Persistent effects of fire severity on ponderosa pine regeneration niches and seedling growth

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A B S T R A C T

Several recent studies have documented how fire severity affects the density and spatial patterns of tree regeneration in western North American ponderosa pine forests. However, less is known about the effects of fire severity on fine-scale tree regeneration niche attributes such as understory plant composition and cover, surface fuel abundance, and soil properties, or how these attributes in turn affect regenerating ponderosa pine growth. Using 1-m^2 plots centered on 360 ponderosa pine seedlings that regenerated naturally after the Pumpkin Fire in 2000 in Arizona, we quantified regeneration niche attributes 13 years post-fire and measured their associations with seedling growth 11–16 years post-fire. Plots were established in a) unburned, b) moderate-severity, and two types of high-severity (100% tree mortality) burns, either c) adjacent to residual live forest edges (high-severity edge plots), or d) > 200 m from any residual live trees (high-severity interior plots). We found that all burned plots had greater understory plant species richness, percent cover of forbs, exotic plants and coarse wood, as well as higher soil pH, sand and gravel content, and lower soil clay content compared to unburned plots. High-severity burn plots had the greatest total understory plant and shrub cover, the most herbaceous fine fuel biomass, and tended to have the highest soil nitrogen content compared to other burn severity classes. Ponderosa pine growth (i.e., stem diameter at root collar (DRC) and length of terminal leader) was lowest in the unburned compared to burned plots, and ponderosa pine terminal leader growth was consistently greater in the high-severity edge plots compared to other severities. Finally, niche characteristics such as overstory tree canopy cover (−), soil phosphate (+), and cover of coarse wood (+), forbs (+), and the native grasses, mountain muhly (+) and squirreltail (−), were important explanatory variables of ponderosa pine growth. Exotic plant cover did not have a negative association with ponderosa pine growth. These results suggest that if ponderosa pine seeds can disperse and germinate, and if seedlings can survive the first few critical years after germination, then low overstory canopy cover and abundant forbs or coarse wood may be associated with increased growth rates. Alternatively, forbs may be responding to the same site benefits as the seedling; and abundant forbs, coarse wood, and fine fuels might also put seedlings at increased risk of mortality from subsequent fire, at least until they are taller and more fire resistant.

1. Introduction

Contemporary wildfires in western North American ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests have increased in size and severity, leaving a mosaic of burn severities including larger, contiguous patches of high-severity fire (100% tree mortality) (Dillon et al., 2011; Singleton et al., 2019). Ponderosa pine is a dominant forest type in the semi-arid southwestern (SW) US. The historical fire regime in SW ponderosa pine forests mainly consisted of frequent low- to moderate-severity fire, which left heterogeneous spatial patterns of surviving trees, in contrast to the large, high-severity burn patches created by recent severe fires (Swetnam and Baisan, 2003; Rodman et al., 2016; Singleton et al., 2019). Ponderosa pine readily regenerates in small openings created by low-, moderate-, and even high-severity fire (Malone et al., 2018; Coop et al., 2019). However, ponderosa pine is poorly adapted to regenerate in large patches of high-severity fire

because it does not re-sprout or have serotinous cones, nor does it maintain long-lived soil seedbanks (Oliver and Ryker, 1990; He et al., 2012). Studies conducted 10 + years after high severity fires found reduced ponderosa pine regeneration densities at distances farther (50–200 m) from seed sources (Chambers et al., 2016; Kemp et al., 2016; Owen et al., 2017; Ziegler et al., 2017; Rodman et al., 2020; reviewed in Korb et al., 2019). Although seedling densities were low, some sparse and spatially heterogeneous, natural regeneration occurred after high-severity fire, even > 200 m from residual seed sources (Owen et al., 2017; Ziegler et al., 2017). To conserve and protect naturally recovering ponderosa pines, and to improve restoration success, it is important to understand post-fire regeneration niches and how they influence seedling growth and survival.

The "regeneration niche" characterizes the fine-scale environmental conditions that are suitable for regeneration processes such as seed germination, seedling establishment and growth (Grubb, 1977; Clark et al., 1999). Ponderosa pine requires several conditions to coincide for successful germination and establishment. These conditions include a favorable climate, a well-prepared seedbed, lack of competing vegetation, sufficient soil moisture, as well as protection from fire, browsing animals or other pests (Pearson, 1950; Schubert, 1974; Savage et al., 1996; Feddema et al., 2013; Iniguez et al., 2016; Rodman et al., 2020). If seedlings survive the high-mortality stage in the first few years after germination, niche components including surrounding plant community characteristics, soil properties, and litter conditions may continue to influence growth of established seedlings (Pearson, 1950; Stein and Kimberling, 2003; reviewed in Dey et al., 2019). Both seedling height and size could be important factors in determining the survival of future disturbances, such as subsequent fires (seedling height) or frost-heaving (greater rooting depth), but there may be tradeoffs between growth rates and survival following drought events (Pearson, 1950; Bailey and Covington, 2002; Bigler and Veblen, 2009; Lloret et al., 2011).

Previous research demonstrates variable effects of fire severity on understory plant communities, soils, and fuels, but it is unclear how these effects translate to ponderosa pine niche characteristics or to seedling growth. Fires create canopy gaps that favor exotic (e.g. Alba et al., 2015) or native (e.g. Abella and Fornwalt, 2015) understory plants that could individually or collectively compete with regenerating pines. Alternatively, understory plants may positively influence growth by acting as nurse objects for regenerating pines, especially under stressful site conditions (Fajardo et al., 2006; Sthultz et al., 2007). Conditions that favor understory plant abundance may also favor ponderosa pine establishment and higher growth rates. Low- or moderate-severity fires rarely induce drastic or long-term soil changes (reviewed in Certini 2005). However, severe fires can induce short-term increases in available soil nutrients (Covington et al., 1991; Covington and Sackett, 1992), followed by either long-term reductions (Smith et al., 2017; Ross et al., 2012) or increases in nutrients (Johnson and Curtis, 2001), depending on the amount of combustion, mineralization, and regeneration. Additionally, severe fire can alter soil structure and increase soil temperature and pH, although effects are often short-lived (Ulery et al., 1993; Robichaud, 2000; Huffman et al., 2001; Neary et al., 2012). In addition, fires create canopy openings that enhance understory biomass production, and moderate to high-severity fires increase coarse woody fuel loads which may provide microsites favoring pine growth, but may eventually put seedlings at risk of burning as the wood decomposes and becomes more flammable (Fajardo et al., 2006; Sabo et al., 2009; Roccaforte et al., 2012; Coppoletta et al., 2016). Finally, within high-severity patches, regenerating ponderosa pines near residual forest edges could have higher growth rates than those found in the far interior because of protection from wind and sun (Oliver and Ryker, 1990; Li and Wilson, 1998) and proximity to available microbial symbionts (Nara, 2006; Grove et al., 2019; Owen et al., 2019). As the amount of area burned continues to increase and accumulate, there is a need for understanding the factors that influence seedling growth in order to ensure sustainable forest management practices, including

reforestation and maintenance burning.

The goal of this study was to understand the fine-scale post-fire environmental influences on the growth of naturally regenerating ponderosa pine seedlings. We examined: 1) understory plant, soil and fuel characteristics surrounding regenerating ponderosa pines 13 years post-fire, and 2) what characteristics were associated with regenerating ponderosa pine growth rates 11–16 years post-fire across different fire severities and unburned areas, after the Pumpkin Fire in 2000 near Flagstaff in northern Arizona. The Pumpkin Fire was selected because it had extensive patches of high- and moderate-severity fire, as well as nearby unburned areas. We tested the following hypotheses about niche characteristics and regenerating ponderosa pine growth: H_1: Understory and exotic species cover will be greater in the high-severity burn plots due to the opening of the tree canopy, but understory plant richness will be greatest in moderate-severity burn plots, consistent with the intermediate disturbance hypothesis (Connell, 1978). H_2: Coarse wood cover and herbaceous fine fuel biomass will be greatest in the high-severity burn plots, but soil properties, litter and fine wood cover will be similar among burn severities because of the length of time since fire. H_3: Regenerating ponderosa pine growth rates will be highest in plots with intermediate amounts of residual overstory canopy cover (moderate burn severity), compared to areas without canopy cover (high-severity), or unburned plots, due to the estimated effects on microsite conditions. H_4: Regenerating ponderosa pine growth rates will have a negative correlation with high residual overstory canopy cover (unburned) and high understory cover (burned or unburned) due to competitive interactions, but a positive correlation with coarse wood (high burn severity interior or edge) and available soil nutrients (burned or unburned).

2. Materials and methods

2.1. Study design

We investigated ponderosa pine regeneration niche attributes (understory plant, fuel, and soil characteristics surrounding seedlings) 13 years post-fire and ponderosa pine growth 11–16 years after the Pumpkin Fire that burned in 2000 in northern Arizona. The Pumpkin Fire burned approximately 6,500 ha, including 1,400 ha of high-severity fire on the Kaibab and Coconino National Forests (http://www.mtbs.gov/; see Owen et al. (2019) for map of fire location and burn severity). Our plots ranged from 2,350–2,600 m elevation, with 3–20% slope and mostly southwest aspects. The mean 16-year (2000–2016) post-fire annual water year (October–September) precipitation was 49.1 cm (Western Regional Climate Center (WRCC): https://wrcc.dri.edu, Accessed 2/15/2019; Fig. S1) and the mean temperature was 7.2 °C (Prism Climate Group: http://prism.oregonstate.edu/, Accessed 10/7/2016). This region receives most of its annual moisture from late-summer rains that typically occur July–August and from winter precipitation. Soils were derived from basalt and ranged from shallow to moderately deep, gravelly sandy to clay loam (WebSoil Survey: http://websoilsurvey.nrcs.usda.gov. Accessed 10/5/16).

We used Monitoring Trends in Burn Severity (MTBS, 2013) maps, ArcGIS 10.1 (ESRI, 2012), and field validation to randomly select three sites within each of four burn severity classes: "unburned," "moderate-severity," "high-severity edge," and "high-severity interior." A single 4-ha (200 × 200 m) plot was established at each site, for a total of twelve 4-ha plots. Unburned plots were not burned in a wildfire or managed fire for the past 50 + years (Crouse, 2019). Unburned areas had high tree densities, ranging from 560 to 1160 trees ha^{-1}. Moderate-severity plots had a spatial heterogeneity of post-fire surviving trees ranging from 120 to 490 trees ha^{-1}, including small patches of high-severity fire < 1 ha in size. Both high-severity edge and interior plots had 100% tree mortality from the wildfire, but high-severity edge plots were established adjacent to forest edges or residual live trees whereas high-severity interior plots were established where no surviving trees were found within at least 200 m from the plot boundaries (see Owen et al.

(2019) for site map, plot photographs and additional site selection criteria).

2.2. Understory plant composition

To test our first hypothesis that burn severity will influence understory cover and species richness, we measured plant cover variables within 1-m^2 (1- × 1-m) quadrats surrounding 30 single ponderosa pine seedlings that naturally regenerated post-fire in each of the 4-ha plots, totaling 360 quadrats. These focal seedlings were randomly selected from the population of seedlings in the plots, which had been spatially mapped during a previous study (Owen et al., 2017). Understory plant cover was measured in August–September 2013. Total plant, life form (forb, graminoid, shrub, and regenerating ponderosa pine), exotic plant, and individual plant species cover were estimated by eight cover classes. We used the following cover classes: 0%, < 1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, and > 95% in each 1- × 1-m frame, a method modified from Daubenmire (1959). We used the midpoints of the cover classes to convert estimates to quantitative values. Plants were identified to species in the field or collected, identified and stored at the USDA Rocky Mountain Research Station (RMRS) herbarium in Flagstaff, Arizona. Scientific nomenclature followed the USDA PLANTS Database (https://plants.usda.gov), and plant nativity followed the Flora of North America (http://beta.floranorthamerica.org). We also determined plant species richness in each quadrat, and estimated percent overstory canopy cover (averaging 5 readings directly over each quadrat) using a vertical densitometer (Geographic Resource Solutions, Arcata, California, USA).

We used generalized linear mixed models (GLMMs) in SAS 9.4 (SAS PROC GLIMMIX, 2017) to test for the effects of fire severity on understory plant cover and richness variables. Fire severity was a fixed effect and site was a random effect. Also included was a residual random effect that modeled heteroscedasticity between treatment levels. We used a beta distribution for proportion of plant cover values, and a negative binomial distribution for richness. Beta distributions that included many zero values were transformed similar to Smithson and Verkuilen (2006). If significant differences were found, we used the post hoc Tukey – Kramer HSD test on least-squares means for subsequent pair-wise comparisons (Kramer, 1956). We present all results as estimated model means with 95% confidence intervals, but true means and standard errors are presented in the supplementary material.

2.3. Surface fuel and soil characteristics

To test the second hypothesis that increasing fire severity will increase surface fuels, we characterized surface fuel cover in the 1-m^2 quadrats surrounding regenerating ponderosa pines by fuel types, 13 years post-fire. We measured percent cover of litter (dead non-woody plant material) together with fine wood (dead wood < 7.62 cm diameter), coarse wood (dead wood ≥ 7.62 cm diameter), stumps (bases of fallen snags), rock, and bare ground cover similar to plant cover variables above. We distinguished between fine and coarse wood using a go/no-go gauge (Brown, 1974). We examined the effects of burn severity on the proportion of fuel cover using GLMMs with beta distributions, fire severity as a fixed effect, and site as a random effect. Finally, we calculated the percentage of quadrats with seedlings growing near coarse wood or stumps out of the total quadrats in each burn severity.

To test the hypothesis that high-severity burns will have the greatest herbaceous fine fuel biomass, we destructively measured it in July 2016 (16 years post-fire) near each quadrat. We measured fine fuel biomass by clipping all live herbaceous plants at ground level in 0.25-m^2 circular frames, at least 1 m east of each seedling quadrat, in a location that best replicated the conditions in the plot. The biomass samples were dried in an oven at 70 °C for 3 days and weighed to the nearest 0.1 g (Moore et al., 2006). We analyzed biomass with respect to fire

severity using a GLMM with a gamma distribution and with fire severity as a fixed effect and site as a random effect, but we found no heteroscedasticity between treatment levels so that term was not included, and family-wise error rate was adjusted for using the Tukey-Kramer method (Kramer, 1956; SAS 9.4; SAS PROC GLIMMIX, 2017).

To explore differences in regeneration niche soil properties among severity classes, we measured the physical and chemical properties of soil from each quadrat in September 2013. Three mineral soil (0–15 cm) samples were collected with a soil corer (3 cm diameter × 15 cm length) within the 1 × 1-m frame from each seedling plot and composited. Soil pH was measured following the method of Carter (1993) with an Orion 550A pH meter (Thermo Electron Corporation, Beverly, MA). Percent silt, sand, and clay were determined by particle size analysis with a hydrometer, similar to Bouyoucos (1962), and percent gravel was determined by sieving and weighing the > 2 mm portion of the sample. Soil aggregate stability (a measure of erodibility) was determined in the field for 5-cm subsurface soils using a soil stability kit (Synergy Resource Solutions, Inc., Bozeman, MT). Soil aggregates were ranked on an ordinal scale of 0 (least stable) to 6 (most stable) ('slake scores') (Herrick, 2000). Percent total soil carbon and nitrogen were measured on a C/N analyzer (ThermoQuest EA Flash 1112, Milan, Italy). Finally, the concentrations of nitrate, ammonium and phosphate (NO_3^-, NH_4^+, PO_4^{3-}) were measured on a Lachat AE Flow Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA) using methods described in Lachat Instruments, Inc. (1990, 2003, 2007). We analyzed silt, sand, clay, gravel, and nutrient concentrations using GLMMs with beta distributions, and soil pH using GLMMs with gamma distributions, with fire severity as a fixed effect and site as a random effect. We analyzed soil aggregate stability (categorical response data 0–6) using an ordered logit model, similar to Agresti (2013). We contrasted severity classes and used Tukey-Kramer comparisons with site as a random effect, as described above.

2.4. Regenerating ponderosa pine seedlings

Tree or seedling age can influence growth rates (Weiner and Thomas, 2001; Johnson and Abrams, 2009); therefore, we estimated regenerating ponderosa pine age by counting branch whorls on each trunk, similar to Shatfet et al. (2007), so that we could include age as a covariate in our analyses. To verify accuracy in the whorl count estimates, we destructively sampled 26 seedlings of various whorl counts outside of our plots and determined pith age by counting growth rings. We compared whorl counts to pith age using multi-response permutation procedures similar to Haire and McGarigal (2010). We found a significant difference between whorl counts and pith age (F = 9.68; p = 0.03), with whorl counts being on average 1.5 years lower than pith age. Therefore, we added 1.5 years to our whorl counts so they would be similar to pith age. It was difficult to find seedlings on the unburned plots that established after the fire, and unburned seedling whorl counts were harder to estimate because some had stunted growth forms, increasing uncertainty of ages compared to seedlings from burned plots.

To test the third hypothesis that regenerating ponderosa pines will have the highest growth rates in moderate-severity burn plots compared to unburned and high-severity burn plots, we measured seedling growth in each quadrat. In September 2016, we measured diameter at root collar (DRC), total height, and annual growth (the length of annual growth of the terminal leader from 2011 to 2015) on regenerating ponderosa pines in each quadrat. We measured DRC at ground level, similar to McPherson et al. (2016). We tested for differences in total height and DRC among severity classes using GLMMs with gamma distributions, with fire severity as a fixed effect, site as a random effect, and estimated seedling age as a covariate. We tested for differences in annual terminal leader growth among severity classes and years, and severity class × year interactions using a repeated measures GLMM with fire severity as a fixed effect and site as a random effect, and a

Table 1

Model estimated means (lower, and upper 95% confidence intervals) for percent canopy cover of total overstory trees, and understory plant, bare ground, different life forms (tree, shrub, forb, graminoid), exotic plants, and species richness among burn severity classes, computed from GLMMs. Different letters indicate significant differences among burn severity classes.

Plant cover and richness	Unburned	Moderate-severity	High-severity edge	High-severity interior	F^{TRT}	p^{TRT}
Overstory tree cover (%)	16.1[a] (8.1, 29.1)	8.9[b] (4.5, 15.6)	0[c] (0, 0)	0[c] (0, 0)	13.53	< 0.01*
Total plant cover (%)	80.6[a] (74.0, 85.9)	84.9[a] (79.4, 89.2)	89.1[b] (84.7, 93.3)	90.4[b] (86.5, 93.3)	8.97	< 0.01*
Bare ground cover (%)	4.9[a] (3.5, 6.9)	2.8[ab] (1.7, 4.3)	1.5[b] (0.8, 2.8)	1.2[b] (0.6, 2.3)	6.87	0.01*
Regenerating ponderosa pine cover (%)	37.5[a] (27.3, 48.9)	40.7[ab] (30.0, 52.4)	57.2[c] (45.5, 68.2)	44.3[b] (30.0, 52.4)	8.27	< 0.01*
Shrub cover (%)	0.1[a] (0.0, 4.3)	6.3[b] (8.6, 33.9)	18.2[c] (21.9, 68.7)	23.9[c] (2.9, 76.4)	11.2	< 0.01*
Forb cover (%)	29.7[a] (7.2, 69.7)	59.6[b] (20.9, 89.2)	57.8[b] (19.7, 88.4)	55.7[b] (18.3, 87.6)	16.92	< 0.01*
Graminoid cover (%)	70.2[a] (64.4, 75.4)	65.7[a] (60.5, 71.1)	58.6[b] (52.6, 64.4)	66.7[a] (60.8, 72.1)	2.78	0.04*
Exotic plant cover (%)	0.2[a] (0.0, 3.6)	12.5[b] (8.9, 17.4)	34.9[c] (29.1, 41.3)	35.2[c] (29.4, 41.5)	16.47	< 0.01*
Total Richness (species m^{-2})	4.9[a] (3.1, 7.6)	7.9[b] (4.9, 12.7)	8.5[b] (5.2, 13.7)	9.0[b] (5.5, 14.6)	39.3	< 0.01*

gamma distribution, and included age as a covariate.

To test the fourth hypothesis that regenerating ponderosa pine growth is influenced by niche variables, we used GLMM to determine the relationship between niche characteristics and ponderosa pine DRC and annual growth rates. Predictor variables included percent overstory canopy cover, soil nutrients (NO_3^-, NH_4^+, PO_4^{3-}), soil pH and percent clay and gravel content, coarse wood, forb, graminoid, shrub, exotic and major species cover (> 10% cover). Response variables included DRC and average 5-year growth rates, with seedling age as a covariate. We used GLMM with fire severity as a fixed effect, site as a random effect, gamma distributions and determined 95% confidence intervals in SAS 9.4 (SAS PROC GLIMMIX, 2017).

3. Results

3.1. Understory plant composition

Regeneration niches differed among severity classes due to differences in overstory tree canopy cover as well as differences in cover of dominant understory species (Table 1; also see Table S1). Overstory tree canopy cover was absent in both types of high-severity burn plots, and lower in the moderate-severity compared to the unburned plots (Table 1). Additionally, we visually observed that seedlings in unburned plots were mostly found in localized openings with lower canopy cover. Regeneration niches in burned plots were characterized by higher forb, higher shrub, and exotic plant cover, and differences in some dominant species cover compared to unburned plots (Tables 1 and 2). All plots had high total plant cover because they included the cover of the central ponderosa pine seedling, but high-severity burn plots had slightly higher total plant cover and 2–3 times greater shrub cover than moderate-severity or unburned plots. Graminoid cover was lowest in the high-severity edge plots. Ponderosa pine seedling cover was greatest in the high-severity edge plots, and exotic plant cover was lowest in the unburned plots (Table 1). All burn types differed from unburned areas in terms of dominant species cover that included the native forbs *Lupinus argenteus* Pursh (silvery lupine), *Bahia dissecta* (A. Gray) Britton (ragleaf bahia) and *Oxytropis lambertii* Pursh (purple locoweed) and the

native grass *Elymus elymoides* (Raf.) Swezey (squirreltail) (Table 2; also see Table S2). *Mahonia repens* (Lindl.) G. Don (creeping barberry; a native shrub) cover was greatest in the high-severity interior plots and intermediate in the high-severity edge compared to the moderate-severity and unburned plots. Finally, higher exotic plant cover on burned plots was dominated by *Bromus tectorum* L. (cheatgrass, an exotic grass), which was absent from unburned plots (Tables 1 and 2).

Plant species richness was lowest in the unburned plots, but similar among other burn severities, contrary to our first hypothesis (Table 1; also see Table S1). We found a total of 82 understory plant species and they were predominantly native and perennial (Table S3). Three species were found only in unburned plots, nine species were found only in moderate-severity plots, five species were found only in high-severity edge plots, and eight species were found only in high-severity interior plots. We found 11 exotic species, mostly in the burned plots. The most common exotic species found in the burned plots were cheatgrass, *Taraxacum officinale* F.H. Wigg. (common dandelion), and *Tragopogon dubius* Scop. (yellow salsify) (Table S3).

3.2. Surface fuel and soil characteristics

Coarse wood cover was similar between all high- and moderate-severity burn plots, but higher in all burned plots compared to the unburned plots, partially supporting our second hypothesis (Fig. 1A). We found that most regenerating ponderosa pines in high-severity burned edge (83%) and interior (77%) quadrats were growing adjacent to coarse wood or stumps, compared to moderate-severity (57%) or unburned (8%) plots (percent of quadrats that contained coarse wood or stumps). The cover of litter plus fine wood, and the cover of rock, were similar among severity classes, but stump cover was higher in all burned compared to unburned plots (Table S4).

Herbaceous fine fuel biomass near ponderosa pine regeneration niches was lowest in the unburned plots, intermediate in moderate-severity plots, and greatest in high-severity burn plots, supporting our second hypothesis (Fig. 1B). Herbaceous fine fuel biomass was three times higher in the high-severity plots, and twice as high in the moderate-severity plots compared to the unburned plots (Fig. 1B).

Table 2

Model estimated means (lower, and upper 95% confidence intervals) for dominant understory plant species cover (> 10% cover in one severity class) among severity classes, computed from GLMMs. Different letters indicate significant differences among severity classes. ◆Indicates non-native, exotic species.

Dominant understory plant species cover (%)	Unburned	Moderate-severity	High-severity edge	High-severity interior	F^{TRT}	p^{TRT}
Bahia dissecta	0.2[a] (0.0, 3.1)	5.4[b] (0.3, 56.3)	14.0[c] (0.6, 81.9)	5.6[b] (0.3, 57.4)	10.42	< 0.01*
Bromus tectorum◆	0.0[a] (0.0, 0.1)	10.0[b] (2.4, 33.3)	13.4[c] (3.1, 42.7)	22.0[c] (4.9, 59.5)	5.83	< 0.01*
Elymus elymoides	1.3[a] (0.3, 5.1)	23.7[b] (6.1, 59.8)	15.1[b] (3.8, 44.0)	13.1[b] (3.4, 39.3)	12.1	< 0.01*
Festuca arizonica	49.7[a] (42.4, 56.9)	30.19[b] (21.6, 40.3)	19.3[b] (9.6, 34.9)	27.7[b] (19.7, 37.4)	7.49	< 0.01*
Lupinus argenteus	3.4[a] (0.2, 37.9)	8.5[b] (0.4, 67.8)	13.9[b] (0.6, 80.0)	9.5[b] (0.5, 70.9)	6.66	0.01*
Mahonia repens	0.0[a] (0.0)	0.1[a] (0.0, 14.0)	3.4[b] (0.0, 95.4)	6.7[c] (0.0, 97.7)	17.91	< 0.01*
Muhlenbergia montana	45.1 (29.5, 61.8)	43.4 (29.4, 58.6)	33.4 (16.7, 55.5)	11.2 (1.5, 51.3)	1.39	0.25
Oxytropis lambertii	0.5[a] (0.1, 16.8)	33.6[b] (15.5, 58.4)	29.8[b] (11.9, 57.0)	34.6[b] (14.1, 63.0)	4.86	< 0.01*

A) Percent coarse wood cover

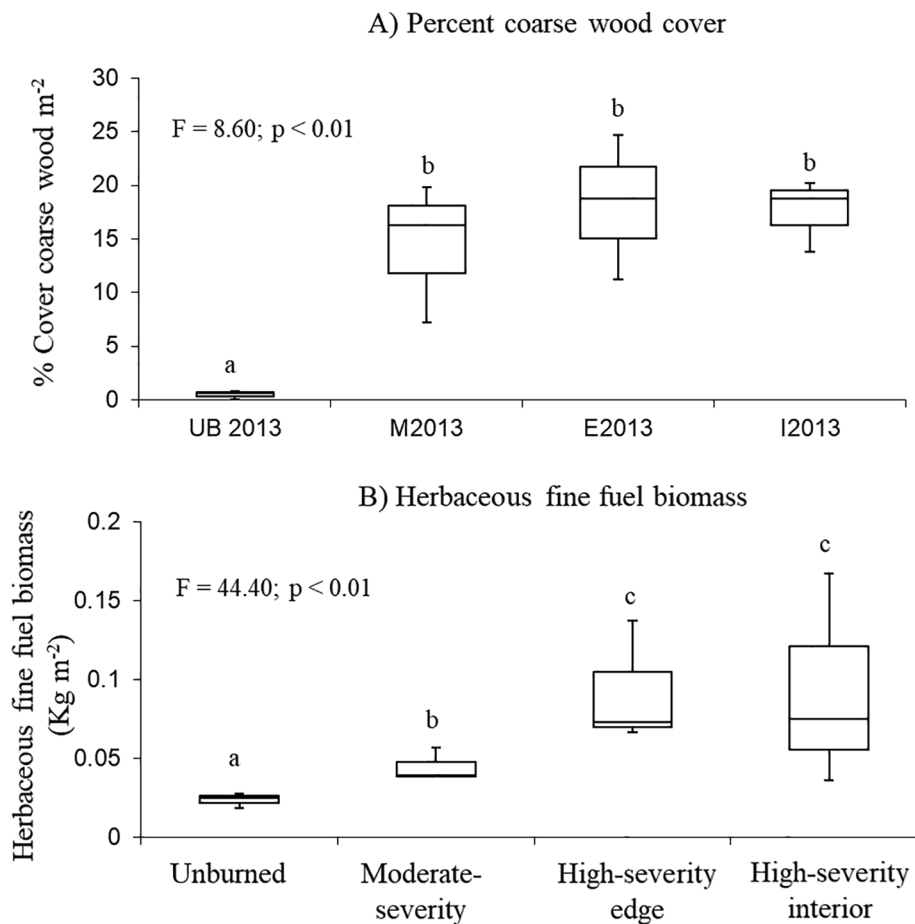## B) Herbaceous fine fuel biomass

Fig. 1. A) Percent coarse wood cover was lowest in the unburned compared to all burned plots. B) Herbaceous fine fuel biomass near regenerating ponderosa pines was lowest in the unburned plots, intermediate in moderate-severity, and greatest in both high-severity edge and interior plots. Boxplots represent the variation between sites and span the first to the third quartile. A center line represents the median, and the "whiskers" above and below the box represent the minimum and maximum values. Model estimated means (lower, and upper 95% confidence intervals) are shown in Table S6.

Table 3
Model estimated means (lower, and upper 95% confidence intervals) soil texture from 0 to 15 cm mineral soil, computed from GLMMs. Sand, silt and clay make up 100% of the < 2 mm portion of the soil sample, and gravel content is a percentage of the entire sample collected. Different letters indicate significant differences among severity classes.

Soil property	Fire severity				F	p
	Unburned	Moderate	High-edge	High interior		
Gravel (% > 2 mm)	19.3[a] (14.3, 25.6)	27.4[c] (21.6, 35.4)	24.2[b] (18.1, 31.7)	28.9[c] (21.8, 37.2)	23.2	< 0.01*
Sand (% < 2 mm)	28.0[a] (23.5, 33.1)	31.2[b] (26.2, 36.6)	31.3[b] (26.4, 36.8)	34.3[c] (29.0, 39.9)	7.3	< 0.01*
Clay (% < 2 mm)	28.5[a] (26.2, 30.9)	27.0[b] (24.7, 29.3)	26.9[b] (24.6, 29.2)	23.4[b] (21.3, 25.6)	7.1	< 0.01*
Silt (% < 2 mm)	43.8 (40.5, 47.2)	41.8 (38.7, 45.1)	41.7 (38.6, 45.0)	42.4 (38.7, 45.1)	0.6	0.62

We found that soil properties differed among severity classes, contrary to our second hypothesis (Table 3; see also Table S5). Percent total C and N were greatest in the high-severity interior burn plots, concentrations of soil NO_3^- and NH_4^+ tended to be higher with increasing burn severity, soil pH was lowest in the unburned plots, and the concentration of soil PO_4^{3-} was similar among severity classes (Table S5). Soil texture was relatively similar across severity classes, with all classified on the interface between loam and clay loam. However, statistical differences were detected in sand content, ranging from ~28% in unburned plots to ~34% in high-severity interior plots, with intermediate levels in high-severity edge and moderate-severity plots. In addition, soil clay content, ranging from ~23 to 28%, was higher in the unburned plots compared to the burned plots (Table 3). Gravel content also differed, ranging from ~19% in unburned plots to ~27% in moderate-severity and ~29% in high-severity interior plots, with intermediate levels (~24%) in high-severity edge plots (Table 3). Percent silt content was similar among severity classes. Finally, soil stability was variable within each of the burn severity classes, with most scores

falling within an intermediate stability range, but similar among severity classes (Fig. S2).

3.3. Regenerating ponderosa pine seedlings

Regenerating ponderosa pines had high survival rates throughout the course of our study; only 4 of the 360 seedlings in our study died between 2013 and 2016 (three in high-severity interior and one in moderate-severity burn plots; estimated ages were 5–6 years old). The estimated year of establishment for post-fire regenerating seedlings ranged from 2001 to 2008 with the majority establishing in 2005, the wettest water year of the study (Fig. S3).

Ponderosa pine growth varied among severity classes and years but was generally highest in the high-severity edge plots, contrary to our third hypothesis (Fig. 2A, B, and C). Ponderosa pine DRC was greatest in the high-severity burned plots, intermediate in moderate-severity, and lowest in the unburned plots (Fig. 2A). Ponderosa pine seedlings were taller in the high-severity edge plots compared to other severity
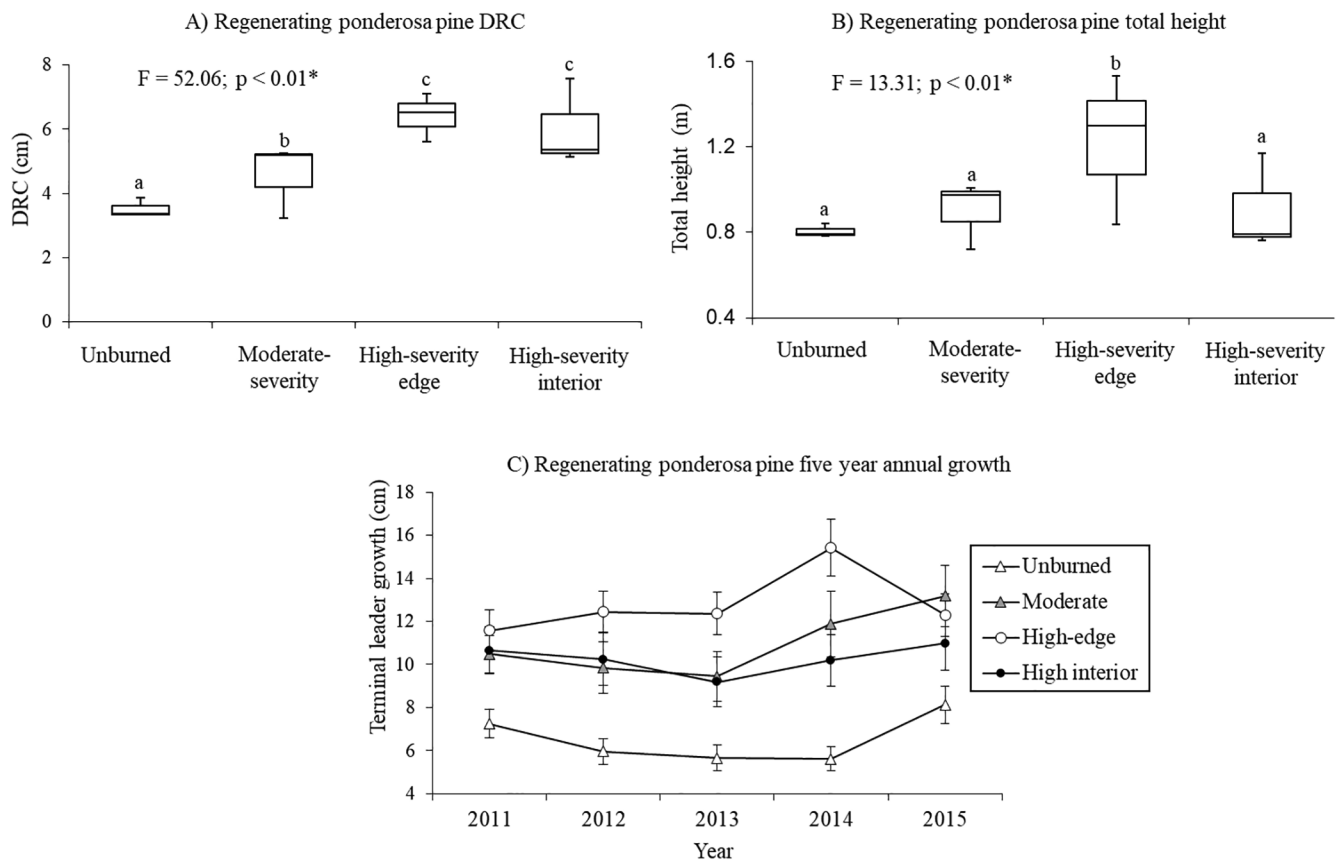
Fig. 2. A) Regenerating ponderosa pine diameter at root collar (DRC) was lowest in the unburned plots, intermediate in moderate-severity, and greatest in both high-severity edge and interior plots. B) Regenerating ponderosa pine total height was higher in high-severity edge plots compared to other severity classes. C) Regenerating ponderosa pine terminal leader annual growth varied among severity class and year but was mostly highest in the high-severity edge plots. Ponderosa pine DRC, total height, and leader growth estimated for 2011–2015 were measured in 2016. Boxplots in A and B represent the variation between sites and span the first to the third quartile. A center line represents the median, and the "whiskers" above and below the box represent the minimum and maximum values. Model estimated means (lower, and upper 95% confidence intervals) are shown in Table S6.

classes, even though seedlings were on average older in unburned plots (Fig. 2B). We found significant severity class × year interactions (F = 2.40; p < 0.01) for terminal leader growth, therefore we analyzed groups separately. Seedlings on unburned plots had the lowest terminal leader growth among the plot types (Fig. 2C). Ponderosa pine terminal leader growth in 2011 (F = 9.06; p < 0.01) was higher in all burned compared to unburned plots (Fig. 2C). Ponderosa pine terminal leader growth in 2012 (F = 12.87; p < 0.01) was greatest in the high-severity plots, and in 2013 (F = 13.41; p < 0.01), and 2014 (F = 17.96; p < 0.01) was greatest in high-severity edge plots, intermediate in both moderate- and high-severity interior plots, and lowest in the unburned plots (Fig. 2C). Finally, ponderosa pine terminal leader growth in 2015 (F = 6.68; p < 0.01) was greatest in the high-severity edge and moderate severity plots and lowest in the unburned plots.

Some niche characteristics were correlated with ponderosa pine seedling growth as we expected (Figs. 3 and 4). For example, there was a positive correlation between ponderosa pine DRC and surrounding percent cover of coarse wood, forbs and mountain muhly, and a positive trend with the concentration of soil phosphate (Fig. 3). Ponderosa pine terminal leader annual growth over 5 years from 2011 to 2015 was partially explained by positive correlations with surrounding percent cover of coarse wood, forbs, and mountain muhly, and soil PO_4^{-3}, and a negative correlation with overstory tree canopy and *E. elymoides* cover (Fig. 4). We also found a trend of positive correlation between ponderosa pine growth rates and percent shrub cover (Fig. 4). Ponderosa pine DRC and growth rates were not correlated with soil pH, clay content, NH_4^+, or NO_3^-, surrounding exotic or other dominant

understory species cover, contrary to our hypothesis (all p > 0.1).

4. Discussion

4.1. Understory plant communities

We found that a wildfire with large, high-severity burn patches had decadal-scale impacts on understory plant composition surrounding naturally regenerating ponderosa pines. Both moderate- and high-severity burn plots had mostly native, diverse and productive understory plant communities, similar to other long-term studies after large, mixed-severity wildfires (Abella and Fornwalt, 2015; Gibson et al., 2016). All burn plots had greater species richness than unburned plots similar to other studies that have shown that understory species richness and productivity can increase with moderate-severity burns (Abella and Fornwalt, 2015; Burkle et al., 2015), and can either increase (Kuenzi et al., 2008; Shive et al., 2013) with high-severity burns, or remain similar between different burn severities (Crawford et al., 2001), in mainly ponderosa pine-dominated forests. The trend of greater forb and shrub cover on our high-severity burn plots was also similar to findings in previous studies (Barton, 2005; Shive et al., 2013; Abella and Fornwalt, 2015). Evidence suggests that severe burning could either lead to a dominance in shrub communities (Savage and Mast, 2005; González-De Vega et al., 2016), or regenerating pine can establish beneath or near shrubs and eventually overtop them (McDonald, 1990; Vankat, 2013). Finally, most of the exotic plant species found on our plots are not considered long-term threats to native communities or ecological function, except for *Bromus tectorum*
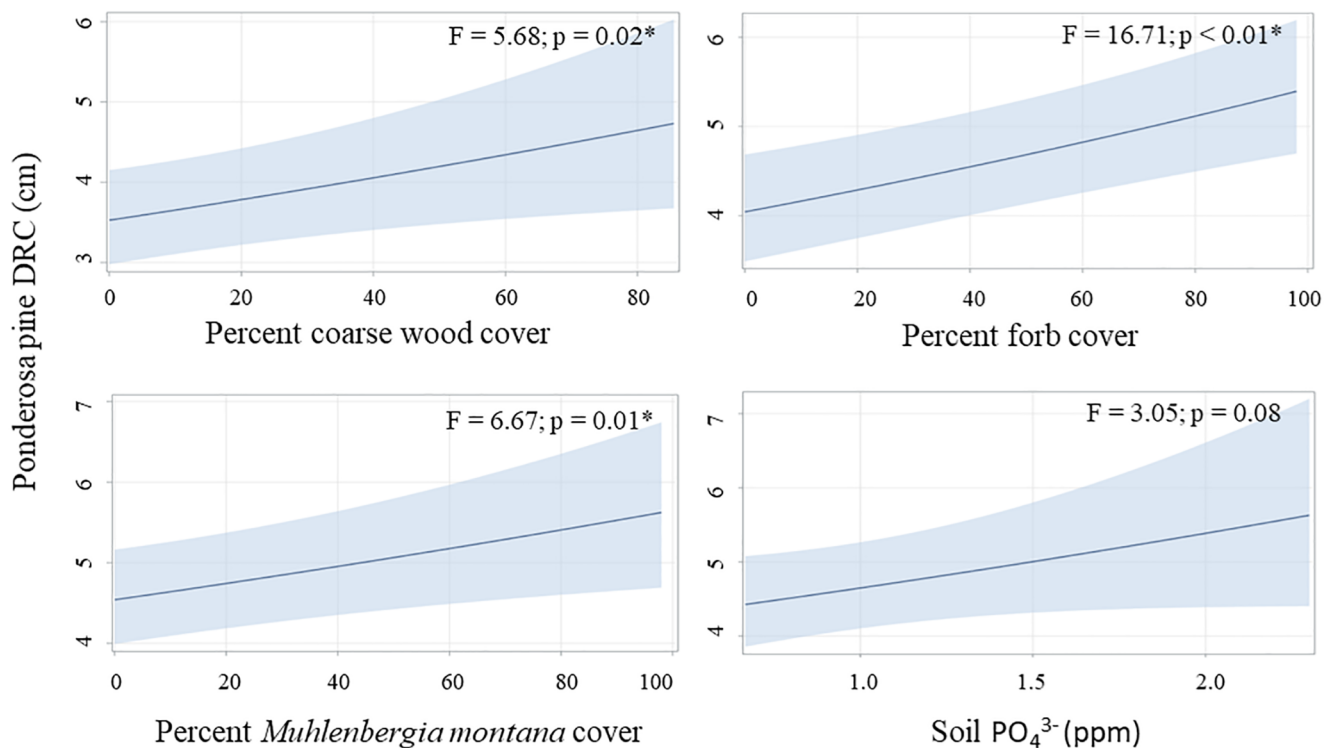
Fig. 3. DRC was partially explained by a positive correlation with surrounding coarse wood, forb and mountain muhly (*Muhlenbergia montana)*, cover. There was a trend for a positive correlation between DRC and the concentration of soil phosphate. GLMM fit is shown with 95% confidence limits.

(cheatgrass) (Sieg et al., 2003; Keane et al., 2008; Fornwalt et al., 2010). Cheatgrass is a highly invasive annual grass that can outcompete native plant species (Young et al., 1987; Keane et al., 2008). We did not find evidence that ponderosa pine growth was impacted by surrounding shrub or exotic species, but forb cover had a positive correlation with ponderosa pine growth.

Both forb and *Muhlenbergia montana* (mountain muhly) cover were important, positively correlated variables for regenerating pine growth, providing evidence for facilitation, or for similar habitat preferences, yet surrounding squirreltail cover was negatively correlated with ponderosa pine growth. Mountain muhly along with squirreltail and *Festuca arizonica* (Arizona fescue) were the most dominant grasses across burn severity classes, but mountain muhly cover was lowest in the high-severity burn plots, and squirreltail cover was lowest in the unburned plots. Mountain muhly is more shade-tolerant than Arizona fescue and squirreltail, and a less-aggressive competitor than Arizona fescue (Pearson, 1942; Larson and Schubert, 1969). There could be a positive interspecific interaction between mountain muhly and regenerating ponderosa pines on sites with some tree canopy (Pearson, 1942). *Muhlenbergia* spp. and forb cover in other studies had positive effects on ponderosa pine seedling densities and survival (Pearson, 1942; Puhlick et al., 2012; Ouzts et al., 2015). Similarly, forb cover may have a positive interspecific interaction with regenerating ponderosa pines in the high-severity burns, providing some protection from wind, sun and frost. This interaction is consistent with the "stress gradient hypothesis," which predicts that with increasing abiotic stresses, facilitative interactions among plants are stronger than competitive interactions, and some species can mitigate stressors to create more favorable habitat by providing some protection from wind and sun (Bertness and Callaway, 1994). Alternatively, the co-occurrence of seedlings with forbs and mountain muhly may simply be due to better conditions for all understory plants in places with low overstory tree canopy cover. Even in the unburned plots, it appeared that regenerating ponderosa pines were mainly found under small canopy openings within the dense forest. Finally, the negative correlation between squirreltail cover and

ponderosa pine growth may be linked to the fact that squirreltail, due to its C3 photosynthetic pathway with growth early in the growing season (Jones, 1998), is a more effective competitor for water than established pine seedlings. This competitive advantage of squirreltail, especially during droughty conditions typical in the spring in Arizona, may contribute to lower pine growth rates. However, Elliot and White (1987) found in a controlled experiment that squirreltail, in contrast to other graminoids, did not reduce growth of newly planted ponderosa pine seedlings. More research is needed to understand this competitive relationship.

4.2. Fuel and soil characteristics

Severe fire led to increases in coarse wood, consistent with other studies (Roccaforte et al., 2012; Bassett et al., 2015), and ponderosa pine growth had a positive correlation with coarse wood cover. We expected coarse wood to have a positive effect on regenerating ponderosa pine growth by providing extra moisture or protection from wind and sun (Sánchez Meador and Moore, 2010; Castro et al., 2011). Flathers et al. (2016) also found that young (1–2 years old) ponderosa pine seedling density and diameter were positively associated with litter cover. Coarse wood can improve the probability of ponderosa pine seedling survival during drought conditions (Hill and Ex, 2020); however, increased coarse wood and fine fuel biomass adjacent to regenerating pine seedlings would also put them at increased risk of mortality from surface fires during dry conditions when coarse wood could contribute to high fire intensity, until the seedlings are taller and more fire resistant (Estes et al., 2012; Westlind and Kerns, 2017). Seedlings were on average < 2 m tall on all severity classes from our study, but if seedlings on the high-severity plots continue to increase in height and diameter, it may help them survive a subsequent low-severity fire (Gaines et al., 1958; Bailey and Covington, 2002; Battaglia et al., 2009).

We expected similar soil properties among severity classes because of the length of time since fire, comparable to studies in ponderosa pine
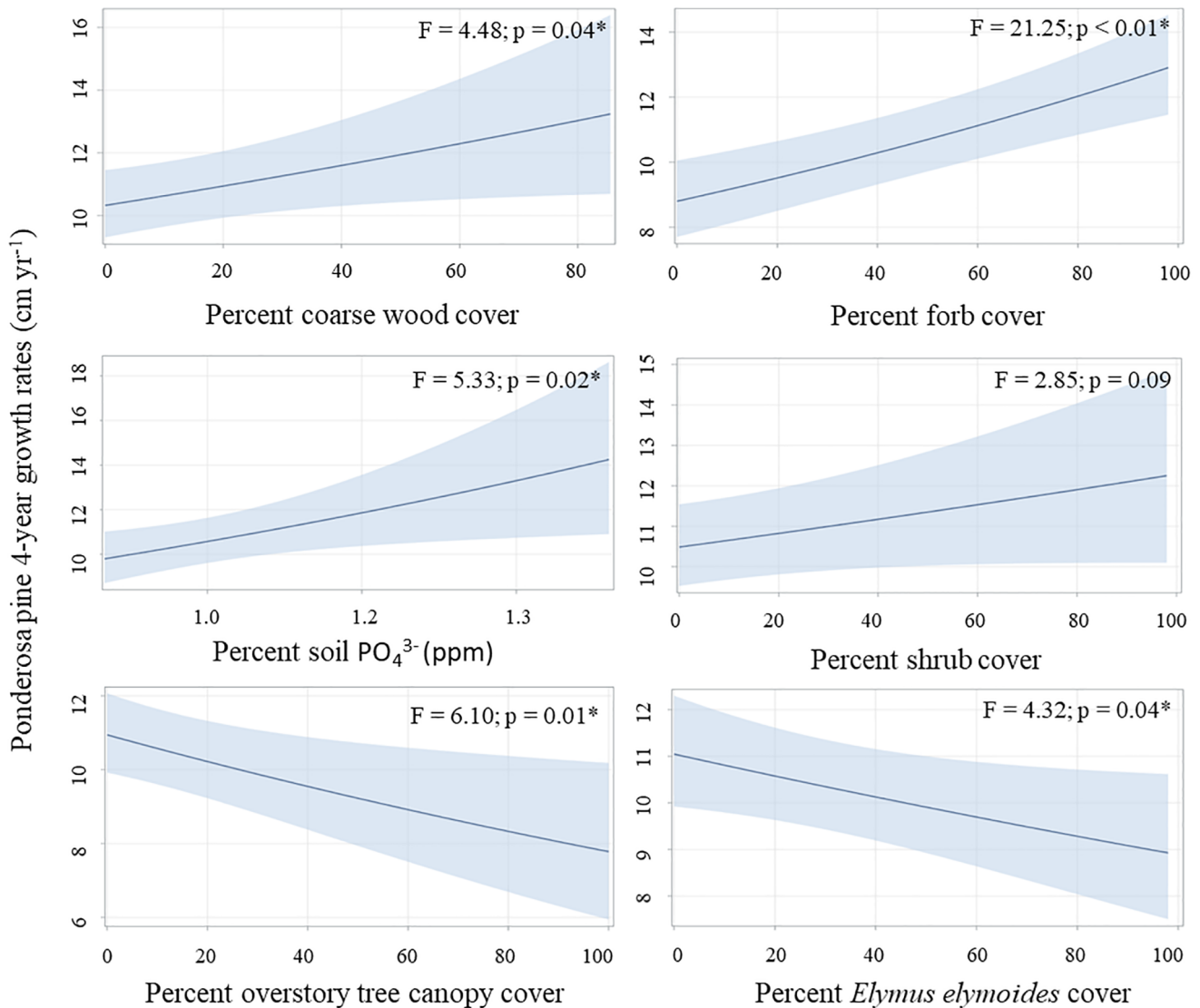
Fig. 4. Ponderosa pine terminal leader annual growth over 5 years from 2011 to 2015 was partially explained by a positive correlation with surrounding percent coarse wood cover, forb cover and soil phosphate, and a negative correlation with percent overstory tree canopy cover and surrounding squirreltail (*Elymus elymoides)* cover. There was a trend for a positive correlation between terminal leader annual growth and shrub cover. GLMM fit is shown with 95% confidence limits.

forests after severe fire (from pile burning) (Covington et al., 1991; Covington and Sackett, 1992), but others have found long-term reductions (DeLuca et al., 2002), or increases (Brais et al., 1995; Turner et al., 2007) in available nutrients and soil pH (reviewed in Certini 2005) after severe fires in boreal forests. Additionally, severe fire can either increase nitrogen mineralization rates (Grady and Hart, 2006), or nitrification rates decades after fires (Kurth et al., 2014) in different ponderosa pine forests, likely from a change in the quality of carbon inputs from overstorny pine needles to more herbaceous inputs. We anticipated that more soil variables, such as available N, would correlate with ponderosa pine growth. There is evidence of N limitation in some ponderosa pine forests (Menge et al., 2012), but on our sites soil PO_4^{3-} was more correlated with plant growth. Previous studies have shown that southwestern ponderosa pines that were fertilized with both N and P had greater diameter growth, but not height (Wagle and Beasley, 1968; Heidmann, 1985). Weathering of mineral P is a slow process, and fine root turnover and the role of symbiotic mycorrhizal fungi in P-uptake are likely contributing to the correlation between PO_4^{3-} and regenerating pine growth (Schlesinger, 1991; Allen, 1991; Delucia et al., 1997). The differences in percent gravel, sand, and clay among our plots, although statistically significant, are probably not

ecologically impactful, and it is unlikely that the differences are the result of variations in fire severity (reviewed in Certini, 2005). Studies such as Puhlick et al. (2012) that have documented effects of soil texture on ponderosa pine regeneration densities incorporated a much larger range in clay content (e.g., 7–28%) than our study incorporated (23–28%). Thus, it is not surprising that we did not find evidence that soil texture influenced seedling growth.

4.3. Ponderosa pine seedling growth after high-severity fire

Our results suggest that if seedlings can establish in the high-severity burns, their growth may not be inhibited by site conditions 11–16 years following the fire, unless they are growing near dense patches of squirreltail. Younger (1–2 years old) ponderosa pine seedling height can be positively associated with overstory basal area (Flathers et al., 2016), but older seedlings and saplings require more sunlight to grow and survive (Chen, 1997), and our results support this. Ponderosa pine seedlings tended to have the greatest growth rates in high-severity edge plots, potentially from receiving some shading and wind protection or connecting to symbiotic soil mycorrhizal networks adjacent to forest edges (Nara, 2006). Results from a recent study in this area

suggest that large patches of high-severity fire have long-term consequences to mycorrhizal sporocarp communities, even on plots adjacent to unburned forests, but greater impacts to mycorrhizal root tip communities in the interior burn patches (Owen et al., 2019). Regenerating ponderosa pines from our study had already survived the high-mortality stage, within the first few years of germination (Pearson, 1950; Shepperd et al., 2006), and their variation in estimated age suggests that regeneration was episodic, similar to findings by Haire and McGarigal (2010). We did not observe any cone-producing ponderosa pine seedlings or saplings on our plots, but if the current seedlings survive and are able to reproduce, their reproduction will help to fill in treeless gaps. Since 2013, only four out of the 360 seedlings we measured died, in contrast to high mortality rates (averaging 75%) of ponderosa pine seedlings planted 5 to 8 years earlier across the SW (Ouzts et al., 2015). However, all seedlings, whether naturally established or planted likely face additional challenges such as fire, drought, herbivory, or disease that could reduce their survival rates (Huffman et al., 2012; Waring and Goodrich, 2012; Savage et al., 2013; Iniguez et al., 2016; Rother and Veblen, 2016). Additionally, even though we found high post-fire ponderosa pine survivorship, establishment in the high-severity burned areas was low, ranging from 20 to 73 ponderosa pine seedlings ha^{-1} (Owen et al., 2017).

5. Conclusions and management implications

Large, high-severity wildfires in ponderosa pine forest are expected to become more common in the future, furthering the challenge for natural ponderosa regeneration, which may already be constrained by climate in some areas (McDowell et al., 2016; Petrie et al., 2016; Stevens-Rumann et al., 2018, Stevens-Rumann and Morgan, 2019; Davis et al., 2019; 2020). Our results indicate long-term changes to understory plant communities and fuel loads from fire, especially severe fire, and some of these variables were associated with ponderosa pine seedling growth 11–16 years post-fire. We found potential evidence of facilitation from some surrounding plant and coarse wood cover. Local adaptations from seedlings that can establish and survive after high-severity fires and surrounding seed sources may be critical for ponderosa pine survival in future climates (Lucas-Borja et al., 2017; Gehring et al., 2017; Patterson et al., 2019). Managers may want to consider the tradeoff of using managed fire to reduce woody fuels or protect post-fire seedlings and seed sources by: 1) postponing prescribed fire treatments around regenerating seedlings until their crowns are taller and they have thicker bark to increase the probability of survival, which may take 15 years or longer in some areas (Bailey and Covington, 2002; Shepperd et al., 2006; Battaglia et al., 2009); 2) burning when woody fuel moisture is high to retain some large branches and logs in high-severity burn patches, because our results indicate they may be important for growth, and others have shown they encourage conifer regeneration and beneficial microbial populations (Sánchez Meador and Moore, 2010; Castro et al., 2011); 3) accept the tradeoff that burning to reduce the heavy surface fuels may result in high regeneration mortality, due to increased fire radiative energy and long duration burning (Monsanto and Agee, 2008; Hudak et al., 2016); or 4) protect ponderosa pine trees near high-severity burn edges so they may provide additional shading and wind protection for regenerating seedlings, and increase seed sources for future regeneration (Stephens et al., 2018; Coop et al, 2019; Dodge et al., 2019).

It is becoming increasingly apparent that predictions of warmer climates and increased occurrences of large, high-severity wildfires should be factored into post-fire treatment plans (McDowell et al., 2016; Abatzoglou and Williams, 2016; Kitzberger et al., 2017). Climate change is predicted to result in large-scale vegetation shifts in southwestern forests (Flatley and Fulé, 2016; Parks et al., 2019). Non-forested high-severity burn patches or alternative vegetation types can be areas of resilience to climate variability and to subsequent fire within portions of the pine-dominant landscape (Coop et al., 2016;

Schoennagel et al., 2017, Parks et al., 2018). However, if management goals are to restore ponderosa forests that are not regenerating naturally, planting pine seedlings in high-severity burn patches could be an option (Ouzts et al., 2015). Planting in low density, spatially heterogeneous patterns would avoid increasing future fire severity (Thompson et al., 2007; North et al., 2019). Our results suggest planted pines may have improved growth near some coarse wood or forb cover, but they may be at risk from future fires until they are tall enough (> 1.2 m to 3 m) to increase their chances of survival (Gaines et al., 1958; Bailey and Covington, 2002; Battaglia et al., 2009).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118502.

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