Forest Ecology and Management 572 (2024) 122321

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

What influences planted tree seedling survival in burned Colorado montane forests?☆

Laura A.E. Marshall [a,*], Paula J. Fornwalt [b], Camille S. Stevens-Rumann [c], Kyle C. Rodman [d], Teresa B. Chapman [e], Catherine A. Schloegel [f], Jens T. Stevens [g]

[a] Forest and Rangeland Stewardship Department, Colorado State University, Fort Collins, CO, USA
[b] USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA
[c] Forest and Rangeland Stewardship Department, Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO, USA
[d] Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ, USA
[e] Monitoring Evaluation and Learning Program, Chief Conservation Office, The Nature Conservancy, Arlington, VA, USA
[f] Colorado Field Office, The Nature Conservancy, Boulder, CO, USA
[g] Department of Biology, University of New Mexico, Albuquerque, NM, USA

ARTICLE INFO

Keywords:
Tree planting
Montane forests
Reforestation
Restoration
Ponderosa pine
Douglas-fir
Wildfire

ABSTRACT

Across the western United States, large, severe wildfires in montane forests are creating treeless patches that can fail to reforest naturally due to a lack of seed sources and a warming climate. Nursery-grown tree seedlings are commonly planted by land managers into these areas to promote forest recovery and resilience, but uncertainty exists about what influences their survival across the landscape. We obtained survival monitoring data that had been collected one growing season after planting for 5656 tree seedlings, which were distributed across nine montane wildfires and four National Forests in Colorado, USA. We used these data to examine how seedling survival varied across a range of factors, including long-term average climatic conditions, post-planting weather conditions, and locations and species of seed lot collection. We found that survival after one growing season averaged 80 % across all plots but ranged from 0 % to 100 %. Survival was greater at cooler, wetter sites and at sites planted in warmer, wetter years. Survival was also greater for ponderosa pine than for Douglas-fir, and when the locally collected seed lot used to produce the seedlings came from a site that was lower in elevation than the planting site. Our results suggest that the location and timing of tree planting, and the plant materials used, play critical roles in planting success in Colorado montane wildfires, and should help land managers optimize post-fire planted seedling survival under both current and future climatic conditions.

1. Introduction

Large, high-severity wildfires are driving forest mortality and constraining natural forest recovery processes around the world (Enright et al., 2015; Coop et al., 2020; van Wees et al., 2021). In western US montane forests, where seed-obligate species like ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) commonly dominate, long distances to seed sources in high-severity burn patches can limit seed dispersal and lead to natural tree regeneration failures (Korb et al., 2019; Stevens-Rumann and Morgan, 2019; Davis et al., 2023). Warm, dry climatic conditions and other factors can create additional barriers to natural tree regeneration and forest resilience (Korb et al., 2019; Davis et al., 2023). Given these constraints, it is likely that many high-severity patches will remain in a non-forested state for the foreseeable future, unless active reforestation strategies such as tree planting are implemented (Stevens et al., 2021; Guiterman et al., 2022; Marsh et al., 2022). Indeed, a backlog of over one million hectares have been identified as potentially in need of active reforestation on US Department of Agriculture (USDA) Forest Service lands alone (USDA Forest Service, 2022), of which severely burned montane forest lands in the western US comprise a sizable proportion. The backlog is projected to increase in future years due to anthropogenic

* Corresponding author.
E-mail address: lamarsh@email.arizona.edu (L.A.E. Marshall).

https://doi.org/10.1016/j.foreco.2024.122321
Received 8 July 2024; Received in revised form 11 September 2024; Accepted 28 September 2024
Available online 18 October 2024

climatic change (Dobrowski et al., 2024).

The 2021 Repairing Existing Public Land by Adding Necessary Trees (REPLANT) Act, a component of the Infrastructure Investment and Jobs Act (Public Law 117–58), has recently provided the USDA Forest Service with a funding mechanism to tackle its reforestation backlog through tree planting. This legislation, together with other public and private initiatives, is expected to relieve some of the bottlenecks in the tree planting pipeline (Fargione et al., 2021) and increase the pace and scale of planting across the western US. Yet tree planting in and of itself is not sufficient to address the reforestation backlog; the planted seedlings must also survive and thrive. Studies that provide clarity into how a wide range of factors affect planted tree seedling performance can help optimize the return on reforestation investments.

As with natural tree regeneration (Korb et al., 2019), the performance of conifer seedlings planted into montane high-severity wildfire patches can be strongly shaped by both the long-term average climate of the site and the weather during the post-planting period. Seedlings planted on warm, dry sites, such as those at lower elevations and on more southerly slopes, commonly have much lower levels of survival and growth than those planted on cool, wet sites (Urretavizcaya and Defossé 2019; Marsh et al., 2022; Marshall et al., 2023). Seedlings planted during warm, dry periods can also have lower survival and growth rates (Schneider et al., 1998; Rother et al., 2015). Planted seedlings can be particularly sensitive to post-planting weather during their first growing season, when they are becoming established (Stahelin, 1941; Schneider et al., 1998).

There are a variety of other site-related factors that may further influence the performance of tree seedlings planted following severe wildfires. For example, sites with longer time intervals between burning and planting often contain higher downed wood loads than sites with shorter intervals (Dunn and Bailey, 2015; Fornwalt et al., 2018; Peterson et al., 2023); downed wood may benefit planted seedlings by providing them with protection from insolation and with access to cooler, moister soils (Hill and Ex, 2020; Owen et al., 2020; Marshall et al., 2023). Sites with longer time intervals can also have higher levels of understory plant abundance (Dunn and Bailey, 2015; Fornwalt et al., 2018); depending on the composition and structure of the understory plant community, its interaction with planted seedlings may range from competitive to facilitative (Ouzts et al., 2015; Owen et al., 2020; Marsh et al., 2023). Sites that burned with extremely high severity can have soils that are altered in their chemical, physical, and biological properties (Cowan et al., 2016), which may negatively affect planted seedling performance (Rhoades et al., 2021). The topographic position of the planting sites, such as whether they are in protected valley bottoms, on slopes, or on exposed ridgetops, may also influence soil moisture and exposure to wind and insolation, thereby influencing seedling survival and growth (Stahelin, 1941; Rodman et al., 2020a; Marsh et al., 2022).

Plant material choices can also influence seedling survival. The target plant concept stresses the importance of choosing plant materials that are well-suited for the planting site (Dumroese et al., 2016; Davis and Pinto, 2021; Andivia et al., 2021). Many of the early provenance studies conducted in montane conifer forests found that the performance of planted tree seedlings varied across seed lots (i.e., collections of seeds from specific populations), where seedlings grown from seed lots that were collected at local, climatically similar sites commonly performed better than seedlings from other seed lots (e.g., Isaac, 1949; Rehfeldt, 1989, 1990, 1993; Sorensen, 1994). Consistent with these studies, the USDA Forest Service has historically directed land managers in the west to use seed lots sourced from the same seed zone and general elevational band (Forest Service Handbook 2409.26 f – Seed Handbook; Bower et al., 2014). However, some more recent studies have identified mismatches between tree populations and both their current and future climates due to ongoing and predicted climate change (Gray and Hamann, 2013; Rehfeldt et al., 2014; Crockett and Hurteau, 2024). Further mismatches can stem from the harsh climatic conditions encountered in high-severity patches relative to their unburned counterparts (Wolf et al., 2021). Together, these factors suggest that using local seed lots from elevation-matched sites may no longer produce the best outcomes, particularly when planting in severely burned forests (Jones, 2013). Assisted population migration (i.e., the movement of seed lots to new areas within the species' range) could address mismatch issues, though there are risks and uncertainties to the approach that may need to be addressed through local studies to help avoid undesired outcomes (Hällfors et al., 2014; Bucharova, 2017; Davis and Pinto, 2021).

In Colorado, hundreds of thousands of hectares of montane forest have been burned by high-severity wildfires in the last few decades (Chapman et al., 2020; Stevens et al., 2021). Natural tree regeneration on these severely burned lands is often insufficient to meet desired forest densities (Chambers et al., 2016; Rodman et al., 2020a, b), creating an active reforestation need and prompting land managers to initiate tree planting programs. We contacted managers on four National Forests in Colorado to acquire data from their planting programs, including seedling survival data that had been collected one growing season after planting. We then used a hierarchical modeling approach to identify how seedling survival was related to a range of factors, including species planted and site attributes reflecting climatic, topographic, and fire characteristics. We also compared the elevation of the planting sites to that of the seed lot collection sites to examine how survival was affected by the upslope or downslope movement of local seed lots.

2. Materials and methods

2.1. Study area and study sites

We conducted our study in Colorado, US, in montane forests that burned with high severity and were subsequently planted with conifer tree seedlings to promote forest recovery. Specifically, we focused on ponderosa pine and Douglas-fir planting units in nine wildfires that burned across lands managed by the Arapaho & Roosevelt National Forests and Pawnee National Grassland (ARP), the Pike & San Isabel National Forests and Cimarron & Comanche National Grasslands (PSICC), the Grand Mesa, Uncompahgre & Gunnison National Forests (GMUG), and the San Juan National Forest (SJ) (Fig. 1; Table 1). These wildfires occurred between 1996 and 2016, and the planting operations occurred between 2005 and 2018 (Table 1). Forests in these planting units had been dominated by ponderosa pine and/or Douglas-fir prior to burning, with lodgepole pine (*Pinus contorta* Dougl.), trembling aspen (*Populus tremuloides* Michx.), Gambel oak (*Quercus gambelii* Nutt.), and other associates also present in some locations.

Management practices related to planting varied across the units, but generally followed the policies, practices, and procedures outlined in national and regional USDA Forest Service directives (especially Forest Service Manual 2470 – Silvicultural Practices, Forest Service Handbook 2409.17 – Reforestation, and Forest Service Handbook 2409.26 f – Seed Handbook). The seed lots used to produce the seedlings were collected from the same seed zones and general elevational bands (within ±300 m) as the planting units. Typically, only one seed lot per species was used in the individual units, though sometimes two or three seed lots per species were used. The seeds were grown into one- or rarely two-year-old containerized seedlings at the Charles E. Bessey Nursery in Halsey, Nebraska. Site preparation, such as salvage logging, was sometimes done in the units prior to planting, and scalping away competing vegetation at the planting microsite was commonly done. Seedlings were hand-planted into the units in March, April, or May. To protect seedlings from high levels of insolation and wind, seedlings were commonly placed on the north or northeast side of objects such as stumps, logs, shrubs, or dead trees. On one National Forest (GMUG), translucent tree tubes were put around seedlings in some units to protect them from insolation, wind, and herbivores.

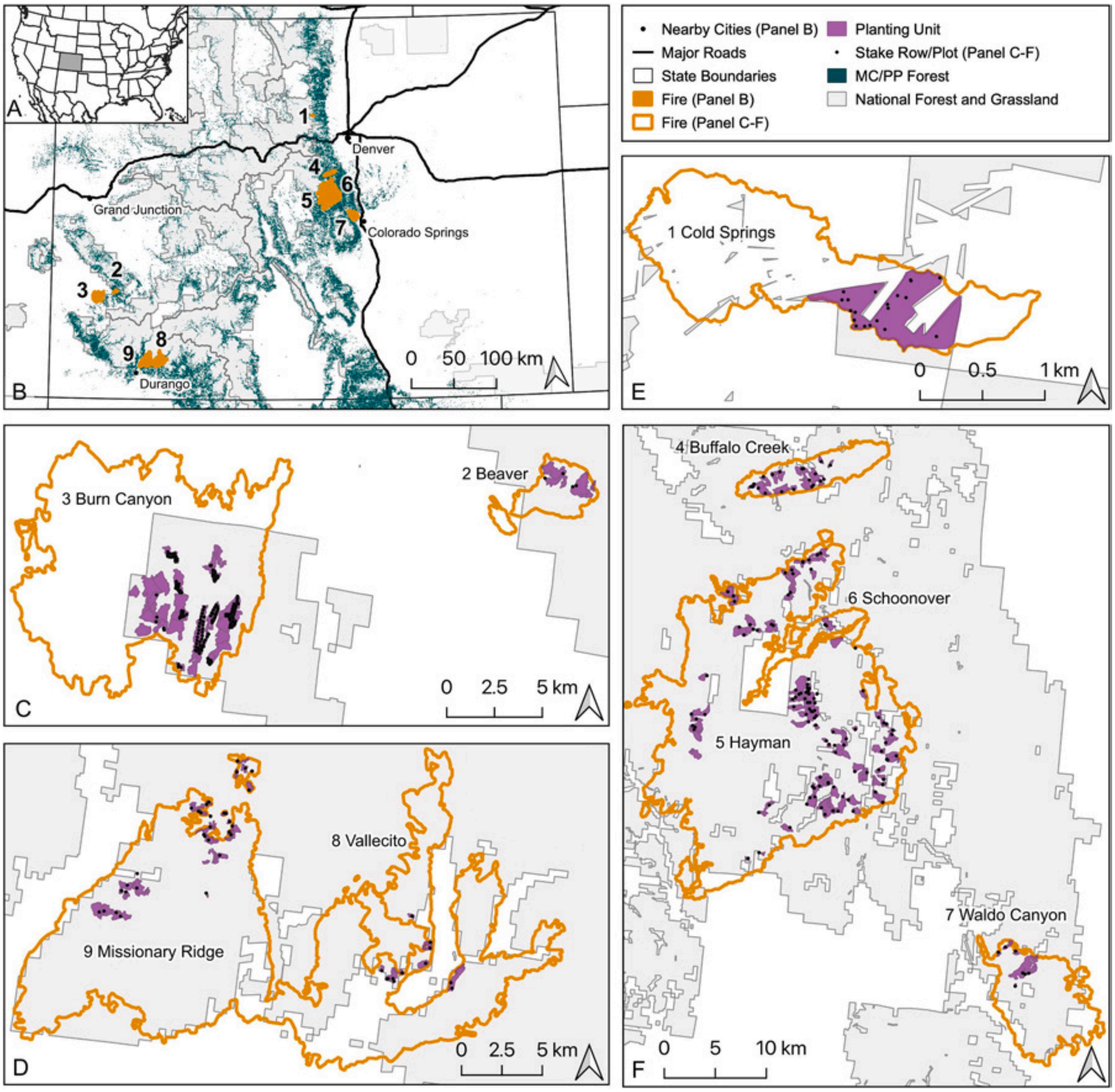

Fig. 1. Study site locations. A: Location of Colorado (gray) within North America. B: Wildfire locations (orange polygons) within Colorado for the nine fires studied with monitored planted seedlings, with montane forest locations underlaid (green polygons). Montane forest (i.e., the ponderosa pine and mixed conifer existing vegetation types) locations were taken from LANDFIRE. Wildfire locations were taken from MTBS (MTBS Data Access: Fire Level Geospatial Data, 2023) and NIFC (National Interagency Fire Center, 2022). The numbers next to each wildfire correspond to those assigned in Table 1. C-F: Location of tree planting units (purple polygons) and survival monitoring stake rows or plots (black points) within wildfires (orange lines).

2.2. Data collection

Planted tree seedling survival was monitored in the planting units by National Forest personnel in accordance with USDA Forest Service directives. To conduct the monitoring, seedlings in planting units were permanently marked at the time of planting, either along variable-length stake rows or in circular fixed-area plots. The median stake row was approximately 60 m long and contained 25 seedlings. Plots, which were only used on the GMUG, were 5.1 m in radius and contained a median of 8 seedlings. The locations of the stake row end points or plot center points, and the species (ponderosa pine or Douglas-fir) of each seedling sampled were also recorded at the initiation of monitoring. In a subsequent survey, seedlings were assessed for survival status (live, dead, or missing) after one growing season; these assessments were generally done in August through November, but were occasionally done the following June. Seedling survival status was also assessed after three growing seasons at many of these stake rows and plots.

2.3. Data acquisition and manipulation: planting data

We contacted personnel at the four National Forests to acquire a variety of implementation and monitoring records for the planting units. Implementation records that we sought for the units included unit boundaries, the species and type of seedling stock planted, the planting date, and the planting methods. We also sought the identity code(s) for the seed lot(s) used to produce the planted seedlings (Forest Service Handbook 2409.26 f – Seed Handbook); embedded in the code(s) is a variety of information, such as the seed zone and the mean elevation (to the nearest 30 m) at which the seeds were collected. Monitoring records that we sought for the units included stake row and plot location(s), monitoring date(s), and species and status for each planted seedling captured by the monitoring. We subsequently extracted, harmonized, condensed, and collated the planting data into a dataset that contained one record for each species planted in each stake row or plot. In total, we acquired data for 145 planting units, 344 stake rows or plots, and 5656 seedlings (Table 1).

Table 1
Summary characteristics of the nine montane Colorado wildfires for which we gathered planted tree survival data, by National Forest. Characteristics reflecting planting implementation (e.g., number of planting units) and monitoring (e.g., number of monitored plots) only capture the planting units incorporated in this study; they do not necessarily capture all units that have been planted and/or monitored in the fire. Monitored plots include both variable-length stake rows as well as fixed-radius plots. Monitoring for survival occurred one and/or three growing seasons (GS) after planting.

Fire	Year burned	Area burned (ha)	Area planted (ha)	Year(s) planted	Number of planting units		Number of monitored plots		Number of monitored seedlings	
					1 GS	3 GS	1 GS	3 GS	1 GS	3 GS
Arapaho and Roosevelt National Forests & Pawnee National Grassland										
1 Cold Springs	2016	200	32	2018	1	1	20	20	200	200
Grand Mesa, Uncompahgre and Gunnison National Forests										
2 Beaver	2010	1000	168	2011	3	3	4	4	300	300
3 Burn Canyon	2002	12,300	1011	2007–2012	19	11	183	54	1761	675
Pike and San Isabel National Forests & Cimarron and Comanche National Grasslands										
4 Buffalo Creek	1996	4700	612	2013–2015	13	13	17	17	425	425
5 Hayman	2002	52,400	3660	2005–2018	88	75	99	84	2475	2100
6 Schoonover	2002	1100	73	2017	2	0	2	0	50	0
7 Waldo Canyon	2012	8100	313	2015–2017	6	4	6	4	150	100
San Juan National Forest										
8 Vallecito	2012	1100	160	2015–2016	9	9	9	9	195	195
9 Missionary Ridge	2002	27,900	427	2018	4	4	4	4	100	100

2.4. Data acquisition and manipulation: additional data

As predictors of tree seedling survival, we identified a set of climatic variables that have been found to relate to natural tree regeneration patterns: total growing season precipitation (April – September; PPT), annual Actual Evapotranspiration (AET), and annual Climatic Water Deficit (CWD) (Table 2; Hankin et al., 2019; Rodman et al., 2020a; Young et al., 2020). AET and CWD are water balance metrics that integrate precipitation, temperature, topography, and soils (Stephenson, 1998). AET (i.e., the actual amount of water entering the atmosphere from transpiration and evaporation) is greatest when conditions are warm and wet, and is commonly interpreted as a measure of productivity. CWD (i.e., potential evapotranspiration (PET), or the amount of water entering the atmosphere from transpiration and evaporation when water is not limited, minus AET) is greatest when conditions are cool and wet, and is commonly interpreted as a measure of water stress. To develop our climatic variables, we retrieved 4-km daily precipitation, potential evapotranspiration, mean temperature, and shortwave radiation flux rasters for the years 1991–2020 from GridMET (Abatzoglou, 2013). AET and CWD were calculated with a modified Thornthwaite-Mather climatic water-balance model following Dobrowski et al. (2013). We then downscaled these data to a 250-m spatial resolution using Gradient-Plus-Inverse Distance Squared (GIDS) interpolation (Nalder and Wein, 1998) following methods in Rodman et al. (2020b). For all raster data, we extracted values at plot center points and stake row end points, and found the mean of raster values across stake row end points. Thirty-year normals (1991–2020; Norms) of each variable were calculated and used as a measure of long-term average site conditions. We also calculated Z-scores relative to 30-year normals (i,e., the difference between the post-planting value and the normal, divided by the standard deviation over the normal period). Z-scores were used as a measure of how the weather during the first post-planting growing season or year deviated from longer-term averages at a site. To calculate or extract climate and other variables from rasters for the points, we used the raster calculator in QGIS (QGIS.org, 2023) and various packages in R (R Core Team, 2023), including *raster*, *sf*, *reshape*, and *dplyr* (Wickham, 2007; Hijmans, 2023; Pebesma and Bivand, 2023; Wickham et al., 2023).

To represent terrain-driven variation in soil moisture and exposure to wind and insolation not captured by AET and CWD, we calculated the predictor Topographic Position Index (TPI; Weiss, 2001) in a 450-m window around each plot center point or stake row end point (Table 2). TPI captures the difference in elevation between a point and the surrounding area, such that a site on a ridge has a positive TPI and a site in a drainage has a negative TPI); for a site in a relatively flat area, TPI is near zero. This 450-m window has been shown to be predictive of natural tree regeneration in the Southern Rocky Mountains and of understory plants in the Colorado Front Range (Rodman et al., 2020a; Demarest et al., 2023). As with climatic variables, we averaged TPI values for stake row end points to obtain a single value.

To incorporate fire severity as a predictor, we retrieved Relative Differenced Normalized Burn Ratio (RdNBR; Miller and Thode, 2007) rasters at a 30-m spatial resolution (Table 2). For fires larger than 405 ha, we retrieved RdNBR rasters developed by the Monitoring Trends in Burn Severity program (MTBS; MTBS Data Access: Fire Level Geospatial Data, 2023). For the one fire (Cold Springs), where severity maps were unavailable through MTBS, we retrieved the RdNBR raster using the Southern Rockies Reforestation Tool (SRRT; Rodman et al., 2022a), which calculates RdNBR following methods in Parks et al. (2021). We again extracted RdNBR value at plots and stake row endpoints, and for stake rows we also found the mean of the endpoints. We excluded four plots where RdNBR was $<$-500, indicating substantially increased greenness after the fire, a result of reburning in multiple fires. We calculated Time Since Fire, another fire-related predictor, from monitoring records as the number of years between the fire and planting.

Finally, we calculated a predictor variable called Seed Lot Movement to describe the elevational movement of seeds from the seed lot collection sites to the planting units, a version of assisted population migration (Table 2). To calculate this variable, we extracted seed lot elevations from the seed lot identity codes; if multiple seed lots of a species were used to plant a unit, we averaged the elevations. Plot and stake row elevations were extracted from 30-m digital elevation model (DEM) layers encompassing all fires (retrieved from USGS Elevation Program (3DEP)), again finding the mean of values at stake row end points. We then differenced the seed lot elevations from the plot and stake row elevations, resulting in positive values when seed lots were moved up in elevation and negative values when seed lots were moved down in elevation.

2.5. Data analysis

All stake rows and plots (hereafter collectively referred to as “plots”) in our final dataset contained planted tree seedling survival data collected after one growing season, but only 60 % of them contained survival data collected after three growing seasons (Table 1). To help determine which time frame to focus on as the response variable in our main analyses, we conducted a preliminary analysis to assess the correlation between one and three growing season survival. We built a single-variable generalized linear mixed model (GLMM) with one growing season survival predicting three growing season survival at the

Table 2
Predictor variables utilized in our modeling approach of planted tree seedling survival after one growing season in nine montane Colorado wildfires. Data were sourced from National Forest personnel and online repositories including GridMET (Abatzoglou 2013), MTBS (MTBS Data Access: Fire Level Geospatial Data, 2023), SRRT (Rodman et al., 2022a), and the USGS Elevation Program (3DEP).

Variable	Data source	Median	Range	Description
Species	National Forests	NA	NA	Tree species planted (*Pinus ponderosa; Pseudotsuga menziesii*)
Norm PPT	GridMET (downscaled to 250 m)	314	245–445	1991–2020 Normal growing season (April – September) total precipitation (mm)
Z-score PPT	GridMET (downscaled to 250 m)	−0.75	−1.4–1.47	Z-score for planting year growing season (April – September) total precipitation relative to Normal
Norm CWD	Derived from GridMET (downscaled to 250 m)	666	419–769	1991–2020 Normal Annual Climatic Water Deficit sum (mm)
Z-score CWD	Derived from GridMET (downscaled to 250 m)	−0.29	−1.30–2.41	Z-score for planting year Annual CWD sum relative to Normal
Norm AET	Derived from GridMET (downscaled to 250 m)	463	416–643	1991–2020 Normal Annual Actual Evapotranspiration sum (mm)
Z-score AET	Derived from GridMET (downscaled to 250 m)	−0.18	−2.25–2.28	Z-score for planting year Annual AET sum relative to Normal
TPI	Derived from 10-m DEM	1	−53–38	Topographic Position Index: relative elevation of a cell compared to the elevation of neighboring cells in a 450-m window
RdNBR	MTBS or SRRT	912	−150–1556	Relative Differenced Normalized Burn Ratio: a measure of burn severity
TSF	National Forests	6	1–19	Time Since Fire: number of years between fire and planting
Seed Lot Movement	Derived from National Forest seed lot code and 30-m DEM	−42	−365–266	Elevational difference (m) between seed lot source location and planting location

plot level, with Fire as a random effect to account for potential spatial correlation and fire-specific operational differences. We used a binomial error structure with a logit link (i.e. logistic regression) and weighted the model by the number of seedlings in a plot. We found that the correlation between model-predicted values for one and three growing season survival was 0.81 (Fig. 2), suggesting that one year survival data could provide meaningful insight into longer-term trends. Therefore, we opted to focus on one-growing-season survival in our main analyses as these data were the most widely available.

Including highly correlated variables in statistical models can make model interpretation challenging. Because we suspected that our climate Norm and Z-score predictor variables were highly correlated, we conducted a series of preliminary analyses to evaluate correlation and reduce variables prior to doing our main analyses. We found that correlation was high, ranging between 0.55 and -0.80 for Norm variables and between -0.71 and -0.80 for Z-score variables. To reduce correlation among predictors, we selected the best Norm and Z-score variables by comparing sample size-corrected Akaike Information Criterion (AICc) scores for separate Norm and Z-score models. Both sets of models contained PPT, AET, or CWD, plus Fire as a random effect. These models indicated that CWD was the strongest predictor among the Norm variables, and AET was the strongest predictor among the Z-score variables. For Norms, the Δ AICc between CWD and PPT, the second-best predictor, was 0.60, and was 35.84 between CWD and AET. For Z-scores, the Δ AICc between AET and CWD was 21.98, and was 32.58 between AET and PPT.

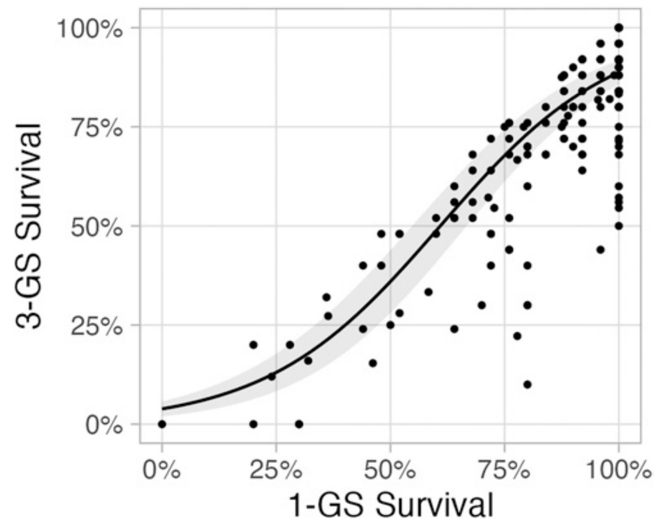

Fig. 2. The predicted relationship (black line with gray 95 % confidence interval) between planted tree seedling survival monitored after one versus three growing seasons (GS). Black points represent the observed survival values in the monitoring stake rows or plots, which were distributed across nine montane Colorado wildfires.

We developed GLMMs to model tree seedling survival from a set of potential "Base" model predictor variables. Included in this potential set of variables were the best Norm and Z-score climate variables from the process described above, plus Species, Time Since Fire, TPI, and RdNBR. We included Fire as a random effect term in our GLMMs. We used a binomial error structure with a logit link (i.e. logistic regression), and modeled the proportion of surviving seedlings following one growing season (response variable) out of all tracked seedlings at a plot (included as 'weights' for each plot). We selected variables for the final Base model using all possible subsets AICc selection, and tested residual distributions using the DHARMa package (Hartig, 2022). Variables in the final Base model had no evidence of strong correlation (i.e., Pearson correlation (r) < 0.5). So that coefficients for continuous and categorical covariates (e.g., tree species) could be interpreted as effect sizes on a comparable scale, we scaled all predictor variables in the manner of Gelman (2008). For visualization and reporting of results, we converted GLMM-predicted probabilities of survival to a percentage for consistency with other metrics derived from field data. We constructed GLMMs in R using the package *lme4* (Bates et al., 2015). Additional packages used for data analysis and figure development were *tidyverse*, *cowplot*, *marginaleffects* and *MuMIn* (Wickham et al., 2019; Wilke, 2020; Arel-Bundock, 2023; Bartoń 2023).

To examine whether and how moving seed lots across elevational gradients relates to tree seedling survival after one growing season, we developed a second GLMM using all variables included in the final Base model, as well as the Seed Lot Movement variable. We developed this model separately because seed lot information was not available for 40 % of the plots. We excluded an additional 21 % of the plots with seed lot data because they were in units that had been planted with multiple seed lots that differed in elevation by >30 m, making Seed Lot Movement imprecise. This "Base Plus Seed Lot" model was constructed in R as described above. We then assessed the effect of Seed Lot Movement by comparing AICc between models with and without this variable.

3. Results

Overall, plot-level survival averaged 80 % after one growing season and 72 % after three growing seasons, though for both time frames it ranged from 0 % to 100 %. At the level of individual fires, mean survival after one growing season was lowest in the Schoonover Fire (50 %) and highest in the Waldo Fire (99.5 %) (Fig. 3). After three growing seasons, mean survival was lowest in the Missionary Ridge Fire (45 %) and highest in the Buffalo Creek Fire (90 %).

3.1. Base model: species, climatic, topographic, and fire characteristics

Our final Base model of one growing season survival included all predictors considered during model selection: Species, Norm Climatic Water Deficit (CWD), Z-score Actual Evapotranspiration (AET), Topographic Position Index (TPI), Relative Differenced Normalized Burn Ratio (RdNBR), and Time Since Fire (TSF) (Table 3). This model had a Δ AICc of 1.97 relative to the next best model, which included all predictors except TSF. Because the Δ AICc of the best model is near the commonly-used cutoff of 2 (Burnham et al., 2011), the effects of TSF should be interpreted cautiously.

Norm CWD had the greatest effect among the predictors (standardized coefficient of −-1.08), followed by Z-score AET (0.56) and Species (-0.29) (Fig. 4A). Survival was greater where Norm CWD was lower, where Z-score AET was higher, and where ponderosa pine was planted rather than Douglas-fir (Fig. 5A-C). Using model-predicted values across the observed range of Norm CWD (419−769), predicted survival was 94 % for the lowest CWD value and 61 % for the highest CWD value, an absolute difference of 33 %. Across the range of observed Z-score AET values (-2.25–2.28), predicted survival was 90 % for the highest AET value and 65 % for the lowest AET value, an absolute difference of 25 %. Predicted survival was 79 % for ponderosa pine and 74 % for Douglas-fir.

Our other predictors had weaker relationships with survival (Figs. 4A, 5D-F). Sites with higher TPI – higher than surrounding areas such as those located on a ridge – had greater survival. Across the range of TPI (-53−38), predicted survival ranged from 59 % at the lowest value to 88 % at the highest value, an absolute difference of 29 %. A longer TSF was associated with greater survival, indicating that plantings many years after fire tended to perform better. Across the range of TSF, predicted survival was 75 % at 1 year after fire, and 84 % at 19 years, an absolute difference of 9 %. More severely burned sites, with higher RdNBR, had greater survival. Across the range of RdNBR (–150–1556), predicted survival was 72 % for the lowest value of RdNBR and 83 % for the highest value, an absolute difference of 11 %. Negative RdNBR values were in small fires and planting units close to the live forest edge.

Table 3
Selection ranking for our top ten Base models of planted seedling survival after one growing season in nine Colorado montane forest wildfires. The ranking demonstrates that the best Base model (i.e., lowest AICc score) occurs when all variables are retained. Variable abbreviations correspond to those in Table 2.

Rank	Included variables	Removed variables	Δ AICc
1	Norm CWD, Z-score AET, Species, TPI, TSF, RdNBR		0
2	Norm CWD, Z-score AET, Species, TPI, RdNBR	-TSF	1.97
3	Norm CWD, Z-score AET, Species, TPI, TSF	-RdNBR	2.53
4	Norm CWD, Z-score AET, TPI, TSF, RdNBR	-Species	3.17
5	Norm CWD, Z-score AET, Species, TPI	-TSF, -RdNBR	5.45
6	Norm CWD, Z-score AET, TPI, TSF	-Species, -RdNBR	5.83
7	Norm CWD, Z-score AET, TPI, RdNBR	-Species, -TSF	6.25
8	Norm CWD, Z-score AET, TPI	-Species, -TSF, -RdNBR	9.93
9	Norm CWD, Z-score AET, Species, TSF, RdNBR	-TPI	17.39
10	Norm CWD, Z-score AET, Species, RdNBR	-TPI, -TSF	17.41

3.2. Base Plus Seed Lot model: seed lot selection

We found that AICc was substantially reduced when the Seed Lot Movement variable was added to the final Base model (Δ AICc 16.9), indicating that the Base model was meaningfully improved with its addition. Indeed, Seed Lot Movement had the third highest standardized coefficient (0.61) in this model, behind Norm CWD (-0.98) and Species (-0.94), which were also among the top predictors in the Base model (Figs. 4A, 4B). The relationship between Seed Lot Movement and

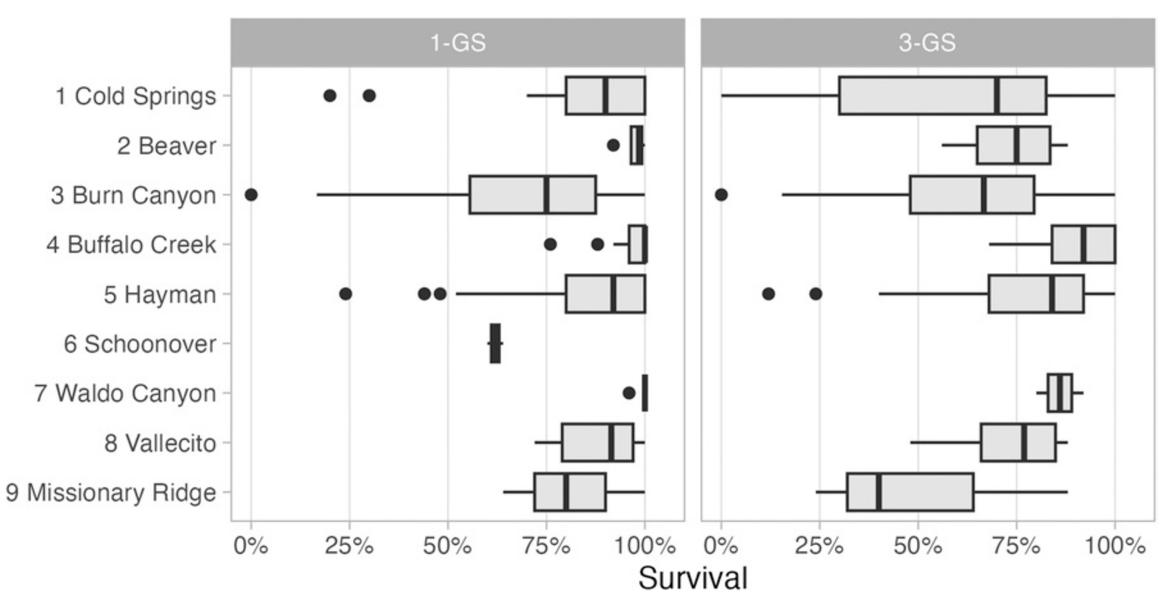

Fig. 3. Boxplots depicting planted tree seedling survival at monitoring stake rows or plots in nine montane Colorado wildfires, at one and three growing seasons (GS) after planting. The numbers for each fire correspond to those assigned in Table 1.

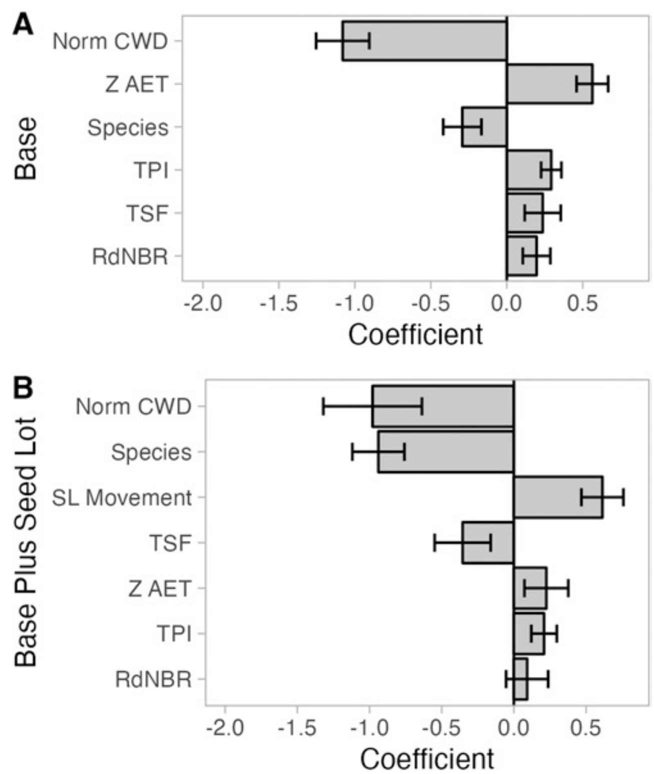

Fig. 4. Standardized coefficients with standard errors for the Base model variables predictive of tree seedling survival after one growing season in nine montane Colorado wildfires (A), and for the Base Plus Seed Lot model variables (B). Variables are arranged in order of importance. Species is categorical (effect of Douglas-fir shown), while other variables are numeric. SL Movement refers to the variable Seed Lot Movement; all other variable abbreviations correspond to those in Table 2.

survival suggested that survival increased when seed lots were sourced from lower elevations; that is, survival increased as seed lots were "moved" up in elevation to the planting sites (Fig. 6C). Seed Lot Movement ranged from -365 m to 266 m. Using the predicted relationship from the model across this range of observed values, survival increased from 50 % when seed lots were moved 365 m down in elevation to 92 % when seed lots were moved 266 m up in elevation, an absolute increase of 42 %. The predictors in the Base Plus Seed Lot model had similar relationships with survival as in the Base model, though in one case (TSF) the direction of the relationship changed (Figs. 4B, 6A-G).

4. Discussion

The scale of tree planting needed after recent high-severity wildfires in western US montane forests is large, and the expectation is that future years will bring even more planting needs (Dobrowski et al., 2024). This study, which incorporated planting data from nine montane fires across four National Forests in Colorado, illustrates both how variable the survival of planted tree seedlings is after the first growing season and how this variability is shaped by a wide range of factors. Factors reflecting long-term climate and post-planting weather conditions, and locations and species of seed lot collection, were the strongest predictors of survival. Other factors — reflecting topographic position, time since fire, and fire severity — affected survival to a lesser degree, but still helped to explain variation in planting outcomes.

4.1. Base model: importance of long-term climate, post-planting weather, and species

We found that Norm Climatic Water Deficit (CWD) — a variable that captures how water stressed a site is on average — was by far the strongest predictor of planted seedling survival (Fig. 4). Seedling survival increased as Norm CWD decreased, suggesting that cooler, wetter, less climatically stressful sites had greater survival than warmer, drier sites (Fig. 5). Warmer, drier conditions put hydraulic stress on seedlings, resulting in mortality through loss of hydraulic conductivity (Simeone et al., 2019). Several studies have similarly documented higher rates of post-fire planted seedling survival on cooler, wetter sites in Colorado and elsewhere (Schneider et al., 1998; Urretavizcaya and Defossé 2019; Marsh et al., 2022; Marshall et al., 2023), as have numerous studies on post-fire natural tree regeneration (Chambers et al., 2016;

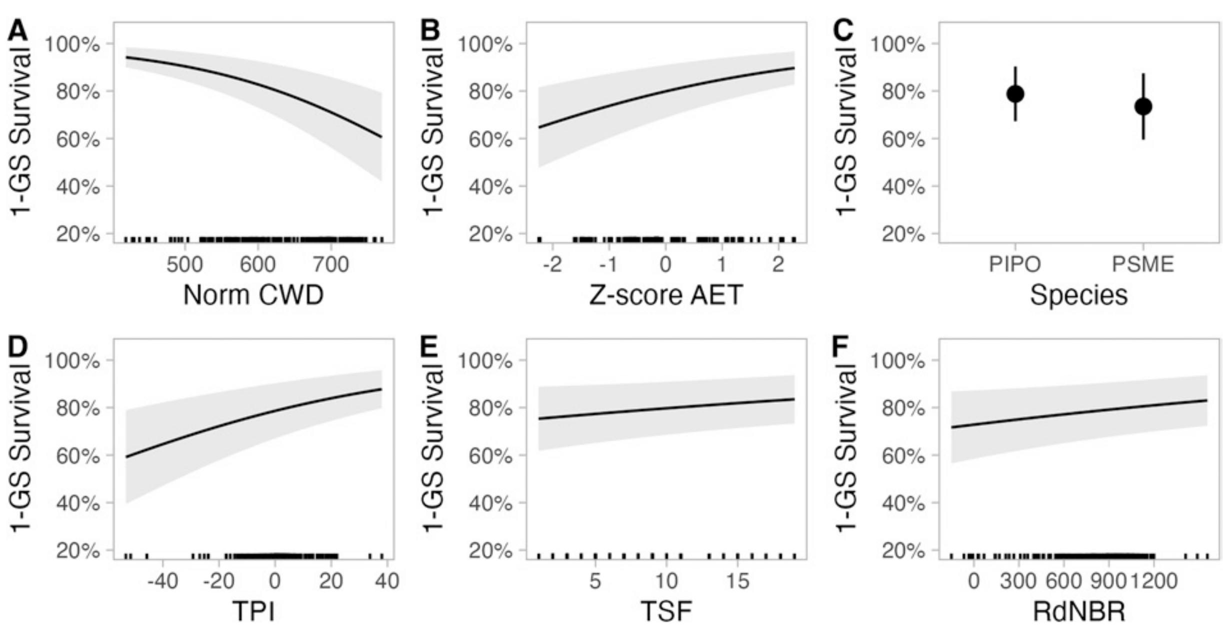

Fig. 5. Model-predicted responses of planted tree seedling survival across nine Colorado montane wildfires after one growing season (GS). Shown here are all predictor variables included in the final Base model, in order of variable importance. Variables are unscaled in this interpretation. Responses for each variable hold the other variables constant, while rug plots show the distribution of the variable across all plots sampled. Variable abbreviations correspond to those in Table 2.

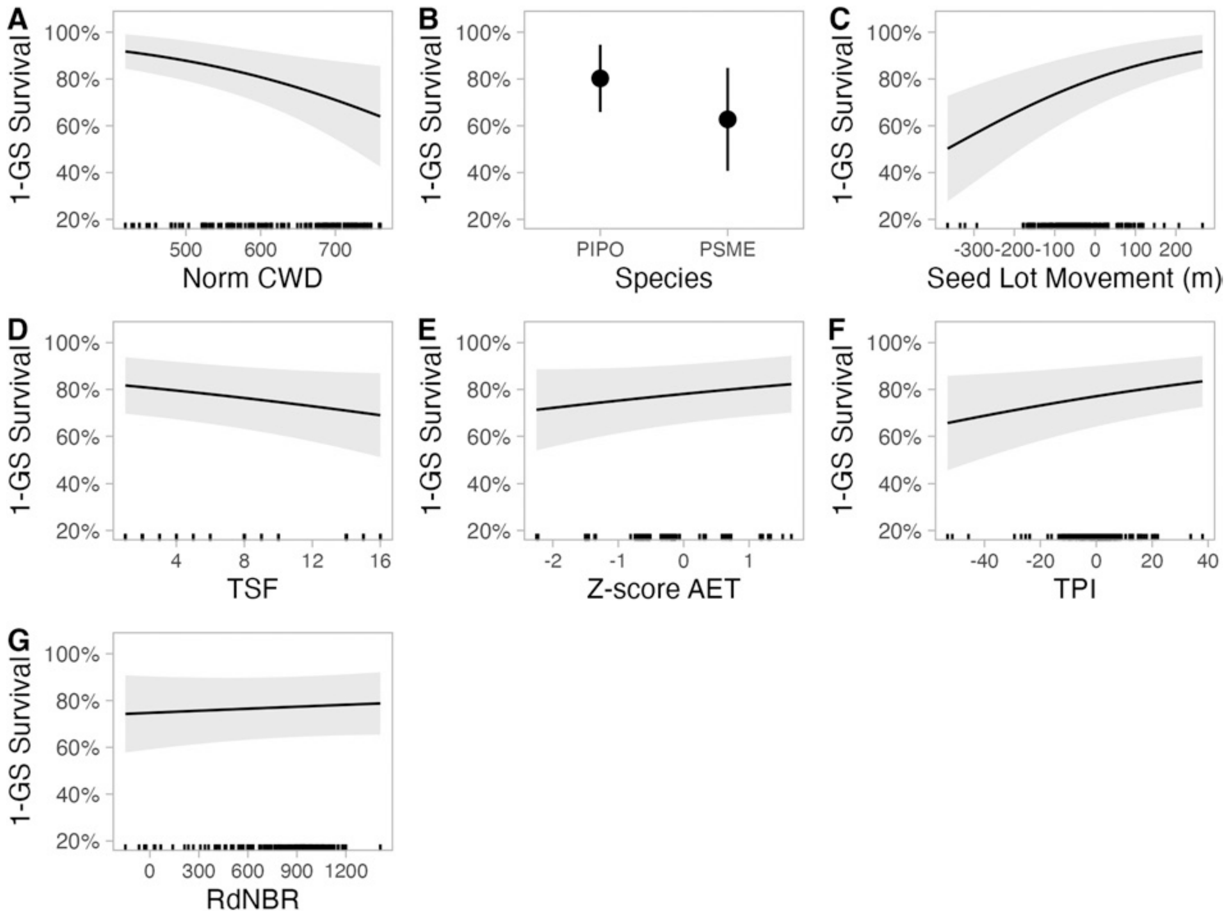

Fig. 6. Model-predicted responses of planted tree seedling survival across nine Colorado montane wildfires after one growing season (GS). Shown here are all predictor variables included in the Base Plus Seed Lot model, in order of variable importance. Variables are unscaled in this interpretation. Responses for each variable hold the other variables constant. Rug plots show the distribution of the predictor variables across all plots incorporated into the model. Variable abbreviations correspond to those in Table 2.

Stevens-Rumann et al., 2018; Kemp et al., 2019; Hankin et al., 2019; Rodman et al., 2020a, 2020b; Davis et al., 2023). Therefore, prioritizing planting in cooler, wetter environments may increase the success of planting programs. However, given the comparatively lower rates of natural regeneration on warm, dry sites, and considering that climate change is expected to exacerbate (Crockett and Hurteau, 2024), planting may also be warranted in climatically stressful areas. Lower planted tree survival rates in warm, dry sites may be accommodated by planting at a higher density and by placing seedlings near shade objects or in water-capturing depressions (Maher et al., 2015; Marsh et al., 2023; Marshall et al., 2023).

Elevated planted seedling survival was highly correlated with higher planting year AET values, similar to findings from natural regeneration and provenance studies (Martínez-Berdeja et al., 2019; Rodman et al., 2020b; Dixit et al., 2021). This indicates that warm, wet years were good for planting, perhaps suggesting that moisture limitations are more detrimental than high temperatures in the year of planting, or that with sufficient water seedlings are able to withstand higher temperatures. Likewise, seedling capacity for growth is driven by physiological mechanisms that are supported by increased moisture availability (Villar-Salvador et al., 2012), and greater root growth may allow seedlings to establish more successfully in harsh environments, benefiting survival (Grossnickle, 2012). While AET Z-score can help to explain planting success, it may be challenging to incorporate into management decision making, given that it is unknown at the time of planting, aside from what can be intuited from seasonal weather forecasts. Planting year weather variation may be accounted for by intentionally planning multi-year planting efforts to reduce the risk of failure due to weather extremes in any one year. With climate change, future weather is expected to become not only warmer but also more variable, creating additional incentive to plant across multiple years (Allen et al., 2010).

Species is another factor where we found a difference in observed planted seedling survival, which may be related to traits controlling species' response to climate and the other drivers (Martínez-Garza et al., 2013). We had much more data available from ponderosa pine than Douglas-fir plantings, so were unable to build species-specific models that might identify species-specific responses. However, species-level differences may lead to differing responses to explanatory drivers, which might be obscured or not captured by our selected model. For example, Douglas-fir tends to be less drought tolerant than ponderosa pine (Crockett and Hurteau, 2024), which could influence model relationships and contribute to higher survival at lower Topographic Position Index (TPI) sites in drainages, as in Rodman et al. (2020a). Indeed, when we ran a single-species model variant of the Base model, we found a significant negative relationship between TPI and survival for Douglas-fir, though the low sample size warrants caution in interpretation. Species-specific environmental response is also important for larger-scale forest development. With climate change, we might expect more drought tolerant species compositions to be favored at early seral stages, especially at lower elevation margins (trailing edge) forests (Rodman et al., 2022b). More drought-adapted populations and species may then become dominant, through natural dispersal and regeneration, or through planting when natural regeneration fails. Surveys of natural regeneration suggest forest composition may be in the process of shifting, often due to fire and drought, with more drought tolerant species finding greater success, especially at trailing edges (Parks et al., 2019; Marshall and Falk, 2020; Guiterman et al., 2022).

In this work, the inclusion of TPI improved the model somewhat. Topographic position affects vegetation establishment and recovery after fire through effects on wind and insolation exposure (Gutiérrez-Jurado and Vivoni, 2012), and through interactions with water storage and movement, promoting heterogeneous recovery across the landscape (Ziegler et al., 2017; Webb et al., 2023). Other topographic indices, such as Heat Load Index and Topographic Wetness Index, have also been found to be useful in predicting habitat suitability and seedling survival (Rodman et al., 2020a; Marsh et al., 2022). Due to the avoidance of planting very steep slopes for operational reasons, the range of TPI at our plots (-53−38) was less than the overall range of TPI across the Southern Rocky Mountain Ecoregion (-67−112), as extracted from 10,000 random points in our study area. The reduced range in the sampling set may affect the explanatory power and relationship found between TPI and planted seedling survival. Moderate positive TPI improved survival in our model, possibly from increased light availability when plot elevation was higher than surrounding areas. At higher TPI, on the unplanted extreme slopes, high insolation and low water availability might alter the relationship with survival.

We used Relative Differenced Normalized Burn Ratio (RdNBR) and Time Since Fire (TSF) as proxies for fire effects that may alter the growing environment. In the model, RdNBR and TSF were less important than other variables, judging by their low standardized coefficients (Fig. 4) and the Δ AICc values relative to the full model when they were removed (Table 3). Additionally, across our two models, the standardized coefficient of TSF changed from a positive in the Base model to negative in the Base Plus Seed Lot subset, while RdNBR had a positive but weak relationship with survival throughout. High RdNBR sites have more aboveground material consumed by fire, and changes to the soil that can reduce natural plant recovery (Cowan et al., 2016; Cardil et al., 2019; Moya et al., 2019), perhaps reducing competition for planted seedlings if the soil has recovered sufficiently. We observed greater survival with longer TSF in the Base model, and a longer TSF may enhance seedling survival through multiple pathways. For example, vegetation recovery can modify microclimatic conditions and improve soil stability, to the benefit of seedlings (Collins and Roller, 2013; Petrie et al., 2016; Stevens-Rumann and Morgan, 2019). Likewise, snag fall over time could alter post-fire environmental conditions, with downed logs providing sheltered sites for planted seedlings (Marshall et al., 2023; Crockett and Hurteau, 2024). If survival is reduced with longer TSF, as we found in the Base Plus Seed lot model, competing vegetation regrowth may be driving the relationship seen at the subset of sites.

4.2. *Base Plus Seed Lot model: importance of seed lot selection*

Our study demonstrates that even small increases in elevation between mean location of seed collection and planting locations can greatly increase seedling survival, which has also been observed in provenance studies (Martínez-Berdeja et al., 2019; Dixit et al., 2021). Experimenting with large elevational range shifts, a form of assisted migration, may be warranted to keep pace with current and projected climate change (Williams and Dumroese, 2013), though bottlenecks such as adequate seed availability and seedling production may complicate planting efforts (Fargione et al., 2021), and risks and unknowns exist with assisted migration (Bucharova, 2017). As we enter increasingly novel climatic conditions, more aggressive experimentation may be warranted to ensure conservation and persistence of many forested landscapes (Coop et al., 2020; Muller et al., 2021). This study reemphasizes the need for location-specific data on collected seed, and the need for a diversity of seed locations to fill the growing need to replant large high severity burned areas.

Work investigating seed transfer guidelines is generally concerned with quantifying and establishing safe limits to moving seeds, as in O'Neill et al. (2014) for distance and Kitzmiller (2005) for elevation. Seed lots in this study generally were planted within ±300 m of the collection elevation, equating to a temperature differential of ±2°C per the environmental lapse rate. Across the range of study elevations (2040–2859 m), CWD, the major climate predictor used, had a difference of 290 mm, as found using a linear model of elevation predicting CWD from 10,000 random points extracted from the model grids used covering the Southern Rocky Mountain Ecoregion. These differences were enough to influence seedling survival, as determined by our model. At greater distances vertically or horizontally, the question of seed transfer becomes one of assisted migration, especially assisted population migration within the current species range limits, where there might be a benefit to future survival by planting seed collected from lower elevation, more arid-adapted populations (Ste-Marie et al., 2011; Williams and Dumroese, 2013). However, moving seed long distances may result in maladaption to local conditions beyond climate, such as biotic interactions (Bucharova, 2017) and day length (Sebastian-Azcona et al., 2019), which could lead to reduced survival in plantings. Fine-scale spatial manipulation of locally-sourced seed with attention to elevation movement, within the current bounds for seed transfer, may instead promote greater survival in outplantings.

We would expect greater survival for seed moved to higher planting elevations due in substantial part to the more mesic environment (Collins and Roller, 2013; Stevens-Rumann and Morgan, 2019), and this has been demonstrated in test elevation transect studies (Martínez-Berdeja et al., 2019; Dixit et al., 2021). In recent work by Dixit et al. (2021), ponderosa pine was planted in common gardens across an elevational gradient in order to investigate genetic and trait effects on survival, and found that growth rates, carbon isotope discrimination, and mortality agents differed across sites and provenances, demonstrating the importance of matching seed source to site in planted seedling survival. Martínez-Berdeja et al. (2019) found similar patterns in survival to our seed lot movement findings in ponderosa pine and Jeffrey pine from differing provenances, planted at differing elevations. More generally, common gardens and provenance experiments have been used to investigate aspects of genetics, growth and survival in many tree species, including ponderosa pine and Douglas-fir, with seeds from across the range of a species grown or planted in one or a few locations (Rehfeldt, 1989; Rehfeldt, 1993; Savolainen et al., 2007; Kolb et al., 2016).

Threshold responses of tree recruitment to environmental variables (Davis et al., 2019), and differing outcomes under climate stress for seedlings of different provenances (Erlichman et al., 2024), suggests that the amount of variation seen across the climatic gradients in this study could have a significant effect on survival when moving tree populations. Planting seedlings above their seed collection elevation may compensate for climate shifts that have already happened, or are in the process of occurring (Gray and Hamann, 2013), and may address the localized hotter, drier conditions found in high severity burns. Utilizing multiple seed lots from the appropriate area may be another way to hedge bets in planting, ensuring a range of genetic sources that could better address uncertainties in future conditions. In all cases, the use of adaptive management practices (Williams, 2011) in planting would allow for adjustments over time leading towards preferred outcomes.

4.3. *Other considerations*

We focused our analyses on response and predictor variables that could be derived either from National Forest planting implementation and monitoring records or from publicly available spatial data. We acknowledge that our response variable – planted seedling survival after one growing season – may not be the best metric for evaluating planted seedling performance, but it was the most consistent variable that we could derive using existing monitoring data. Fortunately, we found that survival after one growing season was strongly correlated to survival after three growing seasons, suggesting that our short-term findings could provide insight into longer-term trends. We also acknowledge that there are many additional predictor variables not included in our analyses that may affect planted seedling survival, perhaps substantially so. Key factors known to be important, and that could potentially be incorporated into future work with our data set, include stock type and quality (Andivia et al., 2021; Villar-Salvador et al., 2012), nursery procedures and conditions (Grossnickle, 2012; Haase and Davis, 2017; Toca et al., 2022; Pinto et al., 2023), procedures and conditions during seedling storage, transport, and planting (McKay et al., 1993; Davis and Pinto, 2021), and localized site conditions in the immediate vicinity of the planted seedling (Maher et al., 2015; Marsh et al., 2023; Marshall et al., 2023).

Our Seed Lot Movement predictor variable was intended to provide insight into the near-term advantages and drawbacks of assisted population migration within wildfire perimeters. Unfortunately, the inputs used to calculate this variable are relatively coarse, because the elevations of the seed lot collection sites are averages rounded to the nearest ~30 m. Despite this coarseness, we found it useful in predicting planted seedling survival. Acquiring finer-scale information about the seed lot collection sites could increase the utility of our approach. Additional insight into assisted population migration could be gained by working with managers to plant experimental units across a broader range of Seed Lot Movement values and by initiating common garden experiments within seed transfer zones.

5. Conclusion

The results of our study illustrate how the location and timing of tree planting after high-severity wildfire, and the plant materials used, can critically affect planting success. We found that in Colorado montane forests, tree seedlings had greater survival at cooler, wetter sites and at sites planted in warmer, wetter years, suggesting site mean and planting year water stress were of high importance for survival. Seedlings also had greater survival when ponderosa pine was planted instead of Douglas-fir, and when seed lots were sourced from lower elevations, indicating the importance of species and provenance choices. In the western US, wildfires are increasing in size and severity (Higuera and Abatzoglou, 2020), climate change is making natural tree establishment more difficult (Davis et al., 2023), and natural regeneration is more likely to fail (Petrie et al., 2023). Planting needs can only increase. Survival of planted seedlings is constrained by seedling climatic limitations (Jackson et al., 2009), which may be an increasing problem in expected future climate conditions. Planting in post-fire areas offers an opportunity to enhance forest resilience, by selecting the best seedling for a site, and the best site among available options, making climate-smart choices that promote desired management outcomes.

Funding

Funding for this project was provided by the Western Wildland Environmental Threat Assessment Center and the Rocky Mountain Research Station of the USDA Forest Service.

CRediT authorship contribution statement

Laura A. E. Marshall: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Conceptualization. **Paula J. Fornwalt:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Camille S. Stevens-Rumann:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Kyle C. Rodman:** Writing – review & editing, Writing – original draft, Software, Methodology, Conceptualization. **Teresa B. Chapman:** Writing – review & editing, Conceptualization. **Catherine A. Schloegel:** Writing – review & editing, Conceptualization. **Jens T Stevens:** Writing – review & editing, Methodology, Conceptualization.

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.

Data availability

Research data will be made available at the USDA Forest Service Research Data Archive.

Acknowledgements

This project would not have been possible without the hard work and dedication of innumerable USDA Forest Service personnel on the Arapaho & Roosevelt National Forests and Pawnee National Grassland, the Pike & San Isabel National Forests and Cimarron & Comanche National Grasslands, the Grand Mesa, Uncompahgre & Gunnison National Forests, and the San Juan National Forest. We are particularly grateful to Kathleen Fialko, Sage Finn, Gretchen Fitzgerald, Ryan Kolling, Christopher Kuennen, Joshua Schutz, Julie Wingate, and Kevin Zimlinghaus, who kindly answered our questions and provided us with volumes of planting records. We also appreciate the help that USDA Forest Service Rocky Mountain Research Station employees Vesper Burjoski and Kirsten Schmidt provided on a wide range of data manipulation tasks.

References

Abatzoglou, J.T., 2013. Development of gridded surface meteorological data for ecological applications and modelling. Int. J. Climatol. 33, 121–131.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259 (4), 660–684.

Andivia, E., Villar-Salvador, P., Oliet, J.A., Puértolas, J., Dumroese, R.K., Ivetić, V., Molina-Venegas, R., Arellano, E.C., Li, G., Ovalle, J.F., 2021. Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide. Ecol. Appl. 31 (6), e02394.

Arel-Bundock, V. (2023). Marginaleffects: Predictions, Comparisons, Slopes, Marginal Means, and Hypothesis Tests. R package version 0.13.0, ⟨https://CRAN.R-project.org/package=marginaleffects⟩.

Bartoń, K. (2023). MuMIn: Multi-Model Inference. R package version 1.47.5, ⟨https://CRAN.R-project.org/package=MuMIn⟩.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67 (1), 1–48.

Bower, A.D., Clair, J.B.S., Erickson, V., 2014. Generalized provisional seed zones for native plants. Ecol. Appl. 24 (5), 913–919.

Bucharova, A., 2017. Assisted migration within species range ignores biotic interactions and lacks evidence. Restor. Ecol. 25 (1), 14–18.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35.

Cardil, A., Mola-Yudego, B., Blázquez-Casado, Á., González-Olabarria, J.R., 2019. Fire and burn severity assessment: Calibration of Relative Differenced Normalized Burn Ratio (RdNBR) with field data. J. Environ. Manag. 235, 342–349.

Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A, M.A., 2016. Patterns of Conifer Regeneration Following High Severity Wildfire in Ponderosa Pine – Dominated Forests of the Colorado Front Range. For. Ecol. Manag. 378, 57–67.

Chapman, T.B., Schoennagel, T., Veblen, T.T., Rodman, K.C., 2020. Still standing: Recent patterns of post-fire conifer refugia in ponderosa pine-dominated forests of the Colorado Front Range. PLoS One 15 (1), e0226926.

Collins, B.M., Roller, G.B., 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landsc. Ecol. 28 (9), 1801–1813.

Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., 2020. Wildfire-driven forest conversion in western North American landscapes. BioScience 70 (8), 659–673.

Cowan, A.D., Smith, J.E., Fitzgerald, S.A., 2016. Recovering lost ground: Effects of soil burn intensity on nutrients and ectomycorrhiza communities of ponderosa pine seedlings. For. Ecol. Manag. 378, 160–172.

Crockett, J.L., Hurteau, M.D., 2024. Ability of seedlings to survive heat and drought portends future demographic challenges for five southwestern US conifers. Tree Physiol. 44 (1) tpad136.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. 116 (13), 6193–6198.
Davis, A.S., Pinto, J.R., 2021. The scientific basis of the target plant concept: An overview. Forests 12 (9), 1293.
Davis, K.T., Robles, M.D., Kemp, K.B., Higuera, P.E., Chapman, T., Metlen, K.L., Peeler, J. L., Rodman, K.C., Woolley, T., Addington, R.N., Buma, B.J., Cansler, C.A., Case, M.J., Collins, B.M., Coop, J.D., Dobrowski, S.Z., Gill, N.S., Haffey, C., Harris, L.B., Harvey, B.J., Haugo, R.D., Hurteau, M.D., Kulakowski, D., Littlefield, C.E., McCauley, L.A., Povak, N., Shive, K.L., Smith, E., Stevens, J.T., Stevens-Rumann, C. S., Taylor, A.H., Tepley, A.J., Young, D.J.N., Andrus, R.A., Battaglia, M.A., Berkey, J. K., Busby, S.U., Carlson, A.R., Chambers, M.E., Dodson, E.K., Donato, D.C., Downing, W.M., Fornwalt, P.J., Halofsky, J.S., Hoffman, A., Holz, A., Iniguez, J.M., Krawchuk, M.A., Kreider, M.R., Larson, A.J., Meigs, G.W., Roccaforte, J.P., Rother, M.T., Safford, H., Schaedel, M., Sibold, J.S., Singleton, M.P., Turner, M.G., Urza, A.K., Clark-Wolf, K.D., Yocom, L., Fontaine, J.B., Campbell, J.L., 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. Proc. Natl. Acad. Sci. 120 (11), e2208120120.
Demarest, A.B., Fornwalt, P.J., Wolk, B.H., Rodman, K.C., Redmond, M.D., 2023. Mechanical forest restoration treatments stimulate understory plants in the Colorado Front Range. For. Ecol. Manag. 548, 121322.
Dixit, A., Kolb, T., Burney, O., Mock, K., Grady, K., 2021. Provenance variation in early survival, growth, and carbon isotope discrimination of southwestern ponderosa pine growing in three common gardens across an elevational gradient. Forests 12 (11), 1561.
Dobrowski, S.Z., Abatzoglou, J., Swanson, A.K., Greenberg, J.A., Mynsberge, A.R., Holden, Z.A., Schwartz, M.K., 2013. The climate velocity of the contiguous United States during the 20th century. Glob. Change Biol. 19 (1), 241–251.
Dobrowski, S.Z., Aghai, M.M., Chichilnisky du Lac, A., Downer, R., Fargione, J., Haase, D.L., Hoecker, T., Kildisheva, O.A., Murdock, A., Newman, S., North, M., Saksa, P., Sjoholm, M., Baribault, T., Buonanduci, M.S., Chambers, M.E., Gonzales-Kramer, L., Harvey, B.J., Hurteau, M.D., Loevner, J., Safford, H.D., Sloan, J., 2024. Mind the Gap'—reforestation needs vs. reforestation capacity in the western United States. Front. For. Glob. Change 7, 1402124.
Dumroese, K.R., Landis, T.D., Pinto, J.R., Haase, D.L., Wilkinson, K.W., Davis, A.S., 2016. Meeting forest restoration challenges: using the target plant concept. Reforesta 1 (1), 37–52.
Dunn, C.J., Bailey, J.D., 2015. Modeling the direct effects of salvage logging on long-term temporal fuel dynamics in dry-mixed conifer forests. For. Ecol. Manag. 341, 93–109.
Enright, N.J., Fontaine, J.B., Bowman, D.M., Bradstock, R.A., Williams, R.J., 2015. Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. Front. Ecol. Environ. 13 (5), 265–272.
Erlichman, A., Sandell, L., Otto, S.P., Aitken, S.N., Ronce, O., 2024. Planting long-lived trees in a warming climate: Theory shows the importance of stage-dependent climatic tolerance. Evolut. Appl. 17 (6), e13711.
Fargione, J., Haase, D.L., Burney, O.T., Kildisheva, O.A., Edge, G., Cook-Patton, S.C., Chapman, T., Rempel, A., Hurteau, M.D., Davis, K.T., Dobrowski, S., Enebak, S., De La Torre, R., Bhuta, A.A.R., Cubbage, F., Kittler, B., Zhang, D., Guldin, R.W., 2021. Challenges to the reforestation pipeline in the United States. Front. For. Glob. Change 4, 629198.
Fornwalt, P.J., Stevens-Rumann, C.S., Collins, B.J., 2018. Overstory structure and surface cover dynamics in the decade following the Hayman Fire. Colo. *For.* 9 (3), 152.
Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. Stat. Med. 27 (15), 2865–2873.
Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. Clim. Change 117 (1), 289–303.
Grossnickle, S.C., 2012. Why seedlings survive: influence of plant attributes. N. For. 43 (5-6), 711–738.
Guiterman, C.H., Gregg, R.M., Marshall, L.A.E., Beckmann, J.J., van Mantgem, P.J., Falk, D.A., Keeley, J.E., Caprio, A.C., Coop, J.D., Fornwalt, P.J., Haffey, C., Hagmann, R.K., Jackson, S.T., Lynch, A.M., Margolis, E.Q., Marks, C., Meyer, M.D., Safford, H., Syphard, A.D., Taylor, A., Wilcox, C., Carril, D., Enquist, C.A.F., Huffman, D., Iniguez, J., Molinari, N.A., Restaino, C., Stevens, J.T., 2022. Vegetation type conversion in the US Southwest: frontline observations and management responses. Fire Ecol. 18 (1), 1–16.
Gutiérrez-Jurado, H.A., Vivoni, E.R., 2012. Ecogeomorphic expressions of an aspect-controlled semiarid basin: II. Topographic and vegetation controls on solar irradiance. Ecohydrology 6, 24–37.
Haase, D.L., Davis, A.S., 2017. Developing and supporting quality nursery facilities and staff are necessary to meet global forest and landscape restoration needs. Reforesta (4), 69–93.
Hällfors, M.H., Vaara, E.M., Hyvärinen, M., Oksanen, M., Schulman, L.E., Siipi, H., Lehvävirta, S., 2014. Coming to terms with the concept of moving species threatened by climate change–a systematic review of the terminology and definitions. PloS one 9 (7), e102979.
Hankin, L.E., Higuera, P.E., Davis, K.T., Dobrowski, S.Z., 2019. Impacts of growing-season climate on tree growth and post-fire regeneration in ponderosa pine and Douglas-fir forests. Ecosphere 10 (4), e02679.
Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6, ⟨https://CRAN.R-project.org/package=DHARMa⟩.
Higuera, P.E., Abatzoglou, J.T., 2020. Record-setting climate enabled the extraordinary 2020 fire season in the western United States. Glob. Change Biol. 27 (1).
Hijmans, R. (2023). raster: Geographic Data Analysis and Modeling. R package version 3.6-26, ⟨https://CRAN.R-project.org/package=raster⟩.
Hill, E.M., Ex, S., 2020. Microsite conditions in a low-elevation Engelmann spruce forest favor ponderosa pine establishment during drought conditions. For. Ecol. Manag. 463, 118037.
Isaac, L.A. (1949). Better Douglas fir forests from better seed. University of Washington Press, Seattle, WA, USA.
Jackson, S.T., Betancourt, J.L., Booth, R.K., Gray, S.T., 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. Proc. Natl. Acad. Sci. 106, 19685–19692.
Jones, T.A., 2013. Ecologically appropriate plant materials for restoration applications. BioScience 63 (3), 211–219.
Kemp, K.B., Higuera, P.E., Morgan, P., Abatzoglou, J.T., 2019. Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10 (1), e02568.
Kitzmiller, J.H., 2005. Provenance trials of ponderosa pine in northern California. For. Sci. 51 (6), 595–607.
Kolb, T.E., Grady, K.C., McEttrick, M.P., Herrero, A., 2016. Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. For. Sci. 62 (6), 641–651.
Korb, J.E., Fornwalt, P.J., Stevens-Rumann, C.S., 2019. What drives ponderosa pine regeneration following wildfire in the western United States? For. Ecol. Manag. 454, 117663.
Maher, C.T., Barber, A.L., Affleck, D.L., 2015. Shelter provided by wood, facilitation, and density-dependent herbivory influence Great Basin bristlecone pine seedling survival. For. Ecol. Manag. 342, 76–83.
Marsh, C., Blankinship, J.C., Hurteau, M.D., 2023. Effects of nurse shrubs and biochar on planted conifer seedling survival and growth in a high-severity burn patch in New Mexico. Usa. *For. Ecol. Manag.* 537, 120971.
Marsh, C., Crockett, J.L., Krofcheck, D., Keyser, A., Allen, C.D., Litvak, M., Hurteau, M.D., 2022. Planted seedling survival in a post-wildfire landscape: From experimental planting to predictive probabilistic surfaces. For. Ecol. Manag. 525, 120524.
Marshall, L.A., Falk, D.A., 2020. Demographic trends in community functional tolerance reflect tree responses to climate and altered fire regimes. Ecol. Appl. 30 (8), e02197.
Marshall, L.A.E., Fornwalt, P.J., Stevens-Rumann, C.S., Rodman, K.C., Rhoades, C.C., Zimlinghaus, K., Chapman, T.B., Schloegel, C.A., 2023. North-facing aspects, shade objects, and microtopographic depressions promote the survival and growth of tree seedlings planted after wildfire. Fire Ecol. 19 (1), 1–12.
Martínez-Berdeja, A., Hamilton, J.A., Bontemps, A., Schmitt, J., Wright, J.W., 2019. Evidence for population differentiation among Jeffrey and ponderosa pines in survival, growth and phenology. For. Ecol. Manag. 434, 40–48.
Martínez-Garza, C., Bongers, F., Poorter, L., 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? For. Ecol. Manag. 303, 35–45.
McKay, H.M., Gardiner, B.A., Mason, W.L., Nelson, D.G., Hollingsworth, M.K., 1993. The gravitational forces generated by dropping plants and the response of Sitka spruce seedlings to dropping. Can. J. For. Res. *23* (11), 2443–2451.
Miller, J.D., Thode, A.E., 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sens. Environ. 109 (1), 66–80.
Moya, D., González-De Vega, S., Lozano, E., García-Orenes, F., Mataix-Solera, J., Lucas-Borja, M.E., de Las Heras, J., 2019. The burn severity and plant recovery relationship affect the biological and chemical soil properties of *Pinus halepensis* Mill. stands in the short and mid-terms after wildfire. J. Environ. Manag. 235, 250–256.
MTBS Data Access: Fire Level Geospatial Data. (2023, April - last revised). MTBS Project (USDA Forest Service/U.S. Geological Survey). Available online: ⟨http://mtbs.gov/direct-download⟩ [accessed June 15, 2023].
Muller, J.J., Nagel, L.M., Palik, B.J., 2021. Comparing long-term projected outcomes of adaptive silvicultural approaches aimed at climate change in red pine forests of northern Minnesota, USA. Can. J. For. Res. 51 (12), 1875–1887.
Nalder, I.A., Wein, R.W., 1998. Spatial interpolation of climatic normals: test of a new method in the Canadian boreal forest. Agric. For. Meteorol. 92 (4), 211–225.
National Interagency Fire Center. (2022, April – last revised). Historic Perimeters Combined 2000-2018 GeoMAC. Available online: ⟨https://data-nifc.opendata.arcgis.com/datasets/nifc::historic-perimeters-combined-2000-2018-geomac/about⟩ [accessed April 22, 2023].
O'Neill, G.A., Stoehr, M., Jaquish, B., 2014. Quantifying safe seed transfer distance and impacts of tree breeding on adaptation. For. Ecol. Manag. 328, 122–130.
Ouzts, J., Kolb, T., Huffman, D., Sánchez Meador, A., 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. For. Ecol. Manag. 354, 281–290.
Owen, S.M., Sieg, C.H., Fulé, P.Z., Gehring, C.A., Baggett, L.S., Iniguez, J.M., Fornwalt, P. J., Battaglia, M.A., 2020. Persistent effects of fire severity on ponderosa pine regeneration niches and seedling growth. For. Ecol. Manag. 477, 118502.
Parks, S.A., Dobrowski, S.Z., Shaw, J.D., Miller, C., 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. Ecosphere 10 (3), e02651.
Parks, S.A., Holsinger, L.M., Voss, M.A., Loehman, R.A., Robinson, N.P., 2021. Correction: Parks et al. Mean composite fire severity metrics computed with Google Earth Engine offer improved accuracy and expanded mapping potential. Remote Sens. 10 (2018), 879. *Remote Sensing*, 13, 4580.
Pebesma, E., & Bivand, R. (2023). Spatial Data Science: With Applications in R. Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016.
Peterson, D.W., Dodson, E.K., Harrod, R.J., 2023. Snag decomposition following stand-replacing wildfires alters wildlife habitat use and surface woody fuels through time. Ecosphere 14 (8), e4635.

Petrie, M.D., Hubbard, R.M., Bradford, J.B., Kolb, T.E., Noel, A., Schlaepfer, D.R., Bowen, M.A., Fuller, L.R., Moser, W.K., 2023. Widespread regeneration failure in ponderosa pine forests of the southwestern United States. For. Ecol. Manag. 545, 121208.
Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For. Ecol. Manag. 361, 328–338.
Pinto, J.R., Sloan, J.L., Ervan, G., Burney, O.T., 2023. Physiological and morphological responses of *Pinus ponderosa* seedlings to moisture limitations in the nursery and their implications for restoration. Front. Plant Sci. 14, 1127656.
QGIS.org (2023). QGIS Geographic Information System. QGIS Association.
R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rehfeldt, G.E., 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii var. glauca*): a synthesis. For. Ecol. Manag. 28 (3-4), 203–215.
Rehfeldt, G.E., 1990. Genetic differentiation among populations of *Pinus ponderosa* from the upper Colorado River Basin. Bot. Gaz. 151 (1), 125–137.
Rehfeldt, G.E., 1993. Genetic variation in the *Ponderosae* of the Southwest. Am. J. Bot. 80 (3), 330–343.
Rehfeldt, G.E., Jaquish, B.C., Sáenz-Romero, C., Joyce, D.G., Leites, L.P., St Clair, J.B., López-Upton, J., 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. For. Ecol. Manag. 324, 147–157.
Rhoades, C.C., Fegel, T.S., Zaman, T., Fornwalt, P.J., Miller, S.P., 2021. Are soil changes responsible for persistent slash pile burn scars in lodgepole pine forests? For. Ecol. Manag. 490, 119090.
Rodman, K.C., Crouse, J.E., Donager, J.J., Huffman, D.W., Meador, A.J.S., 2022b. Patterns and drivers of recent land cover change on two trailing-edge forest landscapes. For. Ecol. Manag. 521, 120449.
Rodman, K., Fornwalt, P., Chapman, T., Coop, J., Edwards, G., Stevens, J., & Veblen, T. (2022a). A Decision Support Tool to Inform Postfire Reforestation of Ponderosa Pine and Douglas-fir in the Southern Rocky Mountains. Research Note RMRS-RN-95. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
Rodman, K.C., Veblen, T.T., Battaglia, M.A., Chambers, M.E., Fornwalt, P.J., Holden, Z. A., Kolb, T.E., Ouzts, J.R., Rother, M.T., 2020a. A changing climate is snuffing out post-fire recovery in montane forests. Glob. Ecol. Biogeogr. 29 (11), 2039–2051.
Rodman, K.C., Veblen, T.T., Chapman, T.B., Rother, M.T., Wion, A.P., Redmond, M.D., 2020b. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. Ecol. Appl. 30 (1), e02001.
Rother, M.T., Veblen, T.T., Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can. J. For. Res. 45 (11), 1607–1616.
Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in trees. Annu. Rev. Ecol., Evol., Syst. 38, 595–619.
Schneider, W.G., Knowe, S.A., Harrington, T.B., 1998. Predicting survival of planted Douglas-fir and ponderosa pine seedlings on dry, low-elevation sites in southwestern Oregon. N. For. 15, 139–159.
Sebastian-Azcona, J., Hamann, A., Hacke, U.G., Rweyongeza, D., 2019. Survival, growth and cold hardiness tradeoffs in white spruce populations: Implications for assisted migration. For. Ecol. Manag. 433, 544–552.
Simeone, C., Maneta, M.P., Holden, Z.A., Sapes, G., Sala, A., Dobrowski, S.Z., 2019. Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. N. Phytol. 221 (4), 1814–1830.
Sorensen, F.C. (1994). Genetic variation and seed transfer guidelines for ponderosa pine in central Oregon. Research Paper PNW-RP-472. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, USA.
Stahelin, R. (1941). Thirty-five Years of Planting on the National Forests of Colorado. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
Ste-Marie, C., Nelson, A., Dabros, A, E., Bonneau, M.E., 2011. Assisted migration: Introduction to a multifaceted concept. For. Chron. 87 (6), 724–730.
Stephenson, N., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25 (5), 855–870.
Stevens, J.T., Haffey, C.M., Coop, J.D., Fornwalt, P.J., Yocom, L., Allen, C.D., Bradley, A., Burney, O.T., Carril, D., Chambers, M.E., Chapman, T.B., Haire, S.L., Hurteau, M.D., Iniguez, J.M., Margolis, E.Q., Marks, C., Marshall, L.A.E., Rodman, K.C., Stevens-Rumann, C.S., Thode, A.E., Walker, J.J., 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. For. Ecol. Manag. 502, 119678.
Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21 (2), 243–252.
Stevens-Rumann, C.S., Morgan, P., 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecol. 15 (1), 1–17.
Toca, A., Moler, E., Nelson, A., Jacobs, D.F., 2022. Environmental conditions in the nursery regulate root system development and architecture of forest tree seedlings: a systematic review. N. For. 53 (6), 1113–1143.
Urretavizcaya, M.F., Defossé, G.E., 2019. Restoration of burned and post-fire logged Austrocedrus chilensis stands in Patagonia: effects of competition and environmental conditions on seedling survival and growth. Int. J. Wildland Fire 28 (5), 365–376.
USDA Forest Service (2022). National Forest System Reforestation Strategy: Growing and Nurturing Resilient Forests. FS-1198. ⟨https://www.usda.gov/sites/default/files/documents/reforestation-strategy.pdf⟩.
van Wees, D., van Der Werf, G.R., Randerson, J.T., Andela, N., Chen, Y., Morton, D.C., 2021. The role of fire in global forest loss dynamics. Glob. Change Biol. 27 (11), 2377–2391.
Villar-Salvador, P., Puértolas, J., Cuesta, B., Peñuelas, J.L., Uscola, M., Heredia-Guerrero, N., Rey Benayas, J.M., 2012. Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival. N. For. 43, 755–770.
Webb, R.W., Litvak, M.E., Brooks, P.D., 2023. The role of terrain-mediated hydroclimate in vegetation recovery after wildfire. Environ. Res. Lett. 18 (6), 064036.
Weiss, A. (2001). Topographic position and landforms analysis. In: Poster presentation, ESRI user conference, San Diego, CA (Vol. 200).
Wickham, H., 2007. Reshaping Data with the reshape Package. J. Stat. Softw. 21 (12), 1–20.
Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4 (43), 1686.
Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.2, ⟨https://CRAN.R-project.org/package=dplyr⟩.
Wilke, C. (2020). cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 1.1.1, ⟨https://CRAN.R-project.org/package=cowplot⟩.
Williams, B.K., 2011. Adaptive management of natural resources—framework and issues. J. Environ. Manag. 92 (5), 1346–1353.
Williams, M.I., Dumroese, R.K., 2013. Preparing for climate change: forestry and assisted migration. J. For. 111 (4), 287–297.
Wolf, K.D., Higuera, P.E., Davis, K.T., Dobrowski, S.Z., 2021. Wildfire impacts on forest microclimate vary with biophysical context. Ecosphere 12 (5), e03467.
Young, D.J., Blush, T.D., Landram, M., Wright, J.W., Latimer, A.M., Safford, H.D., 2020. Assisted gene flow in the context of large-scale forest management in California, USA. Ecosphere 11 (1), e03001.
Ziegler, J.P., Hoffman, C.M., Fornwalt, P.J., Sieg, C.H., Battaglia, M.A., Chambers, M.E., Iniguez, J.M., 2017. Tree regeneration spatial patterns in ponderosa pine forests following stand-replacing fire: Influence of topography and neighbors. Forests 8 (10), 391.