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Environmental Influences on Density and Height Growth of Natural Ponderosa Pine Regeneration following Wildfires

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Abstract: Over the past century the size and severity of wildfires, as well as post-fire recovery processes (e.g., seedling establishment), have been altered from historical levels due to management policies and changing climate. Tree seedling establishment and growth drive future overstory tree dynamics after wildfire. Post-fire tree regeneration can be highly variable depending on burn severity, pre-fire forest condition, tree regeneration strategies, and climate; however, few studies have examined how different abiotic and biotic factors impact seedling density and growth and the interactions among those factors. We measured seedling density and height growth in the period 2015–2016 on three wildfires that burned in ponderosa pine (*Pinus ponderosa*) forests in the period 2000–2007 across broad environmental and burn severity gradients. Using a non-parametric multiplicative regression model, we found that downed woody fuel load, duff depth, and fall precipitation best explained variation in seedling density, while the distance to nearest seed tree, a soil productivity index, duff depth, and spring precipitation as snow best explained seedling height growth. Overall, results highlight the importance of burn severity and post-fire climate in tree regeneration, although the primary factors influencing seedling density and height growth vary. Drier conditions and changes to precipitation seasonality have the potential to influence tree establishment, survival, and growth in post-fire environments, which could lead to significant impacts for long-term forest recovery.

Keywords: *Pinus ponderosa*; post-fire recovery; forest resilience; fire effects; burn severity; forest fire

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1. Introduction

Tree regeneration is a critical aspect of post-wildfire recovery in forested ecosystems, since tree growth is both ecologically and economically valuable. In most forested ecosystems, living trees represent one of the largest and most dynamic carbon pools [1], affecting species interactions in a myriad of ways including through changes in the understory light environment and hydrology [2,3]. Following high-severity wildfire, failure of tree regeneration can result in ecosystem type conversion with potential cascading impacts on system-wide species composition and processes [4–6].

Conifers in the western United States (U.S.) have a variety of regeneration strategies. For many species, fire plays an important role in long-term survival and growth, as evidenced by increased regeneration in burned areas with variable regeneration along burn severity gradients [7–9]. The post-fire environment is often characterized by an increase in nutrient and light availability, but there are also changes in soil properties due to heating, as well as increased potential for soil erosion [10]. Likely due to changing climate as well as changes in fire regimes, conifer regeneration has declined across the western U.S. following fires, highlighting the importance of understanding the dynamic process of post-fire tree recruitment and growth [11].

In the western U.S., the focus of post-fire conifer regeneration research has generally been seedling establishment and density. A wide range of factors have been identified as influencing these processes, including burn severity [7–9], duff depth [12,13], distance to seed source [9,14–16], and post-fire climate [9,17,18]. Distance to seed source is often a predominant factor affecting non-serotinous conifer seedling density post-fire, along with pre-fire tree basal area [9]. Burn severity and patch size (distance to edge/unburned) in turn are important for their influence on distance to seed source, where large, high-severity burn patches create large areas with few to no surviving trees to serve as seed sources. However, for serotinous species, and to a lesser extent for other conifer species in mast years [19], crown mortality does not necessarily mean a removal of the tree as a seed source. Microsite environmental conditions [12–14] such as water availability [5,9,17,18] also create certain windows of conditions where seedling establishment is more likely.

In addition to impacting establishment, factors such as canopy condition and post-fire climate can impact the growth of established seedlings. Light availability strongly impacts conifer seedling growth, particularly for shade intolerant species such as ponderosa pine (*Pinus ponderosa*) [20,21]. Competition for light partially explains one post-fire manipulation study showing that the positive impact of burn severity on height growth of planted boreal species (jack pine [*Pinus banksiana*], black [*Picea mariana*] and white [*Picea glauca*] spruce) was due to lower levels of competing vegetation on higher severity sites [22]. Temperature and water availability also have been shown to impact seedling height growth post-fire, though effects are not always consistent among species, and effects may be strongest when looking at prior-year climate [23–25]. However, seedling height growth as a response variable has been relatively understudied in the context of post-fire environments, with many studies simply using total height to categorize seedling vigor (e.g., [17,26]) or examining height growth of planted seedlings [22,23].

Field-based studies investigating the patterns and drivers of density and growth in natural regeneration following wildfire are fundamental to understanding ecosystem recovery. We examined which environmental variables influenced seedling density and height growth on sites with established naturally regenerated ponderosa pine seedlings approximately 10 years after three large wildfires. We examined sites stratified by elevation, aspect, and burn severity to capture a wide range of site conditions that likely influence long-term tree regeneration following fire. Ponderosa pine is a widespread species across the western U.S. and may be particularly at risk of decreased regeneration success post-fire because of historical management and changing climate [11,27]. Sites with higher water availability, more microsites provided by downed woody fuels or potentially shrubs, and lower inter- and intra-specific competition (lower percent cover of understory plants, lower overstory canopy cover) were predicted to have higher average yearly height growth and seedling density.

2. Materials and Methods

2.1. Sites and Field Methods

Three fires (Hayman, Jasper, and Egley) in ponderosa pine-dominated forests in the western U.S. were sampled. The Jasper Fire (33,794 ha) burned in the Black Hills of southwest South Dakota in 2000, the Hayman Fire (55,893 ha) in the Front Range of central Colorado in 2002, and the Egley Complex (56,800 ha) in Malheur National Forest of central Oregon in 2007. The three locations have generally similar temperature regimes (30 year summer average of 18 °C for Egley and Jasper, 21 °C for Hayman; winter average −2 °C and −3 °C for Egley and Jasper, respectively, and 0 °C for Hayman) but differ in the amount and timing of precipitation. Precipitation at the Egley Fire primarily falls in winter/spring, whereas the areas around the Jasper and Hayman fires receive the majority of their precipitation in spring/summer. Overall, Egley receives only ~50% and 65% of the precipitation that Jasper and Hayman receive (30 year precipitation averages are 264, 525, and 404 mm, respectively).

Field sites were stratified by three variables based on spatial data layers in raster format: (1) burn severity from the Monitoring Trends in Burn Severity (MTBS; www.mtbs.gov, accessed on 18 October 2021) one-year post-fire delta Normalized Burn Ratio (dNBR) classified burn severity product (unburned, low, moderate, high), (2) elevation (high or low, based on the elevation spread of each fire), and (3) aspect. Aspect was transformed to TRASP on a 0–1 scale ranging from cool-wet (0 = 30°) to warm-dry (1 = 210°) based on the topographic solar-radiation index transformation [28]. The total number of sites and year of sampling varied among fires: 19 sites were sampled at Hayman in May/June 2015 (13 years post-fire), 16 sites at Jasper in June 2015 (15 years post-fire), and 41 sites at Egley in May/June 2016 (9 years post-fire).

The MTBS product used to stratify sites is a free product commonly used by both researchers and managers for post-fire ecological studies, impact assessments, and to guide potential restoration. Continuous dNBR values are calculated as pre-fire NBR minus post-fire NBR, where NBR is a normalized ratio calculated from 30 m resolution Landsat near-infrared band (NIR) and short-wave infrared band (SWIR), i.e., (NIR-SWIR)/(NIR + SWIR). Continuous dNBR is then categorized as unburned, low, moderate, or high severity, or increased green based on thresholds determined by the MTBS analyst [29]. The dNBR index is sensitive to changes in green vegetation, bare soil, and char, where areas with higher char and bare soil will have higher NBR values [30,31].

Within each site, five plots were established 30 m apart in a cross formation, with the azimuth defined by the outer plot established upslope of site center according to the dominant slope. Seedlings (≥15 cm and ≤137 cm in height) and saplings (>137 cm in height with a diameter at breast height (DBH) <10 cm) were tallied by full quarters in 5.6 m radius plots until a minimum of six seedlings had been encountered. Up to six representative seedlings or saplings, if they were determined to represent post-fire regeneration based on estimated age, were measured for the length between terminal bud scars to obtain approximate age and yearly growth increments [32]. This analysis focused on the most recent seven complete years of growth (2009–2015 for Egley and 2008–2014 for Hayman and Jasper) because field observations and previous work [32] indicate that bud scars of recent years are more reliably identified.

The distance from each plot to the nearest live mature ponderosa pine assumed to be capable of serving as a seed source (hereafter "seed tree") was recorded. Fractional cover of green vegetation, non-photosynthetic vegetation, mineral soil, and percent char of soil and non-photosynthetic vegetation was visually estimated in a 1 m^2 microplot at the center of each of the five plots. Non-photosynthetic vegetation included woody debris, senesced grass or forbs, tree bark, or leaf and needle litter. Additionally, we measured litter and duff depth, fine woody fuel loads (1, 10, 100 h timelag classes; <1 cm, 1–2.5 cm, and >2.5–7 cm diameter, respectively) were estimated using a photoload guide [33], and canopy cover of the overstory (trees and shrubs exceeding breast height [1.37 m]) was estimated using a convex spherical densiometer.

At each of the four peripheral plots, standing trees were recorded using a 2 m^2/ha basal area factor prism; for each tree the species, vigor (dead, healthy, unhealthy), and DBH was recorded. At only the center plot, all trees were tallied and measured in a 0.02 ha plot (8 m radius). Percent cover of tall shrubs (>1.37 m height) was ocularly estimated, and large downed woody fuel loads (1000-hr timelag class, >7 cm diameter) were estimated using the photoload guide [34] within a 0.01 ha subplot (5.6 m radius) at the center plot only.

2.2. Derived Variable Sources

In addition to field-collected variables, burn severity, post-fire climate, and soil variables were derived from public data sources. Continuous dNBR indicative of burn severity was obtained from the MTBS database. Post-fire climate data were generated using the ClimateNA v.6.21 software package (http://climatena.ca/; accessed on 1 November 2019), which calculates and derives scale-free point estimates of weather data [33]. Weather data were generated for the period 2008–2015 to represent the growth timeframe for seedlings used in this analysis, and then averaged by season within a year: winter (December–February), spring (March–May), summer (June–August), and fall (September–November). Soil variation among sites within a fire and between fires was accounted for with the soil productivity index (soil PI), which ranks soil productivity from 0 (least productive) to 19 (most productive) at 240 m resolution [35]. Soil PI is developed using family-level soil taxonomic information to produce an ordinal index of productivity. The index was chosen because it allowed us to use a consistent index for all three fires that has also been used in previous ponderosa pine seedling research publications (e.g [36]).

2.3. Statistical Methods

Of the total sites sampled, we used 36 sites for this analysis (Hayman = 12, Jasper = 11, Egley = 13) by subsetting only sites that had ponderosa pine seedlings present and that were not planted following the fire (to capture natural tree regeneration vs. planted seedlings). To ensure a roughly balanced sample among fires, sites from Egley were chosen at random from the suitable subsample. Each year's growth was standardized on total seedling height in that year [25], and a site-level average annual growth was determined by averaging the annual growth of all seedlings at a site. The response variable "seedling height growth" therefore represents the average annual height growth for a seedling at a given site for the past seven years of growth prior to sampling, which was standardized to account for the height of the seedling in a given year of growth. Seedling density was calculated as seedlings per hectare based on the number of seedlings counted divided by the area sampled on a site.

Non-parametric multiplicative regression (NPMR) in HyperNiche v.2 [37] was used to determine the influence of and potential interactions among predictor variables on both seedling height growth and density. NPMR allows for predictor variables to interact in non-linear, multiplicative ways to influence the response variables [38]. Each NPMR free search run was done with local mean model and Gaussian weighting, with default medium controls for overfitting, automatic minimum average neighborhood size (number of sites * 0.05), step size of 5, 10% maximum allowable missing estimates, and minimal backtracking search. HyperNiche automatically runs the free search as an iterative process over various combinations of predictor variables, producing thousands of models in the process. To reduce collinearity and duplication among predictor variables, predictor variables with pairwise correlations greater than 0.9 to another predictor variable were dropped in a stepwise approach to retain predictors with the stronger Spearman's rank correlation to average seedling height growth. This resulted in a final set of 39 variables (Table 1) that were included in the NPMR free search to examine their influence on seedling growth; 36 predictor variables were included in the seedling density free search, which excluded seedling density variables (total live seedling density, total dead seedling density, and total live sapling density) that were included as predictor variables for the growth models.

Table 1. Potential predictor variables for non-parametric multiplicative regression (NPMR) models of ponderosa pine seedling density and height growth. Seasonal post-fire climate variables (averaged for the period 2008–2015 to represent post-fire growing conditions) were obtained from ClimateNA (Wang et al. 2016, v. 6.21). Summer was defined as June–August; Fall as September–November; Winter as December–February; Spring as March–May. Burn severity was obtained from MTBS (www.mtbs.gov, accessed on 18 October 2021) and field data were gathered in the summers of 2015 (Hayman and Jasper) and 2016 (Egley). Variables with an asterisk (*) were excluded from the NPMR for seedling density.

Variable	Minimum–Maximum Value
Post-fire climate variables	
Summer mean maximum temperature	22.1–28.2 °C
Fall mean maximum temperature	11.4–18.6 °C
Winter precipitation	54.9–210.6 mm

Table 1. *Cont.*

Variable	Minimum–Maximum Value
Summer precipitation	47.5–292.1 mm
Fall precipitation	92.4–164.3 mm
Fall degree-days above 5 °C	258.1–520.0 degree-days
Fall number of frost-free days	33.0–51.4 days
Winter precipitation as snow	23.3–113.3 mm
Spring precipitation as snow	8.6–112.6 mm
Fall precipitation as snow	2.9–40.3 mm
Winter Hargreaves Reference Evapotranspiration	0.0–25.5 mm
Fall Hargreaves Reference Evapotranspiration	129.0–222.9 mm
Spring Hargreaves Climatic Moisture Deficit	19.4–148.0 mm
Winter relative humidity	43.3–60.8%
Spring relative humidity	48.3–58.5%
Summer relative humidity	44.0–59.3%
Derived variables	
Elevation	1507.1–2858.7 m
Transformed aspect (Roberts and Cooper 1989)	0.0097–0.9960
Slope	0.79–32.15%
Differenced Normalized Burn Ratio	−24.0–717.6
Soil productivity index	6.0–15.0
Field variables	
Distance to nearest cone-bearing tree	2.1–200.0 m
Understory species richness	4.2–17.6
Understory live vegetation cover	5.2–81.0%
Understory non-photosynthetic vegetation cover	14.0–94.4%
Rock cover	0.0–21.4%
Soil cover	0.0–60.0%
Total cover of charred surface components	0.0–141.0%
Tall shrub cover	0.0–2.0%
1000 h woody fuel load	0.0–8.8 kg ha^{-1}
Fine (1, 10, and 100 h) woody fuel load	0.024–1.582 kg ha^{-1}
Litter depth	5.4–39.0 mm
Duff depth	0.0–24.4 mm
Total basal area of live trees	0.0–30.6 m^2 ha^{-1}
Total basal area of dead trees	0.0–23.0 m^2 ha^{-1}
Live sapling density *	0.0–1913.3 stems ha^{-1}
Dead seedling density *	0.0–240.0 stems ha^{-1}
Live seedling density *	20.0–13,360.0 stems ha^{-1}

The lists of models generated by the NPMR process were sorted by the cross-validated R^2 (xR^2) to determine what predictor variables appeared in the majority of the strongest 100 models. This process was used to select the best model for seedling height growth and for seedling density, individually, at which point the models were evaluated for tolerances and sensitivity. Tolerances in NPRM are the standard deviations used in the Gaussian smoothing and must be interpreted based on the range of each predictor; higher tolerance indicates that a variable is less important to the model. Sensitivity values range from 1 to 0, where higher sensitivity indicates that a percent change in that predictor will result in a similar percent change to the estimate of the response variable.

3. Results

The best model for ponderosa pine seedling density included fine woody fuel load, 1000 h woody fuel load, duff depth, and fall precipitation as top predictor variables (Table 2). Scatterplots showed generally positive relationships between seedling density and predictor variables but not necessarily strong linear effects (Figure 1). Using 3D predicted surfaces from the NPMR model, seedling density was consistently greater at higher fine woody fuel loads and greatest with high fine and 1000 h woody fuel loads

(Figure 2A). However, fine woody fuel load interacted with duff depth, which resulted in a marked peak in seedling density at high fine woody fuel load only when duff depth was around 15 mm (Figure 2B). Similarly, fine woody fuel load and fall precipitation interacted resulting in the greatest seedling density at high levels of fine woody fuel loads and fall precipitation (Figure 2C).

Table 2. Selected best models from non-parametric multiplicative regression (NPMR) free search for ponderosa pine seedling density and standardized height growth following large wildfires. Average size is the average neighborhood size, i.e., the average number of sample units that contribute to each point's estimated value on the modeled surface. See Table 1 for variable units and ranges.

Response Variable	Model xR^2	Average Size	Predictor Variable	Sensitivity	Tolerance
Density	0.39	3.49	Fine woody fuel load	0.037	0.62 (40%)
			1000 h woody fuel load	0.030	2.10 (30%)
			Duff depth	0.114	2.02 (10%)
			Fall precipitation	0.035	24.90 (35%)
Height growth	0.57	2.12	Distance to seed tree	0.028	118.76 (60%)
			Soil productivity index	0.033	4.05 (45%)
			Duff depth	0.189	4.04 (20%)
			Spring precipitation as snow	0.652	5.2 (5%)

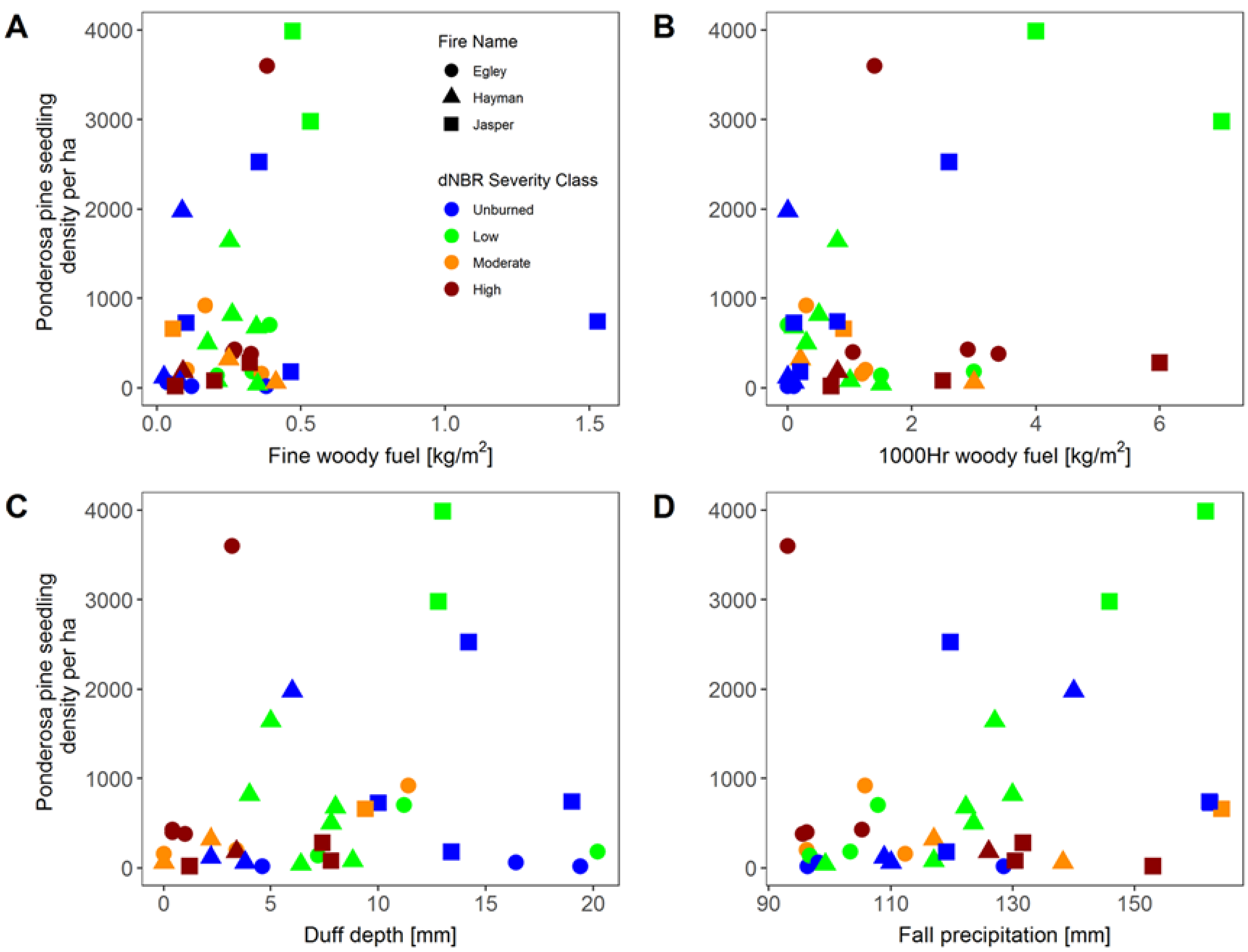

Figure 1. Predictors from best-fit non-parametric multiplicative regression (NPMR) model (see Table 2) for ponderosa pine seedling density across burn severity classes following three large wildfires. Predictors are (**A**) fine downed woody fuel load, (**B**) 1000-hr downed woody fuel load, (**C**) duff depth, and (**D**) fall precipitation.

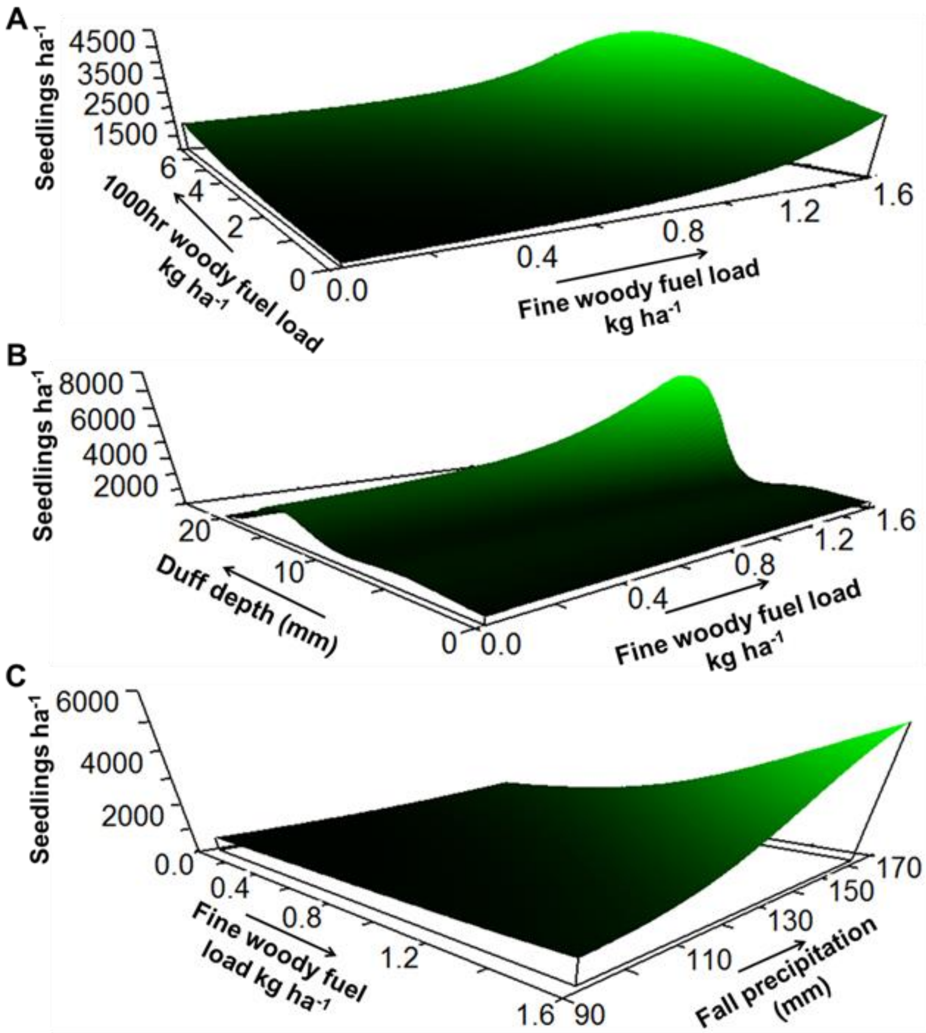

Figure 2. Ponderosa pine seedling density was impacted by fine woody fuel load, which interacted with (**A**) 1000 h woody fuel load, (**B**) duff depth, and (**C**) fall precipitation. Note that *y*-axis ranges and orientation of *x*-axis may vary among panels.

Seedling density was greater at 10–15 mm of duff depth regardless of 1000 h woody fuel load and increased with 1000 h woody fuel loads (Figure 3A). Seedling density was highest at high fall precipitation and high woody fuel load, while at low fall precipitation there was no effect of woody fuel load (Figure 3B). There was a pronounced peak in seedling density at approximately 15 mm duff depth, which increased with fall precipitation (Figure 3C).

The best-fit model for average seedling height growth included distance to nearest ponderosa pine seed tree, soil productivity index (soil PI), duff depth, and spring precipitation as snow (spring PAS) as top predictor variables (Table 2). Scatterplots showed a positive relationship between distance to seed tree and seedling growth (Figure 4A), while seedling height growth somewhat decreased with soil PI, duff depth, and spring PAS (Figure 4B–D). The 3D predictive surfaces from the NPMR analysis showed seedling height growth was greatest with longer distances to seed tree and lower soil PI (Figure 5A). Seedling height growth was also greatest with longer distances to seed tree and increasing duff depth (Figure 5B). Increasing duff depth generally decreased seedling height growth, and seedling height growth was greatest at low soil PI and low duff depth (Figure 5C). The effect of spring PAS on seedling height growth was complex and height growth varied with small changes in spring PAS regardless of other predictors (Table 2), with generally high growth at moderate values of spring PAS.

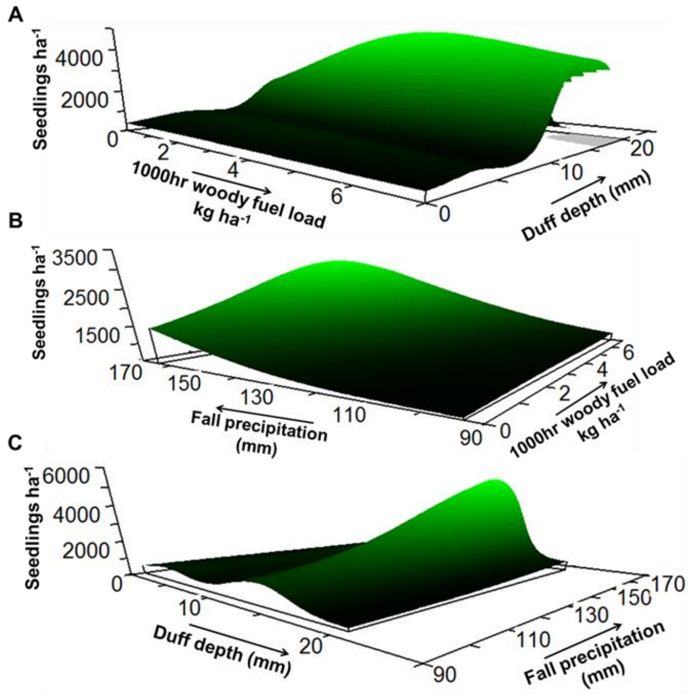

Figure 3. Ponderosa pine seedling density was impacted by 1000 h woody fuel load, which interacted with (**A**) duff depth, (**B**) fall precipitation, and by the interaction of (**C**) duff depth and fall precipitation. Grey areas indicate where the model lacked enough information to reliably predict the response. Note that *y*-axis ranges and orientation of *x*-axis may vary among panels.

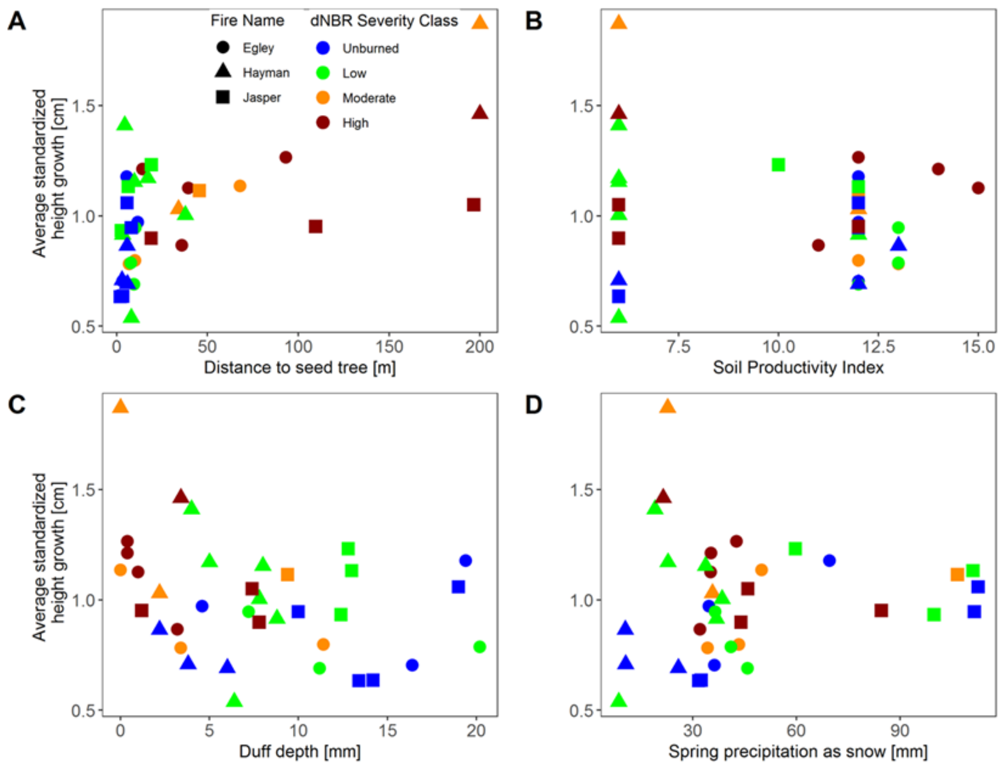

Figure 4. Predictors from best-fit non-parametric multiplicative regression (NPMR) model (see Table 2) for average height growth of ponderosa pine seedlings across a burn severity gradient following three large wildfires. Predictor variables are (**A**) distance to seed tree, (**B**) soil Productivity Index, (**C**) duff depth, and (**D**) spring precipitation as snow.

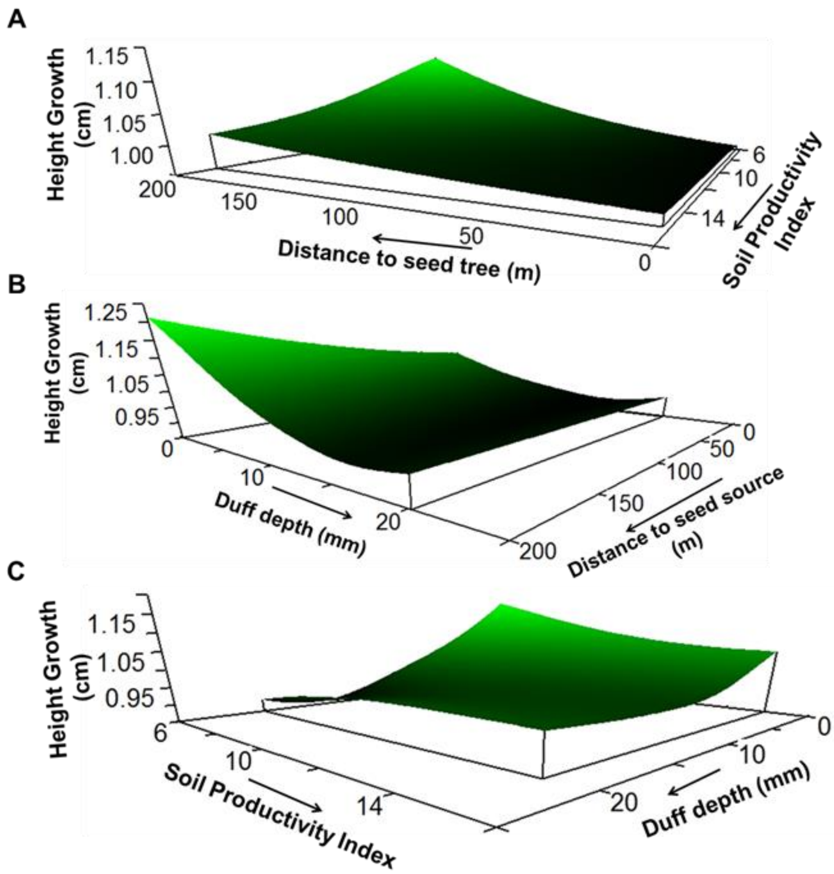

Figure 5. Average annual standardized height growth of natural ponderosa pine regeneration was impacted by distance to nearest seed source and (**A**) soil productivity index (soil PI) and (**B**) duff depth, as well as (**C**) soil PI and duff depth. Note that *y*-axis ranges and orientation of *x*-axis may vary among panels.

4. Discussion

Regeneration of overstory tree species is a critical part of ecosystem resilience to large wildfires; with changing climate and fire regimes, there is increased urgency to understand what biotic and abiotic factors influence tree seedling establishment, survival, and growth in post-fire environments [9,11,39]. Here, ponderosa pine seedling density and height growth were driven by similar predictors, suggesting that post-fire soil surface, overstory, and post-fire climatic conditions influence seedling establishment, survival, and growth in inconsistent ways. This highlights the importance of considering the complex interactions between biotic and abiotic factors and how they influence different aspects of post-fire tree regeneration.

Seedling density, which in this study best represents the survival of established seedlings 9–15 years post-fire, was most influenced by downed woody fuel load (both fine and coarse fuels), duff depth, and fall precipitation. Distance to live seed source has previously been identified as an overriding driver of seedling presence/absence following fires (e.g., [9,40]). Because our analysis specifically focuses on sites with established seedlings, our results highlight more secondary controls on seedling establishment and survival [9]. Understory conditions created by needle litter improve ponderosa pine seedling germination and success post-fire through influencing environmental factors, such as soil temperature and available soil moisture [14,41]. Downed woody fuel has also been found to increase ponderosa pine seedling density following fire for similar reasons, by providing microsites with more favorable temperature and water availability [42]. However, downed woody fuel load had limited impacts on density at sites with little duff or low fall precipitation, while sites with duff depths ~15 mm and higher fall precipitation are where downed woody fuels had a marked positive impact on seedling density. Fall precipitation is likely important because ponderosa pine cone production and seed release are largely seasonal, with the majority of mature seeds released in the fall months [43]. Though many studies have focused on the importance of favorable climate conditions in the subsequent growing season [24,43], higher spring and fall precipitation has been linked to pulses of ponderosa pine establishment in Colorado [44].

Ponderosa pine seedling height growth was influenced by interactions between distance to seed source, soil productivity index (soil PI), duff depth, and spring precipitation as snow (spring PAS). Distance to seed source is likely positively related to growth (i.e., longer distance to seed source relates to greater height growth) because it reflects higher burn severity, lower canopy cover, and thus increased light availability and less overall competition from mature trees. Light availability is known to positively affect conifer seedling height [45–47] and may be more important than water availability [48]. The relationship between seedling height growth and soil PI was inconsistent; our results indicate that lower soil PI has higher variability in growth (having both the highest and lowest height growth) than higher soil PI. Higher soil PI may result in higher growth of competing vegetation that could negatively impact seedling height growth [14] depending on overall soil nutrient availability, though other work has shown positive correlations of forb and other understory species with seedling growth [42]. With deeper duff depth, soil PI was positively associated with seedling height growth, which highlights the importance of considering interactions between variables.

Similarly, spring PAS had a highly non-linear relationship to height growth, making it difficult to predict whether changes in spring PAS (e.g., due to changing climate) would positively or negatively impact height growth. Radial growth of ponderosa pine has been shown to be sensitive to spring and growing season precipitation [24,44]. Ponderosa pine seedling growth and survival were also lower in experimentally warmed plots than in controls, regardless of whether the warmed plots also received additional water [23]. However, Rother et al. (2015) did not manipulate the seasonality of warming, instead raising mean midday temperature by approximately 3–4 °C across the two-year study period. Previous research has also shown evidence for changes in how seedling growth responds to temperature and water deficit in the early vs. late 20th century, indicating that as changing climate pushes more sites to the edge of species' climatic tolerances, there is added complexity in their relationships to climate variables [24].

The only variable significant for both seedling density and growth was duff depth, which had opposing general trends for our two response variables. While duff depth was positively associated with seedling density in most cases, it was negatively associated with height growth. Lower duff values post-fire are often associated with higher burn severity conditions on our sites, which may benefit height growth (via increased light and nutrient availability) for seedlings that can establish on those sites but may result in fewer overall seedlings that successfully establish [8,42,49]. However, these trends were not universal, for example at high soil PI there was no real impact of duff depth on seedling height growth. Our model also shows that the relationship of duff depth to seedling density is non-linear, with a peak in density at approximately 15 mm of duff and a decrease in density at deeper duff depths. Overall, we believe that the stratification of the sites and the intensity of sampling at each site sufficiently captured variability among fires, though of course the number of sites per fire was lower in order to accomplish the broad geographic range of sampling the multiple fires across the western U.S. It is therefore possible that there is additional variation within fires that was not fully captured with our sampling scheme, so it would be interesting to see future work using similar methods with a focus on a single fire to allow for more replication of sites within a fire.

5. Conclusions

Understanding long-term post-fire conifer recovery requires understanding the factors influencing seedling germination and establishment as well as growth and survival. We found that 9–15 years post-fire, ponderosa pine seedling density and height growth were generally impacted by different but related factors. Duff depth was the only predictor present in the best-fit model for both seedling growth and density, but it produced opposite effects. Precipitation was important for both seedling density and height growth, fall precipitation was important for density, while spring precipitation as snow was important for height growth, and the relationship to height growth was highly non-linear.

Overall, seedling density and height growth were driven by burn severity (duff depth, downed woody fuel load, distance to seed tree) as well as post-fire climate. Driest sites have been shown to have lower density of seedlings, and continued changes in climate are pushing more sites outside established climate envelopes to which trees have adapted for successful regeneration [11,40]. The difference in seasonality of precipitation adds nuance to the consideration of post-fire climate and regeneration success, as changing climates may shift precipitations patterns. Post-fire processes are influenced by different factors or by the same factor in opposing ways depending on the site, indicating that future research and management for post-fire forest recovery may need to consider more than seedling establishment and density to offer a complete picture of future forest trajectories under changing climate and burn severity conditions.

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