



Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA



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ABSTRACT

Climate change is expected to increase disturbances such as stand-replacing wildfire in many ecosystems, which have the potential to drive rapid turnover in ecological communities. Ecosystem recovery, and therefore maintenance of critical structures and functions (resilience), is likely to vary across environmental gradients such as moisture availability, but has received little study. We examined conifer regeneration a decade following complete stand-replacing wildfire in dry coniferous forests spanning a 700 m elevation gradient where low elevation sites had relatively high moisture stress due to the combination of high temperature and low precipitation. Conifer regeneration varied strongly across the elevation gradient, with little tree regeneration at warm and dry low elevation sites. Logistic regression models predicted rapid increases in regeneration across the elevation gradient for both seedlings of all conifer species and ponderosa pine seedlings individually. This pattern was especially pronounced for well-established seedlings (≥ 38 cm in height). Graminoids dominated lower elevation sites following wildfire, which may have added to moisture stress for seedlings due to competition for water. These results suggest moisture stress can be a critical factor limiting conifer regeneration following stand-replacing wildfire in dry coniferous forests, with predicted increases in temperature and drought in the coming century likely to increase the importance of moisture stress. Strongly moisture limited forested sites may fail to regenerate for extended periods after stand-replacing disturbance, suggesting these sites are high priorities for management intervention where maintaining forests is a priority.

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1. Introduction

With expected increases in wildfire size and severity in many ecosystems due to ongoing climate change (Westerling et al., 2006; Littell et al., 2010; Rogers et al., 2011; Adams, 2013), preservation of forest ecosystem functions will increasingly depend on post-fire recovery. For example, the presence of trees has critical implications for many landscape functions (Scheffer et al., 2012), highlighting the importance of rapid tree regeneration following stand-replacing disturbance for maintaining ecosystem functions. However, juveniles often have narrower climate niches than adults of the same species (Hogg and Schwarz, 1997; Jackson et al., 2009; Johnstone et al., 2010), so recruitment failures are possible even under climatic conditions that are suitable for maintenance of mature individuals. Therefore, disturbances may drive compositional shifts in ecological communities during an era of climate change (Littell et al., 2010; Johnstone et al., 2010; Moser et al., 2010), but little is known about patterns of natural recovery following severe wildfires in many ecosystems (Keane et al., 2008). Studies on post-fire recovery could increase understanding of community

dynamics, and inform post-fire management, which is often controversial (e.g., DellaSalla et al., 2006).

The potential for an ecosystem to recover (resilience) following wildfire is likely to vary considerably across the landscape, even when initial estimates of fire severity are similar (Díaz-Delgado et al., 2002; Keeley et al., 2008). Some ecosystems have proven highly resilient to large severe disturbances (Rodrigo et al., 2004; Knox and Clarke, 2012), while others show little recovery toward pre-disturbance conditions (Barton, 2002; Rodrigo et al., 2004; Vilà-Cabrera et al., 2012; Lippok et al., 2013). Environmental conditions may influence ecosystem recovery following disturbance by structuring the pre-disturbance community and the conditions at a site during the recovery period (Keeley et al., 2005). Ecosystems with better conditions for re-establishment, survival, and growth may show higher resilience to disturbance (Dynesius et al., 2009). In contrast, stressful environments, particularly drought-stressed ecosystems, have shown limited capacity to recover following disturbance (Díaz-Delgado et al., 2002; Keeley et al., 2005; Johnstone et al., 2010; Vilà-Cabrera et al., 2012). Indeed, the importance of moisture availability for tree regeneration has been documented in forests throughout the world (i.e., Hogg and Schwarz, 1997; Pausas et al., 2004; Calvo et al., 2008; Johnstone et al., 2010; Vilà-Cabrera et al., 2012; Lippok et al., 2013).

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Increases in drought (Schwalm et al., 2012), combined with warming temperatures that exacerbate drought stress (climate change-type drought; Breshears et al., 2005) will increase water stress in the near future with largely unknown consequences for tree regeneration following stand-replacing fire. Studies of post-fire recovery along environmental gradients, such as moisture availability, could help identify thresholds in response to critical limiting factors, and allow identification of sites with low resilience.

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests are widely distributed throughout western North America from Mexico to Canada, across a broad range of environmental settings (Graham and Jain, 2005). Fire severity has already increased in many forests where ponderosa pine is dominant or co-dominant due to historical logging, grazing, and fire suppression (Allen et al., 2002; Hessburg and Agee, 2003), raising concerns that these forests may not be resilient to high severity wildfire (Savage and Mast, 2005). However, post-fire regeneration of ponderosa pine forests has been variable. For example, severe fire has resulted in both strong ponderosa pine regeneration (Ehle and Baker, 2003; Savage and Mast, 2005; Schoennagel et al., 2011; Roccaforte et al., 2012) and a paucity of regeneration (Barton, 2002; Savage and Mast, 2005; Meigs et al., 2009; Roccaforte et al., 2012). Moisture stress has been well documented as a key limiting factor for ponderosa pine regeneration in managed and undisturbed forests (Stein and Kimberling, 2003; Puhlick et al., 2012) and thus could serve as a key barrier to post-fire establishment. Competition from understory vegetation can exacerbate moisture stress for tree regeneration, particularly competition from graminoids with dense fibrous roots that can interfere with early tree establishment (Pearson, 1942; Ehle and Baker, 2003; Balandier et al., 2006). Strong patterns of tree regeneration following wildfire have been documented across elevation and moisture availability gradients in tropical South America (Lippok et al., 2013) and Europe (Moser et al., 2010), but these effects remain poorly studied in many ecosystems, including western North America, despite recent increases in wildfire (Westerling et al., 2006).

We examined tree regeneration in ponderosa pine forests along an elevation gradient spanning more than 700 m that included considerable variability in moisture availability. Increasing temperature and decreasing precipitation interact to increase moisture stress at low elevations (Table 1). We address three specific questions: (i) Do patterns of regeneration vary along an environmental

gradient of moisture stress for all conifer species and ponderosa pine regeneration specifically? (ii) Does the composition of understory competitors vary along the elevation gradient? and (iii) What is the age structure of the sampled seedlings?

2. Methods

2.1. Study site

The Eyerly fire was started by lightning on July 9, 2002 and burned a total of 9362 ha in the Metolius River watershed in the Eastern Cascade Range of Oregon state, with 5188 ha burning at stand-replacing severity (USDA, 2004). Summers in the region are warm and dry, much of the precipitation falls as snow from October to April (Meigs et al., 2009). The Eyerly fire occurred during a multi-year drought in the western U.S. (Schwalm et al., 2012). Prior to the fire, ponderosa pine dominated lower elevations (Table 1) with occasional western juniper (*Juniperus occidentalis* Hook.). Higher elevations were comprised of mixed conifer forests including ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), incense cedar (*Calocedrus decurrens* (Torr.) Florin), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) and western larch (*Larix occidentalis* Nutt.). Soils of the region are well-drained volcanic sandy loams and loamy sands (Meigs et al., 2009). Similar adjacent forests just north of the study area had predominately frequent low-severity fire historically (Weaver, 1959), though the strong variation in vegetation along environmental gradients and frequent ignitions probably led to some mixed severity fire historically in the area (Meigs et al., 2009). Tree density in the Eyerly fire area at the time of the fire was likely higher than before Euro-American settlement due to anthropogenic effects such as fire exclusion (Weaver, 1959; Swedberg, 1973). In the decades immediately preceding the Eyerly fire dispersed clear-cutting has been the main disturbance in the area (Meigs et al., 2009).

The east slope of the Oregon Cascades is characterized by one of the steepest precipitation gradients in western North America (PRISM Group, Oregon St. Univ., <http://prism.oregonstate.edu/>; Meigs et al., 2009) and the area burned by the Eyerly fire is geologically simple (Swedberg, 1973); making it ideal for studying moisture availability gradients. Climate values were calculated for each plot using PRISM (PRISM Group, Oregon St. Univ., <http://prism.oregonstate.edu/>). Annual precipitation ranged from 38 to 86 cm at

Table 1
Characteristics of the 18 plots on the Eyerly fire sorted by elevation.

Plot	Elevation (m)	Aspect	Slope (°)	Trees (ha) ^a	PP ^b trees (ha) ^a	Annual precip. (cm)	Average temp. (°C)	Conifer seedlings (ha)	WE ^c seedlings (ha)	PP ^b seedlings (ha)	PP ^b WE ^c seedlings (ha)
10	641	219	11	183	167	38.4	17.7	0	0	0	0
9	644	171	18	104	80	38.9	17.8	0	0	0	0
11	733	337	6	119	111	39.5	17.0	0	0	0	0
8	757	7	1	159	159	39.7	17.0	76	0	0	0
7	830	225	7	135	135	40.3	16.9	585	0	585	0
19	886	351	10	143	88	43.4	16.7	0	0	0	0
18	897	87	10	135	119	43.4	16.7	0	0	0	0
1	911	351	16	143	143	44.4	16.4	51	0	51	0
4	1023	191	5	72	56	45.6	16.1	25	0	25	0
3	1037	339	3	119	96	45.6	16.1	636	127	331	127
2	1054	23	5	151	151	46.4	15.9	280	25	280	25
17	1096	14	23	159	56	46.3	15.7	25	0	0	0
12	1237	124	7	167	32	72.4	14.1	356	153	127	76
5	1241	124	23	135	127	75.7	14.1	102	51	76	51
13	1269	60	14	183	135	74.3	14.0	840	178	483	127
6	1271	94	9	175	88	86.2	13.6	1807	585	1196	433
16	1296	27	10	143	80	74.3	14.0	967	356	712	280
15	1368	358	5	143	104	83.3	13.4	763	305	687	280

^a Conifer trees ≥ 20 cm DBH prior to wildfire.

^b Ponderosa pine.

^c Well-established (≥ 38 cm in height).

our sites, rapidly increasing along the elevation gradient (Table 1). Predicted mean annual temperature ranged from about 13.4 to 17.8 °C, decreasing at higher elevations (Table 1).

2.2. Sampling

Plots were established in areas with complete stand-replacing wildfire in May of 2012. Candidate stands were selected using maps of fire severity (USDA, 2004) stratifying across the elevation gradient. Stands were selected for inclusion in the study based on public land ownership (77% of the wildfire was on public land), accessibility, isolation from intact forest (at least 50 m to forest, but not more than 300 m to a live tree seed source), presence of mature forest prior to the wildfire (at least three trees ≥ 38 cm diameter at breast height on a plot present before the fire), and no evidence of post-fire logging or tree planting. Plots were established randomly within stands at least 50 m from the edge of roads. Plots were separated by a least 500 m to ensure dispersion and established through much of the fire (Fig. 1), spanning a range of slopes and aspects (Table 1).

Plots consisted of five circular 5-m radius subplots for sampling tree regeneration. One subplot was established at the center of the overall plot with the other four centered at 15 m from the plot center in each cardinal direction. At each subplot the total number of seedlings was recorded for each species. Additionally, the number and species of well-established seedlings (>38 cm in height) were recorded for each subplot. Seedlings were aged by counting bud-scars, an effective method for aging post-fire conifer seedlings in the northwestern US (Urza and Sibold, 2013). *Calocedrus decurrens* and *Juniperus occidentalis* seedlings, which comprised 7% of the total sampled seedlings, were not aged due to difficulties in estimating age from terminal bud scars. Total cover for each understory life-form (forbs, shrubs and graminoids) was visually estimated for each subplot to the nearest 5%. Trees ≥ 20 cm diameter at breast height (1.37 m DBH) present prior to fire were counted on a 20-m radius plot that included all five subplots.

2.3. Statistical analyses

We used logistic regression in SAS (SAS institute, Cary NC, v. 9.3) to evaluate the effects of elevation on the probability of sampling at least one seedling on a subplot. Elevation was strongly collinear with both precipitation and temperature ($R^2 > 0.9$ for both

regressions including a quadratic term for elevation). Because of the high collinearity we included only elevation as a predictor in the statistical models, but interpret the results as a gradient in moisture availability considering the more direct effects of climate and understory competition in our interpretation (Dormann et al., 2013). We calculated heat load index (HLI; McCune, 2007), an index of solar exposure corrected for the difference in warmth between morning and afternoon sun, using latitude, slope and aspect. We included HLI, total plant cover, and pre-fire tree density as potential predictor variables in preliminary models, but none were significant (all P -values ≥ 0.09), so final models include only elevation. Our response variable was the number of subplots with at least one seedling divided by the total number of subplots (5). One seedling per subplot corresponds to 127 trees/ha, near pre-fire stocking for these dry forests (average of 142 trees/ha ≥ 20 cm DBH; Table 1). Models were constructed separately for all species and ponderosa pine. Additionally, models were run for well-established seedlings (≥ 38 cm in height) for all species and ponderosa pine.

Logistic regression models were evaluated, in part, by plotting fitted values with actual values from individual plots. We also evaluated model fit by calculating the area under the curve (AUC) for the receiver operating characteristic (ROC). AUC varies from 0.5 for random to 1.0 for a perfect predictor (Fawcett, 2006). The AUC is equivalent to the probability that a randomly chosen positive instance will be ranked higher than a randomly chosen negative instance (Fawcett, 2006). Hosmer and Lemeshow (2000) suggest the following guidelines for interpreting AUC: 0.7–<0.8, acceptable discrimination, ≥ 0.8 to <0.9, excellent discrimination, and ≥ 0.9 to 1.0, outstanding discrimination (but very rare).

Understory life forms vary considerably in mechanism and timing of competition with tree regeneration (Balandier et al., 2006). We examined the change in graminoid, shrub, and total plant cover with elevation using correlation analysis. Forbs comprised only a small portion of total plant cover (6%) and were not included in the analysis. We inspected model residuals to ensure assumptions of normality, equal variance and independence were not violated.

We graphed the density of seedlings/ha for each age (estimated from counting bud scale scars) for high elevation plots and low elevation plots using a cut-off of 1000 m between elevation groups to examine the age structure of the seedlings sampled in this study. The elevation cut-off of 1000 m was near the median elevation in this study resulting in 10 high elevation plots and eight low elevation plots, with a gap of over 100 m between the two pairs of plots (Table 1).

3. Results

We sampled a total of 253 seedlings a decade following stand-replacing wildfire including 70 well established seedlings (≥ 38 cm in height). The density of tree regeneration varied from entirely absent to an average of 1807 seedlings/ha on individual plots (Table 1), with no seedlings at 6 of the 18 plots on any of the five 78-m² subplots. No well-established seedlings were sampled on the nine plots below 1030 m elevation, whereas eight of the nine plots above 1030 m elevation had well-established seedlings (Table 1). The overall mean seedling density was 362 /ha for all sizes and 98 /ha for well-established seedlings/ha (Table 1). Ponderosa pine regeneration comprised nearly 70% of the sampled seedlings and showed a similar response to overall patterns of regeneration. The average density for ponderosa pine seedlings of any size was 253 /ha and average densities ranged from zero to 1196 /ha on individual plots (Table 1). Well-established ponderosa pine seedlings (≥ 38 cm in height) averaged 77 /ha and average densities on individual plots ranged from zero to 433 /ha (Table 1).

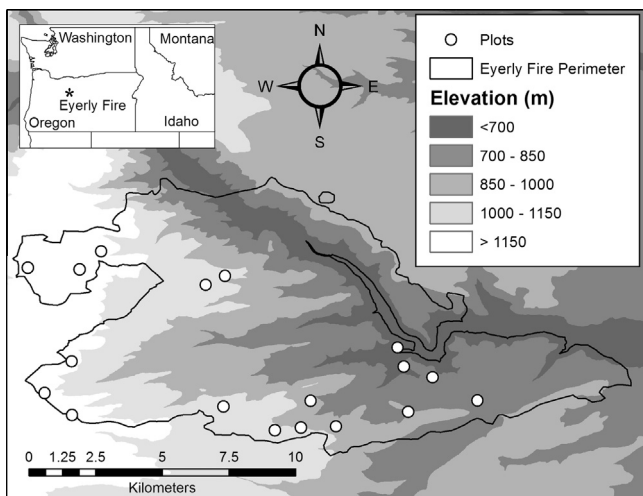


Fig. 1. Map of fire in the northwestern United States and study plots with elevation bands.

Table 2
Results of logistic regression models with elevation as the predictor variable.

Seedling group	Effect size ^a	Std. err.	Wald Chi-Square	P-value	AUC ^b
All species, all sizes	0.007	0.001	24.9	<0.001	0.862
All species, well-established	0.015	0.003	19.8	<0.001	0.951
PP ^c , all sizes	0.009	0.002	25.5	<0.001	0.894
PP ^c , well-established	0.014	0.003	18.3	<0.001	0.940

^a Effect size and standard error are the effects on the odds ratio for a 1 m change in elevation.

^b Area under the curve for the receiver operating characteristic.

^c Ponderosa pine.

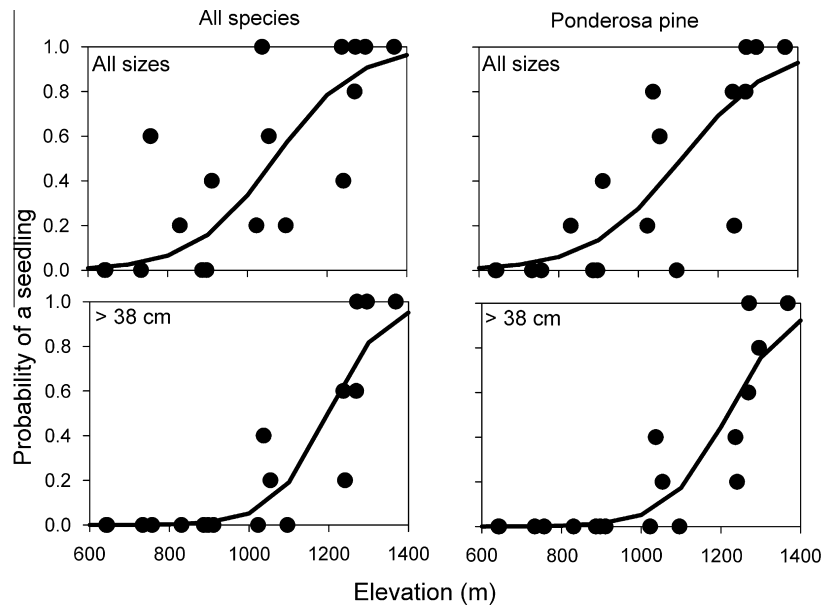


Fig. 2. Modeled logistic regression curves for the probability of seedlings of all sizes and well-established seedlings (≥ 38 cm height) as a function of elevation. Scatterplot points represent the proportion of the five subplots on a plot with at least one seedling.

Elevation had a highly significant effect on the probability of sampling at least one seedling (equivalent to 127 seedlings/ha) on a subplot a decade following wildfire for both all species and ponderosa pine (Table 2). Elevation was also highly significant for well-established seedlings of both all species and ponderosa pine (Table 2). In each case, the probability of sampling a seedling increased sharply with elevation, with large increases over the elevation gradient (Fig. 2). For example, the modeled probability of sampling a seedling of any species or size increased from <5% at the lowest elevations (~600 m) to >90% at the highest elevations (1400 m; Fig. 2). The effects of elevation were even more prominent for well-established seedlings (Fig. 2). The modeled probability of sampling a well-established conifer seedling did not exceed 1% until nearly 900 m elevation, nearly 300 m higher than the lowest plots in this study (Fig. 2). However, the modeled probability of sampling a well-established seedling on a subplot exceeded 95% at the highest elevation plots (Fig. 2).

The area under the curve (AUC) of the receiver operating characteristic (ROC) revealed strong potential for a model with elevation alone to discriminate between randomly selected subplots with and without seedlings (Table 2). This was especially true for well-established seedlings, both of all species and ponderosa pine, where AUC values exceed 0.9 (Table 2), which has been considered outstanding for AUC values in logistic regression (Hosmer and Lemeshow, 2000).

Total plant cover did not vary significantly with elevation in this study ($P = 0.8$; Fig. 3), but understory composition changed from graminoid dominated communities at lower elevations to shrub

dominated communities at higher elevations (Figs. 3 and 5). This change with elevation was highly significant (both P -values < 0.001) for both graminoids and shrubs.

At elevations over 1000 m seedlings sampled 10 years following fire began establishing right after the fire and continued to establish each year until the sample year (Fig. 4). The rapid

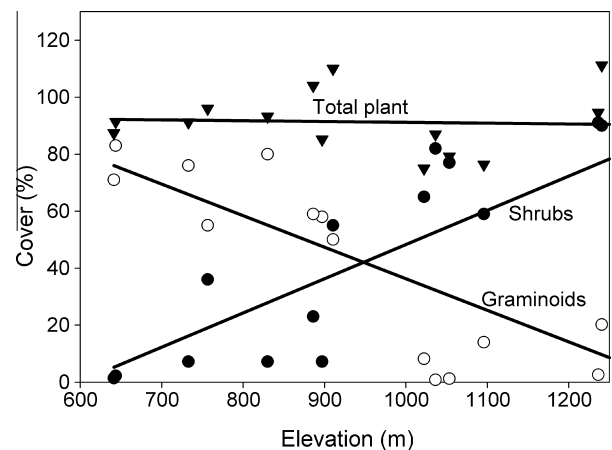


Fig. 3. Relationship of graminoid, shrub, and total plant cover with elevation. Scatterplot points are values from individual plots for graminoids (open circles), shrubs (closed circles) and total plant cover (triangles). Fitted lines are simple linear regression lines.

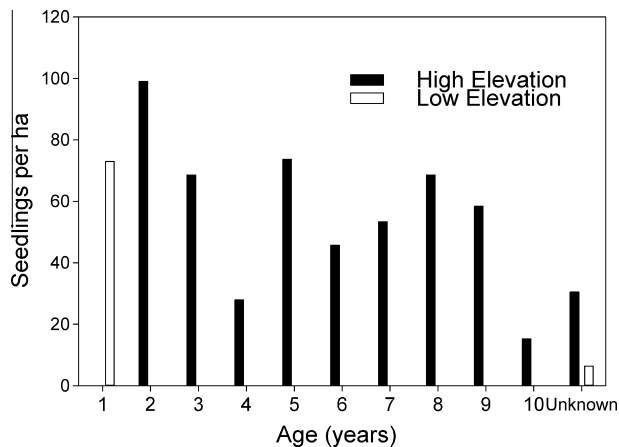


Fig. 4. Age class distribution from counting terminal bud scars at high (>1000 m) and low elevations. Note that *Calocedrus decurrens* and *Juniperus occidentalis* were not included due to difficulties in estimating age from terminal bud scars.

establishment of seedlings following fire at higher elevations resulted in some large seedlings that extended above the shrub layer (Fig. 5a). In contrast, plots below 1000 m were dominated by grasses (Fig. 5b) and had very few seedlings (Fig. 4). Low elevation plots were dominated by 1st (current) year seedlings (Fig. 4), which primarily occurred in clumps (Fig. 5c), suggesting seed dispersal to low elevation plots was ongoing. The lowest elevation plot with any seedlings (Plot 8; Table 1) had only *Juniperus occidentalis* seedlings, which were not included in the age analysis.

4. Discussion

With disturbances likely to serve as catalysts for rapid community change in an era of climate change (Moser et al., 2010; Johnstone et al., 2010; Littell et al., 2010), understanding how effects vary across the landscape is essential for natural resource managers (Harrison et al., 2010). In this study, natural conifer regeneration following stand-replacing wildfire increased strongly across the elevation gradient, which is likely related to increasing moisture availability due to an increase in precipitation and decrease in temperature at higher elevations. This pattern corresponds with studies that have found strong conifer regeneration following stand-replacing fire on more mesic sites (Pausas et al., 2004; Calvo et al., 2008; Shatford et al., 2007; Donato et al., 2009; Moser et al., 2010), and the general trend of higher resilience in more productive or less stressful environments (Larson et al., 2008; Dynesius et al., 2009). In contrast, the lack of regeneration at low elevation sites in this study a decade following wildfire suggests that stand-replacing fire in an era of global climate change could result in delayed regeneration or possible conversion of forest ecosystems to grasslands or shrublands at strongly moisture-stressed sites. While forests sometimes re-establish slowly from unburned edges after fire (Haire and McGarigal, 2010), openings in ponderosa pine forests created by wildfire have persisted for more than a century on harsh south-facing slopes in Colorado, USA (Kaufmann et al., 2000). Similarly, Scots pine in Spain has also shown limited regeneration following wildfire on dry sites, even near edges of intact forest (Vilà-Cabrera et al., 2012). Delays in tree regeneration may lead to increased competition from understory species that more fully occupy the site over time, potentially limiting subsequent regeneration (Schubert, 1974; Roccaforte et al., 2012).

Moisture has been implicated as a key factor influencing post-fire regeneration in other forest types (Hogg and Schwartz, 1997; Calvo et al., 2008; Johnstone et al., 2010; Moser et al., 2010;

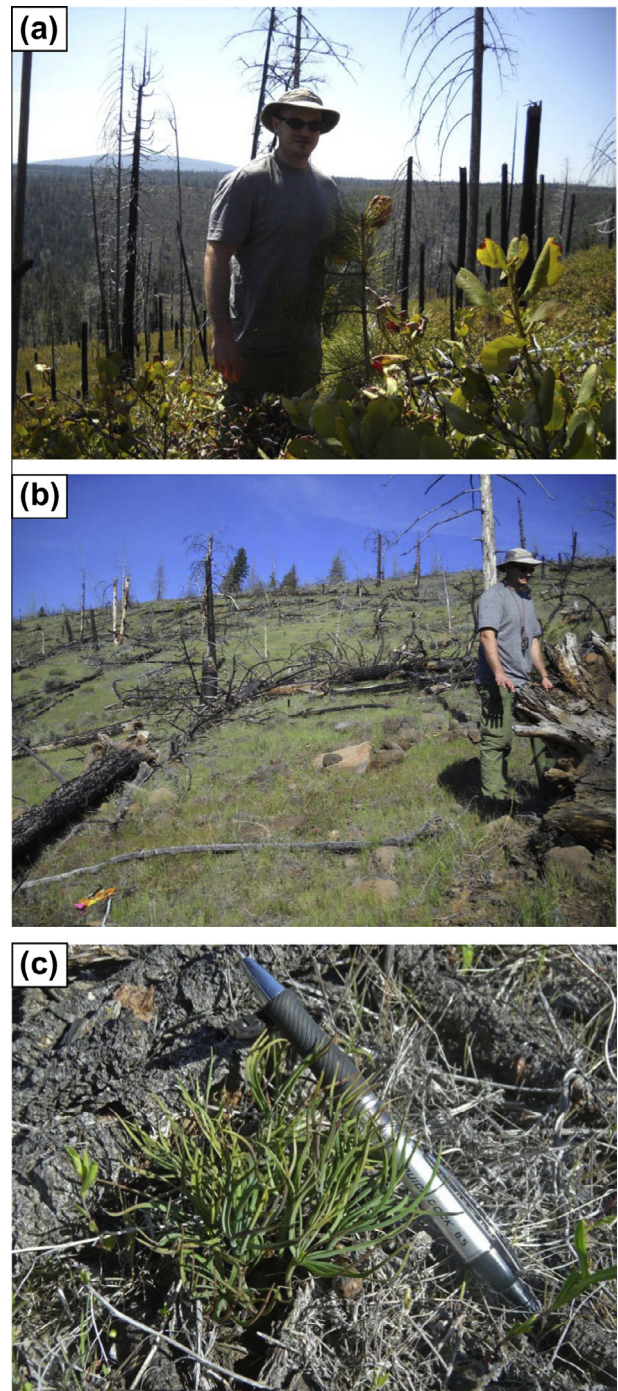


Fig. 5. (a) High elevations plots were dominated by shrubs, but some large seedlings were starting to emerge above the shrub layer, (b) low elevations were dominated by graminoids and had very few large seedlings, and (c) most of the regeneration sampled at lower elevations consisted of first-year seedlings clumps, with pencil included for scale.

Vilà-Cabrera et al., 2012) and has long been recognized as a key factor regulating ponderosa pine regeneration in managed and undisturbed forests (Curtis and Lynch, 1957; Daubenmire, 1968; Puhlick et al., 2012). Tree seedlings in ponderosa pine forests regenerate in the spring, and their taproot must descend more rapidly than the soil desiccates, with low soil moisture limiting the distribution of tree species at low elevations and slope positions with high radiation loads (Daubenmire, 1968). Water availability is critical for seedling survival of high surface temperatures in

undisturbed ponderosa pine forests (Kolb and Robberecht, 1996), which may be even more important after fire with increases in soil temperatures due to removal of vegetation and organic litter and duff layers (Kasischke and Johnstone, 2005). Ponderosa pine can live for centuries, with age reconstruction of an eastern Oregon ponderosa pine forest revealing many trees over 300 years of age (Keen, 1940). Therefore, many of the older pines in this region probably established during the Little Ice Age (~1350 to 1850) when temperatures were cooler, prior to the onset of a warming trend that initiated in the 1920s (Bradley and Jonest, 1993). Continued climate warming will serve to exacerbate moisture limitations and magnify drought effects (Breshears et al., 2005; Littell et al., 2010). These effects may be especially important for regeneration, as large ponderosa pine trees can utilize deep soil water that is recharged by winter precipitation (Kerhoulas et al., 2013).

Ponderosa pine is not serotinous, thus requiring seed dispersal from adjacent areas to reforest stand-replacing wildfires; therefore seed availability has often been considered the limiting factor for regeneration following stand-replacing wildfire (Allen et al., 2002; Bonnet et al., 2005). However, recent genetic reconstructions of isolated ponderosa pine stands suggest multiple seed dispersal events of >10 km at each stand during development (Lesser and Jackson, 2013), raising uncertainty about seed limitations. In contrast, heterogeneity in burn severity may create much shorter distances necessary for seed dispersal throughout much of even very large and severe wildfires. For example, there were few areas more than 400 m from a seed source following the 200,000 ha Biscuit fire (Donato et al., 2009). Even direct application of ponderosa pine seeds following a wildfire in the Southwestern US was not sufficient for stand re-establishment due to high mortality following germination from moisture stress and frost heaving (Reitveld and Hiedman, 1976) further suggesting seed limitation alone may not be responsible for regeneration failures. These results, along with the ongoing recruitment at high elevations and presence of first year seedlings at low-elevations in this study, suggest that site conditions also strongly influence ponderosa pine regeneration following wildfire. The strong pattern across the elevation gradient indicates moisture-stress as a probable key factor limiting regeneration at low elevations, likely due to seedling mortality as documented previously in other forest types (Moser et al., 2010; Lippok et al., 2013).

The composition of understory competitors also varied along the elevation gradient in this study and may have contributed to the observed patterns of tree regeneration. Tree regeneration was relatively frequent despite dense shrub layers at higher elevations. Shrub cover was also positively correlated with tree regeneration in the Klamath Mountains of southwest Oregon and Northern California (Shatford et al., 2007). In undisturbed ponderosa pine forests, shrubs may provide shade that is critical for ponderosa pine regeneration (Keyes et al., 2009). In contrast, grasses, which dominated low elevation plots, start growth earlier and can effectively deplete soil moisture (Reitveld and Hiedman, 1976; Ehle and Baker, 2003). Competition from grasses may have added to the moisture deficit and further negatively impacted regeneration at lower elevations in this study.

Numerous factors may influence tree regeneration (Stein and Kimberling 2003; Pausas et al., 2004; Bonnet et al., 2005), with a suit of factors potentially contributing to the high variability among regeneration densities at high elevations in this study (Table 1). However, elevation alone was strongly predictive of regeneration across the fire despite variation caused by other factors. The multi-year drought in the region at the time of the fire (Schwalm et al., 2012) and extremely strong gradient (with average annual precipitation more than doubling) likely augmented the importance of moisture stress in this study, but also suggest caution in extrapolating of results from this observational study to

sites that vary strongly from the present study site. For example, conifer species with serotinous cones may show strong regeneration across a range of conditions (Rodrigo et al., 2004; Calvo et al., 2008), which may provide adequate regeneration even when post-fire mortality is high (Calvo et al., 2008). Similarly, year-to-year variability in precipitation is important for tree regeneration (Mendoza et al., 2009; Rodriguez-Garcia et al., 2011) and for post-fire recovery in general (Keeley et al., 2005) suggesting other factors may be more important when wet years follow wildfire. However, large fires often occur during multiple years of drought (Robichaud et al., 2006), and even average aridity in the western US by the end of the next century is expected to greatly exceed that found during the drought conditions of this study (Schwalm et al., 2012). Further studies of post-fire regeneration, including experimental manipulations, are needed to confirm patterns found in this study and other recent observational studies (Moser et al., 2010; Lippok et al., 2013) to better understand controls on post-fire regeneration across a range of conditions.

While one seedling per subplot in this study is about equivalent to the pre-fire overstory density measured on our plots (127 seedlings/ha vs. 142 trees/ha pre-fire), the potential for high seedling mortality (i.e., Calvo et al., 2008) suggests caution in extrapolating seedling numbers to predict future forest conditions. However, numerous studies have documented increasing density of ponderosa pine forests in the Eastern Cascades since Euro-American settlement (Weaver, 1959; Swedberg, 1973; Harrod et al., 1999; Hessburg and Agee, 2003), implying historic forests were more open. For example, Harrod et al. (1999) found an average overstory of 50 trees/ha in reconstructions of forest structure prior to Euro-American settlement in ponderosa pine forests of the Eastern Cascades. Furthermore, sparse regeneration may accelerate development of complex forest structure (Donato et al., 2012). This suggests many ecosystem function could be maintained in these dry forests even if subsequent seedling mortality reduces seedling density below stocking levels found prior to wildfire, though further monitoring is needed to determine trajectories of stand development.

Tree regeneration failures following wildfire may greatly reduce ecosystem carbon storage (Kashian et al., 2006; Dore et al., 2012), emphasizing the need for a better understanding of post-fire regeneration dynamics across a range of conditions to guide carbon modeling efforts and the ongoing debate of the potential effects of thinning and burning treatments on carbon storage (i.e., Campbell et al., 2012). The lack of rapid regeneration at low elevations in this study raises questions about findings from recent modeling studies that suggest expansion and increasing carbon storage in dry forests of the Eastern Cascade Range (Rogers et al., 2011) and greater losses of carbon storage in mesic and wet forests relative to dry forests in the Pacific Northwest (Raymond and McKenzie, 2012). How often and how quickly ecosystems return to pre-disturbance conditions is still poorly understood (Dore et al., 2012). While much work remains to be done to understand patterns of post-fire regeneration, a lack of regeneration following high severity fire has frequently been documented for moisture-stressed forests (Barton, 2002; Savage and Mast, 2005; Meigs et al., 2009; Johnstone et al., 2010; Roccaforte et al., 2012; Vilà-Cabrera et al., 2012) suggesting profound effects of stand-replacing wildfire on carbon storage in these forests.

Increasing the capacity for an ecosystem to recover following disturbance (resilience) has emerged as an important strategy for land managers dealing with climate change (Millar et al., 2007; Messier et al., 2013). Restoration treatments utilizing thinning and prescribed burning can effectively reduce fire severity (Pollet and Omi, 2002; Hessburg and Agee, 2003), increasing residual live trees following wildfire. Residual live trees can then provide a seed source that increases the probability of seed availability during

favorable weather years, which is important for regeneration in some ponderosa pine forests (Savage et al., 1996). Furthermore, shading from live trees can facilitate regeneration on the most moisture limited sites in dry forests (Fajardo et al., 2006). The results of this study indicate that dry sites in these forests have less resilience to stand-replacing fire suggesting they are priorities for treatment where maintaining forest is a primary management objective. Alternatively, managers may accept climate change will lead to the loss of forest at some dry low elevation sites and instead facilitate the replacement of forest with native vegetation from drier sites (Fulé, 2008).

5. Conclusions

With predicted increases in fire size and severity with climate change (Westerling et al., 2006; Littell et al., 2010; Rogers et al., 2011), post-fire tree regeneration will be essential for determining ecosystem functions such as wildlife habitat, carbon storage and future disturbance regimes in forested ecosystems. During a multi-year drought in the western US (Schwalm et al., 2012), the resilience of ponderosa pine forests to stand-replacing wildfire varied strongly across a moisture gradient. Relatively mesic high elevation sites in this study had considerably more seedlings, especially well-established seedlings, than low elevation sites, suggesting high elevations may return to forest without management intervention. This concurs with previous studies that found high resilience in productive or less stressful environments (Larson et al., 2008; Dynesius et al., 2009) and strong tree regeneration following stand-replacing wildfire in more mesic forests (Donato et al., 2009; Moser et al., 2010; Lippok et al., 2013). In contrast, results from this and previous studies (Diaz-Delgado et al. 2002; Keeley et al., 2005; Johnstone et al., 2010; Moser et al., 2010; Vilà-Cabrera et al., 2012) suggest that strongly moisture-limited sites are especially susceptible to changes in community composition and ecosystem function in an era of climate change. While further studies on tree regeneration following stand-replacing fire across a broad range of conditions are needed, these results suggest dry sites may be more susceptible to tree regeneration failures following stand-replacing wildfire, which is likely to be exacerbated by strong projected increases in aridity and drought in the coming century (Schwalm et al., 2012). This suggests moisture-stressed sites are priorities for management intervention to increase resilience prior to wildfire or facilitate forest recovery following wildfire where maintaining forest is a management objective.

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