

ARTICLE

Vegetation Ecology

Give seeds a chance? Opportunities and techniques for post-fire reforestation using tree seeding

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Abstract

Altered fire regimes and post-fire tree regeneration failures have the potential to drive forest cover losses throughout western North America, but management practices such as active reforestation may help address these challenges. Planting of nursery-grown tree seedlings currently accounts for the majority of active reforestation in the western United States. Direct tree seeding—an alternative approach that involves dispersing seeds into a project site—is rare but has the potential to supplement planting and increase the pace and scale of reforestation activities, particularly where planting is operationally challenging. In the Southern Rocky Mountains, USA, we used a regionwide spatial analysis to describe (1) the typical locations of post-fire tree planting and (2) the percentage of severely burned forests that are difficult to access using such treatments. In experimental field trials in two Colorado wildfires, we tracked nearly 40,000 seeds over a one-year period to test a range of seed enhancement techniques (seed coating, pelleting, and priming) and operational factors (sowing season, microsite characteristics) that might influence direct seeding outcomes. Nearly two-thirds (63.4%) of post-fire tree planting activities in this region occurred in severely burned areas, near established roads, and on flatter slopes. About one-third (32.2%) of all severely burned forests would be challenging to access using tree planting based on current patterns of implementation. In direct seeding field trials, first-year establishment rates averaged just 0.2% but ranged from 0% to 2.7% across treatments. Untreated seeds had 4× higher establishment rates than those receiving seed

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enhancement techniques. In the older (20-year-old) fire, direct seeding was most effective in sites with bare ground cover; in the more recent (1-year-old) fire, direct seeding was most effective in sites where wood mulch was dispersed during post-fire hillslope stabilization treatments. Direct seeding may help treat vast areas that are difficult to access using tree planting activities. However, increases in seed collection and further exploration of techniques to increase tree establishment rates are needed for this technique to become operationally feasible at broad scales.

KEYWORDS

conifer forests, direct seeding, natural climate solutions, *Pinus ponderosa*, reforestation, seed enhancement techniques, wildfire

INTRODUCTION

Anthropogenic climate change and shifting land use are altering fire activity globally, with important consequences for ecosystems (Burton et al., 2024). In temperate conifer forests of western North America, annual wildfire area and the area burned at high severity have increased since the 1980s (Bowman et al., 2020; Parks et al., 2025). While these forests have co-evolved with fire as an essential process, particular aspects of fire regimes (e.g., fire frequency, fire severity) are now beginning to deviate from the natural range of variability (Higuera et al., 2021; McClure et al., 2024). Altered fire regimes and warming climate conditions are also inhibiting post-fire tree regeneration, which is critical to forest persistence (Coop et al., 2020; Davis et al., 2023). Active reforestation is a widely practiced approach that seeks to accelerate forest recovery using management intervention (Dumroese et al., 2019; North et al., 2019). Where implemented, active reforestation can increase tree density and enhance forest recovery rates following fire (Ouzts et al., 2015; Rodman et al., 2024a; Sorenson et al., 2025). However, there are now at least 1.5 million ha in need of active post-fire reforestation throughout the United States (Dobrowski et al., 2024; USFS, 2022). This accumulated deficit is due to factors such as limited funding, infrastructure, and workforce capacity (Fargione et al., 2021), and creative solutions are needed to address it.

Throughout the western United States, tree planting is the most common method of active reforestation. Tree planting typically involves collecting seeds from cultivated seed orchards or native forests, using these seeds to grow tree seedlings at a nursery, and planting nursery-grown seedlings at a project site (Fargione et al., 2021). Direct seeding—dispersing tree seeds directly into a project site—accounts for just 1% of all reforestation accomplishments on lands of the USDA

Forest Service (USFS), the agency tasked with managing most western US forests (Dumroese et al., 2019). Direct seeding is not widely practiced because seedling establishment and performance can be low relative to tree planting (Grossnickle & Ivetić, 2017; Palma & Laurance, 2015). Yet, seeding may play a valuable role in addressing the reforestation backlog for both economic and operational reasons (Barnett, 2014; Haase & Davis, 2017). Planting projects in the United States typically cost >US\$1 per seedling (Dobrowski et al., 2024; Fargione et al., 2021), whereas direct seeding can be considerably cheaper (Grossnickle & Ivetić, 2017; Palmerlee & Young, 2010). Likewise, aerial platforms may be used with direct seeding to expand the reach of active reforestation projects to sites that are far from roads or have steep, rugged terrain (Aghai & Manteuffel-Ross, 2020; Barnett, 2014; Downer et al., 2024).

While direct seeding may help increase the pace and scale of reforestation activities throughout the western United States, questions remain regarding its utility in post-fire environments. Seed predation by animals (Barnett, 2014; Shepperd et al., 2006; Zwolak et al., 2010) and the hot, dry microclimatic conditions that characterize post-fire landscapes (Wolf et al., 2021) are likely to limit the success of many direct seeding projects. Seed enhancement techniques, such as coating, pelleting, and priming, have helped to mitigate these effects in grassland or shrubland restoration projects (Madsen et al., 2016; Pedrini et al., 2020), but are rarely tested with coniferous trees. However, limited existing research suggests that coating seeds with the natural compounds found in *Capsicum* spp. (i.e., chili peppers) can limit tree seed predation by small mammals (Pearson et al., 2019). Likewise, pelleting seeds—such as by incorporating them into seed balls made from clay or other degradable materials—can reduce seed predation and improve moisture retention when used with herbaceous species and

shrubs (Gornish et al., 2019), and may also increase the success of conifer restoration. Seed priming—hydrating, cold-stratifying, and/or drying seeds—has been shown to expedite germination and improve seed vigor in some species (Pedrini et al., 2020), but is not typically used with the direct seeding of conifers (*but* see Barnett, 2014). Interactions between seedlings and post-fire ground cover can be competitive (Tepley et al., 2017) or facilitative (Marsh et al., 2023), and microsite characteristics are a strong predictor of the success of direct seeding projects (Shackelford et al., 2021). Thus, seed enhancement techniques and microsite selection are critical areas for research to inform direct seeding practices for coniferous trees in post-fire environments (Downer et al., 2024; Grossnickle & Ivetić, 2017).

Here, we evaluate potential opportunities and techniques for direct tree seeding in post-fire landscapes throughout the Southern Rocky Mountains, USA (Figure 1). First, we use a regionwide spatial analysis to describe the typical locations of nursery-based tree planting activities based on factors such as fire severity and site accessibility. Next, we identify fire-affected areas that may need active reforestation but are challenging to access for planting based on current patterns of implementation. Finally, we present the results from two field trials of direct seeding using ponderosa pine (*Pinus ponderosa*), a widespread coniferous tree species. These trials included a range of seed enhancement techniques, sowing seasons (i.e., the season in which direct seeding occurred), and microsite characteristics in an older

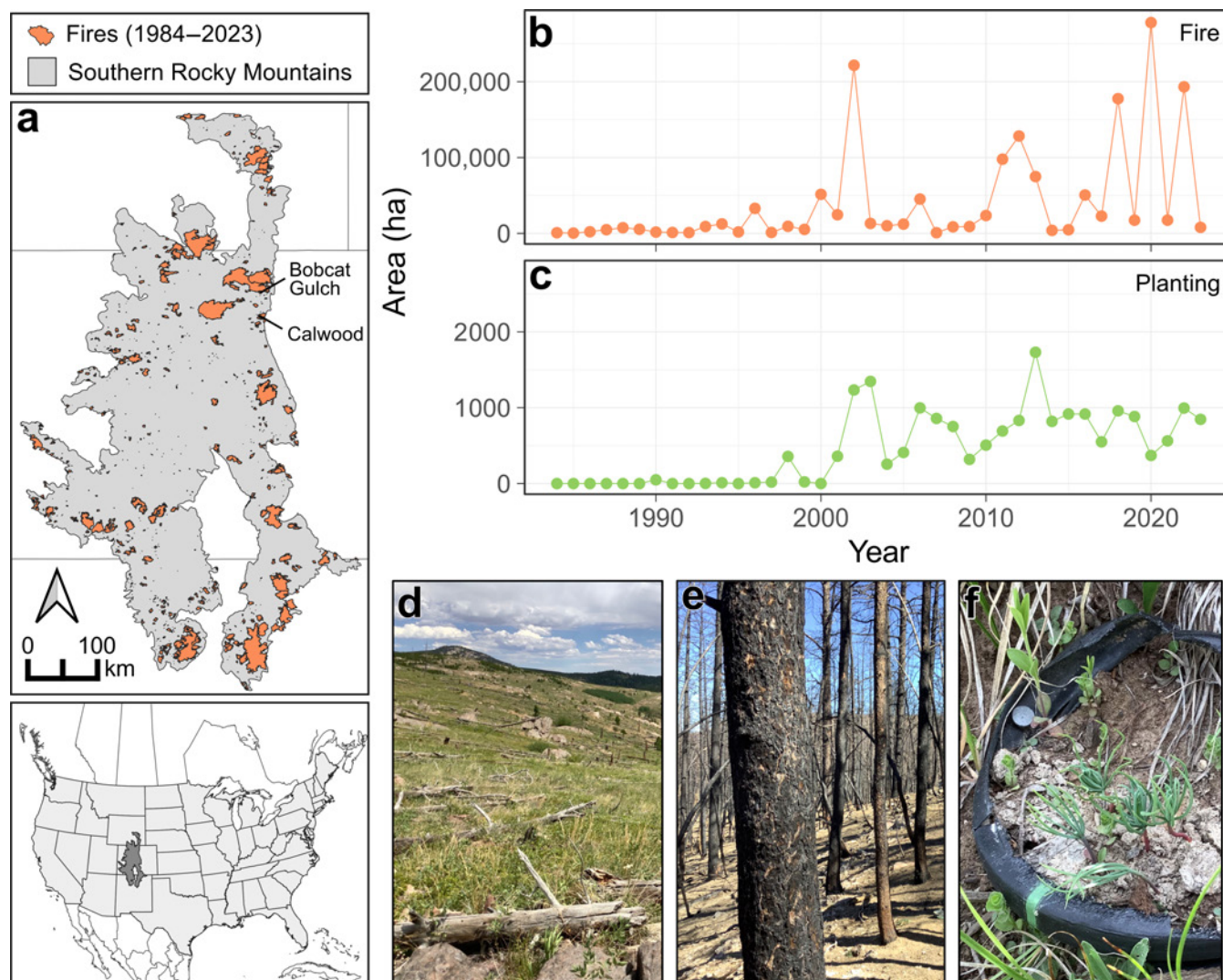


FIGURE 1 (a) The study area (including fire perimeters between 1984 and 2023) in the Southern Rocky Mountains, USA, (b) the annual area burned by wildfire (c), post-fire tree planting activities on USDA Forest Service lands, (d, e) characteristics of the two locations of experimental field trials of direct tree seeding, and (f) a depiction of our direct seeding field trials. (d) The Bobcat Gulch sites burned in 2000 and (e) the Calwood sites burned in 2020; photos (d, e) were taken ca. 2021. Photo credit: C. Schloegel.

(~20 years since fire) and a more recent wildfire (~1 year since fire). We hypothesized that tree plantings would primarily occur in sites with high-severity fire and in more accessible areas (near roads and on more gradual slopes), but that a large percentage of reforestation needs would be found in less accessible sites. Within our experimental seeding trials, we hypothesized that seed coating and pelleting would result in higher establishment rates by limiting animal herbivory and enhancing moisture retention. We also hypothesized that establishment would be highest in microsites with bare ground cover because ponderosa pine establishes well on bare mineral soil (Schubert et al., 1970).

METHODS

Study area

Our study area is located in the Southern Rocky Mountains Ecoregion (SRME) (Level III Ecoregion number 21; US EPA, 2021), which covers 144,462 km² in southern Wyoming, northern New Mexico and central and western Colorado, USA (Figure 1). The SRME is characterized by rugged, mountainous terrain, with elevations ranging from 1142 to 4398 m (USGS, 2021). Mean annual precipitation ranges from 212 to 1847 mm (mean = 589) and mean annual temperature ranges from -5.5 to 12.6°C (mean = 4.6), with greater moisture availability at higher elevations and on the western side of the mountains (1991–2020 climate normals; PRISM, 2023). In order of site moisture availability (dry to wet), typical tree species in the study area include juniper (e.g., *Juniperus monosperma*, *Juniperus osteosperma*, *Juniperus scopulorum*), two-needle piñon (*Pinus edulis*), ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Wilson et al., 2013).

Regionwide spatial analysis of post-fire planting locations and accessibility

To characterize the typical locations of tree planting within the SRME, we acquired spatial datasets describing the locations of operational activities, fire perimeters, and potential drivers of planting need or operational feasibility (Appendix S1). We restricted our analyses to USFS-managed lands because they include over 60% of the forested area in the SRME, and operational records were most complete in these areas (Allred et al., 2021;

USFS, 2025). To identify post-fire plantings in areas that previously had forest cover, we focused on locations that burned between 1987 and 2022 and had ≥10% tree cover in 1986 (70.1% of USFS lands). We excluded designated wilderness areas (USFS, 2025) as no recorded plantings were completed in these locations. For analyses, we converted all planting unit polygons ($n = 905$) into points using a 30-m fishnet grid ($n = 249,525$), aligned with other spatial datasets, and assigned each point a “fire year,” which referred to the last fire that occurred in that location before planting. We then randomly sampled points that were outside of known planting areas, with the same number of planted and unplanted points in each fire year. For each point, we extracted predictor variables of (1) fire-driven canopy loss, (2) slope angle, (3) distance to the closest road, and (4) timber suitability designation. Timber suitability designation is defined by local management plans as any area that can support timber production as a primary management goal (Appendix S1). We expected that each of these variables would influence tree planting decisions by describing ecological change (greater canopy loss would indicate a greater planting need), operational feasibility (slope and distance to road would both influence access for workers and equipment), and administrative prioritization (lands managed as suitable timber would be a higher priority for reforestation).

We used a classification tree approach (Breiman et al., 1984) to predict whether locations were planted or unplanted after fire using the covariates described above. We used a maximum tree depth of two to limit overfitting and assessed model performance using balanced accuracy and area under the curve (AUC) in 20-fold spatially stratified cross-validation. Next, for each terminal node in the model, we calculated the total planting area and the percentage of the study area that was planted. There are some cases where these two numbers differ, for instance, when a node includes a low total planting area because it represents uncommon locations on the landscape, but a high percentage of these locations have been planted. We also described the accessibility of burned sites with a potential reforestation need. To do so, we calculated the 95th percentile values of slope and distance to road from all planting points to identify the near-upper limits of what has been planted. We then identified areas with potential planting need as burned areas that experienced ≥70% canopy loss, a threshold identified in our classification tree analysis. Finally, we quantified the percentage of these areas that were more accessible (i.e., ≤ 95th percentile values of slope and distance to road) or less accessible (i.e., >95th percentile values of either slope or distance to road) using tree planting (Appendix S1: Figure S1). We also conducted a similar analysis across

all forests on all USFS lands (outside of wilderness) to summarize accessibility after theoretical future fire events. We fit the classification tree using the *partykit* package (Hothorn & Zeileis, 2015) and performed spatial data processing using the *terra* package (Hijmans, 2025) in R v. 4.4.0 (R Core Team, 2024).

Experimental field trials

We conducted experimental field trials of direct tree seeding in two wildfires in northern Colorado, USA, to test a range of seed enhancement techniques, microsite characteristics, and sowing seasons (Figure 1, Table 1; Appendix S2). The Bobcat Gulch Fire (40.5° N, 105.5° W; ~2500 m) burned in June 2000, and sowing occurred in December 2020 and April 2021. The Calwood Fire (40.2° N, 105.4° W; ~2300 m) burned in October 2020, and sowing occurred in November 2021, December 2021, and April 2022. Experimental sites in each location were severely burned and had no live trees within 50 m; natural post-fire regeneration of ponderosa pine is very rare beyond 50 m from live trees in this region (Chambers et al., 2016). Ground cover differed considerably between the two locations. Bobcat Gulch had

abundant herbaceous plant cover (Figure 1d) and Calwood had limited vegetation cover at the onset of the experiments (Figure 1e). Treatments and plot design also differed slightly between experiments because we used information from the first experiment (Bobcat Gulch) to update protocols and we also leveraged post-fire hillslope stabilization treatments for Calwood (Table 1; Appendix S2). We sowed a total of 19,200 ponderosa pine seeds on the soil surface at each site. Ponderosa pine was the dominant tree species at each location prior to fire and is the most widely used species for post-fire reforestation in the SRME (Rodman et al., 2024b). We collected all seeds in September 2019 from a single location (40.7° N, 105.5° W; ~2300 m) and they had an estimated germination rate of 89% (USDA Seed Lab, Atlanta, Georgia). In September 2021 (Bobcat Gulch) and September 2022 (Calwood), we recorded the number of ponderosa pine seedlings that germinated and survived through one growing season (hereafter “first-year establishment”). Precipitation during the April–September growing season, an important driver of tree establishment (Rother & Veblen, 2017), was 4.9% above average at Bobcat Gulch and 13.5% below average at Calwood during the course of the experiment (relative to 1991–2020 climate normals; PRISM, 2023).

TABLE 1 Descriptions of ponderosa pine seeding experimental treatments in the Bobcat Gulch and Calwood sites.

Priming	Treatments			Sites ^a	
	Sowing season	Pelleting	Coating	Bobcat	Calwood
No	Winter	Yes	Yes	X	
No	Winter	No	Yes	X	X
No	Winter	Yes	No	X	
No	Winter	No	No	X	X
Yes	Winter	Yes	Yes	X	
Yes	Winter	No	Yes	X	
Yes	Winter	Yes	No	X	
Yes	Winter	No	No	X	
No	Spring	Yes	Yes	X	
No	Spring	No	Yes	X	X
No	Spring	Yes	No	X	
No	Spring	No	No	X	X
Yes	Spring	Yes	Yes	X	
Yes	Spring	No	Yes	X	
Yes	Spring	Yes	No	X	
Yes	Spring	No	No	X	

Note: In Bobcat Gulch, winter sowing occurred on December 21, 2020, and spring sowing occurred on April 7, 2021. In the Calwood experiment, winter sowing occurred on November 19, November 22, and December 3, 2021, and spring sowing occurred on April 8, 2022.

^aThe Calwood sites also had an experimental treatment of ground cover (with equal numbers of plots on mulch and bare ground), whereas the Bobcat Gulch sites had observational ground cover data collected at each plot, but without a balanced, experimental design.

We used generalized linear mixed models (GLMMs) to characterize relationships among response and predictor variables in the experimental studies using the *glmmTMB* package (Brooks et al., 2017) in R. We developed separate models for Bobcat Gulch and Calwood due to differing experimental treatments. For both models, we used a binomial error structure (complementary log–log link; Zuur et al., 2009), where we defined the response as the number of live seedlings (Number Successes) out of the total number of seeds sown (Number Trials). Because our experimental design used a nested structure, we included random intercept terms of (1) transect within site (Appendix S2: Figure S2) for the Bobcat Gulch model and (2) cluster within site (Appendix S2: Figure S3) for the Calwood model to account for potential location-level differences and spatial dependence among samples. We assessed residual diagnostic plots to ensure that model assumptions were met using the *DHARMA* package (Hartig, 2024), and quantified goodness of fit using marginal and conditional R^2 (R^2_m and R^2_c , respectively) using the *MuMIn* package (Bartón, 2024) in R.

RESULTS

Current locations of tree planting and potential accessibility

During our study period (1987–2022), approximately 1.4 million ha burned in the SRME, 41.8% (584,278 ha) of

which met our study criteria—located on USFS lands, outside of wilderness, and with $\geq 10\%$ forest cover in 1986. Overall, 3.8% of the area meeting our study criteria was planted after fire (22,457 ha; $n = 905$ planting units). As expected, fire severity, distance to road, slope angle, and suitable timber designation all helped to identify the locations of tree planting activities in our classification tree model, with a balanced accuracy of 72.1% and an AUC of 0.76. Planted sites often burned at high severity (i.e., $>70.5\%$ canopy loss), were near established roads (i.e., ≤ 815 m distance to road), and on relatively flat slopes (i.e., $\leq 16^\circ$ slope angle) (Figure 2). Of the sites meeting these criteria on USFS lands, 14.9% were planted (i.e., 85.1% of these severely burned and accessible areas remain unplanted), accounting for nearly two-thirds (63.4%) of the total post-fire planting area. However, some less severely burned and less accessible sites were also planted, particularly those that were suitable for timber production. The 95th percentiles of distance to road and slope angle within planting areas were 930 m and 24° , respectively. Based on these road and slope criteria, 32.2% of the area with potential post-fire reforestation needs on USFS lands (i.e., 199,780 ha) would be less accessible to planting (Figure 3; Appendix S1: Figure S1). Likewise, 32.7% of all forests on USFS lands (outside of wilderness) would be hard to access with tree planting, should severe fires occur in the future.

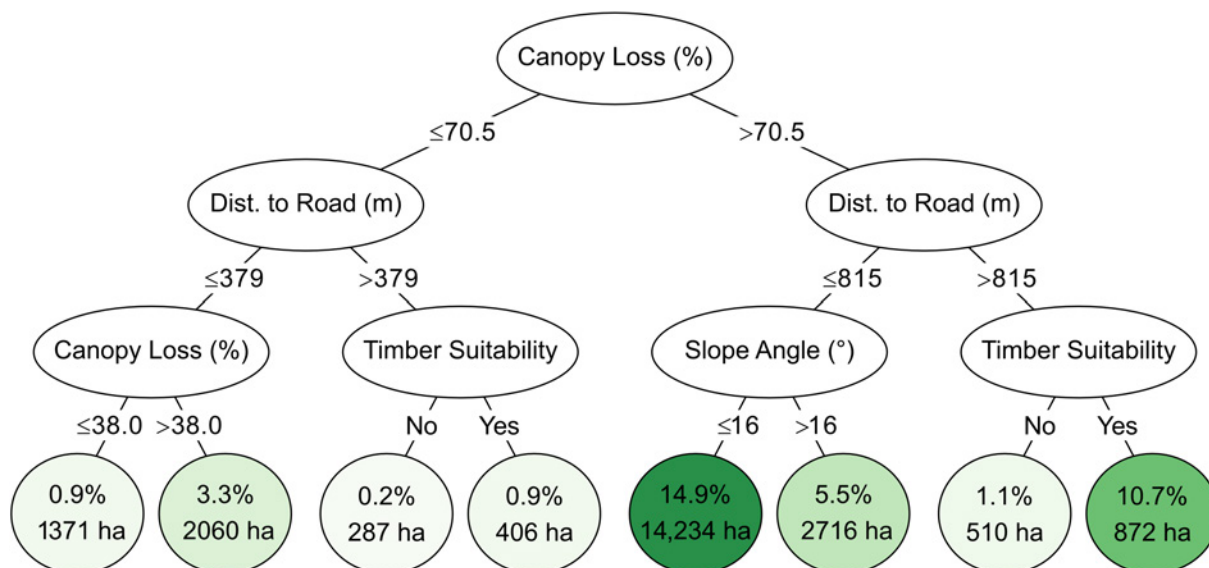


FIGURE 2 Results of the classification tree analysis used to separate planted and unplanted areas on burned USDA Forest Service lands in the Southern Rocky Mountains, USA. Final predictor variables (ovals) created meaningful splits in the data, with splitting thresholds in paths below each variable. In terminal nodes (circles), numbers give the percentage of the total area in each node that was planted and the total planting area, respectively.

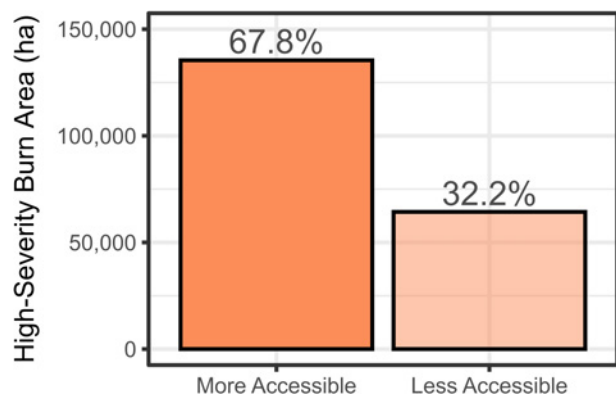


FIGURE 3 A summary of the accessibility of severely burned (>70% canopy loss) USDA Forest Service lands to traditional post-fire tree planting methods in the Southern Rocky Mountains, USA. “Less accessible” areas are defined as sites ≥ 930 m from the closest road, and/or with slope angles $\geq 24^\circ$, the 95th percentiles of each variable within known planting areas. Numbers include areas both with and without records of prior planting.

What techniques can improve the outcomes of direct seeding efforts?

Across our two field experiments, we sowed and monitored 38,400 individual ponderosa pine seeds. Overall, 0.2% ($n = 93$) of these seeds germinated in the first year and survived at least one summer growing season (i.e., 1-year establishment), though numbers ranged from 0 to 2.7% across treatments. Average establishment was relatively low at both Bobcat Gulch (0.3%; $n = 55$) and Calwood (0.2%; $n = 38$), indicating no substantial site-level differences. Our final statistical models suggested that seed enhancement techniques, microsite characteristics, and sowing season all influenced seeding outcomes after the first growing season (Figure 4). Pelleting and coating had strong, consistently negative effects on seedling establishment rates (Figure 4b,c,f). Priming had no detectable effect on establishment (only tested at Bobcat Gulch). In total, seeds without any seed

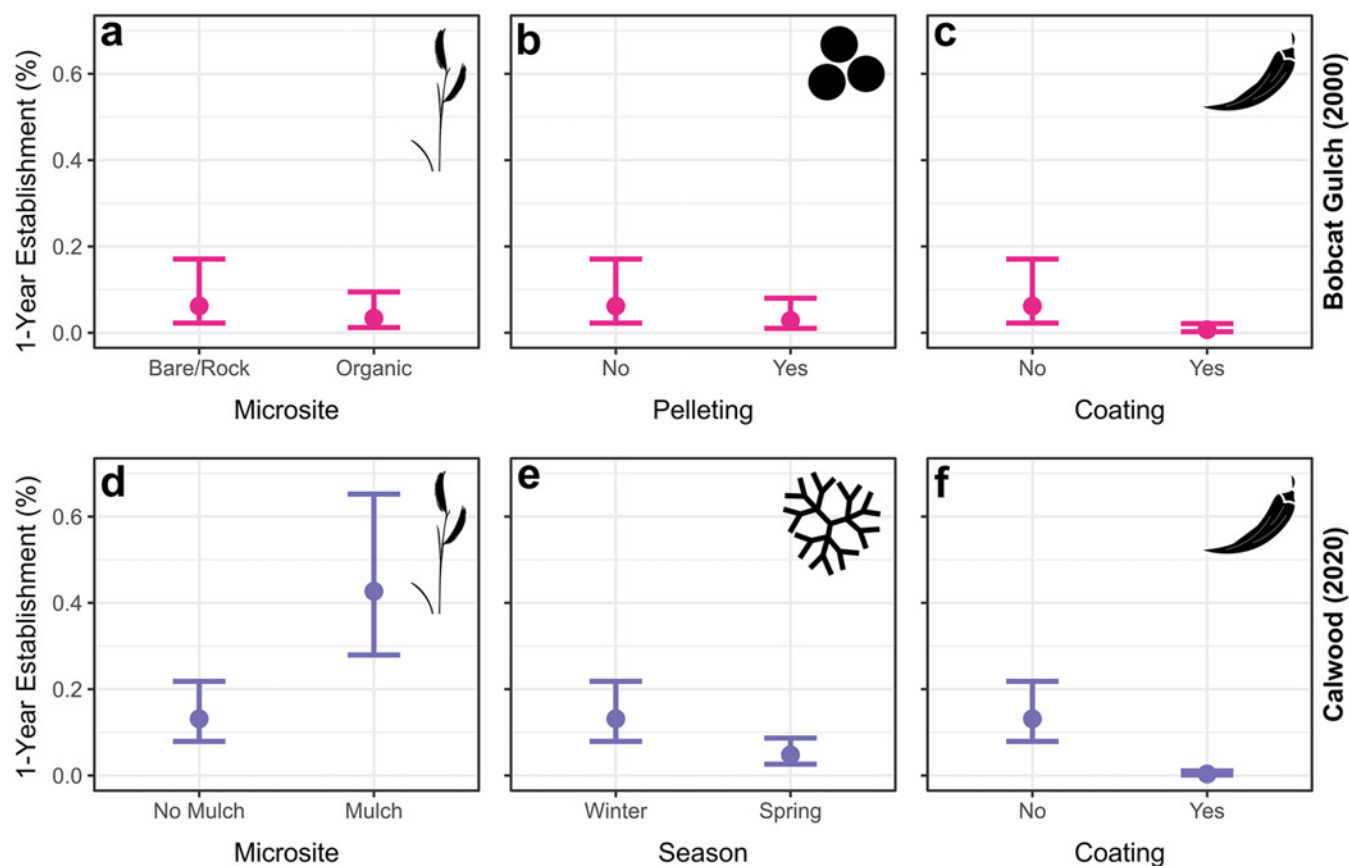


FIGURE 4 Results of final generalized linear mixed models (GLMMs) used to predict one-year germination and survival rates from direct seeding experiments at (a–c) the Bobcat Gulch and (d–f) Calwood sites. Only variables retained in the top model are shown here, and models with partial support are presented in Appendix S3. Points show the conditional mean prediction at different levels of each variable, assuming the average values of random effects and reference levels of other variables. Error bars show ± 1 SE of the prediction. Icons in (a, d) were created by Kim Kraeer and Lucy Van Essen-Fishman, the icon in (e) was created by Tracey Saxby, and icons in (d, f) were created by Nathan Miller; all were obtained via the Integration and Application Network Media Library (ian.umces.edu/media-library).

enhancement techniques established at about 4× higher rates than treated seeds. In the older Bobcat Gulch Fire, establishment rates were slightly higher on plots with bare ground or rocky substrates than on plots with vegetation (Figure 4a). In contrast, at the more recent Calwood Fire, mulch treatments had 3× higher establishment rates than seeding on bare ground (Figure 4d). Sowing season had no measurable effect at Bobcat Gulch, but winter-sown seeds established at 2× higher rates than spring-sown seeds at Calwood (Figure 4e). Fixed-effects terms in the models (i.e., R^2_m) explained 9% and 38% of the total variance in establishment at Bobcat Gulch and Calwood, respectively, and random effects explained an additional 40% (Bobcat Gulch) and 13% (Calwood) (i.e., R^2_c minus R^2_m). After the second growing season at Bobcat Gulch, seedling establishment declined to 0.1% ($n = 24$), and coating and pelleting still had negative effects (Appendix S3: Figure S1).

DISCUSSION

Active reforestation can help restore forest ecosystems in post-fire landscapes (Ouzts et al., 2015; Rodman et al., 2024a; Sorenson et al., 2025); however, significant barriers limit the implementation of reforestation activities (Dobrowski et al., 2024; Fargione et al., 2021; Kildisheva et al., 2023). Using a regionwide spatial analysis, we found that most post-fire tree planting activities occurred in high-severity areas, near established roads, and on flatter slopes, and that nearly a third of the area with potential reforestation need may be difficult to access using tree planting. Direct tree seeding—currently an uncommon practice in the United States (Dumroese et al., 2019)—may help overcome some of the accessibility barriers limiting reforestation in these areas. However, in our two experimental field trials of direct seeding, average first-year seedling establishment rates were very low, and seed enhancement techniques such as coating, pelleting, and priming had either neutral or negative effects on establishment. But other treatments, such as sowing seeds in combination with wood mulch, may be a promising method to incorporate reforestation into common post-fire rehabilitation or restoration activities. Taken together, our findings demonstrate a broad opportunity for direct seeding to reach less accessible areas but also highlight meaningful limitations of such efforts.

Fire-driven forest canopy loss, distance to the nearest road, and slope angle were strong predictors of the locations of recent post-fire tree planting activities in the SRME, with very little planting occurring >930 m from a road or on slopes >24°. The structure of planting contracts is one potential mechanism for these findings,

where costs can be considerably higher for sites >805 m (0.5 miles) from a road. However, even in the most commonly planted sites (i.e., severely burned areas on gradual slopes near roads), only about 15% of potential reforestation needs have been met, suggesting that there are vast areas where nursery-based plantings could still be utilized. Partitioning burned landscapes (e.g., Stevens et al., 2021) into areas that can be reforested using a range of approaches may help increase the pace and scale of management, while also reducing the demand on nurseries and the planting workforce (Fargione et al., 2021). In more accessible areas, tree planting will likely remain the most common method of active reforestation (Dumroese et al., 2019; Haase & Davis, 2017). However, our finding that 32.2% of potential reforestation needs in the SRME were less accessible to traditional planting methods indicates that a portfolio of approaches is needed to address the growing reforestation backlog (Dobrowski et al., 2024). Direct seeding via broadcast or aerial distribution methods may help to treat these hard-to-reach areas (Aghai & Manteuffel-Ross, 2020; Barnett, 2014; Downer et al., 2024).

Our experimental field trials support prior research showing that tree establishment rates following direct seeding can be very low in post-fire environments of the western United States (Perkins, 2015; Rietveld & Heidmann, 1976; Winters & Van Diepen, 2023). Seed inventories and the workforce available for seed collection are also limited in this region, indicating that these resources must be used wisely to optimize reforestation outcomes (Fargione et al., 2021; Kildisheva et al., 2023). Based on our results, direct seeding to achieve a relatively low target density of 100 trees ha^{-1} across a 1000-ha post-fire area could require 3.7 (maximum 2.7% establishment rate) to 41.7 million seeds (average 0.2% establishment rate) or more. Achieving the same result from planting would require <0.3 million seeds (assuming an average sowing rate of 2 seeds per seedling and average first-year survival rates of 79.5%; Bonner, 2008; Rodman et al., 2024a). Still, reforestation using direct seeding typically costs 50%–97% less than tree planting, because seed collection, cleaning, and storage make up just a small fraction of the cost of a planting project (Grossnickle & Ivetić, 2017; Palmerlee & Young, 2010). Direct seeding also promotes flexibility, because sowing can be completed during unexpectedly wet periods that support tree establishment (e.g., Davis et al., 2023; Rother & Veblen, 2017) without a multiyear planning horizon. Yet, for direct tree seeding to become a viable option for broad-scale implementation, efforts are needed to drastically expand seed inventories (Haase & Davis, 2017; Kildisheva et al., 2023) and improve establishment rates. Increased experimentation, such as burying seeds and

testing a range of tree species, is an important topic for future research.

Seed enhancement techniques can improve the outcomes of direct seeding with herbaceous species and shrubs (Gornish et al., 2019; Pedrini et al., 2020), but our findings provide new insight into the use of these techniques with coniferous trees. For example, coating seeds with olfactory and gustatory deterrents has been shown to reduce seed predation by animals (Pearson et al., 2019; Willoughby et al., 2011), yet we observed the remnants of many predated seeds in plots that received a coating treatment that included capsaicin. In fact, seed coating had a strong, negative effect on establishment in both field trials, which might be explained by allelopathic effects of capsaicin, a compound that has been shown to reduce germination and growth of some plant species (Kato-Noguchi & Tanaka, 2003). Likewise, prior research has indicated that pelleting could protect seeds of herbaceous species or shrubs from predation and aid in localized moisture retention (Gornish et al., 2019; Pedrini et al., 2020). However, pelleting was negatively associated with tree establishment in our Bobcat Gulch experiment, perhaps because it delayed seedling emergence (Brown et al., 2019; Jones et al., 2014). Indeed, we observed germination of seeds in pellets in July and August (later than unpelleted seeds), exposing new seedlings to extreme, late-summer weather conditions. Priming is commonly used to expedite and synchronize tree seedling emergence in nursery settings (Bonner, 2008), and we expected that it might increase establishment rates by triggering seed germination early in the spring, a period of elevated soil moisture availability. However, priming had no detectable effect on establishment in the Bobcat Gulch experimental site. Overall, seed enhancement techniques had either neutral or negative effects on tree establishment in our experimental field trials. As these treatments also increase the cost and operational complexity of direct seeding projects, our findings suggest that they may not be justified in post-fire reforestation activities in this region.

Sowing season and microsite characteristics also influenced outcomes in our experimental field trials. For example, winter sowing had roughly twice the establishment rate of spring sowing at Calwood, though sowing season had no effect at Bobcat Gulch. Sowing in the late fall or winter aligns with the natural timing of seedfall for ponderosa pine. It may also expose seeds to longer periods of cold stratification and a greater number of precipitation events that help hydrate and break the seed before the onset of the growing season. In the older Bobcat Gulch Fire, seeding on bare ground microsites enhanced first-year establishment rates, suggesting that there were strong competitive effects between tree

seedlings and other vegetation in the area. Some herbaceous species are known to reduce light availability and soil moisture in upper soil horizons, thereby limiting seedling establishment (Pearson, 1942; Puhlick et al., 2012). Ponderosa pine, in particular, is thought to germinate well on bare mineral soil (Schubert et al., 1970). However, in the more recent Calwood Fire, we found that seeding into areas with wood mulch had about 3× higher establishment rates than seeding into bare areas. Surface temperatures play a critical role in seedling establishment on harsh sites (Holden et al., 2024), and high-severity post-fire environments are often hot, dry, and exposed (Wolf et al., 2021). Wood mulch can help reduce soil surface temperature and enhance moisture retention (Jonas et al., 2019; Santana et al., 2014), thereby increasing seed germination and survival. Aerial distribution of mulch is a common approach to limit hill-slope erosion and post-fire runoff in severely burned areas (Robichaud et al., 2009); our results suggest that leveraging these treatments by dispersing seed into the same areas may help increase the effectiveness of direct seeding efforts in recent fires.

Important limitations to our data and analyses should be recognized. First, because post-fire tree planting is not widespread throughout the SRME (Figure 1), it is possible that planting may be capable of reaching steeper and more distant areas than are currently being treated, albeit at an increased financial cost. Second, our field trials of direct seeding captured outcomes over a relatively short study period in only two fires. Seedling survival rates decrease with time (Marsh et al., 2023; Marshall et al., 2024), as evidenced by approximately 50% declines in establishment rates after the second growing season at the Bobcat Gulch sites. In addition, direct seeding outcomes probably vary with abiotic conditions, as demonstrated by the wide range of establishment rates reported by other studies (Grossnickle & Ivetić, 2017; Palma & Laurance, 2015). Further research is needed to capture the long-term effects of direct seeding treatments across other biophysical settings in the western United States. Nevertheless, our research combining regionwide spatial analyses with two field trials of direct tree seeding demonstrates that there are significant opportunities to incorporate direct seeding in post-fire environments, and that some techniques (e.g., no seed enhancement, dispersal into areas with wood mulch in more recent fires) are more effective than others (e.g., dispersal into heavily vegetated portions of older fires). Such information is valuable to help address management challenges associated with fire-driven forest conversions, which have broad implications for a range of critical ecosystem services in a warming world (Burton et al., 2024; Coop et al., 2020).

AUTHOR CONTRIBUTIONS

Kyle C. Rodman, Catherine A. Schloegel, and Teresa B. Chapman contributed equally to this study. Kyle C. Rodman, Catherine A. Schloegel, and Teresa B. Chapman conceived the ideas and designed the methodology. Catherine A. Schloegel, Teresa B. Chapman, and Mykael Pineda established the field experiment and collected data. Kyle C. Rodman and Teresa B. Chapman analyzed the data. Kyle C. Rodman led the writing of the manuscript, with input from Catherine A. Schloegel and Teresa B. Chapman. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data, analytical code, and statistical model outputs (Rodman et al., 2025) are available from Zenodo: <https://doi.org/10.5281/zenodo.16905578>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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