Marshall *et al. Fire Ecology* (2023) 19:26
https://doi.org/10.1186/s42408-023-00181-8

Fire Ecology

TECHNICAL NOTE

Open Access

North-facing aspects, shade objects, and microtopographic depressions promote the survival and growth of tree seedlings planted after wildfire

Laura A. E. Marshall[1*], Paula J. Fornwalt[2], Camille S. Stevens-Rumann[1,3], Kyle C. Rodman[4], Charles C. Rhoades[2], Kevin Zimlinghaus[5], Teresa B. Chapman[6] and Catherine A. Schloegel[7]

Abstract

Background Planting tree seedlings may help promote forest recovery after extensive high-severity wildfire. We evaluated the influence of growing environment characteristics on the performance of seedlings planted in the 2016 Cold Springs Fire, Colorado, USA. In 2021, four growing seasons after planting, we measured survival, height, and 2021 height growth for 300 ponderosa pine, limber pine, and Douglas-fir seedlings permanently marked along "stake rows." For each seedling, we also recorded one site-level growing environment characteristic, aspect, and two microsite-level characteristics, the presence of coarse wood or other shade object and the presence of water-capturing microtopographic depressions. To examine a potential mechanism through which these growing environment characteristics could influence seedling responses, we also measured summer soil moisture at each ponderosa pine seedling. We used generalized linear mixed models to examine the influence of aspect, shade object presence, and depression presence on seedling survival, height, and height growth, and on soil moisture.

Results The growing environment had a clear influence on tree seedlings. We found greater seedling survival on more northerly aspects, in shade, and in depressions. Across all species, seedlings on north aspects had 37% greater survival than those on south aspects (76% vs. 39%, respectively). Seedlings planted in shaded microsites had 20% greater survival, and seedlings planted in depression microsites had 14% greater survival relative to microsites without shading or depressions, respectively. Seedling height was greater on more northerly aspects and in shade. Likewise, seedling height growth was generally greater on north aspects and in shade, although the influence of aspect and shade depended on species. Soil moisture was greater in depressions.

Conclusions The findings of this opportunistic study demonstrate how positioning seedlings to take advantage of cooler, wetter growing environments can increase their performance in what are often climatically stressful post-fire landscapes. Overall, planting seedlings on north-facing aspects, in shaded microsites, and in depression microsites, practices commonly employed by land managers, were effective at promoting survival and growth, thereby

*Correspondence:
Laura A. E. Marshall
laura.marshall@colostate.edu
Full list of author information is available at the end of the article

facilitating planting success. These practices will likely become ever more relevant as the pace and scale of post-fire planting increases and as planting conditions become more stressful due to ongoing climate change.

Keywords Colorado, High-severity wildfire, Mixed conifer forest, Post-fire planting, Reforestation, Tree seedling survival

Resumen

Antecedentes La plantación de plántulas de árboles puede promover la recuperación del bosque luego de un incendio extenso de gran severidad. Evaluamos la influencia de las características del ambiente de crecimiento en la performance de plántulas plantadas luego del incendio de 2016 en Cold Springs, Colorado, EEUU. En 2021, medimos la supervivencia, altura, y el crecimiento de 300 plántulas de pino ponderosa, pino enano (*Pinus flexilis*) y pino oregón marcadas de manera permanente a lo largo de estacas dispuestas en línea. Para cada plántula, también registramos en cada sitio las características del ambiente de crecimiento, exposición, y dos características a nivel de micrositio, la presencia de troncos gruesos u otros objetos que pudieran "sombrear" el sitio, y también la presencia de depresiones micro-topográficas que pudiesen captar agua. Para evaluar un mecanismo potencial a través del cual esas características pudiesen influenciar las respuestas de las plántulas, también medimos la humedad del suelo durante el verano para cada plántula de pino ponderosa. Para examinar la influencia de la exposición, los efectos del sombreado y la presencia de las depresiones en la supervivencia, altura, crecimiento en altura y en la humedad del suelo, usamos modelos lineales mixtos generalizados.

Resultados El ambiente de crecimiento tuvo una clara influencia en las plántulas de estas especies de árboles. Para todas las especies, las plántulas ubicadas en laderas norte tuvieron un 37% más de supervivencia las ubicadas en laderas orientadas al sur (76% vs. 39%, respectivamente). Las plántulas plantadas en micrositios sombreados tuvieron un 20% más de supervivencia y aquellas plantadas en micrositios con depresiones un 14% más que las que crecieron a pleno sol o en lugares planos, respectivamente. La altura de las plántulas fue mayor en las que crecieron en laderas de exposición norte y en lugares sombreados. Así también, el crecimiento en altura de las plántulas fue generalmente mayor en laderas de exposición norte y en lugares sombreados, aunque la influencia de la exposición y sombreado dependió de la especie. La humedad del suelo fue mayor en las depresiones.

Conclusiones Los resultados de este estudio oportunístico demuestran cómo ubicar las plántulas en el terreno de manera de sacar ventaja de los ambientes más fríos y húmedos que pueden incrementar la performance de las plántulas en lo que frecuentemente son paisajes climáticamente estresados por los incendios. En general, la plantación de plántulas en exposiciones norte, en micrositios sombreados y con micro depresiones, prácticas comunes empleadas por los gestores de tierras, fueron efectivas para promover la supervivencia y el crecimiento, facilitando por lo tanto el éxito de la plantación. Estas prácticas podrían ser mucho más relevantes en tanto la velocidad como la escala de plantación se incremente y las condiciones de plantado se hagan más estresantes debido al avance del cambio climático.

Background

High-severity wildfire activity in montane conifer forests of the US Rocky Mountains has increased in recent decades, threatening forest resilience (Williams et al. 2019; Higuera and Abatzoglou 2021; Coop et al. 2022). In large, high-severity burn patches, natural regeneration of some previously common conifer tree species tends to be rare, putting these areas at risk of conversion to herbland, shrubland, or another vegetation type (Coop et al. 2020; Guiterman et al. 2022). This rarity is often a result of the distance to surviving mature trees, which serve as a necessary source of seeds (Chambers et al. 2016; Kemp et al. 2016; Haffey et al. 2018). Even if surviving trees are present, relatively warm, dry growing environments can challenge natural tree regeneration (Korb et al. 2019). For example, seedling establishment is often poor on south-facing and lower-elevation sites (Chambers et al. 2016; Rother and Veblen 2016; Rodman et al. 2020, and in microsites away from snags, logs, stumps, shrubs, or other protective shade objects (Owen et al. 2017, 2020; Hammond et al. 2021).

Tree seedlings are often planted after fire when natural regeneration is deemed insufficient to restore desired forest conditions and their myriad associated processes and services (Stevens et al. 2021; Guiterman et al. 2022). However, planting tree seedlings is an extremely resource-intensive process, and planting activities in the Rocky Mountains and across the western US have thus far failed to keep up with the identified need (Dumroese et al. 2019; Fargione et al. 2021; Stevens et al. 2021). The 2021 REPLANT Act (Public Law 117 – 58, Title III, Sects. 70,301–70,303) directs the USDA Forest Service to close the planting need over the next 10 years and is expected to help the agency plant 1.2 billion trees across 1.7 million hectares of burned or otherwise deforested land (USDA Forest Service 2022). Proposed legislation, including the Trillion Trees Act and Climate Stewardship Act, addresses planting needs on other jurisdictional and private lands (Neuberger et al. 2021). Moreover, the need for planting is expected to only grow under a warmer climate that is increasingly conducive to high-severity burning (Coop et al. 2022). The pace and scale of planting are therefore expected to increase markedly in the future.

Reforestation guidelines, such as those of the Forest Service (FSH 2409.17_2 2002), offer general recommendations about designing and implementing planting activities to maximize seedling success. For example, guidelines often recommend planting seedlings on north-facing slopes and on the north side of shade objects. These growing environments can be cooler and wetter than their south-facing and unshaded counterparts, reducing seedling hydraulic stress and increasing seedling performance (Simeone et al. 2019). Guidelines also commonly recommend scalping, which removes competing herbaceous vegetation at the planting microsite, and incidentally creates a microtopographic depression that might increase water availability by capturing precipitation. However, while many studies of natural regeneration following high-severity fire provide support for these guidelines (Kemp et al. 2016; Rother et al. 2016; Owen et al. 2017, 2020; Hammond et al. 2021), relatively few studies have focused on planted seedlings (Ouzts et al. 2015; Marsh et al. 2022; Crockett and Hurteau 2022). Additionally, guidelines do not fully address how planting procedures may need to be modified based on species shade tolerance, drought tolerance, or other traits (Silvertown 2004; Andivia et al. 2020). Given the expected increase in post-fire planting across the Rocky Mountains (Stevens et al. 2021), more research is needed to inform the design and implementation of planting activities.

We investigated the effects of growing environment characteristics on planted tree seedling performance following the 2016 Cold Springs Fire, Colorado, USA. This fire burned at predominately high severity across a small parcel of upper-montane forest on the Roosevelt National Forest, creating a patch that was planted in 2018 with ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco), and limber pine (*Pinus flexilis* E. James) seedlings. In 2021, four growing seasons after planting, we surveyed 300 permanently marked seedlings for survival, height, and height growth. We also collected data on seedling growing environment characteristics, noting their site aspect and whether they were planted in microsites near shade objects or in depressions. We used these data to address the following questions: (1) How do seedling survival, height, and height growth vary with respect to aspect, shade object presence, and depression presence? (2) Do responses differ by species? Additionally, to investigate a mechanism through which growing environment characteristics could influence seedling responses, we measured summer soil moisture and asked (3) how does soil moisture vary with aspect, shade object presence, and depression presence? We hypothesized that survival, height, and height growth would be greatest on more northerly sites and in microsites where shade objects and depressions are present. We also hypothesized that the effects of the growing environment would vary by species in accordance with species traits. Last, we hypothesized that soil moisture would be greatest on more northerly aspects, in shade, and in depressions.

Methods

Study site

Our study site was a 37-ha portion of the Roosevelt National Forest that burned in the Cold Springs Fire in July 2016 (Fig. 1 A). Located just northeast of Nederland, Colorado (39.9787°, −105.4732°) at approximately 2550 m elevation, the site was typical of Front Range upper-montane mixed conifer forests prior to burning (Peet 1981; Schoennagel et al. 2011; Evans et al. 2011). Ponderosa pine, Douglas-fir, and lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson) co-dominated stands, with their relative abundance dependent on aspect (from FSVeg [Field Sampled Vegetation]; ARP 2019). Limber pine and trembling aspen (*Populus tremuloides* Michx.) also occurred at or near the site in lesser abundance (ARP 2019). The historical fire regime (prior to ca. 1860) at the site was likely mixed in terms of frequency and severity; historical fires are thought to have occurred every 35 to 100 + years depending on stand, topographic, and climatic conditions, and to have burned with a broad range of fire severities that often included a high-severity component (Schoennagel et al. 2011; Sherriff et al. 2014; McKinney 2019). Long-term mean temperatures at the site ranged from −3°C in January to 17°C in July, and long-term mean annual precipitation averaged 544 mm (1991–2020 climate normals; PRISM 2022). Site topography was rolling with a mix of generally gently sloping north and south aspects. The soils were formed from granitic and gneissic parent materials, which weathered into shallow, skeletal, and excessively drained Alfisols (USDA Natural Resources Conservation Service 2023).

The Cold Springs Fire was a human-ignited wildfire that burned approximately 214 ha before being aggressively suppressed (Fig. 1 A). The majority of the fire burned with moderate to high severity, which resulted

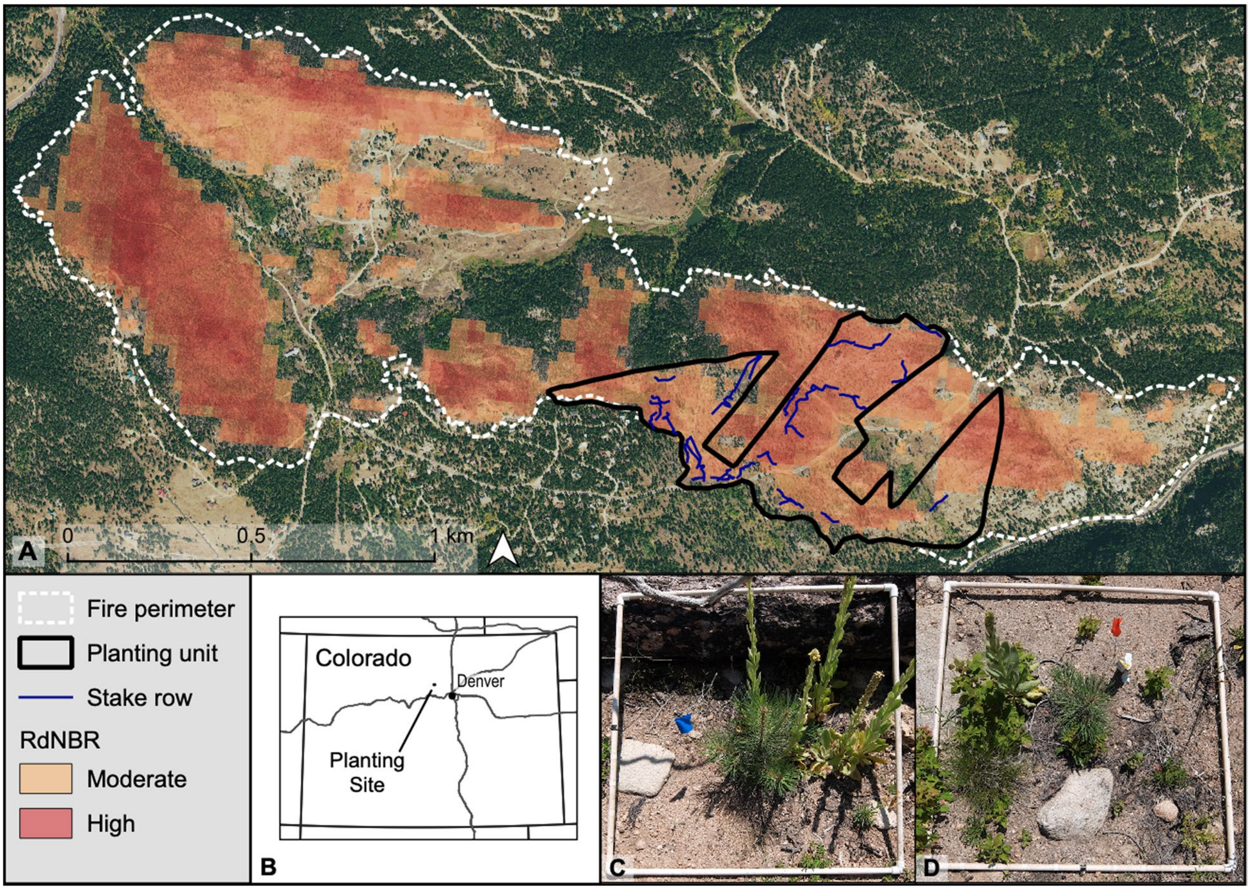

Fig. 1 **A** The Cold Springs Fire perimeter, planting unit, and stake rows. An RdNBR layer from the Southern Rockies Reforestation Tool depicts fire severity (Rodman et al. 2022), with a minimum display threshold of 600 corresponding to areas of field-observed tree mortality. NAIP imagery from September 2019 is also shown (US Geological Survey 2022). **B** The planting unit location within Colorado, with the closest major city and major interstates also shown. **C** and **D** Examples of planted ponderosa pine seedlings in 2021, four growing seasons after planting; seedlings are shaded by a log **C** and unshaded **D**. Photos courtesy: Laura Marshall

in large patches of high tree mortality (Fig. 1 A; Rodman et al. 2022). The study site itself also burned primarily at moderate to high severity, with some trees surviving in small patches along the site perimeter (Fig. 1 A).

Roosevelt National Forest personnel and volunteers planted 1-year-old containerized ponderosa pine, limber pine, and Douglas-fir seedlings at the site in May 2018. The goal of the planting was to help re-establish a mixed conifer forest. Naturally regenerating seedlings of the serotinous species lodgepole pine and the sprouting species trembling aspen were common at the site. However, very few naturally regenerating seedlings of the three seed-obligate, non-serotinous species planted were present away from the surviving trees, and they were not expected to achieve desired densities without intervention. The seedlings were grown by the Charles E. Bessey Tree Nursery in Halsey, Nebraska, from seeds that were collected between 2008 and 2014 at nearby sites of comparable elevation. Following US Forest Service guidelines (FSH 2409.17_2 2002), instructions were given to plant on the north side of shade objects whenever possible. Site preparation activities were minimal but sometimes included scalping the planting location to remove competing herbaceous vegetation. Ponderosa pine was regularly planted throughout the site at 242 seedlings ha^{-1}, limber pine at 52 seedlings ha^{-1}, and Douglas-fir at 7 seedlings ha^{-1}. Annual precipitation since planting was 393 mm in 2018 (72% of the long-term average), 416 mm in 2019 (76%), 403 mm in 2020 (74%), and 439 mm in 2021 (81%) (PRISM 2022).

Data collection

Following planting, Roosevelt National Forest personnel installed and monitored “stake rows” across the planting unit to track seedling survival after one and three growing seasons (FSH 2409.17_2 2002) (Fig. 1 A). Ten stake rows, each with ten seedlings of a single species, were established for the three species planted (30 rows and 300 seedlings total; 100 seedlings per species). Individual seedlings along the rows were permanently marked with wooden stakes and their coordinates were captured with a global positioning system. In September 2018 and October 2020, each seedling was revisited and its live or dead status was recorded. Live seedlings were those with at least some green foliage, while dead seedlings were without green foliage. Missing seedlings, wherein stakes did not have a planted live or dead seedling within an ~ 1-m radius, were assumed to be dead.

In June 2021, we recorded growing environment conditions for each staked seedling. We recorded aspect (degrees magnetic, converted to degrees true) as the general aspect of the area within approximately 20 m of the seedling. If a shade object was present within a 1-m^2 square quadrat centered on the seedling, we recorded the object type and whether it was likely present at the time of planting or was recruited after planting (e.g., due to snag breakup or snag fall). As potential shade objects, we identified snags, logs, stumps, or other objects that would shade the roots of the seedling during summer afternoons. If a depression was present within the 1-m^2 quadrat, we noted it as well. Depressions were subjectively identified as microtopographic concavities of the soil surface at the seedling that would allow water to collect. Although depression dimensions were not measured at Cold Springs, at similar planting sites nearby, they had an average depth of 28 mm and average volume of 1532 cm^3 (Marshall, unpublished data). When a seedling was missing but its stake was not, site and microsite characteristics were recorded at the stake. When a stake was missing in 2021, the seedling was dropped from the analysis (8/300 trees). Seedlings were equally distributed across aspects, with 50% on northerly (less than 90° and greater than 270°) slopes and 50% on southerly slopes (between 90 and 270°). Meanwhile, 29% of seedlings were situated near shade objects and 32% were in depressions.

In October 2021, four growing seasons after planting, we recorded the live or dead status for all seedlings and the height (mm) and 1-year height growth (mm) of live seedlings. We assessed live or dead status as described above. We measured height as the length of the seedling's above-ground woody stem. We measured height growth as stem growth during 2021, or the length of the stem between the tip and the first internode. Height growth was measured for 2021 as it was most likely to relate to the present growing environment; for example, we estimated that up to 21% of seedlings may have had post-planting changes in shade object condition due to snag dynamics.

We measured volumetric soil moisture content within the rooting zone (upper 10 cm of mineral soil) of each ponderosa pine seedling in July and August 2021 to characterize soil moisture (Hydrosense II, Campbell Scientific, Logan, UT). According to the nearest weather station (CoCoRaHS station CO-BO-75), conditions prior to both soil moisture sampling events were relatively dry. On July 14, the day before the July sampling, 1-mm precipitation was recorded; before that, 6 days had passed without precipitation. Trace rain fell on August 18, the day before the August sampling, and 2 mm fell 2 days prior to that. Sampling was restricted to only ponderosa pine seedlings to minimize potential temporal changes in soil moisture within each sampling event; this took approximately 4 h (1030 to 1430). We made three to five measurements within 20 cm of the base of each seedling, or if the seedling was missing, near the stake. We also took repeated measurements at one seedling over the course of each sampling event to track temporal trends, which were minimal.

Data analysis

To describe various elements of planting success, we used seedling survival, height, and height growth as response variables in our analyses. We also used soil moisture as an additional response variable. Soil moisture measurements were purged of obvious outliers, averaged for each seedling and sampling event, and then averaged across the two sampling events.

As potential predictors of each seedling response variable, we considered aspect, shade object presence, depression presence, and tree species. For analysis of aspect, we folded it around a north-south line such that 0° is north and 180° is south (Folded aspect = 180 - |Aspect – 180|) (McCune and Keon 2002). For descriptive and graphical interpretation, we also binned aspect to a binary north- or south-facing category. We binned shade and depression measurements to present or absent for both analysis and interpretation. Predictors were binned to make findings easy for managers to incorporate into planting activities. We assessed all individual predictors, as well as the two-way interaction terms of aspect by species, shade object presence by species, and depression presence by species, as we expected that species might respond differently to growing environment conditions. For soil moisture, we included the predictor aspect, shade object presence, and depression presence. Species and species interactions with other predictors were not included because soil moisture was only measured for ponderosa pine. Data used in the analysis are available at the USDA Forest Service Research Data Archive (Marshall et al. 2023).

We used generalized linear mixed models (GLMM) to characterize relationships among response and predictor variables. Models were constructed in R using the *glmmTMB*, *DHARMa*, and *MuMIn* packages (Neuwirth 2014; Brooks et al. 2017; Wickham et al. 2019; Müller 2020; R Core Team 2021; Bartoń 2022; Hartig 2022). We analyzed response variables at the seedling level, and included stake row as a random intercept term in each model to account for the manner in which the data were collected. We used a binomial distribution (logit link) for survival, a Gaussian distribution (identity link) for height and soil moisture, and a gamma distribution (log link) for height growth. We used an all-possible subsets model selection procedure (i.e., “dredge” function in MuMIn package) to identify the best combination of predictors of each response variable, where the top model was the one that minimized the second-order Akaike Information Criterion (AICc). We assessed residual diagnostic plots to ensure that model assumptions were met and to confirm goodness of fit.

Results

Cumulative seedling survival rates dropped notably over the first three growing seasons after planting (2018 to 2020) but exhibited only a minor decrease between the third and fourth (2021) growing seasons (Fig. 2). Of the 300 monitored seedlings, 80% survived to the end of the first growing season, while 59% and 58% survived to the end of the third and fourth growing seasons, respectively. Survival was relatively consistent across species, with 61% of planted ponderosa pine, 57% of limber pine, and 55% of Douglas-fir seedlings surviving to the end of four growing seasons.

Seedling survival through the fourth growing season was related to all three growing environment factors, with no differences attributed to species or species

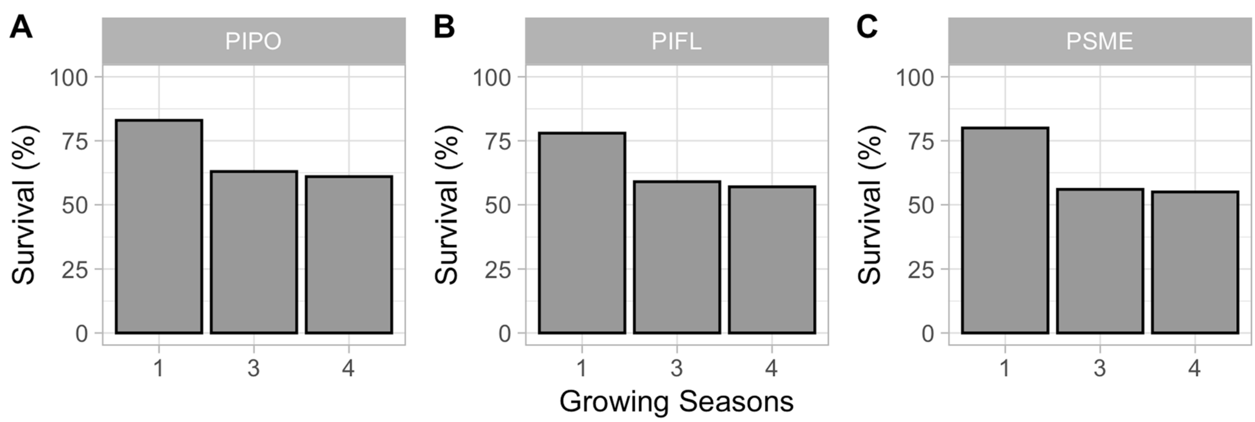

Fig. 2 Planted seedling survival by species at the end of growing seasons one (September 2018), three (October 2020), and four (October 2021). Species are ponderosa pine (*Pinus ponderosa*, PIPO, **A**), limber pine (*Pinus flexilis*, PIFL, **B**), and Douglas-fir (*Pseudotsuga menziesii*, PSME, **C**)

Table 1 Results (coefficients (coef) and *p*-value (p-val)) of final generalized linear mixed models (GLMMs) used to predict 4-year planted seedling survival, 4-year height, 2021 height growth, and summer 2021 soil moisture in the 2016 Cold Springs fire near Nederland, Colorado. Coefficients are only shown for fixed effect terms that were included in the final GLMMs based on all-possible subsets model selection. Terms that were included in at least one final GLMM but not in a particular GLMM are indicated by dashes, while terms that were not included in any of the final GLMMS were excluded altogether. Species are ponderosa pine (*Pinus ponderosa*, PIPO) and Douglas-fir (*Pseudotsuga menziesii*, PSME)

Model variables	*Survival*		*Height*		*Height growth*		*Soil moisture*	
	Coef	*P-val*	*Coef*	*P-val*	*Coef*	*P-val*	*Coef*	*P-val*
Folded aspect (° from north)	−0.016	< 0.001	−0.338	0.024	−0.005	0.186	-	-
Shade object presence (Yes)	0.621	0.067	37.83	0.004	0.728	< 0.001	-	-
Depression presence (Yes)	0.789	0.025	-	-	-	-	0.317	0.101
Species (PIPO)	-	-	164.11	< 0.001	1.071	< 0.001	-	-
Species (PSME)	-	-	116.88	< 0.001	0.331	0.218	-	-
Folded aspect by species (PSME)	-	-	-	-	−0.008	0.004	-	-
Shade object presence by species (PIPO)	-	-	-	-	−0.397	0.080	-	-
Shade object presence by species (PSME)	-	-	-	-	−0.664	0.005	-	-

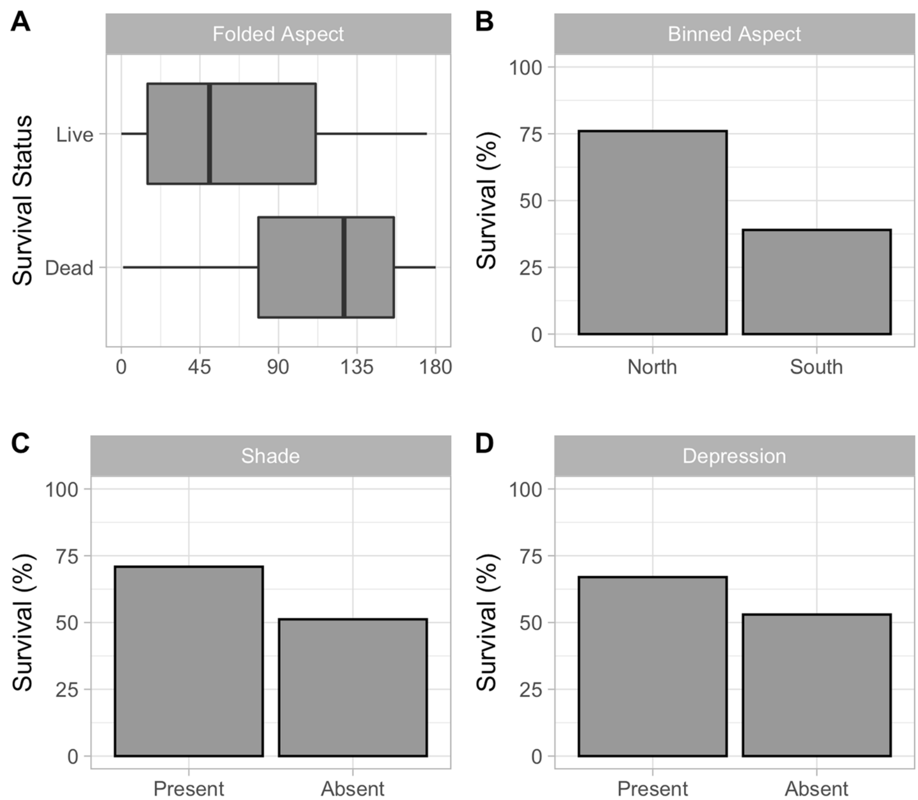

Fig. 3 Planted seedling survival in October 2021, four growing seasons after planting, relative to variables included in the final model: folded aspect (° from north) **A**, shade object presence **C**, and depression presence **D**. Panel **B** shows aspect in binary north- or south-facing bins and is included for interpretation only

interactions (Table 1, Fig. 3). Survival across all species was greater for seedlings with more northerly aspects (folded aspect closer to 0°) than with more southerly aspects (closer to 180°). Binning aspect into a binary category for interpretation, measured seedling survival on north-facing aspects was 37% greater than for those on south-facing aspects (76% versus 39%, respectively). Additionally, survival for seedlings near shade objects was 20% greater than for those not near shade objects (72% versus 52%, respectively), while survival for seedlings in depressions was 14% greater than for those not in depressions (67% versus 53%, respectively).

The height of live seedlings varied with aspect, shade object presence, and species, but the effects of aspect and shade were not species-dependent in our final model (i.e., no interaction terms) (Table 1, Fig. 4). Across all species, heights were greater for seedlings with more northerly aspects, such that seedlings in the north-facing aspect category were 65 mm taller than those in the south-facing category (261 mm vs. 197 mm, respectively). Heights were also 37 mm greater near shade objects than not near shade objects (263 mm vs. 226 mm, respectively). Overall, ponderosa pine seedlings were the tallest (305 mm), and limber pine seedlings were the shortest (142 mm); Douglas-fir seedlings were of intermediate height (271 mm).

Both aspect and shade object presence affected 2021 height growth rates for live seedlings, although their influence depended on species (Table 1, Fig. 5). More northerly aspects benefitted Douglas-fir height growth, such that measured growth was 26 mm greater for the north-facing aspect category (36 mm) than for the south-facing category (10 mm). In contrast, shade object presence affected height growth for both ponderosa pine and Douglas-fir. Ponderosa pine height growth was 20 mm greater near shade objects (103 mm) than not near shade objects (83 mm). Although a significant difference was detected, Douglas-fir seedlings had no measured height growth difference when considering shade object proximity (32 mm near and away from shade).

Summer soil moisture near ponderosa pine seedlings was affected only by depression presence (Fig. 6). Mean soil moisture measured at seedlings located in

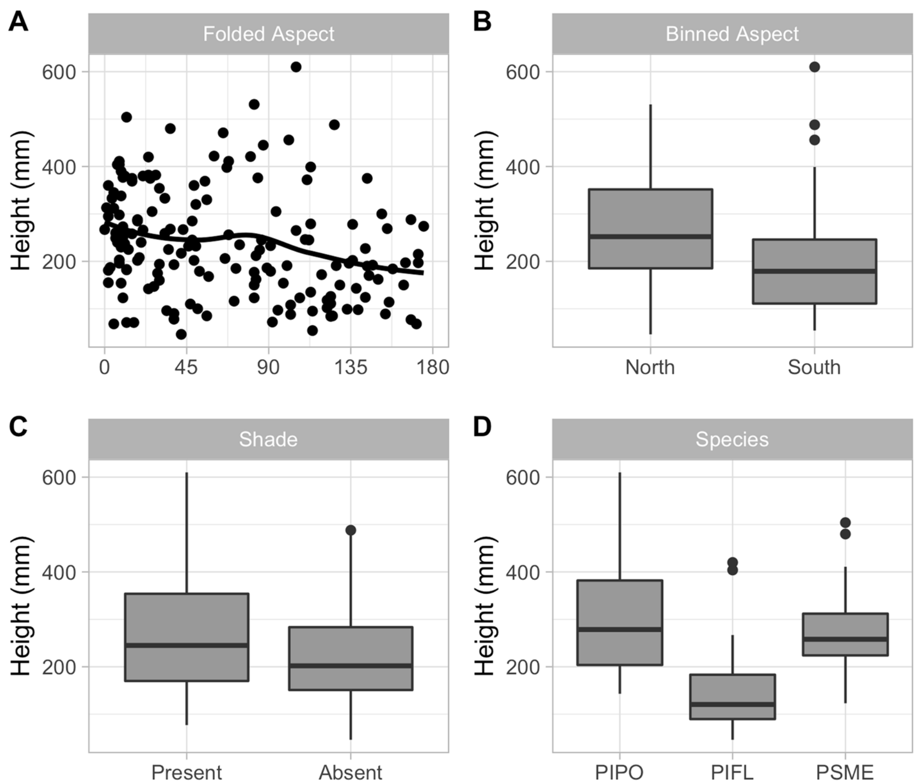

Fig. 4 Height of live seedlings in October 2021, four growing seasons after planting, relative to variables included in the final model: folded aspect (° from north, with a loess smooth line added for interpretation) **A**, shade object presence **C**, and depression presence **D**. Panel **B** shows aspect in binary north- or south-facing bins and is also included for interpretation. Species are ponderosa pine (*Pinus ponderosa*, PIPO), limber pine (*Pinus flexilis*, PIFL), and Douglas-fir (*Pseudotsuga menziesii*, PSME)

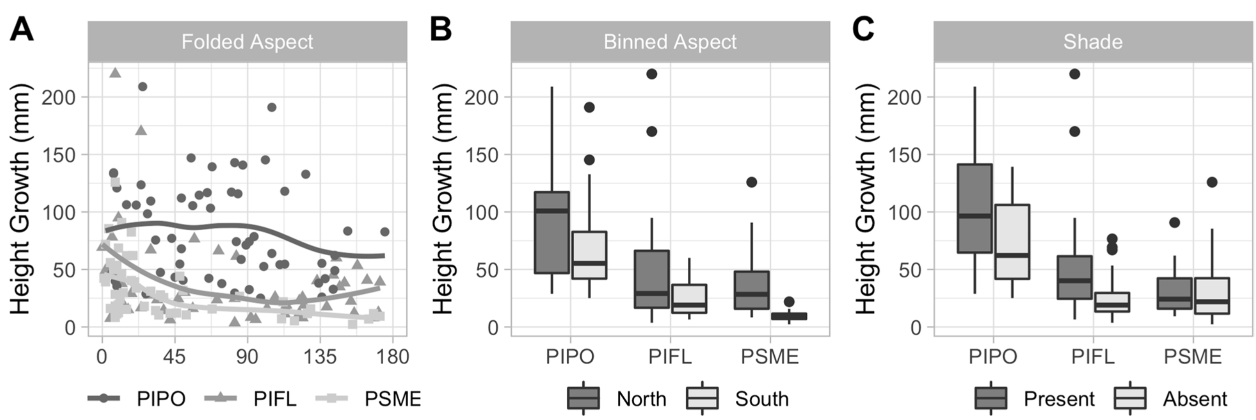

Fig. 5 Height growth of live seedlings at the end of the fourth growing season after planting, relative to variables included in final model: folded aspect by species (° from north, with a loess smooth line added for interpretation) **A,** and shade object presence by species **C**. Panel **B** shows aspect in binary north- or south-facing bins and is also included for interpretation. Species are ponderosa pine (*Pinus ponderosa*, PIPO), limber pine (*Pinus flexilis*, PIFL), and Douglas-fir (*Pseudotsuga menziesii*, PSME)

depressions was 3.8%, while moisture at seedlings not in depressions was 3.2%. Aspect and shade object presence did not have an effect on soil moisture as measured during the relatively dry and warm summer months.

Discussion

Tree planting after high-severity wildfire is playing an increasingly important role in forest recovery in the US Rocky Mountains, and the body of research available to

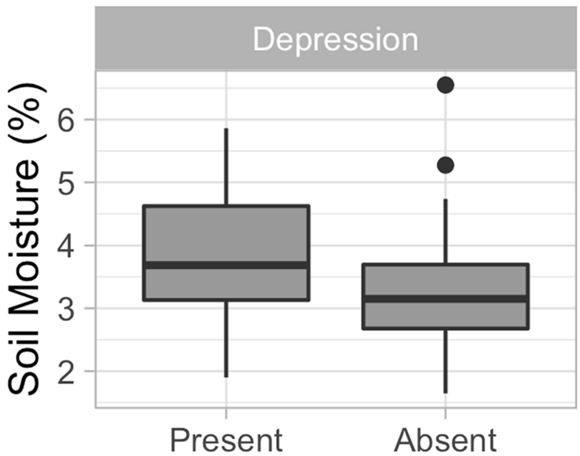

Fig. 6 Percent soil water content (soil moisture) measured at ponderosa pine seedlings in summer 2021, the fourth growing season after planting, relative to depression presence. Depression presence was the only variable included in the final model

directly guide this land management activity is small but growing (Ouzts et al. 2015; Marsh et al. 2022; Crockett and Hurteau 2022; Rodman et al. 2022). A planting and monitoring program initiated by Roosevelt National Forest personnel after the 2016 Cold Springs Fire in the Colorado Front Range provided us with a unique opportunity to examine how the growing environment affects the performance of planted seedlings. Our findings indicate that positioning seedlings to take advantage of cooler, wetter sites (i.e., north aspects) and microsites (i.e., near shade objects and in depressions) can increase their survival and growth in what are often otherwise climatically stressful post-fire landscapes (Wolf et al. 2021; Marsh et al. 2022). These practices, which are already commonly employed by land managers, will likely become increasingly relevant as the pace and scale of post-fire planting continues to grow and as conditions on the ground continue to become more stressful due to climate change.

In the Cold Springs Fire, seedlings planted on more northerly aspects had considerably greater survival, height, and height growth than those planted on more southerly aspects. The effect of aspect on survival was particularly notable: across all species, seedlings in the north-facing aspect category had survival rates that were nearly double those of their counterparts in the south-facing category. Cooler and wetter soil and air conditions, as well as lower insolation levels, all likely contributed to higher seedling survival and growth on more northerly aspects (Hoecker et al. 2020). Interestingly, we failed to detect an effect of aspect on summer soil moisture. Perhaps this was because little precipitation fell prior to the sampling events, or because our sampling was limited (only ponderosa pine seedlings were sampled for soil moisture, and only two sampling events were conducted). The survival rates we documented with respect to aspect ultimately may result in stand development patterns that will be comparable to those typically arising from natural regeneration processes (Kemp et al. 2016; Rother and Veblen 2016; Ziegler et al. 2017), with denser stands on northerly aspects than on southerly aspects. Even so, given the resource-intensive nature of planting, actions that improve survival rates on southerly aspects may be desirable. These actions may include leveraging microsite conditions (e.g., shade objects and depressions).

Indeed, shade objects, which in our study were primarily various forms of dead woody vegetation (i.e., snags, logs, and stumps) that shaded seedling roots during summer afternoons, increased the survival and growth of planted seedlings. As with aspect, the benefits of shade objects were most apparent for survival, with rates 1.4 times greater for seedlings near shade objects than away from them. Shaded microsites have been found to benefit both naturally regenerating and planted seedlings elsewhere (Maher et al. 2015; Hill and Ex 2020; Owen et al. 2020) and likely confer this benefit by buffering them against extreme insolation and soil and air temperatures during summer afternoons (Maher et al. 2015; Crockett and Hurteau 2022; Marsh et al. 2022). Shaded microsites may also increase the amount of soil moisture available to seedlings, which could increase survival (Hoecker et al. 2020; Rhoades et al. 2020), although as with aspect, we were unable to detect summer soil moisture differences between classes. While our findings clearly support the common practice of planting seedlings adjacent to shade objects to increase their performance (FSH 2409.17_2 2002), areas with a substantial risk of repeat fire may require a modified approach. This is because seedlings planted next to shade objects may be more likely to die during a reburn if the object combusts (Collins et al. 2018). Mortality during a reburn could be amortized by planting a subset of seedlings away from shade objects or by planting seedlings in widely spaced clusters (nucleation planting) within a fire or planting unit to distribute the risk of repeat fire across a broad area (North et al. 2019; Stevens et al. 2021).

Small microtopographic depressions likewise increased planted seedling performance, although less so than the other growing environment factors we examined. Moreover, depressions increased soil moisture, although the increase was very minor. The depressions we encountered in the Cold Springs Fire may have been an artifact of scalping to remove competing vegetation at the planting location. If true, then our findings suggest that this practice could be adjusted to make larger or deeper depressions, as is commonly done in dryland agroforestry

(Ramón Vallejo et al. 2012); wider or deeper depressions may potentially benefit seedlings by capturing more precipitation.

In our model, seedling responses to growing environment factors were relatively consistent across species; only for height and height growth were species or species interaction terms (aspect by species and shade object presence by species) retained in the top models. That there were few species effects may reflect the fact that all species occurred at or near the site prior to the fire (ARP 2019) and that locally sourced seeds were used to produce the seedlings. Nonetheless, species trait differences may still explain why seedlings of limber pine, a relatively slow-growing species (Steele 1990), were considerably shorter than those of ponderosa pine or Douglas-fir. Species trait differences may also explain why only Douglas-fir, which is less drought-tolerant than ponderosa pine and limber pine (Niinemets and Valladares 2006), had greater height growth on more northerly aspects than on more southerly ones.

This opportunistic study provides important quantitative information about how growing environment characteristics can influence the survival and growth of tree seedlings planted after wildfire in the US Rocky Mountains. However, it also highlights additional research needs. For example, evaluating the influence of aspect, shade objects, and depressions at other post-fire sites would help clarify the generalizability of our findings. Additionally, exploring how other relevant factors affect seedlings, such as long-term and post-planting climate, would help further refine planting procedures. At Cold Springs, the long-term climate appears to be moderately to highly suitable for seedlings (Rodman et al. 2022), which may have contributed to the relatively high rates of seedling survival and growth that we observed. However, conditions in the years following planting were generally warmer and drier than average (PRISM 2022), which may have compromised seedling survival and growth relative to what otherwise would be expected (Davis et al. 2019). Future studies targeting topics such as these would help to further expand the science available to land managers, and allow them to better optimize planting efforts in the face of an increasingly growing need.

Acknowledgements
The authors thank Robert Hubbard for his insights on the study and Marisa Granados, Joshua Ling, and Maria Vicini for their assistance with field data collection and data entry.

Authors' contributions
PF, LM, CS, KR, TC, and CS conceived the study. LM, PF, KZ, and CR developed the data collection methods and collected the data. LM and KR analyzed the data with input from PF and CS. LM and PF wrote the draft manuscript and all authors provided substantial comments and edits. All authors read and approved the final manuscript.

Funding
This work was supported by a grant from the USDA Forest Service, Western Wildland Environmental Threat Assessment Center. Additional support was provided by the Rocky Mountain Research Station and the Arapaho and Roosevelt National Forests and Pawnee National Grassland of the USDA Forest Service. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

Availability of data and materials
The data used in this study are available in the USDA Forest Service Research Data Archive (Marshall et al. 2023).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Forest and Rangeland Stewardship Department, Colorado State University, Fort Collins, CO, USA. [2]USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. [3]Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO, USA. [4]Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ, USA. [5]USDA Forest Service, Arapaho & Roosevelt National Forests and Pawnee National Grassland, Boulder, CO, USA. [6]Monitoring Evaluation and Learning Program, Chief Conservation Office, The Nature Conservancy, Arlington, VA, USA. [7]Colorado Field Office, The Nature Conservancy, Boulder, CO, USA.

Received: 9 November 2022 Accepted: 24 March 2023
Published online: 25 April 2023

References

Andivia, E., P. Ruiz-Benito, P. Díaz-Martínez, N. Carro-Martínez, M.A. Zavala, and J. Madrigal-González. 2020. Inter-specific tolerance to recurrent droughts of pine species revealed in saplings rather than adult trees. *Forest Ecology and Management* 459: 117848.

ARP [Arapaho and Roosevelt National Forests and Pawnee National Grassland]. 2019. Field Sampled Vegetation Spatial Database. US Department of Agriculture, Forest Service, Arapaho and Roosevelt National Forests and Pawnee National Grassland. Available online at the following link: https://www.fs.usda.gov/nrm/fsveg/. Accessed 27 Oct 2019.

Bartoń, K. 2022. MuMIn: Multi-Model Inference. R package version 1.46.0. https://CRAN.R-project.org/package=MuMIn.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9 (2): 378–400.

Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine–dominated forests of the Colorado Front Range. *Forest Ecology and Management* 378: 57–67.

Collins, B. M., J. M. Lydersen, R. G. Everett, and S. L. Stephens. 2018. How does forest recovery following moderate-severity fire influence effects of subsequent wildfire in mixed-conifer forests? *Fire Ecology* 14 (2): 1–9.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, E. Whitman, T. Assal, B. M. Collins, K. T. Davis, S. Dovrowski, D. A. Falk, P. J. Fornwalt, P. Z. Fulé, B. J. Harvey, V. R. Kane, C. E. Littlefield, E. Q. Margolis, M. North, M. Parisien, and S. Prichard and KC Rodman. 2020. Wildfire-driven forest conversion in western north american landscapes. BioScience 70(8), 659–673.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. M. Ritter, and C. M. Hoffman. 2022. Extreme fire spread events and area burned under recent and future climate in the western USA. *Global Ecology and Biogeography* 31 (10): 1949–1959.
Crockett, J. L., and M. D. Hurteau. 2022. Post-fire early successional vegetation buffers surface microclimate and increases survival of planted conifer seedlings in the southwestern United States. *Canadian Journal of Forest Research* 52 (3): 416–425.
Davis, K.T., S.Z. Dobrowski, P.E. Higuera, Z.A. Holden, T.T. Veblen, M.T. Rother, S.A. Parks, A. Sala, and M.P. Maneta. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences* 116 (13): 6193–6198.
Dumroese, R. K., N. Balloffet, J. W. Crockett, J. A. Stanturf, and L. E. Nave. 2019. A national approach to leverage the benefits of tree planting on public lands. *New Forests* 50: 1–9.
Evans, A. M., R. G. Everett, S. L. Stephens, and J. A. Youtz. 2011. Comprehensive fuels treatment practices guide for mixed conifer forests: California, Central and Southern Rockies, and the Southwest. JFSP Synthesis Reports. 12.
Fargione, J., D. L. Haase, O. T. Burney, O. A. Kildisheva, G. Edge, S. C. Cook-Patton, T. Chapman, A. Rempel, M. D. Hurteau, K. T. Davis, S. Dobrowski, S. Enebak, R. De La Torre, A. A. R. Bhuta, F. Cubbage, B. Kittler, D. Zhang, and R. W. Guldin. 2021. Challenges to the reforestation pipeline in the United States. *Frontiers in Forests and Global Change* 4: 8.
Guiterman, C. H., R. M. Gregg, L. A. Marshall, J. J. Beckmann, P. J. van Mantgem, D. A. Falk, J. E. Keeley, A. C. Caprio, J. D. Coop, P. J. Fornwalt, C. Haffey, R. K. Hagmann, S. T. Jackson, A. M. Lynch, E. Q. Margolis, C. Marks, M. D. Meyer, H. Safford, A Dunya Syphard, A. Taylor, C. Wilcox, D. Carril, C. A. F. Enquist, D. Huffman, J. Iniguez, N. A. Molinari, C. Restaino, and J. T. Stevens. 2022. Vegetation type conversion in the US Southwest: Frontline observations and management responses. *Fire Ecology* 18 (1): 1–16.
Haffey, C., T. D. Sisk, C. D. Allen, A. E. Thode, and E. Q. Margolis. 2018. Limits to ponderosa pine regeneration following large high-severity forest fires in the United States Southwest. *Fire Ecology* 14 (1): 143–163.
Hammond, D. H., E. K. Strand, P. Morgan, A. T. Hudak, and B. A. Newingham. 2021. Environmental influences on density and height growth of natural ponderosa pine regeneration following wildfires. *Fire* 4 (4): 80.
Hartig, F. 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.5. https://CRAN.R-project.org/package=DHARMa.
Higuera, P. E., and J. T. Abatzoglou. 2021. Record-setting climate enabled the extraordinary 2020 fire season in the western United States. *Global Change Biology* 27 (1): 1–2.
Hill, E. M., and S. Ex. 2020. Microsite conditions in a low-elevation Engelmann spruce forest favor ponderosa pine establishment during drought conditions. *Forest Ecology and Management* 463: 118037.
Hoecker, T. J., W. D. Hansen, and M. G. Turner. 2020. Topographic position amplifies consequences of short-interval stand-replacing fires on postfire tree establishment in subalpine conifer forests. *Forest Ecology and Management* 478: 118523.
Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the US northern Rockies. *Landscape Ecology* 31 (3): 619–636.
Korb, J. E., P. J. Fornwalt, and C. S. Stevens-Rumann. 2019. What drives ponderosa pine regeneration following wildfire in the western United States? *Forest Ecology and Management* 454: 117663.
Maher, C. T., A. L. Barber, and D. L. Affleck. 2015. Shelter provided by wood, facilitation, and density-dependent herbivory influence Great Basin bristlecone pine seedling survival. *Forest Ecology and Management* 342: 76–83.
Marsh, C., D. Krofcheck, and M. D. Hurteau. 2022. Identifying microclimate tree seedling refugia in post-wildfire landscapes. *Agricultural and Forest Meteorology* 313: 108741.
Marshall, L. A. E., P. J. Fornwalt, C. S. Stevens-Rumann, K. C. Rodman, C. C. Rhoades, K. Zimlinghaus, T. Chapman, and C. A. Schloegel. 2023. Seedling and growing environment measurements from a tree planting unit in the 2016 Cold Springs Fire, Colorado, USA. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2023-0014.
McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of vegetation science* 13 (4): 603–606.
McKinney, S. T. 2019. Systematic review and meta-analysis of fire regime research in ponderosa pine (Pinus ponderosa) ecosystems, Colorado, USA. *Fire Ecology* 15 (1): 1–25.
Müller, K. 2020. here: A Simpler Way to Find Your Files. R package version 1.0.1. https://CRAN.R-project.org/package=here.
Neuberger, J., A. Rudee, and H. Leslie-Bole. 2021. 7 Policy Proposals to Restore US Trees: How Do They Compare? Commentary: World Resources Institute. https://www.wri.org/insights/us-policy-trees-natural-infrastructure.
Neuwirth, E. 2014. RColorBrewer: ColorBrewer Palettes. R package version 1.1-2. https://CRAN.R-project.org/package=RColorBrewer.
Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76 (4): 521–547.
North, M. P., J. T. Stevens, D. F. Greene, M. Coppoletta, E. E. Knapp, A. M. Latimer, C. M. Restaino, R. E. Tompkins, K. R. Welch, R. A. York, D. J. Young, J. N. Axelson, T. N. Buckley, B. L. Estes, R. N. Hager, J. W. Long, M. D. Meyer, S. M. Ostoja, H. D. Safford, K. L. Shive, C. L. Tubbesing, H. Vice, D. Walsh, C. M. Werner, and P. Wyrsch. 2019. Tamm Review: Reforestation for resilience in dry western US forests. *Forest Ecology and Management* 432: 209–224.
Ouzts, J., T. Kolb, D. Huffman, and A. S. Meador. 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. *Forest Ecology and Management* 354: 281–290.
Owen, S. M., C. H. Sieg, A. J. S. Meador, P. Z. Fulé, J. M. Iniguez, L. S. Baggett, P. J. Fornwalt, and M. A. Battaglia. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. *Forest Ecology and Management* 405: 134–149.
Owen, S. M., C. H. Sieg, P. Z. Fulé, C. A. Gehring, L. S. Baggett, J. M. Iniguez, P. J. Fornwalt, and M. A. Battaglia. 2020. Persistent effects of fire severity on ponderosa pine regeneration niches and seedling growth. *Forest Ecology and Management* 477: 118502.
Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. *Vegetatio* 45 (1): 3–75.
PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data created 1 Dec 2021. Accessed 8 Feb 2022.
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Ramón Vallejo, V., A. Smanis, E. Chirino, D. Fuentes, A. Valdecantos, and A. Vilagrosa. 2012. Perspectives in dryland restoration: approaches for climate change adaptation. *New Forests* 43 (5): 561–579.
Rhoades, C. C., R. M. Hubbard, K. Elder, P. J. Fornwalt, E. Schnackenberg, P. R. Hood, and D. B. Tinker. 2020. Tree regeneration and soil responses to management alternatives in beetle-infested lodgepole pine forests. *Forest Ecology and Management* 468: 118182.
Rodman, K. C., T. T. Veblen, M. A. Battaglia, M. E. Chambers, P. J. Fornwalt, Z. A. Holden, T. E. Kolb, J. R. Ouzts, and M. T. Rother. 2020. A changing climate is snuffing out post-fire recovery in montane forests. *Global Ecology and Biogeography* 29 (11): 2039–2051.
Rodman, K., P. Fornwalt, T. Chapman, J. Coop, G. Edwards, J. Stevens, and T. Veblen. 2022. *SRRT: a decision Support Tool to inform Postfire Reforestation of Ponderosa Pine and Douglas-fir in the Southern Rocky Mountains. Research note RMRS-RN-95*. 12 p. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.
Rother, M.T., and T.T. Veblen. 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. *Ecosphere* 7 (12): e01594.
Schoennagel, T., R. L. Sherriff, and T. T. Veblen. 2011. Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration. *Ecological Applications* 21 (6): 2210–2222.
Sherriff, R.L., R.V. Platt, T.T. Veblen, T.L. Schoennagel, and M.H. Gartner. 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *Plos One* 9 (9): e106971.
Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19 (11): 605–611.
Simeone, C., M. P. Maneta, Z. A. Holden, G. Sapes, A. Sala, and S. Z. Dobrowski. 2019. Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. *New Phytologist* 221 (4): 1814–1830.
Steele, R. 1990. Pinus flexilis James. Limber pine. In *Silvics of North America, volume 1: conifers. Agriculture Handbook 654*, 348–354. Washington, DC: U.S. Department of Agriculture, Forest Service.

Stevens, J. T., C. M. Haffey, J. D. Coop, P. J. Fornwalt, L. Yocom, C. D. Allen, A. Bradley, O. T. Burney, D. Carril, M. E. Chambers, T. B. Chapman, S. L. Haire, M. D. Hurteau, J. M. Iniguez, E. Q. Margolis, C. Marks, L. A. E. Marshall, K. C. Rodman, C. S. Stevens-Rumann, A. E. Thode, and J. J. Walker. 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. *Forest Ecology and Management* 502: 119678.
Wickham, H., M. Averick, J. Bryan, W. Chang, L. D'Agostino, R. McGowan, G. François, A. Grolemund, L. Hayes, J. Henry, M. Hester, T. L. Kuhn, E. Pedersen, S. M. Miller, K. Bache, J. Müller, D. Ooms, D. P. Robinson, V. Seidel, K. Spinu, D. Takahashi, C. Vaughan, K. Wilke, and Woo, and H Yutani. 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4 (43): 1686.
Williams, A. P., J. T. Abatzoglou, A. Gershunov, J. Guzman-Morales, D. A. Bishop, J. K. Balch, and D. P. Lettenmaier. 2019. Observed impacts of anthropogenic climate change on wildfire in California. *Earth's Future* 7 (8): 892–910.
Wolf, K.D., P.E. Higuera, K.T. Davis, and S.Z. Dobrowski. 2021. Wildfire impacts on forest microclimate vary with biophysical context. *Ecosphere* 12 (5): e03467.
US Geological Survey. 2022. USDA-FPAC-BC-APFO Aerial Photography Field Office National Agriculture Imagery Program (NAIP) (published 20190924). https://www.usgs.gov/the-national-map-data-delivery. Accessed April 29, 2022.
USDA Forest Service. 2022. National forest system reforestation strategy growing and nurturing resilient forests. *National Forest System FS* -1198: 32 p.
USDA Forest Service. 2002. FSH 2409.17– Silvicultural Practices Handbook Chap. 2 – Reforestation. 97 p.
USDA Natural Resources Conservation Service. Web Soil Survey. Available online at the following link: http://websoilsurvey.sc.egov.usda.gov/. Accessed 02/28/2023.
Ziegler, J. P., C. M. Hoffman, P. J. Fornwalt, C. H. Sieg, M. A. Battaglia, M. E. Chambers, and J. M. Iniguez. 2017. Tree regeneration spatial patterns in ponderosa pine forests following stand-replacing fire: influence of topography and neighbors. *Forests* 8 (10): 391.

Publisher's Note