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Tree regeneration, understory development, and biomass dynamics following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest

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ABSTRACT

Processes initiated by wildfire largely determine ecological characteristics of forested landscapes in subsequent decades, including vegetation composition, habitat quality, carbon balance, and probability of fire recurrence. Post-fire biomass dynamics have rarely been observed directly for high-elevation forests of the Pacific Northwest. We examined changes in total biomass and its components (attrition of coarse woody debris (CWD), growth of shrubs and herbaceous plants, and tree recruitment) over the first 15 years following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest in Oregon, using permanent plots representing random samples of four levels of fire-severity, from unburned to >90% tree mortality. Understory vegetation was transformed by fire, inasmuch as only shrubs were detected in unburned plots, while burned plots also had significant amounts of graminoids and forbs. Conifer recruitment was sparse in plots with high fire-severity two years after fire, but was abundant after 15 years. Recruitment was predominantly mountain hemlock and most were seedlings <1 m tall. The breakage of snags and resulting increase in logs created microsites (north sides of logs) conducive to tree regeneration. Mass of understory vegetation and conifer regeneration was far outweighed by CWD. Toppling, fragmentation, and advancing decay of snags resulted in a decrease in snag mass and an increase in log mass. The loss of snag mass exceeded the increase in log mass, resulting in an overall decline. For some portions of the burned area, particularly areas of high fire-severity, it may be more than a century before the growth of live trees balances the loss of mass of CWD.

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1. Introduction

Processes initiated by wildfire largely determine ecological characteristics of forested landscapes in the subsequent decades. While even intense fires consume only a small fraction of aboveground biomass, primarily finer material such as leaves, twigs, litter, and duff (Donato et al., 2013), mortality of susceptible tree species (e.g., those with thin bark, shallow roots, and/or low-hanging branches, Cope, 1992; Tesky, 1992) can result from fires of relatively low intensity. Mortality converts live trees to snags, downed logs, and finer material, and serves as a starting point for disintegration and decay. Vegetation typically returns to burned areas, though species composition and vegetation physiognomy may or may not resemble previous conditions (Keane et al., 2008). Attrition of dead material, growth of shrubs and herbaceous plants, and recruitment of trees following wildfire are among the main determinants of the subsequent dynamics of vegetation composition, habitat quality, carbon balance, and probability of fire recurrence (Agee and Huff, 1987; Donato et al., 2013; McKinley et al., 2011).

For high-elevation forests of the Pacific Northwest, there has been limited study of the component processes, either through direct observation (e.g., Acker et al., 2013; Brown et al., 2013), or reconstruction of the effects of past fires (e.g., Agee and Smith, 1984; Chappell and Agee, 1996; Dickman and Cook, 1989; Little et al., 1994). Among these component processes, most research has addressed post-fire tree regeneration, with fewer observations of dynamics of herbaceous or shrubby vegetation or coarse woody debris (CWD). Furthermore, most studies of post-fire tree recruitment have focused on forests dominated by various species of true fir (*Abies*), with less attention devoted to forests of mountain hemlock (*Tsuga mertensiana*) (e.g., Agee and Smith, 1984; Brown et al., 2013; Chappell and Agee, 1996; Dickman and Cook, 1989; Little et al., 1994). In addition, in contrast to past work we combine

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the component processes to comprehensively evaluate changes in total aboveground biomass following wildfire.

Tree regeneration following wildfire in high-elevation forests in the Pacific Northwest tends to lag wildfire by one to several decades (Agee and Smith, 1984; Chappell and Agee, 1996; Little et al., 1994), though it may begin promptly after fire (Brown et al., 2013). Lodgepole pine (*Pinus contorta*) may dominate post-fire tree regeneration, due to its prolific seed production, light, dispersible seed, and ability to germinate and thrive in conditions of disturbed soil and full sunlight (Chappell and Agee, 1996; Dickman and Cook, 1989; Lotan and Critchfield, 1990). Though mountain hemlock also has relatively light seeds (Minore, 1979), it tends to produce heavy cone crops only at intervals of three years or longer (Woodward et al., 1994), and requires partial shade to thrive as a seedling (El-Kassaby and Edwards, 2001). In addition, germination of mountain hemlock seed requires a degree of warming usually not present until August, which leaves little time before low temperatures and snow accumulation curtail growth (El-Kassaby and Edwards, 2001). However, proximity of mature, seed-bearing trees, whether as surrounding unburned forest, or individual surviving trees, can outweigh differences between species with respect to germination and establishment requirements (Agee and Smith, 1984; Chappell and Agee, 1996; Donato et al., 2009).

In the first decade following fire in high-elevation forests, due to life-history traits such as persistent seed banks and ability to resprout (Miller, 2000), shrubs can be the dominant life-form, especially in patches of high fire severity lacking a seed source of lodgepole pine (Brown et al., 2013; Chappell and Agee, 1996). In such situations, shrub dominance may persist indefinitely (Chappell and Agee, 1996). While nonnative, invasive plants can increase following fire, such invasions are uncommon in high-elevation ecosystems (Anzinger and Radosevich, 2008; Zouhar et al., 2008).

Mass of CWD is likely to be in the initial stages of a long-term decline by the end of the first decade following wildfire in high-elevation forest (Acker et al., 2013). Though a majority of snags may remain standing, and attrition is most likely for smaller snags, both breakage of standing snags and decreasing wood density due to decay lead to a decrease in mass of snags. Mass of logs increases as snags fall and break, but the amount may or may not balance the loss of snag mass, due to decay and fragmentation (Acker et al., 2013; Brown et al., 2013).

The purpose of this study was to quantify and compare the changes in total aboveground biomass and its components over the first 15 years following a wildfire in a mountain hemlock forest in Oregon (Acker et al., 2013). We examined understory vegetation, tree regeneration, established trees, and CWD, using previously existing permanent plots augmented after the fire. We expected that tree regeneration would be relatively sparse during this period, given the common observation of a lag following fire. We also expected that tree regeneration would be more common where downed logs provided protection from desiccation, i.e., in close proximity to logs, especially on the north (shaded) side. Though understory species, particularly shrubs, are likely to be prominent, we expected they would have a minimal effect on biomass dynamics, due to their small contribution to older forests in the region (see e.g., Smithwick et al., 2002). Thus, we hypothesized that biomass dynamics during this period would be dominated by changes in mass of CWD, and consequently would show a small decline. We were able to take advantage of permanent plots which were monitored annually for the first 10 years after the fire and again at year 15. The plots were arranged to provide random samples of four levels of fire-severity, from unburned to >90% tree mortality (Acker et al., 2013).

2. Materials and methods

2.1. Study area

The study area is in the Torrey-Charlton Research Natural Area (TCRNA) on the crest of the Cascade Range in central Oregon, at approximately 43°46′ north latitude and 121°59′ west longitude. TCRNA is in the Willamette and Deschutes National Forests, at an elevation of approximately 1700 m. The topography consists mostly of gentle, west-facing slopes; soils, classified as Typic Cryorthents, are derived from volcanic ash, pumice, and glacial till, with ash and pumice in the thin surface layers, and are excessively drained (Acker et al., 2013; Legard and Meyer, 1973, 1990). The climate consists of snowy winters, persistent, deep snowpacks, and brief, cool and dry summers (Jackson, 1985). At the nearby Irish Taylor Snotel site (43°48′, 121°45′, 1689 m elevation; USDA NRCS, 2011), between 1997 and 2011 the average annual precipitation was 172 cm (on water-year basis, i.e., Oct. 1 to Sept. 30), with snow cover beginning by mid-November and lasting until at least mid-June in most years. The average mean minimum temperature in January was −7.3 °C, the average mean maximum temperature in July was 21.8 °C. Vegetation is mostly old-growth forest (⩾350 years old) dominated by mountain hemlock, with an understory of grouse huckleberry (*Vaccinium scoparium* Leib. ex Coville) and a sparse herbaceous layer (Salix Associates, 1998).

In August, 1996 much of TCRNA was burned by the Charlton Fire, a lightning-caused fire which covered over 3700 ha (Gardner and Whitlock, 2001; Salix Associates, 1998). Fire severity varied spatially, although the majority of the area within the burn experienced >90% tree mortality (Acker et al., 2013; Gardner and Whitlock, 2001).

2.2. Data collection

We investigated post-fire tree regeneration, the dynamics of live trees, snags, and downed logs, and understory development across four fire severity classes:

1. Unburned (>90% surviving trees)(abbreviated below as U).
2. Partial mortality (>10% and <90% surviving trees)(PM).
3. High mortality (<10% surviving trees), tree crowns scorched (HM-S).
4. High mortality (<10% surviving trees), tree crowns consumed (HM-C).

The two high-mortality classes represent contrasting effects of fire on foliage in tree crowns. Fire-killed trees in the HM-S class still held their dead needles when observed from the air shortly after the fire. Fire-killed trees in the HM-C class lacked foliage but generally retained branches. We used this distinction to structure our observations largely to investigate whether the presence (HM-S) or absence (HM-C) of litter inputs following fire would have an effect on tree regeneration composition and density.

We used pre-existing permanent plots and randomly located additional plots to sample three replicates of each fire severity class (12 plots total). Following the fire in 1996, we chose among the 20 plots that were established in 1976 (Salix Associates, 1998), regularly spaced along a west-to-east transect. The transect is located near the southeast boundary of the fire, and includes both burned and unburned plots. We excluded several plots from consideration either due to missing center stakes or extensive tree mortality prior to the fire due to *Phellinus weirii* root-rot. Of the remaining plots, five were unburned. We selected three at random for this study. For the other three fire-severity classes, there were fewer than three pre-existing plots per class (one in PM, two each in HM-S and HM-C). To complete the sample, we selected polygons at random in the general vicinity of the existing plots from a fire severity map we developed by interpretation of post-fire imagery. We established plots at random locations within these polygons, after confirming that the fire effects on the ground matched the mapped fire severity category.

Sampling occurred annually from 1997 through 2006, and again in 2011. In 1997 we were unable to enumerate seedlings and saplings by species and measure understory vegetation at all plots before the first snowfall, so the first year with a complete set of observations of tree regeneration and understory is 1998. Plots are circular with a radius of 17.84 m (0.1 ha.). Plots were on gentle terrain (slopes ranged from 1% to 20%, median 8%). Aspects were west (i.e., between 225° and 315°) for seven plots, south (i.e., between 135° and 225°) for four plots, and north (327°) for one plot. Densities of live and dead stems, and the various mass components, were converted to quantities per hectare, correcting for the effect of slope on plot area.

Within each plot, we established two belt transects, 2 × 14 m each, divided into seven 2 × 2-m quadrats. The belt transects were oriented west-to-east, to the north and south of the center of each plot. The endpoints of the inside edges of each belt transect were located 10 m from the center of the plot, in the sub-cardinal directions (i.e., NW, NE, SE, SW). In each quadrat we recorded the number, size, and species of seedlings and saplings. Seedlings (<1.37 m tall) were tallied in 10-cm height classes and saplings in dbh (diameter at breast height, 1.37 m) classes up to 5 cm. Initial seedbed conditions in each quadrat were characterized by estimating percent cover of different substrates in 1998. We measured cover of understory vascular plants using the line-intercept method (Greig-Smith, 1983), along two, 14-m long lines in each plot, situated on the inside edge of each belt transect. Live trees ($\geqslant$5 cm dbh) were tagged and measured in 1997, 2001, 2006, and 2011. We measured snags and logs (100% census in each 0.1 ha plot) in 1997, 2002, 2005 and 2011, collecting dimensional measurements to allow computation of volume. Measurements consisted of dbh and height for snags, and multiple diameters (mostly three, i.e., each end and the middle, in a few cases only the end diameters) and length (within plot only) for logs. We also measured a small number of "blobs," defined as "piles of decomposed bark and wood that accumulate around the base of large conifer snags," recording diameter and height (Harmon and Sexton, 1996). We recorded decay class of each piece, from least decayed (class 1) to most decayed (class 5), using separate definition schemes for snags and logs (Cline et al., 1980; Maser et al., 1988; Harmon et al., 2011)

In 2011 we carried out a supplementary study of spatial relationships between downed logs and tree regeneration. We set criteria concerning log size and position to ensure that logs would cast shade during the probable time of hottest conditions (i.e., late afternoon in late July). Logs included in the supplementary study were on or within 10 cm of the ground, had large-end diameters $\geqslant$22 cm, and were $\geqslant$3 m long to the point where they tapered to a diameter of 10 cm. The axis of each log was oriented within a 30-degree zone bounded by 75–105 degrees on the east end and 255–285 degrees on the west end. We selected up to three logs per plot for the supplementary study, choosing logs at random in plots with more than three that met the criteria. We recorded tree regeneration at fixed distances along and extending out from each log, separating observations into four, 1 m by 0.25 m quadrats, starting at the edge of the log out to a distance of 1 m. We also recorded tree regeneration directly beneath logs, where it occurred. Both south and north sides of logs were observed.

The methods we used to calculate biomass from dimensional measurements varied by mass component. We used allometric models based on cover for forbs and graminoids, and cover plus height for shrubs, obtained from Halpern and Means (2011). For tree seedlings and saplings we used Agee's (1983) models for seedling mass as a function of height (Agee defined seedlings as including individual stems up to 3 m in height, largely overlapping with the stems we recorded as saplings). For the smallest size-class of seedlings (height <10 cm), it was necessary to develop an alternative approach, since Agee's model predicted negative mass. In 2014 we collected 20 seedlings of mountain hemlock adjacent to the study area, ranging in height from 1 to 20 cm. Seedlings were dried at 60 °C to constant mass (24 h). We regressed mass on height and evaluated the regression for the mid-point of the smallest size-class of seedlings (i.e., height of 4.5 cm). For saplings, it was necessary to first convert measured diameters to heights. For this purpose we constructed regression models using data from Forest Inventory and Analysis plots (FIA Data Mart, 2014) for surrounding counties and elevations similar to our plots. For live trees, we estimated biomass using existing relationships between diameter and height (Garman et al., 1995), mass of bole wood, bark, branches (Zhou and Hemstrom, 2010), and foliage (Halpern and Means, 2011).

Snag and log measurements were converted to volume and then to mass using allometric equations and values of wood density pertaining to the species and decay class (Harmon et al., 2008). For snags we used bole-only allometric equations from Zhou and Hemstrom (2010), which predict volume from dbh and height. For broken snags, we compared measured height to intact height predicted from species-specific models in Garman et al. (1995), and used the taper equation of the Kozak and others (as described in Avery and Burkhart, 1994), with species-specific taper coefficients (S. Garman, pers. comm.) derived from dendrometer measurements in the western U.S. (Harmon and Franklin, 2015). We converted bole wood volume to mass using species- and decay-class specific values of wood density from Harmon et al. (2011); for decay class 5 we used values developed for decay class 4, as recommended by Harmon et al. (2011). For bark mass, we applied species-specific ratios of bark volume to wood volume (Harmon and Franklin, 2015) to bole wood volume estimates for each snag. We accounted for the tendency of bark volume to decrease as decay progresses (Harmon et al., 2011) by applying decay-class specific adjustment factors (Domke et al., 2011). Bark volume was then converted to mass using species-specific bark densities (Zhou and Hemstrom, 2010), holding density constant across decay classes as in Harmon (2005). For the majority of logs, which had three diameter measurements, we used Newton's equation to calculate volume (i.e., $L * (A_1 + (4 * A_2) + A_3)/6$, where L is piece length, A_1 is the cross-sectional area at one end, A_2 is cross-sectional area in the middle, and A_3 is the cross-sectional area at the other end.). For pieces with diameter measurements at just the ends, volume was calculated with Smalian's equation for the frustum of a paraboloid (i.e., $L * (A_1 + A_2)/2$). The volume of blobs was calculated with length and a single diameter measurement (i.e., $L * A_1/2$), under the assumption that the top diameter = 0. Mass was then determined by multiplying volume by density constants specific to species and decay class (Harmon et al., 2008). In 2014, at each plot we identified and measured the distance to the closest live trees of major species (noble fir (*Abies procera*), Pacific silver fir (*A. amabilis*), lodgepole pine, mountain hemlock) which likely were cone-bearing in the years immediately after the fire. We used a maximum distance of 150 m from the center of each plot to accommodate the probable dispersal distance of the best-dispersed of the species (mountain hemlock, Burns and Honkala, 1990).

2.3. Statistical analysis

We used analysis of variance (ANOVA) to assess differences among the fire-severity levels with respect to densities of tree seedlings, live trees, and snags, and changes in mass components. To assess whether residuals met the assumption of normality, we inspected them graphically using quantile-quantile plots (QQ-plots) and applied the Shapiro-Wilks test (Crawley, 2007). When the normality assumption did not hold, we transformed response values with the square-root (for strictly positive response values) or log (for responses that included negative values, after adding an integer to shift all responses to positive values) functions (Sokal and Rohlf, 1981). If the transformed data still did not meet the normality assumption, we applied the non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1981). To determine which fire-severity classes differed from one another, we used Tukey's test of Honest Significant Differences (Crawley, 2007). In cases where we did not find significant differences among burned classes, we addressed our overall hypotheses concerning changes in total mass or mass components by combining data across all burned severity classes and applying t-tests.

To evaluate the relationship between tree regeneration and downed logs, we transformed counts of seedlings and saplings in quadrats to presence of regeneration irrespective of regeneration category (i.e., seedling or sapling), species, or size (see Section 3.5). We used generalized mixed effects models to carry out logistic regression of presence of tree regeneration in proximity to downed logs. Mixed effects models are appropriate when predictors include factors for which the particular levels are of interest (e.g., distance from log, north versus south side), and factors for which the particular values are not inherently meaningful, but rather the degree of variability is of interest (i.e., plots, logs within plots)(Bolker et al., 2008). The former are referred to as "fixed effects," while the latter are referred to as "random effects." We used the *glmer*( ) function in the *lme4* R library to implement the models (Bates and Maechler, 2009). We selected models by starting with all fixed effects in the model and fitting varying levels of random effects (Zuur et al., 2009). We compared performance among these models using Akaike's Information Criteria (AIC; Bolker et al., 2008), using the model with all fixed and random effects ("full model") as the standard for comparison (Burnham and Anderson, 2010). The full model contained fixed effects for fire severity, side of log, and distance from log, plus all pairwise interactions, and random intercepts for plots, and logs within plots. After selecting the appropriate number of random effects, we determined the significance of the fixed effects from results of individual t-tests in the model output. We then generated a final model by eliminating non-significant fixed effects. We excluded from logistic regression areas directly beneath logs, since the area sampled varied from log to log and between measurement locations depending on the shape and placement of each log.

We used R for all data analysis and graphics (R Core Team, 2014). We set α to 0.05 for all tests of significance.

3. Results

3.1. Seedbed conditions

All seedbed conditions were present on all plots, but the distribution varied with fire severity (Fig. 1). Litter was the most common substrate for potential tree regeneration after the fire in all but one of the plots. In both U and PM plots, litter accounted for the majority of the seedbed cover. Mineral soil and rock together accounted for almost a third to over half of the seedbed cover in the HM-S and HM-C plots (Fig. 1).

3.2. Proximity of cone-bearing trees

Trees judged to be cone-bearing were found within the threshold distance of 150 m of all plots, with the distance increasing by fire severity. Cone-bearing trees occurred on all the U plots, whereas the nearest cone-bearing trees to HM-C plots ranged from about 50 to almost 140 m (Table 1). Mountain hemlock was the most common cone-bearing species. Cone-bearing lodgepole pine also grew within 150 m of most plots, except for the HM-C severity class where only one plot had a lodgepole pine within the threshold distance. Among burned plots, few of the plots had either Pacific silver fir or noble fir within 150 m.

3.3. Understory vegetation

Over the entire 15 years of study, the patterns of cover by life-forms of understory plants varied with fire severity. In the HM-C severity class, graminoids were the predominant life-form, followed by shrubs and then forbs. In both HM-S and PM plots, shrubs were the predominant life-form, followed by graminoids and then forbs. Understory cover in the U plots consisted solely of shrubs. Across all plots, the three life-forms were each dominated by one or two species. Ross' sedge (*Carex rossii*) and long-stolon sedge (*Carex inops*) accounted for 85% and 11% of cover of graminoids, respectively. Forb cover was mostly fireweed (*Chamerion angustifolium*) and white hawkweed (*Hieracium albiflorum*) (82% and 14%, respectively). Grouse huckleberry accounted for 98% of shrub cover. Over the course of the study, we identified 14 understory plant species through line-intercept measurements (six forbs, six graminoids, and two shrubs).

Graminoid cover increased over the course of the study on nearly all of the burned plots, amounting to over 10% on several plots at the end of the study (Fig. 2). Forb cover peaked soon after the fire on most of the burned plots. Following the peak, forb cover declined or disappeared on some plots, and increased on others. Shrub cover increased initially on most of the burned plots, after which it declined in most cases. One of the plots in the HM-C severity class had no shrub cover over the entire course of the study. On the U plots shrub cover was variable from year to year and declined over time (Fig. 2).

3.4. Tree regeneration

Tree seedlings (<1.37 m tall) were present in most but not all plots in the burned area two years after the fire, with densities varying by fire severity (Table 2). Only one of the three plots in HM-C severity class had tree seedlings in 1998. That year, mean densities of tree seedlings varied from <200 ha^{-1} in the HM-C severity class to >13,000 ha^{-1} in the U plots. Most of the seedlings on burned plots, including all seedlings on plots in both high mortality classes, were in the smallest size-class (i.e., <10 cm tall; Table 2). In each severity class, the majority of seedlings were mountain hemlock in 1998. Across all severity classes, 76% of seedlings were mountain hemlock and 22% were Pacific silver fir.

In 2011, 15 years after the fire, all plots had >1000 seedlings ha^{-1}; densities increased on both HM-S and HM-C plots between 1998 and 2011. Seedlings in the smallest size class accounted on average for <30% of seedlings in all the burned severity classes and did not account for more than 50% of seedlings in any of the plots in the high mortality classes (Table 2). By contrast, seedlings in the smallest size-class comprised the majority of seedlings in all U plots in both 1998 and 2011 (Table 2). Total seedling density did not differ significantly among severity classes in 2011 (Table 2).

Although the size-distribution had shifted to larger seedlings at 15 years after the fire, the majority of seedlings were still <30 cm tall (64% over all severity classes). Seedlings 1 m or taller com-

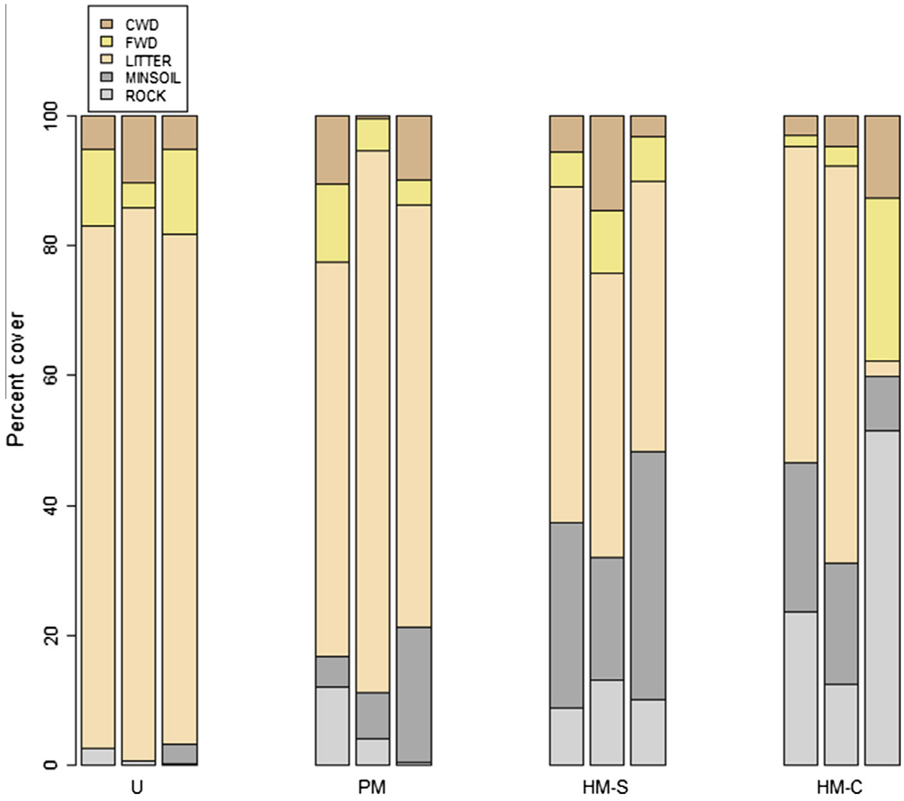

Fig. 1. Seedbed conditions two years after the Charlton fire, plots grouped by fire-severity class. Each bar represents one plot.

Table 1
Proximity of closest trees judged likely to have been cone-bearing immediately after the Charlton Fire by fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed). N signifies the number of plots (maximum of three) with an individual of the species within 150 m of the center of the plot.

Fire-severity	Pacific silver fir		Noble fir		Lodgepole pine		Mountain hemlock	
	N	Distance (m)	N	Distance (m)	N	Distance (m)	N	Distance (m)
U	3	29[a] (6–72)	0	n.a.	3	30 (5–67)	3	1 (0–3)
PM	1	26	2	93 (44–142)	2	69 (2–137)	3	30 (8–72)
HM-S	0	n.a.	1	89	3	57 (27–93)	3	47 (32–73)
HM-C	1	96	0	n.a.	1	146	3	95 (52–138)

[a] Distance values are means, with ranges in parentheses.

prised 5% of the total over all severity classes 15 years after the fire. There were no significant differences among fire-severity classes in the densities of seedlings of different sizes at 15 years after the fire (Table 3). In all of the burned classes, seedlings 30–99 cm tall were nearly equal to or somewhat greater in abundance than seedlings 10–29 cm tall (Table 3). Over all plots in the burned classes, the average density of seedlings ⩾10 cm tall was 4401 ha^{-1}; the average density of seedlings ⩾30 cm tall was 2578 ha^{-1}.

Mountain hemlock continued to account for the majority of tree seedlings in all severity classes 15 years after the fire (Table 2). Across all severity classes in 2011, 74% of seedlings were mountain hemlock and 22% were Pacific silver fir. The remaining 4% were predominantly lodgepole pine, with western white pine (*Pinus monticola*) and unidentified true fir species also present.

Saplings (⩾1.37 m tall and <5 cm dbh) were sparse in all severity classes, including U, both two and 15 years post-fire. Two years after the fire, saplings were present in only U and PM plots (mean densities 357 and 238 ha^{-1}, respectively). At 15 years post-fire, saplings were present in U, PM, and HM-S plots (mean densities 179, 238, and 179 per ha, respectively). Most of the saplings were mountain hemlock in both years (80% in 1998, 73% in 2011). Other species of saplings were lodgepole pine and Pacific silver fir.

3.5. Proximity of tree regeneration to downed logs

Among U and PM plots, suitable logs were found on two of three plots per severity class, whereas all three plots had suitable logs in both HM-S and HM-C severity classes. The target number of three suitable logs per plot occurred on HM-S and HM-C plots, but not on U and PM plots (averages 1.5 and 2 logs per plot, respectively). Due to the presence of more numerous and generally longer logs on HM-S and HM-C plots, the average number of measurement locations was greater on HM-S and HM-C plots (eight and 11, respectively), than on U and PM plots (two and five measurement locations, respectively). Nearly all the regeneration stems we tallied were seedlings of mountain hemlock. Most seedlings were less than 30 cm tall (84%). Given the lack of diversity of tree regeneration with respect to species and size, we analyzed all tree regeneration as a single entity.

The frequency of tree regeneration in proximity to logs was generally greater on U plots than burned plots (Table 4), mostly varying between 25% and 50%. In U and PM plots, frequency of regeneration was similar on both north and south sides of logs. In contrast, in HM-C and HM-S plots, seedlings were sparse on the south side of logs, particularly compared to the first one

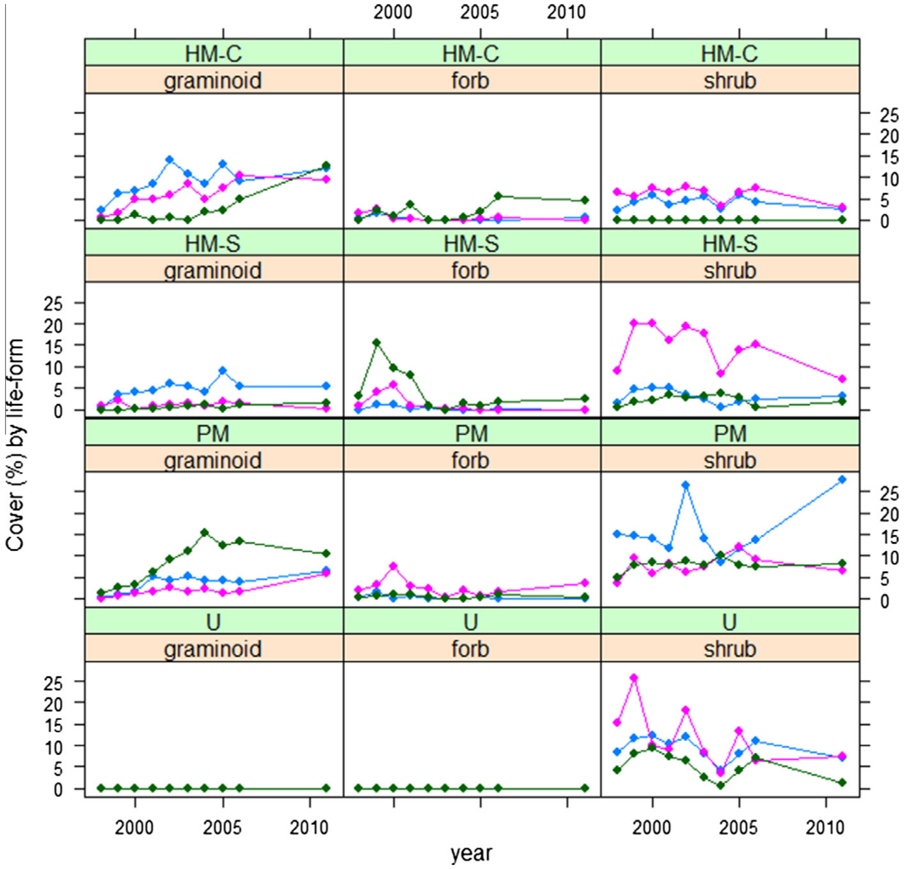

Fig. 2. Changes in cover of graminoids (principally sedges (*Carex* spp.)), forbs (principally fireweed (*Chamerion angustifolium*)), and shrubs (principally grouse huckleberry (*Vaccinium scoparium*)) in plots grouped by fire-severity class over course of study, as indicated from line-intercept measurements. Each line represents an individual plot. No graminoids or forbs were observed on any of the three unburned plots over the entire study.

Table 2
Tree seedlings, two (1998) and 15 (2011) years post-fire, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Density of seedlings in 1998 (ha^{-1})	Percent-age of mountain hemlock among seedlings, 1998	Percent-age of seedlings <10 cm in height, 1998	Density of seedlings in 2011 (ha^{-1})	Percent-age of mountain hemlock among seedlings, 2011	Percent-age of seedlings <10 cm in height, 2011
U	13218 ± 4962^{a} (3594–20128)	87 ± 8 (72–95)	82 ± 2 (80–85)	7232 ± 2612^{a} (3774–12352)	76 ± 16 (45–100)	68 ± 5 (58–76)
PM	8049 ± 3340^{a} (2021–13555)	73 ± 25 (24–100)	77 ± 23 (31–100)	5960 ± 2427^{a} (2572–10663)	71 ± 29 (14–100)	20 ± 11 (0–38)
HM-S	1268 ± 267^{ab} (743–1617)	100 ± 0 (100–100)	100 ± 0 (100–100)	9188 ± 2148^{a} (6871–13479)	94 ± 3 (90–100)	28 ± 1 (27–30)
HM-C	180 ± 180^{b} (0–539)	67[A]	100[A]	2035 ± 573^{a} (1072–3055)	91 ± 5 (83–100)	27 ± 10 (17–47)

Notes: Values are means ± standard errors, with ranges in parentheses. Values followed by same superscript in a column are not significantly different (ANOVA, $p > 0.05$).

[A] Only one plot had seedlings in 1998, so standard error undefined.

Table 3
Tree seedlings ⩾10 cm tall and saplings, 15 years post-fire, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Density of seedlings 10–29 cm tall (ha^{-1})	Density of seedlings 30–99 cm tall (ha^{-1})	Density of seedlings 100–136 cm tall (ha^{-1})	Density of saplings (ha^{-1})
U	1493 ± 954^{a} (539–3401)	777 ± 260^{a} (359–1253)	299 ± 158^{a} (0–537)	180 ± 180^{a} (0, 539)
PM	1744 ± 1402^{a} (0–4518)	2896 ± 1268^{a} (1429–5422)	540 ± 178^{a} (184–723)	241 ± 241^{a} (0, 723)
HM-S	3188 ± 2001^{a} (1114–7189)	3088 ± 441^{a} (2600–3968)	371 ± 371^{a} (0–1114)	182 ± 104^{a} (0, 361)
HM-C	538 ± 103^{a} (359–715)	778 ± 317^{a} (179–1258)	60 ± 60^{a} (0–180)	0^{a}

Notes: Values are means ± standard errors, with ranges in parentheses. Values followed by same superscript in a column are not significantly different (ANOVA, $p > 0.05$).

Table 4
Frequency of tree regeneration in proximity to downed logs, as a function of position (north vs. south) and distance from log (in 25 cm increments), 15 years post-fire. Averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	North side of logs				South side of logs			
	Quadrat 4	Quadrat 3	Quadrat 2	Quadrat 1	Quadrat 1	Quadrat 2	Quadrat 3	Quadrat 4
U	0.25 ± 0.25 (0–0.5)	0.25 ± 0.25 (0–0.5)	0.5 ± 0 (0.5–0.5)	0.5 ± 0 (0.5–0.5)	0.5 ± 0 (0.5–0.5)	0.25 ± 0.25 (0–0.5)	0.25 ± 0.25 (0–0.5)	0.25 ± 0.25 (0–0.5)
PM	0.31 ± 0.19 (0.12–0.5)	0 ± 0 (0–0)	0.06 ± 0.06 (0–0.12)	0.19 ± 0.19 (0–0.38)	0.25 ± 0.25 (0–0.5)	0.06 ± 0.06 (0–0.12)	0.12 ± 0.12 (0–0.25)	0.12 ± 0.12 (0–0.25)
HM-S	0.07 ± 0.07 (0–0.2)	0.1 ± 0.06 (0–0.2)	0.15 ± 0.05 (0.1–0.25)	0.43 ± 0.03 (0.4–0.5)	0.07 ± 0.07 (0–0.2)	0.07 ± 0.07 (0–0.2)	0.03 ± 0.03 (0–0.1)	0.08 ± 0.08 (0–0.25)
HM-C	0.02 ± 0.02 (0–0.06)	0 ± 0 (0–0)	0.02 ± 0.02 (0–0.06)	0.25 ± 0.13 (0–0.44)	0 ± 0 (0–0)	0 ± 0 (0–0)	0.02 ± 0.02 (0–0.06)	0.02 ± 0.02 (0–0.06)

Notes: Quadrats 1 through 4 are from 0 to 25 cm, 25 to 50 cm, 50 to 75 cm, and 75 to 100 cm away from the log, respectively. Values are means ± standard errors, with ranges in parentheses. Data for quadrat 0 (directly beneath the log) are not shown, since the area sampled varied from log to log and between measurement locations depending on the shape and placement of each log.

(HM-C) or two (HM-S) quadrats on the north side (i.e., those closest to the logs).

The full model with random effects for both plots and individual logs was more plausible than the model with random effects for plots only (AIC 340.2 vs. 348.8, respectively). Significant fixed effects were side of the log, distance from log, and the interaction of the two (Table 5). Probability of occurrence of tree regeneration was lower on the south side of logs and decreased with distance from logs; the interaction moderated the effect of distance from logs on their south sides.

3.6. Live trees

In keeping with criteria for plot selection, live trees ($\geqslant$5 cm dbh) were present on all PM plots one year after the fire but were sparse to absent on high mortality plots (Table 6). The pattern was very similar 15 years after the fire, with HM-C and HM-S plots having significantly fewer trees than U plots (Table 6). At both time-points, mountain hemlock accounted for 86% of live trees across all plots. The only other species that accounted for >10% of trees on plots with > 100 trees ha^{-1} was lodgepole pine, which represented about 40% of trees on one PM plot in both years. Other species present as live trees, in decreasing order of abundance, were Pacific silver fir, noble fir, western white pine, ponderosa pine (*Pinus ponderosa*), and western hemlock (*Tsuga heterophylla*).

3.7. Snags

One year after the fire, snags on burned plots ranged from about 400 to 1300 ha^{-1}, compared to fewer than 300 ha^{-1} on U plots. Fifteen years after the fire, snags on burned plots ranged from 100 to 600 ha^{-1} (Table 7). Most of the snags were mountain hemlock (75% one year after the fire; 90% 15 years after the fire). Pacific silver fir accounted for 16% of snags one year after the fire; most of these were on one of the HM-C plots and nearly all had fallen by 15 years after the fire. The integrity of snags was transformed over the course of the study: one year after the fire nearly all the snags on burned plots had intact boles, whereas 15 years after the fire nearly all the remaining snags had broken boles (Table 7). The height of these broken snags averaged 7–8 m, representing about one-third of the live-tree height predicted from regional models of height as a function of dbh (Garman et al., 1995).

Table 6
Density of live trees, one and 15 years post-fire, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Density of live trees in 1997 (ha^{-1})	Density of live trees in 2011 (ha^{-1})
U	1245 ± 503^{a} (322–2055)	1275 ± 516^{a} (292–2035)
PM	351 ± 247^{ab} (51–840)	317 ± 272^{ab} (41–860)
HM-S	17 ± 12^{b} (0–40)	27 ± 15^{b} (0–50)
HM-C	0 ± 0^{b} (0–0)	7 ± 3^{b} (0–10)

Notes: Values are means ± standard errors, with ranges in parentheses. Values followed by same superscript in a column are not significantly different (ANOVA, $p > 0.05$).

3.8. Biomass dynamics

The components that dominated biomass dynamics varied between burned and unburned plots and by fire severity. Live trees accounted for at least 75% of biomass on all U plots throughout the study, whereas only on one burned plot (PM) did live trees ever account for more than half of the total (Figs. 3 and 4). On PM plots, live trees accounted for 0.2–52% of mass in all years (9–38% of mass the first year after the fire), while live trees always accounted for less than 1% of biomass on plots with high mortality. Snags always accounted for the majority of mass on HM-S plots, and for most observations of plots in the PM or HM-C severity classes. For one of the three HM-C plots, logs accounted for the majority of mass after 15 years. Understory vegetation accounted for less than 1% of mass on all plots throughout the study. Tree regeneration accounted for less than 1% of mass throughout the study with the exception of one PM plot in which it varied between 1% and 2% of the total (Figs. 3 and 4).

Log mass one year after the fire was lower on most burned plots than on unburned plots (Fig. 3), which could be due to consumption of logs in the fire.

Change in total mass between one to two years post-fire and 15 years post-fire was not significantly different among fire

Table 5
Parameter estimates for fixed effects from the most parsimonious model fit to the data concerning proximity of tree regeneration to downed logs.

	Estimate	Std. Error	z value	P-value for z
Intercept	−0.3231	0.5349	−0.604	0.545849
South side of log	−2.9528	0.7663	−3.853	0.000117
Distance from log	−0.8569	0.1975	−4.338	0.00001
Interaction of south side and distance	0.8824	0.3002	2.939	0.003290

Table 7
Density of snags, one and 15 years post-fire, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Density of snags in 1997 (ha^{-1})	Percentage of snags with broken boles, 1997	Density of snags in 2011 (ha^{-1})	Percentage of snags with broken boles, 2011	Heights of snags with broken boles, 2011
U	147 ± 75^{a} (40–291)	35 ± 14 (17–64)	80 ± 25^{a} (30–111)	79 ± 11 (67–100)	8.2 ± 1.4 (2.2–19.4)
PM	606 ± 106^{ab} (453–810)	12 ± 2 (9–16)	361 ± 144^{a} (101–600)	89 ± 5 (80–97)	7.1 ± 0.5 (1.4–24.1)
HM-S	479 ± 14^{a} (453–499)	11 ± 1 (10–12)	350 ± 35^{a} (282–395)	100 ± 0 (100–100)	8.1 ± 0.5 (1.6–29.2)
HM-C	994 ± 160^{b} (755–1298)	12 ± 5 (3–19)	411 ± 133^{a} (151–590)	77 ± 16 (47–100)	6.7 ± 0.4 (1.4–29.4)

Notes: Values are means ± standard errors, with ranges in parentheses. Values followed by same superscript in a column are not significantly different (ANOVA, $p > 0.05$).

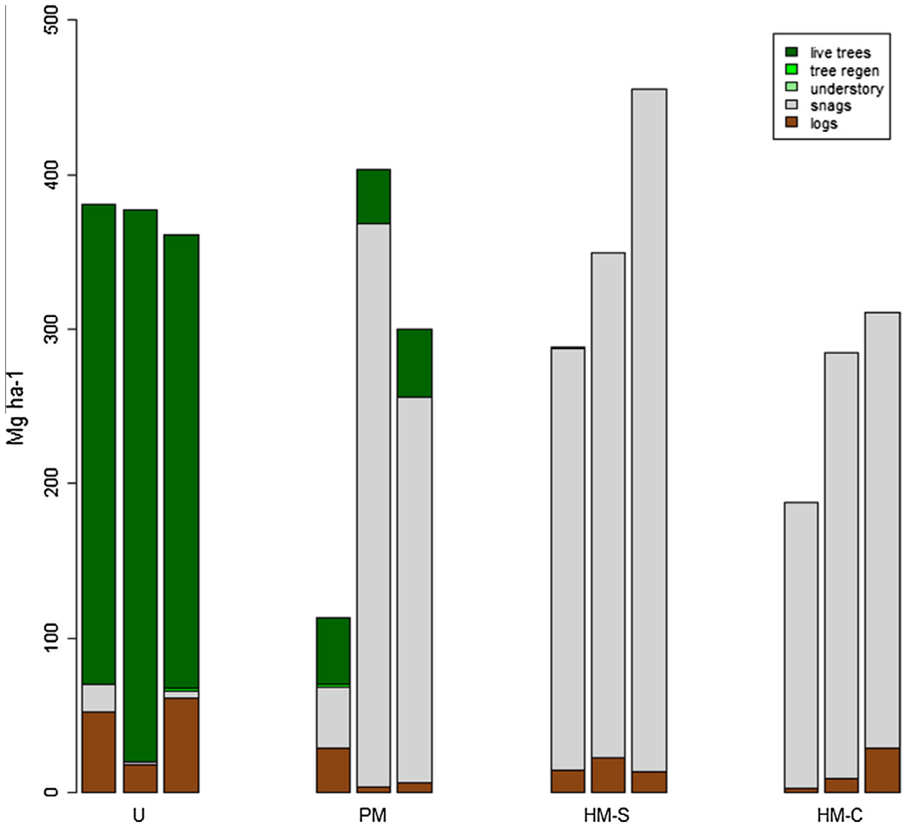

Fig. 3. Distribution of mass one to two years post-fire on plots grouped by fire-severity class.

severity classes (Table 8). For the burned plots as a group, however, total mass decreased significantly over time ($p = 0.001$ for two-tailed *t*-test, mean change −74 Mg ha^{-1}, 95% CI −108 to −40 Mg ha^{-1}). Change in snag mass was significantly different between U plots and the two high-mortality classes (Table 8); snag mass increased on two of three U plots and decreased on all burned plots. Change in log mass over the interval was not significantly different among fire severity classes (Table 8). For the burned plots as a group, however, the increase in log mass over time was significant ($p = 0.0002$ for one-tailed *t*-test, mean change 72 Mg ha^{-1}, lower 95% CI 50 Mg ha^{-1}).

4. Discussion

In the first 15 years after a wildfire in a mountain hemlock forest, understory vegetation has been transformed and there has been abundant but variable recruitment of conifer seedlings. Conifer regeneration has not included lodgepole pine, the species considered the most common early-seral tree for this type of forest. For the most part, tree regeneration has not grown to large seedling (i.e., ⩾1 m in height), sapling, or tree size. In terms of mass, changes in understory plants and conifer regeneration have been far outweighed by CWD dynamics. Toppling, fragmentation, and advancing decay of snags have resulted in a decrease in snag mass and an increase in log mass. The loss of snag mass has exceeded the increase in log mass, resulting in an overall decline of biomass.

Our plots constituted a random sample across fire severities in the southeast corner of the Charlton Fire. The relatively small number of plots may have limited our ability to detect significant differences among fire severity classes, for example in density of tree regeneration 15 years after the fire (Tables 2 and 3). Thus, any effects on tree regeneration of litter inputs due to whether or not tree crowns were consumed were too subtle to be detected with our study design. The small amount of live tree mass on PM plots the first year after the fire (i.e., between 9% and 38%) suggests that in the portion of the fire we studied, severity in the area mapped as partial mortality was more often than not towards the higher end of the range.

Structural diversity of understory vegetation has increased due to fire, inasmuch as only shrubs were detected in unburned plots, while burned plots had significant amounts of graminoids and

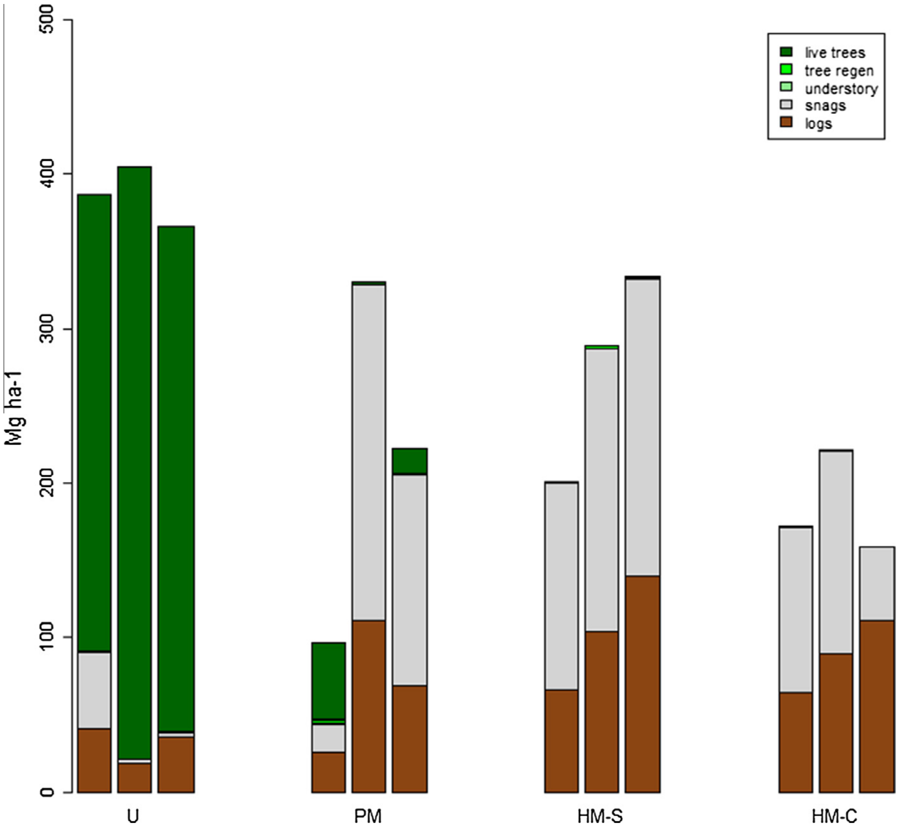

Fig. 4. Distribution of mass 15 years post-fire on plots grouped by fire-severity class.

Table 8
Change in total aboveground biomass, mass of snags, and mass of logs from one to two years to 15 years post-fire, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Change in total aboveground biomass 1997/1998 to 2011 (Mg ha^{-1})	Change in snag mass 1997–2011 (Mg ha^{-1})	Change in log mass 1997–2011 (Mg ha^{-1})
U	12 ± 8^{a}	10 ± 11^{a}	−12 ± 8^{a}
	(5–28)	(−2 to 31)	(−25 to 1)
PM	−56 ± 19^{a}	−94 ± 38^{ab}	56 ± 32^{a}
	(−77 to −17)	(−147 to −21)	(−3 to 108)
HM-S	−90 ± 18^{a}	−177 ± 36^{b}	86 ± 22^{a}
	(−122 to −61)	(−249 to −139)	(51–126)
HM-C	−77 ± 40^{a}	−152 ± 46^{b}	75 ± 7^{a}
	(−152 to −16)	(−235 to −78)	(62–82)

Notes: Values are means ± standard errors, with ranges in parentheses. Values followed by same superscript in a column are not significantly different (ANOVA, $p > 0.05$). For change in log mass, means were compared with the Kruskal-Wallis test due to lack of normality.

forbs in addition to shrubs. The interaction between species' life history and fire severity largely explains the spatial and temporal distribution of the various life forms of understory plants. Grouse huckleberry can persist through fires that do not completely consume the forest floor (as we observed) by sprouting from shallow rhizomes, though seedling recruitment following fire is rare (Johnson, 2001). This is consistent with the relative abundance of grouse huckleberry on PM plots. Ross' sedge commonly dominates recently-disturbed areas in a wide variety of environments in western North America, largely due to recruitment from residual seeds in duff or soil (Anderson, 2008). Fireweed, by contrast, is represented in a wide variety of disturbed locations due to abundant airborne seeds, rather than persistence in the seed bank (Pavek, 1992). An early peak in cover of fireweed, followed by decline or disappearance, has been observed in a variety of habitats. However, the previously-reported mechanism for decline with closure of a forest canopy (Pavek, 1992) does not apply in this case, given the abundant light in the burned plots. All the species we detected with line-intercepts measurements were natives. The absence of nonnative, invasive plants is consistent with earlier studies in upper montane environments of the Pacific Northwest (reviewed by Anzinger and Radosevich, 2008), and mirrors patterns observed with riparian corridors in montane areas (Planty-Tabacchi et al., 1996). Possible explanations include environmental limitations such as excessive winter cold or short duration of the growing season, and/or lack of proximate seed sources (Anzinger and Radosevich, 2008; Jones et al., 2010).

Though tree regeneration was sparse on the most severely burned plots two years after the fire, by 15 years post-fire all but one of the burned plots had numbers of conifer seedlings exceeding the numbers of live trees on unburned plots. On the remaining burned plot, seedling density exceeded 80% of average density of live trees on unburned plots. The breakage of snags and resulting increase in logs created microsites (north sides of logs) conducive to tree regeneration. Conifer seedlings on burned plots are evidently growing, as nearly all seedlings two years after the fire were <10 cm in height while most were >10 cm in height 15 years after the fire. Throughout the course of the study, most conifer seedlings were mountain hemlock. Lodgepole pine would be expected to colonize burned areas in this forest type (Hemstrom et al., 1987), due to both removal of tree canopy and exposure of mineral soil (Lotan and Critchfield, 1990). However, effective dispersal of lodgepole pine is often limited to 60 m (Lotan and Critchfield, 1990); most burned plots did not have cone-bearing individuals of lodgepole pine within that distance. In contrast, effective dispersal of seed of mountain hemlock has been observed more than 100 m from parent trees (Means, 1990); all but one of the burned plots had cone-bearing individuals of mountain hemlock within that distance. Proximity of seed sources has influenced patterns of post-fire seedling establishment.

Between one and 15 years post-fire, many snags on burned plots fell, and the overwhelming majority of those that remained standing had broken boles. This led to a decrease in snag mass and an increase in log mass, but the increase in log mass was only about half the decrease in snag mass. The progression of decay and hence decreased wood density has contributed to the discrepancy (Acker et al., 2013). Fragmentation of fallen pieces to less than the minimum length and/or width to be measured as logs (i.e., 1.5 m and 10 cm, respectively, Harmon et al., 2008) has likely also contributed to the discrepancy. Snags or portions of snags may have fallen outside of plot boundaries, and thus have not been measured. However, on average these would be balanced by snags or portions of snags that fell into plots.

In the first 15 years following wildfire in a mountain hemlock forest, total biomass has declined due to snag attrition, decay, and fragmentation. While understory vegetation is not likely to ever constitute sufficient mass to balance the decline, conifer recruitment has been abundant and is likely to eventually balance the loss of biomass due to fire. This raises the question of how long it may take for trees to add significant mass. We can bracket the possible contribution of live trees to biomass dynamics over the next century by use of current observations of these plots and published information on growth and allometry of mountain hemlock, along with some simplifying assumptions.

Given that current seedling density on burned plots approaches or exceeds average live-tree density on unburned plots, it is reasonable to use the current range of density of live trees on the unburned plots to bracket possible future conditions on the burned plots (i.e., 290–2030 trees ha^{-1}, Table 6). This may, in fact, overestimate the lower end of the range of future tree densities, given that some mortality is to be expected as seedlings grow to become mature trees (Franklin et al., 1987). In this forest type, mountain hemlock typically reaches a height of 15 m by age 100 (Hemstrom et al., 1987). Such a tree would have a mass of 144 kg, using the same set of relationships we used to estimate live tree mass. So as a first approximation, biomass of live trees on the burned plots 100 years after the fire could vary between 42 and 292 Mg ha^{-1}. Given the current size-distribution of tree seedlings (Table 3), it is reasonable to assume that biomass of live trees will be lower, on average, for areas burned at high severity than for areas burned with lower severity. Thus, it is possible that for some portions of the burned area, even after a century, the growth of live trees may not balance the loss of mass due to decay and fragmentation of CWD that has occurred since the fire. To return to the amount of mass present before the fire may take even longer. Such an extended period of decline would be greater than that reported for forests in the region at lower elevations (e.g., Janisch and Harmon, 2002). Given the expectation of increased occurrence of fire in western North America in coming decades due at least in part to a changing climate, understanding the trajectory of tree regeneration, dead wood decomposition, and accumulation of biomass and carbon following wildfire in mountain hemlock and other forest types is an important part of projecting the role of forests as sinks or sources in the global carbon cycle (Loehman et al., 2014; McKinley et al., 2011). Continued observation of the Charlton Fire will make it possible to determine whether or not tree regeneration in the first 15 years post-fire will eventually contribute to an accumulation of aboveground biomass that balances losses due to attrition of CWD. Detecting these and other patterns would be facilitated by increasing the sample size and spatial representation across the Charlton Fire, as well as making corresponding observations of other recent, large fires in mountain hemlock forest in the Pacific Northwest.

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