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Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA

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Abstract

We investigated the effect of fire severity and environmental conditions on conifer tree regeneration 11 years after an autumn wildfire in the western Oregon Cascade Range. Conifer tree seedlings, including those of *Pseudotsuga menziesii*, established promptly and at high densities following fire, in contrast to long establishment periods documented for many other sites. *P. menziesii*, *Tsuga heterophylla* and *Thuja plicata* comprised 99.0% of the seedlings measured in the study. *Pseudotsuga* seedling density was greater on sites that had burned with moderate and high severity compared to low fire severity. *Tsuga* seedling density was greater on north aspects than on south aspects. *Tsuga* and *Thuja* seedling densities were correlated with pre-fire conspecific basal area. Coexistence of the three principal conifer species was more likely on sites that burned with moderate severity. We attribute the rapid initial establishment of *Pseudotsuga* observed in this study to the persistence of a canopy seed bank—a biological legacy not normally associated with *Pseudotsuga* forests. Environmental factors, fire severity and disturbance timing influence seedling establishment patterns, shaping future stand composition and development.

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1. Introduction

Disturbances play important roles in structuring the coniferous forests of western North America (e.g. Agee, 1993; Veblen et al., 1994; Franklin et al., 2002). Disturbances vary in type, extent, intensity and frequency with different combinations leading to unique post-disturbance conditions. Fire ranks as one of the most important disturbances in forests of the Pacific Northwest, including *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) forests, and facilitates recruitment of trees by seeds (Hemstrom and Franklin, 1982; Agee, 1993). Research on fire history in *Pseudotsuga* forests in the past two decades has added to the understanding of forest dynamics in the region (Agee, 1991, 1993). For decades wildfire was stressed as virtually always occurring as a stand-replacing disturbance. It is now understood that

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moderate and low severity fire influence forest population dynamics and structure in *Pseudotsuga* forests (Stewart, 1986; Morrison and Swanson, 1990; Zenner, 2005), and variation in fire severity follows a regional climatic gradient (Agee, 1993).

The theory of natural regeneration following fire in *Pseudotsuga* forests has evolved significantly during the last century, reflecting the rich history of forest research in the Pacific Northwest. The early descriptions of stand initiation were carried out on sites disturbed by stand replacing wildfire or clearcut harvest (Hofmann, 1917, 1924; Isaac, 1943). These observations led to a widely accepted model for stand initiation in which *Pseudotsuga* quickly occupied the site with relatively high and uniform stocking, followed by later invasion of the site by *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Thuja plicata* Donn ex D. Don (western red cedar) (Munger, 1940). More recently, several investigators reported long establishment periods for *Pseudotsuga* based on tree ring reconstruction studies (Franklin and Hemstrom, 1981; Franklin et al., 1988; Stewart, 1986; Yamaguchi, 1993; Tappeiner et al., 1997; Poage and Tappeiner, 2002), although some reconstruction studies in the region have documented rapid site occupancy by *Pseudotsuga* following disturbance, providing continued support for the historical model of stand establishment (Franklin and Hemstrom, 1981; Gray and Franklin, 1997; Winter et al., 2002). Inferences drawn from stand reconstructions must be made cautiously because only a partial record of stand history is present in the material studied (i.e. those structures that have not been lost to decay). Additionally, it is difficult to differentiate with reconstruction techniques, for example, slow invasion of a site by trees from pulses of tree establishment following periodic moderate severity disturbances (Zenner, 2005). Therefore, studies of stand initiation immediately following the stand initiating disturbance are better suited to investigating the ecological processes involved in colonization of a site by trees.

In this article, we document density and composition of coniferous tree regeneration 11 years after the 1991 Warner Creek burn. Our study was motivated by the debate in the literature over competing post-fire succession models for *Pseudotsuga* forests (e.g. Poage and Tappeiner, 2002; Winter et al., 2002). We addressed two primary research questions in our investigation. (1) Does the regeneration present 11 years after fire at Warner Creek support the historical model for stand initiation (rapid occupancy of the site by *Pseudotsuga*) or the contemporary model (slow initial *Pseudotsuga* establishment), and what are the important contributing factors to the observed patterns of *Pseudotsuga* regeneration? (2) How are patterns of conifer tree regeneration at Warner Creek, in terns of seedling density and regeneration composition, related to variation in fire severity, environmental conditions and pre-fire stand composition? The purpose of this study is to improve understanding of post-fire successional pathways in *Pseudotsuga* dominated forests and to provide information to forest managers and scientists about factors affecting conifer tree regeneration following fire.

2. Methods

2.1. Study species

P. menziesii, *T. heterophylla* and *T. plicata* are the principal conifer tree species in *Pseudotsuga* forests of the Pacific Northwest. In these forests *Pseudotsuga* is a long-lived, early seral dominant (Franklin et al., 2002). Very long-lived *Thuja* is capable of regenerating under a canopy and persisting in old-growth, gap-phase forests, however low seedling and sapling densities are typical and recruitment into the canopy and population maintenance in old-growth stands are not fully understood (Daniels, 2003). The shade-tolerant *Tsuga* is considered to be the climax dominant throughout many *Pseudotsuga* forests – including the area described in this paper – and consequently these forests are also known as the *T. heterophylla* Zone (Franklin and Dyrness, 1988).

Tsuga and *Thuja* both have light wind dispersed seeds and are considered to be prolific seed producers (Minore, 1990; Packee, 1990). *Tsuga* seeds are held in small cones 2–3 cm long with light cone scales while *Thuja* produces very small (1–1.5 cm long), leathery to woody cones (Preston, 1989). *Pseudotsuga* seeds are also wind dispersed, however seed production varies, with light seed crops complimented by occasional mast years (Isaac, 1930; Reukema, 1982); seeds are produced in woody cones 5–12 cm in length (Preston, 1989). The light seeds of *Tsuga* are known to disperse hundreds of meters (Packee, 1990). *Pseudotsuga* and *Thuja* are also capable of long-distance dispersal, however most seeds fall within 100 m of the parent tree, with seeds of *Thuja* tending to disperse relatively shorter distances than seeds of *Pseudotsuga* (Hermann and Lavender, 1990; Minore, 1990). *Tsuga* regeneration is known to strongly prefer organic substrates in old-growth *Pseudotsuga* forests (Christy and Mack, 1984), however mineral soil is the preferred substrate in the exposed conditions typical following fire (Packee, 1990). *Pseudotsuga* and *Thuja* seedlings establish and develop best in a mineral soil rooting medium (Hermann and Lavender, 1990; Minore, 1990). *Thuja* is capable of vegetative reproduction (Minore, 1990); however, this regeneration method is not important following fire.

Pseudotsuga is the most fire adapted of the three species; old *Pseudotsuga* trees resist fire with their thick bark, and relatively deep roots and high crowns (Agee, 1993). *Tsuga* and *Thuja* are considered to be poorly adapted to fire due to their thin bark, shallow roots and deep, low-reaching crowns, and are consequently termed fire "*avoiders*" (Agee, 1993).

2.2. Study area

The Warner Creek burn is in the southern portion of the Willamette National Forest in the central western Oregon Cascade Range, USA (43°43′N, 122°13′W). The fire burned from 10 October 1991 to 23 October 1991, with the fire perimeter encompassing a 3669 ha area, including most of Bunchgrass Ridge and the upper Kelsey Creek basin. A summary of fire behavior and weather conditions during the fire event is available (Walker and Rogers, 1991). Within the fire perimeter 30.4% of the stands were completely killed, 38.9% experienced partial mortality and 30.7% underburned or did not burn (i.e. no overstory mortality; Kushla and Ripple, 1997). Despite the incendiary origin of the fire, the Warner Creek burn falls within the range of variation for natural ignitions in the central Oregon Cascades. While most ignitions occur in July and August, at least 10% of natural ignitions occur during the autumn months in western Washington, and this figure is greater in the central Oregon Cascades (Agee, 1993).

The study area has a Mediterranean climate characterized by cool, wet winters which receive most of the 120–200 cm of annual precipitation, and hot dry summers. Within the fire perimeter *T. heterophylla* Zone forests dominate lower elevations, while at upper slope locations *Abies amabilis*, and at the highest and coldest sites, *Tsuga mertensiana* become the climax tree species (Franklin and Dyrness, 1988). The study area was restricted to the *T. heterophylla* Zone (Franklin and Dyrness, 1988). For additional details on the physical and biological characteristics of the study area see USDA (1993).

Target study areas within the burn perimeter were identified by spatial analysis with ArcView 3.2 software (ESRI, Redlands, CA) conducted on geospatial data provided by Willamette National Forest. Pre-fire stand age class spatial data were overlain with a fire perimeter map and a digital elevation model to identify the study area. The study area was defined as those areas within fire perimeter with a pre-fire stand age >150 years and situated below 1400 m elevation. These criteria yielded a spatially discontinuous study area of 1231.6 ha.

2.3. Field methods

Sampling was conducted between July and September 2002. The study area was systematically sampled with plots located on a 500 m × 200 m grid of random origin, a design intended to provide proportional representation of post-fire conditions. This design resulted in a total of 116 potential sample plots distributed systematically across the study area. Seventy-two of these plots were measured. Thirteen plots were visited but not measured because the sites did not burn. The remaining 31 plots were not visited because dangerous terrain and cliffs barred access or due to limited time resources. We therefore cannot assume that proportional sampling was achieved. Subsequent analysis takes the unbalanced design into consideration.

Pre-fire conditions and fire effects were sampled with circular 500 m^2 plots, in which all live and dead stems were tallied, identified to species, and measured at breast height (1.37 m above ground level). Dead stems were identified to species using bark texture. Particularly on high severity sites, dead *Tsuga* and *Thuja* stems had sometimes shed much of their thin bark and were alternately differentiated by the distinctive neiloid stem form characteristic of *Thuja* (Minore, 1990). Pre-fire stand composition was estimated as the sum of residual green tree and standing dead basal areas. Standing dead trees that had extensively charred sapwood at the time of sampling were considered to be already dead at the time of the fire (i.e. pre-fire snags), and therefore were not included in the estimate of pre-fire stand composition. Downed trees that appeared to have originated from fire killed trees based on visual clues (e.g. downed trees with charred bark but lacking char on sapwood and heartwood exposed by stem breakage) were also measured at 1.37 m above former ground level and included in the pre-fire total. Downed, fire killed trees were encountered infrequently; most were located on one sample plot which was partially affected by a small soil slump. Post-fire conditions were defined at the basal area of residual green trees present at the time of sampling, plus the basal area of trees that appeared to have died recently (1–3 years) based on visual clues such as retention of foliage, cones and fine twigs (Chappell and Agee, 1996). While fire may have been an inciting factor in the mortality of trees that died immediately prior to sampling in 2002, it was not the direct cause, and therefore trees that died recently were included in the post-fire residual green tree basal area figure. Fire severity was calculated as percent basal area mortality:

$$\text{Fire severity} = \frac{\text{pre-fire BA} - \text{post-fire BA}}{\text{pre-fire BA}} \times 100$$

Because some delayed fire-caused mortality likely occurred in the years following fire, our calculation may slightly overestimate immediate (first-year) fire severity. Agee and Huff (1987) reported that while 28.7 $\mathrm{m}^2\,\mathrm{ha}^{-1}$ of tree basal area survived the first year following fire in an old-growth *Pseudotsuga-Tsuga* forest in western Washington, residual basal area dropped to 0 $\mathrm{m}^2\,\mathrm{ha}^{-1}$ by year 3 post fire. The high severity fire studied by Agee and Huff (1987) was predominantly characterized by crown scorch, as opposed to crown consumption, which would have killed trees outright. We interpret this as a worst-case estimate for delayed overstory mortality at Warner Creek, because much of the area burned with low and moderate severity (for which we expect less delayed mortality), and also because large areas at Warner Creek burned with crown fire. While our calculation may slightly overestimate immediate (first-year) fire severity, total fire severity is accurately represented by our method since we include an adjustment (Chappell and Agee, 1996) for trees that died immediately prior to sampling from causes not related or indirectly related to fire (e.g. bark beetle attack).

Four, circular 10 m^2 subplots were systematically located in each 500 m^2 plot. In each subplot all coniferous tree seedlings were counted and identified to species. Seedlings less than 0.05 m were not considered to be fully established and therefore were not considered. Percent ground coverage of shrubs, herbs, and rocks >10 cm in diameter and exposed bedrock was visually estimated for all 10 m^2 subplots. Plot level values for seedling densities and percent coverage of rocks, shrubs and herbs were calculated as the mean of the four subplots.

2.4. Data analysis

Two-factor ANOVA, with fire severity and aspect as independent variables, was used to test for differences in mean seeding density by species at different factorial combinations. Three fire severity levels, low (0–20% basal area mortality), moderate (20.1–80% basal area mortality), and high (>80.1% basal area mortality) were used. These classes are unequal with respect to percent canopy area removed but are relatively balanced in terms of the conditions experienced by establishing seedlings (Chappell and Agee, 1996). Two aspect classes each spanning 180° and centered on 45° (north) and 225° (south), respectively (Stage, 1976), were used as a proxy for environmental conditions because insolation, which influences air and soil moisture and temperature (Silen, 1960; Geiger, 1965) is related to aspect. Tukey multiple comparisons were used to analyze factor level effects. The Tukey procedure is appropriate for unplanned multiple comparisons and is conservative when sample sizes are unequal (Neter et al., 1996). Seedling densities were log-transformed before performing statistical analyses in order to meet the underlying assumptions of the statistical tests. We used Spearman rank correlation analysis to explore for relationships between untransformed seedling densities and other independent variables.

We evaluated the effect of disturbance severity on species coexistence within the tree seedling cohort with contingency table analysis (4 × 3 table: number of species equal to 0, 1, 2 or 3; fire severity = high, moderate, low). Post hoc partitioning of the original contingency table into 2, 4 × 2 tables, and subsequent analysis of the standardized residuals facilitated inferences about the relationship between disturbance severity and species coexistence. The level of significance for all test statistics was set at $\alpha = 0.05$. The family level confidence coefficient for Tukey multiple comparisons of factor level means was set at 0.95.

Because we studied an unplanned natural disturbance event, we were restricted to a pseudoreplicated design (Hurlbert, 1984; Wiens and Parker, 1995). However, case studies of natural disturbance events still provide valuable information about disturbance effects (e.g. Turner et al., 1997). Results from case studies of disturbances must be interpreted appropriately; generalization of results beyond the study site must be couched in terms of limitations of the study design.

3. Results

Natural conifer tree regeneration, including *Pseudotsuga*, established promptly after the Warner Creek burn (Fig. 1), supporting the historical model of rapid *Pseudotsuga* establishment following disturbance. Seedling densities are lowest on sites that burned with low severity and substantially greater on sites that burned with moderate or high severity (Tables 1 and 2). Despite the high mean seedling densities across the study area full restocking at Warner Creek was not complete 11 years after fire; while 69 of the 72 sample plots had conifer seedling densities $\geq$250 seedlings ha^{-1}, the remaining three sample plots contained no conifer seedlings (data not shown). The majority of sites, however, are well stocked with tree seedlings. Conifer tree regeneration was overwhelmingly dominated by three species, *P. menziesii*, *T. heterophylla* and *T. plicata*. *Abies amabilis* Dougl. Ex Forbes (Pacific silver fir), *A. grandis* (Dougl. Ex D. Don) Lindl. (grand fir), *A. procera* Rehd. (noble fir), *T. mertensiana* (Bong.)

Fig. 1. A within-stand view of a high severity patch at Warner Creek. The site shown is several hundred meters from the nearest green trees, yet is well stocked with *Pseudotsuga* seedlings (photo by Jerry F. Franklin).

Table 1
ANOVA results for seedling density analysis

	d.f.	ms	F	P
Pseudotsuga menziesii				
Aspect	1	37.43	4.68	0.0341*
Severity	2	66.09	8.26	0.0006***
Interaction	2	2.31	0.29	0.7501
Residual	66	8.00		
Tsuga heterophylla				
Aspect	1	131.67	11.71	0.0011**
Severity	2	90.41	8.04	0.0001***
Interaction	2	2.70	0.24	0.7871
Residual	66	11.25		
Thuja plicata				
Aspect	1	70.10	4.99	0.0289*
Severity	2	51.97	3.70	0.0300*
Interaction	2	5.22	0.37	0.6909
Residual	66	14.05		

Data were natural logarithm transformed ($\ln[X + 1]$) before statistical analysis.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Carr. (mountain hemlock), *Calocedrus decurrens* (Torr.) Florin (incense cedar) and *Taxus brevifolia* Nutt. (Pacific yew) together accounted for only 1.0% ($n = 32$) of the seedlings measured during the study and only 19.4% of plots ($n = 14$) contained one or more of these minor species (data not shown). Statistical analysis is restricted to the three most common species.

3.1. Seedling density

Fire severity and environmental conditions are significant factors in determining patterns of tree regeneration following fire. *Pseudotsuga* seedling density was sensitive to both aspect (Table 1; 2-factor ANOVA, $F_{0.05,1,66} = 4.68$, $P = 0.034$) and fire severity (Table 1; 2-factor ANOVA, $F_{0.05,2,66} = 8.26$, $P = 0.0006$). *Pseudotsuga* seedling density could not be separated by aspect class with Tukey comparisons of factor level means. However, *Pseudotsuga* seedling densities were greater on sites that burned with high and moderate severity compared to sites that burned with low severity (Table 2; $q_{0.95,3,60} = 4.86$, $0.001 < P < 0.01$, and $q_{0.95,3,60} = 4.76$, $0.001 < P < 0.01$, respectively). *Tsuga* density was strongly related to aspect (Table 1; 2-factor ANOVA, $F_{0.05,1,66} = 11.71$, $P = 0.0011$) and fire severity (Table 1; 2-factor ANOVA, $F_{0.05,2,66} = 8.04$, $P = 0.0001$). *Tsuga* seedling densities were significantly greater on north aspects compared to south aspects (Table 2; $q_{0.95,2,60} = 4.55$, $0.001 < P < 0.01$). *Tsuga* seedling density was greater on sites that burned with moderate severity compared to low severity sites (Table 2; $q_{0.95,3,60} = 5.07$, $0.001 < P < 0.01$). *Tsuga* seedling density on high severity sites could not be differentiated from low or moderate severity sites with Tukey comparison of factor level means. Both aspect and fire severity were significant for *Thuja* at the 0.05 level (Table 1; 2-factor ANOVA, $F_{0.05,1,66} = 4.99$, $P = 0.0289$, and $F_{0.05,2,66} = 3.70$, $P = 0.0300$, respectively). However, comparisons of factor level means did not reveal any statistically significant patterns for *Thuja*. Statistical interaction between aspect and fire severity was not significant for any of the three principal species.

Table 2
Tukey multiple comparisons of seedling density for factor level means

	Seedling density[1] (seedlings ha^{-1})				
	Severity			Aspect	
	High	Moderate	Low	North	South
P. menziesii	4462 a[2]	1514 a,b	111 c	731 d	1131 d
T. heterophylla	140 a,b	1296 b	47 a	961 c	43 d
T. plicata	9 a	208 a	36 a	95 b	18 b

Tests are within rows and factors (i.e. severity or aspect) only.

[1] Values are back-transformed from $\ln(X + 1)$.

[2] Letters (a–d) denote different mean values—cells that share a common letter are not statistically different at the $\alpha = 0.05$ level.

Spearman rank correlation analysis revealed additional relationships between seedling density and other independent plot variables. *Pseudotsuga* seedling density was positively correlated with shrub cover and negatively correlated with percent cover of rocks (Table 3). *Tsuga* and *Thuja* seedling density showed positive correlations with pre-fire conspecific basal area and negative correlations with shrub cover (Table 3).

3.2. Species composition and coexistence

Composition of the seedling cohort, in terms of relative composition of the three principal species, *Pseudotsuga*, *Tsuga*, and *Thuja*, was strongly related to aspect. *Pseudotsuga* dominates on south aspects while *Tsuga* and *Thuja* comprise a greater portion of the seedling cohort on north aspects (Fig. 2).

Table 3
Spearman rank correlation coefficients between tree seedling density and independent variables measured for each sample plot

	P. menziesii	*T. heterophylla*	*T. plicata*
Elevation	−0.109	0.180	−0.087
Pre-fire total basal area	−0.073	−0.031	0.033
Pre-fire *P. menziesii* basal area	−0.100	−0.222	−0.137
Pre-fire *T. heterophylla* basal area	0.040	0.611**	0.145
Pre-fire *T. plicata* basal area	0.008	0.146	0.570**
Percent coverage rock	−0.261*	−0.121	−0.086
Percent coverage shrubs	0.261*	−0.244*	−0.373**
Percent coverage herbs	0.159	−0.137	−0.101

* $P < 0.05$.
** $P < 0.01$.

Coexistence between *Pseudotsuga*, *Tsuga*, and *Thuja* in the seedling cohort is related to fire severity ($\chi^2_{0.05,6} = 19.88, 0.001 < P < 0.005$). Partitioning the contingency table revealed that for high and low severity fire species coexistence is not related to disturbance severity ($\chi^2_{0.05,3} = 1.32, 0.75 < P < 0.90$). However, when high-plus-low severity fire was compared to moderate severity fire, species coexistence was significantly affected by fire severity ($\chi^2_{0.05,3} = 18.23, 0.001 < P < 0.005$). Coexistence of seedlings of all three principal tree species was more likely on sites that burned with moderate severity than on sites that burned with low or high severity based on the standardized residual values. Results are similar when minor species are included in the calculation of species richness.

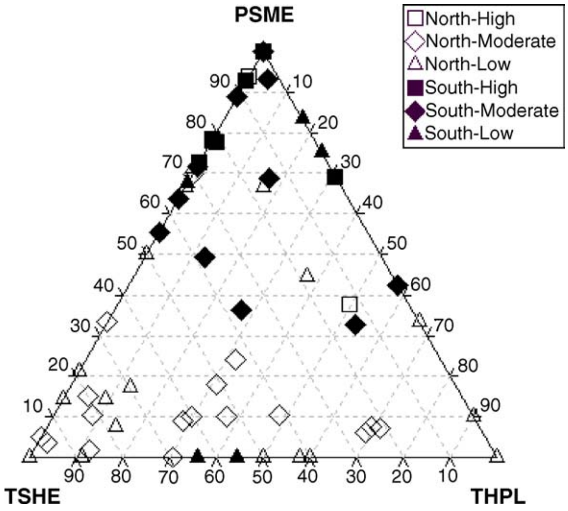

Fig. 2. Trilinear plot of relative seedling composition showing stratification in relative species composition according to aspect. Increasing distance from a vertex corresponds to a decrease in the relative density of the species associated with the vertex. Sites with all three species present plot as points entirely within the triangular plot area. Points located along one of the legs of the triangular plot represent study sites occupied by only the two species connected by the leg of the triangle. For example, a point on the line between PSME and THPL represents a site with both *Pseudotsuga* and *Thuja* seedlings. Points which plot at a vertex on the figure are sites occupied by only the species associated with the vertex; e.g. a point at the vertex labeled TSHE represents a site occupied by *Tsuga* only.

4. Discussion

4.1. Pseudotsuga establishment

Conditions 11 years after fire at Warner Creek support a model for stand development that includes rapid and dense colonization of disturbed sites by *Pseudotsuga*, particularly on sites that experienced high severity disturbance. However, it is apparent that *Pseudotsuga* forests can establish and develop via several different pathways (Poage and Tappeiner, 2002; Winter et al., 2002; Zenner, 2005). Clearly, forests throughout the *Pseudotsuga* region have highly individualistic establishment patterns and a flexible conceptual model for stand establishment is required. Given the wide range of possible establishment patterns, an interesting and important goal is to understand the factors that give rise to a particular observed establishment pattern. We consider this question in the specific case of *Pseudotsuga* establishment following the Warner Creek burn.

Biological legacies persisting on sites after disturbance influence ecological processes as the new sere develops (Franklin et al., 2000). A particularly important type of biological legacy in some ecosystems is the canopy seed bank produced by tree species that have serotinous cones, which survive stand-replacing fire and subsequently open to shed seeds that initiate the new stand (Agee, 1993). *Pseudotsuga*, however, does not produce serotinous cones; seeds are shed from cones annually during autumn and winter. The year in which Warner Creek burned, 1991, was heavy seed crop year for *P. menziesii* (USDA, 1991). While parts of the fire burned at a high intensity that scorched or even consumed canopy foliage, much of the ripe cone crop apparently survived the autumn fire. This unexpected biological legacy from the previous stand – a canopy *Pseudotsuga* seed bank – provided propagules to immediately colonize the site following the fire. Although there were no direct measurements of canopy seed bank survival or seed rain at Warner Creek, the presence of a *Pseudotsuga* canopy seed bank is supported by several facts. First, *Pseudotsuga* seeds in cones can survive substantial heating and scorch (Hofmann, 1924). Second, *Pseudotsuga* seed dissemination is a protracted process, with only one-third to one-half of seeds released from cones by late October (Reukema, 1982). Additionally, large seed crops, like the 1991 crop, tend to be released later with up to two-thirds of seed retained in cones until mid December (Reukema, 1982), thus a substantial portion of the seed would have not yet been released at the time of the Warner Creek fire in mid October. Finally, after the first post-fire growing season most sites at Warner Creek were well stocked with total seedling densities ranging ‘‘from several hundred to several hundred thousand seedlings per acre’’ based on regeneration surveys in 20 stands (Bailey, 1993).

There is also evidence for the canopy seed bank phenomenon in the historical record. Gray and Franklin (1997) found that *Pseudotsuga* establishment and stand density following the 1902 Siouxon burn was uniform over distances of up to 3 km from unburned stand edges and hypothesized that a canopy seed bank may have survived the fire, explaining the observed prompt and uniform regeneration. Their hypothesis was not without basis: Isaac (1943) and Munger (1940) reported observations of *Pseudotsuga* canopy seed banks surviving fire at sites throughout the region. The conditions at Warner Creek and historical accounts suggest that the survival of a canopy seed bank in non-serotinous species may be more common than expected. Based on timing of lightning ignitions (Agee, 1993) we expect that as much as 10–20% of fires in western Oregon and Washington *Pseudotsuga* forests could potentially have surviving canopy seed banks, although seed bank size will vary depending on annual seed production.

The canopy seed bank phenomenon very likely contributed to the conflicting early theories of *Pseudotsuga* regeneration following fire in the Pacific Northwest (Hofmann, 1917, 1924; Isaac, 1935, 1943). Following the 1902 Yacolt burn *Pseudotsuga* seedlings ‘‘almost uniformly covered the area’’ (Hofmann, 1917, p. 4), with first-year *Pseudotsuga* seedling densities frequently exceeding 1235 seedlings ha^{-1}. From these circumstances Hofmann (1917, 1924) concluded that an on-site seed source must have been present immediately after the fire and advanced his infamous ‘‘seed stored in the forest floor’’ hypothesis, which was ultimately rejected after the work of Isaac (1935, 1943). It appears, however, that one element of Hofmann’s (1917, 1924) theory was correct: an on-site seed source was present immediately following the 1902 Yacolt burn, but it was in the canopy, not the forest floor.

4.2. Seedling density

The dense tree regeneration reported here (Section 3; Fig. 1) is consistent with earlier observations of forest regeneration at Warner Creek and at least one other study of natural regeneration in a *Pseudotsuga-Tsuga* forests following fire. Brown et al. (1998) observed seedling densities ranging between 398 and 24303 seedlings ha^{-1} 1–2 years after fire at Warner Creek. Huff (1995) observed copious *Tsuga* regeneration but comparatively few *Thuja* seedlings following fire in the Western Olympic Peninsula of Washington State.

The observed pattern of increasing *Pseudotsuga* seedling density along the gradient of low to high severity fire is likely due to the relative shade-intolerance of *Pseudotsuga*. Germinants grow well in partial shade, but older seedlings are more likely to survive in high light conditions (Hermann and

Lavender, 1990). The relative insensitivity of *Pseudotsuga* seedling density to aspect is likely due to *Pseudotsuga*'s tolerance of xeric conditions (Hermann and Lavender, 1990).

The historical observation that abundant shade tolerant conifer regeneration, particularly *Tsuga*, occurs on north-facing slopes (Isaac, 1943) was supported at Warner Creek. The low densities observed for *Thuja* and *Tsuga* on southern aspects are probably related to stressful environmental conditions. Zenner et al. (1998) postulated that *Tsuga* would be less successful on south aspects because *Tsuga* loses hydraulic conductivity at higher water potentials than *Pseudotsuga* (Brix, 1978). Drought stress is likely an important limiting factor for *Tsuga* seedling establishment. However, soil surface temperatures will be much higher on south aspects as well. Silen (1960) found that soil surface temperatures exceeded temperatures lethal to *Pseudotsuga* seedlings on south-facing clearcuts almost twice as frequently as on north-facing clearcuts. Because both *Tsuga* and *Thuja* seedlings are quite sensitive to high surface temperatures (Minore, 1990; Packee, 1990), it is reasonable to conclude that surface temperatures have played a role in regulating *Tsuga* and *Thuja* seedling densities, particularly on south aspects.

In light of the results of the correlation analysis, some caution is required regarding the interpretation of the ANOVA and multiple comparisons results for *Tsuga* and *Thuja*. While not conclusive, the positive correlation between seedling density and conspecific basal area for *Tsuga* and *Thuja* indicates that seed source may be a confounding factor, exaggerating the inferred effect of fire severity and aspect on shade tolerant seedling density. Seed source limitation is known to be an important factor in conifer seedling recruitment. Beach and Halpern (2001) found seed availability to be more limiting than competition or substrate for conifer regeneration in managed riparian forests. Seed source relationships are important in explaining patterns of shade-tolerant conifer recruitment in the southern Washington Cascades (Keeton and Franklin, 2005) and in the Oregon Coast Range (Schrader, 1998).

Tsuga and *Thuja* seedling density responded negatively to shrub cover while *Pseudotsuga* seedling density was positively correlated with cover of shrubs. It is unlikely that shrubs facilitate *Pseudotsuga* recruitment; shrub species are known to compete with conifer tree seedlings (Isaac, 1943; Pabst and Spies, 1999). Rather, the positive correlation of *Pseudotsuga* density with shrub cover is likely due to the combination of high mean *Pseudotsuga* seedling density on high and moderate severity south aspect sites and the tendency of shrub cover to be higher on south aspect sites at Warner Creek (data not shown). The opposite trend for *Tsuga* and *Thuja* may be attributable to the relative lack of shrub cover on north aspect sites (data not shown), where the shade-tolerant conifers reached their peak abundance.

4.3. Species coexistence

A primary goal of ecological science is to elucidate mechanisms that facilitate species coexistence. Many mechanisms have been proposed, including disturbance (Connell, 1978), habitat partitioning (Duncan, 1991) and chance (Hubbell, 2001). The Intermediate Disturbance Hypothesis (Connell, 1978) predicts that diversity will be maximized under intermediate disturbance regimes.

The three principal conifer tree species found at Warner Creek are more likely to coexist on sites that burned with moderate severity. This pattern may be due to the greater variation in local conditions (i.e. mosaic of shade, partial shade and full sunlight) at moderate severity sites, which facilitates coexistence between species with different environmental and competitive tolerances (Connell, 1978). We cannot be certain that this is the case at Warner Creek since microenvironmental conditions were not directly measured. However, when considered in terms of the species' autecology, this idea seems plausible. It is unlikely that *Pseudotsuga* will successfully colonize many low severity sites, particular those with high residual overstory canopy cover, due to its relative shade intolerance. *Tsuga* and *Thuja* have likely been excluded by more extreme temperature and moisture conditions on high severity sites, especially those on south aspects. Sites that burned with moderate severity are likely to have conditions intermediate between these extremes, and therefore will be more tolerable to a broader group of species. The positive correlation between *Tsuga* and *Thuja* seedling density and pre-fire conspecific basal area suggests that local seed source may influence the occurrence of these species on some sites, confounding the effect of fire severity. We conclude that data from Warner Creek provide preliminary support of the idea that disturbance severity influences species coexistence during post-fire stand establishment in *Pseudotsuga* forests, but caution that additional research is needed to fully explore the relationship between fire severity and tree seedling coexistence.

4.4. Future stand development at Warner Creek

Zenner's (2005) recent work provides a conceptual framework for considering future stand development at Warner Creek. Both of the major developmental trajectories for *Pseudotsuga* forests described by Zenner (2005), the catastrophic/maturation model and the chronic/partial fire model, are present at Warner Creek. Stands that burned with low and moderate severity are now midway along the chronic/partial fire structural development continuum. Structural development in stands that experienced high severity fire has been essentially ''reset'' to the earliest stages the catastrophic/maturation model, cohort establishment and canopy closure (Franklin et al., 2002). Zenner (2005) identifies two unique pathways within the catastrophic/maturation model: the ''successional/gap processes'' pathway where *Pseudotsuga* dominates the regenerating cohort and eventual successional replacement by *Tsuga* and *Thuja* is necessary to complete structural development, and the ''structural'' pathway which occurs when a mixed *Pseudotsuga-Tsuga*/*Thuja* cohort establishes following fire. Although both of these pathways are present at Warner Creek, it appears that the successional/gap processes pathway, where *Pseudotsuga* dominates regeneration, is more common, particularly on south aspect sites (Fig. 2). The structural pathway of the catastrophic/maturation model was reported as being related to a long establishment period (Zenner, 2005), which is not a characteristic of the Warner Creek burn. Since establishment at Warner Creek has been quite prompt, and also because tree species coexistence was greatest on moderate severity sites, we would expect relatively few of the high severity sites at Warner Creek to follow the structural pathway within the catastrophic/maturation model.

The effect of rapid and dense tree seedling establishment on structural development – a result of the canopy seed bank in the case of *Pseudotsuga* – will be profound. The high seedling densities will result in intense intercohort competition, both within and between species. Diameter growth slows dramatically with increasing initial stand density, resulting in tall, thin and unstable trees (Oliver and Larson, 1996; Miller et al., 2004). Dense initial establishment can lead to poor differentiation and depressed height growth (Oliver and Larson, 1996), slowing structural development. High initial density also results in small crowns, limiting tree response to changes in stand density (Oliver and Larson, 1996) and delaying the development of tree-level structural features such as large diameter branches (Franklin et al., 2002). Current conditions indicate that large diameter *Pseudotsuga* will develop slowly on high severity sites at Warner Creek.

5. Conclusions

Study of conifer tree regeneration 11 years after the 1991 Warner Creek fire in the central western Oregon Cascades has yielded a number of insights about factors regulating tree seedling establishment and coexistence. Prominent among these discernments is recognition of the potential for a canopy seed bank in non-serotinous species, a subtle but important type of biological legacy in *Pseudotsuga* forests. Seed availability is only one of many factors that ultimately determine community composition and developmental trajectory. However, we emphasize it here because the presence of a canopy seed bank appears to have been an important factor in determining the post-fire *Pseudotsuga* regeneration and structural development pathways at Warner Creek.

Ecological effects of disturbance are linked to the intra-annual timing of the disturbance event (Crawley, 2004). The post-fire conditions at Warner Creek illustrate how the type and number of biological legacies left following disturbance can vary depending on an organism's phenological status. The case of a non-serotinous canopy seed bank surviving fire arises only when the timing of the disturbance coincides with the presence of mature seed crop still held in cones. This scenario could potentially occur in any coniferous system where the fire season overlaps with seed maturity and may be particularly important for species with larger cones, which should better insulate seeds from fire.

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