	Non-CHANA2 Germinants	% Non-CHANA2 Germinants
Summit	6	2	5	13	34.2
Mid-slope	3	3	5	11	28.9
Toeslope	5	2	7	14	36.8
Non-CHANA2 Germinants	14	7	17	38	
% Non-CHANA2 Germination	36.8	18.4	44.7		

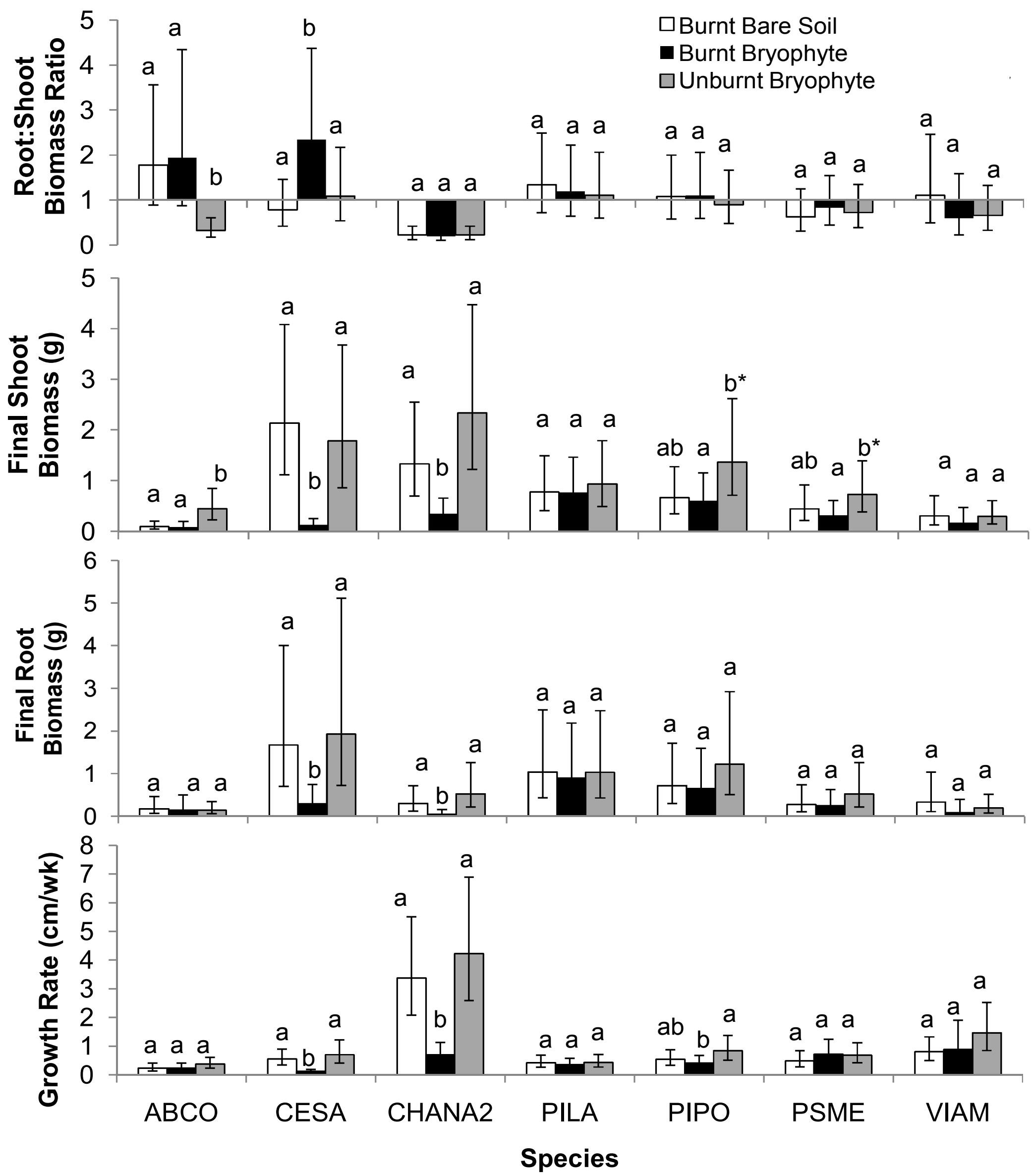


Figure 4.3. Growth rate and dry root:shoot biomass for seven species in three seedbeds from greenhouse experiment. Values are medians and 95% confidence intervals. Different letters indicate significance at $p \leq 0.05$ within species except * are significant at $p < 0.08$. Species codes are ABCO = *Abies concolor*, CESA = *Ceanothus sanguineus*, CHANA2 = *Chamerion angustifolium*, PILA = *Pinus lambertiana*, PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii* and VIAM = *Vicia americana.*

Table 4.8. Seedling survival from field seeding study. CHANA2 = *Chamerion angustifolium*. All values are numbers of seeds unless stated as percentages. All germinants other than CHANA2 were conifers.

1-Yr Survival						
Slope Position	Bryophyte Seedbeds	Bare Soil Seedbeds	Scalped Seedbeds	Survival Yr 1 (#)	Survival Yr 1 (%)	% non-CHANA2 Germinants Survived
Summit	4	2	3	9	50	69.2
Mid-slope	3	1	3	7	38.9	63.6
Toeslope	2	0	0	2	11.1	14.3
Total Survival	9	3	6	18		47.4
% Yr 1 Survival	50	16.7	33.3			
% Non-CHANA2 Germinants Survived	64.3	42.9	35.3			

2-Yr Survival						
Slope Position	Bryophyte Seedbeds	Bare Soil Seedbeds	Scalped Seedbeds	Survival Yr 2 (#)	Survival Yr 2 (%)	% non-CHANA2 Germinants Survived
Summit	1	2	2	5	83.3	38.5
Mid-slope	1	0	0	1	16. 7	9.1
Toeslope	0	0	0	0	0	0
Total Survival	2	2	2	6		15.8
% Yr 2 Survival	33.3	33.3	33.3			
% Non-CHANA2 Germinants Survived	14.3	28.6	11.8			

CHAPTER 5 – CONCLUSION

This research characterized early post-fire succession and species interactions in severely burnt plantation forests. This research also evaluated the effects of a range of post-fire restoration options, based on conifer planting and vegetation removal, on early-seral vegetation and plant communities on two contrasting aspects. As part of the Timbered Rock Reforestation, Stand Development and Fuels study, this research contributes to understanding of post-fire recovery in managed mixed conifer forests, the impacts of early post-fire management on native plant communities and successional processes, early stand dynamics and techniques for restoring late-successional components to severely burnt plantations. Additionally, this research contributes to the understanding of species interactions, particularly effects of bryophytes on germination and establishment of vascular plants. Forest managers can benefit from the information provided on short-term effects of conifer planting and vegetation removal on plant communities and structural layers and microsite effects on germination and establishment of early-seral vascular plants and conifers. The goal of this research project was to understand natural (chapter two) and management (chapter three) influences on early-successional dynamics of plant communities in severely burnt plantations at two different scales. Environmental factors influencing plant community dynamics were examined at the stand scale (chapter two) and microsite scale (chapter four).

Vegetation composition in mixed conifer forests appeared to be resilient to the interacting effects of natural (chapter two) and human-caused disturbances (chapter three), demonstrated by rapid establishment of residual native vegetation prior to restoration and similar within-block plant community compositions following restoration. Differences in plant community composition and species distributions appeared to be due to vegetation removal and environmental factors at the stand and the microsite scales. At the stand scale (chapter two), plant community composition was influenced by fire severity, previous plant community composition, topography, site history and species life history traits. At the microsite scale (chapter four), early-seral bryophytes established preferentially in microsites with undisturbed soil with low to moderate litter and overstory cover. Early-seral bryophyte seedbeds influenced germination and establishment of vascular plants.

Secondary succession among structural layers in burnt plantations followed an initial floristics model with rapid vegetation establishment in the absence of vegetation removal (chapter two). Investigations into microsites and impacts of bryophytes on germination and establishment of plants supported this conclusion for early-seral burnt bryophytes (chapter four). Early-seral burnt bryophytes did not appear to facilitate the establishment of early-seral herbs or shrubs, at least not of the species examined. Lack of facilitation was demonstrated by burnt bryophyte seedbeds decreasing growth and biomass of early-seral species compared to burnt bare soil seedbeds. However, late-seral or unburnt bryophytes may have a facilitative effect for conifers, because growth and germination of some conifers were higher on unburnt bryophyte seedbeds compared to other seedbeds in a greenhouse study. As succession progresses, canopy cover and litter cover will increase with increasing tall shrub cover in areas without vegetation removal (chapter two). Increased canopy cover and litter cover will result in a decrease of early-seral bryophytes. The resulting shift in bryophyte species from early- to late-seral species (chapter two) could increase the number of microsites suitable for conifer establishment.

In contrast to succession among structural layers, succession within structural layers did not necessarily conform to floristics theories and may differ between individual structural layers. Succession within and among structural layers occurred at different rates and with different drivers. Succession within structural layers appeared to be driven by differential species resistance or resilience to fire, regeneration mode, growth rates and site adaptations rather than attributes of structural layers as a whole. Succession among structural layers was driven by structural layer growth and colonization rates which constrain the rate at which different structural layers are able to occupy sites. Restoration activities, particularly vegetation removal, appeared to alter the rate at which succession among structural layers occurred. The elimination of the tall shrub layer delayed the transition to a shrub dominated system.

Multiple trajectories of succession were evident due to initial differences in species composition (chapter two) and vegetation removal treatments (chapter three). Specifically, the presence of *Ceanothus integerrimus* in high abundance altered successional trajectories (chapter two), which may have important implications for post-fire nitrogen dynamics. *Ceanothus* spp. fix nitrogen in root nodules and presence of nitrogen fixing shrubs can increase community nitrogen compared to areas without shrubs (Zatvitkovski and Newton 1968; Binkley et al. 1982; Busse et al. 1996). Multiple successional trajectories could result in divergent plant community compositions in areas with and without restoration treatments. Alteration of successional trajectories in areas with vegetation removal appear to be due to lower tall shrub cover and, on harsh aspects by the final year of study, higher cover of annual and exotic species than areas without vegetation removal. Vegetation removal lead to increased microsite litter cover, decreased microsite canopy cover, and eliminated microsites beneath shrubs (chapter four). Alteration of microsite characteristics that are important habitat features contribute to alter plant community composition, which occurred with vegetation removal. Vegetation removal decreased cover of all trait groups with primarily shrub cover (early-seral, late-seral, nitrogen fixers, evergreen shrubs, deciduous shrubs, evaders, endurers, natives and sub-shrubs) and increased cover of trait groups with primarily herbaceous cover (annuals, invaders, perennials, exotics, graminoids and ferns) compared to areas without vegetation removal. The removal of the tall shrub layer allowed the extended dominance of herbaceous and bryophyte species, in place of the transition to a shrub dominated community (as occurred in untreated plots, see chapter two). Scalping appeared to have significant impacts on the bryophyte layer but not the herbaceous layer due to the prevalence of perennial and disturbance invading herbs and coincident timing of scalping with the summer growing season. However, bryophytes were also recovering the year after scalping following the winter-spring growing season.

While differences between plant community composition and structural layer cover on harsh and moderate aspects were smaller than expected in untreated areas (chapter two), differences in plant community composition were amplified by varying responses to vegetation removal on these aspects (chapter three). In areas without vegetation removal, all structural layers had higher cover on moderate aspects than harsh aspects, probably due to lower overall cover of vegetation on harsh aspects. Cover of the low shrub layer and several trait groups responded differently to vegetation removal on moderate and harsh aspects. Trait groups with primarily shrub species, invader cover and cryptogam communities were more responsive to vegetation removal on moderate aspects than on harsh aspects. Differences in cover for trait groups with primarily herb cover between areas with and without vegetation removal were more pronounced on harsh aspects than on moderate aspects.

Knowledge of the natural recovery of plantations following wildfire will help in understanding the benefits and shortcomings of restoration activities. This understanding may be particularly important in areas where intensive forest management is not the management objective. Plantation management requires an understanding of the natural vegetation and its effects on conifer growth and establishment. While there is a plethora of information on the effects of shrubs and herbaceous vegetation on conifer survival and growth, limited information exists on the effects of early-seral bryophytes on conifer germination and establishment. Chapter four fills part of this gap for bryophytes, particularly early-seral bryophytes. Information on seedbed effects can help managers more efficiently implement post-fire restoration.

These results provide information about vegetation recovery in plantations with and without post-fire restoration and about bryophyte seedbed effects on germination and establishment of early-seral vascular plants and conifers. The conclusions drawn from this research are limited to the period immediately following fire and restoration and mixed conifer forests or similar ecosystems. Long-term consequences of fire and post-fire restoration on vegetation in burnt plantations have not been evaluated. Succession of these communities will continue for many decades. In the absence of conifer planting, it is likely that areas with vegetation removal would rapidly recover from the effects of vegetation removal with limited long-term consequences due to the short term nature of the vegetation removal and sprouting ability of most shrubs. However, the purpose of vegetation removal is to shift the competitive advantage to conifers. If this is achieved, it will result in significant long-term changes in vegetation due to a shift from shrubs and hardwoods to conifer dominated forest (e.g. Zhang et al. 2008). Trajectories of areas that were planted without vegetation removal are likely to vary depending on the amount of shrub cover on each site. On the other hand, intensive shrub removal may not be necessary if the management objective is ecosystem recovery, given that conifer survival is high under abundant shrub cover (Lopez-Ortiz 2007; Shatford et al. 2007).

One concern with vegetation removal is potential for increased cover of exotic species. Exotic species that are allowed to gain a foothold have the potential to eliminate native vegetation, particularly in high resource environments (Blumenthal 2005), such as areas where vegetation has been removed. In this study, exotic species increased with vegetation removal on harsh aspects, which may be equally limiting to native and exotic species. When removing vegetation on harsh aspects, exotic species should be monitored especially in areas with resident populations of these species.

Evaluating the role of microsite conditions on species distributions in diverse ecosystems is a difficult task. The multitude of interacting factors that can influence dispersal, germination and establishment make it very difficult to determine specific factors influencing species distributions. Additionally, factors are likely to vary in different locations and over time. In chapter four, separation of bryophyte effects from microsite effects on germination and establishment of vascular plants was not possible due to the failure of the field seeding trial. Soil moisture, nutrient status and depth components need to be examined to more clearly understand the mechanisms by which early-seral bryophytes influence germination and establishment of vascular plants. More in-depth field analysis of bryophyte and other early-seral species impacts on conifer establishment will allow further insights into potential for and limitations to natural plantation recovery following wildfire. Additionally, microsite suitability and habitat requirements change over time (Jones and del Moral 2005). Microsites change over time due to changes in vegetation, woody debris, and litter conditions. The role of microsites is altered due to changes in species resource use (Whittaker 1993).

Finally, the spatial scale of examination needs to be considered when interpreting results of the study. Interpretation of successional processes, which operate at multiple spatial scales, appear to vary by the scale of measurement and treatment averages may not be indicative of subplot or plant scale differences. For example, study plots were not large enough to examine interactions with wildlife that could drastically affect successional trajectories and plant communities. Scale of measurement also affects inferences about microsite heterogeneity (Bonnet et al. 2005; Mills and Macdonald 2005; Cutler et al. 2008). The small scale utilized in this study for measurement of microsites was deliberately chosen due to interest in bryophytes and because, in the presence of propagules, germination and establishment success are largely determined by small scale environmental factors. Larger microsite or mesosite factors may be as or more important in determining species distributions following severe fire in plantation forests, particularly in the presence of varying dispersal capabilities and seed sources.

This research was designed to examine the effects of conifer planting and vegetation removal and environmental factors on vegetation succession and plant communities during the regeneration process. The Timbered Rock Reforestation, Stand Dynamics and Fuels Study, is designed to be a long-term study of the stand development aimed at creating a suite of restoration options that could meet changing management goals, particularly increasing late successional characteristics and decreasing risk of repeated fire. The study will also examine other ecosystem components: including dead and live fuel dynamics and planted and natural conifer establishment and long-term vegetation, fuel and overstory dynamics. The continued monitoring of these study plots will allow long-term research needs to be met and increase understanding of forest management effects on plant communities, stand development and forest succession. Examination of vegetation, natural and artificial regeneration and fuel dynamics will provide a detailed picture of the succession of burnt plantations with and without restoration. The current results underscore the importance of abiotic and biotic interactions at multiple scales in determining the initial conditions for, and response to, restoration activities.

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APPENDICES.

APPENDIX A. TREATMENT AND SAMPLE PLOT LAYOUT.

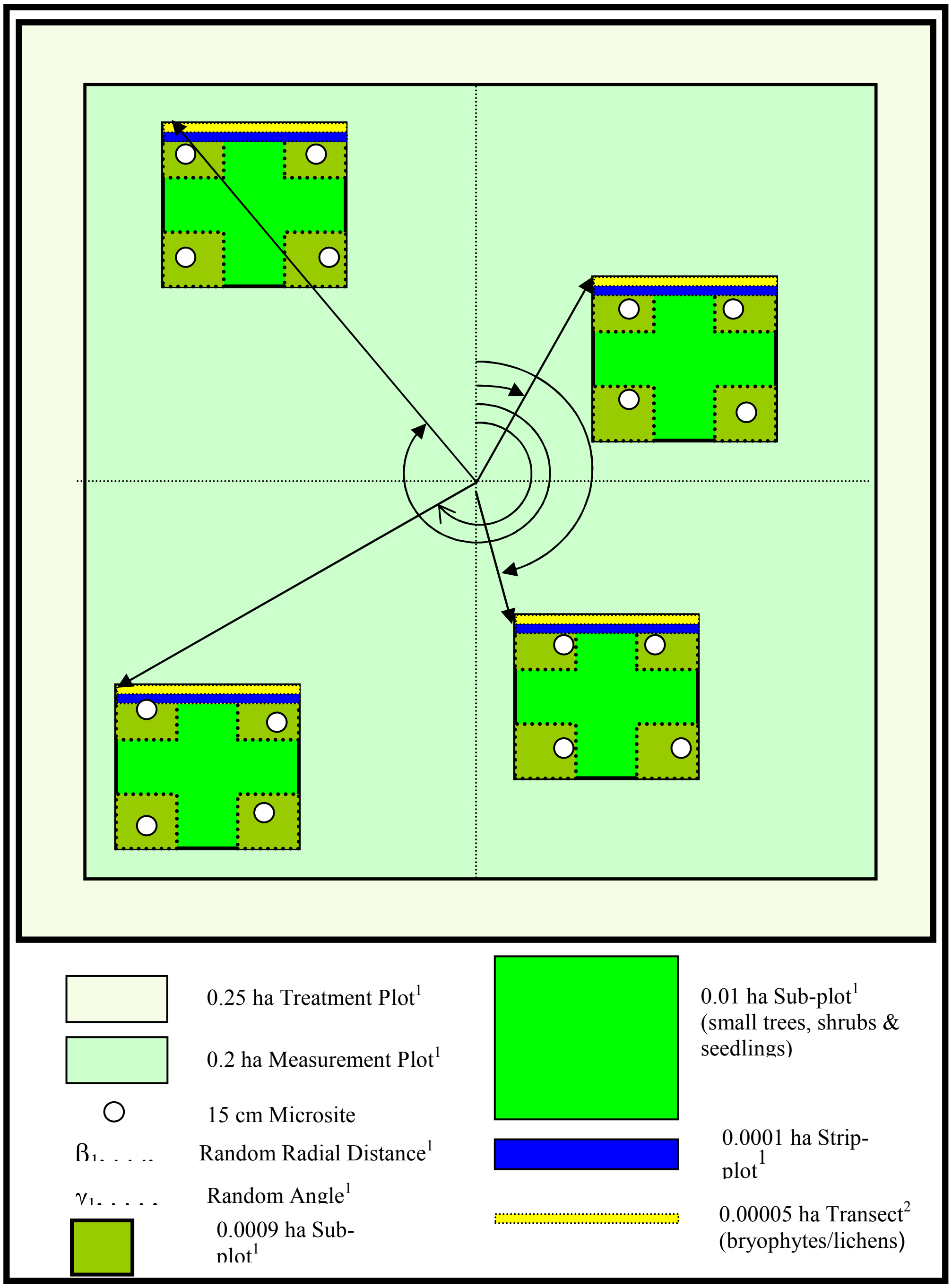

Figure A.1. Treatment and sample plot layout (Schematic originally developed by PNW Research Station).

APPENDIX B. SPECIES LISTS AND TRAIT GROUP DESIGNATIONS.

Table B.1. Vascular plant species list and trait group designations. Fire = fire response, Weed = weediness, Av=avoider, En = endurer, Ev = evader, I = invader, R = residual, c = conifer, a = annual herb, p = perennial herb, g = graminoid, f = fern, b = bryophyte, ss = sub-shrub, eg = evergreen shrub, d = deciduous shrub, e = early-seral, l = late-seral, we = weedy exotic, wn = weedy native, n = native, ex = exotic and nf = nitrogen fixer. Blank indicates undefined status except for N-fix and weediness which indicate non-fixer and not weedy respectively.

		Trait Groups					
Scientific Name	**Common Name**	**Fire**	**Growth Form**	**Weed**	**Origin**	**N-fix**	**Seral State**
Abies concolor [Tree]	white fir	Av/I	c		n		l
Acer circinatum [Tall]	vine maple	En	d		n		e/l
Acer macrophyllum [Tall/ Tree]	big leaf maple	En	d		n		l
Achlys triphylla	deer footed vanilla leaf	En	p		n		l
Adenocaulon bicolor	trail plant	En	p		n		l
Agoseris grandiflora	bigflower agoseris						
Agoseris heterophylla	annual agoseris	EV/En	p		n		
Agoseris sp.	agoseris	Ev			ex		
Agoseris retrorsa	spearleaf agoseris						
Agrostis sp.	bent Grass	EV/En	pg		n		e
Aira caryophyllea	silver European hairgrass	I/Ev	ag	we	ex		
Amelanchier alnifolia [Tree]	Saskatoon serviceberry	En	d		n		
Anaphalis margaritacea	pearly everlasting	I/En	p	wn	n		
Anemone deltoidea	Columbian windflower	EV/En	p		n		
Anemone oregana	blue windflower	EV/En	p		n		l
Antennaria arcuata	box pussytoes						
Apocynum androsaemifolium	dogbane	En	p		n		
Aquilegia formosa	western columbine	En	p		n		
Arbutus menziesii [Tall/ Tree]	madrone	I/En	eg		n		
Arctostaphylos columbiana	hairy manzanita	I/Ev	eg		n		e
Arctostaphylos patula	green leafed manzanita	I/En	eg		n		e
Arctostaphylos viscida	sticky whiteleaf manzanita						
Arnica cordifolia	heartleaf arnica						
Arnica sp.	unknown arnica						
Arnica latifolia	broadleaf arnica	En	p		n		e/l

Table B.1 (Continued.)

			Trait Groups				
Scientific Name	**Common Name**	**Fire**	**Growth Form**	**Weediness**	**Origin**	**N-fix**	**Seral State**
Arnica spathulata	hairy arnica	En	p		n		e
Asarum marmoratum	wild ginger	En	p		n		e/l
Asyneuma prenanthoides	California harebell	Ev/En	p		n		
Boschniakia strobilacea	Calfornia ground cone	Ev/En	p		n		
Bromus hordeaceus	softbrome	I	ag	we	ex		e/l
Bromus sp.	brome sp.						
Bromus tectorum	cheatgrass	I	ag	we	ex		e/l
Calocedrus decurrens Tree	incense cedar	Av/I	c		n		e/l
Calochortus tolmiei	cat's ears	En	p		n		
Campanula scouleri	Scouler's harebell	Ev/En	p		n		e
Cardamine oligosperma	little western bittercress	I/Ev	p/a		n		
Carex sp.	sedge		g		ex		
Ceanothus integerrimus Tall	deer brush	Ev	d		n	nf	e
Ceanothus sanguineus Tall	redstem ceanothus	Ev	d		n	nf	e
Cerastium arvense	field chickweed	I	p		n		e
Chamerion angustifolium	fire weed	I/En	p	wn	n		e
Chimaphila umbellata	prince's pine	Av/En	ss/p		n		l
Chrysolepis chrysophylla Tall/Tree	chinquapin	En	eg		n		e/l
Cirsium arvense	Canada thistle	I/En	p	we	ex		e
Cirsium sp.	thistle				ex		
Cirsium vulgare	bull thistle	I	a	we	ex		e
Clarkia purpurea	winecup clarkia						
Clarkia rhomboidea	diamond clarkia	I	a		n		e
Claytonia perfoliata	miner's lettuce	Ev	a	wn	n		e
Claytonia sibirica	candy flower	Ev	p/a		n		e/l
Clinopodium douglasii	yerba buena	Ev/En	ss/p		n		
Collomia heterophylla	varied leaf collomia	I	a		n		
Conyza canadensis	horseweed	I	p/a	wn	n		l
Coptis laciniata	Oregon goldenthread	En	p		n		e/l
Cornus nuttallii Tall/Tree	Pacific dogwood	En	d		n		e/l
Corylus cornuta var. *californica* Tall	hazelnut	En	d		n		e/l
Crepis capillaris	hawksbeard	I	a	we	ex		e
Crepis sp.	Hawksbeard sp.				ex		
Cynoglossum grande	Pacific hound's tongue	En	p		n		e
Cynosurus echinatus	Hedgehog dogtail	I	ag	we	ex		
Cystopteris fragilis	Fragile fern	En	pf		n		

Table B.1 (Continued.)

Scientific Name	Common Name	Fire	Trait Groups Growth Form	Weed iness	Ori gin	N-fix	Seral State
Daucus pusillus	Queen Anne's lace	I	a	we	ex		e
Deschampsia elongata	tufted hair grass	En	pg		n		e/l
Dicentra formosa	Bleeding heart	En	p		n		
Dichelostemma congestum	ookow	En	p		n		
Dodecatheon hendersonii	mosquito bills	En	p		n		e
Elymus glaucus	Blue wild rye		pg		n		e
Epilobium brachycarpum	Tall annual willowherb	I	a		n		
Epilobium ciliatum	Fringed willowherb		p	wn	n		
Epilobium sp.	Unk epilobium				ex		
Epilobium minutum	Chapparal willowherb	I	a	wn	n		
Equisetum arvense	field horsetail		pf	wn	n		e/l
Erechtites minima	Fireweed	I/Ev	p/a		n		
Erodium cicutarium	redstem stork's bill	I	a	we	ex		e
Euchiton japonicus	Father and child plant	I	a	we	ex		
Eurybia radulina	rough leaved aster	I/Ev	p		n		
Festuca sp.	Fescue		g		ex		
Festuca occidentalis	desert fescue	I/En	a	wn	n		e/l
Fragaria vesca	wild strawberry	En	p		n		e
Galium aparine	cleavers	I	a	wn	n		
Galium sp.	cleaver sp.	I	a		ex		
Galium triflorum	sweetscented bedstraw	Ev/En	p		n		e/l
Garrya fremontii Tall	bearbrush	I/En	eg		n		e/l
Gaultheria shallon	salal	En	eg		n		e
Geranium dissectum	cut leaf geranium	I	a	we	ex		e/l
Geranium molle	dove foot geranium						
Heuchera micrantha	crevice alumroot	En	p		n		
Hieracium albiflorum	white flowered hawksbeard	Ev	p		n		
Hieracium sp.	hawkweed.	Ev			ex		
Holodiscus discolor Tall	oceanspray	Ev/En	d		n		e/l
Hypericum perforatum	St. John's wort	I/En	p	we	ex		e
Hypochaeris radicata	false dandelion		p	we	ex		
Iris chrysophylla	wild iris	En	p		n		
Juncus ensifolius	rush	En	pg		n		
Lactuca muralis	wild lettuce	I	a	we	ex		e
Lactuca saligna	thin leaf lettuce	I	a	we	ex		
Lactuca serriola	prickly lettuce	I	a	we	ex		

Table B.1 (Continued.)

Scientific Name	Common Name	Fire	Trait Groups Growth Form	Weed iness	Ori gin	N-fix	Seral State
Lathyrus polyphyllus	leafy pea	I/Ev	p		n	nf	
Leucanthemum vulgare	oxeye daisy	I	p	we	ex		e
Lilium columbianum	tiger lily	En			n		
Linnaea borealis ssp. *longiflora*	twin flower	Ev/En	ss/p		n		l
Lonicera ciliosa	orange honeysuckle	En	ss/p		n		
Lonicera hispidula	pink honeysuckle	En	ss/p		n		
Lotus corniculatus	bird's-foot trefoil	I		we	ex	nf	e
Lotus crassifolius	big deervetch						
Lotus sp.	trefoil						
Lotus micranthus	desert deervetch	I	a	we	ex	nf	
Lotus unifoliolatus	American bird's foot trefoil	I	a	wn	n	nf	e
Luzula comosa	woodrush	En	pg		n		
Madia exigua	threadstem madia	I	a		n		
Madia madioides	woodland madia	I	a		n		
Mahonia nervosa	Oregon grape	En	ss/eg		n		l
Mahonia piperiana	Oregon grape	En	eg		n		
Maianthemum racemosum	false solomon's seal	I/En	p		n		e/l
Maianthemum stellatum	stellate false solomon's	I/En	p		n		e/l
Marah oreganus	wild cucumber	En	p		n		e
Melica sp.	oniongrass	En	pg		n		l
Melica harfordii	Harford's oniongrass						
Melica subulata	Alaska oniongrass						
Microseris douglasii	Douglas' silverpuffs				ex		
Mimulus guttatus	monkey flower	Ev/En	p		n		e
Mitella diversifolia	angle leaf mitrewort	En	p		n		
Moehringia macrophylla	largeleaf sandwort	Ev/En	p		n		l
Montia diffusa	miner's lettuce	I	a	wn	n		
Navarretia squarrosa	skunk weed	I/Ev	a		n		
Nemophila parviflora	small flowered nemophilla	I/Ev	a		n		
Osmorhiza berteroi	sweetroot	Ev/En	p	wn	n		l
Phacelia heterophylla	varied leaf phacelia	En	p/a		n		
Philadelphus lewisii [Tall]	mock orange	En	d		n		e
Phlox adsurgens	woodland phlox	Ev/En	p		n		
Pinus lambertiana [Tree]	sugar pine	I/En	c		n		e
Pinus ponderosa [Tree]	ponderosa pine	I/En	c		n		e/l

Table B.1 (Continued.)

Scientific Name	Common Name	Fire	Trait Groups Growth Form	Weed iness	Ori gin	N-fix	Seral State
Piperia elegans	orchid	En	p		n		l
Plagiobothrys nothofulvus	rusty popcornflower	I/Ev	a		n		e
Plagiobothrys tenellus	Pacific popcorn flower						
Plantago lanceolata	California plantain	I	p/a	we	ex		
Poa sp.			g		ex		
Polystichum imbricans	narrowleaf sword fern	En	pf		n		
Polystichum munitum	sword fern	I/En	pf		n		e/l
Potentilla glandulosa	sticky cinquefoil	Ev	p		n		e
Potentilla gracilis	slender cinquefoil						
Prosartes hookeri var. *hookeri*	Hooker's fairy bells	En	p		n		l
Prunus emarginata Tree	bitter cherry	Ev/En	ss/d		n		e
Pseudognaphalium californicum	lady's tobacco						
Pseudognaphalium canescens ssp. *thermale*	Wright's cudweed						
Pseudotsuga menziesii Tree	Douglas-fir	I/En	c		n		e/l
Pteridium aquilinum	bracken fern	I/En	pf		n		e
Pyrola picta	white-veined wintergreen						
Quercus chrysolepis Tall/Tree	canyon live oak	En	eg		n		e/l
Quercus kelloggii Tall/Tree	California black oak	En	d		n		e/l
Ribes cruentum	Sierra gooseberry	I/Ev/En	d		n		l
Ribes lobbii	gummy gooseberry	Ev/En	d		n		e/l
Ribes sanguineum Tall	red flowering currant	Ev/En	d		n		e/l
Rosa canina	dog rose	I	p		ex		
Rosa gymnocarpa	wood rose		ss/d		n		e/l
Rosa spithamea	ground rose	En	ss/d		n		
Rubus armeniacus	Himalayan blackberry	I/En	eg		ex		e
Rubus leucodermis Tall	blackcap raspberry	I/Ev/En	d		n		e/l
Rubus parviflorus Tall	thimbleberry	I/Ev/En	ss/d		n		e
Rubus ursinus	trailing blackberry	I/Ev/En	ss/d		n		e
Rupertia physodes	forest scrurfpea	I/En	p		n	nf	
Salix sp. Tall/Tree	willow	En	d		n		e
Sambucus sp. Tall	elderberry	I/Ev/En	d		n		

Table B.1 (Continued.)

Scientific Name	Common Name	Fire	Trait Groups Growth Form	Weed iness	Ori gin	N-fix	Seral State
Sanicula crassicaulis	Pacific black snakeroot	Ev/En	p		n		
Senecio sylvaticus	woodland ragweed		a	we	ex		e
Solanum parishii	Parish's nightshade	I/Ev/En	p		n		
Sonchus asper	prickly sow thistle	I	a	we	ex		e
Stephanomeria virgata	wirelettuce	I	a		n		
Symphoricarpos mollis	creeping snowberry	En	ss/d		n		
Synthyris reniformis	snow queen	En	p		n		l
Taraxacum officinale	dandelion	I/En	p	we	ex		e
Tellima grandiflora	fringeplant	En	p		n		
Tonella tenella	lesser baby innocence	I/Ev	a		n		e
Torilis arvensis	bur chervil	I	a	we	ex		e
Toxicodendron diversilobum Tall	poision oak	En	d		n		e/l
Tragopogon dubius	goat's beard	I/En	p	we	ex		e
Trientalis borealis	star flower	En	p		n		
Trifolium sp.	clover				ex		
Trillium ovatum	trillium	En	p		n		
Trisetum canescens	tall trisetum	Ev/En	pg		n		e
Triteleia hyacinthina	white brodiaea	En	p		n		
Vaccinium parvifolium	huckleberry	En	d		n		
Vancouveria hexandra	goosefoot	En	p		n		l
Veronica americana	American brooklime	I	p		n		
Vicia americana	American vetch	I/Ev	p	wn	n	nf	e/l
Viola sempervirens	evergreen violet	Ev/En	p		n		
Vulpia sp.	Vulpia sp.		g		ex		
Vulpia myuros	rattail fescue	I	a		ex		e
Whipplea modesta	common whipplea	En	ss/p		n		
Xerophyllum tenax	bear grass	En	p		n		e/l

Nomenclature based on USDA (2007).

Tree indicates species considered trees for seedling surveys.

Tall indicates shrubs that had at least one shrub over 1.3 m.

Table B.2. Cryptogam species list and trait group designations. I = invader, R = residual, ss = short lived, ll = long-lived, a = acrocarpous, p = pleurocarpous, ft = fruiticose, fl = foliose, st = simple thalloid, ct = complex thalloid, l = leafy liverwort. Blank indicates undefined.

Scientific Name	**Fire Response**	**Longevity**	**Growth Form**
Bryophytes			
Antitrichia californica	R	ll	p
Aulacomnium androgynum	I	ll	a
Brachythecium velutinum	I		p
Bryum argenteum	I	ll	a
Bryum capillare	I	sl	a
Ceratodon purpureus	I	sl	a
Claopodium whippleanum			p
Dicranum scoparium	R	ll	a
Didymodon sp.			a
Didymodon vinealis	I	ll	a
Ditrichum ambiguum	I		a
Ditrichum pusillum	I		a
Epipterygium tozeri	I		p
Eurhynchium oreganum	R	ll	p
Fissidens dubius			a
Fissidens sp.	I	sl	a
Fissidens sublimbatus			a
Funaria hygrometrica	I	sl	a
Grimmia pulvinata	R	ll	a
Homalothecium fulgescens	R	ll	p
Homalothecium sp.			p
Hypnum subimponens	R	ll	p
Isothecium myosuroides	R		p
Leptobryum pyriforme	I	sl	a
Leucolepis acanthoneuron	R	ll	p
Orthotrichum sp.	R		p
Plagiomnium venustum	R		p
Pohlia longibracteata			a
Polytrichum juniperinum	R	ll	a
Polytrichum piliferum	R	ll	a
Racomitrium heterostichum	R	ll	p
Scleropodium touretii	R	ll	p
Timmiella crassinervis	I		a
Tortula princeps	R	ll	a
Tortula subulata			a
Weissia controversa	I	sl	a
Weissia sp.	I	sl	a

Table B.2 (Continued).

Scientific Name	**Fire Response**	**Longevity**	**Growth Form**
Hornworts			
Anthoceros sp.	I	sl	
Lichens			
Cladonia sp.	I	ll	ft
Letharia vulpina	R	ll	ft
Nephroma sp.	R	ll	fl
Peltigera sp.	R	ll	fl
Liverworts			
Cephalozia lunulifolia			l
Cephaloziella divaricata			l
Fossombronia sp.	I	sl	st
Jungermannia rubra			l
Jungermannia sp.			l
Marchantia polymorpha	I		ct
Pellia sp.			st

Nomenclature based on USDA (2007).

APPENDIX C. INDICATOR SPECIES FOR BLOCKS.

Table C.1. Vascular plant indicator species for blocks with indicator values (IV) of p < 0.05. Higher values mean that the species is more restricted to that particular group. Tall shrubs and hardwood trees that were indicators for the same sites as low shrubs were combined and indicated by (- tall) and highest indicator value reported. WBEC, FC2, FC3, SPC4 and SPC5 = block codes (See Table 2.A1).

Vascular Plant Indicators		
Species	**Block**	**IV**
Acer circinatum (-tall)	SPC5	51.7
Acer macrophyllum - tall	WBEC	56.7
Achyls triphylla	SPC4	40.7
Agoseris sp.	WBEC	57.7
Aica caryophyllea	FC3	73.6
Anemone deltoidea	WBEC	36.5
Apocynum androsaemifolium	FC3	65.8
Arbutus menziesii (-tall)	FC2	45.4
Arctostaphylos columbiana	FC2	79.9
Arnica latifolia	FC2	31.9
Arnica spathulata	FC2	29.1
Asarum marmoratum	WBEC	34.7
Asyneuma prenanthoides	SPC5	49.7
Bromus tectorum	FC3	49.5
Campanula scouleri	WBEC	41.1
Cardamine oligosperma	WBEC	41.3
Carex sp.	FC2	36
Ceanothus integerrimus	FC2	35.6
Ceanothus sanguineus	SPC5	44.3
Chimaphylla umbellata	SPC4	28
Chrysolepis chrysophylla	FC2	28.4
Claytonia perfoliata	SPC5	86.6
Claytonia sibirica	SPC5	62.4
Clinopodium douglasii	FC3	32.3
Corylus cornuta var. *californica*	FC3	37.8
Corylus cornuta var. *californica* - tall	FC3	33.6
Cynosurus echinatus	FC3	54
Dicentra formosa	SPC5	48.5
Elymus glaucus	WBEC	49
Erechtites minima	FC3	48.3
Euchiton japonicum	FC3	70.3
Eurybia radulina	FC3	53
Fragaria vesca	WBEC	64.3
Galium triflorum	SPC5	64.6

Table C.1 (Continued)

Species	**Block**	**IV**
Iris chrysophylla	FC3	58.4
Lathyrus polyphyllus	SPC5	58.8
Lilium columbianum	FC2	50
Lonicera hispidula	SPC4	44
Lotus micranthus	FC3	56.9
Luzula comosa	SPC5	35.2
Madia exigua	FC3	64.9
Madia madioides	WBEC	66.8
Mahonia nervosa	SPC5	36
Mahonia piperiana	FC3	32.1
Maianthemum racemosum	WBEC	52
Maianthemum stellatum	WBEC	29.3
Melica sp.	WBEC	57.2
Moehringia macrophylla	WBEC	29.3
Osmorhiza berteroi	WBEC	41
Phacelia heterophylla	SPC5	45.6
Polystichum imbricans ssp. *imbricans*	SPC4	39.8
Polystichum munitum	SPC5	45.9
Pseudotsuga menziesii	FC2	49.7
Quercus kelloggii - tall	WBEC	91
Ribes lobbii	WBEC	53.1
Rosa gymnocarpa	WBEC	63.5
Rosa spithamea	FC2	45.6
Rubus leucodermis	SPC5	60
Rubus leucodermis - tall	SPC5	44.8
Rubus ursinus	WBEC	33.4
Salix sp.	SPC5	49.4
Stephanomeria virgata	SPC4	29.6
Symphoricarpos mollis	WBEC	65.5
Synthyris reniformis	FC3	46.6
Tellima grandiflora	SPC5	41.9
Torilis arvensis	WBEC	82.7
Trientalis borealis ssp. *latifolia*	SPC4	53.3
Vaccinium parvifolium	FC2	50.1
Viola sempervirens	WBEC	37.8
Vulpia myuros	FC3	74.4
Whipplea modesta	FC2	33
Xerophyllum tenax	FC2	44.6

Table C.2. Cryptogam indicator species for blocks with indicator values (IV) of $p \leq 0.05$. Higher values mean that the species is more restricted to that particular group.

Cryptogam Indicators		
Species	**Block**	**IV**
Ceratodon purpureus	SPC5	24.6
Fissidens sp.	FC3	36.5
FUNGI	FC3	53.5
Homalothecium group	FC3	39.7
Leptobryum pyriforme	FC2	60.1
Weissia group	FC3	45.1

Table C.3. Indicator traits for blocks with indicator values (IV) of $p \leq 0.05$. Higher values mean that the trait is more restricted to that particular group.

Trait	**Block**	**IV**
Deciduous Shrubs	WBEC	27.6
Conifers	FC2	42
Evergreen Shrubs	FC2	35.4
Exotics	FC3	35
Weedy Exotics	FC3	35
Annual Herbs	FC3	30.8

APPENDIX D. NMS AXIS CORRELATIONS FROM CHAPTER 2.

Table D.1. Strong correlations ($R^2 \geq 0.20$) between environmental factors, species and traits for vascular plant ordination shown in Figure 2.1a and 2.1c. Traits were relativized by row totals before calculations. ^{t}Tall shrub of a given species. ^{s}Seedling of a given species. R = richness, BA = basal area, I=Index., unburnt = unburnt forest, other conifer = other than *P. menziesii,* Age = plantation age at time of burn, Year = year post-fire.

	Axis		
Factor	**1**	**2**	**3**
Burn Date	.	0.66	.
% Dead BA	-0.56	.	.
Hardwood BA	.	0.46	.
% Live BA	0.56	.	.
BA other conifers	0.62	.	.
Total BA	-0.49	.	.
Distance to unburnt	.	0.57	.
Elevation	0.49	.	.
Fern R	-0.46	.	.
Forb Cover	.	0.54	.
Graminoid Cover	.	.	-0.56
Age	0.45	.	.
Herb Cover	.	0.57	-0.49
Heat load I	.	-0.37	.
Low Shrub Cover	.	0.49	-0.73
Slope	-0.77	.	.
Tall Shrub R	.	0.66	.
Tall Shrub Cover	.	0.49	.
Total R	.	0.47	.
Year	.	.	-0.68

	Axis		
Trait Group	**1**	**2**	**2**
Deciduous shrubs	.	0.83	.
Early-seral	.	0.49	.
Evader	.	0.56	.
Evergreen Shrubs	.	-0.76	.
Fern Cover	-0.60	.	.
Graminoid Cover	.	.	-0.51

	Axis		
Species	**1**	**2**	**3**
Acer circinatum	-0.60	.	.
Acer circinatum ^{t}	-0.70	.	.
Acer macrophyllum ^{s}	.	0.47	.
Acer macrophyllum ^{t}	.	0.61	.
Agoseris sp.	.	0.49	.
Asarum marmoratum	.	0.47	.
Mahonia nervosa	-0.53	.	-0.52
Asyneuma prenanthoides	-0.50	.	.
Ceanothus integerrimus	.	.	-0.64
Chrysolepis chrysophylla	.	-0.52	.
Chimaphila umbellata	.	-0.52	.
Corylus cornuta ^{t}	.	0.62	.
Collomia heterophylla	0.52	.	0.48
Elymus glaucus	.	0.52	.
Chamerion angustifolium	.	0.58	.
Polystichum munitum	-0.67	.	.
Pseudotsuga menziesii	.	-0.48	.
Quercus kelloggii^{t}	0.47	.	.
Ribes sanguineum	.	0.56	.
Rosa gymnocarpa	.	0.49	.
Rosa spithamea	.	.	-0.49
Rubus leucodermis	-0.52	.	.
Rubus leucodermis^{t}	-0.51	.	.
Rubus parviflorus	.	0.66	.
Rubus ursinus	.	0.58	.
Symphoricarpos mollis	.	0.48	.
Tellima grandiflora	-0.45	.	.
Torilis arvensis	.	0.49	.
Trientalis borealis	-0.49	.	.
Vancouveria hexandra	.	0.48	.
Whipplea modesta	.	.	-0.62

Table D.2. Strong correlations ($R^2 \geq 0.20$) between environmental factors, species and traits for cryptogam community ordination shown in Figure 2.1b and 2.1d. Traits were relativized by row totals before calculations. R = richness, BA = basal area.

	Axis		
Environmental Factor	**1**	**2**	**3**
% Dead BA	-0.68	.	.
% Live BA	0.68	.	.
BA other conifers	0.47	.	.
BA Douglas-fir	0.65	-0.45	.
Distance to stream	-0.45	.	.
Low shrub	.	0.52	.
Slope	-0.51	.	.
Tall Shrub R	.	.	0.46
Total Vascular R	0.45	.	.

	Axis		
Trait Group	**1**	**2**	**3**
Bryophyte	.	.	-0.47
Evaders	.	0.46	.
Evergreen shrubs	.	.	-0.50
Fungi	0.55	.	.
Liverwort	0.51	.	-0.54

	Axis		
Cryptogam Species	**1**	**2**	**3**
Aulacomnium androgynum	0.66	.	-0.57
Bryum argenteum	.	0.60	.
Bryum capillare	.	0.59	.
Ceratodon purpureus	.	0.70	.
Didymodon vinealis	.	.	-0.59
Fissidens	0.65	.	.
Fossombronia	0.52	.	.
FUNGI	0.57	.	.
Homalothecium group	0.52	.	.
Polytrichum juniperinum	.	.	-0.61
Weissia group	0.74	.	.

APPENDIX E. MRPP/MRBP FROM CHAPTER 3 INCLUDING ALL BLOCKS.

Table E.1. A-statistics and p-values for differences in plant community and trait composition among all restoration treatments and between planting only versus control treatments large sub-block and vegetation removal (VR) versus no vegetation removal (NVR) on two aspects (harsh and moderate) from MRBP/MRPP in all five blocks. All differences were considered individually without regard to other groups. * Analyzed with MRPP and included the control and monoculture treatments on both aspects. Due to the need for balanced groups in MRBP, partial datasets were used for blocked factors as follows: restoration treatments included five restoration treatments and one control treatment on one aspect, NVR/VR by aspect included high-density treatments with and without vegetation removal on two aspects, NVR/VR (harsh) and (moderate) included high-density treatments with and with vegetation removal on one aspect. Significant p-values (≤ 0.05) and relatively strong A-statistics (> 0.1) are in bold.

Community		Vascular Plant Year Two		Combined Year Three		Cryptogam Year Three		Trait Year Two	
Group	**Group (#)**	**A**	**p**	**A**	**p**	**A**	**p**	**A**	**p**
Treatments	6	-0.1	0.98	0.006	-0.01	0.57	0.12	-0.03	0.76
Control/ Planting only	3	-0.02	0.92	-0.005	-0.06	0.89	0.76	-0.06	0.95
NVR/VR*	2	0.05	**0.013**	0.07	0.02	0.14	0.07	0.02	0.09
NVR/VR by aspect	4	-0.007	0.51	0.02	**0.20**	**0.005**	**0.002**	**0.20**	**0.006**
NVR/VR (harsh)	2	-0.01	0.69	0.03	**0.17**	**0.03**	**0.03**	**0.13**	**0.04**
NVR/VR (moderate)	2	0.02	0.1	0.04	**0.42**	**0.03**	**0.02**	**0.44**	**0.02**
Community		**Vascular Plants Year Four**		**Combined Year Four**		**Cryptogam Year Four**		**Trait Year Four**	
Group	**Group (#)**	**A**	**p**	**A**	**p**	**A**	**p**	**A**	**p**
Treatments	6	-0.05	0.81	0.01	-0.03	0.64	0.06	-0.02	0.67
Control/ Planting only	3	-0.02	0.96	-0.01	-0.08	0.90	0.97	-0.06	0.95
NVR/VR*	2	**0.11**	**0.000**	0.07	**0.10**	**0.003**	**0.000**	0.09	**0.0009**
NVR/VR by aspect	4	0.09	0.11	0.04	**0.25**	**0.01**	**0.000**	**0.22**	**0.005**
NVR/VR (harsh)	2	0.04	**0.02**	0.04	0.08	0.26	**0.02**	0.03	0.37
NVR/VR (moderate)	2	0.04	**0.03**	0.06	**0.43**	**0.04**	**0.02**	**0.39**	**0.02**

APPENDIX F. NUMBER OF SEEDLINGS PER SEEDBED USED IN CHAPTER 4 ANALYSES.

Table F.1. Number of seedlings per seedbed used in growth, germination (germ.) and biomass (includes root and shoot weight and root:shoot ratio) analyses. Growth numbers greater than 5 resulted from a seedling dying and then germination of a new seedling corrected for using growth rate over time. Species codes are ABCO = *Abies concolor*, CESA = *Ceanothus sanguineus*, CHANA2 = *Chamerion angustifolium*, PILA = *Pinus lambertiana*, PIPO =*Pinus ponderosa*, PSME = *Pseudotsuga menziesii* and VIAM = *Vicia americana.*

	Seedbed	ABCO	CESA	CHANA2	PILA	PIPO	PSME	VIAM
Germ.	Burnt bryophytes	5	5	5	5	5	5	5
	Burnt bare soil	5	5	5	5	5	5	5
	Unburnt bryophytes	5	5	5	5	5	5	5
Biomas	Burnt bryophytes	3	5	5	5	5	5	2
	Burnt bare soil	4	5	5	5	5	5	3
	Unburnt bryophytes	5	4	5	5	5	5	4
Growth	Burnt bryophytes	5	5	5	5	5	5	2
	Burnt bare soil	5	6	5	5	5	4	5
	Unburnt bryophytes	5	5	5	5	5	4	4