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Tamm reviews

Tamm review: Current and recommended management practices for the restoration of whitebark pine (*Pinus albicaulis* Engelm.), an imperiled high-elevation Western North American forest tree[☆]

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ABSTRACT

Whitebark pine (*Pinus albicaulis* Engelm.) is an ecologically important subalpine and treeline forest tree of the western U.S. and Canada. It is categorized as endangered by the IUCN and by Canada under the Species at Risk Act and was recently proposed for listing in the U.S. as threatened under the Endangered Species Act. Whitebark pine populations are declining nearly rangewide primarily from the spread and intensification of *Cronartium ribicola* J.C. Fisch., the exotic, invasive pathogen that causes white pine blister rust (WPBR); recent, large-scale outbreaks of mountain pine beetles (MPB) (*Dendroctonus ponderosae* Hopkins); altered fire regimes; and, multiple impacts from climate change. For more than two decades, researchers and managers within the U.S. Forest Service and Canadian forestry agencies have been developing restoration and conservation tools and techniques to help mitigate these threats. Four conservation and restoration principles for whitebark pine were previously emphasized: (1) conserve genetic diversity, (2) promote WPBR resistance, (3) protect seed sources, and (4) deploy restoration treatments, while mitigating for climate change. These principles are served by ten additional management or conservation actions that form the basis of a restoration and adaptive management plan but apply primarily to regions with moderate to high levels of WPBR and MPB outbreaks. Where the pathogen and MPB are absent or present at low levels, managers can implement proactive management to build resilience to prevent the future loss of ecological function. Here, we review the key management actions currently used for whitebark pine conservation and restoration in the U.S. and Canada, which include gene conservation, increasing natural genetic resistance to *C. ribicola*, cone collections, growing and planting seedlings or directly sowing seeds, protecting seed sources, prescribed fire and silvicultural thinning to reduce competition in late seral

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communities, proactive intervention, stand health surveys and monitoring, and monitoring the impacts of restoration for adaptive management. This review is the outcome of an experts' workshop held in association with the development of the National Whitebark Pine Restoration Plan (NWPRP), a collaborative U.S. multi-agency and tribal effort initiated in 2017 in consultation with the U.S. Forest Service and facilitated by the non-profit organizations, the Whitebark Pine Ecosystem Foundation and American Forests.

1. Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is an ecologically important subalpine and treeline forest tree distributed throughout the Sierra Nevada-Cascade crest, the northern coastal ranges of the western U.S. and Canada, and the northern Rocky Mountains from the southern Greater Yellowstone (~42°) to about 55° N latitude in Canada (Fig. 1A). Whitebark pine communities provide ecosystem services including snow retention and redistribution; large, nutritious seeds sought by a diversity of wildlife; plant protection (facilitation) on harsh subalpine and treeline sites; and, comparatively rapid regeneration after fire and other disturbances (Tomback et al., 2001a; 2001b, 2011, 2016). Whitebark pine was an important episodic food resource both culturally and historically for several western Native American tribes (Moerman, 1998; Tomback et al., 2011). The pine is considered both a keystone and foundation species, given that its communities promote biodiversity at high elevations and provide locally stable conditions for other plant and animal species (Tomback et al., 2001a, 2011, 2016; Ellison et al., 2005; DeGrasssi et al., 2019).

Estimates of the areal extent of whitebark pine in the U.S. vary greatly, depending on sources and assumptions, such as historical, potential, or current range. The U.S. Fish & Wildlife Service (2018) estimated the entire North American distribution of whitebark pine to encompass ~ 32.6 million ha (~80,600,000 acres)—with 70% in the U.S. distribution and 88% of the U.S. distribution on federal lands. COSEWIC (2010) estimated the range at about 34 million ha, with ~ 15 million ha in the U.S. (44%) and ~ 19 million in Canada (66%). Keane et al. (2012) estimated the U.S. distribution at ~ 5.8 million ha based on a combination of geospatial information and modeling, and Goeking and Izlar (2018) estimated 4.1 million ha based on U.S. Forest Service, Forest Inventory and Analysis (FIA) data.

The largest U.S. land manager for whitebark pine is the U.S. Forest Service (~74% of land area), followed by the National Park Service (10%), and BLM (4%) (U.S. Fish & Wildlife Service, 2018). The remaining 12% is administered primarily by Native American tribes, states, and private landowners. The U.S. Fish & Wildlife Service (2018) has divided the U.S. whitebark pine range into ten distinct ecoregions (Fig. 1B). COSEWIC (2010) estimates that 76% of the Canadian distribution of whitebark pine is in British Columbia and 24% in Alberta; in these provinces, whitebark pine is found primarily on Canadian federal or provincial Crown lands with some occurrence on tribal lands.

Whitebark pine has the largest geographic distribution of any forest tree evaluated across multiple government jurisdictions for listing as a threatened or endangered species. It is categorized as endangered by the IUCN (Mahalovich and Stritch, 2013, https://www.iucnredlist.org/species/39049/2885918) and by Canada under the Species at Risk Act (Government of Canada, 2012). The species was recently proposed for listing in the U.S. as threatened under the Endangered Species Act (U.S.

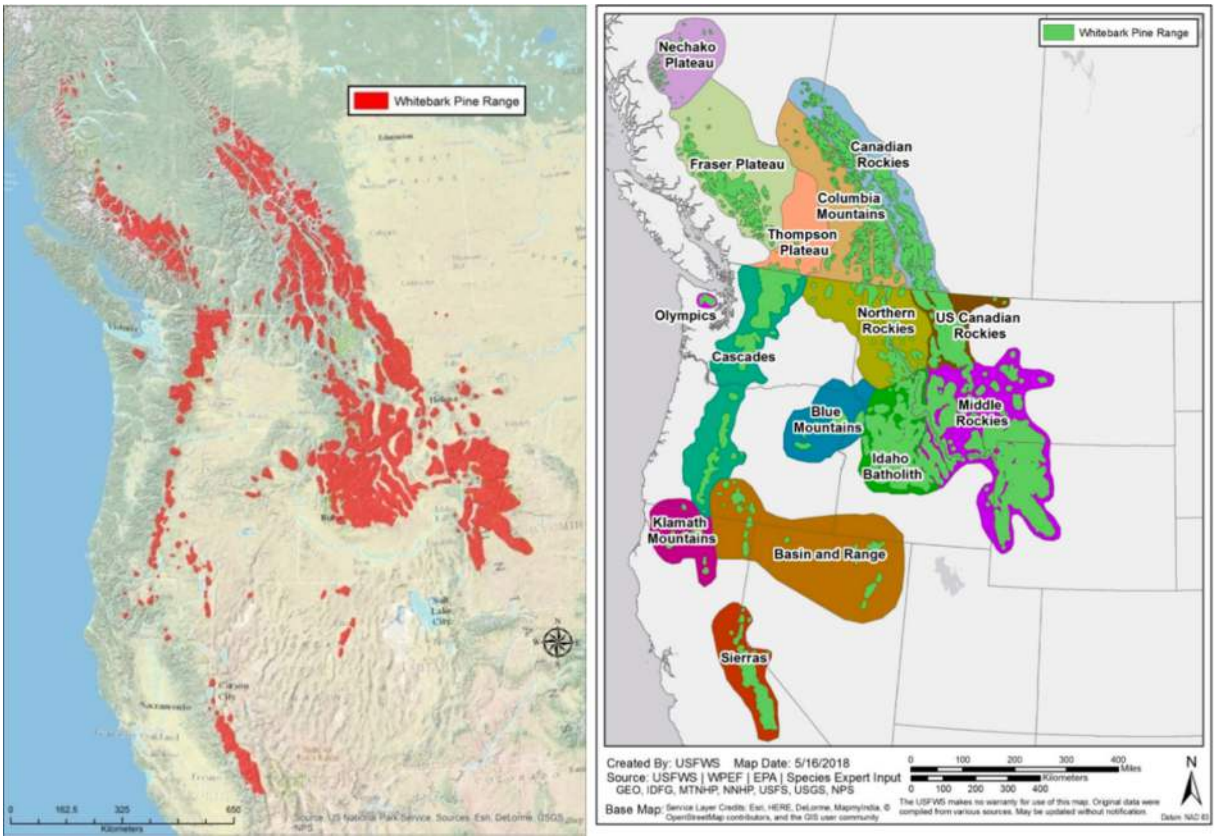

Fig. 1. A. The U.S. and Canadian distribution of whitebark pine (*Pinus albicaulis* Engelm.) https://whitebarkfound.org/wp-content/uploads/2014/05/Whitebark-Pine-Range-New-02.jpg. B. Fifteen ecoregions identified by the U.S. Fish & Wildlife Service (2018) within the U.S. and Canadian distribution of whitebark pine.

Fish and Wildlife Service, 2020), with the listing decision to be finalized in 2022.

Whitebark pine populations are declining across most of the species' range in both the U.S. and Canada, primarily as a result of infection by *Cronartium ribicola* J.C. Fisch., the exotic, invasive pathogen that causes white pine blister rust (WPBR) (COSEWIC, 2010; Environment and Climate Change Canada, 2017; U.S. Fish and Wildlife Service, 2018, 2020). In five-needle white pines, *C. ribicola* infection leads to crown mortality, which reduces seed and pollen cone production, and to tree mortality (McDonald and Hoff, 2001; Geils et al., 2010; Tomback and Achuff, 2010; Schwandt et al., 2010). Another significant threat to whitebark pine includes widespread mortality of mature trees during large-scale outbreaks of mountain pine beetles (MPB) (*Dendroctonus ponderosae* Hopkins). Although unprecedented whitebark pine mortality from MPB occurred from about 1999 to 2009 in Idaho, Montana, and Wyoming, the outbreaks have declined in these regions, and WPBR infection levels have increased (Gibson et al., 2008; Shanahan et al., 2016). Other threats include altered fire regimes from both historical fire exclusion and more frequent and severe fires from climate warming trends, and other climate change impacts. Climate warming not only alters whitebark pine distribution at both local and regional scales and changes fire regimes, it is driving native bark beetle outbreaks (Logan et al., 2003; Gibson et al., 2008; Tomback and Achuff, 2010; Schwandt et al., 2010; Keane et al. 2017a; 2017b; Shepherd et al., 2018; Goeking and Iszlar, 2018). Regional declines in seed source abundance and health decreases the effectiveness of whitebark pine's obligate avian seed disperser, Clark's nutcracker (*Nucifraga columbiana* Wilson) (Tomback,1978, 1982; Hutchins and Lanner, 1982; McKinney et al., 2009; Barringer et al., 2012), reducing regeneration rates, especially after wildfire (Leirfallom et al., 2015; Stevens-Rumann et al., 2017).

For more than 25 years, all three branches of the U.S. Forest Service—the National Forest System, State and Private Forestry, and Research and Development—have been developing various tools and techniques to mitigate the causal agents of decline in whitebark pine within its U.S. range. Canadian federal and provincial forestry agencies have also pioneered and used similar approaches to whitebark pine management. This review will primarily emphasize specific strategies and techniques developed in the U.S. for managing whitebark pine but also references relevant Canadian work.

Since 1990, there have been multiple workshops, conferences, and proceedings devoted to whitebark pine ecology, threats, and restoration, with both U.S. and Canadian participation. The first overview of this information was published in the landmark collected volume edited by Tomback, Arno, and Keane (2001c). The first chapter (Tomback et al., 2001a) presented the case for timely management intervention across much of whitebark pine's range followed by chapters summarizing information on whitebark pine biology, population genetic structure, ecology, and threats. The book's final section highlighted new information on restoration approaches, including Burr et al. (2001) on collecting cones, germinating seeds, and growing seedlings; Hoff et al. (2001) on strategies for identifying *C. ribicola* resistance in individual trees and developing integrated management programs for planting seedlings and other actions to build resilience in whitebark pine; and, Keane and Arno (2001) on use of prescribed fire and silviculture thinning to prevent loss of whitebark pine in successionally advanced stands. The first five-year management plan for whitebark pine was written by the Pacific Northwest region of the U.S. Forest Service (Aubry et al., 2008) (Table S1). Another landmark publication was a special issue of *Forest Pathology* edited by Shaw and Geils (2010); the papers in this journal issue outlined the major threats to five-needle white pines represented by WPBR and detailed the components of a continent-wide pathosystem. This publication was followed by Keane et al. (2012), which synthesized and described rangewide conservation and restoration approaches for whitebark pine at individual tree to landscape scales.

Agency assessments over the last 20 years indicate the spread of WPBR not only poses an existential threat to whitebark pine but also to other western five-needle white pines (e.g., Samman et al., 2003; Schwandt, 2006). The other most severely impacted pines include western white pine (*P. monticola* Dougl.), limber pine (*P. flexilis* James), and sugar pine (*P. lambertiana* Dougl.) (Tomback and Achuff, 2010; Goeking and Windmuller-Campione, 2021, this issue). WPBR has also invaded populations of southwestern white pine (*P. strobiformis* Engelm.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and the northern populations of foxtail pine (*P. balfouriana* Balf.) (McDonald and Hoff, 2001; Tomback and Achuff, 2010; Schwandt et al., 2010; Goeking and Windmuller-Campione, 2021, this issue; Schoettle et al., 2022, this issue). Great Basin bristlecone pine (*P. longaeva* D.K. Bailey) is yet uninfected by *C. ribicola* (Goeking and Windmuller-Campione, 2021, this issue; Schoettle et al., 2022, this issue). Like whitebark pine, most of these pines are somewhat fire-dependent, moderately shade-intolerant, and susceptible to successional replacement (Tomback and Achuff, 2010). Management treatments and strategies to restore whitebark pine may serve as a template for restoration of other western five-needle white pines (see Tomback and Sprague, 2022, this issue; Schoettle et al., 2022, this issue).

Limber pine, sugar pine, and northern populations of southwestern white pine are also reliably dispersed by Clark's nutcrackers (e.g., Lanner and Vander Wall, 1980; Samano and Tomback, 2003; Murray and Tomback, 2010; Turner et al., 2011), which can facilitate the spread of WPBR-resistant genotypes from trees surviving infection. Nutcrackers, however, are energy-sensitive foragers and will emigrate from regions experiencing low cone production (e.g., Vander Wall and Balda, 1981; McLane et al., 2017). Therefore, under conditions of declining forest health, cones from the few trees that are genetically resistant to *C. ribicola* may be removed by pine squirrels [*Tamiasciurus hudsonicus* (Erxleben, 1777) and *T. douglasii* (Bachman, 1839)] or the seeds consumed by nutcrackers (McKinney and Tomback, 2007; McKinney et al., 2009; Barringer et al., 2012). Given that population-level genetic resistance to *C. ribicola* is key to whitebark pine viability, several large-scale applied programs to identify and develop resistant planting stock have been underway for more than 15 years (Sniezko et al., 2011).

Basic management approaches for whitebark pine were previously summarized by Keane et al. (2012, 2021, this issue), which presented a workflow sequence to guide the selection of whitebark pine communities and stands for restoration and the appropriate conservation approaches. The four restoration principles emphasized in Keane et al. (2012) were (1) conserve genetic diversity, (2) promote rust resistance, (3) protect seed sources, and (4) employ restoration treatments. These principles are served by ten management or conservation actions, summarized here, which could in part be considered both a workflow and adaptive management strategy (Table 1). Where populations of whitebark and other five-needle white pines are yet to be invaded by *C. ribicola*, a proactive approach to building resilience to prevent the loss of ecological function and a management framework has been recommended by Schoettle and Sniezko (2007) and Schoettle et al. (2019a).

Several agency conservation plans for whitebark pine have been developed specific to different geographic areas and distributions, with an inter-agency plan currently under development in California and a transboundary plan nearing completion for the Crown of the Continent (Jenkins et al., 2022, this issue) (Table S1). Most plans describe stand conditions that require specific restoration, conservation, or protective actions in relation to the current health status of their whitebark pine communities. For example, Keane et al.'s (2012) range-wide strategy and Keane et al. (2021, this issue) provide general guidance for assessments and restoration applications at different landscape scales, from range-wide to tree level. Spatial layers and health status information are used for management decisions about where to restore whitebark pine and selecting appropriate restoration applications and actions. However, a few plans, such as the National Whitebark Pine Restoration Plan (NWPRP, Tomback and Sprague, 2022, this issue), the Crown of the Continent Ecosystem High Five Working Group Restoration Strategy

Table 1
Four guiding principles (category 1) or basic tenets, and ten conservation, restoration, and management actions divided into two categories (2 and 3) for whitebark pine. These can be used to construct a workflow plan for management, modified from Keane et al. (2012). WPBR = white pine blister rust; MPB = mountain pine beetle(s).

Action	Explanation
1. Basic tenets	
Conserve genetic diversity	The genetic diversity across the range of whitebark pine is a conservation priority to provide genetic variation for adaptation to all ecological settings and abiotic conditions represented by whitebark pine range-wide but also for adaptation to climate change and challenges from insects and native and exotic disease.
Promote rust resistance	WPBR, caused by the exotic fungal pathogen *Cronartium ribicola*, is the primary agent of whitebark pine decline. By planting seedlings with genetic rust resistance in declining stands, managers can build resilience to the disease and ensure healthier future populations. Planting seedlings with genetic resistance in stands prior to WPBR invasion or at low levels of WPBR will increase future stand resilience and promote sustainability upon invasion.
Save seed sources	Mature cone-producing trees with known genetic resistance to WPBR and stands of trees with high frequencies of genetic resistance must be protected from destructive disturbances, including MPB outbreaks, wildland fire, and commercial timber cutting. Unique stands that occupy unusual ecological conditions, peripheral populations, or have unusually high genetic diversity are also priority for protection.
Apply restoration treatments	Restoration treatments are applied in response to whitebark pine community decline caused by MPB outbreaks, WPBR, and advanced succession and proactively to build resistance to the spread and intensification WPBR and to encourage natural regeneration, especially in areas of high natural genetic resistance.
2. Initial work for restoration planning	
Assess condition	Assess trends in whitebark pine health and successional status at local scales in designated geographic areas.
Plan activities	Use assessment information to plan appropriate conservation and restoration actions.
3. Application of specific management actions relevant to stand conditions	
Reduce disturbance	Implement restoration treatments that reduce the risk of impacts such as competition, fire, or MPB attack on whitebark pine.
Collect seeds	Collect whitebark pine seeds for multiple purposes, including gene conservation for the species, conservation of genetic diversity, and growing WPBR-resistant seedlings for planting.
Grow seedlings	Grow seedlings from potentially WPBR-resistant seed sources for resistance screening trials to identify parent trees with genetic resistance and operationally for seedling planting from screened trees with known genetic resistance.
Protect seed sources	Protect known resistant (elite) trees that have been identified through screening efforts from both wildfire and MPB attack.
Implement treatments	Use ecological restoration treatments that include silvicultural techniques and prescribed fire to create opportunities for whitebark pine regeneration and to reduce competing vegetation and fuels.
Plant seedlings	Plant whitebark pine seedlings grown from the seeds of WPBR- resistant trees. Plant in areas with suitable seedbeds, such as recent natural and prescribed burns or stands that have experienced heavy mortality from MPB. Planting techniques following established protocols will increase seedling survival. An alternative to seedling planting is to sow seeds directly into suitable seedbeds.
Monitor activities	Monitor restoration treatments to determine their efficacy and whether they must be reapplied. Also, monitor plantings to determine if mortality from WPBR is greater than expected from the likely frequency of genetic resistance among seedlings, and thus whether seed sources need to be reevaluated.
Conduct research	Develop new and more cost-efficient methods and restoration techniques, including the use of genomics to identify genetic resistance to WPBR in individuals.

(Jenkins et al., 2022, this issue), and the Whitebark Pine Strategy for the Greater Yellowstone Area, identify a subset of whitebark pine's range in different geographic regions, using specific biological criteria, for priority application of conservation and restoration actions (Table S1). The conditions within these selected areas determine which of the proposed restoration actions are applied.

Here, we review key management approaches used for whitebark pine conservation and restoration, some of which have arisen from practice and are not codified. This paper is the outcome of a 2017 workshop in association with the National Whitebark Pine Restoration Plan (NWPRP), a collaborative U.S. milti-agency and tribal effort initiated in 2017 in consultation with the U.S. Forest Service and facilitated by two non-profit partners, the Whitebark Pine Ecosystem Foundation (https://whitebarkfound.org/our-work/national-whitebark-pine-restorationplan/) and American Forests (https://www.americanforests.org/). Information developed during the workshop is summarized here with additional description and appropriate updates.

As articulated by workshop organizers, the overarching goal of whitebark pine conservation and restoration is to develop and sustain healthy and resilient whitebark pine communities in the face of current and future challenges.

2. Guiding principles to provide context to conservation actions and restoration treatments

1. *C. ribicola*, infectious only to five-needle white pines and its alternate hosts, is the most persistent and widely distributed threat to whitebark pine populations, affecting all life stages (Kendall and Keane, 2001; McDonald and Hoff, 2001; Schwandt, 2006; Tomback and Achuff, 2010; Schwandt et al., 2010). The combination of WPBR and MPB reduces seed production and accelerates population losses.

2. *C. ribicola* is still spreading and infection is intensifying across the range of whitebark pine (e.g., Retzlaff et al., 2016; Shanahan et al., 2016; Tomback et al., 2016; Goeking and Izlar, 2018; Rochefort et al., 2018; Shepherd et al., 2018; Thoma et al., 2019, Dudney et al., 2020).

3. Planting seedlings and potentially directly sowing seeds, using source trees found to have moderate to high genetic resistance to WPBR, are the primary means to return or maintain functional whitebark pine on the landscape, especially in geographic regions where *C. ribicola* infection has led to high mortality (Hoff et al., 1980, 1994, 2001; Bingham, 1983; Hagle et al., 1989; McDonald and Hoff, 2001; Tomback and Achuff, 2010; Keane et al., 2012; Keane et al. 2017a; 2017b; Sniezko et al., 2011; Sniezko and Koch, 2017; Schoettle et al., 2019a). Several other approaches to combat WPBR, such as eradicating native *Ribes* (the common alternate host of *C. ribicola*) and applying fungicidal controls, have been tried unsuccessfully during the early history of its detection and spread in five-needle white pines, (e.g., Maloy, 1997; Neuenschwander et al., 1999; McDonald and Hoff, 2001).

4. Trees found to have genetic resistance to WPBR are the current and future seed sources for developing resistant populations. Protecting these trees from MPB, in areas where beetles are active (e.g., Kegley and Gibson, 2004; Progar, 2003; Bentz et al., 2005; Kegley et al., 2010) and from wildfire is important. Resistant tree locations and fire-protection strategies can be integrated into forest management plans (Keane et al., 2012; Keane, 2018)

5. Climate change potentially affects whitebark pine regeneration, distribution, and abundance; promotes MPB outbreaks; and, alters fire regimes (Westerling et al., 2006, 2011; Warwell et al., 2007; Chang et al., 2014; Buotte et al., 2016; Stevens-Rumann et al., 2017). Its effects on the spread of *C. ribicola* geographically and infection dynamics depend on regional climate scenarios (Sturrock et al., 2011; Kliejunas, 2011); however, blister rust has infected treeline populations even at whitebark pine's northern limits (Tomback et al., 2016).

6. Restoration treatments at local to regional geographic scales are potentially more effective if they include climate change mitigation (Keane et al., 2021, this issue). Mitigation strategies may include

thinning competing species to increase vigor of surviving trees, using appropriate genotypes to grow seedlings for planting or for direct seed sowing, deciding where to plant seedlings or sow seeds within the local distribution, and determining where and when to apply thinning or prescribed fire treatments (Keane et al., 2013, 2017a,b; Ireland et al., 2018; Keane et al., 2021, this issue). Given that some treatments are experimental, monitoring and adaptive management are needed to test whether treatments are performing as expected and for unintended consequences.

7. In areas where whitebark pine is still relatively healthy, proactive management can be a priority (Samman et al., 2003; Schoettle and Sniezko, 2007; Keane and Schoettle, 2011; Schoettle et al., 2019a). Proactive actions may include gene conservation collections to capture genetic diversity for archiving, genetic screening of cone-producing trees to determine the frequency and distribution of *C. ribicola* resistance, establishment of seed orchards or clone banks of resistant parent or progeny selections, and planting seedlings with resistance to WPBR to increase genetic resistance in target populations. If natural genetic resistance is present in populations at moderate to high levels, light prescribed burning—while avoiding crown scorch and bole charring damage to whitebark pine—and thinning create open and more favorable seedbeds, which may encourage natural establishment of seedlings with rust resistance. Diversifying the age class structure of whitebark pine across the landscape as well as thinning treatments will help limit future MPB outbreaks.

8. Management of whitebark pine is both complicated and expedited by the pine's dependence on Clark's nutcracker and further complicated by cone-cutting by pine squirrels (*Tamiasciurus*). Where cone crops are much reduced, seeds from resistant trees may be lost to pre-dispersal predation or not dispersed by nutcrackers (McKinney and Tomback, 2007; McKinney et al., 2009; Barringer et al., 2012). In stands where WPBR resistance has increased through seedling planting, direct seed sowing, or natural regeneration, and trees reach maturity, nutcrackers will potentially spread genetic resistance in coming decades by caching whitebark pine seeds in adjacent areas and to distances as far as ~ 32 km from seed sources (Tomback, 1978; Lorenz et al., 2011).

3. Conservation and restoration actions and applications.

In this section, key management practices and treatments for conservation and restoration identified by Keane et al. (2012) are briefly described. Some practices will vary geographically or by whitebark pine ecoregion (Fig. 1B). A list of estimated whitebark pine conservation and restoration treatment costs is provided in Table S2 under Appendix A.

3.1. Conserve genetic diversity: Seed collections and archiving.

Seed collections are an important means of preserving genetic diversity for whitebark pine and other five-needle white pines, as populations decline from WPBR and MPB (Hoff et al., 2001). Seed collections from different geographic areas may be used for determining the distribution of genetic diversity within and among populations and for assigning seed zones, establishing common gardens for determining adaptive traits including cold hardiness and drought tolerance, and for assessing regional differences in genetic resistance to WPBR (e.g., Bower and Aitken, 2006; Mahalovich and Hipkins, 2011; Warwell and Shaw, 2017). They may also be used as part of climate change mitigation protocols, as these are developed (e.g., Keane et al., 2021, this issue).

In the U.S., many National Forests, National Parks, Bureau of Land Management field offices, and several Native American tribes have collected seeds from their whitebark pine populations and from populations of other five-needle white pines to archive and conserve genetic diversity. Seed collections have also been made in Canada by Alberta and British Columbia forestry agencies, Parks Canada, and non-profits (e.g., Bulkley Valley Research Centre - Whitebark Pine (bvcentre.ca) (Environment and Climate Change Canada, 2017). In some cases, the seedlots have been planted out and represent both *in situ* and *ex situ* genetic conservation. The U.S. Forest Service supports a gene conservation program for native plants and operates several seed storage facilities that are used for *ex situ* conservation. The agency states that "*The development and use of genetically appropriate plant material can help maintain genetic diversity and protect plant populations in their natural habitat (*in situ *conservation). Establishing and supporting* ex situ*, or off-site, seed banks is an additional important aspect of gene conservation, and provides an insurance policy against the loss of wild populations.*" https://www.fs.fed.us/wildflowers/Native_Plant_Materials/genetics/conservation.shtml.

Recent studies indicate that if whitebark pine seeds are stored at cold temperatures (−11 to −18 °C) with low humidity, they may remain viable for a decade or more (e.g., Bower et al., 2011; Sniezko et al., 2017). Whitebark pine seeds collected from 1978 to 2009 and recently tested had germination rates ranging from 0 to 96%, with mean germination success across all collections of about 47% (Sniezko et al., 2017). Longevity of seed viability may depend in part on protocols used in field collection, seed extraction, and seed storage.

3.2. Promote genetic resistance to WPBR

The primary means to enhance resilience to WPBR in whitebark pine is to increase the frequency of genetic resistance within populations, thus artificially accelerating natural selection for resistant genotypes. This entails identification of seed trees with rust resistance and then planting progeny from these trees. Planting seedlings serves to promote rust resistance and as a restoration treatment. In the following sections, we define key terminology related to the identification of blister rust resistance and the utilization of genetic resistance for restoration.

3.2.1. Terminology related to WPBR resistance in seed sources used for restoration

A specialized set of terms, defined below, is generally applied to trees and seedlings by U.S. Forest Service and Canadian genetic resource managers at tree nursery facilities that screen seed sources for blister rust resistance (e.g., Mahalovich and Dickerson, 2004; Pigott et al., 2015). The terminology comes from long-standing tree improvement and breeding programs that are gradually being integrated with new genomic, forest management, and climate modeling approaches (e.g., Wang et al., 2010; Wheeler et al, 2015). These terms will be frequently used in discussion throughout this review.

Genetic resistance: Whitebark pine trees show quantitative genetic resistance to WPBR (i.e., additive resistance). Quantitative resistance is based on polygenic inheritance of genes with allele frequencies that differ among individuals and populations. Thus, phenotypes span a resistance continuum (e.g., Sniezko et al., 2007; 2011; 2018; Murray and Strong, 2021); and, although progeny of most whitebark pine parent trees have survival of 0 to 30% in screening trials for resistance, progeny of some parent trees show survival of 30 to 90% (Sniezko, unpublished data). Because not all progeny from a seed tree with high quantitative resistance will inherit the same combination of genes that confer resistance, managers must determine which screened trees provide the highest proportions of resistant offspring among the trees tested, particularly in comparison to the most susceptible (least resistant) seed tree genotypes. Furthermore, a high number of seed trees with some heritable resistance must be identified to provide adequate genetic diversity for operational seedling production or for direct seeding to help ensure continual evolution of the species in the face of biotic and abiotic challenges. Establishing seed orchards and using controlled pollination improves the frequency of progeny with resistance, can increase numbers of seeds per tree, and may be used to diversify the mechanisms that confer resistance, but useful seed production requires about two decades of orchard growth and development.

Seed tree (general with unknown resistance): A healthy, cone-bearing tree for seed collection selected from an area of moderate to low to no WPBR. Thus, the tree is one of many healthy trees within a stand. The tree has not yet undergone screening for blister rust resistance. Seed trees, if geo-referenced and tagged, can be candidates for resistance screening to obtain baseline frequencies of resistance in threatened populations and, if shown to have resistance (designated an *elite tree*, see below), provide *in situ* seed sources for growing seedlings for planting.

Plus tree (putatively resistant seed tree): A relatively healthy geo-referenced and tagged tree from a stand with high infection level and mortality from WPBR. The tree is a promising candidate for resistance screening, but resistance is not yet confirmed.

Elite tree (resistant seed source): A seed or plus tree confirmed through resistance screening to have heritable (genetic) resistance (i.e., reduced susceptibility) to WPBR. The level of resistance provided to progeny may be evaluated in relation to other screened trees to date within the same stand or from the same geographic area. The results of resistance screening must be confirmed with field trials under natural conditions, which will also monitor durability of resistance.

Putatively resistant seedlings: Seedlings grown from seeds from plus trees, with the assumption that a proportion of the seedlings will have some degree of genetic resistance. Often, seeds from several trees are combined into a bulked lot with unknown resistance for operational seedling production. Putatively resistant seed lots can be screened to provide an estimate of the frequency of resistance for determining appropriate planting densities. This approach may not accomplish restoration goals where WPBR hazard is high, if genetic resistance to WPBR has not been confirmed in seed sources.

Resistant seedlings: Seedlings grown from elite tree seeds, or seeds from a mix of elite trees and unscreened plus trees. Since wind-pollinated seeds of elite parent trees will be used, there will be a wide continuum of susceptibility within seedlots, and seedling survival in high WPBR areas may be 50% or lower because of cross-pollination or recombination. Not all seedlings will carry resistance traits, but seedling survival is expected to be greater than for seedlings grown from untested plus trees alone. Bulked seed lots can be screened to provide a better estimate of the frequency of resistance for determining appropriate planting densities.

Seeds with improved resistance: Seeds harvested from a seed orchard consisting of resistant genotypes adapted to a given seed zone. In the seed orchard, all elite parents will have some degree of resistance, and resistance will be expected to be higher than from the field collections of elite trees, since the pollen parent as well as the seed parent are resistant (elite trees in the field, by contrast, may be pollinated by susceptible and resistant trees). Controlled pollination from within the seed orchard can increase the frequency of progeny with some resistance to WPBR as well as the overall frequency of genes that confer resistance. Regional seed orchards, i.e., one or more seed orchards within a given seed zone, are considered the most efficient approach to operational production of seeds for direct seeding or for growing seedlings with resistance to WPBR.

3.2.2. Seed zones and plus or seed tree selection

Seeds from any tree within a designated seed zone will generally be adapted to most environments within that seed zone (Vander Mijnsbrugge et al., 2010; Bower et al., 2014). Seed zones represent a larger geographic scale of adaptation than tree provenances or ecotypes (Heslop-Harrison, 1964). The rationale for identifying seed zones is to minimize the loss of planted seedlings or trees from maladaptation. Seed zones also serve as the basis for selecting plus trees for genetic screening. Thus, seeds from elite trees from one location hypothetically can be used to grow and plant seedlings in suitable habitat anywhere within that seed zone. Seed zone designation can be improved and expanded as more genetic information and results from common garden and genomic studies become available and may incorporate distributional changes expected with climate warming.

The range of whitebark pine in the northern Rocky Mountains, Inland West, and Great Basin has been provisionally divided into seed zones based on integrating the distribution of genetic variation and results from common garden studies (Mahalovich and Hipkins, 2011) (Fig. 2A). The range of whitebark pine in Washington and Oregon has also been divided into seed zones which are used in the USFS Region 6 Restoration Program (Aubry et al., 2008) (Fig. 2B, C). These seed zones only generally correspond to whitebark pine ecoregions. Refinement of seed zones, which optimizes local adaptation, awaits advances in physiological genomics for whitebark pine (e.g., Aitken et al., 2008; Wheeler et al., 2015; Lind et al., 2017).

For restoration application, seed zones require identification for all geographic regions within whitebark pine's range. For the Inland Mountain West, at least 100 plus (or a combination of plus and seed) trees were previously recommended per seed zone for resistance screening, and for small or isolated distributions, 50 plus and seed trees (Mahalovich and Dickerson, 2004; Vander Mijnsbrugge et al., 2010). An initial screen of about 100 plus or seed trees from a seed zone would provide an estimate of the frequency of resistance within a given seed zone, which can then be used to project the number of trees needed for screening to meet a target number of confirmed resistant parent trees to use in restoration. Resistance screening must be performed to confirm genetic resistance to WPBR regardless of the infection level within a stand or forest (whether the tree is a plus tree or seed tree), because a healthy tree within an area with high levels of blister rust might be an "escape" tree and not genetically resistant.

Current recommendations are to identify at least 100 elite trees for each seed zone through screening so that restoration plantings capture adequate genetic diversity (e.g., Frankham et al., 2014). The target number of plus trees or seed trees identified for screening will ultimately depend on the frequency of trees (families) found to have relatively higher levels of genetic resistance to WPBR within a seed zone, and this can vary greatly geographically (e.g., Mahalovich et al., 2006; Mahalovich and Hipkins, 2011; Sniezko et al., 2018). For example, in the Pacific Northwest, where the overall average frequency of 'usable' resistance (sensu Hoff et al., 2001; Sniezko et al., 2020) across the range is about 25%, 400 trees or more must be screened to identify 100 or more elite trees. However, in some forests the frequency of resistance will be much higher or lower (Sniezko et al., 2018).

For populations not yet invaded by *C. ribicola*, proactive rust resistance screenings of seed trees will be needed to identify elite trees. Alternatively, elite trees identified from other seed zones that are climatically similar could be used as provisional seed sources. Prioritizing plus tree and seed tree screening for heritable resistance across the range of whitebark pine is integral to restoration efforts. Developing a pool of rust-resistant elite trees in each seed zone is required for restoration actions and could also incorporate modest climate change mitigation. Determining the extent of climate and edaphic adaptation that we can expect of whitebark pine genotypes from a given seed zone might also be useful for climate change mitigation along with increasing WPBR resistance. Mixing resistant genotypes through seedling planting at a given location with those from a seed zone just to the south or from a climate zone projected to be similar to the future climate in a region could be an effective and proactive strategy to build WPBR resistance but also resilience to the impact of climate change.

Stand-level criteria have been developed to provide guidance for plus tree selection for resistance screening, where WPBR is prevalent (Hoff et al., 2001; Mahalovich and Dickerson, 2004; Shoal et al., 2008). The likelihood of finding potentially resistant trees is highest in stands most heavily impacted by WPBR (e.g., high infection rates). In general, selected plus trees will be those relatively free of WPBR in comparison to other trees within the same stand.

Prior to plus tree selection within a given whitebark pine stand, Mahalovich and Dickerson (2004) recommend surveying 100 trees for WPBR symptoms to obtain base-line information on stand infection rate. They recommend that the survey also include the percent trees killed by MPB, and whether recent mortality from WPBR is apparent. In regions

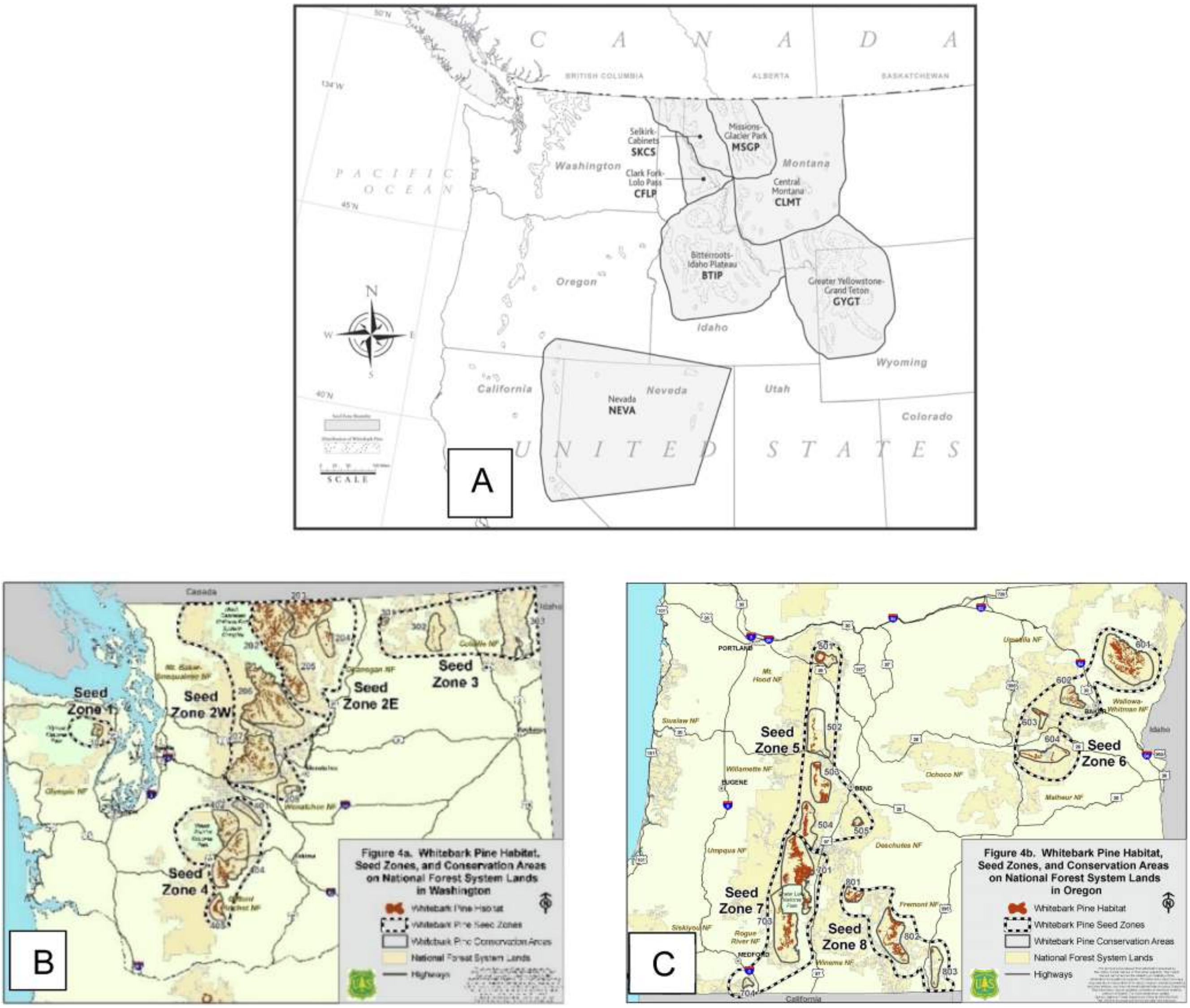

Fig. 2. A. Candidate seed zones identified for whitebark pine in the Inland West and Great Basin (source: Mahalovich and Hipkins, 2011) and B. in Washington and C. in Oregon (source: Aubry et al., 2008).

where WPBR is just invading, these selection criteria must be modified, depending on the prevalence of WPBR infection and mortality (Table 2). In areas with low to little incidence of WPBR, seed tree selection is based solely on optimizing phenotypes for tree health, crown volume, sturdiness for climbing, and cone production.

3.2.3. *Screening for genetic resistance*

Resistance screening for whitebark pine and other high elevation five needle pines currently entails a protocol whereby seedlings grown from seed or plus trees are exposed to high densities of *C. ribicola* spores under controlled conditions (e.g., Sniezko et al., 2011). The seedlings are then tracked over time to determine if they develop blister rust symptoms or show resistance, and if resistance is demonstrated, the specific resistance phenotypes are identified. Resistance mechanisms originally identified include needle shed, short-shoot, and bark reaction (Hoff et al., 1980; Hoff et al., 2001), and resistance mechanisms identified from screening work by Mahalovich et al. (2006, Table 1) include: needle lesion frequency, early stem symptoms, bark reactions, canker tolerance, no spots, needle shed, and short-shoot. The underlying genetic mechanisms and their inheritance are still being investigated (Sniezko and Johnson, unpublished data); but, it is clear that resistance in whitebark and other white pine species is quantitative (Sniezko et al., 2020; Weiss et al., 2020), which strengthens the likelihood of its durability. Resistance screening is currently being conducted at several government facilities in the U.S. and Canada (Sniezko et al., 2011; Murray and Strong, 2021). Common standards and evaluation protocols would enable comparison of resistance traits range-wide. The following protocols provide guidance for standardizing procedures.

Including seeds in each screening trial from the same seed lots that have been previously tested and shown to be fully susceptible to infection by *C. ribicola*, (i.e., susceptible “controls”) enables calibration of inoculation effectiveness among screening trials. Many whitebark pines are highly susceptible, and 100% of progeny from these susceptible trees are expected to become infected during the resistance screening process, if screening conditions are sufficient. Confidence in screening trial results are greater when spore loads are set at a level that achieves 100% infection of known susceptible individuals, which can serve as controls for given inoculation and culture conditions. Thus, adequate seed collections in storage from susceptible individuals are important to use for “calibration” of conditions, i.e, as controls, especially since these trees *in situ* may become scarce over time. In addition, including one or more known resistant (elite tree) controls in testing ensures that the rust spore

Table 2
Basic stand-level criteria to provide guidance for plus and seed tree selection for WPBR resistance screening. Stand-level criteria will vary with the geographic region and prevalence of WPBR infection and mortality. In the Inland Mountain West region, where criteria were first developed, WPBR prevalence is generally high (modified from Mahalovich and Dickerson, 2004). WPBR = white pine blister rust.

Stand-level criteria for areas with high incidence and mortality of WPBR:
• The best plus tree candidates are large with well-developed crowns that support moderate to good pollen and seed cone production. Minimum age varies with elevation and location. High elevation trees a minimum of 50 to 80 years of age may have adequate cone production, whereas low elevation trees may grow faster and meet criteria at earlier ages.
• Plus trees that are easily and safely climbed, with spreading crowns, are most efficiently utilized.
• The plus trees selected should be free of insect-infestation and other diseases.
• In stands with infection levels ranging from 50 to 90%, trees with no more than five cankers are preferred as plus trees.
• Plus trees separated by at least 60–90 m (200–300 feet) avoid pollination by the same trees and diversify genotypes.
• Where blister rust mortality and infection levels are moderate to high, trees that have few cankers and show tolerance to cankers are good plus tree candidates for screening.
• In the case of widely-spaced or isolated trees on the landscape, healthy trees may be “escapes” from infection rather than resistant, where WPBR infection is high.
Stand-level criteria for areas with zero to low (single digit) WPBR infection levels:
• In areas of zero to low infection rates, selection of seed trees is based on phenotypes that reflect tree vigor, since indicators of resistance, such as few cankers or absence of WPBR symptoms, are not applicable under these conditions.
• Desirable characteristics for seed tree selection, given low incidence of WPBR and thus limited infection, include good potential pollen and seed cone production (high crown volume), no symptoms of insect infestation or disease, vigorous growth, and suitability of tree for climbing.

inoculum level is not so high that all levels of resistance are overcome. Inoculum from diversified sources (mixed population of basidiospores, harvested from different populations of susceptible *Ribes* spp., the primary alternate hosts to *C. ribicola*) improves the rigor of screening trials.

Whitebark pine seedlings grown for screening trials are usually inoculated when 2 to 3 years of age and sufficiently developed. Currently, seedling post-inoculum scoring protocols differ according to seed zone or geographic region (e.g., Mahalovich et al., 2006; Sniezko et al., 2008, 2011), but standardization would facilitate comparisons among these areas. Infection symptoms and resistance reactions, however, are expressed in seedlings at different and variable time periods post-inoculation, depending in part on growing conditions.

Field trials, which usually are based on out-planting seedlings from plus trees or seed trees, including susceptible controls, in forested areas with known WPBR hazard, provide further tests of resistance and susceptibility under natural infection conditions (see Cartwright et al., 2022, this issue). Field trials verify the efficacy of the seedling screening trials, which are conducted under artificial conditions, and the durability and stability of resistance (Sniezko et al., 2020; Cartwright et al., 2022, this issue). They test whether the original inoculum source and spore density were adequate and whether the resistance expressed in the artificial inoculation trials is expressed under field conditions. As in the controlled screening trials, inclusion of families known to be fully susceptible to WPBR serve as controls in field trials to test whether seedlings are sufficiently challenged by the pathogen. In many cases, it takes more than a decade before high infection levels are evident in field trials.

Studies comparing living and dead trees from the recent, large-scale MPB outbreak have indicated that certain whitebark pine phenotypes are more resistant to MPB infestation (e.g., Raffa et al., 2017; Kichas et al., 2020). It is yet unknown how selection for genetic resistance to WPBR may affect resistance to MPB attack (but see Holtz and Schoettle, 2018), and in general how selection for certain resistant phenotypes will affect adaptation. When the genetic bases for WPBR and MPB resistant phenotypes are elucidated, potential trade-offs can be assessed, as well as environmental effects. All forest trees evolved under diversifying selection, given an array of pests and pathogens and environments (e.g., Peláez et al., 2020), which is why genetic diversity must be prioritized and maintained in whitebark pine management.

3.2.4. The utility of seed orchards as an operational seed source

The overarching rationale for whitebark pine seed orchards is to facilitate access to seeds with a high likelihood of resistance to WPBR for growing seedlings for operational planting. Once at least 30 elite (resistant) trees are identified for a given seed zone, one or more seed orchards may be developed for shared stakeholder use. A seed orchard is developed at a prepared site by planting enough rootstock to support the target number of trees and then grafting a scion (a shoot or branch) from a selected elite tree to each rootstock, but grafting may also be done in the greenhouse in advance of rootstock planting. The use of rootstock and grafting is generally expected to lead to cone and pollen production at a younger age relative to starting with seedlings. Cost-benefit analyses and tree improvement programs have supported the utility of developing conifer seed orchards with superior phenotypes for commercial seed production (e.g., Li et al., 1999; Wu et al., 2015). The process for developing whitebark pine seed orchards with trees resistant to WPBR was based on the western white pine model, which has also proven to be successful (Fins et al., 2002).

Optimally, a whitebark pine seed orchard will be comprised of a minimum of 30 to 60 unrelated elite trees from within a designated seed zone, representing the diversity of rust-resistance mechanisms identified within the seed zone. Furthermore, trees added to the seed orchard, or new grafts applied over time, will increase genetic diversity. Molecular marker studies of the orchard trees could potentially provide useful information on both the genetic variation represented and genetic limitations relative to natural populations.

The establishment of seed orchards has both pros and cons. The most important anticipated benefits of seed orchards include the improvement of tree progeny through cross-pollination, the availability of scion for developing orchards and other applications, and the decreased cost of harvesting seeds relative to dispersed elite trees. The scion for grafted orchard trees can originate from either the parent trees (backward selection) or progeny selections from resistance screening. Within orchards, genes for resistance can be contributed by both the seed and pollen parents, increasing the strength of resistance to *C. ribicola*, as observed for western white pine (Hoff et al., 1973; 2001). Given that orchard trees are in a single location, they can be more easily protected from insect infestation and diseases as well as from fire than individual trees dispersed across the landscape. Multiple orchards within a seed zone, however, potentially offer redundancy in case of loss of one seed orchard from these hazards. In addition, fertilizer and hormone treatments or other methods to induce seed and pollen cone production have been applied to orchard trees to stimulate tree growth and cone production, rather than depending on natural cone cycles (Li et al., 2021). Although costly to establish, seed orchards become highly cost-effective over time, given that collecting seeds with similar levels of genetic diversity would require visiting many different trees locations within a seed zone (Wu et al., 2015).

The preceding benefits are countered by the concern that placing high value trees within a small area may actually increase the likelihood of pathogen spread, insect infestation, or loss from fire. Other issues may arise: Nascent seed orchards in the Custer-Gallatin National Forest have experienced instances of scion graft incompatibilities and site damage from pocket gophers (*Thomomys* spp., Wied-Neuweid) (C.R. Demastus, unpublished data). Operational cone production will also take two decades or more of tree growth after orchard establishment. Often, only about 20% of orchard trees produce the majority of seeds, which reduces the genetic diversity of progeny, and in some years few to no cones might be produced (R.A. Sniezko, unpublished data). Furthermore, each seed orchard represents a significant cost and commitment for maintenance, management, and protection, not to mention rootstock development and tree maturation time, which delay benefits. Finally, the individual trees within seed orchards optimally reflect the genetic diversity within a seed zone, requiring numerous trees or augmentation over time.

Several seed orchards are in different stages of development in the U. S. and Canada (e.g., Murphy, 2014; Konen, 2014). Because whitebark pine grows slowly and does not produce many cones until at least five or six decades in age, seed orchards are a long-term commitment.

3.3. Seedling production: Cone collections, seed germination, growing and planting seedlings

Procedures used for cone collection and growing seedlings for whitebark pine were developed for operational seedling production but also for growing seedlings for resistance screening (Burr et al., 2001). They may vary somewhat among nursery facilities, but the basic approaches have been in practice now for more than 20 years.

3.3.1. Cone collections, seed germination, and growing seedlings

Within a geographic region, managers collect cones in years of good production, whether cones are collected from seed trees, plus, or elite trees, to make efficient use of field crews and to guarantee sufficient harvest. The frequency of good cone crops varies geographically but may be predicted in advance by first-year conelets (McCaughey and Tomback, 2001). Trees are first climbed in early summer by certified crew members, using standard climbing and safety gear to reach the upper crown, where most cones are produced. The climbers carefully enclose healthy whorls of cones in hardware cloth or, preferably, light screen envelopes (i.e., cages) on each tree while cones are still unripe and developing (Fig. 3) (Burr et al., 2001). Protection prevents cone cutting by squirrels and removal of seeds by Clark's nutcrackers. Trees are climbed again in late August to early September to evaluate the state of seed development through sampling seeds from a few cones and to remove cages and collect the intact cones when ripe (e.g., Burr et al., 2001). For shorter trees or those with cone-producing branches within 2–6 m off the ground, a tree-tong may be used to cage and remove cones (Murray, 2007a). Burr et al. (2001) describe cone treatment and interim storage.

Seed extraction, storage, germination, and seedling growing protocols have been successfully implemented at an operational level for producing thousands of seedlings for planting (e.g., Burr et al., 2001; Kolotelo et al., 2001; Sniezko et al., 2017a; Robb, 2020a,b) (Fig. 3). An effective protocol implemented at Dorena Genetic Resource Center to prepare seeds for germination uses a 30-day warm stratification at 10° C to further embryo development followed by a 110-day cold stratification at 1 or 2° C. Seeds are then placed in an environmentally controlled germinator with day/night temperatures of 19° C/16° C and a 12 hr photoperiod (L. Riley, personal communication). For stored seeds, Bower et al. (2011) were able to germinate seeds non-responsive to this protocol after a second but longer round of cold stratification. Protocols for planting seeds with emerging radicles and for greenhouse production are described by several sources (e.g., Burr et al., 2001; Kolotelo et al., 2001; Robb, 2020b).

3.3.2. Planting seedlings/sowing seeds

Planting seedlings and sowing seeds from resistant seed sources are critical management actions for whitebark pine restoration that spread genetic resistance to WPBR. These efforts spread genes for rust resistance while restoring whitebark pine populations. Only seed sources with high resistance levels are suitable for use, unless the seeds are from an area with known high frequencies of blister rust resistance. Utility of resistance, hence seedling survival, will be improved if plantings are targeted to areas with low to moderate WPBR hazard (Schoettle et al., 2019a).

Operational planting of whitebark pine seedlings has been ongoing for more than two decades. The efficacy of an alternative method, which involves sowing seeds—often called "direct seeding"—has yet to be adequately tested; it has been used in several exploratory projects with mixed outcomes (Schwandt et al., 2007; 2011; DeMastus, 2013; Pansing et al., 2017; Pansing and Tomback, 2019). If effective, this method has the potential to decrease costs relative to seedling planting and decrease logistical constraints associated with access and jurisdictional regulations. However, there remain challenges to large-scale implementation. Losses of high proportions of unprotected caches to rodents remain one of the major drawbacks to direct seeding, given the high cost of seed collection and especially if seeds have resistance to WPBR. Recommendations for planting and direct seeding microsites (Table 3) also include some mitigation for climate change (e.g., Keane et al., 2013; Ireland et al., 2018).

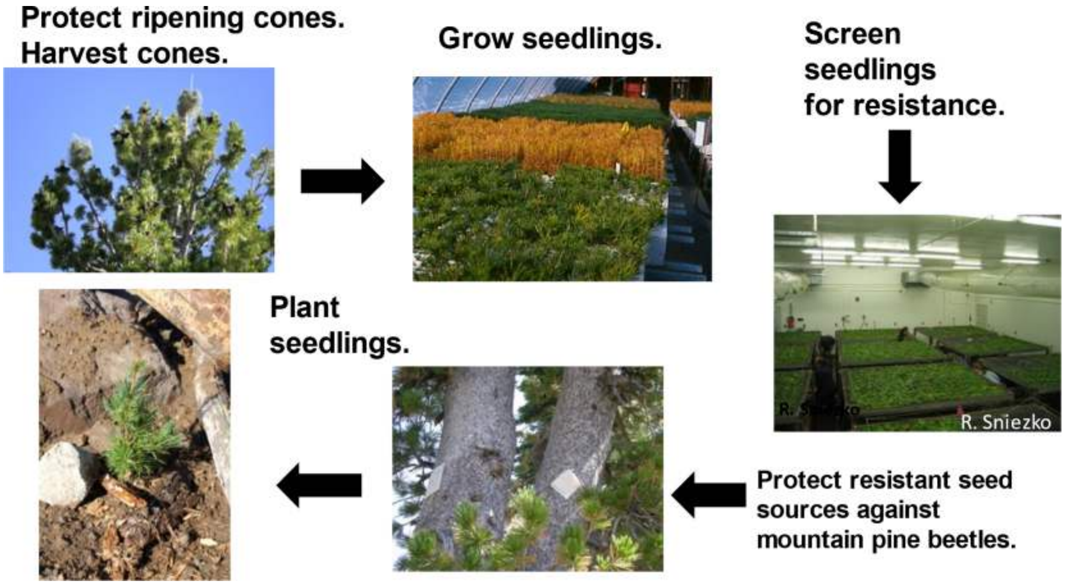

Fig. 3. Steps involved in growing seedlings for screening for genetic rust resistance and operational planting: Cone collecting, growing seedlings, applying blister rust inoculum, protecting plus and elite trees, and planting seedlings in protected microsites. Photo credit, unless otherwise noted: D.F. Tomback.

Table 3
Planting guidelines for whitebark pine seedlings, modified from McCaughey et al. (2009). Many of these guidelines may also apply to microsite choices for direct seeding. B. Preliminary guidelines for whitebark pine direct seeding, modified from Pansing et al. (2017) and Pansing and Tomback (2019). WPBR = white pine blister rust.

A. Planting guidelines for seedlings and for direct seeding.

- Grow and plant seedlings or sow seeds from seed sources that are known to have genetic resistance to WPBR.
- Plant robust seedlings with well-developed root systems.
- Use planting densities of 175–300 seedlings per acre. Planting density may vary geographically and with seed source and expectations of seedling mortality. Consider sowing at higher densities for direct seeding, given the likelihood of seed loss to rodents.
- Plant or sow in competition-free environments, avoiding encroachment by larger or more shade-tolerant conifers.
- Include areas for planting or direct seeding recently burned by wildfire, which provide suitable, competition-free seedbeds.
- Where required, prepare potential planting or seeding sites by using prescribed burning to eliminate vegetation.
- Where feasible, plant or sow in stands with high mortality from MPB to speed up regeneration, take advantage of open conditions.
- Before planting or sowing, wait for bark to slough off trees first in stands with high MPB mortality or plant seedlings away from dead trees, or seedlings may be damaged or covered.
- Avoid dense vegetation, grasses, and beargrass (*Xerophyllum tenax*) in the immediate vicinity of the planted seedling or seed cache. Dense vegetation and these specific plants compete with conifer seedlings.
- Provide shade for seedlings for part of the day on southern and western aspects by using natural objects (rocks, fallen trees, deadfall), but avoid stumps and post-fire snags in areas of known root disease. In most plantings, wood debris can be positioned to provide shade.
- Plant or sow seeds during moist or cooler periods if possible, avoiding summer heat and drought. The most favorable times will vary geographically.
- Plant or sow in areas with lower WPBR hazard (conditions unfavorable to blister rust). It is more cost-effective to avoid planting or sowing in high hazard sites, although this may be necessary to restore areas with high mortality from WPBR.
- Consider inoculation of greenhouse seedling growth medium with ectomycorrhizal (ECM) fungi to improve seedling growth and survival (Cripps and Grimme, 2011). Natural ECM colonization can occur in the field, e.g., is there whitebark pine growing nearby? ECM fungi may not be present in large burns or in areas without whitebark pine for many years.
- For climate change mitigation, select moister aspects and microsites for planting or sowing within the tolerance range of whitebark pine seedlings, but avoid areas of competing vegetation. Northern aspects and cooler slopes may be important for planting at lower latitudes.
- Plant first at the highest elevations within the targeted area or burn for climate change mitigation.
- Consider planting some seedlings in upper subalpine-lower treeline ecotone (just below or transitioning to flagged and krummholz) communities; these do not require seedbed preparation. These areas are important for snow retention and watershed protection and they are where trees are responding to warming effects.
- Consider hedging bets for climate change mitigation by including seeds from seed sources from warmer aspects or from latitudes a few degrees to the south to provide resilience for climate change. Information based on a tolerance analysis would be highly valuable.

B. Guidelines specific to direct seeding.

- Consider direct seeding (seed sowing) as a logistically efficient alternative to planting seedlings in some areas within whitebark pine's range, and especially remote or Wilderness Areas (Schwandt et al., 2011; Pansing et al., 2017).
- Use seeds from elite trees or other seed sources likely to have genetic resistance to WPBR. The limited availability of these seeds may restrict application.
- Consider likely losses to rodent predation with respect to numbers of seeds sown and desired seedling densities. Sowing seeds at lower densities may reduce rodent pilferage.
- Do not scarify or stratify seeds for direct seeding, since they will experience natural stratification conditions.
- Sow seeds, as noted, in sites similar to those recommended for seedlings (above).

3.4. *Protecting seed sources*

Plus trees, elite trees, and seed orchards must be protected from threats. The primary threats are pests and disease—especially MPB—and wildland fire. Elite trees and established seed orchards, must have the highest priority for protection, given that they are the sources of putatively WPBR-resistant planting stock for restoration efforts and represent an investment of resources.

For short-term protection of whitebark pine trees against MPB, options include use of the anti-aggregation pheromone verbenone in one of several forms or preventive insecticides. MPBs naturally produce verbenone to disperse adult beetles away from a fully colonized tree (e.g., Seybold et al., 2006). Verbenone is chemically synthesized and available commercially in slow-release pouches that can be stapled or tacked onto trees (USDA Forest Service, 2011a) and in a wax emulsion matrix applied with a caulking gun (SPLAT^R Verb) (Fettig et al., 2016). Verbenone products require reapplication every year (USDA Forest Service, 2011a). Where there is MPB activity, either verbenone product can be used to treat a stand or individual trees. Verbenone is also available in the form of tiny, inert polymeric flakes that can be aerially applied to pine stands by small aircraft (Gillette et al., 2012); this form would be the most time and cost-efficient for remote whitebark pine stands.

Verbenone does not always protect all treated trees, including whitebark pine, particularly when MPB populations are extremely high (e.g., Kegley and Gibson, 2004; Progar, 2003; Bentz et al., 2005; Kegley et al., 2010). Preventive insecticides, such as carbaryl or pyrethroids such as bifenthrin or permethrin, can be 100% effective in protecting individual trees from MPB, but application is labor intensive because the boles of individual trees must be sprayed thoroughly (USDA Forest Service, 2011b). Carbaryl is effective for two years, but the pyrethroids must be reapplied every year (USDA Forest Service, 2011b). Additional management actions that might reduce the risk of local MPB activity and reduce fire intensity include thinning stands by removing all non-whitebark pines stems 4 in and greater in diameter and even by carefully applying prescribed fire (Keane et al., 2012; Sturdevant et al., 2015; Keane et al., 2020).

Plus trees, elite trees, and seed orchards especially must be protected from wildland fire by incorporating their locations into the agency unit's fire management plan (Keane et al, 2012). If trees are threatened by wildland fire, protective measures such as suppressant foam, wet or dry lining, and foil wraps may be carefully applied to individual trees (e.g., Murray, 2007b). The Wildland Fire Decision Support System (https://wfdss.usgs.gov/wfdss/wfdss_home.shtml) is a fire management tool used by federal agencies and tribal jurisdictions. The WFDSS provides support for fire managers and analysts who make tactical decisions for fire incidents. Spatial data can be entered into a management unit's WFDSS layers for plus and elite whitebark pine trees and high value whitebark pine stands, as well as for stands that could benefit from application of fire.

Murray et al. (2021), working in British Columbia, Canada, found that whitebark pine trees purposefully retained after high elevation logging operations have high mortality over the succeeding five-years, predominantly from wind-throw. They recommend several practices, such as selecting shorter trees for retention and clustering retained trees, to reduce whitebark pine loss. Although the retained trees in clusters were primarily whitebark pine, the results imply that any tree species might protect retained whitebark pine.

3.5. *Reducing competition in successionally advanced communities*

The primary objective of the following restoration treatments is to retain mature, cone-bearing whitebark pine in late-seral communities by reducing competition from encroaching faster-growing, shade-tolerant conifers and thus prolong whitebark pine's ability to persist and produce cones, especially under climate change (e.g., Keane et al., 2021, this issue) or to create openings for natural regeneration. Referring to treatments applied to successionally-advanced whitebark pine stands, Keane and Arno (2001, p. 367) state that "…ecosystem restoration must emphasize the return of ecosystem processes rather than historical stand characteristics to succeed over the long term…"

On productive subalpine forest sites, whitebark pine is a minor to major component of seral communities, which are periodically renewed by wildland fire (e.g., Arno, 1980, 2001; Arno and Hoff, 1990; Tomback et al., 1990; 1993). Over time, whitebark pine trees in these communities are replaced by faster-growing, shade-tolerant species, although a small number of whitebark pine attain sufficient size and survive into late seral stages (Pfister et al., 1977; Campbell and Antos, 2003). Since European settlement, in many regions fire regimes have been altered and return intervals protracted, including regions where successional whitebark pine communities are abundant (Brown et al., 1994; Keane et al., 2002; Van Wagner et al., 2006).

Seral whitebark pine communities are well-represented in the Greater Yellowstone Area and throughout the northern Rocky Mountains of the U.S. and Canada up to about 50° N (Arno, 2001). On localized sites and across more extensive areas, seral communities with relatively frequent fire have been described from the Oregon and Washington Cascades and in west-central Idaho, and eastern Oregon (Arno, 2001; Murray and Siderius, 2018). Seral communities may exist on local sites in the Sierra Nevada Range but are yet undescribed.

The Great Basin Ranges, much of the Sierra Nevada, areas within the Pacific Northwest, coast ranges, and regions north of about 50° N in Canada are dominated by open communities of “climax” or self-replacing whitebark pine at subalpine and treeline elevations. These communities may support pure stands of whitebark pine, or whitebark pine co-dominant with other conifers (e.g., Arno and Hoff, 1990; Tomback and Achuff, 2010). In these regions, whitebark pine grows on steep, rocky slopes, with poor soils or arid climates—conditions unfavorable to competing conifers (Arno and Hoff, 1990; Arno, 2001; Tomback et al., 2016); fire occurs less frequently and is not essential for whitebark pine regeneration. For these communities, prescribed fire and silvicultural treatments are unnecessary to maintain whitebark pine.

Keane and Arno (2001) pioneered the application of silvicultural techniques and prescribed burning to restore successional whitebark pine communities at five experimental restoration sites in west-central Montana from about 1995 to 2002. These sites were monitored pre-treatment and 1 to 5 years post-treatment and have been evaluated with respect to outcome (Keane and Parsons, 2010a,b). These treatments can be further refined with respect to specific site conditions.

3.5.1. *Silvicultural treatments*

The objective of silvicultural treatment is to remove competing, faster-growing conifers in successionally-advanced stands in order to retain cone-producing whitebark pine, encourage whitebark pine regeneration, reduce fire hazard, and/or enhance fuels for prescribed burning. Application of silvicultural treatments may also protect plus or elite whitebark pine trees from wildland fire.

Treatments must be tailored to individual stands. Silvicultural treatments, which encourage natural regeneration, may be particularly useful for proactive restoration efforts aspiring to maintain resilience within communities by ensuring multiple age classes (e.g., Schoettle and Sniezko, 2007; Keane and Schoettle, 2011).

Given that successional whitebark pine stands are widely-distributed throughout much of the U.S. northern and the southern Canadian Rocky Mountains, specific silvicultural treatments have been developed for these regional ecosystems, e.g., Keane and Arno (2001), Keane and Parsons (2010a, b), Keane et al. (2012, p. 73-83), and Keane (2018), but many require further monitoring and evaluation of outcomes to determine long-term efficacy and effects (Maher et al., 2018). Silviculture treatments for other regions may also be useful but require development and testing through adaptive management. Murray et al. (2021) provide guidelines for retaining mature trees in commercial harvests.

Silviculture treatments are most cost-effective when target stands are near roads and on gentle terrain for easier access by crews. Types of treatments vary by objective; they are briefly described below, based on Keane et al. (2017c) and Keane (2018), with recommended modifications for adaptation to climate change in Keane et al. (2021, this issue).

Stand-level thinning: For this treatment, generally all faster-growing conifers are cut at a stand-level scale. Thinning can be followed by prescribed fire to reduce competing understory conifers and clonal regeneration but must be applied cautiously to prevent scorching cone-bearing whitebark pine.

Selection cutting: This treatment is performed at a sub-stand scale, in which groups of competing trees are removed from designated sites, typically over an area of 0.1 to 1.0 ha. The cut is meant to mimic a mixed severity fire. Canopy fuels are removed in these openings, thus decreasing potential for torching and stand-replacing fire. This treatment also reduces overstory competition to facilitate growth of mature whitebark pine trees and promotes natural regeneration through nutcracker caching to diversify whitebark pine age structure.

Tree-level thinning (daylighting): For this cutting, all competing conifers are cleared in a circle around a high value, cone-bearing whitebark pine, such as a plus or elite tree, in a radius greater than the height of the canopy. This treatment approach has not been evaluated for long-term effectiveness, but it reduces the risk of high-severity fire (Sturdevant et al., 2015).

Spot fuels treatments: Here, both canopy and surface fuels are reduced near mature, cone-bearing whitebark pine trees—especially high value trees. Fuel reduction treatments include cutting, clipping, and scattering encroaching understory and overstory.

Girdling: This treatment can rapidly kill competing trees within a whitebark pine stand. Trees must be girdled below the lowest branches to be killed. Leaving dead trees in place, however, may increase fire hazard (Keane, 2018).

Nutcracker openings: This treatment creates circular clearcuts of ca. 10 to 50 ha (~25 to ~ 124 acres) to encourage seed caching by Clark’s nutcrackers and to mimic effects of mixed severity burns or, for the larger openings, stand-replacing burns. These openings may also be burned by prescription to remove all understory and slash and simulate natural burned seedbeds to attract nutcrackers for seed caching.

There are caveats regarding silvicultural thinning treatments, particularly at a stand-scale. To reduce the risk of wildfire and secondary bark beetles from moving from slash into whitebark pine, slash piles can be removed from treatment areas or burned (Keane, 2018). Also, the process of removing understory conifers increases the likelihood of *Ribes* spp. spread, because seeds in the soil seed bank germinate in response to disturbance (Zambino, 2010). Finally, long-term monitoring is needed to determine the efficacy and effects of different treatment types.

3.5.2. *Prescribed fire as a restoration tool and wildland fire management*

Successional whitebark pine communities are periodically renewed by fire. The U.S. and Canadian Rocky Mountain distributions of whitebark pine and some areas in the Pacific Northwest and Intermountain regions historically sustained frequent fire. Whitebark pine communities in the Rocky Mountains usually experienced three types of fire regimes: non-lethal (surface), mixed-severity, and stand-replacing (lethal) (Arno, 1980, 2001; Morgan et al., 1994). Mixed-severity and stand-replacing fire regimes were most common, and typical return intervals ranged from fewer than 50 years to more than 400 years (Arno, 2001).

Wildland fire management involves wildfire suppression, wildland fire use, restoration treatments, and fire mitigation. Keane et al. (2021, this issue) provides additional guidelines integrating wildland fire management and the impacts of climate change.

3.5.2.1. Prescribed fire as a restoration tool: Rocky Mountains. There are pros and cons to the use of prescribed fire as a management tool to reduce competition in successionally advanced whitebark pine forests. Prescribed burning cannot be controlled as tightly as silvicultural techniques, and prescribed fire risks killing mature whitebark pine, including plus and elite trees. Whitebark pine has thin bark which makes it highly susceptible to fire, and there is evidence that even minor bole scorching can kill mature trees (Hood et al., 2008). Prescribed fire, however, can remove competing understory more effectively than silvicultural treatments and can also be applied to remote locations. All three historical fire regimes in whitebark pine communities can be simulated with prescribed fire for specific applications. Low-intensity prescribed fire, for example, simulates non-lethal surface fires and removes conifer seedlings, saplings, and small diameter trees, which reduces canopy density and raises canopy height. Moderate-intensity prescribed fire produces a mixed severity fire, which opens canopies, reduces competition, and creates clearings that can act as nutcracker openings. High-intensity prescribed fire mimics the effects of stand-replacing fire, which kills trees over a large area, removing competition and creating open, burned seedbeds that act as fuel-breaks and provide opportunities for regeneration (Keane, 2018). As with silvicultural treatments, the benefits of prescribed fire as a restoration tool require confirmation through monitoring and evaluation both short and long-term post-fire.

All three prescribed fire treatments may benefit from fuel augmentation prior to burning, which results in a more flexible burning window. Furthermore, patchy prescribed burns may pose less risk to cone-bearing whitebark pine trees (Keane et al., 2020). General prescriptive guidelines for treatments are based on Keane and Parsons (2010 a,b), Keane et al. (2012, p. 73-83), and Keane (2018) for successional whitebark pine communities in the northern Rocky Mountains. Keane (2018, Tables 1 and 3) offers preliminary guidelines for use or avoidance of prescribed fire for the different ecoregions of whitebark pine in the U.S. and Canada (Fig. 1B).

3.5.2.2. Wildland fire management. Wildfires in whitebark pine communities can either be fully suppressed, partially suppressed, or allowed to burn under prescribed conditions (Keane et al., 2012; Keane, 2018). Suppression actions may not always be effective, because many large wildfires are driven by weather; and, under extreme conditions, suppression attempts will not save whitebark pine. Each suppression alternative has specific goals, as described below:

Full suppression: Achievement of full suppression requires that crews extinguish fires while they are still small. The goal is to protect high value mature, cone-producing whitebark pine stands with known plus or elite trees or known high rust resistance, or early successional stands dominated by whitebark pine. The downside is that full suppression will allow the continued accumulation of live and dead biomass, thereby increasing the risk of high severity wildfires.

Partial suppression: This effort requires active suppression during initial stages of wildfire. However, flame retardant or water drops are not used for suppression because of potential harm to high value whitebark pine trees.

Wildland fire use: Wildland fires are most often lightning-ignited wildfires in prescription and allowed to burn under an existing fire plan. They may be used for ecological restoration under prescribed conditions.

Stand-replacing, uncontrolled wildfires may also benefit whitebark pine communities that are experiencing advancing succession and poor health conditions. They create opportunities for planting rust-resistant seedlings as well as openings and seedbeds favorable to natural regeneration. Natural regeneration is useful where local WPBR resistance is sufficient, a process that supports proactive restoration.

The potential for stand-replacing wildfire requires a plan to protect high value whitebark pine trees or stands. Their precise locations must be available to managers, especially in national forests. As discussed above under Protecting Seed Sources (section 3.4), managers can incorporate spatial data for high value whitebark pine trees and stands into an agency unit or tribal fire management plan or use the Wildland Fire Decision Support System.

3.6. Proactive intervention approaches

In forest communities where *C. ribicola* is at low levels or not yet invaded, the implementation of several management actions is proposed to increase whitebark pine resilience to anticipated future infection and increasing levels of infection (Samman et al., 2003; Schoettle and Sniezko, 2007; Schoettle et al., 2019a). The proactive approach is focused on preparing the landscape through silvicultural treatments (e.g., increasing age class diversity, planting with WPBR-resistant seedlings) and protection treatments (i.e., protection against MPB and fire) before or in the early stages of *C. ribicola* invasion to facilitate an increase in the frequency of genetic resistance to WPBR and reduce future loss of ecosystem function from *C. ribicola* (e.g., Proactive Strategy, Schoettle et al., 2019b). Proactive management is an especially suitable option for whitebark pine in the Basin and Range, Klamath Mountains, and Sierras ecoregions, but also at its northern limits along the Canadian Coastal Ranges in British Columbia and in the Rocky Mountains (e.g., Goeking and Izlar, 2018; Shepherd et al., 2018; Nesmith et al., 2019; Schoettle et al., 2022, this issue) (Fig. 1B).

Proactive management actions have been developed for other five-needle white pine species (Schoettle et al., 2011; Schoettle et al., 2019b) but will require modification for application to whitebark pine ecosystems. The goals include: (1) increase population resilience to *C. ribicola* by planting resistant seedlings in recent burns and canopy openings created by MPB mortality or other disturbances; (2) implement silvicultural treatments to promote natural regeneration to diversify population age class structure and provide young cohorts for rapid selection by WPBR upon invasion; (3) implement silvicultural treatments to reduce competition to maintain cone-producing trees within a stand; and, (4) protect trees against MPB and fire to maintain genetic diversity and a viable population size, which will also maintain ecosystem services and resilience to disturbance during future naturalization of *C. ribicola* (Schoettle and Sniezko, 2007). Resilience with respect to climate change may also be developed with restoration projects focused on stands and sites where whitebark pine will be retained or will inhabit in the near future (Keane et al., 2021, this issue) (Table 4).

All ten management actions in Table 1 that incorporate the four basic principles (conserve genetic diversity, promote rust resistance, save seed sources, and employ restoration treatments) can be incorporated into a management plan for proactive conservation. The timing and application of the implementation of these actions, however, are different for proactive management (see Table 2). For example, the collection of seeds for WPBR resistance screening begins prior to, or early in, the rust invasion when *C. ribicola* infection and WPBR-caused tree mortality are low or absent; therefore, the selection of seed trees is not based on field

Table 4

Proactive restoration actions to develop whitebark pine population resiliency for regions or areas where *Cronartium ribicola* either has not yet invaded or WPBR is at low levels. These actions are based on the guiding principles, conservation actions, and restoration treatments for whitebark pine described in Table 1 and modified from Schoettle and Sniezko (2007) and Keane et al. (2012). WPBR = white pine blister rust.

- Healthy seed trees are to be selected for resistance screening, and the distribution of resistance to WPBR on the landscape determined. Where resistance levels are high, they can be utilized by facilitating natural regeneration.
- Individual-tree seed collections are useful for archiving genetic diversity. After genetic resistance screening testing, additional seed collections from known susceptible trees are valuable to serve as controls for future resistance and field trials. Extra seeds from resistant trees can be used for planting or direct seeding projects.
- Climate change mitigation can be incorporated into planting plans by ensuring high levels of genetic diversity are present.
- Removal of competing vegetation by prescribed fire or silvicultural thinning will reduce successional processes and encourage natural regeneration, especially in areas where genetic resistance to WPBR is highest.
- Planting resistant seedlings or direct seeding under good growing conditions will enhance the frequency of natural genetic resistance and provide resilience against WPBR, diversify age structure, and help maintain a viable population size.
- Planting plans optimally include appropriate sites that also provide some mitigation for climate change.
- Ideally, landscape-scale forest management will reduce MPB risk. By managing other hosts, MPB impacts on whitebark pine may be reduced. Treatments at a stand level, such as daylighting or thinning, may increase resilience to MPB.

phenotypes that may indicate putative resistance to WPBR (i.e., technically they are not “plus trees”; see Section 3.2.1). Instead, these seed trees will be randomly sampled with respect to WPBR resistance traits, which enables estimates of natural (unselected) frequencies within a population and provides guidance for proactive management decisions (Schoettle et al., 2012; 2014; 2019a, 2019b). For example, if genetic resistance is relatively high within a population, treatments to protect cone-bearing trees and to promote natural regeneration to increase population size and diversify the age class structure may build resilience. If the frequency is low, planting WPBR-resistant seedlings to increase population size and genetic resistance is an appropriate strategy (Schoettle et al., 2019a). Furthermore, timely seed collections potentially capture the full genetic diversity of these relatively healthy populations, including rare alleles that may be lost from WPBR-caused mortality (Kim et al., 2003). These and additional proactive practices are currently being implemented for other high elevation five-needle white pines (e.g., Schoettle et al., 2013, 2019b; Schoettle and Coop, 2017; Waring et al., 2020) and can be utilized in the remaining healthy whitebark pine populations as *C. ribicola* continues to spread.

3.7. Health and stand condition status and trends: Surveys and monitoring

One-time surveys or the construction of plot networks for monitoring (repeated surveys over time) are fundamental to determining whitebark pine stand health conditions and thus which conservation or restoration actions are indicated. All management actions outlined in Table 1, but especially under heading 2, *Assess condition* and *Plan activities*, depend on knowing the health status of whitebark pine stands. One-time surveys have been conducted in many areas, and permanent monitoring plots and networks have been implemented in multiple regions. Repeated monitoring entails obtaining geolocations of plot ends, marking plots, and tagging trees for accurate remeasurement (Tomback et al., 2005). Both one-time surveys and remeasurement of plot networks have provided essential information on whitebark pine health status. Examples of permanent plot networks include those established by Parks Canada (Smith et al., 2008, 2013; Shepherd et al., 2018), British Columbia (Murray and Moody, in press), the Greater Yellowstone Whitebark Pine Monitoring Working Group (Shanahan et al. 2016; Greater Yellowstone Whitebark Pine Monitoring Working Group, 2011, 2016), Region 6 of the U.S. Forest Service (A.D. Bower, personal communication), and the National Park Service for Sierra Nevada parks (Nesmith et al., 2019; Dudney et al., 2020).

One of the first long-term monitoring protocols was developed by Tomback et al. (2005) in the attempt to standardize whitebark pine health surveys. This protocol was subsequently modified for use in establishing plot networks, e.g., in the Canadian Rockies by Parks Canada (Smith et al., 2008) and in the Greater Yellowstone Ecosystem (Greater Yellowstone Whitebark Pine Monitoring Working Group, 2011). The expense and effort in developing monitoring networks and continued monitoring over time can only be justified if the data gathered are used for decision-making, such as triggering conservation actions or development and implementation of a restoration plan, especially as whitebark pine health status declines.

Appropriate sampling design is extremely important for statistical analysis and inference. Consultation with an expert in statistics or in inventory and monitoring will ensure that sampling protocols within an administrative unit or region are designed appropriately. Random sampling, incorporating elevation and aspect, that is constrained by access or safety considerations is the most defensible design approach. Plot or transect-based protocols with tagged trees are most effective for long-term monitoring efforts (e.g., Greater Yellowstone Whitebark Pine Monitoring Working Group, 2011) or the use of a random point-based protocol for rapid one-time surveys. In stands or areas currently with little or no WPBR, we recommend that the sampling frame (i.e., the larger area from which samples are drawn) include areas of projected high risk, such as near streams, lakes, on northerly slope faces, or in locations with higher humidity, for early detection of infection (e.g., Van Arsdel, 1972; Smith-McKenna et al., 2013; Cleaver et al., 2017; Thoma et al., 2019).

Aside from basic skill sets involving navigation, setting up plots, and taking tree diameters, as well as outdoors safety, those working on surveys must know the forest trees, forest health symptoms, and conifer seedlings by species. Identification of the variable symptoms of WPBR infection and MPB infestation require training and experience (Hoff, 1992; Hunt and Meagher, 1992; Gibson et al., 2009). Good binoculars (preferably 10 x) are essential for examining tree crowns for WPBR cankers (Tomback et al, 2005). Sporulating cankers confirm active WPBR infection, but three of five symptoms co-occurring on a tree also signal infection: resin weeping, branch flagging, rodent bark stripping, roughened bark, and branch or stem swelling (Hoff, 1992; Hunt and Meagher, 1992; Tomback et al., 2005; Greater Yellowstone Whitebark Pine Monitoring Working Group, 2011).

In addition, periodic examination of plus trees and especially elite trees for blister rust infection may detect changes in rust virulence or intensity. Since elite trees have been rated based on resistance in their progeny, they serve as sentinels that can signal major increases in local blister rust spore loads if they become infected (Sniezko and Koch, 2017).

4. Monitoring and adaptive management for restoration projects

4.1. Integrating monitoring into project planning and management

Whitebark pine restoration remains, to a large extent, experimental, and practitioners are still exploring the methods to achieve desired conditions. In particular, the long-term benefits of prescribed burning and silvicultural treatments require monitoring and evaluation; to date, variable outcomes have been reported (e.g., Maher et al., 2018). Consequently, monitoring project success and applying outcomes to improve future project implementation are essential to the restoration process (Gann et al., 2019). A monitoring plan must be developed in concert with restoration project planning. Furthermore, assessment of the effectiveness of a restoration project requires clear, measurable management objectives that are identified in the project planning phase. Project objectives need to include measurable descriptions of what the treatment is intended to accomplish, such as the specific target (e.g., basal area of competing conifers), the amount and direction of change (e.g., 40% reduction), and timeframe (e.g., 5 years) in which objectives are to be met (Elzinga et al., 1998). If project objectives are developed without addressing how the project will be monitored, project success may not be verifiable.

Designing the monitoring plan at the time of project development ensures that any required baseline or reference data can be collected in advance of treatment implementation. Determining whether objectives have been met may require pre-treatment baseline data from the project area and sometimes from control areas (Osenberg et al., 2006). *Control areas* are in proximity and similar in condition to treated areas. Assessment of objectives also may require data from *reference areas*, which are areas with attributes that can be used as benchmarks for success. Additionally, assessing treatment effects sometimes requires information about treatment implementation, such as fire severity or basal area removed, that can only be collected during and immediately after treatment. If the monitoring objectives are not developed until after treatments are implemented, the opportunity to collect required data will be lost.

Finally, designing the monitoring program during project development ensures that time and resources are adequate to maximize learning from the treatment and monitoring effort. For example, monitoring efforts must include the time and cost for data management and analysis, which are essential for determining whether the restoration treatment met objectives or requires supplemental work or a different strategy. This evaluation process is integral to the use of adaptive management to ensure that goals are met for the restoration of whitebark pine.

In summary, without adequate resources, data may be collected but never analyzed or used to understand the outcome of treatment, and thus not used to improve future restoration projects for whitebark pine.

4.2. Guiding principles for monitoring

There are three general categories of monitoring that are relevant to the restoration of whitebark pine (Larson et al., 2013). Most restoration treatments have components that require all three approaches to monitoring.

Implementation monitoring: Did the treatment go as planned? Implementation monitoring requires collecting data during and immediately after the treatments are deployed related to the treatment itself, such as flame length, tree mortality, crown scorch, etc., or how many seedlings were planted per acre (hectare), and what were the subsequent temperature and moisture conditions?

Efficacy monitoring: Were the project objectives met? Approaches to efficacy monitoring depend on the monitoring question. (1) If the question is *whether a particular performance condition has been met* (e.g., specific basal area target for mature whitebark pine), data can be collected *after* treatment. Here, the comparison is condition *after* treatment with respect to the stated performance variables. (2) If the question is *whether the site has been restored* with respect to treatment objectives, best practice is to sample and compare treated areas after treatment with a set of reference areas (Gann et al., 2019). (3) If the question concerns *whether change has occurred after treatment and how much change*, monitoring requires sampling the treated sites *both before and after treatment* (Osenberg et al., 2006). Efficacy monitoring does not address whether the treatments themselves affected site conditions (i.e., specific causal effects of the treatment).

Effects monitoring: What were the effects of the treatments that were implemented, including unintended consequences (both positive and negative)? The only way to determine if and how much a treatment actually altered stand conditions (i.e., had a causal effect) is to measure key variables in both treated and control sites both before and after treatment (Osenberg et al., 2006). Although this type of monitoring is the most intensive in terms of data needs, it helps avoid confounding treatment effects, such as variation in fuels, with environmental variation, which may include spatial and temporal variation such as the influence of topography, recent precipitation, or differences in tree or understory density.

Appropriate timeframes must be selected for monitoring and assessing outcomes. Several examples of key points to include in a monitoring protocol for restoration treatments and conservation actions are presented in Table 5.

4.3. Failing to meet objectives

If efficacy and effects monitoring reveal that project objectives were not met, managers must first determine from implementation monitoring whether the treatment was applied correctly. If the treatment was applied correctly and objectives were not met, managers have two choices: (1) reapply the treatment but modify it in a way likely to achieve project objectives (e.g., more severe fire), or (2) determine whether a different treatment may be indicated to achieve project objectives. This evaluation and revised approach comprise the adaptive management component of restoration treatments.

Thus, well-designed monitoring is essential not only to determine whether project objectives were met, partly met, or not met, but also to provide clarity as to the reason. This information enables managers to improve treatments and align them better to specific community characteristics.

Table 5

Key points to consider in the design of monitoring protocols for several important restoration treatments. These guidelines may be tailored to fit the goals of each project. For all restoration treatments and conservation actions, if objectives are not met, then managers must first determine from implementation monitoring whether the treatment was applied correctly. If treatment was applied correctly and objectives were not met, managers have two choices: 1) Reapply the treatment but modify it in a way likely to achieve project objectives (e.g., more severe fire), or 2) determine whether a different treatment approach may be indicated to achieve project objectives. This evaluation comprises the *adaptive management* component of restoration treatments.

A. Planting seedlings/sowing seeds: determine surviving seedling density.
- Sampling: 1 yr, 5 yr, 10 yr.
- Random points with plots established.
- Plot type and size for density measurements.
- Stratification of random points in planting area by aspect, soils, and other habitat conditions.
- Sample across the entire restoration planting area.
- Generate sample sizes.

B. Silvicultural thinning and daylighting: reducing encroachment (competition) on whitebark pine.
- Sampling: 3 yr, 5 yr, 10 yr
- Area treated or daylighting replicates.
- Pre-thinning sampling for baseline; use random points to generate plot locations.
- Random points for thinning over large areas: control and treated areas.
- Select points from within the entire treated area.
- For selected daylighting, sampling within a subset of treated areas.
- Thinning or daylighting: plots stratified by aspect, forest variation.
- Generate sample sizes.

C. Prescribed burning: creating burned seedbed promoting whitebark pine regeneration; reducing competition; renewing successional processes for whitebark pine establishment.
- Identify primary goals.
- Sampling: 3 yr, 5 yr, 10 yr
- Pre-burn sampling for baseline composition.
- Random points for sampling.
- Stratify by burn severity, topography, pre-burn forest composition
- If comparable pre-burn forest, generate control plots in unburned control as well as treatment plots.

D. Plus or seed tree selection for resistance screening and adaptive management.
- Each seed zone needs a target number of plus or seed trees (e.g., 100) for the purpose of identifying rust-resistant individuals through screening and for determining the prevalence of genetic resistance. For a given seed zone, determine the starting number of plus or seed trees.
- Decide on a target number of elite trees, such as 100 genetically resistant whitebark pine determined through screening, for restoration planting and direct seeding that represents reasonable genetic diversity. (See text for discussion).
- Of the plus or seed trees identified and then screened within a seed zone, determine how many have progeny that show relatively moderate to high genetic resistance and could be considered elite trees for cone harvesting and orchard development.
- If there are fewer than 100 elite trees that come from screening, additional plus or seed trees need to be identified and screened.
- Providing new elite trees as seed sources over time for restoration and building resilience increases genetic representation, which is important for adaptation to changing environmental conditions. Forestry genetics experts are an excellent resource for consultation and guidance.

5. Current and future whitebark pine restoration: The restoration imperative

The management and conservation actions reviewed in this paper represent a varied arsenal of tools and approaches developed over time to conserve and restore whitebark pine. The main challenge is to fund and mobilize timely implementation of proactive and active restoration and conservation actions across the range of whitebark pine at a scale that will build resilience into relatively healthy populations and eventually restore functional ecosystems in rapidly declining populations. If whitebark pine is listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service, 2020), this will provide further impetus for organized agency response. The U.S. Fish and Wildlife Service listing proposal itself [Proposed Rule Issued Under Section 4(d) of the Act] recognizes restoration treatments described here as required for recovery of the species.

Given the challenge of a vast U.S. distribution, the interagency National Whitebark Pine Restoration Plan identifies 20 to 30% of the U.S. whitebark pine range to be prioritized for restoration across federal and tribal administrative units (Tomback and Sprague, 2022, this volume). The plan can facilitate acquiring the resources for restoration through federal agency and tribal government partnerships with non-profit organizations, corporate donors, and private individuals. This restoration plan, once implemented, will take a minimum of 15 years to accomplish, requiring commitment of all partners.

The major threats to whitebark pine require integrated management approaches and the harnessing of new technologies over time. For example, during the last 20–25 years we experienced an outbreak of bark beetles across much of the American and Canadian West that led to widespread mortality within many conifer species (e.g., Logan et al., 2003; Raffa et al., 2008). This threat fostered the development of ways to reduce beetle-caused mortality in high value trees and protect accessible whitebark pine stands. However, as important conifer hosts for bark beetles regenerate during this century, and if forests are not proactively managed to reduce host homogeneity and diversify stand age, we are likely to see a resurgence of outbreaks in several decades, given inciting factors such as warming minimum temperatures and drought, as well as renewed concerns about watershed-scale losses of cone-bearing trees (Negrón and Huckaby, 2020).

C. ribicola represents the ultimate threat to whitebark pine and other western five-needle white pine species, especially as it spreads to the remaining uninfected areas across whitebark pine's range and intensifies in previously infected populations (e.g., Thoma et al., 2019; Dudney et al., 2020). Fortunately, many populations of whitebark pine have WPBR-resistance levels sufficient to support restoration efforts (Mahalovich et al., 2006; Sniezko et al., 2008, 2018). Although whitebark pine is considered highly susceptible to WPBR, the species appears to have quantitative resistance, which should be more durable than the major gene resistance found in several other white pine species. In addition, trees with relatively high levels of resistance have been found in the Cascades of Washington and Oregon and in the Inland West (Mahalovich et al., 2006; Mahalovich and Hipkins, 2011 (Table 1); Sniezko et al., 2018). Testing these resistant seedlots under field conditions, as WPBR infection prevalence increases, will verify their utility.

Building genetic resistance into populations is the highest priority among restoration actions, including those populations where blister rust infection levels are currently low (Aubry et al., 2008; Keane and Schoettle, 2011). A whitebark pine genomics initiative currently in progress has the potential to expedite the identification of resistance genotypes in the field and identify appropriate genotypes for planting under different environmental conditions, including drought and warm temperatures (Lind et al., 2017; Sniezko and Liu, 2022, this issue). Field application is developing, but currently, traditional screening processes are the only reliable means of identifying resistant seed sources for restoration. The utility of traditional screening (e.g., Sniezko et al., 2011; Murray and Strong, 2021) will remain important for validating novel genomic techniques, and field plantings will require monitoring to examine durability of resistance (Telford et al., 2014; Sniezko et al., 2020). These screening methods are also robust enough to accomplish the goal of finding enough resistant parents across the U.S. range; but, genomic and other biotechnological advances may help us to achieve this faster and at lower cost and reveal the underlying genetic basis of resistance.

Climate change has multiple ramifications for whitebark pine management. For example, a major complication to whitebark pine management has been shifts in fire regime to larger and more severe fires, as climate warming has increased temperatures and altered snowpack and timing of snowmelt, creating prolonged periods of summer and fall drought (Westerling et al., 2011; Cansler and McKenzie, 2014). These conditions create new uncertainties in all forest types from lower elevation to treeline with respect to regeneration timeframes and alternative vegetation types, and for whitebark pine, whether areal extent will be diminished (Enright et al., 2015; Pansing et al., 2020). Where possible, repeat sampling of permanent plots (e.g., Amberson et al., 2018) may help reveal long-term trends in stand dynamics. The stability of WPBR resistance under different environments and a changing climate will also require monitoring (Sniezko et al., 2020).

Other climate warming implications concern management strategies to accommodate changes in distribution of whitebark pine on local landscapes (McKenney et al., 2007; Chang et al., 2014; Keane et al., 2017a,b; Maher et al., 2020). For example, restoration treatments can be targeted to refugia or topography where whitebark pine is predicted to persist (Keane et al., 2013; Landguth et al., 2017; Ireland et al., 2018; Keane et al., 2021, this issue). Distributional or biophysical modelling of whitebark pine under various climate scenarios could inform restoration priorities and practices.

In decades to come, new technologies will provide new restoration tools and applications to make restoration projects more cost-effective. Meanwhile, the challenge is to make significant progress in building resilience to WPBR, managing MPB outbreaks, and integrating restoration and climate change. The future of whitebark pine and the diverse communities that it supports are at stake.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

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