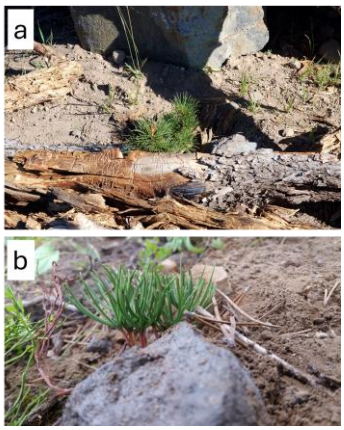

Seeding of whitebark pine (*Pinus albicaulis*) in western north American subalpine forests: Development and application

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Abstract

The rapid decline of whitebark pine (*Pinus albicaulis* Engelm.), a keystone species of upper subalpine and treeline elevational zones across many of the higher mountains of the western United States and Canada, has prompted the development of restoration strategies and practical restoration applications. Whitebark pine has been federally listed as 'threatened' in the United States, which elevates the restoration imperative. Seeding potentially provides a low-cost means of establishing the species in remote areas with limited access and/or land use constraints, but this restoration tool still lacks sufficient advancement to ensure operational success. We present an overview of whitebark pine ecology, outline the factors leading to its decline, summarize ongoing conservation efforts and restoration strategies, and review the available literature on seeding whitebark pine to identify barriers that challenge successful operationalization. Informing and advancing land management for conservation of whitebark pine will require refining seeding protocols by monitoring and reporting on trials to mitigate the main barriers to this application. Additional research is required to reduce seed pilferage by rodents, improve sowing techniques, identify favorable sowing microsites for improved seeding outcomes, and develop a reliable supply chain for seed resistant to introduced disease.

Keywords

whitebark pine, forest restoration, direct seeding, Clark's nutcracker, seed pilferage

Contents

Note
This paper is a part of a Special issue on International Practices for Regenerating and Restoring Forest Trees by Seeding, edited by Emile S Gardiner and John A Stanturf

1 Whitebark pine distribution, ecology, and ecosystem services

Whitebark pine (*Pinus albicaulis* Engelm.), an ecologically important species in rapid decline (Figure 1a), inhabits the upper subalpine and treeline elevational zones across many of the higher mountains of the western United States and Canada (Arno and Hoff 1990; McCaughey and Schmidt 2001; Olgilvie 1990). About 88% of whitebark pine's range in the United States occurs on federal (public) lands managed by the U.S. Forest Service, National Park Service, and Bureau of Land Management; and in Canada, whitebark pine occurs primarily on federal and provincial lands (COSEWIC 2010; U.S. Fish and Wildlife Service 2021). Indigenous lands in both nations comprise a portion of the whitebark pine distribution. The rapid decline of whitebark pine populations, especially in the northern Rocky Mountains, has been of management concern for more than 25 years (Tomback et al. 2001a), leading to multiple regional and range-wide restoration strategies and plans, as well as the development of restoration tools and applications, including seeding (Tomback et al. 2022).

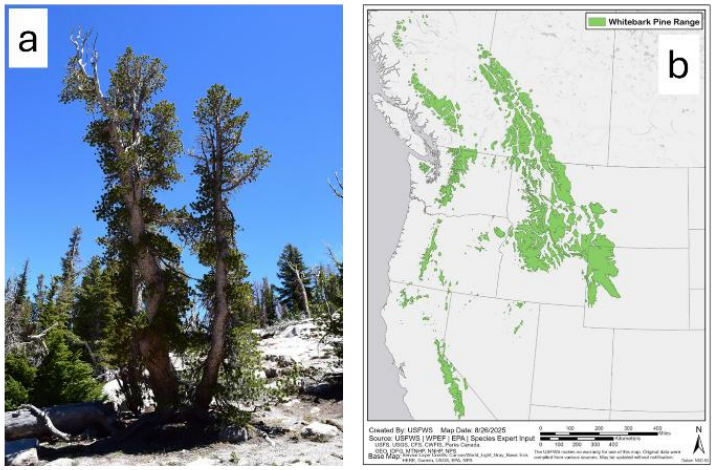

Figure 1. (a) Whitebark pine (*Pinus albicaulis* Engelm.), Sierra Nevada, California. (b) The U.S. and Canadian distribution of whitebark pine. (Photo credit: (a) D.F. Tomback); (b) Map modified from: U.S. Fish and Wildlife Service (2021); range data updated from U.S. Fish and Wildlife Service(2023). https://www.sciencebase.gov/catalog/item/66cf792ad34e98e8a924c06a).

Whitebark pine has two distinct distributional segments: the western portion ranges from about 36 to 55° N latitude, from the southern Sierra Nevada Range north through the coastal ranges of Canada; and the Rocky Mountain portion from about 42 to 54° N latitude, from the Greater Yellowstone Region north through the southern Canadian Rocky Mountains (Figure 1b). Whitebark pine may be a minor to major component of forest communities, which comprise three distinct types with intergradation. Successional communities occur on productive sites in the upper subalpine forest zone, depend on periodic fire for renewal, and are most common across the central and northern Rocky Mountains of the U.S. and adjacent southern Canada (Arno and Hoff 1990). Whitebark pine is an early seral species in these communities, gradually replaced by faster-growing, shade-tolerant species over time, with some individuals persisting late into succession (Campbell and Antos 2003). Whitebark pine in climax communities, which occur on windy sites with poor soils, is self-replacing through seedling establishment; whitebark pine climax communities are

the most widely occurring whitebark pine communities across the species' range. Whitebark pine is also a component of treeline communities and assumes a dominant role especially east of the Continental Divide on windy, dry slopes (Arno and Hoff 1990; Tomback et al. 2016a).

The life history of whitebark pine has been shaped by coevolution with its principal seed disperser, Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae) (Lanner 1990; Tomback and Linhart 1990). Seed dispersal by nutcrackers influences the ecology, distribution, and population structure of whitebark pine (Tomback 2001, 2005) and informs seeding methods. In late summer and fall, nutcrackers harvest seed from whitebark pine cones and bury seed caches (typically 1 to 15 seeds per cache) throughout mountain terrain across the elevational gradient from lower treeline to the alpine zone above the upper treeline (Hutchins and Lanner 1982; Tomback 1982, 2001). Seed in suitable sites that are not retrieved by nutcrackers or pilfered by rodents (Order Rodentia) may germinate after one to several years, leading to regeneration (Tomback 1982; Tomback et al. 2001b). Cache site selection by nutcrackers, in conjunction with environmental potential for seed germination and seedling survival and growth, determines where whitebark pine establishes in mountain terrain (Table 1) (Tomback 2001; Lorenz et al. 2011). Seed dispersal in seed clusters often produces multi-genet tree growth forms; and local and long-distance seed dispersal influences population structure at stand, watershed, and regional levels (Tomback and Linhart 1990; Tomback 2005). The distinctive morphology of whitebark pine appears adapted for this interaction: upward-trending branches bearing cone whorls at their tips; cones that remain closed when ripe (indehiscent); large, wingless seeds; and seed morphology and physiology that enable seed to remain viable for years in a soil seed bank (Lanner 1990; Tillman-Sutela et al. 2008; Tomback and Linhart 1990).

Table 1. Characteristics of Clark's nutcracker (*Nucifraga columbiana*) cache sites for whitebark pine (*Pinus albicaulis* Engelm.) seed that potentially impact restoration practice. Information is based on Lorenz et al. (2011), Hutchins and Lanner (1982), and Tomback (1978, 1982, 2001). Note: nutcrackers also place a portion of their caches above ground within trees (e.g., crotch of a fork), but these caches have no regeneration potential (Lorenz et al. 2011; Tomback 1978).

Range of distance seed is moved from the source tree: ~0 m to 33 km
Substrates: mineral soil, volcanic gravel (pumice), conifer needle litter (duff)
Number of seed per cache: $\bar{x}$ = 3–4, range = 1 to 15
Distance between caches: $\bar{x}$ = 67 ± 69 cm (SD), range = 10 to 300 cm
General cache environments: within different forest community types; steep, open slopes; rocky cliffs; talus slopes; rocky rises; meadows; streambanks; lower treeline shrub and tree communities to upper treeline and tundra communities.
Specific cache sites: around tree bases, next to rocks, next to deadfall, next to fallen branches, in sparse vegetation, among tree roots, and in open areas (no feature).

Whitebark pine provides important ecosystem services across its range. Given its broad latitudinal distribution, whitebark pine communities are diverse, varying in tree associates and understory composition (Arno and Hoff 2001; Tomback et al. 2001a; Tomback and Achuff 2010). Whitebark pine stands growing at the highest subalpine elevations and treeline communities redistribute and retain snowpack (Farnes 1990; Tomback et al. 2016a). Its large seeds are an important food for numerous granivorous birds and small mammals as well as bears (*Ursus* spp.); and whitebark pine communities on harsh high elevation sites provide habitat, shelter, nest, and burrow sites for diverse wildlife, including birds of prey (Order Accipitriformes, Falconiformes, and Strigiformes), cervids (including elk (*Cervus canadensis)*, deer (*Odocoileus spp.)*, and moose (*Alces*

alces)), and carnivores (Order Carnivora) (Tomback and Kendall 2001; Tomback et al. 2016a). Tolerance of whitebark pine for harsh environmental conditions and poor soils provides protection (facilitation) for the establishment of other plant species (Callaway 1998; Tomback et al. 2016b); and seed dispersal by nutcrackers leads to comparatively rapid regeneration after fire and other disturbances (Tomback et al. 1993, 2001b). In addition, whitebark pine was an important food resource historically and culturally for several western Native American and First Nation tribes (Moermond 1998; Tomback et al. 2011). Whitebark pine is considered both a keystone and foundation species, given that its communities promote biodiversity and provide locally stable conditions for other plant and animal species (DeGrassi et al. 2019; Ellison et al. 2005; Tomback et al. 2001a).

2 Whitebark pine decline and conservation efforts

The ongoing population losses in whitebark pine are reflected in its global and national conservation status. Whitebark pine is categorized as 'endangered' by the International Union for the Conservation of Nature (Mahalovich and Stritch 2013) and by Canada under the Species at Risk Act (Government of Canada 2012), and it is listed as 'threatened' by the U.S. under the Endangered Species Act (U.S. Fish and Wildlife Service 2022).

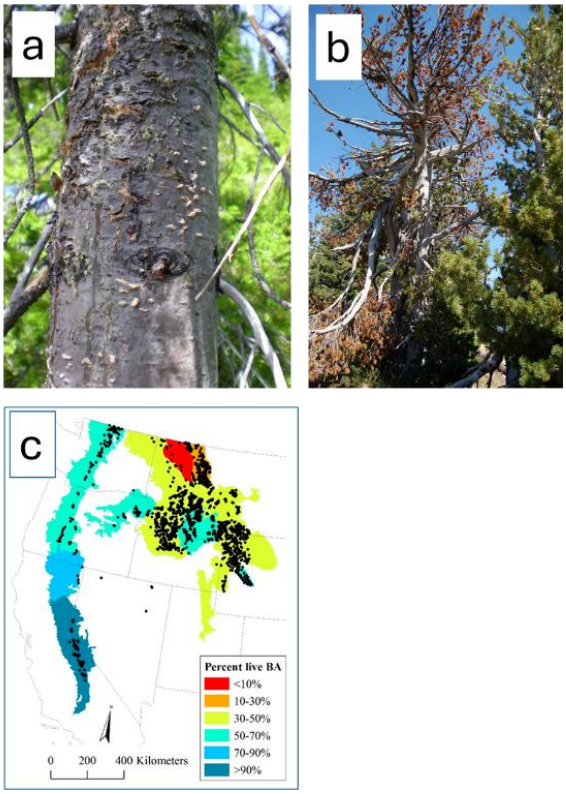

Figure 2. Mortality agents in whitebark pine (*Pinus albicaulis* Engelm.) and extent of decline. (a) Potentially fatal white pine blister rust stem canker in whitebark pine. (b) Whitebark pine killed by mountain pine beetles (*Dendroctonus ponderosae*). (c) From Goeking and Izlar (2019), depicting locations of 1,406 forest inventory plots (black dots) with percentage living basal area of standing whitebark pine trees with diameters ≥ 2.54 cm at breast height within each eco-province, based on plots measured between 2007 and 2016. (Photo credits: (a, b) D.F. Tomback).

The current major threat to whitebark pine is the exotic fungal pathogen *Cronartium ribicola*, which causes the disease white pine blister rust (WPBR) (Figure 2a), that continues to spread throughout the range of whitebark pine (McDonald and Hoff 2001; Tomback and Achuff 2010; U.S. Fish and Wildlife Service 2021). WPBR canopy infections reduce seed production, and stem infections kill trees. Additionally, recent outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have killed mature whitebark pine at an unprecedented scale (Figure 2b; Gibson et al. 2008; Schwandt et al. 2010; Tomback and Achuff 2010). Lastly, historical fire regimes have been altered by fire exclusion and more recently by climate change, which is leading to more frequent, larger, and increasingly severe fires (e.g., Higuera et al. 2021; Keane et al. 2022; Tomback et al. 2022). Climate change is also expected to drive whitebark pine distributional changes (Parks et al. 2025). Compiled U.S. Forest Service Forest Inventory and Analysis data indicated that 51% of standing whitebark pine in the U.S. was dead, with the Northern U.S. Rocky Mountain populations in greatest decline primarily due to WPBR (Figure 2c; Goeking and Izlar 2018). Loss of local and regional seed production decreases the effectiveness of seed dispersal by Clark's nutcracker (Barringer et al. 2012; McKinney and Tomback 2007; McKinney et al. 2009), reducing regeneration rates especially after wildfire (Leirfallom et al. 2015; Stevens-Rumann et al. 2017).

Although the U.S. Fish and Wildlife Service currently is developing the Whitebark Pine Recovery Plan as mandated by the Endangered Species Act, several agencies and inter-agency collaborations previously developed conservation and restoration plans or strategies. A few of these focus on specific restoration treatments or protective actions (e.g., Keane et al. 2012), while others also prioritize a subset of the whitebark pine range for restoration treatments, recognizing the scale of the undertaking even within a region (Jenkins et al. 2022; Tomback and Sprague 2022; Tomback et al. 2022). The primary restoration and conservation approaches and actions used to restore whitebark pine are reviewed in Tomback et al. (2022) and listed in Table 2.

A key restoration strategy is to plant seedlings that are genetically resistant to WPBR (Table 2) (Figure 3), with seeding being piloted as an alternative in areas with limited access and/or land use constraints (Keane et al. 2022; Tomback et al. 2022). Seedling planting is intended to increase the frequency of WPBR-resistant genotypes within populations and compensate for reduced natural regeneration caused by decreasing seed production. Natural resistance to *C. ribicola* exists within whitebark pine populations, and recommended seed sources for seeding and seedling production should be those trees confirmed to have usable genetic resistance to WPBR (Sniezko and Liu 2022). Screening parent trees for genetic resistance to WPBR involves a lengthy (up to 10 years) multi-step process (Figure 4) (Cartwright et al. 2022). Individuals with putative resistance to WPBR must be identified; cones must be collected from trees and processed for storage and screening. Subsequently, seeds are germinated, and seedlings are grown for 2 to 3 years before seedlings are inoculated with WPBR via exposure to high concentrations of *C. ribicola* spores. Trees are then monitored for an additional 3 years before a resistance determination and grade is applied (Sniezko et al. 2023). Elite trees, i.e., those with confirmed resistance to WPBR, then must be protected from other threats including mountain pine beetles (Figure 4).

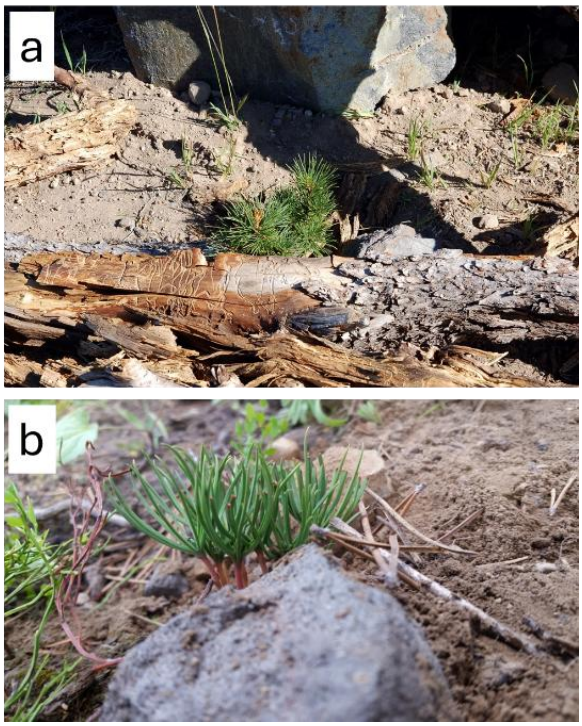

Figure 3. (a) Restoration plantings of whitebark pine (*Pinus albicaulis* Engelm.) seedlings that are from seed sources genetically resistant to white pine blister rust, Crater Lake National Park, Oregon. (b) Natural whitebark pine regeneration in a seedling cluster. Clusters result from the tendency of Clark's nutcrackers (*Nucifraga columbiana*) to bury several seed per cache and to cache near objects such as rocks and fallen trees. (Photo credits: D. F. Tomback).

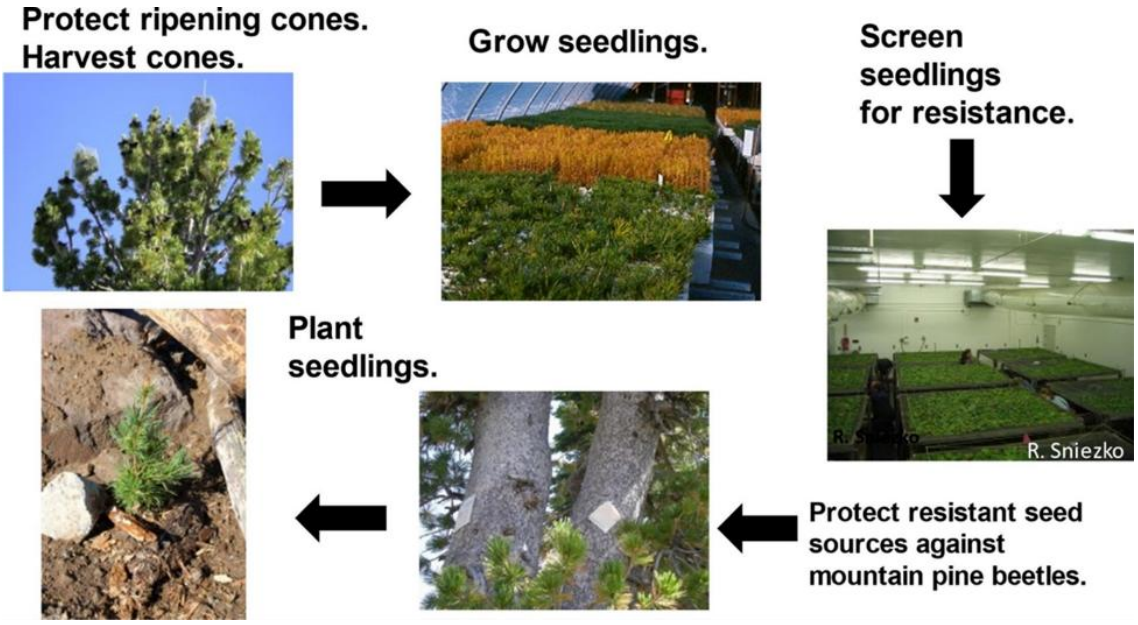

Figure 4. Steps in growing seedlings for screening for genetic resistance to white pine blister rust and for operational planting: Cone protection and harvest, growing seedlings, applying blister rust inoculum, protecting trees with genetic resistance to white pine blister rust from mountain pine beetle (*Dendroctonus ponderosae*) attack, and planting seedlings in protected microsites. (Photo credits: unless otherwise noted, D.F. Tomback; modified from Tomback et al. (2022)).

Table 2. Summary of conservation actions and restoration treatments for whitebark pine (*Pinus albicaulis* Engelm.) from Tomback and Sprague (2022). See Tomback et al. (2022) for guiding principles and a review of currently recommended actions and treatments and Keane et al. (2012, 2022) for basic restoration and conservation principles and restoration approaches under climate change. WPBR = white pine blister rust. MPB = mountain pine beetle (*Dendroctonus ponderosae*).

1. Conserve genetic diversity
● Seed collections for seed archiving.
2. Promote genetic resistance to WPBR
● Identify seed zones across the whitebark pine range.
● Select candidate trees (seed trees and plus—i.e., putatively resistant—trees) for WPBR-resistance screening.
● Screen for genetic resistance to identify trees with useable resistance (elite trees).
● Identify sufficient numbers of resistant trees to conserve genetic diversity.
● Develop seed orchards where appropriate for operational seed production.
3. Grow seedlings to restore populations and build resilience to WPBR and climate change
● Collect cones from elite trees and drought-tolerant trees or those from environments considered similar to future climate change scenarios.
● Optimal goal is to find trees with both WPBR-resistance and drought tolerance.
● Grow seedlings.
● Plant seedlings or sow seed, especially in climate change refugia.
4. Protect trees with known blister rust resistance or high value stands
● Protect trees from attack by MPB.
● Protect trees from fire.
5. Reduce competition in successionally advanced communities
● Apply various silvicultural treatments, depending on conditions and goals.
● Use prescribed fire as a restoration tool.
● Manage wildfires.
6. Implement treatments proactively to build resilience in healthy whitebark pine communities
7. Assess whitebark pine health and stand conditions
● Implement surveys to assess health status and trends.
● Monitor stand health and conditions over time.
8. Develop monitoring plans for restoration treatments and conservation actions
● Integrate monitoring into project planning and management.
● Use monitoring outcomes to adjust treatments for successful restoration and conservation, i.e., adaptive management.

3 Rationale for use of seeding

Although planting WPBR-resistant nursery-grown seedlings will remain the key restoration action for whitebark pine, seeding is being explored as an additional tool for the restoration toolkit. There are two major rationales or justifications for exploring the efficacy of seeding as an alternative to seedling planting and as a restoration practice for whitebark pine. First and foremost, accessibility and/or land use constraints may limit where restoration activities are feasible. Much of the whitebark pine distribution is at high elevations on steep slopes in remote and/or inaccessible terrain where planting becomes infeasible to execute. Additionally, about 29% of the whitebark pine range is within federally designated wilderness (Tomback et al. 2001a; U.S. Fish and Wildlife Service 2021). In the case of the latter, interpretation of the 1964 Wilderness Act by organizations and agencies may restrict the transportation and planting of seedlings in federally designated wilderness (Tomback et al. 2022). Seeding involves less manipulation or 'trammeling,' especially if seed is collected from and sown at the targeted location. With respect to general application, seeding is viewed as a method

to restore whitebark pine in inaccessible high elevation terrain, where transporting and planting seedlings becomes challenging if not prohibitive. Given that burned seedbeds are optimal conditions for planting seedlings and seeding, field crews can make use of high elevation burns on steep terrain for sowing seed with far less effort than required for planting. Accessibility and logistical constraints are further expected to become more pointed with a changing climate. Climate change may accelerate whitebark pine decline, progressively shifting suitable habitat to higher elevations (e.g., McKenney et al. 2007; Schrag et al. 2007; Warwell et al. 2007; Hansen et al. 2016; Park et al. 2025). This upward contraction may further isolate potential restoration sites that may act as climate refugia, amplifying the logistical challenges of accessing and restoring sustainable populations. Seeding may facilitate restoration in areas that are priorities for intervention but would otherwise be omitted due to logistical or land-use constraints.

The second rationale for seeding is to reduce costs for restoration projects. For operational seedling production, the cost of nursery facility care plus planting per whitebark pine seedling is more than $3, but this price does not include the expenses of tree climbers, cone caging, cone harvest, transportation, and storage, etc. In contrast, estimated costs for seeding are about $0.20 per seed cache without including costs of harvesting seeds and transportation (Tomback et al. 2022). The trade-off is the efficacy of seedling planting versus seeding. Details are provided below.

4 Development of seeding in whitebark pine ecosystems

The use of seeding to restore whitebark pine communities has a comparatively recent history. Whitebark pine seed is characterized by an underdeveloped embryo, physiological dormancy, and mechanical barriers to germination, requiring specialized treatments and stratification protocols for seedling production in nurseries (McCaughey and Tomback 2001). The primary objectives of the first studies were to examine germination and seedling emergence rates with and without seed treatments, but also the efficacy of treatments to reduce rates of rodent pilferage and different microsite types. Most of the exploratory seeding studies have been implemented in the northwestern United States and the Greater Yellowstone Region.

The objectives of McCaughey (1993), the first documented seeding study, were to compare germination rates of untreated whitebark pine seed between surface-sown seed and buried seed (Table 3). For this study, McCaughey (1993) used a recent clearcut on Palmer Mountain, Gallatin National Forest, Montana, USA. His study deployed 2,880 filled seeds collected nearby, varied shade levels and substrate, and enclosed all plots in wire mesh cloth cages with edges buried to exclude seed predators. Each surface-sown seed was matched by a buried seed within the same subplot. Over three years, significantly more buried seed than surface-sown seed germinated. Seed germination did not differ statistically by shade level or substrate type, although more seedlings emerged from shaded treatments and litter layer treatments. The study indicated that most buried seed that are protected from rodent predation will germinate over time, and that whitebark pine seed often experiences delayed germination—a fact later substantiated for naturally dispersed whitebark pine seed (Tomback et al. 1993, 2001b).

Table 3. Development of seeding as a restoration tool for whitebark pine (*P. albicaulis*). Results of studies that explored the efficacy of various treatments to increase germination rate, reduce losses to rodents, and increase seedling survival are summarized here. See text for additional details. NF = national forest.

Reference	Location	Site preparation	Treatments	Duration	Results
McCaughey (1993)	Palmer Mountain, Gallatin NF, MT, USA.	Clearcut.	1 buried seed; 1 surface seed per treatment. Shade levels (0%, 25%, 50%). Substrate mineral soil, litter. Wire cloth enclosures.	3 years	% Germination: - 56% buried vs. 7% sown on surface. - 60% shaded vs. 47% unshaded. - 60% mineral soil vs. 51% duff.
Schwandt et al. (2007)	Vinegar Hill, Umatilla NF, OR, USA.	Small burn scars from slash pile burning.	Warm stratification. Seed scarification. Scarification and warm stratification. Control. Above 4 treatments in wire cloth enclosures. Rodent repellent Thiram®. [1] Rodent repellent cayenne pepper.[2] No repellent. Logs provided afternoon shade.	9 months (see below)	Only 94 of 700 seeds germinated. Highest germination from both warm stratification treatments. <10% germination for other treatments.
Schwandt et al. (2011)	Vinegar Hill, Umatilla NF, OR, USA. Mt. Bachelor, Deschutes NF, OR, USA. Fairy Lake, Gallatin NF, MT, USA. Thompson Peak, Lolo NF, MT, USA. Ulm Peak, Kootenai NF, MT, USA. Gold Pass, ID, USA Panhandle NF, ID, USA.	Burn scars from natural or prescribed fire.	Warm stratification. Seed scarification. Warm stratification and seed scarification. Control. <u>Vinegar Hill</u>: Above treatments in wire cloth enclosures. Shade provided by logs, snow fences, trees, or snags. <u>Vinegar Hill & Mt. Bachelor only</u>: Rodent repellent Thiram®. [1] Rodent repellent cayenne pepper.[2] No repellent. Mt. Bachelor only Rodent repellent Ropel®.[3] <u>Other sites added</u>: 3 seed caches buried next to planted 2 yr-old seedlings.	Vinegar Hill, 2+ years. Mt. Bachelor, 2+ years. Other study sites (see below)	Vinegar Hill and Mt. Bachelor had the highest germination in the first year with additional germination in the second year but none beyond. Treatments including warm stratification produced the highest seed germination in both study areas (25–72%). Seeds treated with rodent repellents had the lowest germination (8–18%). Preliminary results for the other study areas indicated variable germination, but warm stratification treatments produced the highest percentage germination.
DeMastus (2013)	Fairy Lake[4] and Pioneer Mountain, Custer Gallatin NF,[5] MT, USA. Thompson Peak, Lolo NF, MT, USA. Ulm Peak, Kootenai NF, MT, USA. Gold Pass, ID, USA. Panhandle NF, ID, USA. Toboggan Ridge, Clearwater NF, ID, USA.	Burn scars from natural or prescribed fire (Schwandt et al. 2011). Preparation probably similar for Pioneer Mountain and Toboggan Ridge but not described.	Warm stratification. Seed scarification. Warm stratification and seed scarification. Control. Per treatment block, each treatment both in open and in wire cloth enclosure. 3 or 4 seed caches buried next to planted 2 yr-old seedlings. Soil and below ground temperatures measured in all study areas.	Schwandt et al. (2011) study areas, 3 years. Pioneer Mountain and Toboggan Ridge, 2 years.	The warm stratification had the highest germination rate across study areas (≥41%). Seedling survival rates were study-area specific and varied by treatment. Nursey grown seedlings had higher survival rates than seedlings that emerged during the study. Seedling survival was slightly higher under wire cloth enclosures. Temperature differences did not impact germination rates.

[1]Tetramethylthiuram disulfide [2]*Capsicum annuum* L. [3]Benzyldiethy l[(2,6 xylyl carbamoyl) methyl ammonium sacchari and thymol [4]Fairy Lake study area unsuitable and data not included in final data analysis by Demastus (2013). [5]Custer and Gallatin National Forests merged administratively in 2014.

Schwandt et al. (2007) investigated whether seed treatments (e.g., stratification, scarification) could speed up germination and reduce rodent predation (Table 3). In 2005, they established a trial on Vinegar Hill, Umatilla National Forest, Oregon, USA, using 700 locally sourced whitebark pine seeds. In the study area, small burn scars were selected as sites to install five replicates, with 140 seeds per replicate divided among seven treatments. Three treatments were designed to speed up germination rates, with a fourth control treatment, and all four treatments were enclosed in wire mesh cloth. Two additional treatments tested different substances for efficacy as rodent repellents with a third control treatment (no repellent), and these two rodent repellent treatments and control were exposed to predation. Logs were positioned to provide shade during the afternoon for each replicate. The experimental study area was revisited nine months after installation. Investigators found that the treatments with the highest germination rates were the two with warm stratification. Despite low germination rates overall, the study indicated that treatments potentially could speed up germination.

In 2006, Schwandt et al. (2011) added treatments for seeding, comparing germination success, seedling survival rates, and comparing the survival of seedlings produced from seeding to the survival of nursery-grown seedlings on the same sites, and they also added study areas. They expanded their seeding study beyond Vinegar Hill, Oregon, to Mt. Bachelor, Oregon, and in 2009 to three sites in Montana—Fairy Lake, Thompson Peak, Ulm Peak—and one in Idaho, USA—Gold Pass (Table 3). About 1,000 seeds were obtained near each study area and sown with five replicates of four basic treatments, 20 seeds per treatment. There were additional treatments in some study areas and differences in the setups. Three treatments facilitated seed germination and were compared with an untreated control. The Mt. Bachelor study area also included three rodent repellent treatments and a treatment where small peat pots were used to provide a moist environment for the seed. The 2009 trials also included sowing seed caches adjacent to nursery-grown seedlings in the Montana and Idaho study areas (Table 3). Half the treatments were protected from rodent predation by wire mesh cloth enclosures, and all treatments were shaded (Table 3). The 2005 and 2006 results indicated that most germination occurred in the spring following sowing. Warm stratification treatments were more effective than scarification in facilitating germination. Rodent repellents reduced germination, and the peat pots were destroyed by rodents. At Vinegar Hill, only 20% of seed germinated overall, and most of the cotyledon seedlings were killed by high temperatures after emergence. For Mt. Bachelor, 72% of the caged, warm stratified seed germinated, and seedling survival was greater on cool, northern slopes than on warm aspects. For the 2009 trials, preliminary results indicated that warm stratification of seed produced the highest germination of all treatments or the control, with an average of 47%.

The study objectives for DeMastus (2013) were similar to those of Schwandt et al. (2011) but also included questions about the influence of soil surface and sub-surface temperatures (monitored by sensors and data loggers) (Table 3). His research continued the Schwandt et al. (2007, 2011) studies, using the Fairy Lake, Thompson Peak, Ulm Peak, and Gold Pass study areas noted above; and in 2010, he added the Yellowstone Club ski area in Montana, and Toboggan Ridge in Idaho. The methods did not state whether shade protection for treatment blocks was still provided in these areas, as described in Schwandt et al. (2011). For each study area, DeMastus (2013) collected 800 whitebark pine seeds from local seed sources, using 20 seeds per treatment. Among the

blocks, he planted either 34 or 100 two-year-old-seedlings, paired with caches of 3 or 4 seeds, depending on the study area. Data were collected for three years at the sites established in 2009, and for two years at the site established in 2010. Sites differed in maximum and minimum temperatures and extreme weather events, but no association with germination was established. Overall, warm stratification produced the highest average percent germination for most of the sites. Seedling survival was highest across treatments at the Toboggan Ridge site followed by Thompson Peak, with the lowest survival at Ulm Peak, and thus appeared to be site-specific and to vary by treatment. Germination rate was similar between seed with and without wire mesh cloth cover, nursery-grown seedlings had higher survival than seedlings grown from sown seed, seed sown in multi-seed and single-seed caches had similar germination rates overall, and the survival of seedlings from seed sown in clusters vs. single seeds was similar. The slight block dependent advantage of wire mesh cloth enclosures on seedling survival was not considered great enough to justify the work required to deploy the enclosures.

Pansing et al. (2017) approached seeding with a different set of objectives. They aspired to assess, through artificial caches closely simulating nutcracker caches, whether spatial patterns of cache pilferage, germination, and seedling survival might modify the initial spatial pattern of caches made by Clark's nutcrackers and how these modifications may differ between subalpine forest and the alpine treeline ecotone. The studies, although intended to reveal patterns at a local landscape scale, provided important basic information on variation in the success of seeding based on a rigorous experimental design. Pansing et al. (2017) investigated seeding in two locations in the Northern Rocky Mountains: White Calf Mountain, Montana, on the eastern front of Glacier National Park, and Tibbs Butte, Shoshone National Forest, on the Beartooth Plateau within the Greater Yellowstone Ecosystem. Seed was collected from trees within 11 km of these study sites the fall prior to deployments. Seed was sorted to remove low-weight and insect-damaged seeds, and over-wintered at 1.5 °C (cold stratification). In 2012 the researchers created 735 seed caches across both sites, varying cache size from 1 to 7 based on a Poisson distribution of seed cache size and stratifying the placement of caches in two ways—by whitebark pine forest community type (upper subalpine forest or alpine treeline ecotone), as well as among microsites commonly used by Clark's nutcrackers (rock bases, tree bases, or open terrain) (Tomback 1978). Caches were created in the nearest assigned microsite type to randomly generated points; each cache was buried ca. 2.5 cm under substrate. Seed caches were checked in 2013 for rodent pilferage and seed germination and in 2014 for additional seed germination and seedling survival. Ungerminated caches were excavated to document rodent pilferage in 2013, and any remaining seed was carefully reburied. They found that one or more seeds were pilfered from 54% of caches. Of the pilfered caches, 75% lost all seeds and 25% retained one or more seeds. Odds of pilferage were higher at treeline relative to the subalpine, indicating higher risk of seed theft by rodents at treeline. On Tibbs Butte, one or more seeds in 64% of remaining caches germinated in 2013, and one or more additional seeds in 36% of the remaining caches germinated by 2014. In total, one or more seeds germinated in 85% and 46% of the remaining caches by 2014 on Tibbs Butte and White Calf Mtn., respectively.

These results from Pansing et al. (2017) highlight the importance of recognizing delayed germination in whitebark pine, even with cold stratification treatments, when investigating seeding efficacy. At Tibbs Butte, the odds of cache germination, i.e., one or more seeds germinating per cache, were higher at treeline than in the subalpine

forest, and odds of germination were higher near rocks than trees. First year cache survival, i.e., one or more seedlings surviving per cache, ranged from 19% in the subalpine forest of White Calf Mtn. to 77% at treeline on Tibbs Butte. The odds of seedling survival were higher at treeline on Tibbs Butte and adjacent to objects (i.e., rocks and trees) relative to open microsites, suggesting that protection at treeline may improve seedling survival outcomes. Similar to the findings of DeMastus (2013), no association between cache germination and cache size was detected.

Pansing and Tomback (2019) continued to follow the seed caches created on Tibbs Butte through 2018 to assess five-year seedling survival. In 2018, they could relocate 162 caches that held one or more seedlings in 2013—68 of the 162 caches contained at least one surviving seedling. Known fate modeling suggested that annual seedling survival rates ranged from 57% in the subalpine forest to 99% at treeline in 2016. Odds of survival were 2.6 times higher at treeline than in the subalpine and varied substantially by year. A model including year and elevation zone, and another including year, elevation zone, and microsite had similar evidence AIC scores suggesting microsites may be influential despite non-significant microsite differences, potentially due to small sample sizes. Year may be a surrogate for annual differences in weather variables such as snowpack, precipitation, or temperature.

Hankin et al. (2023) explored variation in the performance of seedlings produced by seeding in three high elevation five needle white pines (*Pinus* spp. L.), including whitebark pine. Their work aimed to estimate local adaptation and phenotypic plasticity in emerging whitebark pine and other high elevation white pine seedlings, focusing on the impact of weather during emergence and seedling survival. Importantly, it represents the only research published to date on whitebark pine seeding in the southern Sierra Nevada, which comprises a genetically and ecologically distinct population of the species (Richardson et al. 2002; Syring et al. 2016; U.S. Fish and Wildlife Service 2021). Hankin et al. (2023) established a common garden experiment using two whitebark pine seed sources sown in six locations across California and Nevada. Whitebark pine consistently had low emergence rates—between 0.3% and 8.5% in 2020 and 2021 across the six sites, with 0.5% emergence at both sites where whitebark pine is native. The remaining four sites were outside of the whitebark pine range. They found that the establishment environment, specifically summer soil moisture, was the strongest predictor of emergence and abundance of whitebark pine. Further, they identified that the seed source from the drier location, i.e., the site that had higher summer climatic moisture deficit, produced seedlings with a higher root to shoot ratio and lower biomass growth rate.

The studies summarized in Table 3 provide guidance for seeding projects. They indicated that cached whitebark pine seed had much higher germination rates than surface-sown seed and that whitebark pine seed may germinate over a period of several years. Furthermore, warm stratified seed germinated at a higher rate than untreated or scarified seed, rodent repellent reduced seed germination rates, seedling survival varied by study area and by treatment, and that the use of wire mesh cloth enclosures only slightly increased seed germination and seedling survival. The studies by Pansing et al. (2017) and Pansing and Tomback (2019) indicated that seeding that simulated natural caches across a local landscape experience high losses to small mammals, but the remaining caches had >50% cumulative seed germination rates over two years. Seedling survival was surprisingly high at treeline at the Tibbs Butte study area, showing promise for this restoration approach, especially when considering the potential impacts of

climate change. The Hankin et al. (2023) paper demonstrated the importance of summer moisture for seed germination in arid environments, which is substantiated by field studies (Tomback et al. 1993, 2001b) and suggests that sites for seeding must be carefully chosen.

5 Seed procurement and preparation

Seed collection for whitebark pine is a costly and labor-intensive process. Most seed is wild-collected, although seed orchards are being developed across the range of the species to facilitate easier collection. Ideally, seed is collected from elite parent trees, although in many locations it is still being collected from trees that are putatively resistant to WPBR or have unknown levels of resistance.

Because whitebark pine seed is sought by wildlife, cone collection protocols differ substantially from other conifer species. In mid spring, trees are surveyed for cone production, and individual trees are identified for collection. In late spring or early summer (June through early July, depending on the geographic region), climbers access trees and place wire mesh cages around developing cones to prevent seed predation by nutcrackers and squirrels. Climbers return to harvest cones once seed has ripened in mid-September through October. Cones are then sent for processing to extract seed and prepare it for storage and later use in restoration plantings.

Research assessing important whitebark pine traits, including WPBR resistance, climate adaptation, drought resistance, and mountain pine beetle resistance is at different stages, but the objective is to inform seed collection and restoration activities. Protocols for harvesting seed and growing seedlings from parent trees with known WPBR resistance are well established and benefit from more than 60 years of research on other white pines (Burr et al. 2001; Schwandt et al. 2010). Efforts are underway to identify key genes that confer WPBR resistance, climate adaptation, and other traits, aided in part by the recently described whitebark pine genome (Figueroa-Corona et al. 2024; Neale et al. 2024; van Mantgem et al. 2023). The highest priority is to identify parent trees with WPBR resistance without the need to screen seedlings. Restoration efforts would be further facilitated by the ability to identify seed sources and to develop protocols to promote climate adaptation, drought resistance, and mountain pine beetle resistance. Climate adaptation focuses restoration efforts on topography and sites where whitebark pine is likely to persist but also can potentially employ assisted migration of better adapted genotypes from areas within the whitebark pine range where current climate is similar to future climate predictions (Tomback et al. 2022). Historically, forest tree seed has always been collected from local sources within designated seed transfer zones with the understanding that local sources are best adapted to local environments. Yet evidence indicates that many tree species are already maladapted to current climates where they are found, suggesting that local seed may not be best, especially as the climate continues to change (Rehfeldt et al. 2012). Current guidance for whitebark pine suggests avoiding movement among seed zones, but this is being reevaluated (Tomback et al. 2022).

The management reality is that whitebark pine seed available for restoration activities is scarce. In general, there are seed shortages for restoration purposes across the western United States, and the lack of work capacity limits the number of seed collections even in years with good cone production (Fargione et al. 2021). Further, loss of existing whitebark pine seed sources from WPBR, mountain pine beetles, and wildfire

reduces the number of genotypes we can conserve and use in reforestation activities. Expanding the funding and workforce with skills to collect whitebark pine cones will be integral to the success of future restoration activities including seeding.

6 Seeding protocol

Seeding protocols for whitebark pine share some of the recommendations made for seedling planting, such as avoiding the following conditions: closed canopy, steep slopes, dense understory vegetation, moist swales, and deep friable soils, especially with signs of pocket gopher (Family Geomyidae) disturbance (McCaughey et al. 2009; Tomback et al. 2022). Because whitebark pine historically has regenerated well in post-fire seedbeds, especially in the Northern Rocky Mountains, many managers have targeted comparatively recent burns or burned sites prior to seedling planting to avoid competition and understory plants (Keane et al. 2012; Perkins 2015; Jenkins et al. 2022). Planted seedlings and seeded caches established on southern or western slope aspects are expected to fare better if they are located near natural or artificial shade objects (e.g., McCaughey et al. 2009; Casper et al. 2016). Seeding microsites for most of the studies reviewed above were distributed within the confines of study blocks or plots, but other distribution patterns in relation to natural microsites and certain topography, as well as lower densities, may be more favorable.

Although specific seeding implementation protocols do not exist yet, aside from general site recommendations (Tomback et al. 2022), Pansing et al. (2017) established an experimental, inference-based, and replicable approach that facilitates monitoring of seed pilferage, seed germination, and seedling survival over multiple years. Although sound inference is not necessary to seeding implementation, it is integral to developing sound best management practices and improving outcomes, and it can be integrated with operational seeding to monitor and improve outcomes. Importantly, the methods used simulate Clark's nutcracker caching behavior, under the assumption that this will lead to the highest germination and seedling survival, at least in certain microsites. In addition to selecting the number of seeds per cache from an empirically derived Poisson distribution of seed cache sizes (Tomback 1978; Hutchins and Lanner 1982), burying seed at a similar depth to nutcracker caches (~2.5 cm; Tomback 1978) and creating seed caches at microsites known to be used by nutcrackers (rock, tree, open; Tomback 1978), Pansing et al. (2017) developed a method to precisely relocate caches so they can be excavated to monitor seed pilferage. At each selected cache site, a high precision GPS unit is used to collect and store the location of the cache. To further facilitate cache relocation for monitoring, a square PVC frame (20 cm x 20 cm) and two 8-inch nail spikes are used to mark the location of the cache. Seeds are sown in one vertex of the PVC frame, and one nail spike is hammered into each vertex adjacent to the seed cache (Figure 5). The seed cache is always created upslope of the nail spikes for open microsites and on the northeast side of the object for rock and tree microsites to protect seedlings from excessive sun, high temperatures, and strong winds. A numbered aluminum identification tag is attached to one of the nail spikes to facilitate data collection. When managers return to caches for monitoring, GPS navigation can be used to identify the general vicinity of the cache, and the PVC frame is placed around the nail spikes to identify exactly where the cache was created. Once the location is identified, the cache can be dug up to count the number of seeds remaining in the cache and/or identify seedlings germinated from the cached seed. This approach to locating seedlings

has shown to be effective over as many as 5 years (Pansing and Tomback 2019). In the last few years, this suite of methods has been adopted by various federal agencies for experimental trials examining the utility of seeding as a restoration tool.

Figure 5. Monitoring framework as developed by Pansing et al. (2017). The PVC frame is placed such that two nail spikes are visible in two opposing vertices of the frame. The seed cache is located in the vertex nearest the tree. Between this marking process and GPS coordinates, it is possible to track individual seed caches and even dig up seeds to assess cache pilferage. (Photo credit: E.R. Pansing).

For operational application, seeding configurations and selection criteria for seeding may be developed to better align with management goals and desired future conditions. For example, there may be an established tree density target. However, there may be trade-offs between the density of seeded caches and the probability of attracting rodents to the planting projects, and site weather conditions or water balance characteristics may impact demographic processes. A thorough understanding of the impacts of uncontrollable variables on site selection and planning will be necessary to ensure long-term success. Even in operational applications, monitoring will be key to developing and improving best practices.

Currently, information about soil types that best support seeding is limited; soil types vary considerably across the range of whitebark pine, a product of regional and local geological history as well as local ecological processes (Arno and Hoff 1990). Research is just beginning to examine the impact of water balance variables on planted seedlings, sown seed, and whitebark pine recruitment (e.g., Laufenberg et al. 2020; Hankin et al. 2023), focusing on factors such as evapotranspiration (AET) thresholds and soil moisture, and their association with growth rates and root to shoot ratios. For example, Laufenberg et al. (2020) found that whitebark pine seedling growth rates were highest when cumulative growing season AET was greater than 350 mm. Research into water balance variables associated with seeding may provide key recommendations for restoration protocols that minimize water deficit. Water balance studies may help managers understand the requirements of whitebark pine early growth stages, and especially the impact of water balance on whitebark pine seed germination and seedling establishment.

7 Monitoring

Given that seeding as a restoration tool for whitebark pine is still very much under development, monitoring outcomes becomes an essential component of seeding projects (Tomback et al. 2022). The geographic variation in climate and biophysical conditions across the whitebark pine range will likely require that seeding protocols vary at scales from local to regional. As projects are developed and implemented, managers should include monitoring strategies during the planning phase so they may assess project outcomes to improve future protocols. Projects can also be developed with a learning component through stratification of seeding efforts by microsite, slope aspect, elevation, and habitat characteristic, such as burn severity or canopy closure. The major monitoring challenge for seeding is devising some way to mark cache sites that is compatible with agency restrictions and land use types.

There are guiding principles for ecological restoration monitoring that are relevant for achieving 'active adaptive management' in seeding applications (Hutto and Belote 2013; Larson et al. 2013; Gann et al. 2019). These are used in a broader sense for plant ecological restoration but can be applied to seeding specifically. For example, *implementation monitoring* can be used to assess how seeding was performed for the project and could include variables such as weather, seed density, number of seeds per 'cache,' seeding depth, and microsite types. A monitoring strategy should capture the variation in implementation with sufficient sample sizes so that comparisons within each variable are possible. *Efficacy monitoring* in principle examines whether project restoration objectives were met, or some progress can be documented towards objectives, such as density of seedlings produced and seedling survival rates after a designated timeframe. Monitoring considerations might include when to sample, such as after years 1, 3, and 5, how much of the project to sample, and how to distribute monitoring across the project (Tomback et al. 2022).

Because whitebark pine seeding is still under development as a restoration tool, implementation and efficacy monitoring will enable us to better understand how to improve outcomes and reduce outcome variation, ensure operational efficiency, and confirm that restoration objectives are being met. Monitoring seeding presents its own unique challenge. Whitebark pine seed must be buried to maximize germination, and returning to the exact location of a seed cache is difficult. This challenge is even greater when seed caches must be dug up to assess cache pilferage rates. Marking caches is necessary to ensure that information on the cache location is sufficiently accurate that pilferage and lack of germination are not confounded, and naturally regenerating seedlings are not confused with seedlings generated from seeding (see Figure 3b). Confounding pilferage and germination failure can prohibit identification and testing of solutions specific to each recruitment phase. Although monitoring methods have been developed, some key aspects of seeding life history, such as number of years required for successful establishment, which informs optimal monitoring timelines and frequencies, remain to be determined.

8 Challenges to operationalizing seeding

Although seeding holds promise for whitebark pine restoration, substantial barriers remain to effective operationalization. Solutions to these challenges are likely to vary in utility depending on geographic context, land-use designation, and implementation phase.

Seed pilferage by rodents is one of the most significant barriers to implementation and social acceptance. Various mitigation techniques, such as wire mesh cloth cages, cayenne pepper, and the fungicide Thiram, as discussed above (Schwandt et al. 2006; Schwandt et al. 2011; DeMastus 2013), along with emerging technologies like seed crowns and nursery pods (e.g., W. Scott Laseter, personal communication, Marc Swackhamer personal communication), have shown promise but also mixed results. However, protective installations including wire mesh cloth and seed crowns are often prohibited in proposed and designated Wilderness Areas; they add substantial labor and costs for both installation and removal; and they require extra site trips for removal. Pilferage is a critical concern, because whitebark pine seed collection is costly, time-intensive, and laborious (Tomback and Sprague 2022), making "wasted" seed a significant resource loss. However, comparative studies have yet to assess seed efficiency between seeding and greenhouse-grown seedlings. DeMastus (2013) found higher survival rates of outplanted seedlings compared to combined seed germination and seedling survival rates for directly sown seeds. However, comparisons of survival of outplanted seedlings to germination and seedling survival of sown seed overlook nursery processes that obscure seed use efficiency. For example, nursery germination rates for whitebark pine range from 28% to 90%, and personnel will often place two seeds in each seedling container to optimize space in greenhouse settings (Olsen et al. 2016). Assumptions that seeding wastes more seed than outplanted seedlings have not been assessed and require examination.

Another barrier is the uncertainty in outcomes associated with seeding. Whitebark pine seed collections can be a limiting factor in the initiation of operational seedling planting or seeding projects. The priority is to grow seedlings or sow seed that have some genetic resistance to WPBR (Tomback et al. 2022). Given that the overall success of seeding projects currently is highly variable, there is a reluctance to invest seed from resistant seed sources, time, and personnel costs. On the other hand, seeding is one of the only restoration tools that is permitted for use in Wilderness Areas, which comprise a high proportion of some federal lands, such as National Park units and many National Forests of the U.S. Forest Service and are predicted to comprise a relatively higher proportion of whitebark pine habitat less impacted by climate change in the foreseeable future (Parks et al. 2025). As we work to better understand and reduce the variation associated with seeding outcomes, managers need to evaluate the tradeoffs between uncertain outcomes and the consequences of not restoring priority areas.

Monitoring seeding outcomes presents additional logistical challenges, as consistent year-to-year measurements necessitate marked installations to relocate caches and their seedlings (e.g., Figure 5). Existing studies rely on specific markers to facilitate re-measurement and data consistency (e.g., Schwandt et al. 2007; Pansing et al. 2017), yet use of these markers is often restricted in Wilderness Areas. Furthermore, if seeding is being implemented by agencies, more reporting of outcomes from seeding trials would benefit managers across agencies, underscoring an urgent need for broader dissemination of trial results. Published findings will be critical for refining protocols and guidance for land managers, ultimately bolstering the success of seeding operations.

Finally, current guidance on seeding lacks specificity regarding optimal techniques and locations, primarily because recommendations have been constrained by geographically limited trials with small sample sizes. Modifications to standard seedling planting densities, for example, may be required to align with the unique needs of seeding and to mitigate pilferage rates. Preliminary evidence suggests that microsite

selection may significantly influence seeding outcomes (e.g., Pansing et al. 2017), yet further research is needed to offer land managers informed, location-specific recommendations.

9 The road ahead

Better understanding of the factors affecting variation in seeding outcomes and how managers can increase seeding success may be essential before we see general adoption of this method as a restoration tool for whitebark pine. Although variation in outcomes from site-specific differences, including soils, regional and local weather, and climate change impacts, are expected, methodical, controlled research spanning multiple sites, regions, and years will be required to refine recommendations to land managers. As additional information on the impacts of site-specific characteristics on whitebark pine seeding success becomes available, we need to encourage managers to disseminate the results.

Despite ongoing challenges, interest in the use of seeding for whitebark pine restoration is expanding across federal lands in the western U.S. While there is still work to be done to standardize outcomes and develop protocols adaptable to diverse geographies and jurisdictions, seeding is emerging as a valuable tool in the whitebark pine restoration toolkit. Land managers increasingly recognize its potential, particularly in hard-to-access areas where traditional seedling planting is impractical or restricted. As more data from seeding trials become available—alongside best management practices and a boost in seed collection efforts across the West—seeding is poised to become a more widely adopted method for restoring whitebark pine in remote high-priority locations that would otherwise remain unrestored. Inaction could potentially result in local extirpation of this important forest resource.

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