Andrus *et al. Fire Ecology* (2022) 18:29
https://doi.org/10.1186/s42408-022-00153-4

Fire Ecology

ORIGINAL RESEARCH

Open Access

Spatial and temporal drivers of post-fire tree establishment and height growth in a managed forest landscape

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Abstract

Background: In seed-obligate conifer forests of the western US, land managers need a better understanding of the spatiotemporal variability in post-fire recovery to develop adaptation strategies. Successful establishment of post-fire seedlings requires the arrival of seeds and favorable environmental conditions for germination, survival, and growth. We investigated the spatiotemporal limitations to post-fire seedling establishment and height growth in dry to moist mixed conifer forests with and without post-fire forest management treatments (salvage logging, grass seeding) in areas burned from low to high severity. In 2011, we measured post-fire seedling establishment year, juvenile density (seedlings and saplings), and height growth (annual and total) in 50 plots with six conifer species in the School Fire (2005), Blue Mountains, WA, USA. In 2021, we remeasured the plots for post-fire juvenile density and height growth.

Results: Post-fire juvenile tree densities appeared sufficient for self-replacement of forest (> 60 stems ha^{-1}) in 96% of plots in 2021 (median 3130 stems ha^{-1}), but densities were highly variable (range 33–100,501 stems ha^{-1}). Annual seedling establishment was positively correlated with cooler, wetter climate conditions during the summer of germination (July–September) and the growing season of the subsequent year (April–September) for multiple tree species. We found lower juvenile densities at greater distances to seed sources and with higher grass cover, while salvage logging had no effect. Annual height growth was shorter on warmer, drier topographic positions for three species, whereas annual height growth was associated with climate variability for one species. Shifts in height class structure from 2011 to 2021 were, in part, explained by differences among species in annual height growth.

Conclusions: Abundant and widespread tree seedling establishment for multiple conifer species after fire was strong evidence that most burned sites in the present study are currently on a trajectory to return to forest. However, post-fire establishment may be constrained to brief periods of cooler, wetter climate conditions following future fires. Long-term monitoring of post-fire recovery dynamics is needed to inform management activities designed to adapt forests to climate change and future disturbances, which will collectively shape future forest structure and composition.

Keywords: Conifer forest, Wildfire, Burn severity, Post-fire tree regeneration, Post-fire treatments, Salvage logging, Grass seeding, Remeasurement

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Resumen

Antecedentes: En bosques de coníferas del oeste de los EEUU que se reproducen estrictamente por semilla, los gestores de tierras necesitan de un mejor entendimiento sobre la variabilidad espacio- temporal en la recuperación post fuego en paisajes manejados, para desarrollar estrategias de adaptación. El establecimiento exitoso de plántulas post fuego requiere de la disponibilidad de semillas y de condiciones ambientales favorables para su germinación, sobrevivencia, y establecimiento. Investigamos las limitaciones espacio-temporales en el establecimiento y altura de plántulas en bosques mixtos de coníferas (entre secos y húmedos) con y sin tratamientos posteriores al evento de fuego (tala rasa y siembra de pastos) en áreas quemadas con baja y hasta alta severidad. En 2011, medimos el establecimiento post fuego, la densidad de juveniles (plántulas y árboles jóvenes) y año de establecimiento, crecimiento en altura (anual y total) en 50 parcelas con seis especies de coníferas en el incendio de School (School Fire, 2005), en las Montañas Azules (Blue Mountains, WA, EEUU). En 2021 las parcelas fueron re-medidas para determinar densidad de juveniles y crecimiento en altura.

Resultados: Las densidades de plantas juveniles de coníferas parecieron ser suficientes como para lograr un autoreemplazo del bosque (>60 plantas ha^{-1}) en el 96% de las parcelas en 2021 (mediana de 3.130 tallos ha^{-1}), aunque sus densidades fueron altamente variables (rango desde 33 a 100.501 fustes por ha^{-1}). El establecimiento anual de plántulas se correlacionó positivamente con condiciones climáticas frescas y húmedas durante el verano luego de su germinación (julio a septiembre) y con la estación de crecimiento del año subsiguiente (abril a septiembre) para muchas especies de árboles. Encontramos una menor densidad de juveniles a mayores distancias de las fuentes de semilla, con más cobertura de pastos, y en exposiciones sur, mientras que la tala rasa no tuvo efectos. El crecimiento en altura fue más bajo en posiciones topográficas más secas y cálidas para tres especies, mientras que el crecimiento en altura fue asociado con la variabilidad climática para una especie. Las desviaciones en la altura de las diferentes clases de estructura desde 2011 a 2021 fueron en parte explicadas por diferencias en el crecimiento anual en altura entre especies.

Conclusiones: El abundante y territorialmente amplio establecimiento de plántulas de diversas especies de coníferas luego de incendios, es una evidencia muy fuerte de que la mayoría de los sitios quemados reportados en el presente estudio está en una trayectoria de retorno a constituirse nuevamente en bosques. Por supuesto, el establecimiento post fuego parece ser condicionado por breves períodos de frío y humedad que siguen a los futuros fuegos. El monitoreo a largo plazo de la dinámica de la recuperación post fuego es necesaria para informar sobre las actividades de manejo diseñadas para adaptar esos bosques al cambio climático y a disturbios a futuro, los que colectivamente darán lugar a la formación de la estructura y composición de ese futuro bosque.

Background

The density and height of tree seedlings in the first few years to a decade after fire can be indicative of the future forest canopy and are critical for informing land management decisions, such as the need for post-fire treatments (Millar and Stephenson 2015; Larson et al 2022). However, unexpected shifts in vegetation composition and structure do occur in the decades following fire (Gill et al 2017), and changing climate is expected to further alter post-fire trajectories (Enright et al 2015; Johnstone et al 2016; Coop et al 2020). Repeated monitoring of demographic rates (reproduction, growth, mortality) after fire at the same sites can help forecast shifts in tree species composition and structure and improve post-fire management. In the context of increased annual area burned and area burned as stand-replacing fire in forest ecosystems since ~2000 (Abatzoglou and Williams 2016; Kitzberger et al 2017; Parks and Abatzoglou 2020), understanding where forests are expected to recover after fire and how forests may change over time is a pressing forest management issue, especially in moist mixed conifer forests actively managed for timber production and other values (Vose et al 2018).

Recovery of forest ecosystems from fire is necessary to maintain the current extent of forest cover and associated ecosystem services, such as soil stability, carbon sequestration, and wildlife habitats (Thom and Seidl 2015). Recently observed conversions of forest to non-forest vegetation types and shifts in tree species distributions following fire potentially indicate long-term changes in vegetation structure and function (Johnstone et al 2016; Seidl et al 2017; Coop et al 2020; Hill and Field 2021). Following wildfire, recovery of seed-obligate conifer forest communities to a pre-disturbance structure and composition (i.e., resilience) is supported by post-fire survivors (i.e., resistance) and establishment of new trees (Grime 1977). New seedling establishment occurs when seeds disperse from surviving trees or fire-killed trees (serotinous species only) into burned areas and environmental conditions are suitable for germination and survival (i.e., regeneration niche; Grubb 1977). Seedlings have minimal reserves (e.g., carbon stores), small canopy and root systems, and a poor ability to withstand the high temperatures and low soil moistures found on the soil surface in environments burned with moderate to high severity (Jackson et al 2009; Wolf et al 2021). Timing of seedling establishment after fire and variability in height growth among species can result in markedly different outcomes for vegetation trajectories (Tepley et al 2017). A better understanding of spatiotemporal limitations to seedling establishment and height growth is necessary to develop strategies and tools to adapt forest ecosystems to climate change and more frequent fire.

Seed availability is the initial determinant of post-fire seedling germination, whereas a multitude of factors affect the survival of seedlings and height growth. The spatial configuration of fire-killed trees creates variability in distance to and quantity of available seeds (Turner 2010), and annual seed delivery varies with the infrequent production of large seed crops (Kelly 1994). When seeds are available, survival and growth of seedlings are modified by the topographic effects on soil moisture (Donato et al 2016; Hoecker et al 2020; Stewart et al 2021), competition from understory vegetation (Povak et al 2020; Owen et al 2020), species traits (Harvey et al 2016; Rodman et al 2020; Hoecker and Turner 2022), soil substrates (Burns and Honkala 1990), and subsequent disturbance (Turner et al 2019; Busby et al 2020). Most researchers have focused on the factors affecting the spatial variability in post-fire seedling density (as reviewed by Stevens-Rumann and Morgan 2019), whereas few researchers have examined factors affecting height growth, a critical factor for forecasting the future forest canopy. Trees that grow faster are more likely to outcompete other individuals (trees, shrubs) and may also have traits to protect against heat from future fire (e.g., higher canopy base height and thicker bark; Rodman et al 2020).

Post-fire management activities, including salvage logging and seeding of grasses (Leverkus et al 2021) and mulching (Bontrager et al 2019), may also alter the density and growth of natural (i.e., not planted) tree seedlings. Salvage logging, often conducted within 1–2 years post-fire, removes some or all merchantable fire-killed and fire-damaged trees (Peterson et al 2009). The machinery used in salvage operations, such as feller bunchers and skidders, may have positive (e.g., exposes mineral soils and reduces competition from understory vegetation), negative (e.g., damage to seedlings or surviving trees and soil disturbance), or no effect on post-fire regeneration (Donato et al 2006; Povak et al 2020; Leverkus et al 2021). Another common post-fire management practice is seeding of native and non-native grasses, with the intended goal of reducing soil erosion and limiting the expansion of invasive species into burned areas (Robichaud et al 2006; Peppin et al 2010). Sites seeded with grasses supplement naturally establishing vegetation and can result in high cover of grasses (Morgan et al 2015). Increased competition for resources (e.g., soil moisture and nutrients) may thereby reduce post-fire establishment of conifer species (Beyers 2004; Bontrager et al 2019; Jonas et al 2019). Understanding the shorter (first few years) and longer-term (one to multiple decades post-fire) consequences of post-fire management practices for tree regeneration can inform the management of post-fire landscapes (e.g., tree planting), particularly in working forest landscapes where timber production is a high priority and state and federal laws in the USA require prompt reforestation of timber producing stands following wildfire (U.S. Government 1976; Peppin et al 2010).

The Blue Mountains ecoregion (Washington and Oregon, USA) experienced ~100 fires of >10,000 ha from 2000 to 2021 (MTBS 2021). Timber and other forest products, as well as recreation and wildlife, are an important source of income for local economies (Hamilton et al 2016). Increasing air temperatures over the last several decades has reduced late spring snowpack as well as summer soil and fuel moisture (Stewart et al 2005; Hamlet et al 2007; Clifton et al 2018), and these trends are expected to continue (Davis et al 2017). Increased fire activity is expected to catalyze changes in dry to moist mixed conifer forest communities, such as decreases in forested area, lower canopy cover within forested areas, and shifts toward more drought-tolerant species (Kerns et al 2018). Researchers have identified key limitations to the densities of post-fire seedling establishment (e.g., seed availability and moisture deficit) in the Blue Mountains (Downing et al 2019; Boag et al 2020), but the following aspects of post-fire ecosystem recovery have yet to be explored: (1) the influence of interannual climate on seedling establishment for multiple conifer species (but see Hankin et al 2019 in northern Rockies), (2) drivers of the spatial and temporal variability in annual height growth (but see Littlefield 2019 in the eastern Cascade Mountains), (3) shifts in post-fire tree composition and structure over time, and (4) the implications of post-fire management practices for regeneration (but see Povak et al 2020for effects of salvage logging in neighboring ecoregions).

Our overall objective was to investigate the spatial and temporal limitations to post-fire seedling establishment and rates of forest recovery in dry to moist mixed conifer forests. We measured (6 years post-fire in 2011) and remeasured (16 years post-fire in 2021) 50 plots with natural post-fire regeneration in the School Fire (2005), a managed forest landscape in the Blue Mountains. Specifically, we asked the following: (1) How did post-fire stem densities (stems ha^{-1}) compare to silvicultural stocking recommendations and pre-fire stem densities? (2) How did the composition and structure of post-fire regeneration change 6 to 16 years post-fire? (3) How was post-fire seedling establishment affected by the interannual variability in climate? (4) How was post-fire seedling density (stems ha^{-1}) affected by topography, seed availability, and post-fire management? (5) How was annual height growth influenced by topography, burn severity, competition from tree regeneration, and interannual variability in climate? We discuss our expectations (see Table 1 for expected effects of predictor variables) and the implications of our research results for land managers in the context of climate change.

Methods

Study area

Our study area encompasses the forested areas of the School Fire in the northern Blue Mountains (Umatilla National Forest), in southeastern Washington State (Fig. 1 A). Between July and August 2005, the School Fire burned 20,923 ha of grass and agricultural lands and dry to moist mixed conifer forest in mountainous terrain (elevation range of plots, 1230–1600 m). The Blue Mountains are characterized by hot, dry summers and cool, snowy winters. The annual precipitation is ~700mm, and the mean monthly maximum temperatures are ~18°C in July and August and the mean monthly minimum temperatures are −0.4°C in December and January (1981–2010 climate normals extracted at 46.2733, −117.4950; 1318 m; PRISM 2019). Mean annual temperatures increased 0.06 °C per decade from 1895 to

Table 1 Predictor variables and expected direction of effect in analyses of annual post-fire establishment, post-fire juvenile stem density, and annual height growth (HG) increment with median and range of plot data. Expected effects ("+" positive, "–" negative, "NT" not tested) were based on prior studies (see superscript numbers and footnotes) in the Blue Mountains ecoregion or neighboring ecoregions

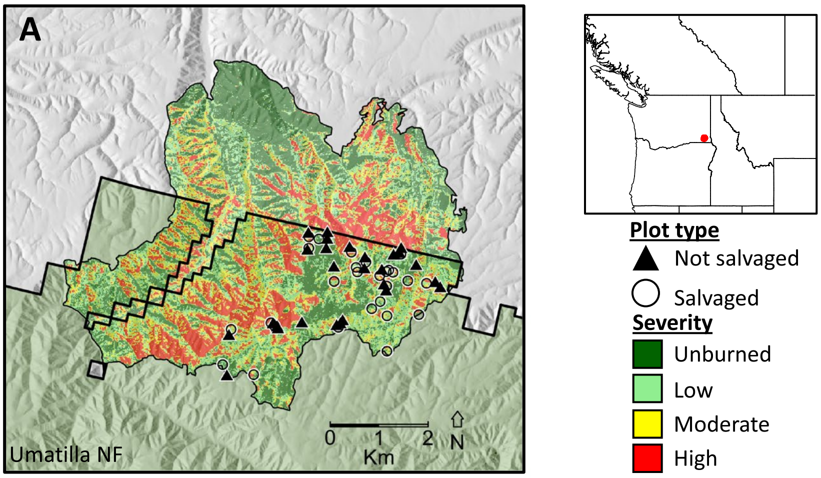
		Expected effect by analysis			
Predictor variable	**Description (units)**	**Establishment**	**Density**	**Annual HG**	**Median (min.–max.)**
Fire					
Distance to seed source	Distance (m) from the plot center to the nearest surviving conspecific conifer with evidence of seed cones (i.e., mature)	NT	–[a,b]	NT	29 (0–260)
Burn severity	Relative differenced Normalized Burn Ratio (unitless). Larger values indicate higher burn severity	NT	–[a]	+	521 (−41–1167)
Topography					
HLI	Heat load index (unitless) from 0 (coolest) to 1 (warmest)	NT	–[a,b]	–	0.66 (0.33–0.91)
Transformed aspect	Beers transformed aspect (unitless) from 0 (warmer, drier aspects) to 2 (cooler, wetter aspects)	NT	+[c]	+	0.64 (0–1.99)
Climate					
SPEI	Monthly, seasonal, or water year Standardized Precipitation Evaporation Index (unitless). Negative values indicate warmer, drier annual climate conditions, while positive values indicate cooler, wetter conditions	+[d]	NT	+/–[d]	NA
Understory					
Grass (%)	Cover of grass (%)	NT	–[a]	NT	11 (0–88)
Forbs (%)	Cover of forbs (%)	NT	+/–[a]	NT	18 (0–73)
Shrubs (%)	Cover of shrubs (%)	NT	+/–[a,b]	NT	20 (0–65)
Trees					
Juvenile density	Density of post-fire seedlings and saplings (stems ha^{-a})	NT	NT	–	4417 (17–100,500)
Juvenile height	Height of seedlings and saplings (cm)	NT	NT	+	240 (40–470)
Management					
Salvage logged	Salvage logged (22 plots) or not salvage logged (28 plots)	NT	+/–[c]	–	NA

[a] (Boag et al, 2020)

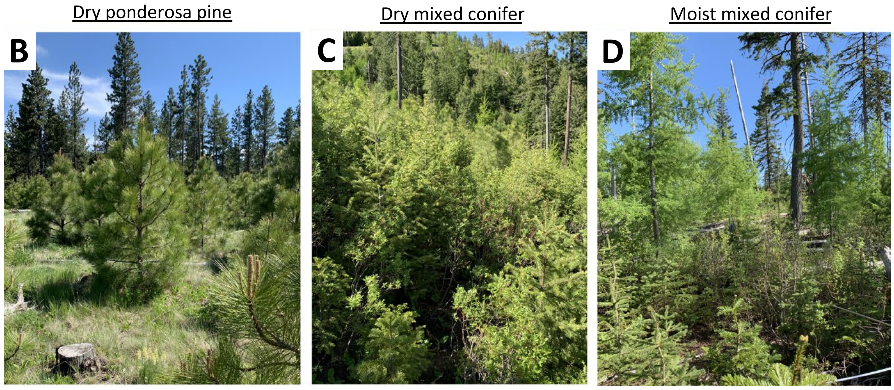
[b] (Downing et al, 2019)

[c] (Povak et al 2020)

[d] (Littlefield 2019)



Examples of three postfire forest trajectories



Dry ponderosa pine Dry mixed conifer Moist mixed conifer

Fig. 1 **A** Burn severity (MTBS 2021) and locations of salvaged and not salvaged plots (50 plots total) in the School Fire (2005), Umatilla National Forest, southeastern Washington State, USA (inset). **B**–**D** Examples of the three initial post-fire forest trajectories, including **B** dry ponderosa pine, **C** dry mixed conifer (ponderosa pine, Douglas fir, and grand fir), and **D** moist mixed conifer (western larch, lodgepole pine, Engelmann spruce, and dry mixed conifer species). Photo credit: R. Andrus

2013, and global climate models project temperatures will increase an additional 2.4 to 3.1 °C by 2050 relative to 1970–1999 (Halofsky et al 2018). Annual precipitation has not significantly changed, and model projections do not agree on the direction of change in future annual precipitation (Clifton et al 2018). Soils are ashy loamy sand derived from basalt layers, loess deposits, and volcanic ash (NRCS 2012).

Tree species composition and structure vary with elevation and topographic aspect in the northern Blue Mountains (Daubenmire 1956; Franklin and Dyrness 1990). Lower-elevation forests (~1200 m) are composed of nearly pure stands of ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson). At slightly higher elevations, ponderosa pine intermixes with Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) to create dry mixed conifer forests. Moist mixed conifer forests are found at the highest elevations and moister sites in the School Fire and may also include western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). In the context of warming climate, differences in species' fire-related traits and life history strategies, such as bark thickness, seed mass, and drought tolerance, may affect the recovery of tree populations and community assembly (see Additional file 1: Table S2 for a summary of tree species fire-related traits; Weiher et al 2011).

Fire is an important component of the disturbance regime in forests of the Blue Mountains (Agee 1996). Fire history reconstructions indicate that fires were both frequent and large from ~1550 to 1900, though few fires occurred after 1900 (Heyerdahl et al 2001; Johnston et al 2017). Prior to ~1900, Indigenous peoples inhabited and used fire on the landscape for multiple purposes (e.g., to promote desired plant species; Robbins and Wolf 1994). Decreases in fire activity from 1900 to ~2000 in dry to moist forest types resulted from multiple interacting factors, such as domestic livestock grazing, timber harvesting (e.g., cutting of large-diameter fire-resistant trees), road building, and suppressing fires (Agee 1996). Consequently, vegetation and fuel compositions and structures, particularly in lower-elevation forests, differ from reconstructions of forests in the late 1800s (Hessburg et al 2000; Hessburg et al 2005), but it is not clear how land use history has affected fire regimes in recent decades. Nevertheless, large stand-replacing patches, resulting from increasingly contiguous fuel structures and extremely warm, dry weather conditions, may reduce the chances for forest recovery.

Post-fire management in the school fire

The burn severity of the School Fire (2005) was 22% high, 23% moderate, 31% low, and 32% unburned (Fig. 1B; MTBS 2021). In the decade prior to the School Fire, 37% of the total burned area experienced timber harvest and partial cutting and 10% of the total burned area was mechanically thinned and prescribe burned (Moy 2010). Salvage logging and aerial seeding of grasses occurred following the School Fire. Salvage logging occurred during the winter months from 2005 to 2009, with the majority occurring during the winter of 2006–2007 and in areas burned with high severity. Prior to 2007, dead and dying trees were harvested. After 2007, all surviving trees with > 50% live basal area cambium and all trees (live or dead) > 53 cm diameter at breast height (dbh) were retained, while other trees were eligible for cutting (USDA Forest Service 2007). Aerial seeding of locally grown, native, and perennial grass species occurred immediately post-fire in 712 ha of areas burned at high severity in the School Fire (for grass species and seeding rates, see Additional file 1: Table S1). The goal of aerial seeding treatments as part of Burned Area Emergency Rehabilitation (BAER) was to reduce the spread of non-native plant species into the burned area, and non-native species were not abundant post-fire (Morgan et al 2015). Graminoid cover peaked 2 years post-fire and was much higher 6 years post-fire in seeded (~30% average canopy cover) compared to non-seeded areas (3% average canopy cover; Morgan et al 2015).

Post-fire regeneration field sampling design

We relocated and surveyed 50 permanent vegetation plots (monumented with rebar) with natural post-fire tree regeneration in summer 2021 that were initially measured in summer 2011 (Droske 2012; Table 1). Permanent plots were originally installed to investigate the long-term effects of burn severity and salvage logging on non-arboreal vegetation communities after fire (see Morgan et al 2015). Plots were stratified across three burn severity classes (low, moderate, high) based on a Burned Area Reflectance Classification map (U.S. Department of Agriculture, Remote Sensing Applications Center, Salt Lake City, UT) and presence/absence of salvage logging (field validated prior to plot installation). Burn severity classes were validated with field measurements of fire-caused tree mortality (high >70%, moderate 20–70%, and low <20% overstory tree mortality) by Morgan et al 2015) 1 year post-fire. None of the plots sampled was replanted with trees following fire or salvage logging according to local management records and examination of seedlings within the plots.

In July 2011, Droske (2012) randomly selected 42 of the 72 permanent vegetation plots and added 13 randomly located post-fire regeneration plots in areas with natural post-fire tree regeneration (55 plots total). Plots were stratified by salvage or non-salvage logging and three burn severity classes (low, moderate, high). In summer 2021 (May, June, September; the study area closed due to fire in July and August), we successfully relocated 50 of the 55 plots and only included remeasured plots in the present study. The 50 plots were salvage logged (22 plots) or not salvage logged (28 plots) and in low (10 plots), moderate (12 plots), or high (28 plots) burn severity. We sampled high-severity plots at a higher rate because lower abundances of post-fire regeneration were expected. In July 2011 and summer 2021, all seedlings (<1.4m tall) and saplings (>1.4m tall to <10cm dbh) were counted by species and measured for total height in 60-m-long belt transects perpendicular to the slope contour with plot center at the transect midpoint. To account for variability in post-fire seedlings and saplings (hereafter, juveniles) density, the transect width varied from 1 to 10 m to ensure that a minimum of 30 post-fire juveniles of the most abundant species were present. In 2011, establishment year was estimated for all seedlings by counting the number of annually formed terminal bud scars, a reasonably accurate estimate of seedling age for seedlings < 6 years old (e.g., ~70% accuracy for western larch, lodgepole pine, and Engelmann spruce; Urza and Sibold 2013).

To examine spatial and temporal variability in height growth, annual height growth (distance between internodes or bud scars) was measured in 2011 (seedling germination year to 2010) and 2021 (from 2011 to 2020, excluding the partial growth measurement in 2021). Tree selection protocols varied slightly by sample year. In 2011, annual height growth was measured for all seedlings in the belt transect. In 2021, annual height growth was measured on the tallest 6–10 (depending on availability) individuals in or within 5m of the transect in a subset of plots burned at moderate to high severity.

For each plot, we measured multiple biophysical factors that affect post-fire recovery (Table 1). To quantify pre-fire and post-fire stem density, we counted trees (> 10 cm dbh) and saplings and recorded status (pre-fire snag, killed by fire, or survived fire) in an 8-m-radius plot (200 m^2) at plot center 1 year after fire (only available for 40 of 50 plots). In 2021, we conducted the same assessment for all trees that survived the fire in a 11.3-m-radius plot (400 m^2). From the plot center, we measured the distance to the nearest living conspecific adult tree using a laser rangefinder for each species of seedling establishment found in the plot in 2011 (accuracy checked in 2021). The percent cover of grass, shrubs, and forbs was estimated in three 1-m^2 quadrats (2011) or four 4-m^2 quadrats (2021) and averaged at the plot scale.

Biophysical predictors of post-fire recovery derived from spatial datasets

To account for topographic and burn severity effects on post-fire recovery, we extracted remote sensing and GIS-derived spatial datasets at the plot locations (see Table 1 for each variable by analysis). For burn severity, we used RdNBR (relative differenced Normalized Burn Ratio (Miller and Thode 2007)), a burn severity index derived from pre- and post-fire Landsat imagery (30m) (MTBS 2021). For topographic variables, we included heat load index (HLI; McCune and Keon 2002) and Beers transformed aspect (Beers et al 1966).

Analytical methods

Comparing post-fire stem densities to silvicultural stocking recommendations and pre-fire stem densities (question 1)

To assess the likelihood for post-fire recovery to forest (i.e., resilience), we compared post-fire stem densities to local silvicultural stocking recommendations and pre-fire stem densities. On lands managed by the USDA Forest Service in the Blue Mountains, minimum stocking recommendations range from ~60 trees ha^{-1} in lower elevation and drier forest types to >350 trees ha^{-1} in higher elevation and cooler-moister forest types (Powell 1999), and these stocking rates were used in similar post-fire regeneration studies of dry to moist mixed conifer forest types in the PNW (Povak et al 2020; Boag et al 2020). Specifically, we compared post-fire stem density (sum of juveniles and surviving trees) for each plot to four post-fire stem density thresholds: (1) presence of post-fire stems, (2) 60 stems ha^{-1}, (3) 350 stems ha^{-1}, and (4) pre-fire stem density of trees and saplings.

Examining changes in species composition and structure over time (question 2)

To understand how the post-fire forest composition and structure changed over time, we classified each plot into one of three post-fire stand types based on the species composition in 2011: (1) dry ponderosa pine (>80% post-fire ponderosa pine seedlings), (2) dry mixed conifer (>80% post-fire ponderosa pine, Douglas fir, or grand fir seedlings), and (3) moist mixed conifer (>20% post-fire lodgepole pine, western larch, or Engelmann spruce seedlings). Then, we computed the medians of post-fire stems ha^{-1} by species and year (2011, 2021) for seedlings and saplings within each stand type.

Climate effects on post-fire seedling establishment (question 3)

To examine if post-fire seedling establishment was affected by the interannual variability in climate, we related the Standardized Precipitation Evaporation Index (SPEI) to the sum of annual post-fire tree density by species (standardized to the hectare) from 2006 to 2011 (year of establishment not measured 2012–2020) using Spearman's correlations. SPEI is a multi-scalar drought index that accounts for the effects of temperature and precipitation on soil moisture availability (Vicente-Serrano et al 2010). SPEI was computed in R programming software (Begueria and Vicente-Serrano 2017; R Core Team 2020) using monthly precipitation and temperature data extracted from a central location and average elevation within the School Fire (1970–2020; PRISM 2019). We tested the effect of spring (April–June), summer (July–September), growing season (April–September), and water year (October–September) SPEI, all of which are known to affect post-fire seedling establishment (Rother and Veblen 2016; Littlefield 2019), for the germination year and 1-year lags. To account for potentially confounding effects, we removed plots that were salvage logged or burned at low severity (29 plots removed), because salvage logging created additional soil disturbance from 2005 to 2007, and the microclimate of areas burned with low severity was likely cooler and moister than plots burned with moderate to high severity (Wolf et al 2021). To account for sample size limitations (six observations of annual seedling establishment per species) and the failure to detect potentially meaningful relationships between climate and establishment year (i.e., type II error), we evaluated statistical significance with an $\alpha = 0.10$.

Biophysical factors affecting post-fire juvenile stem density (question 4)

To test biophysical factors affecting the density of post-fire juvenile stems (density model) in plots with species presence, we constructed generalized linear mixed models (GLMMs) with a negative binomial distribution ("glmmTMB" package in R; Brooks et al 2017). We constructed separate GLMMs for density of (1) all species combined, (2) ponderosa pine, (3) Douglas fir, and (4) grand fir. Sample sizes of western larch (only present in 16 plots), lodgepole pine (8 plots), and Engelmann spruce (12 plots) were too small for individual models. In all models, we tested the following candidate biophysical predictor variables (see Table 1 for descriptions and expected effects): (1) HLI, (2) Beer's transformed aspect, (3) RdNBR, (4) distance to conspecific seed source, (5) grass (%), (6) forbs (%), (7) shrubs (%), and (8) salvage logging. RdNBR was strongly and positively correlated with distance to conspecific seed source (Spearman's $\rho = 0.67$, $P < 0.01$), and both variables had a similar effect on the density of post-fire stems. We selected distance to the seed source, because it is the result of burn severity and better represents the biological seed limitation to post-fire regeneration. We chose to test for the effects of total grass cover (rather than include a variable for plots seeded with grass), because competition from grasses results from the combined effects of natural regeneration and seeding of grasses and only 10 of 50 plots were seeded with grasses (i.e., unbalanced sampling). To account for plot remeasurement, we included "plot" as a random effect. All continuous predictor variables were standardized to allow comparison of model coefficients. Beginning with a full model of uncorrelated predictor variables, we selected the best predictor variables within each group (see Table 1 for groups) by minimizing the Akaike information criterion (AIC; Bozdogan 1987). To evaluate whether predictor variables improved model fit, we used an AIC threshold of 2 points, such that predictor variables that decreased AIC by >2 points were considered to have improved model fit. Model residuals were checked for dispersion with the "DHARMa" package in R (Hartig 2018).

Testing the influence of climate variability on height growth (question 5)

To test how height growth varied spatially (e.g., with topography), we constructed one GLMM with a Gaussian distribution ("glmmTMB" package in R). Specifically, we tested whether total annual height growth (average height growth over 5 years, 2016–2020) was affected by topography, stem height, burn severity, density of post-fire regeneration (i.e., competition), and tree species (ponderosa pine, Douglas fir, and grand fir; sample sizes of other species were too small). Annual height growth over 5 years accounted for the interannual variability in growth. We included "plot" as a random effect to account for measurements of multiple species within each plot. Standardization of predictor variables, model trimming, and residual diagnostics were completed using the same approach as the post-fire stem density models (see above).

To test how the interannual variability in climate affects the rate of post-fire recovery, we related an annual height growth chronology from 2006 to 2020 to monthly SPEI using Spearman's correlations. Plot-level chronologies of annual height growth increments were created by species using standard dendrochronological techniques ("dplR" package in R; Bunn 2010). To remove the age and height-related growth trend, annual height growth of individual trees was detrended with a linear regression model by dividing the raw growth increment measurement for each year by the regression value to produce a standardized growth index series (following Littlefield 2019). Individuals within plots and then plots within species were averaged annually using a biweighted robust mean (Bunn 2010) to produce a standardized height growth index by species from 2006 to 2020. We correlated monthly SPEI from March of the year prior to growth (to account for lagged effects) to October of the year of growth to the height growth index.

Results

Post-fire juvenile density and surviving tree density

For post-fire juveniles (seedlings and saplings), we counted 3812 and 4552 stems in 2011 and 2021, respectively. The median post-fire juvenile density of all species was 2083 stems ha^{-1} in 2011 and 3130 stems ha^{-1} in 2021, but density was highly variable (e.g., 33–100,501 stems ha^{-1} in 2021) (Fig. 2; Additional file 1: Table S3). Among post-fire juveniles, ponderosa pine, Douglas fir, and grand fir were present in >70% of plots in 2011, while western larch, Engelmann spruce, and lodgepole pine juveniles occurred in <35% of plots (Additional file 1: Table S3). Grand fir was less frequently encountered in plots than ponderosa pine or Douglas fir juveniles (2021 only), but when present, grand fir was on average more abundant than ponderosa pine or Douglas fir in both 2011 and 2021. The mean abundance of post-fire stems ha^{-1} increased from 2011 to 2021 for all species, except western larch.

Few plots had trees (134 live trees counted) that survived fire and lived to 2021 (38%), with a plot median of 0 stems ha^{-1} (range, 0–324 stems ha^{-1}) (Additional file 1: Table S3). Live ponderosa pine trees occurred in 28% of post-fire plots and were the most common species that survived fire.

All plots had post-fire juvenile stems present in 2011 and 2021 (Additional file 1: Table S3). When comparing post-fire juveniles and surviving trees to local stocking recommendations, we found that 18% (2011) and

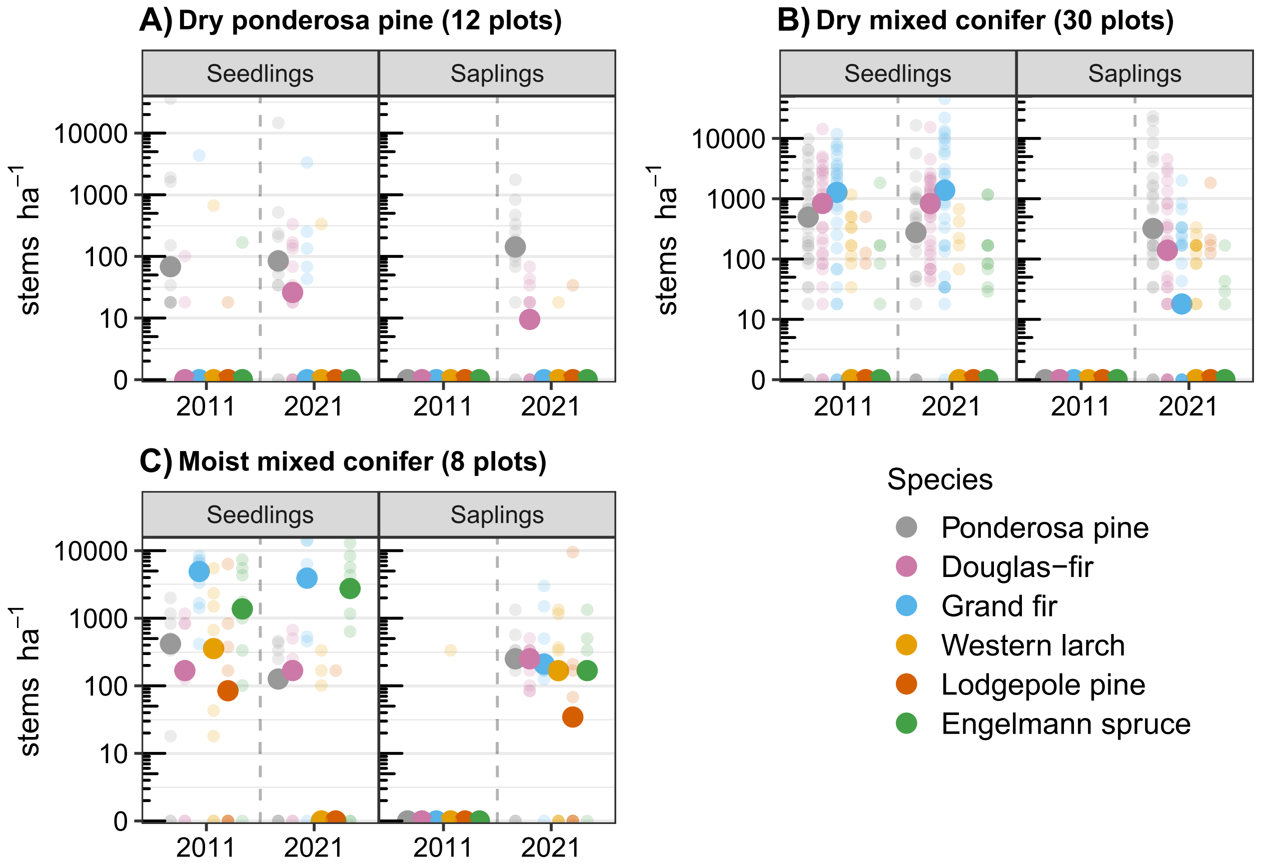


Fig. 2 Median (large solid dots) of plot (small dots) estimates of post-fire seedling (<1.4m tall) and sapling (>1.4m tall) density (stems ha^{-1}) in 2011 and 2021 by species for **A**–**C** three initial post-fire trajectories. Trajectories were grouped based on the species composition in 2011 to illustrate changes in species composition and structure from 2011 to 2021. Data were collected in 2011 and 2021 in the School Fire, Blue Mountains, WA, USA

4% (2021) of the 50 plots contained < 60 live stems ha^{-1} and 28% (2011) and 16% (2021) contained < 350 live stems ha^{-1}. Pre-fire stem densities of trees and saplings (median 3000 stems ha^{-1}, range 600–9600 stems ha^{-1}) were higher than stocking recommendations. Comparing stem densities within plots, post-fire stem densities were lower than pre-fire stem densities in 38% (2011) and 33% (2021) of plots (result only for 40 plots with pre-fire stem densities). Plots containing < 60 live post-fire stems ha^{-1} did not include any surviving trees and were generally found on warmer, drier aspects [mean transformed aspect 0.48 (warmer, drier) for all plots containing <60 stems ha^{-1} compared to 0.87 (cooler, wetter) in all other plots].

Changes in post-fire juvenile composition and structure from 2011 to 2021

The cumulative effects of post-fire establishment timing, juvenile densities, and growth rates by species resulted in changes in species composition and stand structures from 2011 to 2021 by initial post-fire trajectory (Fig. 2). For all initial trajectories from 2011 to 2021, the density of post-fire saplings increased for most species (Fig. 2) and post-fire seedling densities were roughly equivalent or decreased for most species, except Douglas fir (Fig. 2A), grand fir (Fig. 2B), and Engelmann spruce (Fig. 2C). In dry ponderosa pine stands, many ponderosa pine seedlings transitioned from the seedling to sapling size class and these plots continued to be dominated by ponderosa pine (Fig. 2A). In dry mixed conifer stands, the decrease in ponderosa pine seedlings (median, −28%) was a result of in-growth into the sapling size class (Fig. 2B), and ponderosa pine followed by Douglas fir was the most common and tallest species in the sapling size class. In moist mixed conifer stands, recruitment into the sapling size class from 2011 to 2021 resulted in lower densities of seedlings for most species, except Engelmann spruce (median, +63%) (Fig. 2C). Nearly all lodgepole pine and western larch seedlings transitioned to the sapling size class between 2011 and 2021 (Fig. 2C).

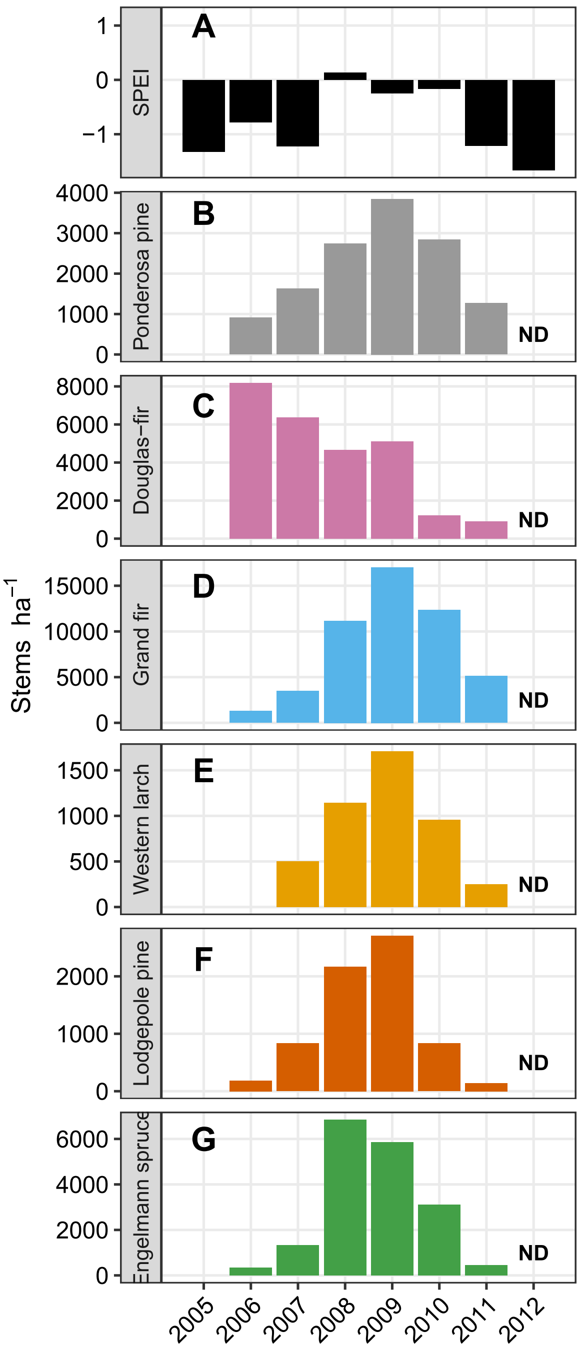


Fig. 3 **A** Standardized Precipitation Evaporation Index (SPEI; July 1 to September 31) and sum of post-fire, annual seedling establishment (stems ha^{-1}) from 2006 to 2011 for **B** ponderosa pine, **C** Douglas fir, **D** grand fir, **E** western larch, **F** lodgepole pine, and **G** Engelmann spruce. Only plots that burned at moderate to high severity and without salvage logging were included to reduce the effects of confounding factors. Positive values of SPEI indicate cooler and wetter conditions, while negative values indicate warmer and drier conditions. Note the *y*-axis scale varies by species. "ND" indicates no data available. Data were collected in July 2011 in the School Fire (2005), Blue Mountains, WA, USA

Effect of climate on seedling establishment

The density of annual post-fire seedling establishment increased from 1 year post-fire (2006) to a peak in 2008 or 2009 for all tree species, except Douglas fir (Fig. 3). Climate conditions were cooler and wetter (positive SPEI) during the summer (July–September) and growing season (April–September) from 2008 to 2010 relative to the 2 to 3 years before and after this period (Fig. 3A; Additional file 1: Fig. S2). Annual establishment was positively correlated with summer SPEI during the germination year ($\rho > 0.54$; $P < 0.09$) for grand fir, Engelmann spruce, and ponderosa pine and growing season (April–September) SPEI of the following year ($\rho > 0.70$; $P < 0.10$) for grand fir, lodgepole pine, ponderosa pine, and western larch (see Additional file 1: Table S5 for all correlations by species). In contrast, the establishment of Douglas fir occurred during a warmer, drier period (2006–2009) and was negatively correlated to spring and growing season SPEI during the germination year ($\rho > -0.89$; $P = 0.03$). Snow-water equivalent had no effect on establishment ($\rho < 0.43$; $P > 0.34$; Additional file 1: Fig. S2). Following 2011, growing season climate conditions were generally warm and dry (median SPEI −1.10, range −1.92–0.21) as were summer climate conditions (median SPEI −0.83, range −1.66–0.16; Additional file 1: Fig. S2).

Effect of biophysical factors on post-fire stem density

Post-fire juvenile densities were most strongly related to distances to seed sources, and percent grass cover, though the strength of the relationship varied by species in the four GLMMs (Fig. 4). Post-fire juvenile densities for grand fir, Douglas fir, and all species decreased with distance to seed sources (ΔAIC > 2, Fig. 4A, B). The distance from seed sources where the predicted post-fire juvenile density decreased below 350 stems ha^{-1} (silvicultural stocking metric) was 220m for ponderosa pine, 100m for Douglas fir, and 295m for grand fir (Fig. 4B). Greater percent grass cover was associated with lower post-fire juvenile densities in all four GLMMs (ΔAIC > 2; Fig. 4A, C). More southerly facing slopes, as indicated by the transformed slope aspect, were related to higher post-fire juvenile densities for Douglas fir only (ΔAIC > 2). Comparing plots seeded with perennial grasses (n=10) and not seeded (n=40), seeded plots had 150% higher grass cover, were located at lower elevations, and had 190% fewer juveniles (Additional file 1: Fig. S3). Salvage logging (0–4 years following fire) had no effect on post-fire juvenile densities 6 or 16 years after fire (ΔAIC < 2).

Effect of biophysical factors on post-fire stem height growth

Annual height growth varied among plots and by species (Additional file 1: Table S4). Annual height growth

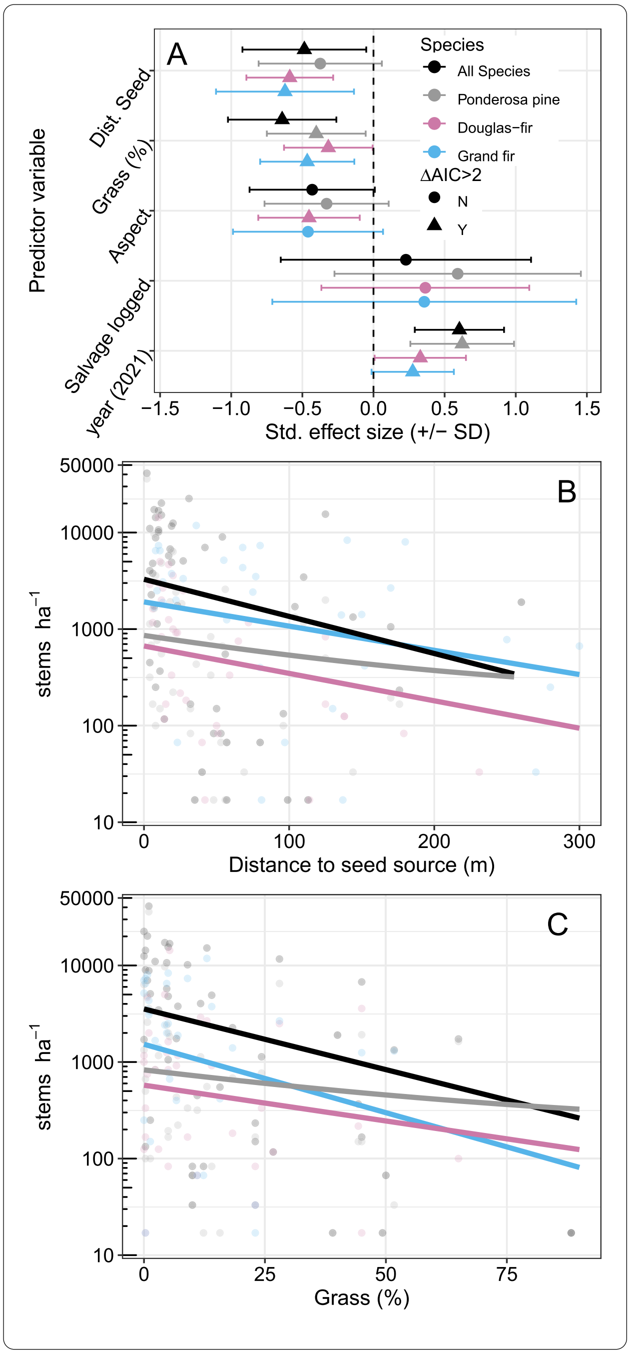


Fig. 4 **A** Results of four post-fire stem density generalized linear mixed models (i.e., coefficients) and modeled stem density (line) with varying **B** distance to seed source and **C** percent grass cover, assuming median values for other model predictors in 2011. Separate models were created for (1) all species, (2) grand fir, (3) Douglas fir, and (4) ponderosa pine. Final models of post-fire stem density included the following predictor variables: distance to the seed source, percent grass cover, transformed topographic aspect, salvage logging (presence/absence), and year of survey (see Table 1 for all variables considered); symbol shape in **A** indicates whether each predictor variable improved model fit (i.e., change in AIC > 2pts). **A** Predictor variables were standardized to allow comparison and error bars are 95% confidence intervals on coefficient estimates. **B**, **C** Note the *y*-axis is on a log scale (i.e., models appear linear), and points are the observed values in 2011. Data were collected in 2011 and 2021 in the School Fire, Blue Mountains, WA, USA

was greater in cooler, wetter site conditions (lower HLI) and in taller trees but varied by species in the GLMM (Fig. 5A–C). Salvage logging had no effect (Fig. 5A). Douglas fir was the fastest growing species followed by ponderosa pine, and grand fir grew the slowest (Fig. 5A), though this hierarchy varied with height (Fig. 3B). For a 250-cm-tall sapling, Douglas fir would on average grow 30.5 cm in height per year (± 3.5 cm), which was ~4 cm more than ponderosa pine and 6.5 cm more than grand fir. The difference in annual height growth was 4 cm between a warm, dry site (HLI $= 0.8$) compared to a cooler, wetter site (HLI $= 0.4$).

The interannual variability in climate was related to annual height growth for ponderosa pine, but not Douglas fir or grand fir (Fig. 6; Additional file 1: Fig. S4). For ponderosa pine, greater annual height growth was negatively correlated to SPEI (warmer, drier conditions) during the spring (April–June) of the year prior to growth ($P < 0.05$ for April to June) and the spring of growth ($P < 0.05$ for June; Fig. 6), and this result was consistent across most plots (>60%) (Additional file 1: Fig. S4).

Discussion

Abundant, natural post-fire tree establishment and fast height growth rates of juvenile trees in most plots imply that dry to moist mixed conifer forests are rapidly recovering following the School Fire. High abundances of post-fire regeneration, similar to those observed in the School Fire, were also found following multiple fires in the southern Blue Mountains (Downing et al 2019; Boag et al 2020). However, we did observe very low abundances of post-fire regeneration (<60 stems ha^{-1}) 16 years following high-severity fire in plots (4%) near the forest-grassland ecotone where forests in the Blue Mountains and western US appear to be more vulnerable to conversion from forest to non-forest or require longer periods to recover (Downing et al 2019; Stevens-Rumann and Morgan 2019; Boag et al 2020). Here, we show that the number of plots not meeting silvicultural stocking recommendation and pre-fire stem densities decreased from 2011 to 2021, evidence that seedlings are continuing to establish in warmer, drier sites. Below, we discuss the spatiotemporal drivers of post-fire seedling establishment and growth, the shift in the post-fire forest communities 6 to 16 years post-fire, and the implications of warming climate and shifting fire regimes for forest management.

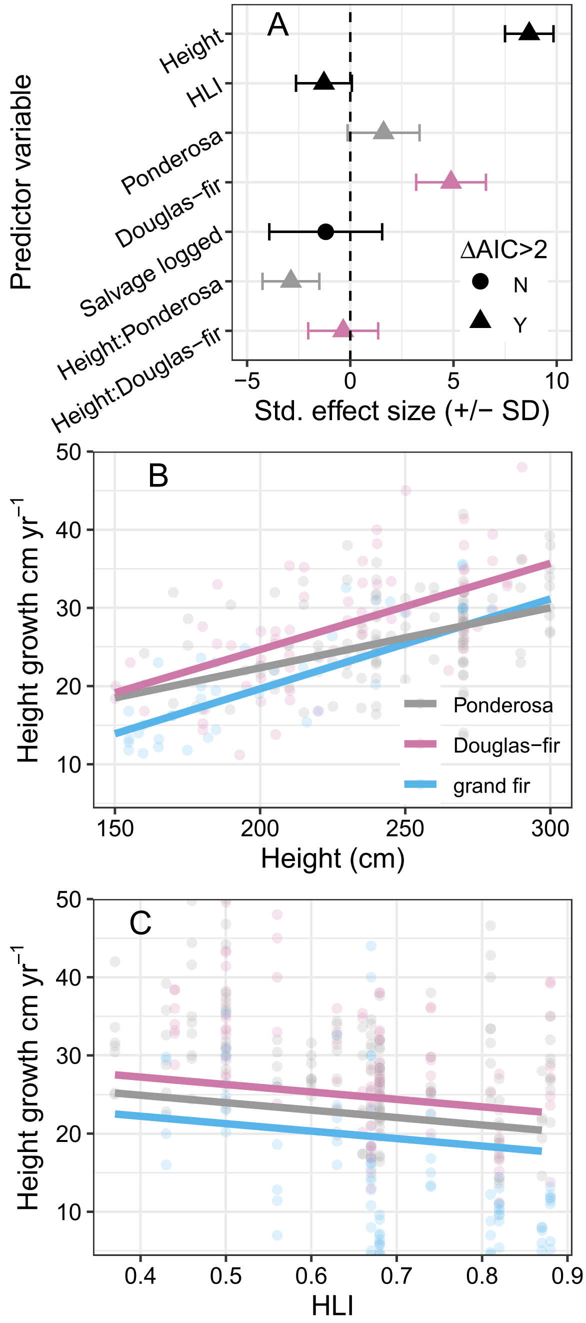


Fig. 5 **A** Results of annual post-fire height growth generalized linear mixed model (i.e., coefficients) and marginal effects of **B** stem height (cm) and **C** heat load index (HLI) on annual height growth (cm year^{-1}), assuming median values for other model predictors. Grand fir is the reference species in the model. **A** Predictor variables were standardized to allow comparison and error bars are 95% confidence intervals on coefficient estimates. Larger HLI values indicate warmer, drier conditions. Data were collected in 2021 in the School Fire, Blue Mountains, WA, USA

Our finding that post-fire juvenile densities decreased with distance to seed sources (Fig. 4B) is consistent with prior studies of post-fire regeneration in conifer forests of the Blue Mountains (Downing et al 2019, Boag et al 2020) and the western US (Kemp et al 2016, Stevens-Rumann and Morgan 2019). Limited post-fire conifer establishment is often observed beyond ~200 m from surviving trees in the western US (Stevens-Rumann and Morgan 2019), but we found densities of seedlings that exceeded minimum stocking thresholds (60 stems ha^{-1}) 200–300 m from seed sources (i.e., long-distance dispersal). Additionally, we expected to find differences among species in dispersal limitations based on seed mass such that ponderosa pine (heaviest seeds) would be more severely limited by dispersal distance than Douglas fir and grand fir (both medium-weight seeds). However, Douglas fir juvenile density dropped below 350 stems ha^{-1} (silvicultural stocking threshold) much closer to seed sources (~100 m) compared to ponderosa pine (~220 m) and grand fir (~295 m). Other studies have found that dispersal distances of the same focal species more closely track their respective seeds' mass (Kemp et al 2016). Differences among studies could be attributed to the choice of the response variable (e.g., stem density versus probability of presence), while inconsistent seed mass effects on dispersal distance limitations inferred from successful establishment may be attributed to variability among species in seed predation, seed quantity, and seedling survival rates (Zwolak et al 2010) or wind and local topography.

When seeds were available, higher abundances of post-fire seedling establishment coincided with cooler and wetter summer climate conditions during the year of and the year following germination for all species, except Douglas fir, in the 6 years following the School Fire (Fig. 3). Similarly, cooler and wetter spring climate conditions (year of germination and subsequent year) were associated with higher post-fire establishment for lodgepole pine, ponderosa pine, and western larch in the neighboring eastern Cascade Mountains (Littlefield 2019). Our finding that post-fire Douglas fir seedlings were less sensitive to high summer moisture deficits than ponderosa pine was also observed in post-fire regeneration in the Rocky Mountains (Davis et al 2019) and is supported by the higher resistance of young Douglas fir to hydraulic failure (Miller and Johnson 2017). However, the anomalous response of post-fire Douglas fir seedling establishment to climate compared to other species and no effect of climate on post-fire ponderosa pine establishment in the southern Blue Mountains (Downing et al 2019) stresses the need to relate annual climate to more accurate estimates of post-fire establishment ages from tree rings across gradients in topo-climatic variability (Hankin et al 2018). In summary, our results imply that

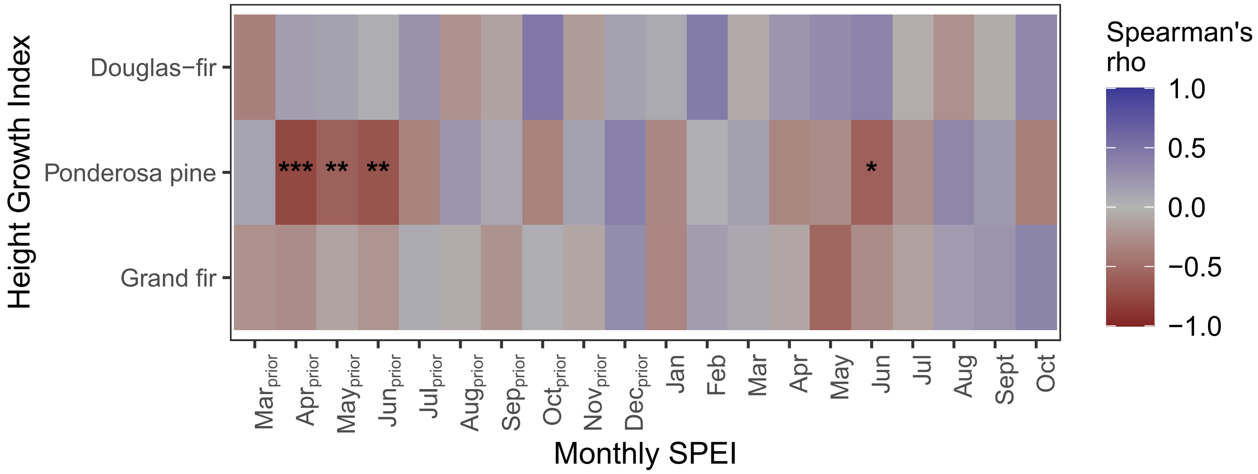


Fig. 6 Spearman's rank correlation coefficients for the relationship between annual height growth index and monthly Standardized Precipitation Evapotranspiration Index (SPEI) from March prior to the growth year to October of the growth year for the period 2006–2020 for Douglas fir (11 plots), ponderosa pine (15 plots), and grand fir (8 plots) in the School Fire. More positive values of SPEI indicate cooler and wetter conditions. Negative correlations (red squares) indicate that annual height growth increased under warmer and drier conditions. Annual height growth was averaged across all sites because site-level relationships were similar across plots (see Additional file 1: Fig. S4). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

increasing summer soil moisture deficits will likely limit post-fire seedling establishment for multiple species in dry to moist mixed conifer forests following future fires.

Abrupt transitions in aspect, created by complex topography (e.g., steep canyons, mountains, and plateaus), were a key driver of spatial variability in post-fire regeneration in our study and in the southern Blue Mountains (Boag et al 2020). Our finding that the sites with the lowest densities of post-fire juveniles (i.e., < 60 stems ha^{-1}) were found on more southerly aspects where warmer, drier conditions may be limiting survival of post-fire seedlings is consistent with our expectations. However, we also found that abundances of post-fire Douglas fir juveniles were higher on more southerly topographic aspects where conditions are warmer and drier (Fig. 4). This counter-intuitive result may be attributed to the forest types burned in the School Fire; drier mixed conifer forests, including higher abundances of Douglas fir, inhabit the more southerly aspects and mesic mixed conifer forests, including lower abundances of Douglas fir, inhabit more northerly aspects.

Post-fire seedling establishment determines where forests will recover, whereas height growth rates determine the individuals that have the competitive advantage over other vegetation and the development of fire-resistant traits (e.g., bark thickness and crown base height). Three species in dry mixed conifer forests grew faster in cooler, wetter topographic locations (Fig. 5), which may be attributed to the longer persistence of soil moisture during the annual summer drought. Interestingly, the inter-annual variability in climate only affected ponderosa pine height growth (Fig. 6). Ponderosa pines in the School Fire are growing in relatively cooler, wetter geographic locations compared to their distribution in the PNW (Additional file 1: Fig. S1). Warmer and drier spring climate during the year preceding and year of growth may promote photosynthesis for carbon gain and growth earlier in the growing season when soil moisture is greater relative to later in the growing season. In contrast, no effect of annual climate on height growth for grand fir and Douglas fir may indicate optimal climate conditions for height growth. Further research is needed to determine whether the complex response of height growth to topography and annual climate observed in the School Fire is indicative of species responses throughout their distributions.

Differences among species in post-fire seedling establishment densities and annual height growth influenced changes in post-fire stand composition and structure from 2011 to 2021 (Figs. 2, 3, 4, 5, and 6) and can help infer stand structure and composition in the upcoming decades in the absence of future disturbance. In general, the 2011 stand structure and composition were largely indicative of the structure and composition in 2021. This is most clearly illustrated by the ponderosa pine stands. Ponderosa pine established in higher abundances than Douglas fir by 2011 and ponderosa pine was ten times more abundant than Douglas fir in the sapling size class in 2021. However, faster height growth rates of Douglas fir than ponderosa pine suggests that a small component of Douglas fir will likely be included in the next forest canopy. In dry mixed conifer stands, Douglas fir and ponderosa pine are expected to form the next forest canopy, because of their greater total height in 2021 and faster growth rates than grand fir. However, grand fir, a more shade-tolerant and abundant species in the School Fire, will likely continue to be well represented in smaller diameter classes within these stands. In moist mixed conifer stands, the diverse mix of tree species (up to six species) and the spatial variability in species compositions, such as a few monotypic stands of lodgepole pine, complicate generalizations about the composition of the future forest canopy. In contrast to other stand types, higher abundances of post-fire seedlings in 2011 did not necessarily equate to higher abundances of post-fire saplings in 2021 by species in moist mixed conifer stands. This discrepancy can, in part, be attributed to differences in height growth rates, but monitoring is necessary to evaluate how multiple demographic rates (e.g., recruitment to large-size classes and mortality) will interact to shape the next forest canopy.

Management implications

Adapting forests to future climate conditions and altered disturbance regimes is a critical challenge for natural resource managers and scientists (Millar and Stephenson 2015; Vose et al 2018; Halofsky et al 2018). Robust scientific knowledge of forest ecosystem responses to wildfire that address climate change impacts and societal values (e.g., timber and recreation) is needed to inform science-based management (Higuera et al. 2019). We found that the patchiness of surviving trees created by low to high burn severity and the high abundances of juvenile trees post-fire, especially on higher elevation sites, is a sign of forest resilience at the stand scale. This finding strongly contrasts with mounting evidence for widespread tree regeneration failure following fire in some lower-elevation, dry forests (Davis et al 2019, Rodman et al 2020, but see Stevens-Rumann et al 2022). Depending on management objectives, tree species compositions and structures in the School Fire may need to be managed to promote species and stand structures that are less vulnerable to future climate conditions and disturbances (Millar et al 2007; Larson et al 2022).

Climate change is increasing growing season dryness and in turn affecting tree species distributions in the Inland Northwest (Rehfeldt et al 2006; Rehfeldt et al 2008), with more obvious effects on warm, dry topographic positions. Areas where densities of post-fire regeneration in the School Fire fell below stocking recommendations were more commonly located on warm, dry aspects (i.e., marginal sites), the same areas where planted seedlings are expected to experience low survival rates (Stevens-Rumann and Morgan 2019). Slower recruitment of post-fire seedlings, lower density forests, and large areas of non-forest on more southerly aspects are common in the Inland Northwest (Hessburg et al 2005). Accepting fire-caused transitions from forest to non-forest vegetation types in marginal sites may be beneficial for increasing landscape heterogeneity (Turner and Gardner 2015), promoting biodiversity (Lindenmayer and Franklin 2002), and conserving financial resources associated with post-fire management.

Our research also addresses the potential implications of salvage logging and seeding of grasses for post-fire tree regeneration. We found no significant effect of salvage logging on juvenile density or height growth 6 or 16 years after fire (Figs. 4 and 5), which is consistent with neutral to slightly higher post-fire regeneration densities observed >15 years after fire in similar forest types in the neighboring eastern Cascades and Okanogan ecoregions (Povak et al 2020). One possible explanation for not observing an effect of salvage logging in our study was that climate conditions suitable for post-fire establishment did not occur until after salvage logging was completed.

Of greater significance to stand-scale recovery was the seeding of native grasses, which created notably higher grass cover and was associated with lower densities of tree seedlings 6 and 16 years after fire (Fig. 4). Early and rapid establishment of post-fire tree seedlings is critical for determining longer-term forest trajectories, because grasses and shrubs can increase competition for key resources (e.g., soil moisture, nutrients, light) in the first few years following fire (Droske 2012; Tepley et al 2017) and negatively affect seedling survival (Barclay et al 2004). While grass seeding can promote early and rapid colonization of grasses to increase soil stability in post-fire environments (Robichaud et al 2013), greater cover of grasses may reduce the density of post-fire seedlings and slow post-fire forest recovery (Barclay et al 2004).

Conclusions

Current trends toward increasing area burned and unfavorable climate conditions for post-fire seedling establishment are expected to continue, highlighting the need to understand complex forest ecosystem responses to fire over time. Our research identifies biophysical limitations and post-fire management effects on post-fire seedling establishment and annual height growth, two key properties of post-fire forest recovery. Abundant post-fire seedling establishment and rapid height growth of multiple species imply that most stands will likely recover to forest following the School fire. However, high spatiotemporal variability in densities of post-fire seedling establishment and differences among species in height growth—resulting from limitations created by climate, topography, grass cover (supplemented with grass seeding), and species life history strategies—will likely lead to a heterogenous post-fire forest landscape. Long-term monitoring of post-fire recovery dynamics is needed to determine how and when climate change and future disturbances will affect height growth and survival to shape the future forest structure and composition.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-022-00153-4.

Additional file 1: Supplementary information for spatial and temporal drivers of post-fire tree establishment and height growth in a managed forest landscape.

Acknowledgements
We thank I.W. for helping in the field, D.H. for reviewing an earlier version of this manuscript, and the Umatilla National Forest for logistical support. Additionally, we thank the guest editor and two anonymous reviewers for their constructive criticism on earlier versions of this manuscript.

Authors' contributions

Authors 2–6 are ranked alphabetically rather than in order of contribution. As described in the methods, the design of the present study was based on a Master of Science thesis written by C.D. and advised by P.M. at the University of Idaho. R.A.A., M.F., A.H., and A.J.H.M designed the present study. R.A.A. and M.F. collected the field data. R.A.A. performed the statistical analyses. R.A.A. led the writing of the manuscript. All authors helped revise the manuscript and gave final approval for publication.

Funding
The initial measurements of the post-fire regeneration plots were supported in part by funds provided by the Rocky Mountain Research Station and the Umatilla National Forest, Forest Service, US Department of Agriculture, through agreement 08-JV-11221634-236 with the University of Idaho; by the USDA/USDI Joint Fire Science Program (Project 06-1-2-03); and by the University of Idaho. The remeasurement was supported by USDA NIFA, McIntire Stennis Project WNP00009.

Availability of data and materials

The datasets analyzed in the current study are available from the corresponding author.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 1 March 2022 Accepted: 26 October 2022
Published online: 05 December 2022

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