



Microsite conditions in a low-elevation Engelmann spruce forest favor ponderosa pine establishment during drought conditions

Edward M. Hill*, Seth Ex

Department of Forest and Rangeland Stewardship, Colorado State University, 1472 Campus Delivery, Fort Collins, CO 80523 USA



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ABSTRACT

Warming climate in U.S. forests may limit future viability of dominant high-elevation species at their lower elevation range limits but favor more drought-adapted sympatric species, potentially contributing to species distribution changes. Adaptive management may address future uncertainty in species distributions by facilitating regeneration of multiple species with contrasting silvics. However, the success of this approach will depend on suitable microsite conditions, the effects of which are not well understood across species and forest types. These concerns are present in the southern Rocky Mountain region, where current and future climate may restrict Engelmann spruce regeneration but benefit sympatric species like ponderosa pine. We used a planting experiment to systematically evaluate microsite conditions which support critical first-season survival and root growth of these contrasting species in a low-elevation spruce forest during a droughty 2018 growing season. Our assessment targeted species responses to variation in canopy cover generated by different silvicultural regeneration treatments, with and without additional shelter from coarse woody debris. We also considered microsite variables of seedling size, vegetation and litter cover, soil moisture and depth, and competition from established tree regeneration. Survival of ponderosa pine was nearly twice that of Engelmann spruce, but the relative effects of microsite variables were similar. Coarse woody debris shelter improved the probability of survival by approximately 357%, though the effect was stronger for spruce. Influences of canopy cover were minimal and opposite our expectations; spruce was marginally inhibited by canopy cover, while pine was positively influenced by more dense canopy. Smaller seedling heights improved the probability of survival for both species by 179% compared to mean seedling heights. Pine root growth was 150% greater in open versus dense canopy microsites and limited in coarse woody debris shelter. We discuss likely site and physiological factors underlying these results. This study provides insight into the factors which define suitable microsites for first-season establishment for these species in rapidly changing low-elevation spruce forests, especially during drought conditions. We discuss implications for adaptive management and silviculture, concluding that regeneration efforts which seek to improve forest resilience to climate-related changes in species viability could consider more drought-adapted, sympatric species as viable supplements to moisture-dependent species at their current lower range limits.

1. Introduction

Adaptive forest management seeks to address potential climate change impacts on forest dynamics, such as more frequent disturbance and altered species habitat suitability, but adaptive management practices appropriate for specific regional settings and forest types are not yet well understood (e.g., Kemp et al., 2015; Sousa-Silva et al., 2018). The practice of adaptive management is often hindered by both uncertainty in the precise mechanisms and outcomes of projected ecological change as well as a lack of precedent and systematic evaluation of relevant management options for species of concern (Keenan,

2015; Fahey et al., 2018). In a recent, extensive survey of climate adaptation practices in forest management across Europe, lack of relevant information and technical knowledge (e.g. expected species performance) accounted for 57% of reported obstacles to implementation of adaptive concepts (Sousa-Silva et al., 2018). Similar surveys of forest managers and planners in North America have echoed these sentiments (Kemp et al., 2015; Halofsky et al., 2018). These concerns have in part been resolved through development of broadly applicable adaptation frameworks rooted in the concepts of “resistance” and “resilience” (DeRose and Long, 2014) and are increasingly incorporated into operational-scale field trials of different management practices

* Corresponding author at: Colorado State University, Department of Forest and Rangeland Stewardship, 1472 Campus Delivery, Fort Collins, CO 80523-1472.
E-mail addresses: emhill@rams.colostate.edu (E.M. Hill), seth.ex@colostate.edu (S. Ex).

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(e.g., Nagel et al., 2017; Yousefpour et al., 2017; Halofsky et al., 2018; Fahey et al., 2018). However, adaptive approaches seek to contend with uncertainty in the outcomes of environmental change, which are dependent on ecological responses and feedbacks occurring at local to regional geographic scales (Jacobs et al., 2015; Messier et al., 2016; Fischer, 2018). These relationships are readily evident in many fundamental ecological processes in forests which are non-linear and change in direction and magnitude over space and time, such as the dynamics of density dependent mortality, competitive interactions among species, and tree growth responses to changing light or climate conditions (Messier et al., 2016). The magnitude of complexity (both ecological and practical) presented by non-linear processes and feedbacks creates “moving targets” for adaptive management, such as when and to what extent shifts in habitat suitability for different species could occur, which are best addressed at local to regional scales (Keenan, 2015; Fischer, 2018). Consequently, there is a need to better understand mechanisms of change as they relate to environmental and practical concerns in local- and regional-specific management applications (Keenan, 2015; Kemp et al., 2015; Lawrence, 2017; Fahey et al., 2018; Sousa-Silva et al., 2018).

While the climate-related processes that could drive changes to forests are complex, the restrictive nature of conditions suitable for seedling establishment relative to adult survival suggests that tree regeneration is a likely mechanism of shifts in species distributions and forest cover as a result of climate change (Bell et al., 2014; Copenhagen-Parry et al., 2017). Consequently, regeneration conditions are a central focus for adaptive management and silviculture, for which tree regeneration is a fundamental concern. These concerns are likely to be amplified in areas that are marginal relative to the general distribution of a species (Bell et al., 2014; Dobrowski et al., 2015), such as lower and upper elevation range extents (Kroiss and HilleRisLambers, 2015). Regeneration in these areas will depend in part on species-specific adaptations to abiotic extremes or variability (e.g., Ibáñez et al., 2007; Larson and Funk, 2016) and the availability of microsite conditions suitable to survival and growth of seedlings. For example, recent assessments of potential species range shifts in the Pacific Northwest indicate that varying tolerances for snowpack and canopy cover conditions were strong differentiators between species with respect to microsite suitability for recruitment above treeline (Kroiss and HilleRisLambers, 2015). Adaptive approaches to regeneration in such circumstances, to contend with future uncertainty, may therefore include managing for a diversity of species with different adaptations to current or expected environmental conditions (Aitken et al., 2008; Hof et al., 2017; Long et al., 2018). Success in these regeneration efforts will depend in part on more thorough accounting of biophysical microsite influences for species of interest (Lembrechts et al., 2018), especially those affected by silvicultural practices (Chmura et al., 2011; Larson and Funk, 2016; Anderson and Puettmann, 2017). For instance, the amount and spatial distribution of overstory density resulting from silvicultural treatments can favor or disfavor species through their effects on the biophysical environment, such as penetration of light and precipitation, understory vegetation density, and microhabitats of soil biota (Jacobs et al., 2015). Regeneration is therefore a critical consideration in adaptive management that is responsive to the uncertain outcomes of climate change, necessitating greater understanding of microsite influences on the performance of species of interest, especially in sensitive marginal distribution areas.

Adaptive approaches to regeneration in the southern Rocky Mountain region will likely need to consider greater frequency of growing season drought conditions resulting from reduced snowpack and increased summer temperatures in the future (Lukas et al., 2014). These anticipated changes may restrict survivorship of mesic, high-elevation species, especially at their lower elevation range (marginal) limits (Conlisk et al., 2017; Kueppers et al., 2017), while favoring or expanding that of more xeric, montane species (Rehfeldt et al., 2014; Elsen and Tingley, 2015). Persistence of current dominant species and

expansion of sympatric species where high-elevation and montane species overlap in this region, like mesic mixed-conifer forests, will be dependent on the availability of microsite conditions which support survival and growth of young trees/regeneration each species. Microsite factors most important in this regard may include soils (texture and nutrient content), site moisture characteristics, and competitive or facilitative effects (i.e. shade or shelter) from understory and overstory vegetation cover. Silvicultural practices can precipitate, facilitate, or constrain tree regeneration by direct and indirect alteration of these biophysical microsite characteristics within a forest site (Nyland, 2016; Chen et al., 1999). Most notably, management of structural conditions like density of canopy trees can influence microsite temperature and moisture relations for juvenile trees (Chen et al., 1999; Aussenac, 2000; Gray et al., 2002; von Arx et al., 2013; Davis et al., 2019) and will often be used to target regeneration of different species based on their tolerances for exposed or sheltered conditions (e.g., Long et al., 2018). In this way, silvicultural practices directly influence the presence and distribution of niche conditions for different species which are desired for regeneration. The prevailing vulnerability and uncertainty of climate change impacts on these forests present novel backdrops against which to evaluate mechanisms of successful regeneration. More precise understanding of microsite conditions that are limiting for successful regeneration of different species in these forests will help to inform effective silvicultural practices and ensure future forest viability.

In the southern Rocky Mountain region, the vulnerability of dominant high-elevation species to changing climate is a concern for management of regeneration in low-elevation Engelmann spruce (*Picea engelmannii*) forests. Engelmann spruce is a highly moisture dependent species, and young seedlings may be acutely dependent on microsite influences that facilitate moisture availability, particularly in low-elevation forest stands (Conlisk et al., 2017; Kueppers et al., 2017) and at young life-stages (Hill et al., 2019). Engelmann spruce has been historically difficult to regenerate in this region with even-aged (e.g. clearcut regeneration treatments) silvicultural systems, while uneven-aged, selection-based systems have generally led to greater success (Alexander, 1987; Davy, 2016). Silvicultural practices which retain sufficient canopy cover and coarse woody debris on the forest floor may help create regeneration niches with relatively high moisture availability (e.g., Day, 1963, 1964; Ronco, 1967, 1970; Davy, 2016). For instance, research on tree-density related effects from silvicultural practices suggests that Engelmann spruce typically favor low (Hill et al., 2019) to intermediate (Alexander et al., 1985) amounts of canopy cover in selection-based regeneration treatments, or artificial or topographic sheltering in the absence of canopy cover (e.g. clearcuts; Alexander, 1966, 1984; Jacobs, 2011). Further complicating Engelmann spruce regeneration efforts, recent modeling studies suggest that climate warming will significantly limit spruce seedling germination and survival (Conlisk et al., 2017; Kueppers et al., 2017) and effectively preclude spruce persistence in marginal portions of its range within 40–50 years (Rehfeldt et al., 2015). However, Engelmann spruce is an important species in this region for conservation efforts via (adaptive) forest management, due to its value as a timber species, role in wildlife habitat (e.g. elk), and aesthetics and recreation (CFRI, 2017). It is crucial to develop more precise knowledge of microsite influences supporting Engelmann spruce persistence in these forests experiencing meso-scale climate changes which are increasingly divergent from typical spruce habitat. Projected declines in Engelmann spruce viability in these forests and its regional socioeconomic importance necessitate this renewed focus on conditions supporting its persistence.

Ponderosa pine (*Pinus ponderosa*) is a sympatric species in this region which may be better adapted to forecasted changes, especially for its superior ability to withstand drought and better leverage warmer conditions for growth (e.g., Rehfeldt et al., 2014; Carroll et al., 2017). Ponderosa pine may not depend on silvicultural practices which emphasize retaining overstory tree density or shelter (Shepperd et al., 2006) to the same extent as Engelmann spruce in low-elevation spruce

forests. Ponderosa pine regeneration may instead benefit from resource environments characteristic of open canopy conditions at higher elevations relative to its core range (Korb et al., 2019), as repeatedly documented both after disturbance (Chambers et al., 2016; Rother and Veblen, 2016; Francis et al., 2018; Fialko, 2018) and in intact forests (Stein, 1988; Puhlick et al., 2012). Whether or not ponderosa pine would naturally disperse to low-elevation spruce forests is unresolved, but dispersal of its heavy seeds typically declines exponentially from live seed sources and is especially limited beyond about 50 m (Chambers et al., 2016). Therefore, regeneration potential of ponderosa pine in these forests may in part be dependent on small-scale, long-term natural movements or active assisted migration by management, such as through planting. However, it is unclear to what extent ponderosa pine's characteristic dominance of comparatively moisture limited montane forests and the prevailing mechanisms determining its regeneration success translate into a relative advantage in actively changing low-elevation Engelmann spruce forests, specifically for young seedlings typically more sensitive to hot and dry conditions (e.g., Petrie et al., 2016). Uncertainty in climate-driven outcomes in these forests underscores the importance of assessing the performance of ponderosa pine in the same regeneration environments as Engelmann spruce, to evaluate the relative availability of suitable microsite conditions for pine.

Because of anticipated climate change effects in low-elevation Engelmann spruce forests in the southern Rocky Mountains, adaptive management in these areas might consider reforestation using both Engelmann spruce and ponderosa pine to limit the possibility of total regeneration failures, and to maintain resilience to uncertain climate change outcomes. Our objective in this study was to determine how microsite conditions affect survival of Engelmann spruce seedlings in a low-elevation spruce forest, and how their effects differed for a sympatric species with contrasting shade and drought tolerance traits. We chose to focus our study specifically on conditions which support first-season establishment of planted seedlings because obstacles to establishment in this period are particularly acute (Grossnickle, 2012) and therefore critical to account for in reforestation efforts. However, we recognize that seed availability, germination, and new germinant survival can be substantial constraints on natural regeneration processes. Because shade or shelter has been shown to be an important factor for establishment of these species in the southern Rocky Mountains (e.g., Alexander, 1987; Shepperd et al., 2006) and is directly manipulated by silvicultural treatments, we chose to focus our evaluation of microsites on these influences, while also accounting for other microsite conditions such as size of seedlings, understory vegetation cover, and soil moisture (e.g. Pinto et al., 2012; Puhlick et al., 2012; Newsome et al., 2016). We expected Engelmann spruce to be favored in higher shade relative to unshaded environments but expected pine to be less influenced by shade. Our study illuminates the limiting factors that define suitable regeneration microsites for seedlings of these contrasting species in rapidly changing Engelmann spruce forests, specifically during drought conditions and the acute stresses of first-season, planted seedling establishment. Our findings can inform adaptive management by identifying components of the microsite environment that are conducive to Engelmann spruce and ponderosa pine seedling establishment, thus supporting efforts to mitigate undesirable effects of climate change in these forests.

2. Methods

2.1. Study area

We established a planting experiment to study microsite conditions in May 2018 in a recently harvested timber sale on the Uncompahgre National Forest in southwest Colorado (~38° 26' N, 108° 25' W; Fig. 1). This site falls within areas of projected declines in future Engelmann spruce habitat suitability which intersect with projected expansion for

that of ponderosa pine (Mathys et al., 2014; Rehfeldt et al., 2014, 2015). The site ranges from 2714 to 2805 m (mean 2,760 m \pm 21.6) elevation in an Engelmann spruce-dominated forest on the Uncompahgre Plateau. Topography is northerly in aspect with slopes less than 10% on average (USDA NRCS, 2018). Soils are characterized by minimal organic layers, low water holding capacity, and shallow bedrock (25–76 cm depth; Hughes et al., 1995; USDA NRCS, 2018). Engelmann spruce is the dominant tree species in the study area (~49% of total basal area), while ponderosa pine is a co-dominant overstory species in northern portions of the study area (but < 3% of total basal area). Pockets of Douglas-fir (*Pseudotsuga menziesii*) are also present (~11% of total basal area), and aspen (*Populus tremuloides*) is abundant in both the canopy and understory (~22% of total basal area). Though subalpine fir (*Abies lasiocarpa*) is also a ubiquitous associate throughout the area (~16% of total basal area), mortality of canopy fir at the time of study was close to 100% due to previous western spruce budworm (*Choristoneura freemani*) activity. The study area included no visual evidence of previous large-scale disturbance. Fire return intervals in these cool-moist mixed conifer forests are on the order of hundreds of years, and the most recent stand-replacing fire likely occurred in 1879 when much of the Uncompahgre Plateau forests were consumed by severe fire (Baker, 2017).

Data from a SNOTEL site 3.9 km from the study site indicate that the area receives about 845 mm annual precipitation on average (1987–2017 data from SNOTEL site 409, ~2870 m, 38°25' N, 108°23' W, <https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=409>), which is highly dependent on snow precipitation. Growing season (May–September) precipitation accounts for only about 26% of annual totals and arrives predominantly in July–September. Temperatures average 12.8° C during the growing season and typically reach their annual average maximum (30.7° C) in July or August. Conditions during our study period (May–October 2018) diverged considerably (Fig. 2) from these average conditions. Notably, average temperatures over the growing season period were 1.6° C higher, and precipitation, totaling only 7.87 cm, was 36% of the average over this period. Additionally, precipitation accumulation was highly variable, with over 50% coming during July 2018 and zero accumulation recorded in June 2018. While temperatures during this period were within the range (one standard deviation) of the long-term record variability (Fig. 2), the lack of late season precipitation (August–September) was outside this range. More importantly, winter precipitation (October 2017–April 2018), when the majority of annual precipitation is expected to accumulate, in the 2018 water year was only 38% of average (well outside the range of long-term variability) and temperatures 2.28° C higher on average (Fig. 2). The consequences of these water year patterns resulted in considerable drought during our study period, conditions which may reflect climate changes which have been predicted to occur in this region (Lukas et al., 2014).

2.2. Experimental design and measurements

We randomly located 206 plots within the study area (Fig. 1) for planting tree seedlings and examining the effects of microsite (~1 m²; Gray and Spies, 1997) characteristics on their performance. We stratified sampling across three canopy environments which differed with respect to density of canopy trees resulting from different silvicultural regeneration treatments. These canopy strata included: (1) group-selection openings with little to no canopy cover; (2) individual-tree selection areas with variable canopy cover; and (3) no treatment areas with continuous canopy cover (Fig. 1). Sixty-nine plots were established in both group-selection and no treatment strata, and 68 in the individual-tree selection canopy stratum. Study area delineation and point generation were accomplished using geospatial data processing tools available in ArcMap 10.5.1 (ESRI Inc., Redlands, CA, USA).

Plot layout was designed to accommodate planted seedlings for both species, manipulation of woody debris microsite shelter, and

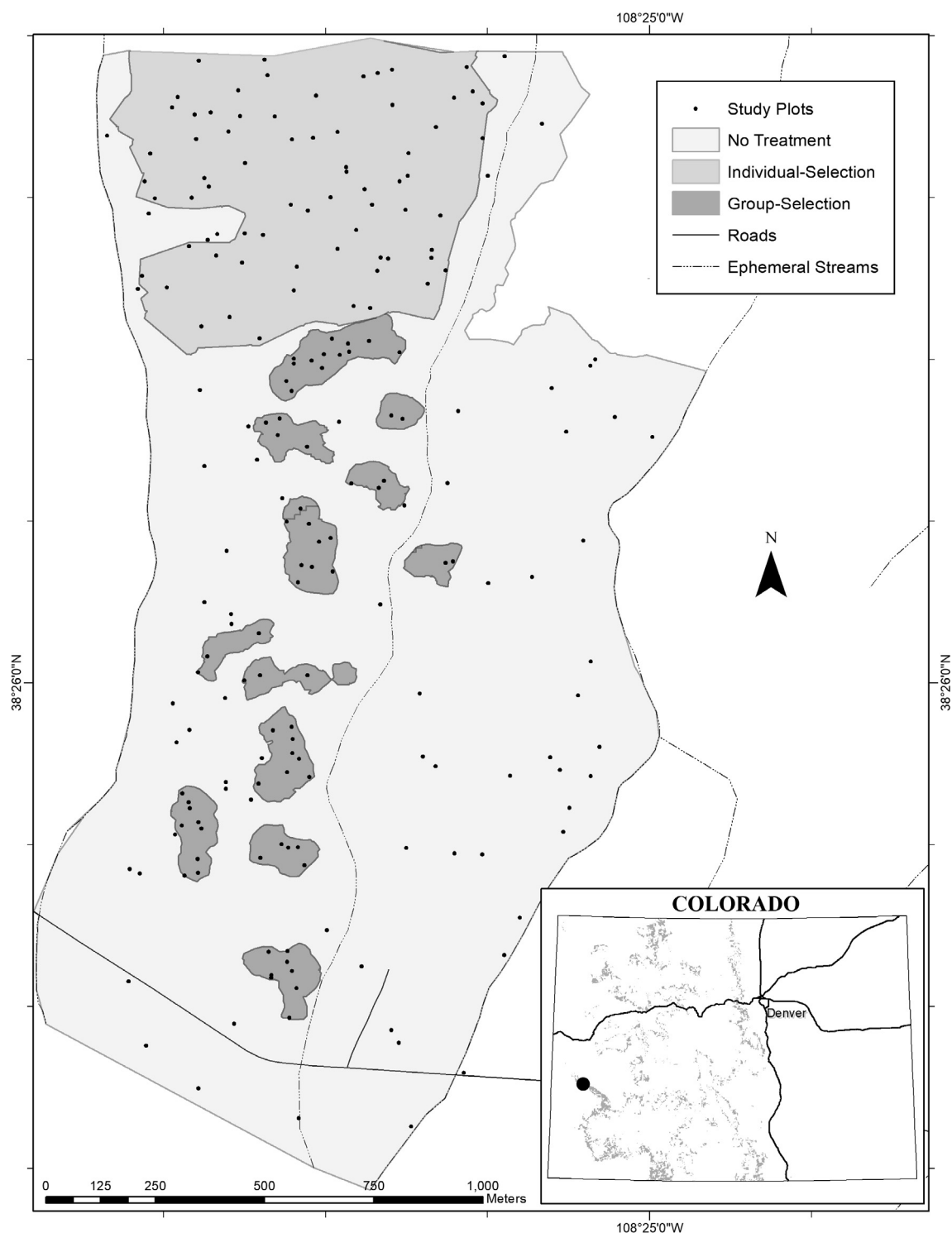


Fig. 1. The study was located on the Uncompahgre Plateau in southwest Colorado (black circle, locator map). Gray detail on the Colorado locator map shows area of overlap in predicted Engelmann spruce habitat declines and ponderosa pine habitat increases (Mathys et al., 2014). The study area was established in a recently harvested timber sale area. In the harvest area (data via Todd Gardiner, personal communication, April 11, 2018), dark shading indicates group-selection treatment openings and medium shading indicates individual-tree selection treatment area. No treatment (unharvested) areas are indicated by light shading. Elevation of the area ranges from 2,714 to 2,805 m, and slopes are largely < 10% with northerly aspects. Plots in our study are indicated by circles; two seedlings of each species were planted at each plot location, one with coarse woody debris shelter and one without. All data, unless otherwise indicated, were retrieved from the USDA NRCS Geospatial Data Gateway (USDA NRCS, 2018).

measurements of biophysical microsite variables potentially affecting seedling survival and growth (Fig. 3). Around each plot center, a 1 m² area was established, with each side of the square set perpendicular to the four cardinal directions and corners of the square serving as

seedling planting locations. Coarse woody debris from the site was placed on the north side of each plot to create microsite shelter (“CWD shelter”) for each seedling planted on the northern corners at a given plot (Landis, 2010; Davy, 2016). We chose the nearest piece of CWD to

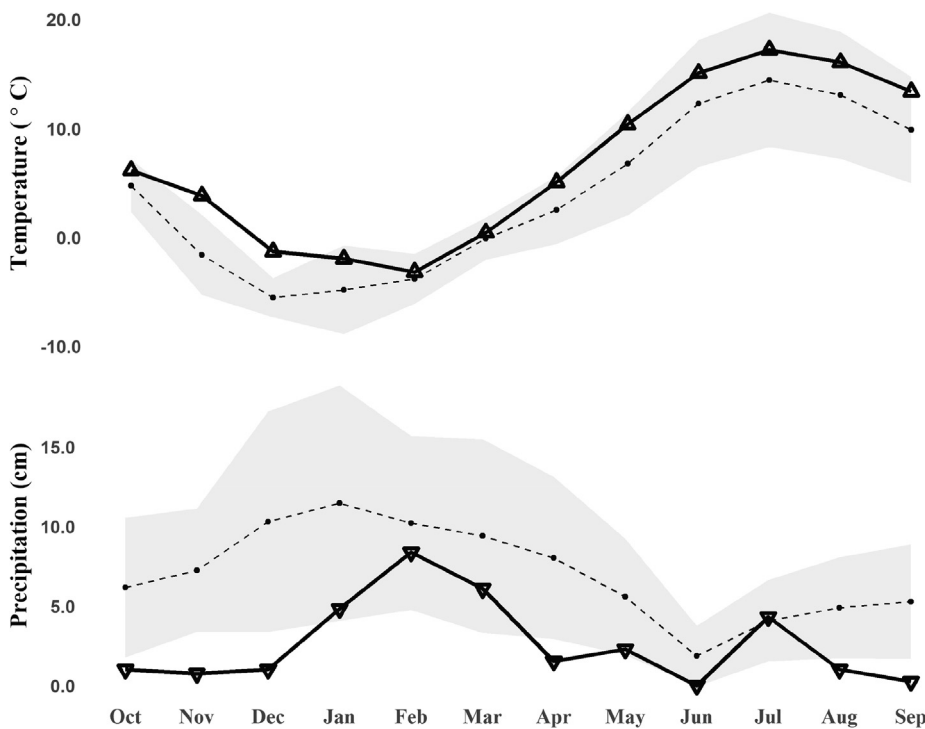


Fig. 2. Temperature (top panel) and precipitation (bottom panel) for the long-term average (1987–2017; dashed line with solid points; shaded area represents one standard deviation) and the 2018 water year (October 2017–September 2018; solid line with open triangle points), inclusive of our study period growing season (May–September 2018). The exceptionally warm and dry winter months (October–April) were particularly consequential for subsequent growing-season drought conditions. Climate data were downloaded from the Columbine Pass USDA NRCS SNOTEL site (site 409, ~ 2870 m, 38°25' N, 108°23' W, <https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=409>).

plot center which had a diameter of at least 7.6 cm, or 75% of the minimum target height (10.2 cm; Richard Gilbert, personal communication, July 20, 2018) of our seedlings to ensure sufficient shelter (e.g., Maher et al., 2015). Data from prior work on the effects of CWD shelter for Engelmann spruce regeneration in nearby harvest openings suggest that temperatures are significantly lower (5.5 °C on average) than ambient on the north side of CWD shelter (≥ 5 cm diameter) and significantly enhance germination and seedling survival (Davy, 2016).

We planted 824 Engelmann spruce and ponderosa pine seedlings (412 of each; 2 per species per plot) in June 2018 over the course of five days. Seedlings were 1–0 containerized (108.2 cm³ plug volume; Richard Gilbert, personal communication, July 20, 2018) stock grown at U.S. Forest Service facilities (Bessey Nursery, Halsey, Nebraska). Seedlings were planted on plot corners (Fig. 3) so that one seedling of each species was planted with CWD shelter (Fig. 3 positions 1–2) and one of each species was planted without CWD shelter (Fig. 3 positions 3–4). The number of seedlings planted of each species per plot was chosen to allow for greater number of plots within a canopy stratum to capture within-stratum density gradients, and to limit any possibility of direct seedling competition given the small plot size. Hoedad tools were used to remove surface vegetation and debris in a circle of ~15 cm radius at each planting position (Landis, 2010), and subsequently used to plant each seedling. At the time of planting we measured diameter at root collar (DRC) and height from DRC to the top of the terminal bud for each seedling. Size was measured to account for the potential effects of planting stock size on survival (e.g., Davis and Jacobs, 2005; Grossnickle and MacDonald, 2018).

The effects of canopy tree density, or canopy cover, on seedling regeneration environments (Chen, 1997; Holmgren et al., 2012; von Arx et al., 2013; Davis et al., 2019) were estimated with hemispherical photographs taken at each plot center. Photographs were taken in pre-dawn and overcast sky conditions 30 cm above ground height (max seedling height) using a camera mounted on a self-leveling mechanism equipped with a fish-eye lens (24MP DSLR Compact OMount, Regent Instruments, Inc., Québec, Canada). We processed each photograph using WinSCANOPY Pro 2016a software (Regent Instruments, Inc., Québec, Canada) to obtain estimates of percent openness of the canopy, which can be representative of available photosynthetically active

radiation and exposure to atmospheric fluctuations in temperature and moisture (e.g., Frazer et al., 1997). For added comparability with more standard silvicultural treatment metrics (e.g., Alexander, 1987; Shepperd et al., 2006), we also sampled basal area of overstory trees (≥ 5 cm diameter at breast height, DBH) with variable-radius plots using a 2.30 basal area (m² ha⁻¹) factor prism. Canopy openness was strongly negatively correlated (Pearson's $r = -0.82$) with basal area across plots.

Other biophysical microsite variables which had potential to positively or negatively affect the resource environments of seedlings were sampled at each plot center (Fig. 3). Counts of advanced regeneration (< 5 cm diameter at breast height) within a fixed area plot of 3.6 m radius from plot center were recorded for 0.5 m height classes. Established juvenile trees can be either competitive or facilitative influences for younger seedlings (e.g., Callaway, 1998). Percent cover of vegetation, litter/debris, and bare soil were estimated in 5% increments within 0.5 m² quadrat situated about plot center (Fig. 3). We took cover estimates to account for potential productivity and competition within a given microsite relevant to these species (e.g., Day, 1963, 1964; Fleming et al., 1998; Pinto et al., 2012; Puhlick et al., 2012; Ouzts et al., 2015; Newsome et al., 2016). It is possible that the direct effects of vegetation on seedlings were muted by preparation of planting positions, but were still a possible microsite influence on moisture retention and competition or on light availability (e.g. overtopping). Soil cores (0–20 cm) were extracted using a 2.2 cm dia. corer from each plot center during 3 consecutive days (same weather conditions) in July 2018 to estimate relative moisture availability at a given plot location (Kolb and Robberecht, 1996; Puhlick et al., 2012; Gill et al., 2015). Soil samples were weighed in the field, bagged, and oven dried at 105 °C to constant mass (Saxton and Rawls, 2006) for determining gravimetric water content (GWC). Depth to restriction was recorded in all plots where the 20 cm depth was not possible. Finally, elevation was recorded at each plot to account for any potential effects of differences across the site.

2.3. Seedling performance: survival and root growth

Our measures of seedling performance relative to microsite

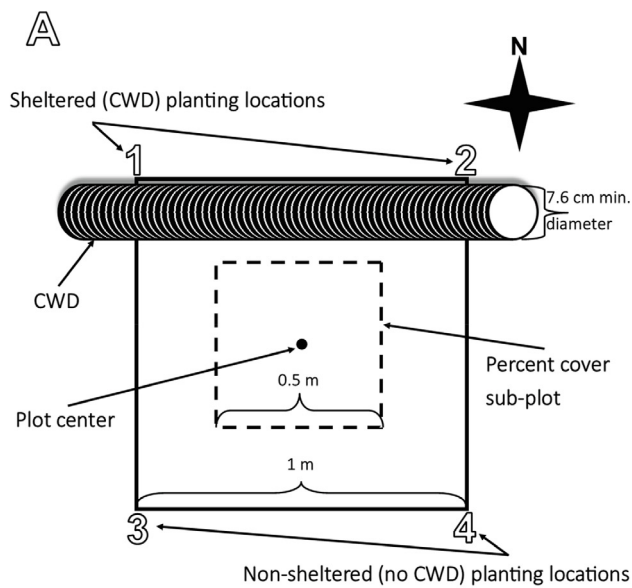
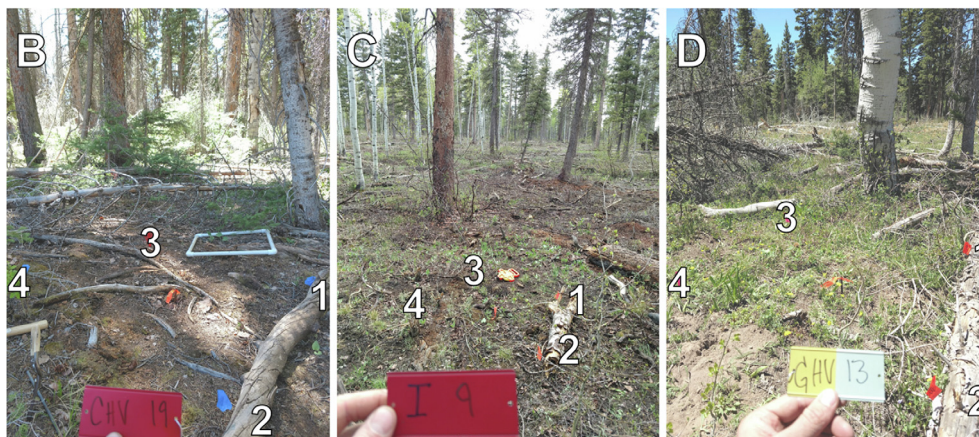


Fig. 3. Plot design (A) structured around randomly generated points (plot center), and example photos (B–D) of plot layout in each canopy stratum (no treatment, individual-tree selection, and group-selection, respectively). Seedling planting positions are indicated by corresponding numbers (1–4) in each figure panel (A–D). Plots were 1 m², oriented with sides perpendicular to cardinal directions. Coarse woody debris, at least 7.6 cm diameter, was placed at the north edge of each plot for the CWD shelter treatments. One seedling of each species, Engelmann spruce and ponderosa pine, was planted with CWD shelter (positions 1 and 2), and one of each species planted without CWD shelter at plot corners (positions 3 and 4). Hemispherical photographs were taken at plot center to estimate canopy cover. Subplots (0.5 m²) were used to sample vegetation, bare soil, and litter/debris cover around plot center. Counts of advanced regeneration (< 5 cm DBH) were tallied by 0.5 m height classes in 3.6 m radius fixed plots originating at plot center. Soil cores were also taken at plot center to estimate soil moisture at each plot.



conditions included survival and root growth (e.g. Davis and Jacobs, 2005; Grossnickle, 2018), the latter estimated by total root biomass (Grossnickle, 2005a; Grossnickle, 2012) at the end of the study period. Accumulation of root biomass was considered the most important growth metric for seedling establishment in the first season after planting (e.g., Davis and Jacobs, 2005), because aboveground biomass was not expected to differ meaningfully after one season, particularly in drought conditions (Grossnickle and MacDonald, 2018). Changes in seedlings heights at the end of the season were, in fact, zero on average. However, in order to contextualize root biomass with seedling size, we evaluated root biomass relative to aboveground biomass (i.e. root:shoot ratio). Plots were surveyed at the end of October 2018 to assess seedling survival. All surviving seedlings were carefully excavated with shovels to process for biomass sampling. Excavations were made far enough around and under seedlings so as to limit the possibility of root breakage; these efforts were made easier by wet soils and having advanced knowledge of the exact location of root plugs from the time of planting. Biomass sampling consisted of washing soil from the roots of each seedling, separating aboveground and belowground components at the root collar, oven drying at 55° C to constant mass, and weighing for dry mass.

2.4. Statistical analysis

2.4.1. Survival

We analyzed individual seedling survival for each species relative to sampled microsite conditions. We first used non-parametric permutation tests (for their flexibility with non-normally distributed data; *rcompanion* package in R, Mangiafico, 2019) to understand how species survival and microsite conditions like shade, moisture, and competition. Because our sampling design included paired observations of survival for a species at each plot location, we used mixed effects (random intercepts) to account for non-independence inherent in this design (Harrison et al., 2018). Furthermore, because our research questions primarily concerned the influences of canopy cover (openness) and CWD shelter, we included these variables *a priori* in all models. All models were developed with the *lme4* package (Bates et al., 2015) in R

(version 3.4.1, R Core Team, 2017).

We expected microsite characteristics other than canopy cover and CWD shelter to account for some variation in survivorship of both species. However, because certain variables may be more or less important in a model conditional on the presence of others, we considered all possible combinations of variables retained from dimension reduction as equally valid final candidate models. Interactions were considered for our openness variable and CWD shelter treatment, openness and soil GWC (e.g. Gray et al., 2002; Davis et al., 2019), and height and DRC (Grossnickle, 2005b). We also considered the potential for a non-linear relationship of survival with openness (e.g. Holmgren et al., 2012). However, no interactions or non-linear terms had greater support than corresponding univariable terms and so were not considered further. We evaluated multicollinearity among predictor variables selected for final model development, though no high correlations (Pearson's $|r| > 0.65$) were detected. We used biological reasoning, interpretability, and corrected Akaike's Information Criteria (AIC_c; Burnham and Anderson, 2002) to compare candidate models (models within $\Delta AIC_c < 6.00$ were assumed to have similar support; Harrison et al., 2018). However, in choosing a single final model for facilitating interpretation, models with similar support ($\Delta AIC_c < 6.00$) were further evaluated for their classification performance since we sought a final model with high discriminatory power for distinguishing survivors and non-survivors for each species. Specifically, we favored sensitivity (ratio of true positive predictions to all actual positives) and positive predictive value (PPV; ratio of true positive predictions to all positive predictions).

Model fit of our final selected models included assessment of classification metrics as well as computing area under the receiver operating characteristic curve (AUC, Fawcett, 2006; pROC package, Robin et al., 2011). AUC is commonly used as a measure of model fit for the discriminatory power of a model assessed across all possible thresholds distinguishing the probability of a successful event. AUC is maximized with high sensitivity and PPV. We made our fit assessments without using independent data and acknowledge potential inflation of these assessments as a result, though this did not substantially affect our interpretation of model effects. Individual model term estimates were examined for strength of support, or significance, with 95% confidence intervals. Where confidence intervals overlapped zero, estimates were considered statistically insignificant. Finally, we examined the relative strength of effect for each model term by comparing standardized model coefficient estimates.

2.4.2. Growth: Root biomass

The root:shoot biomass data were non-normal with non-constant variance and attempts at transformation were unsuccessful at resolving these issues. Therefore, we used non-parametric permutation tests (rcompanion package in R, Mangiafico, 2019) to examine differences (significance set at $\alpha = 0.05$) in root:shoot biomass among canopy strata, or silvicultural treatments. We also tested for root:shoot biomass differences between our CWD shelter treatments (sheltered or not sheltered).

3. Results

3.1. Microsite conditions

Microsite conditions were variable across canopy strata, with most differences reflecting contrasting canopy cover conditions across the strata (Table 1). Mean canopy openness across sampling strata, or treatment types, was 47.10% (± 16.52 SD) and ranged from 10.02% to 77.24%. Differences in mean canopy openness among strata were significant ($P \leq 0.01$ for all pairwise comparisons), with mean openness lowest in the no treatment stratum (28.56% ± 7.80), intermediate in the individual-tree selection stratum (49.89% ± 8.28), and highest in the group-selection stratum (62.90% ± 9.21). Size of CWD shelter

Table 1
Summary characteristics (mean \pm SD) for microsite variables considered for survival models of both species. Bolded and italicized figures indicate a significant difference across canopy strata for each reported microsite variable; corresponding superscripted letters indicate pairwise differences between canopy strata for each reported microsite variable, where strata sharing the same letter are not significantly different.

Canopy Stratum	Plots	Basal Area (m ² ha ⁻¹)	Canopy Cover (%) openness)	Coarse Woody Debris shelter size (cm)	Soil Moisture* (%)	Soil Depth (cm)	Bare Soil (%)	Litter/Debris (%)	Vegetation** (%)	Mean Adv. Regen. Height† (m)	Adv. Regen. Count†
No harvest	69	25.12 (± 10.72) ^a	28.56 (± 7.84) ^a	16.51 (± 4.77)	14.21 (± 5.45) ^a	17.56 (± 3.21)	10.22 (± 18.22)	61.52 (± 24.68)	47.61 (± 28.71) ^a	4.99 (± 3.57) ^a	23.73 (± 13.61) ^a
Individual-tree selection	68	14.45 (± 8.59) ^c	49.89 (± 8.33) ^c	16.32 (± 5.51)	16.98 (± 9.75) ^b	16.76 (± 3.81)	9.34 (± 15.31)	71.03 (± 23.49)	36.99 (± 26.87) ^b	2.40 (± 2.49) ^b	8.84 (± 10.69) ^b
Group-selection	69	4.13 (± 4.58) ^b	62.90 (± 9.26) ^b	15.40 (± 3.73)	20.22 (± 13.30) ^b	17.01 (± 3.96)	9.42 (± 15.71)	66.09 (± 23.12)	36.59 (± 27.61) ^b	2.96 (± 3.31) ^b	12.22 (± 15.68) ^b

* Estimated by gravimetric water content.

** Vegetation is a summation of cover measurements for graminoid, forb, shrub, and moss life-forms.

† Sample sizes for advanced regeneration ("Adv. Regen.") were 60 for no harvest, 69 for group-selection, and 57 for individual-tree selection overstory types.

(16.07 cm \pm 4.72) was not different across strata ($P = 0.38$ – 0.83 for pairwise comparisons). On average, this size exceeded the minimum requirement of 75% of the mean seedling height for both species (18.95 cm \pm 3.14 for Engelmann spruce, 12.62 cm \pm 3.58 for ponderosa pine). Soil GWC was low and highly variable across all strata on average (17.14% \pm 10.26) but increased significantly ($P \leq 0.01$ for all pairwise comparisons) with canopy openness across strata. In contrast, soil depth was similar across strata (mean 17.11 cm \pm 3.66). Surrounding advanced regeneration (all site species) was significantly greater ($P \leq 0.01$ for pairwise comparisons) in number and average height in the no treatment stratum (count 23.73 \pm 13.56, height 4.99 m \pm 3.56) as compared to both individual- and group-selection treatment strata (count 10.69 \pm 13.68, height 2.71 m \pm 2.97). Ground cover by both vegetation and litter/debris at plots across strata were inversely related and highly variable, with significant differences ($P = 0.01$ – 0.04 for pairwise comparisons) occurring between the no treatment stratum (47.61% \pm 28.55 vegetation; 61.52% \pm 24.54 litter/debris) and both individual- and group-selection treatment strata (36.77% \pm 27.12 vegetation; 68.80% \pm 23.27 litter/debris).

3.2. Engelmann spruce survival

Survival of individual Engelmann spruce seedlings was low (77 of 412 total individuals; 18.69% \pm 39.02). Survival was significantly higher ($P \leq 0.01$ for pairwise comparisons) in individual- (26.50% \pm 44.28) and group-selection (21.01% \pm 40.89) treatment strata as compared with the no treatment stratum (8.70% \pm 28.28). Survival with CWD shelter was significantly greater ($P \leq 0.01$) at over 200% of the survival without CWD shelter (25.24% \pm 43.55 and 12.14% \pm 32.73, respectively) across canopy strata.

Our selected final model of Engelmann spruce survivorship included effects of seedling height, soil GWC, and soil depth in addition to canopy openness and CWD shelter (Fig. 4). The effect of overstory openness on Engelmann spruce survival was slightly positive ($\beta_{\text{Open}} = 0.55 \pm 0.27$), while the relationship with the absence of CWD shelter was very strongly negative ($\beta_{\text{CWD}} = -1.62 \pm 0.47$), the effect of seedling height was strongly negative ($\beta_{\text{Ht}} = -0.96 \pm 0.35$), and the effects of soil GWC and depth were strongly positive

($\beta_{\text{SWWC}} = 0.85 \pm 0.30$ and $\beta_{\text{Depth}} = 0.72 \pm 0.28$). Variation among plots was high (random effects standard deviation 2.10). Influences on predicted survival probabilities was strongest for CWD shelter treatments, over 463% higher for sheltered versus unsheltered seedlings on average (Fig. 5). In contrast, changes in predicted survival were minimal over observed canopy openness values. Over the observed range of soil GWC percentages, predicted probability of survival increased most sharply above the mean observed moisture content (17.14%), resulting in an increase in survival probability of 196%. Seedling height at planting also strongly influenced survival probability in our model, suggesting a nearly 203% increase in survival probability with a one standard deviation (3.14 cm) decrease in height from the mean (18.95 cm) observed height. Changes in predicted probabilities of survival with soil depth influences were comparatively minimal, but less variable overall.

All coefficient estimates were reliable as no confidence intervals (95%) included zero, though reliability for the canopy openness estimate was marginal (lower CI bound = 0.06). The model fit to our data as assessed by AUC was exceptional (AUC = 0.98, 95% confidence interval of 0.97–0.99), indicating that the model was able to discriminate well between Engelmann spruce survivors and non-survivors. From a confusion matrix constructed at a probability of success threshold of 0.50, only 4 observed non-survivors were classified incorrectly (98.81% specificity), while 43 of 77 (55.84%) of observed survivors were classified successfully (sensitivity), resulting in a PPV of 91.49%. Overall accuracy was 90.78% (95% confidence interval of 87.56%–93.39%). Predicted survival probabilities were mostly very low (mean 0.16 \pm 0.01, median 0.05), but were as high as 0.96.

3.3. Ponderosa pine survival

Survival of individual ponderosa pine seedlings was greater than Engelmann spruce but still low (143 of 412 total individuals; 34.71% \pm 47.66) across strata. Ponderosa pine survival was similar across canopy treatment strata, with no significant differences ($P = 0.40$ – 0.83 for pairwise comparisons). Survival with CWD shelter was significantly higher ($P \leq 0.01$) and 198% of the survival without CWD shelter (46.12% \pm 49.97 and 23.30% \pm 42.38, respectively).

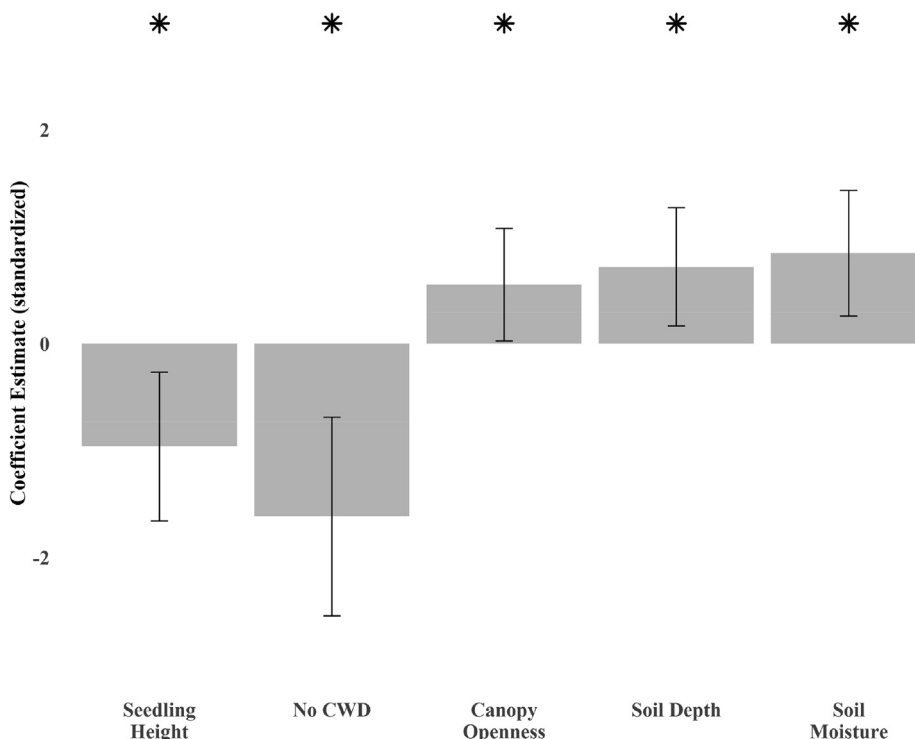


Fig. 4. Standardized effects for final selected Engelmann spruce survival model coefficient estimates. Covariates include seedling height at planting (“Seedling Height”), coarse woody debris shelter treatment (model estimate for effect of no shelter), canopy openness (%), soil depth, and soil GWC (“Soil Moisture”). Vertical lines indicate 95% confidence intervals. Asterisks indicate significant effects.

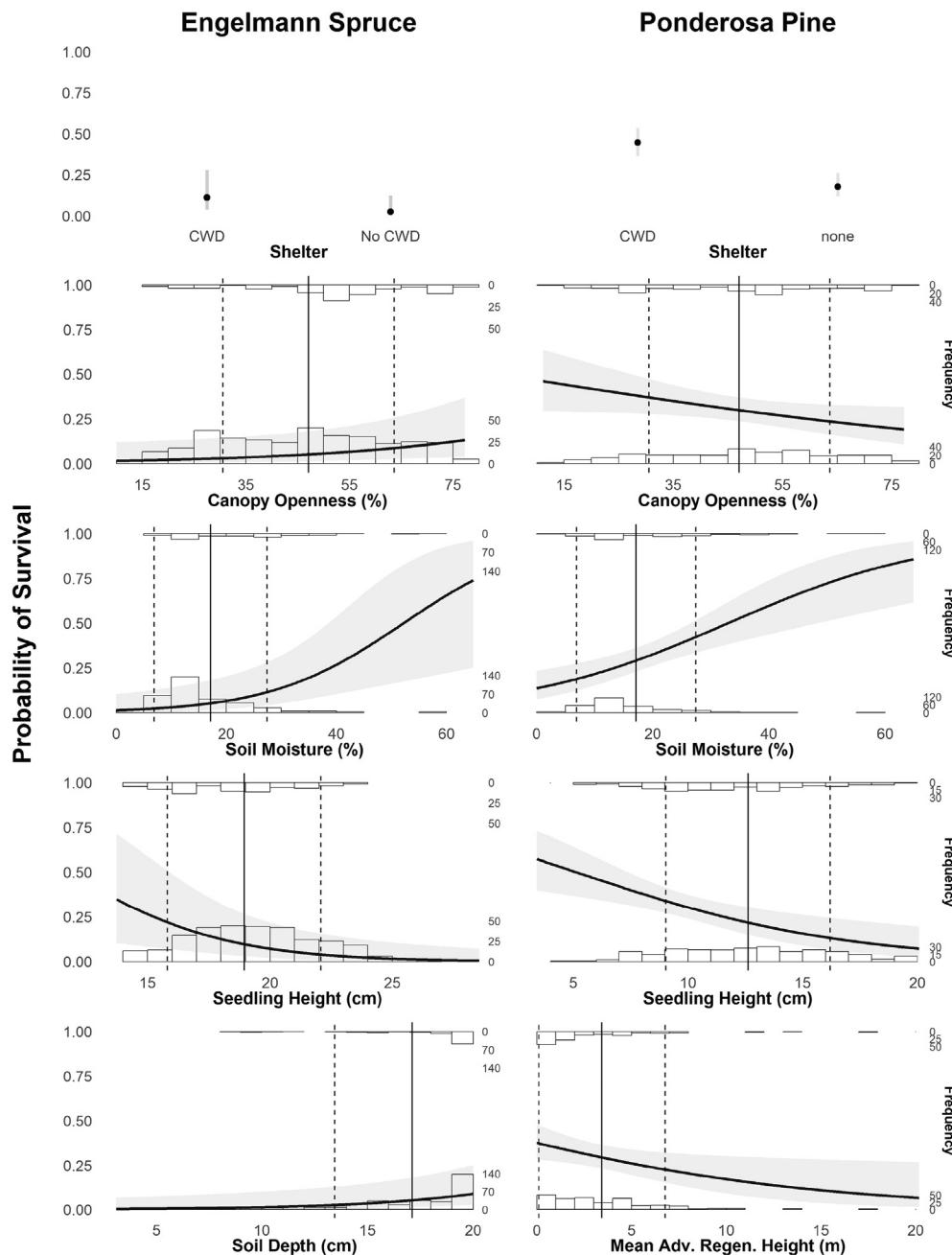


Fig. 5. Predicted mean effects of microsite variables in the final selected survival models for Engelmann spruce (left column) and ponderosa pine (right column). Covariates for both species include coarse woody debris shelter treatment (CWD shelter or no shelter), canopy cover (% canopy openness), seedling height at planting, and percent soil moisture (GWC). The Engelmann spruce final survival model also included soil depth, and the ponderosa model also included mean height of surrounding advanced regeneration trees ("Mean Adv. Regen. Height"). Predictions were made across observed values of each variable. Predicted survival is indicated by the solid black line (points for CWD shelter effects), and gray bands (bars for CWD shelter effects) on either side of the line show 95% confidence intervals for predicted mean survival. Frequency distributions (frequency on secondary y-axis) of observed survivorship are displayed with histograms for each continuous covariate. Vertical black lines indicate the mean (solid) and one standard deviation (dashed) of observed values for each continuous covariate, aiding interpretations of model effects. All effects were significant.

The final selected model fit to our ponderosa pine survivorship data included estimates for canopy openness and CWD shelter, seedling height, soil GWC, and average height of advanced regeneration. All effects were negative, except for a positive relationship with soil GWC (Fig. 6). The effects of openness were minimal and negative ($\beta_{\text{Open}} = -0.32 \pm 0.16$), but survival was very strongly negatively related to the absence of CWD shelter ($\beta_{\text{CWD}} = -1.32 \pm 0.28$). Effects of seedling height were moderate and negative ($\beta_{\text{Ht}} = -0.61 \pm 0.19$), soil GWC had a moderate positive effect ($\beta_{\text{SWC}} = 0.58 \pm 0.15$), and the effects of mean advanced regeneration height were small and negative ($\beta_{\text{RHt}} = -0.35 \pm 0.16$). Variation among plots was moderate (random effects standard deviation 0.79). Similar to Engelmann spruce, the strongest relative influence on ponderosa pine survival probability in our model resulted from CWD shelter treatments, which showed 251% higher probability of survival in sheltered versus unsheltered treatments, though predictions were highly variable in both cases (Fig. 5). Influences of canopy openness and mean height of advanced

regeneration both had similarly small influences on ponderosa pine survival probability. For both predictors, one standard deviation decreases from mean observed values (47.99% mean canopy openness, 16.49% SD; 3.45 m mean advanced regeneration height, 3.34 m SD) both resulted in differences in survival probability of only about 0.07. Soil GWC had a strong influence on probability of survival for ponderosa pine as well, resulting in a nearly 145% increase in survival probability with a one standard deviation (10.65%) increase from the observed mean (17.44%). For ponderosa pine, the influence of seedling height at planting was a strong negative influence on survival, with a roughly 155% increase in survival probability given a one standard deviation (3.58 cm) decrease from the mean observed height (12.70 cm).

All coefficient estimates were reliable as no confidence intervals (95%) included zero, though the canopy openness estimate was again marginal in reliability (upper CI = -0.02). Calculation of AUC suggested good fit for our final selected ponderosa pine survivorship model

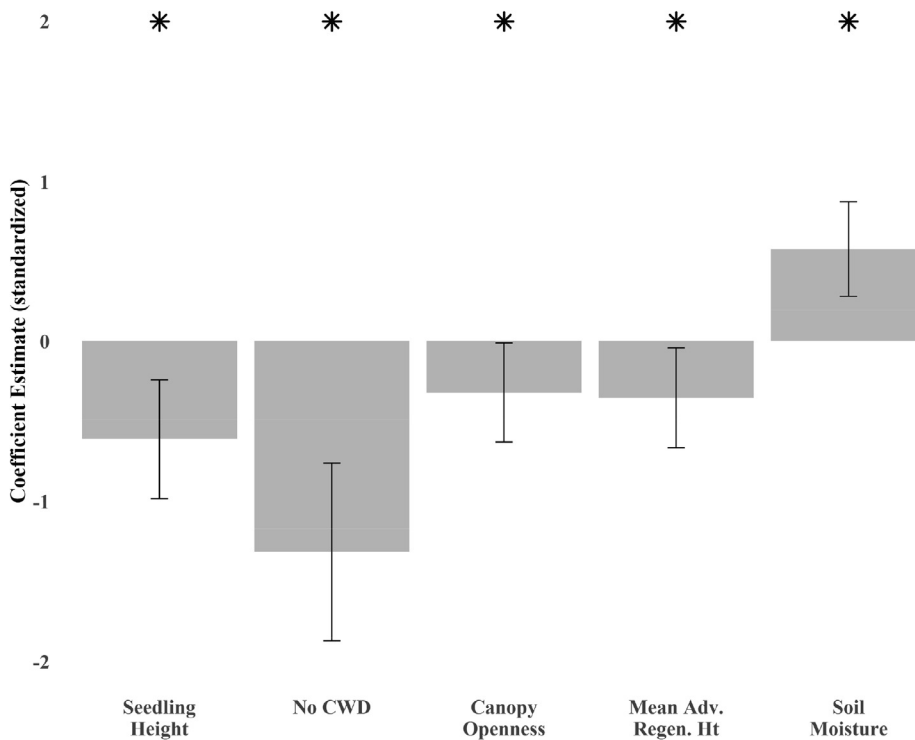


Fig. 6. Standardized effects for final selected ponderosa pine survival model coefficient estimates. Covariates include seedling height at planting (“Seedling Height”), coarse woody debris shelter treatment (model estimate for effect of no CWD shelter), canopy cover (percent canopy openness), mean height of advanced regeneration (“Mean Adv. Regen. Ht”), and soil GWC (“Soil Moisture”). Vertical lines indicate 95% confidence intervals. Asterisks indicate significant effects.

(AUC = 0.85, 95% confidence interval of 0.81–0.90). Given a confusion matrix constructed on a 0.50 probability of success threshold, only 14 observations of non-survival were misclassified by the model (94.29% specificity), but more observations of survival were misclassified than correctly classified (63 of 127 correct, 49.61% sensitivity). With relatively few false positives predicted by the model, PPV was 81.82%, while overall accuracy was 79.03% (95% confidence interval of 74.54–83.06%). Predicted probability of survival from our ponderosa pine survival model was generally low (mean 0.33 ± 0.01 , median 0.29), but about twice that of our Engelmann spruce model on average.

3.4. Root biomass

Permutation tests for differences in root:shoot biomass showed contrasting responses between species to canopy strata (silvicultural treatments) and CWD shelter treatments (Fig. 7). Engelmann spruce root:shoot biomass for surviving seedlings was lower in the no treatment canopy stratum (0.34 ± 0.04 , $n = 11$) compared to the group-selection stratum (0.56 ± 0.06 , $n = 28$) and the individual-tree selection stratum (0.60 ± 0.09 , $n = 30$). However, these differences were not significant ($P = 0.16$ for each). Engelmann spruce root:shoot biomass was higher for non-sheltered seedlings (0.69 ± 0.12 , $n = 22$) than for CWD sheltered seedlings (0.48 ± 0.04 , $n = 47$), but this difference was marginally insignificant ($P = 0.07$). Ponderosa pine root:shoot biomass for surviving seedlings was also lower on average in the no treatment stratum (0.46 ± 0.02 , $n = 41$) compared to group-selection (0.63 ± 0.03 , $n = 43$) and individual-tree selection (0.71 ± 0.05 , $n = 42$) treatment strata. Between no treatment and each treatment strata, these differences were significant ($P < 0.01$ in both cases), but not between treatment strata ($P = 0.16$). Root:shoot biomass of ponderosa pine seedlings was significantly different ($P < 0.01$) between CWD shelter treatments (0.56 ± 0.02 for sheltered, $n = 84$, 0.68 ± 0.04 for no shelter, $n = 42$).

4. Discussion

Adaptive silviculture for responding to climate change should

carefully account for microsite influences on the regeneration environment because regeneration largely determines success of adaptive practices (Spittlehouse, 2005; Anderson and Puettmann, 2017; Nolan et al., 2018; North et al., 2019). In low-elevation Engelmann spruce forests of the southern Rocky Mountains, it is expected that viability of spruce populations will sharply decline with warming climate conditions (Rehfeldt et al., 2015; Conlisk et al., 2017; Kueppers et al., 2017), while sympatric species like ponderosa pine may be favored by such conditions (Rehfeldt et al., 2014). We used a planting experiment to evaluate microsite conditions which support planted seedling survival through the critical first growing season for Engelmann spruce, the current dominant species, and ponderosa pine, a sympatric species with contrasting shade and drought tolerance characteristics. Influences of microsite conditions in this study were similar in strength and direction for both species, likely indicative of a particularly critical period of “coupling” (Grossnickle, 2012), or acclimation of planted seedlings to the field environment in the first season following planting (Dumroese et al., 2016; Grossnickle, 2018). Coupling, achieved especially through root growth into the surrounding soil for moisture and nutrient capture, is essential for seedlings to overcome planting stress (Grossnickle, 2012). These establishment stresses were likely further intensified by drought conditions during the study, which limit growth. Our results show that survival of both species was strongly benefitted by dead shade from coarse woody debris shelter but not from canopy cover. While expected for Engelmann spruce, we did not anticipate such a strong benefit from shade for ponderosa pine, nor did we anticipate the relative unimportance of canopy cover for differentiating species microsite preferences. Despite similarities, the greater survivorship and root growth responses of ponderosa pine relative to Engelmann spruce suggests that available microsites in these forests may better support first-season establishment of ponderosa pine during drought conditions. While few studies have directly compared survival of these species, greater survivorship of ponderosa pine in resource-limited (especially moisture-limited) environmental conditions is not unexpected given their regeneration requirements. Germinant seedlings of both species see extremely low survival rates on average in highly resource-stressed environments such as after severe fire or intensive harvesting (e.g., commonly $< 10\%$; Alexander and Noble, 1971; Noble and Alexander,

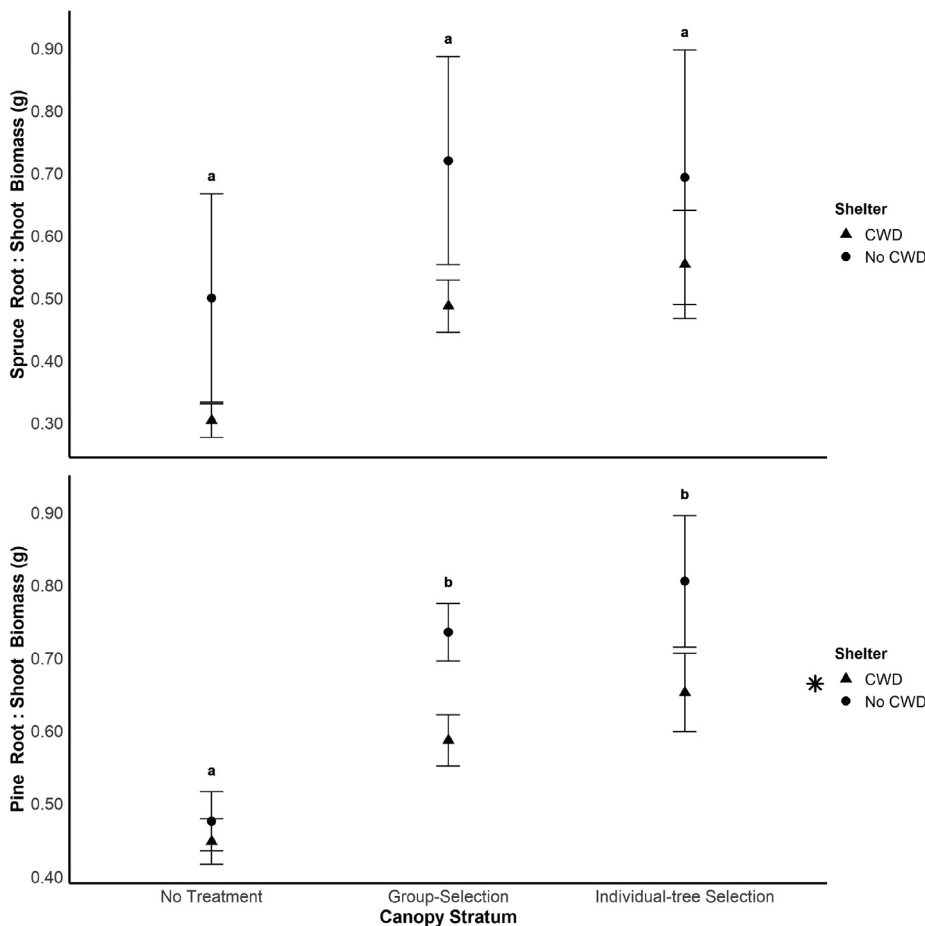


Fig. 7. Root:shoot biomass for Engelmann spruce (top panel) and ponderosa pine (bottom panel) by canopy treatment strata (silvicultural regeneration treatment type) and coarse woody debris shelter. Vertical bars from each point indicate standard error of the observed proportion of survival for each treatment. Coarse woody debris-sheltered seedlings are indicated by triangles, and non-sheltered seedlings are indicated by circles. Differences in biomass were significant between no treatment and the two treatment strata for pine but not spruce. Significant differences between canopy environments are indicated by bolded lowercase letters; environments sharing the same letter do not differ significantly in mean survival. Significant differences between coarse woody debris shelter treatments are indicated by an asterisk adjacent to the treatment legend.

1977; Alexander, 1984; Fiedler et al., 1985; Johnson and Fryer, 1996; Callaway et al., 1996; Bonnet et al., 2005; Keyes et al., 2007; Castanha et al., 2013; Kueppers et al., 2017). However, first-year and older seedlings of ponderosa pine might typically see greater survival on average compared to Engelmann spruce seedlings over several years when evaluated in these environments (e.g., commonly 5–50% for spruce and 25–85% for pine, but often highly variable; Larson and Schubert, 1969; Noble and Ronco, 1978; Elliott and White, 1987; Stein, 1988; Schauer et al., 1998; Parish and Antos, 2005; Maher and Germino, 2006; Shepperd et al., 2006; Coop and Givnish, 2008; Jacobs, 2011; Pinto et al., 2011; Gill et al., 2015; Rother et al., 2015; Ouzts et al., 2015; Newsome et al., 2016). Conversely, in years or on sites without considerable moisture limitations, both species can experience high survival rates (e.g., > 80%; Larson and Schubert, 1969; Lopushinsky and Beebe, 1976; Stein, 1988; Coates et al., 1991; Chen, 1997; Steen et al., 2008; Waterhouse et al., 2010; Pinto et al., 2011; Ouzts et al., 2015; Rother et al., 2015). This underscores ponderosa pine's elevated tolerance of stresses experienced in our study, suggesting differences in survival were likely driven by species differences in drought tolerance.

Our experiment took place over one growing season characterized by a marked drought on a marginally productive low-elevation Engelmann spruce-dominated site. Our results thus offer a relatively limited but important window into conditions which define suitability of regeneration microsites for these contrasting species under stressful growing conditions on a site likely to experience significant climate-change effects. Drought conditions experienced during the study allowed for valuable insight into stresses which are expected to be more frequent in these areas, making our results especially relevant to adaptive forest management efforts in marginal conditions. The magnitude of the effect of coarse woody debris shelter was likely inflated in

our study due to drought conditions, but facilitating influences of shelter may be seen even in years which are more typical relative to long-term climate records. Engelmann spruce and ponderosa pine seedlings, both natural and planted, commonly benefit from sheltering influences which facilitate moisture retention and temperature moderation during establishment, especially at vulnerable young life-stages (e.g. Keyes et al., 2007; Maher et al., 2005; Bonnet et al., 2005; Davy, 2016; Alexander, 1984). However, the short duration of this study and drought conditions during the period of observation may have muted differences between species. The effects of species-specific life history characteristics may become expressed more in response to microsite conditions, such as canopy cover (shade) and competition or facilitation from surrounding understory vegetation, when drought is not a predominant factor. As such, it could be possible over multiple seasons to see ponderosa pine favored in higher light environments, outcompeting the slower-growing spruce, which may tend toward partial shade microsites (e.g., Chen, 1997). Evidently, disentangling seedling responses, natural or planted, to variation in microsite conditions over multiple seasons presents a clear and useful opportunity for additional research. Our results contribute valuable evidence for regional adaptive management that may consider alternative or supplemental species plantings to enhance forest resilience to the effects of climate change. Below we provide detailed discussion of the site and physiological features which likely underly our first-season outplanting performance results.

4.1. Seedling performance: survival and root biomass

The facilitative influence of coarse woody debris shelter in our study was unambiguously important, resulting in nearly twice the survivorship as compared to non-sheltered seedlings of both species (Fig. 5). The benefits of coarse woody debris shelter for young trees can be many

(Harmon et al., 1986; Gray and Spies, 1997), but we expect that its primary influence on seedlings in this study was preventing direct radiation from reaching young, non-woody stem tissue, especially because the study occurred during a growing season marked by high temperatures and extremely low precipitation (Helgerson, 1989; Maher et al., 2015; Davy, 2016). For young seedlings (Landis, 2010), protecting non-hardened, succulent stem tissue from high temperatures may be especially important for preventing cellular damage and subsequent girdling of the stem (Alexander, 1984; Seidel, 1986), leading to internal physiological failure (Helgerson, 1989; Kolb and Robberecht, 1996). Furthermore, sheltering influences of coarse woody debris may also lower ambient air temperatures and raise relative humidity at the soil surface surrounding the seedling (Castro et al., 2011; Jia-bing et al., 2005), increasing available moisture for seedlings (Feller, 2003). In contrast to facilitating influences that can come from surrounding vegetation, coarse woody debris has no actively competitive interactions with seedlings (McTague and Tinus, 1996). Competition for moisture is undoubtedly more acute during both drought conditions and first-season establishment processes (like root growth), underscoring the importance of a non-competitive source of temperature and moisture moderation. The importance of non-competitive shelter has been demonstrated for Engelmann spruce in alpine treeline environments, where seedlings sheltered by boulders had over 65% greater survival than those sheltered by surrounding vegetation (Resler et al., 2005). Results of vegetative sheltering of ponderosa pine have been mixed (reviewed in Korb et al., 2019), but survival through drought conditions has been shown to increase dramatically when not in direct competition with surrounding vegetation due to increased soil moisture availability (e.g., Pinto et al., 2012). Our results are also consistent more generally with documented positive relationships of regeneration survival or densities with woody debris in environments likely to have high abiotic stress after high-impact disturbance events like intensive harvesting (Alexander, 1966; Fajardo et al., 2007) and severe fire (Keyes et al., 2007) and demonstrate this effect persists for ponderosa pine in a putatively more mesic forest relative to its typical regional altitudinal range.

The average size of our coarse woody debris shelter (Table 1) was greater than average heights of ponderosa pine (+3.5 cm) and less than those of Engelmann spruce (−3.0 cm), which may help explain contrasting root biomass results for each species. Though coarse woody debris was beneficial for ponderosa pine survival, it may have reduced light for growth relatively more for pine than for the taller, more shade-tolerant Engelmann spruce (e.g., Chen, 1997; Sheppard et al., 2006). Whereas root growth for Engelmann spruce was not significantly affected by coarse woody debris shelter treatments, ponderosa pine root growth was significantly greater in the unsheltered treatments (Fig. 7). Our survival and growth results collectively suggest ponderosa pine seedlings may have experienced light limitations for growth in sheltered microsites, which in part resulted in less change in predicted probability of survival between sheltered and unsheltered microsites as compared to Engelmann spruce.

In contrast to the strong positive influence of coarse woody debris shelter for both species, the effects of canopy cover were overall only minimally important for seedling survival in our study. Modeled canopy effects on Engelmann spruce survival marginally favored greater openness (Figs. 4 and 5), whereas the effects on ponderosa pine survival indicated preference for greater canopy cover (density). While canopy buffering influences on sub-canopy environments can be substantial, drier sites have less buffering capacity relative to wetter sites (von Arx et al., 2013; Davis et al., 2019). We suspect that moderating influences of canopy in our study, for facilitating moisture availability, were largely nonexistent due to the severe moisture deficit during the study period. Ponderosa pine seedlings, in contrast to Engelmann spruce, may have been able to benefit from temperature buffering effects (i.e. shade) of intermediate canopy density microsites and simultaneously withstand the relative paucity of moisture in these microsites compared to

less dense microsites (Stein and Kimberling, 2003; Holmgren et al., 2012). Soil moisture decreased significantly with canopy cover (Table 1), potentially offsetting the beneficial effects of shade for Engelmann spruce. In their meta-analysis of species responses to interacting shade and drought effects, Holmgren et al. (2012) report similar non-linear survival results for shade-intolerant species, with possible benefits realized only in intermediate levels of shade (e.g. 40–60% full light), and neutral results for shade-tolerant species when drought was a driving site factor. Canopy effects on Engelmann spruce survival may have been marginal because while spruce benefitted from temperature moderation of canopy cover, it was more impacted by competition for moisture from canopy trees than ponderosa pine (e.g., Hill et al., 2019). Seedling responses to canopy cover appear to reflect a trade-off between greater moisture availability but increasing exposure to high temperatures and thus desiccation, or decreased moisture availability but increasing shelter from high temperatures, as evidenced by the strong modeled positive influence of microsite soil moisture at mean canopy cover (Fig. 5).

Though differences in canopy cover between individual- and group-selection strata were significant (Table 1), survival of both species was not significantly different between these treatment strata. Consequently, both species were apparently insensitive to the relative uniformity of canopy conditions in group-selection areas as compared to the relative variability in canopy conditions in individual-tree selection areas. It is possible that our observed levels of canopy openness were not sufficiently broad on average to have greater influence on survival responses. Moreover, despite the effects of canopy cover on understory light environments (and thus microclimatic conditions) in similar forests in the region (e.g., Cannon et al., 2019), differences in canopy environments can be obscured by other microsite conditions (e.g., Pelz et al., 2018). The strength of effect for coarse woody debris shelter, directly adjacent to our seedlings, in both species' survival models here likely account for some of the sheltering influences that canopy cover can provide, since these influences are typically strongest close to the forest floor (Davis et al., 2019). Ultimately, these results reflect potential complications for explaining seedling survival relative to canopy cover, since these relationships can be dependent on temporal variation in moisture availability and other influences acting on seedling environments, especially those in direct proximity to seedlings (e.g. Bonnet et al., 2005).

For ponderosa pine survival, the competition for light and moisture which we expected to observe with canopy density may be more evident in the negative relationship with surrounding advanced regeneration and root growth responses to light environments (Figs. 5 and 7). Ponderosa pine's sensitivity to the presence of surrounding advanced regeneration may result from the crowns of these juvenile trees, mostly shade tolerant conifers, occupying space close to the ground and thus impeding adequate light availability for pine seedlings (Coates et al., 2003; Ligot et al., 2014). Additionally, surrounding advanced regeneration were likely to have had more established root systems, thus outcompeting ponderosa pine seedlings for limited soil moisture and nutrients (Potvin and Dutilleul, 2009; Lei et al., 2012). Similar relationships may be reflected in reports of ponderosa seedling densities having negative associations with the occurrence of sapling and canopy trees at short distances (5 m) (Keyes et al., 2001). Moreover, the effects of canopy cover on root biomass for pine showed that root growth on average was restricted – nearly 150% less on average – in the higher density no treatment stratum (Fig. 7), where advanced regeneration was significantly greater (Table 1) relative to other canopy strata. Since root growth depends on both light for carbohydrate accumulation and moisture availability (Grossnickle, 2005a, 2018), the occurrence of lower soil moisture in dense canopy microsites likely contributed to these results (Rother et al., 2015). This is consistent with the feedback (Davis and Jacobs, 2005; Pinto et al., 2016; Grossnickle, 2005a, 2012, 2018) between moisture availability, root growth, and capacity for uptake of moisture which may have resulted in the correlation between

higher observed survival in harvested areas as compared to unharvested.

The influence seedling height roughly doubled predicted survivorship at smaller compared to larger observed height values for both species (Fig. 5). Seedling size attributes like height and root collar diameter are typically associated with advantages in outplanting environments, especially for resource acquisition due to more developed root systems and height advantages for outcompeting other vegetation (e.g. Grossnickle, 2005b; Pinto et al., 2011). However, it has also been suggested that these advantages are negated in particularly stressful site conditions (Dumroese et al., 2016; Grossnickle, 2012; Pinto et al., 2016), which is presumably the case in our study. From a physiological perspective, where moisture limitations are a prevalent, seedling survival can be limited by greater aboveground development (e.g. height), since greater surface area of foliage requires more soil moisture for root systems to support (Stewart and Bernier, 1995; Grossnickle, 2018). In our results, predicted survival was particularly sensitive to lower ranges of observed heights as compared to higher (Fig. 5), suggesting that first-season establishment during drought conditions is benefitted by smaller seedlings.

4.2. Implications for adaptive silviculture and conclusions

We provide evidence here for the overwhelming benefit of shelter provided by coarse woody debris. While planting strategies in western U.S. silviculture often include leveraging shelter (e.g., stumps, logs) in post-disturbance outplanting environments (e.g. Landis, 2010), our results suggest a change in survival probability that would justify more active inclusion or manipulation of these shelter elements, especially if hot and dry conditions are likely. We also show that important microsite influences for first-season establishment may not be reliably approximated by canopy or overstory tree density estimates (and thus by regeneration treatment type), since the effects of canopy density on seedling environments are conditional on site moisture. This result underscores variability in canopy buffering effects on temperature and moisture, which may be greatly reduced on dry sites or in drought conditions. Microsite conditions supporting establishment may be better represented by more immediate (proximate) influences on individual seedlings, such as dead shade, soil characteristics, other juvenile trees, and seedling height. With respect to seedling height, nursery practices for drought-hardening seedlings prior to outplanting have provided mixed results in field trials (e.g., Grossnickle, 2012; Pinto et al., 2016), but our results suggest that height is a major determinant of responses to drought conditions for these species (Lopushinsky and Beebe, 1976). For both Engelmann spruce and ponderosa pine on harsh sites or in severe drought conditions these effects may be most relevant during the critical period of first-season establishment.

Our results have important implications for regeneration efforts of these species in low-elevation Engelmann spruce forests in the southern Rocky Mountains and more broadly for approaches to mixed sympatric species regeneration in marginal distribution areas experiencing climate change-driven impacts on species habitat suitability. For seedlings of species with contrasting silvics, severely hot and dry environmental conditions combined with seedling physiology in first-season coupling phases may result in similar relative effects of microsite variables on survival. Yet, in our study these effects were ultimately more limiting as factors in first-season establishment for the less drought-tolerant species. Ponderosa pine, a habitat generalist, may be comparatively better suited to available conditions in these low-elevation Engelmann spruce forests during establishment, especially considering anticipated changes toward warmer temperatures and variable precipitation. Consequently, regeneration practices focused on resilience and maximizing outplanting success in these forests in the southern Rocky Mountain region could consider the potential successes of supplementing dominant species with species better adapted to future

conditions. These findings may help spur additional experimentation with alternative candidate reforestation species, and highlight opportunities to resolve inter-annual variation in microsite conditions and species responses to this variation, as well as the effects of planting stock characteristics such as size and provenance.

CRediT authorship contribution statement

Edward M. Hill: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Project administration, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Seth Ex:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118037>.

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