

GENETIC RESISTANCE TO WHITE PINE BLISTER RUST IS KEY BUT HOW IT IS MANAGED WILL DETERMINE THE FUTURE OF HIGH ELEVATION FIVE-NEEDLE PINES

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The North American high elevation five-needle white pines (Figure 1) define the forest-alpine ecotone in many mountain systems and provide watershed protection and wildlife habitat. Climate change is projected to be rapid and heightened in these same habitats, highlighting the importance of genetic diversity and adaptive capacity of the species that occupy them (Millar et al. 2007). The five-needle pines are also being challenged by an invasive fungal pathogen, *Cronartium ribicola*, that was introduced to North America in the early 1900s and causes the lethal disease white pine blister rust (WPBR) on five-needle white pines (subgenus *Strobus*) (Figure 2). All the high elevation five-needle white pines of North America are susceptible to *C. ribicola*. The disease spread rapidly through host ranges in the moist forests of the northwest and east and continues to spread, though more slowly, into the drier habitats of the southern Rockies, Great Basin, and southwest. WPBR has killed many five-needle white pines in the north, though wasn't detected in Colorado until the late 1990s and has yet to be found on trees in Utah or most of Great Basin (see map in Jacobi et al. 2018). As the pathogen continues to spread and the disease intensifies, the populations currently less affected may too follow the same trajectory as those to the north if effective management intervention is not pursued.



Figure 1: The high elevation five-needle pines. Clockwise from the upper left: Great Basin bristlecone pine (*Pinus longaeva*), Rocky Mountain bristlecone pine (*P. aristata*), foxtail pine (*P. balfouriana*, photo: Wikipedia), whitebark pine (*P. albicaulis*), southwestern white pine (*P. strobiformis*), and limber pine (*P. flexilis*, photo: CT Holtz). Photos by author unless otherwise noted.

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Figure 2: *Cronartium ribicola* fruiting on a limber pine branch and the bole of a Rocky Mountain bristlecone pine tree.

How do we prioritize limited management resources across these remote and harsh landscapes for the greatest benefit to the five-needle pine species and likelihood of sustaining or restoring ecosystem services into the future? Traditionally, management is focused in the crisis areas, those that have the highest mortality or impact. However, if only crisis areas receive attention, the currently healthy five-needle pine ecosystems will progressively degrade as the pathogen continues to spread. Also, the crisis-centric management approach neglects that management options are often not equally effective under different forest conditions, and successful restoration is less likely in severely impacted areas. Thus, to manage the high elevation white pine species for future persistence and health, one needs to look beyond the crisis areas and across the full spectrum of ecological conditions. Therefore, both Proactive and Restoration Strategies have been developed for the high elevation five-needle pines (Figure 3). Both have the same long-term management goal of sustaining, restoring, and promoting self-sustaining pine populations in the presence of WPBR and other stresses to support ecosystems processes and services into the future (e.g. Schoettle & Snieszko 2007, Keane & Schoettle 2011, Keane et al. 2012, Schoettle et al. 2019b). The opportunities and timing of interventions to achieve this goal are however different. The Proactive Strategy approach focuses on augmenting natural processes in healthy pine populations to increase forest resilience to mitigate WPBR impacts upon invasion such that ecosystem function and services are sustained throughout the naturalization process of the rust. The approach of the Restoration Strategy is to restore the already impacted populations and impaired ecosystems to re-establish natural processes and ecosystems services.

Fortunately, the five-needle pines have some genetic resistance to *C. ribicola* even though they lack a shared evolutionary history with the pathogen. Although the frequency of resistance is very low, it provides the genetic variation on the landscape on which natural selection can operate. Both complete resistance (R

gene, qualitative resistance) and partial resistance (slow rusting, quantitative resistance) types exist in the North American five-needle pines, though not all mechanisms appear to be present in all species. Characterizing and screening for resistance to WPBR in the high elevation five-needle pines began with inclusion of these species in cross species comparison in the mid-1900s and have been a focus since the mid-1990s (see summary by King et al. 2010). The screening process includes growing individual tree seedling families for 6-18 months, exposing them to basidiospores of *C. ribicola* under controlled conditions suitable for spore germination and tree infection, and assessing disease development and resistance phenotypes for 4-6 years post-inoculation. Seedlings with resistance can be planted in gardens or used for scion to generate grafted material for clone banks. In addition, the performance of the progeny can be used to infer the resistance of the seed tree, and that seed tree can be used as scion for grafted material and as a seed source for restoration plantings. If the seed trees are in stands that are not heavily impacted, the baseline genetic frequency of the resistance to WPBR in the sampled population can also be inferred and used in management decisions (Kinloch 1992, Schoettle et al. 2014, 2019a). Identification of resistance in individuals and families may be possible with molecular tools, offering the potential for marker assisted selection (MAS) (e.g. Liu et al. 2016, 2019). The investigations into disease resistance have provided evidence that all the five-needles pines are susceptible to WPBR as well as (1) demonstrating that each species has at least some heritable genetic resistance, (2) seed trees with resistance can be identified to provide seed for restoration plantings or incorporation into breeding programs, and (3) baseline frequency of some genetic resistance traits at the population scale can be estimated for use in management decisions.

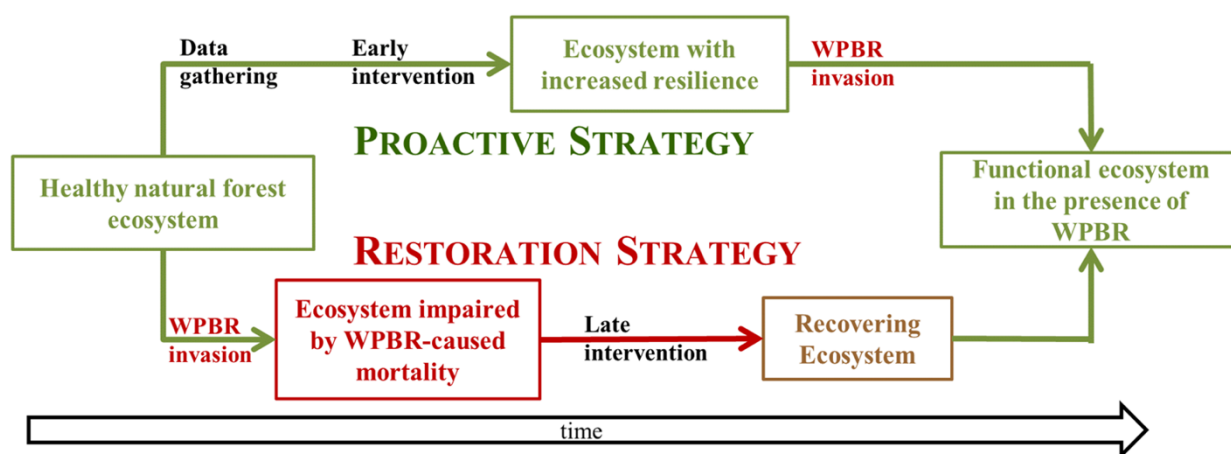


Figure 3: A schematic of pathways for facilitating sustainable natural forest ecosystems in the presence of a nonnative invasive species.

Deployment strategies to increase the frequency of genetic resistance in natural forests (as opposed to plantation forests) using regeneration management were not well developed, hence the regeneration for resilience (R4R) framework was advanced to provide a decision structure to prioritize limited resources and utilize natural and artificial regeneration management to offer the best likelihood of success in positioning stands and landscapes to support multi-generational self-sustaining pine populations in the presence of WPBR (Schoettle et al. 2019a). The complexity of natural ecosystems makes mitigating disease impacts more difficult than in managed forests. Sustaining natural forest resilience in the presence of an invasive species requires maintenance of the host population's recovery and adaptive capacity on a landscape spatial and multi-generational temporal scale. Regeneration management, whether it be planting genetically resistant seedling stock, maintaining and augmenting the size of host species populations, or generating a diverse mosaic of stand ages across a landscape, can foster forest adaptation and mitigate

impacts caused by invasive species such as *C. ribicola*. Natural regeneration offsets mortality and is therefore a stabilizing force in forests. Regeneration also provides the individuals and genetic combinations to support the dynamic natural selection for genetic resistance and other traits important for long-term adaptation in a changing climate.

Positioning forests for accelerated adaptation to new conditions while sustaining viable population sizes will promote resilience (Schoettle & Snieszko 2007, Keane & Schoettle 2011). Therefore, the management approach must incorporate a long-term and evolutionary perspective which also incorporates adaptation to climate change. Unfortunately for the high elevation five-needle pines, generation time is very long, and the stressors directly affect all nodes of the regeneration cycle (Figure 4). The high elevation five-needle pines are not well equipped for rapid adaptation to novel stresses such as those imposed by the introduction of *C. ribicola* in a changing climate. Reducing the effect of disease on survival and fecundity by increasing heritable disease resistance is essential to sustaining many of these populations and ecosystems services. Numerous trials are underway to discern geographic patterns of genetic WPBR resistance to identify parent trees for seed collections and populations for protection. Ultimately, an increase in the frequencies of resistance in populations over the landscape will help establish a new equilibrium from which pine species and associated ecosystems will have the best opportunity to exist and function in the presence of the permanent residence of *C. ribicola*.

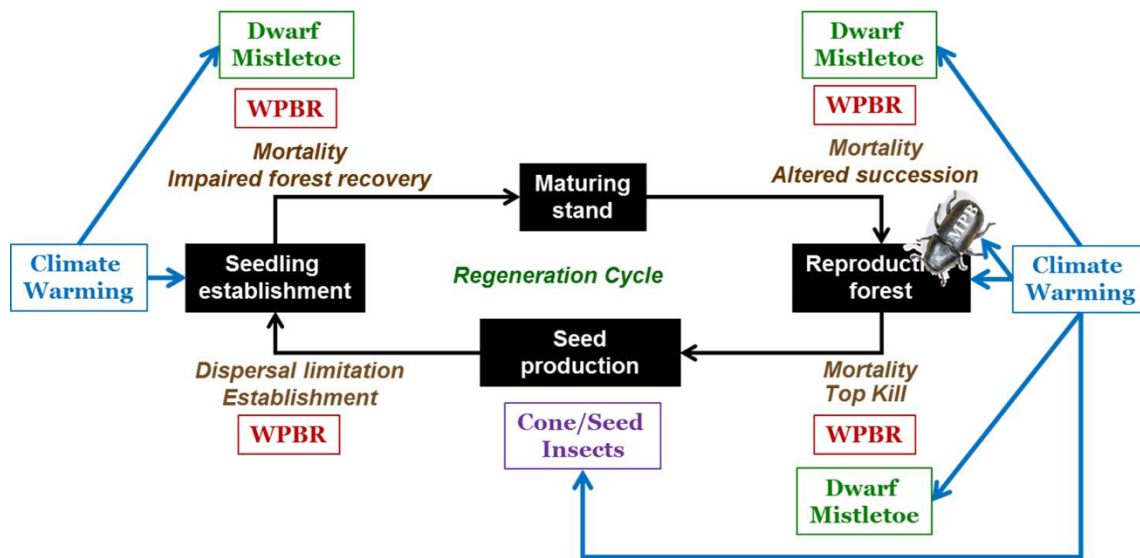


Figure 4: High elevation five-needle pine regeneration cycle and damage agents (from Schoettle et al. 2019b). White pine blister rust (WPBR) affects the regeneration cycle at all points (brown text), while mountain pine beetle (MPB) only impacts larger mature trees, and cone and seed insects only impact seed production. Dwarf mistletoe can infect trees of all ages. Climate change may directly impact insect populations, seedling establishment, and tree growth and may indirectly affect other interactions within the cycle.

Ecological condition and context determine the likelihood of success of management interventions to mitigate impacts of WPBR. In populations heavily impacted by WPBR, the remaining seed trees may be too few to support natural regeneration even with management intervention. Likewise, rust pressure can be so high that it will overcome the expression of WPBR-resistance, reducing the efficacy of artificial regeneration with resistant seedling stock as well. Management has a low probability of successfully rebuilding a

population under these conditions; triaging these areas in favor of managing areas with less rust pressure may be a better investment. In threatened but currently healthy populations, interventions to increase natural regeneration can help increase population size while early planting of seedling stock with disease resistance traits will enable them to begin to mature and offset mortality of the reproductive overstory trees as the disease intensifies over time. The R4R framework encourages looking beyond the crisis areas for other opportunities to conserve the species and prevent population extirpation.

These interventions entail integrating genetic resistance information into an ecological context to prioritize and inform regeneration interventions to restore and sustain healthy landscapes. The R4R decision framework highlights opportunities across stand conditions and discourages management in areas where management has a low probability of success (Schoettle et al. 2019a). The framework has been applied to prioritize management within target regions and can also be applied across a full species range to prioritize actions by probability of success to prevent species extinction. The framework was used in the development of the Proactive Limber Pine Conservation Strategy in the Greater Rocky Mountain National Park Area (Schoettle et al. 2015, 2019b) and prioritizing treatments for a Restoration Strategy for whitebark pine in a pilot area within the Crown of the Continent Ecosystem (Jenkins et al. 2019).

Rocky Mountain National Park (RMNP) is at the infection front for *C. ribicola* in Northern Colorado, and the park has a responsibility to prevent ecosystem impairment. The Proactive Limber Pine Conservation Strategy for the Greater Rocky Mountain National Park Area is an outcome of a partnership between RMNP and the USDA Forest Service. The Strategy focuses on timing specific monitoring and interventions efforts to inform management to sustain healthy limber pine populations and ecosystems during invasion and naturalization of WPBR, thereby putting limber pine on a trajectory that does not lead to ecosystem impairment in the future (Schoettle et al. 2015, 2019b, Cleaver et al. 2017). During this collaboration, a high frequency of complete resistance to WPBR in limber pine populations in RMNP and surrounding areas was discovered revealing a unique feature of this area's ecology (Schoettle et al. 2014). That we have this information and the other site-based genetic and disturbance ecology information before the limber pine populations have been invaded by WPBR is unique. This situation justified developing a conservation strategy specific to the greater RMNP area.

The major focal areas for management activities are (1) Promote ex situ and in situ conservation - continue and expand efforts to collect and archive limber pine genetic diversity through seed collections and protect limber pine trees from mountain pine beetle, WPBR, and fire to minimize mortality when and where land designations and management objectives permit; (2) Increase population size and sustain genetic diversity - increase the number of limber pine trees on the landscape through planting or seeding, or both, immediately to offset future mortality and to sustain viable self-sustaining populations; (3) Locate treatments to maintain durability of complete WPBR resistance - minimize selective pressure on the rust by planting trees with a range of susceptibilities only in low-WPBR-risk areas to reduce the probability of the proliferation of genotypes virulent to the complete resistance in limber pine; (4) Discover, develop, and deploy local quantitative WPBR-resistant sources - research quantitative (polygenic) WPBR resistance types in limber pine in the greater RMNP area and establish a clone bank of these genotypes (which can be protected from fire and other stresses) to provide seed for future plantings, and (5) Monitor pines and rust - Monitor for limber pine health, early detection of WPBR, and WPBR virulence. The Proactive Conservation Strategy was adopted by the park in 2015 and has served as a model for ongoing proactive conservation efforts for Rocky Mountain bristlecone pine, Great Basin bristlecone pine, as well as southwestern white pine and can be applied to other healthy portions of the distribution of limber pine and for those for foxtail pine and whitebark pine also.

The R4R framework has also been applied to the very heavily impacted area of the Crown of the Continent Ecosystem (CCE - northern Montana, southern British Columbia and Alberta; <https://www.crownmanagers.org/five-needle-pine-working-group>). The decision space is constrained by high impacts, but the landscape can still be stratified by forest condition and context to allocate treatment resources to have the highest likelihood of restoring whitebark pine within the CCE. It is well documented that five-needle pine forests in the CCE have declined significantly due to a combination of biotic and abiotic stressors. The High Five Working Group of the Crown Managers Partnership was formed to prioritize and advance collective efforts to effectively monitor, conserve, and restore five-needle pines across the complex jurisdictional boundaries of the CCE. The working group developed a proof of concept methodology for whitebark pine restoration within a US portion of the CCE (Jenkins et al. 2019). Future applications will cover the full CCE including both whitebark and limber pine. The strategy integrates existing data sources, expert opinion, and modeling within a GIS platform. Areas were first identified where whitebark pine is capable of existing on the landscape and then rated related to (1) conservation value as defined as those areas currently providing ecosystem services or capable of providing ecosystem services and then (2) the threats/stressors that have reduced, or are likely to reduce, conservation value were identified and quantified. Restoration actions were then prioritized based on the likelihood of successfully benefitting whitebark pine under each of the stressor's levels such that areas where stressors negatively impacted the potential success of the treatments were assigned a lower priority using an adaptation of the R4R framework. Finally, all factors were integrated, and priority core areas are defined for focused restoration in the future. The outcome of this effort is a draft methodology to identify priority areas for restoration within the CCE and for the National Whitebark Pine Restoration Strategy within the USA and can serve as a model for restoration strategies for other areas impacted by WPBR including the northern distributions of whitebark, limber, and foxtail pines.

Timely management approaches that incorporate both ecological context and an evolutionary perspective increase the likelihood of successfully sustaining high-mountain pine ecosystems into the future. The R4R framework highlights opportunity for increasing the resilience of both WPBR-threatened and impacted high elevation five-needle pines ecosystems across western North America. In healthy but threatened ecosystems, acting now will increase forest resilience to position the ecosystems to develop fewer impacts, and need less restoration, in the future, and the R4R framework encourages managers to not wait until the ecosystems are impaired to begin managing for increased resilience. In impacted systems, R4R recommended prioritizing management in locations that have the greatest likelihood of successfully restoring function and to look for opportunities beyond the heavily impacted areas that often attract most of the attention but have a poor prognosis. The same framework can be used when trying to prevent range-wide species endangerment by prioritizing treatments across a diversity of current stand conditions and WPBR hazards to increase the likelihood that at least some populations avoid extirpation. When prioritizing limited resources, context is critical. Accepting that some habitats may not support sustainable populations in the future, even with intervention, is essential for making good treatment investment decisions. The future of the high elevation five-needle pine ecosystems may depend on it.

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