

Vegetation succession among and within structural layers following wildfire in managed forests

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Abstract

Question: How does vegetation develop during the initial period following severe wildfire in managed forests?

Location: Southwestern Oregon, USA.

Methods: In severely burned plantations, dynamics of (1) shrub, herbaceous, and cryptogam richness; (2) cover; (3) topographic, overstory, and site influences were characterized on two contrasting aspects 2 to 4 years following fire. Analysis of variance was used to examine change in structural layer richness and cover over time. Non-metric 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 burned plantations, following an initial floristics model of succession among structural layers. Succession within structural layers followed a combination of initial and relay floristic models. 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, and the fire regime. Succession among and within structural layers can follow different successional models and trajectories, oc-

curs at different rates, and is affected by multiple interacting factors.

Keywords: Aspect; Bryophytes; Cryptogams; Early-seral; Fire severity; Initial floristics; Managed forests; Mixed conifer forest; Mixed severity fire; Pacific Northwest; Plant community; Relay floristics; Succession.

Nomenclature: USDA (2007)

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

Introduction

Disturbance is a major driver structuring vegetation heterogeneity and plant communities (Pickett & White 1985; Naveh 1994; Laughlin et al. 2004). Many ecosystems are resilient to natural disturbances, and adaptation of plant species to specific disturbance regimes results in rapid recovery (Traubaud 1994; Kimmins 1997; Barnes et al. 1998; DeBano et al. 1998; Laughlin et al. 2004). Succession, i.e., directional change in vegetation over time, is reinitiated by catastrophic disturbances and varies among ecosystems and disturbance regimes. Two types of theory of succession exist, equilibrium- and non-equilibrium-based theories. Equilibrium-based successional theories predict ordered progression through successional states to a fairly stable endpoint (sensu Clements 1916). Non-equilibrium successional theories predict multiple successional pathways due to variation in abiotic and disturbance characteristics. In general, non-equilibrium successional theories have been more widely accepted in recent decades (Whittaker 1975; Connell & Slayter 1977; Noble & Slatyer 1980; Naveh 1994; Bradstock et al. 2005).

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; Whit-

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taker 1975; Pickett & White 1985) and disturbance regimes (Agee 2005; Bradstock et al. 2005). Some of the variability in successional models and theory is due to a failure to define the temporal phase or context (i.e., within versus among life forms) of succession (Grace 1991). For this purpose, Noble & Slatyer (1980) recognized two temporal phases of succession: (1) the immediate post-disturbance phase (initial state) when species abundance is determined by regenerative processes, and (2) later succession when species interactions and resource competition determine abundance. While the immediate post-disturbance phase is a brief portion of the entire community succession, change in dominance by small-stature plants can only be detected during this phase since their dominance may be restricted to one generation (West & Chilcote 1968; Dyrness 1973; Halpern et al. 1997). In addition, patterns evident in initial successional phases may strongly influence later succession states (Pickett & White 1985; Turner et al. 1997; Barnes et al. 1998; Ghermandi et al. 2004).

Initial states and vegetation succession are partially determined by pre-disturbance conditions, including previous management activities (DeGrandpre et al. 1993; Stuart et al. 1993; Turner et al. 1999; Fahey & Puettmann 2007; Penman et al. 2008). Effects of, and response to, disturbance in managed landscapes are derived from an interaction between 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 to become dense, even-aged conifer plantations. This type of management increases fire severity due to resultant high fuel loads, low branches, and continuous fuel arrangement, compared to uncut or partially cut forests (Weatherspoon & Skinner 1995; Thompson et al. 2007). In addition, dense overstory cover associated with plantations in the self-thinning or stem exclusion stage (e.g., Oliver & Larson 1996) may lead to reductions in understory abundance and diversity (Schoonmaker & McKee 1988; Halpern 1989; Spies 1991; Naveh 1994; Bailey et al. 1998). The distinctive vegetation composition and structure of plantations can alter post-fire successional dynamics compared to those in unmanaged forests (Stuart et al. 1993; Weatherspoon & Skinner 1995; Thompson et al. 2007).

Initial and relay floristics models of succession (Egler 1954) are useful for understanding early succession in managed forests because these models (1) focus on patterns of initial regeneration that may be evident in the immediate post-disturbance phase of

succession (Noble & Slatyer 1980), (2) predict measurable shifts in diversity and abundance, and (3) are sufficiently descriptive to be useful for developing forest management strategies (Egler 1954; Kimmins 1997). The relay floristics model predicts that vegetation cohorts replace one another over time due to the creation of more hospitable habitats and changes in propagule availability (Clements 1916; Titus & del Moral 1998). Alternatively, the initial floristics model predicts that most species are present in early-seral stages; subsequent successional dynamics are created by changes in the species or species group abundances (Halpern 1989; Trabaud 1994; Debussche et al. 1996). While floristics models are derived from equilibrium-based succession theory, models based on equilibrium theory can help explain mechanisms behind successional pathways, even in a non-equilibrium successional context.

The main objective of this study was to improve understanding of initial vegetation succession following severe wildfire in plantation forests 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.

Post-fire plantations may exhibit a lack of residual sprouting species due to a depauperate pre-fire understory, as often found in dense plantations (Schoonmaker & McKee 1988; Halpern 1989; Spies 1991; Naveh 1994; Bailey et al. 1998). Furthermore, high fire severity in plantations may delay regrowth or kill locally abundant sprouting shrubs (Halpern 1988; DeBano et al. 1998; Agee 2005). This lack of sprouting species could encourage succession among structural layers that follows a relay floristics model. In this scenario, increasing diversity in herbaceous and shrub structural layers and decreasing diversity in the bryoid layer would precede the transition between these structural layers. Alternatively, if plantations retained a significant portion of their pre-fire and pre-harvest understory vegetation, succession is more likely to follow an initial floristics model among structural layers. In these cases, high species diversity across all structural layers would occur early in succession with changes in structural layer dominance over time.

Succession within structural layers occurs simultaneously with succession among structural layers (Cremer & Mount 1965; Uhl et al. 1981; Spies 1991; DeGrandpre et al. 1993; de las Heras et al. 1994; Trabaud 1994). Succession within structural

layers that follows a relay floristics model would be reflected in increasing stress tolerator diversity and decreasing ruderal (sensu Grime 2001) diversity preceding a transition in dominance from ruderal to stress-tolerant species within each structural layer. Alternatively, succession within structural layers that follows the initial floristics model would be reflected in a high diversity of ruderal and stress-tolerant species in early succession within a given structural layer and changes in life form (ruderal to stress-tolerant) dominance over time.

While floristics models may explain the patterns of change within and among structural layers, site conditions and disturbance effects are expected to affect initial states and successional progression. Variation in topography, fire severity, site history, and abiotic conditions could lead to differences in plant community composition and successional trajectories. Alternatively, impacts of management may have homogenized plantations, resulting in little variation in plant communities and successional trajectories due to fire effects or site conditions.

Methods

Study area

The Timbered Rock fire occurred within the Western Cascades physiographic province, near the intersection of the Klamath and Cascade Mountains, primarily within the *Abies concolor* and mixed conifer forest zones (Franklin & Dyrness 1973). Southwestern Oregon has a mixed severity fire re-

gime, with an average fire return interval of 5 to 75 years (Sensenig 2002). The regional climate is Mediterranean, with warm, dry summers and mild, wet winters. Long-term weather data for nearby Prospect, Oregon, indicate that 89–152 cm of annual precipitation falls primarily between October and May. Average high temperatures range from 24°C to 30°C in the summer and from 8°C to 12°C in the winter (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?orpros>).

The 2002 wildfire burned 11 000 ha with varying severity in late summer. *Pseudotsuga menziesii* plantations <35 years of age occupied approximately 40% of the burned area. The study was conducted within five *P. menziesii* plantations (blocks) in three different watersheds, selected for moderate to high fire severity, sufficient plantation size for study implementation, and lack of other planned restoration activities (USDI 2003). While replication was low, the five plantation locations spanned the elevation range of mixed-conifer forest within the fire perimeter. Prior to the fire, plantations averaged 283 tph *P. menziesii*, 500 tph hardwoods (*Arbutus menziesii*, *Acer macrophyllum*, *Quercus chrysolepis*, and *Chrysolepis chrysophylla*), and 45 tph of other conifers (*A. concolor*, *Pinus ponderosa*, *Pinus lambertiana*, and *Calocedrus decurrens*). See Table 1 for more detailed site description by plantation.

Study design

Within each block, four plots were established on one generally uniform aspect (large sub-block), and two plots were established on a contrasting aspect

Table 1. 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 *P. menziesii* and *Pinus ponderosa*. Abbreviations are as follows: WBEC = West Branch Elk Creek, FC = Flat Creek, SPC = Sugar Pine Creek, 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, BA = Basal Area, 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	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 BA (%)	54–84	49–100	55–75	91–100	99–100
Total BA (m ² ha ⁻¹)	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

(small sub-block: Fig. 1) 2 years post-fire. 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 plots within each sub-block. Treatments on the large sub-block were: 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 were: 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° to 360° and moderate aspects ranged from 44° to 160°. 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. Although replication was low, the dispersion of plantations at the watershed scale and plots on contrasting aspects at the block scale provided representation of a full range of landscape conditions, contributing to a broad environmental frame of inference.

Plots were planted with 40% *P. menziesii* and 20% each of *Pinus lambertiana*, *P. ponderosa*, and

C. decurrens. Vegetation removal consisted of manual cutting of tall vegetation, focused on woody shrub stems in years 2 through 4 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 3 post-fire. One high-density NVR plot on the harsh aspect was accidentally scalped.

Data collection

Within each plot, slope (%), aspect (°, corrected for declination), and basal area (BA: $\text{m}^2 \text{ha}^{-1}$) by species of live and dead overstory conifer and hardwood trees [$> 5\text{-cm}$ diameter at breast height (dbh)] were measured. Aspect was converted to a heat load index (McCune & Grace 2002, p. 24). Percentage dead overstory BA was used as a continuous measure of fire severity, with lower severity having a lower percentage of overstory mortality. Additional data were retrieved from United States Department of Interior records (plantation age at time of fire) or derived from a Geographical Information System [watershed, elevation, and distance from plot center to nearest edge of unburned forest (≥ 0.16 ha) and downhill stream (first to fourth order)].

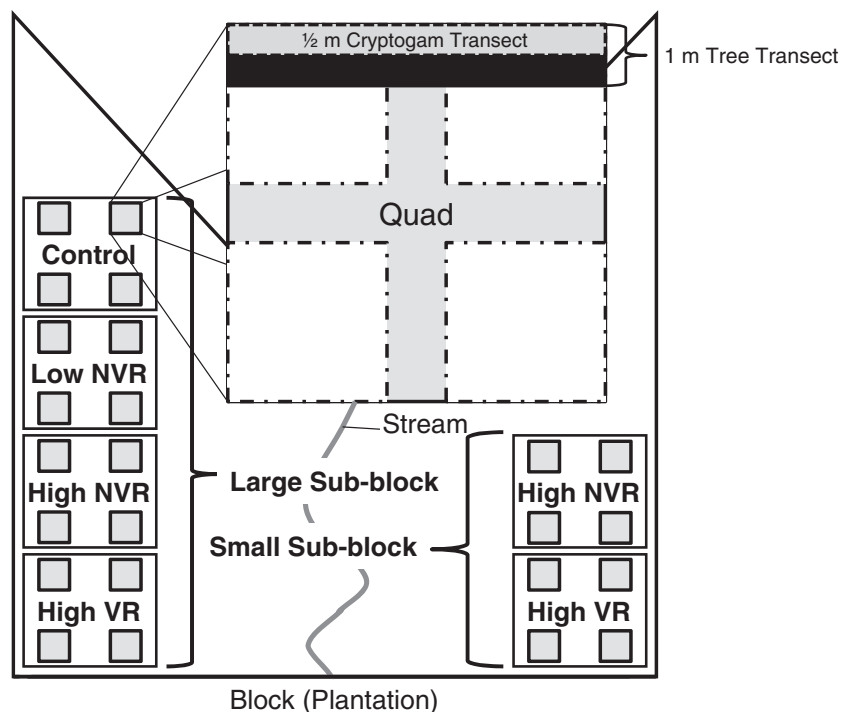


Fig. 1. Plot and quad layout within one block (plantation), with treatments labeled within plots. Subplot and transect layout within one quad (inset). Plot layout was replicated in five blocks. High = high-density, Low = low-density, NVR = no vegetation removal, and VR = vegetation removal.

Vascular plant percentage cover data were collected in three summers, years 2 through 4 post-fire. In order to provide a consistent measure of irregularly-shaped shrubs ≥ 1.3 m and hardwood trees ≤ 5 -cm dbh (tall shrubs), individual tall shrub percentage cover was measured as [canopy area (width \times length: cm²)/quad area (cm²) 100]. Length was measured along the long axis of each tall shrub, and width was recorded at an arbitrary point perpendicular to the long axis, not the widest point. This arbitrary location of the width axis measurement decreased the potential upward bias of using rectangular projection for tall shrubs. Individual tall shrub cover was then summed by species. Tall shrubs were measured in each of four permanently marked 0.01-ha square sub-plots (quads) that were randomly dispersed (with the restriction that each fit within one quadrant) within each plot (Fig. 1). Total tall shrub cover per quad was the sum of all individual tall shrub covers minus visually estimated overlap among neighbors. Total (maximum cover = 100%) and individual species percentage cover was estimated for low shrubs (shrubs and hardwood trees < 1.3 m), forbs, ferns, grasses, and combined herbaceous species by visual estimation in four 3 m \times 3 m (0.009 ha) square subplots per quad (Fig. 1). Natural tree seedlings were counted in a 1 m \times 10 m transect on the upslope side of each quad and converted to seedling density ha⁻¹. Non-vascular plant cover data were collected by one observer in the summers of years 3 and 4 post-fire in a 0.5 m \times 10 m transect on the upslope side of each quad in 20 contiguous 0.5 m \times 0.5 m subplots. Percentage cover was estimated by approximately log-scaled cover class: (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 (adapted from McCune et al. 1997) for individual species (except fungi) and for bryophytes, liverworts, lichens, and fungi across taxa.

Vascular plants and cryptogams were determined to the species level when possible, otherwise to the genus level or life-form group. Due to the difficulty of identifying extremely small or immature samples, several bryophytes were lumped into species groups (*Weissia controversa* includes *Timmiella crassinervis*; *Homalothecium* includes *Brachythecium velutinum*, *Claopodium whippleanum*, *Homalothecium fulgescens*, and *Isothecium myosuroides*; *Bryum capillare* includes *Pohlia longibracteata*).

To examine correlations between species traits and community patterns, trait groups (i.e., a set of

species that have similar biological characteristics, possess similar niches, and respond in similar ways to environmental factors) were defined based on USDA (2006, 2007), Hickman (1993), Spies (1991), Wang & Kembell (2005), Lawton (1971), Vitt et al. (1988), and personal experience. Vascular plants were classified into trait groups based on 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 and perennial forbs or graminoids, ferns, sub-shrubs, evergreen and 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). Cryptogams were classified into trait groups based on disturbance response (invading or residual) and longevity (short- or long-lived).

Data analysis

Mixed model 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 trait groups from non-metric multidimensional scaling (NMS) were used to examine the general patterns of species richness and cover and succession among and within structural layers in burned plantations on contrasting aspects. Correlations of environmental factors with NMS gradients and MRPP were used to examine effects of site conditions in influencing successional patterns, while avoiding assumptions of linearity among community variables (McCune & Grace 2002).

For all analyses, data were aggregated at the plot level, and tall shrubs and low shrubs of the same species were analyzed separately. Vascular plants and cryptogams were analyzed separately due to lack of year 2 cryptogam data, continuous (vascular plants) versus categorical (cryptogams) cover measures, and to allow comparisons between groups, which have been demonstrated to respond differently to gradients and follow different successional patterns (McCune & Antos 1981).

Repeated measures ANOVA was performed using a general linear mixed model in PROC MIXED, SAS (version 9.1 SAS Institute Inc., Cary, NC, US), 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. 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 examine the effects of aspect while controlling for planting density, with vegetation removal (NVR/VR), aspect (harsh/moderate), and year (3 years for vascular plants and 2 years for cryptogams) as explanatory variables. Within the two-way factorial, differences between aspects in treatments without vegetation removal only were examined using contrast statements. Second, due to a lack of interaction between aspect and year in the first analysis 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 (3 years for vascular plants and 2 years for cryptogams) as explanatory variables.

Log-transformed values (graminoid and fern cover) were used when necessary to meet model assumptions of normality and constant variance (Ramsey & Schafer 2002), as assessed using PROC UNIVARIATE, and plots of residual versus predicted and residual versus normal percentile. The most appropriate repeated measures covariance structure was selected for each response variable. 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 years 3 and 4, which was removed from analysis. To investigate differences between years and aspects, multiple comparisons were adjusted with the Tukey Honest Significant Difference (1949) adjustment.

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 magnitude of cover between different species (McCune & Grace 2002). Species that occurred in less than 5% of the plots (63 vascular and 20 cryptogam species) were deleted to reduce the noise in the dataset. In the vascular plant community, two treatments (Control and Low-density NVR) were labeled as multivariate outliers but were retained since removal did not yield significant improvement. Sørensen distance was used in multivariate analysis, unless otherwise specified, because

it works well for community data even with high beta diversity (McCune & Grace 2002).

NMS analyses used PC-ORD (version 5.1, MjM Software, Gleneden Beach, OR, US) autopilot “slow-and-thorough” setting, with random starting configurations and 250 runs of real data; obtaining three-dimensional solutions with final instability of <0.00001 . The resulting vascular plant community ordination was aligned by fire severity (indicated by % dead BA) on axis 1, so the cryptogam community was rotated to maximize percentage dead BA on axis 1 for comparison. 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 unburned 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 changes in plant communities over time, remeasured plots were connected using 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 & Grace 2002).

MRPP (Mielke 1984), a non-parametric method for testing group differences, was used to compare watersheds, blocks, aspects, and year for both communities using PC-ORD (version 5.1, MjM Software, Gleneden Beach, OR, US). 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 (Dufrene & Legendre 1973) was used to determine which species and trait groups 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.

Results

Two hundred and twenty-two taxa were observed across all treatments: five conifers, 33 shrubs and hardwood trees, 134 herbs (six ferns, 20 graminoids, and 108 forbs), and 50 cryptogam taxa (35 bryophytes, eight liverworts, and six lichens). Thirty-two

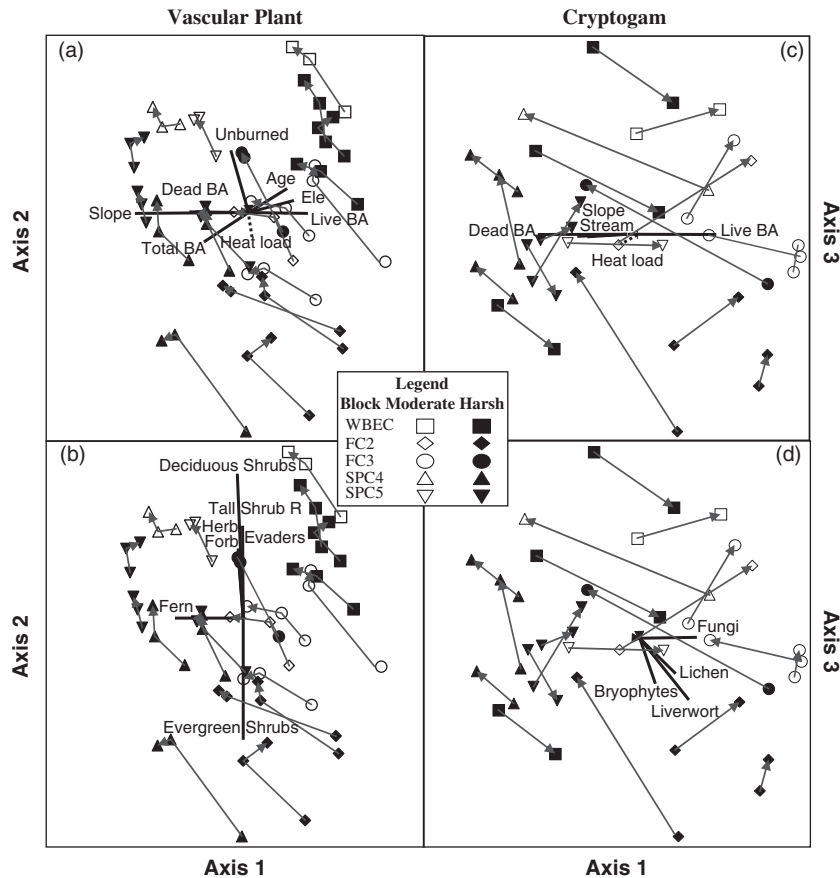


Fig. 2. Three-dimensional NMS ordinations of vascular plant (**a** and **b**; $R^2 = 69\%$ for all three axes) and cryptogam (**c** and **d**; $R^2 = 81.8\%$ for all three axes) post-fire communities for treatments without vegetation removal. Successional arrows (gray) connect the same plot through years. Environmental (**a** and **c**) and trait (**b** and **d**) variable joint plots are overlain. Angles and length of joint plot lines (black) represents the direction and strength of relationships with environmental variables (Moderate = moderate aspect, harsh = harsh aspect, BA = basal area, Dead BA = % dead BA, Live BA = % live BA, Ele = elevation, Age = plantation age at time of burn, R = Richness, Stream = distance to stream and Unburned = distance to unburned forest). Cryptogam community axes were rigidly rotated to align % live BA with axis 1. All correlations have $R^2 \geq 0.2$ except dashed lines are $R^2 \geq 0.08$.

exotic vascular species were documented (two shrubs, four graminoids, and 26 forbs). The most common species for each were: conifer *P. menziesii*; hardwood trees *A. menziesii* and *Q. chrysophylla*; shrubs *Ceanothus integerrimus*, *Rubus ursinus*, and *Mahonia nervosa*; herbs *Chamerion angustifolium*, *Epilobium brachycarpum*, and *Whipplea modesta*; and bryophytes *Funaria hygrometrica* and *Ceratodon purpureus*. The most common exotics were the herbs *Lactuca serriola*, *Senecio sylvaticus*, and *Cirsium vulgare*. Gradients in species composition were related most strongly to heat load index ($R^2 = 36\%$), time since fire ($R^2 = 18.6\%$), and fire severity ($R^2 = 14.2\%$) for the vascular plant community, and fire severity ($R^2 = 36.1\%$), heat load index ($R^2 = 26.5\%$), and time since fire ($R^2 = 19.2\%$) for the cryptogam community (Fig. 2: time since fire not shown).

Succession among structural layers

Succession among structural layers followed a pattern of dominance shifting from low to progressively taller structural layers (Fig. 3). Vegetation cover increased rapidly over time following wildfire in upper structural layers (Fig. 3a: $F_{2,44} = 28-138$, $P < 0.0001$ for year in all structural layers) but declined in the bryoid layer ($F_{1,26} = 17.2$, $P < 0.003$). Average bryophyte cover class in year 3 was 3.9 (95% CI: 3.5, 4.3) and 3.4 in year 4 (95% CI: 3.0, 3.9). 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. 3a). Average cover of tall shrubs, low shrubs, and graminoids increased over the 3 years (Fig. 3a). Combined low and tall shrub cover was greater than herb cover on both aspects by year 4.

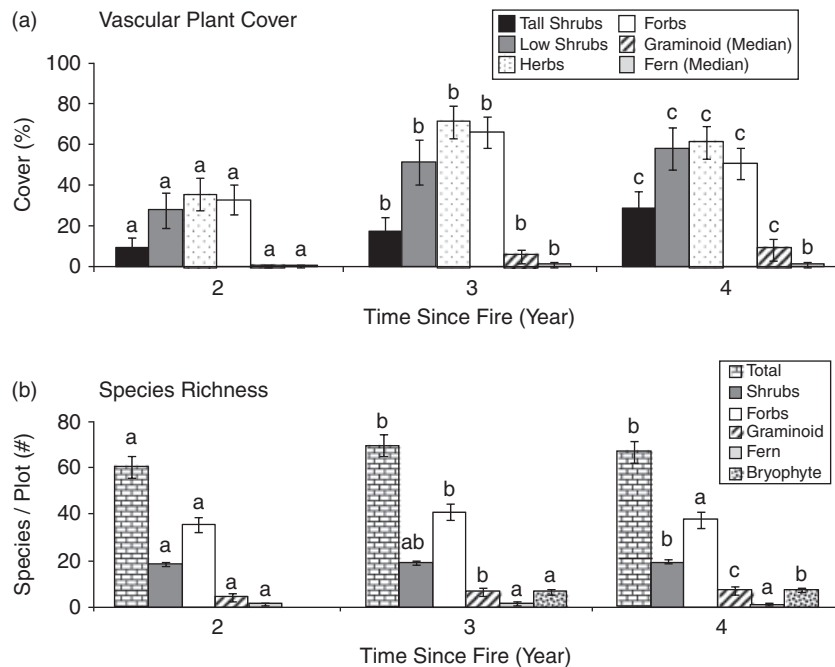


Fig. 3. Vascular plant percentage cover (a) and species richness per plot (b) by time since fire on harsh and moderate aspects combined in treatments without vegetation removal for different structural layers and life-form groups. Values are means and lines are 95% confidence intervals. Within each structural layer or life form, years with different letters were significantly different at $P \leq 0.05$ level. There was no difference in cover or richness between aspects for any structural layer or life form. Bryophytes were not measured in year 2.

Total species richness increased over the 3 years (Fig. 3b: $F_{2,44} = 17.6$, $P < 0.0001$ for year). Average total species richness per plot peaked in the third year post-fire due to increases in forb and graminoid richness (Fig. 3b: $F_{2,44} = 8.6-40.9$, $P \leq 0.0007$ for year). Average total species richness declined in year 4 due to decreased forb species richness (Fig. 3b). Bryophyte richness per plot increased from the third to the fourth year (Fig. 3b: $F_{1,28} = 9.8$, $P < 0.004$ for year). Shrub richness increased slightly by the end of the study (Fig. 3b: $F_{2,44} = 3.3$, $P < 0.04$ for year).

Succession within structural layers

Plant community composition changed over time for cryptogams and vascular plants (see correlations with time since fire above). For both communities, composition differed by year based on MRPP, but with small within-group homogeneity (Table 2). Succession within the herbaceous layer from early-seral to later-seral species was occurring by the fourth year. Early-seral herbs (*Collomia heterophylla* and *Montia diffusa*) that decreased over time and herbaceous trait groups associated with early-seral environments (invaders, annuals, and herbaceous species) were indicators of year 2 and

Table 2. MRPP/MRBP results for differences 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	
	A	P	A	P
Individual factors (MRPP)				
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)				
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

year 3, respectively (Tables 3 and 4). Meanwhile, herbaceous traits (perennial forbs, enduring herbs, and graminoids) and species (*Iris chrysophylla* and *Whipplea modesta*) associated with later-seral environments were indicators of, and correlated with, year 4 (Tables 3 and 4; Fig. 2). Succession was also

Table 3. 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. Tall indicates that the tall (> 1.3 m) shrub of that species was the indicator. Trait group 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 = subshrub, 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.

Indicator Species	Trait Groups	IV	Indicator Species	Trait Groups	IV
Harsh Aspect			Year Two		
<i>Luzula comosa</i>	EN, pg, n	87.2	<i>Collomia heterophylla</i>	I, a, n	89
<i>Asyneuma prenanthoides</i>	EN/EV, p, n	83.6	<i>Montia diffusa</i>	I, a, Wn	56.6
<i>Arnica latifolia</i>	EN, p, n, e/l	66.7	Year Three		
<i>Xerophyllum tenax</i>	EN, p, n, e/l	64.7	<i>Nemophila parviflora</i>	I/EV, a, n	77.5
<i>Chimaphylla umbellata</i>	AV, ss/p, n, l	40	<i>Fragaria vesca</i>	EN, p, n, e	76.6
Moderate Aspect			<i>Senecio sylvaticus</i>	I, a, Wex, e	71.2
<i>Madia madioides</i>	I, a, n	92.9	<i>Didymodon vinealis</i>	I, b, ll	65.4
<i>Agoseris</i> sp.	EV, f, ex	84.4	<i>Lactuca serriola</i>	I, a, Wex	63.8
<i>Galium triflorum</i>	EV/EN, p, n, e/l	80.9	<i>Asyneuma prenanthoides</i>	EN/EV, p, n	60
<i>Fissidens</i> sp.	I, b, sl	77.7	<i>Funaria hygrometrica</i>	I, b, sl	54.3
<i>Epilobium ciliatum</i>	I, p, Wn	76.2	<i>Epilobium ciliatum</i>	I, p, Wn	53
<i>Cirsium vulgare</i>	I, a, Wex, e	73.6	<i>Crepis capillaris</i>	I, a, Wex, e	50.7
<i>Weissia</i> group	I, b, sl	72.4	<i>Epilobium minutum</i>	I, a, Wn	47.1
<i>Rubus ursinus</i>	I/EN/EV, d/ss, n, e	68.6	<i>Euchiton japonicum</i>	I, a, Wex	45.1
<i>Corylus cornuta</i> var. <i>californica</i> - tall	EN, d, n, e/l	65.7	<i>Stephanomeria virgata</i>	I, a, n	45.1
<i>Homalothecium</i> group	R, b, ll	64.9	<i>Erechtites minima</i>	I/EV, p, n	44.5
<i>Acer macrophyllum</i> - tall	EN, d, n	60	<i>Poa</i> sp.	g	31.2
FUNGI			<i>Galium aparine</i>	I, a, Wn	85.1
<i>Achyls triphylla</i>	N/A	52.6	Year Four		
<i>Lotus micranthus</i>	EN, p, n, l	47.3	<i>Bryum capillare</i> group	I, b, sl	80.7
Non-Indicator Species			<i>Ceanothus integerrimus</i>	EV, d, n, nf, e	71.4
<i>Acer circinatum</i>	EN, d, n, e/l	NA	<i>Festuca occidentalis</i>	I/EN, pg, Wn, e/l	64.8
<i>Mahonia nervosa</i>	EN, eg/ss, n, l	NA	<i>Elymus glaucus</i>	EN, pg, n, e	55.9
<i>Polystichum munitum</i>	I/EN, fe, n, e/l	NA	<i>Cirsium vulgare</i>	I, a, Wex, e	54
<i>Aulacomnium androgynum</i>	I, b, ll	NA	<i>Iris chrysophylla</i>	EN, p, n	52.7
<i>Bryum argenteum</i>	I, b, ll	NA	<i>Deschampsia elongata</i>	EN, pg, n, e/l	50.7
<i>Ceratodon purpureus</i>	I, b, sl	NA	<i>Whipplea modesta</i>	EN, ss/p, n,	48.9
<i>Eurhynchium oregonum</i>	R, b, ll	NA	<i>Ceanothus sanguineus</i>	EV, d, n, e, nf	41.8
<i>Hypnum subimponens</i>	R, b, ll	NA	<i>Rubus leucodermis</i> - tall	I/EN/EV, d, n, e	34.7
<i>Leucolepis acanthoneuron</i>	R, b, ll	NA	<i>Trisetum canescens</i>	EN/EV, pg, n, e	25.3
<i>Polytrichum juniperinum</i>	R, b, ll	NA	<i>Leptobryum pyriforme</i>	I, b, sl	25.2

Table 4. Vascular plants indicator trait groups for aspects and years in treatments without vegetation removal. All indicator trait groups had $P \leq 0.05$. Higher indicator values (IV) mean that the trait is more restricted to that particular group.

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

occurring within the cryptogam layer, Indicator species for year 3 were short-lived invaders (*Didymodon vinealis* and *Funaria hygrometrica*: Table 3). Longer-lived colonizers [*Bryum capillare* (year 4 indicator), *Bryum argenteum*, and *Ceratodon purpureus*] were positively correlated with time since fire. Three bryophytes associated with older-forest floors (*Hypnum subimponens*, *Eurhynchium oregonum*, and *Leucolepis acanthoneuron*: Vitt et al. 1988) colonized by year 4.

Successional trajectories of vascular plant communities were similar in all plots, except for plots dominated by *Ceanothus integerrimus* (Fig. 4). While most cryptogam communities were moving in the same general direction over time, several divergent cryptogam trajectories occurred (Fig. 4).

Role of site conditions

Site conditions were important in influencing vascular plant community composition within

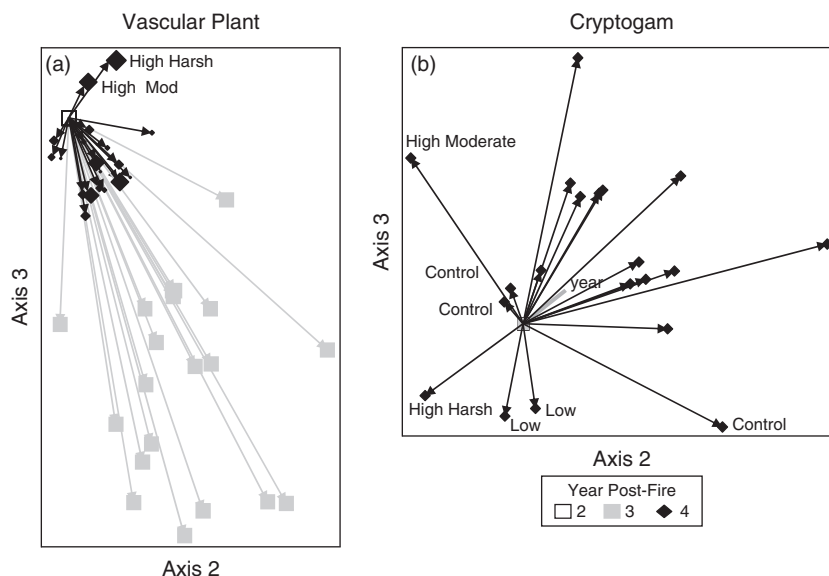


Fig. 4. Relative length and direction of successional trajectories over time of (a) vascular plant community for 3 years and (b) cryptogam community for 2 years in treatments without vegetation removal only from NMS ordinations shown in Fig. 2. Origin represents the year 2 centroid for changes from year 2 to 3 (gray arrows) and the year 3 centroid for changes from year 3 to 4 (black arrows). Arrows indicate direction and rate of change between years, and grey line is correlated environmental variable ($R^2 \geq 0.200$). (a) Size of the year-4 symbols indicates the amount of *Ceanothus integerrimus* cover. Treatments with divergent trajectories are labeled. High = high-density, Low = low-density, Harsh = harsh aspect, Mod = moderate aspect.

burned plantations but were less important for the cryptogam community (Fig. 2). The importance of site condition was indicated by larger differences among blocks than within blocks and among watersheds than within watersheds, regardless of time since fire in NMS and MRPP. Block had the greatest within group homogeneities (Table 2). ISA detected many indicator species for blocks (Table 5).

Community differences among blocks arose from differences in site conditions – fire severity, topography, and aspect – and species life-history traits. Vascular plant community composition in areas with relatively low fire severity (indicated by lower % dead BA) was correlated with high elevation and plantation age at time of fire, whereas that of areas with higher fire severities was correlated with high total basal area and steeper slopes (Fig. 2). Cryptogam community composition in areas with high fire severity was also correlated with steeper slopes. 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), and several bryophyte species/groups

(*Aulacomnium androgynum*, *Fissidens* sp., *Homolothecium* group, and *Weissia* group).

Aspect and heat load index influenced plant community composition, as indicated by grouping of communities on moderate aspects near the upper end of the axis correlated with heat load index (Fig. 2). Correlations with heat load index were stronger for individual years (data not shown). Harsh and moderate aspects in WBEC grouped with the moderate aspects of other blocks. WBEC had a number of characteristics that differ from the other blocks, including younger stand age at time of burn, more moderate slopes, and higher elevation (Table 1). While differences in plant community composition between aspects were evident in NMS, differences were not discernable based on MRPP, except for the cryptogam community in year 4 (Table 2). In the vascular plant community, evergreen shrubs and hardwood trees (Fig. 2) were associated with higher heat load index, while deciduous shrubs and hardwood trees, forbs, and herb cover, tall shrub richness (Fig. 2), and moderate aspect indicator species (*A. macrophyllum*, *Agoseris* sp., and *Rubus ursinus*: Table 3) and trait groups (evader species: Table 4) were correlated with low heat load index. In the cryptogam community, bryophyte, lichen and liverwort cover, and cover of *Polytrichum*

Table 5. Total number of indicator species with $P \leq 0.05$ per block, aspect, and year in treatments without vegetation removal.

Group	Vasc. plants	Cryptogam	Total species	Trait groups
Block				
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
Aspect				
Harsh	5	0	5	0
Moderate	10	4	14	6
Year				
Two	2	.	2	0
Three	11	2	13	6
Four	9	2	11	10

juniperinum, *A. androgynum*, and *D. vinealis* were correlated with higher heat load index.

There were no differences in cover or richness of structural layers on different relative aspects ($F_{1,4} = 0.1-3.2$, $P > 0.14$ for aspect). Seven trait groups were indicators for moderate aspects based on ISA, but there were no indicator trait groups for harsh aspects (Tables 4 and 5), suggesting that all life forms were less abundant under putatively more stressful conditions.

Discussion

The data support the initial floristic model of succession (Egler 1954) among structural layers, shown by constant species richness per plot in upper structural layers coupled with a shift in the dominance of structural layers over time. Forest succession among structural layers is associated with progressively larger plants dominating over time, e.g., succession from bryoid layer to tree dominance (Cremer & Mount 1965; Dyrness 1973; Uhl et al. 1981; Halpern 1988; Tatoni & Roche 1994; Trabaud 1994; Esposito et al. 1999; Wang & Kembal 2005). Fire-responding cryptogams can occupy mineral soil and reproduce as soon as moisture becomes available in the winter (Shaw & Goffinet 2000), and thus cryptogams are the primary early cover, especially in severely burned areas (Dyrness 1973; Esposito et al. 1999; Wang & Kembal 2005). Typically, sprouting residual and invading herbaceous species become the primary cover within one to two growing seasons following disturbance (Uhl et al. 1981; Tatoni & Roche 1994; Trabaud 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, such as southwestern Oregon, abundance of sprouting shrubs can decrease the time needed to reach shrub dominance (Arianoutsou-Faraggitaki 1984; Trabaud 1994; Ojeda et al. 1996; Ghermandi et al. 2004). Early succession among structural layers in burned 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 determine the rate at which different structural layers are able to occupy sites.

Succession within structural layers followed both initial and relay floristics models. Succession within structural layers was driven by differential species resistance or resilience to fire, regeneration mode, growth rate, and site adaptations, rather than the characteristics of structural layers as a whole. Slow transitions from early-seral to late-seral cryptogam dominance have been documented (DeGrandpre et al. 1993; de las Heras et al. 1994) and appear to be occurring in the current study due to asexual reproduction and slow lateral spread of stress-tolerant species. This slow transition, coupled with a lack of late-seral cryptogams, in early succession indicates that relay floristics may be occurring in the bryoid layer. However, facilitating effects of early-seral vegetation, such as increasing nutrient availability, were not tested to determine if relay floristics was occurring. In contrast, herbaceous layer transition from ruderal to stress-tolerant occurred rapidly due to the short-lived nature of invasive annuals (Grime's ruderal species: West & Chilcote 1968; Halpern et al. 1997) and rapid clonal expansion by native perennial and graminoid species (Grime's competitive or stress-tolerating species: Halpern 1989; Tatoni & Roche 1994; Debussche et al. 1996; Ojeda et al. 1996). Shrub and hardwood tree cover was assumed to be directly related to pre-fire shrub and hardwood trees abundance, due to post-fire regeneration mode of sprouting or seedling establishment from a seed bank for all shrubs. In contrast to the bryoid layer, sprouting of pre-fire vegetation in the herb and shrub layers, coupled with invasion by ruderal species, contributes to the presence of early- and late-seral species simultaneously, as predicted by the initial floristics model.

While floristics models are able to explain the transitions occurring within and among structural

layers, factors associated with the previous vegetative community, mixed severity fire regime, and underlying environmental factors contribute to observed differences in initial states of plant community composition following fire. Deterministic (pre-disturbance plant community, life-history characteristics, and topography) and stochastic (disturbance regime and site history) factors contribute to initial states of plant community composition. Geographic location, an indicator of landscape heterogeneity due to differences in stand histories, local disturbance impacts, and abiotic factors contribute to plant community heterogeneity following fire in temperate forests (Turner et al. 1997), boreal forests (Purdon et al. 2004; Wang & Kembball 2005), and the Mediterranean (Arevalo et al. 2001), as well as following forest management activities in the Pacific Northwest (Halpern 1989; Bailey et al. 1998; Fahey & Puettmann 2007). Landscape heterogeneity is inherent in mixed severity fire regimes due to variability in fire frequency, severity, and landscape patterns (Agee 2005). Other impacts of the fire regime relate to fire severity, which may control succession within structural layers by determining survival of residual/late-seral species (Uhl et al. 1981; Turner et al. 1999; Wang & Kembball 2005) and succession among structural layers by determining the rate of transition between structural layers.

Species composition and life-history traits drive plant community composition and successional trajectories among and within structural layers (Connell & Slayter 1977; Noble & Slatyer 1980; Thornburgh 1982). Multiple successional trajectories occurred within structural layers due to differing species composition and may have long-term effects on succession among structural layers (Bradstock et al. 2005). Initial dominance of a particular species or species groups determined successional pathways in the current study, as hypothesized by Thornburgh (1982) for xeric, mixed conifer forests. Following fire, differences in shrub and hardwood tree composition were also linked to differing plant community compositions on contrasting aspects (Ghermandi et al. 2004; Purdon et al. 2004). Differences in environmental conditions associated with aspect contribute to differing plant community compositions (Whittaker 1960; Kadmon & Harari-Kremer 1999) and to variation in fire intensities and severities in Mediterranean ecosystems (Beaty & Taylor 2001; Mermoz et al. 2005). Dominance by evergreen species on harsh aspects may slow succession within structural layers due to decreased light (Purdon et al. 2004) and slower growth compared to deciduous species, resulting in

the persistence of a bryophyte–herbaceous co-dominance, as demonstrated following severe disturbance (Cremer & Mount 1965; Esposito et al. 1999; Wang & Kembball 2005).

Temporal and spatial variability are defining components of mixed severity fire regimes (Agee 2005) and result in highly variable plant community compositions among stands. Mixed conifer forests appear to be adapted to highly variable disturbance, based on the ability of burned plantations to rapidly re-establish native vegetation. Succession within structural layers appeared to be significantly slower and occurred at different rates for each structural layer (McCune & Antos 1981; Penman et al. 2008). The potential for initial and relay floristics to act in concert is consistent with Egler's (1954) concept of vegetation development, and is indicative of the importance of the disturbance regime in succession. However, this study addressed an immediate post-disturbance phase of plantation succession, a limited view into the full succession of these communities. Future successional trajectories and states will be influenced by subsequent fire recurrence, species interactions, and resource competition, but eventually mixed conifer forests should reestablish on these sites. 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 burned plantations are unknown.

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