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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 ($\geqslant$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.

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 (Diaz-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).