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Return of the King: Western White Pine Conservation and Restoration in a Changing Climate

Western white pine is so named for the light color of its wood. The timber was used for everything from window and door frames to shelving, paneling, and furniture.
Photo by Susan McDougall, USDA-NRCS Plants Database.

To look out on the forested landscape of today's Interior Northwest—northern Idaho and western Montana—is to observe a forested ecosystem that looks and functions dramatically differently from that which an early settler to the area would have seen over a century ago. During and prior to the late 1800s and early 1900s, the forests of the Interior Northwest were dominated by western white pine (*Pinus monticola*)–"King Pine" as it came to be known–a species unmatched in its ecological and eventual economic significance to the region. But western white pine experienced a series of devastating events during the early- to mid-20th century when the species became a casualty of overharvesting, pine beetle damage, lack of fire-mediated opportunities for regeneration, and, perhaps most significantly, an invasive fungal pathogen that causes white pine blister rust disease.

This quadruple setback means that today, western white pine covers less than 10% of its historical range and at far lower densities than a century ago. The forests of the Interior Northwest are instead dominated by grand fir, western hemlock, western redcedar, and Douglas-fir–shade-tolerant, fire-intolerant (except Douglas-fir) species that are less deeply rooted and more vulnerable to insects, root disease, blow-downs, fire mortality, and

SUMMARY

Western white pine (*Pinus monticola*) is a species that used to dominate the forests of the Interior Northwest prior to the expansion of the Northern Pacific Railroad in the late 19th century. Its foundational role contributed to a landscape that was resilient, fire-adapted, and provided abundant suitable habitat for terrestrial and aquatic species. However, substantial harvesting and the early 20th century introduction of the invasive fungal pathogen that causes white pine blister rust disease combined with other factors to fundamentally alter the forested landscape of the Interior Northwest, reducing the extent of western white pine by 90%. As a result, other tree species that are generally fire-intolerant, less economically valuable, and more vulnerable to insects and disease now dominate a landscape that is regularly subject to fire. Now, as managers seek to restore damaged and degraded ecosystems in the Inland Northwest, new research is shedding light on the genetic structure and diversity of western white pine populations. While it would seem that many of these populations went through a bottleneck related to overharvesting and blister rust pathogen, research is demonstrating that much genetic diversity remains. This diversity is greatest in southern populations, which existed well before northern populations; significantly, southern populations are also more threatened by climate change than northern populations. The scientists' research can go a long way toward helping to inform western white pine conservation and restoration efforts in an era of climate change.

post-fire fungal infections. Considering the ecology and fire history of the region, today's forest composition yields an ecosystem that is less resilient, diverse, and productive.

The concept of ecological restoration—the practice of restoring damaged, degraded, or destroyed ecosystems—has been increasingly embraced by the forest management community. Now, with the advent of a changing climate, promoting ecosystem resilience and smart ecological restoration policies is ever more critical. "Right place, right time, right species" is a mantra that belies the complexity and nuance of restoring ecosystems as the climatic backdrop–temperature, precipitation, and the timing and duration of weather events–continues to shift. Yet, despite the complexity and uncertainty associated with these changes, scientists and land managers are recognizing that restoring western white pine to the landscape may be one of our best options for responding to climate change. From its incredible ability to sequester carbon (thereby mitigating climate change) to its climatic adaptability, western white pine restoration could be a harbinger of future forest health and ecosystem resiliency. But, in order to begin to implement appropriate strategies for restoration, it's critical to understand the western white pine at a deeper level. It's time to roll up our sleeves, hark back to biology class, and revisit what we know about evolution and genetics.

Western white pine is distributed widely across the western landscape–its historical range stretches from the northern Rocky Mountains (northern Idaho and western Montana), to the Cascade Mountains (Washington and Oregon), to northern California and the Sierra Mountains.

Genetics 101

Western white pine is a widely distributed species across the western landscape. Its historical range stretches from the northern Rocky Mountains (northern Idaho and western Montana), to the Cascade Mountains (Washington and Oregon), to northern California and the Sierra Mountains. Within this broad range, individual populations of trees convey both adaptive and neutral genetic variation as a result of evolutionary forces.

Adaptive genetic variation implies natural selection at work–genes are being selected for, and individuals and populations are being shaped by specific conditions or adaptive pressures. Neutral genetic variation, on the other hand, is the term for genetic variation that does not have any direct effects on fitness. But, precisely because these genes are "neutral," the effects of selection have not obscured the patterns of evolutionary history that they reveal. Therefore, these genetic markers can tell us a lot about migration, gene flow, and dispersal among sub-populations. And because genetic variation is the raw material for future adaptation, greater genetic variation within or among populations can enable greater flexibility and responsiveness to future selection pressures.

All totaled, different individuals and populations are bound to possess both neutral and adaptive variation. But the scale and significance of this variation, and its implications for restoration, were not understood until recently.

Variety is the Spice of Life

As a way to begin to understand western white pine more deeply and perhaps to inform "smart restoration" of the species in an era of climate change, researchers at the U.S. Forest Service Rocky Mountain Research Station (RMRS) started with the fundamental building block of genetics–DNA. RMRS Researchers Bryce Richardson, Marcus Warwell, and Ned Klopfenstein, collaborating with Mee-Sook Kim from Kookmin University in Seoul, South Korea, and emeritus scientists Jerry Rehfeldt and Geral McDonald, used DNA-based markers to assess genetic variation. Specifically, they analyzed the DNA fingerprint of individuals within a

"Southern populations existed well before the northern populations," said Research Geneticist Bryce Richardson. "The climate change that is occurring today is a distinct threat to these southern populations that contain the highest genetic diversity."

species to assess neutral genetic variation across populations. "This approach is a useful way to assess genetic diversity and population structure for white pine populations—it simply tells researchers which populations are genetically similar or dissimilar to each other or how much genetic variability exists within populations. But, the markers typically do not convey explicit information about adaptation," said Professor Kim.

The researchers found a complex pattern of genetic diversity and relationships among the many sub-populations of western white pine with an overall trend toward three distinct population clusters or "metapopulations": a Pacific Northwest metapopulation encompasses the northern Rockies and stretches west to the Pacific and south through the Cascades to central Oregon; a Siskiyou Mountain metapopulation in southern Oregon and Northern California; and a Sierra Nevada metapopulation stretches throughout much of this mountain range in California.

The researchers then examined the populations that comprised each metapopulation to better understand the genetic diversity within and between populations. What they found, said Research Geneticist Bryce Richardson, "conforms to a pattern we've seen over and over again in temperate plant species, where we tend to see higher genetic diversity in southern populations than northern populations." The theory is that western white pine (and other temperate plant species) only expanded to more northern climates after the last glacial maximum, at the start of the Holocene (the current geological epoch that began 12,000 years ago). Simply put, "southern populations existed well before the northern populations," said Richardson.

This bit of information might seem inconsequential until we think of the ways that the climate is changing–therein lies the "ah-ha!" moment. Southern populations contain more genetic variation, and genetic variation is the raw material for adaptation. And, as Richardson noted, "The climate change that is occurring today is a distinct threat to these southern populations that contain the highest genetic diversity." Armed with this heightened understanding of western white pine genetics, we now have a better-informed basis for conservation strategies.

In metaphorical terms, only collecting seed from some sub-populations or collecting sample sizes that are too small and therefore not representative of a sub-population's diversity would be like only half filling the bookshelves in a library. On the other hand, collecting seed from all sub-populations, especially the more diverse southern populations, is essential if we wish to create a seed bank that is more fully representative of the diversity in the species. Doing so will further facilitate flexibility, responsiveness, and, ultimately, adaptation as restoration proceeds in the face of climate change.

However, this ecological story doesn't stop here. Questions of how the climate might change can influence decisions on where western white pine should be restored. Research conducted by Rehfeldt and others has revealed substantial phenotypic plasticity of western white pine with respect to changes in climate. "Western white pine is a generalist with respect to climate. Within an ecotype, seed from any suitable white pine climate can be moved to another suitable white pine climate and be expected to exhibit relatively normal, healthy growth. This is not true

Orange-yellow spores of Cronartium ribicola*, the cause of white pine blister rust on white pine.* *Photo by Deems Burton, USDA Forest Service, Pacific Southwest Research Station.*

“Western white pine is a generalist with respect to climate. Within an ecotype, seed from any suitable white pine climate can be moved to another suitable white pine climate and be expected to exhibit relatively normal, healthy growth. This is not true for most other major conifer species,” said Geneticist Marcus Warwell.

for most other major conifer species,” said Warwell. Beyond understanding western white pine’s genecology, the question on almost any land manager’s mind in the Interior Northwest is bound to be “What about white pine blister rust?,” the disease caused by the invasive fungal pathogen that nearly wiped King Pine entirely from the landscape within the past century. In order to more fully inform future land management decisions, it is necessary to step into the past and understand something about the history and biology of this incredible species.

Ecology of the Western White Pine

Western white pine is a type of five-needle pine that gets its name from the light color of its wood. The tree typically has a whitish stem near the top with distinctive thin, grey, furrowed bark (younger trees have smooth bark) and cones that can grow to be a foot long. Absent disease, individual trees can easily live to be 350 years old and grow to be 150 feet tall, with the oldest specimens exceeding 500 years and 220 feet.

In the 1930s, the Civilian Conservation Corps tried unsuccessfully to eliminate blister rust host, Ribes, from the landscape by pulling, spraying, and even bulldozing the shrubs.

Western white pine typically prefers moister climates (with between 30 and 60 inches of precipitation per year) and grows well in deep, porous soils. It thrives in the Inland Northwest specifically because the jet stream from the Pacific carries moisture up and over the Cascade Mountains, depositing more precipitation on the northern Rockies than is typical throughout most of the rest of the mountain range. Despite its need for higher levels of precipitation, the tree can nonetheless tolerate environmental fluctuations, including drought and cold–both of which can be climatic features of the Interior Northwest.

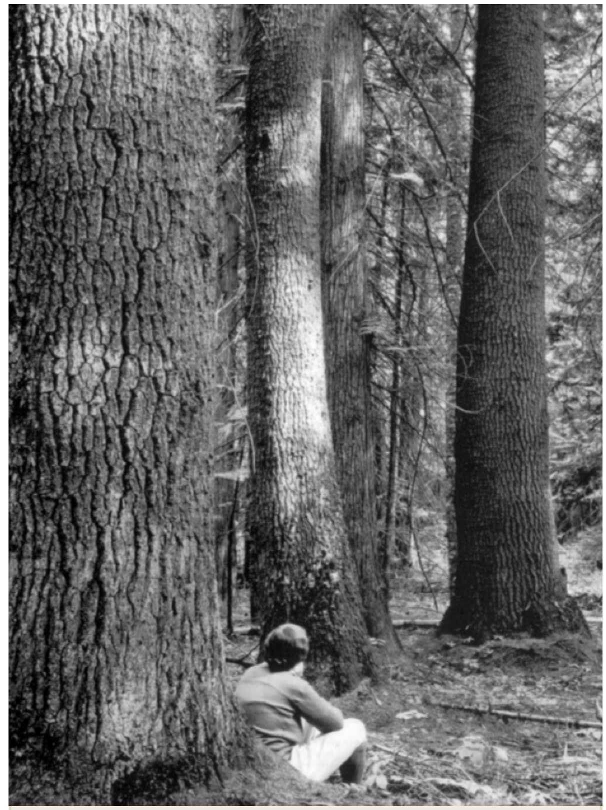
Historically, western white pine typically comprised 15 to 80% of Interior Northwest forests. In 1900, this tree covered more than 2 million acres in Idaho alone. Today, the extent of white pine has been reduced by more than 90%. Such a drastic reduction in prevalence has resulted in equally drastic implications for forest health given the region’s ecology. Despite the moist conditions that typically befall these forests from autumn to spring, shifts in the summer jet stream now carry Pacific moisture further north, creating summer droughts, while weak air masses simultaneously generate thunderstorms with copious lightning strikes. The western white pine evolved with this ecological backdrop and is considered a fire-adapted species. Indeed, this pine requires full sun for regeneration and the species is dependent on high-intensity, stand-replacing fires to promote regeneration. Now, where western white pine used to dominate, shade-tolerant species that are vulnerable to the characteristic recurrent fires (and cannot regenerate well after stand-replacing fires) and are far more susceptible to native diseases create a canopy of species that are inferior in terms of providing fast growth, timber quality, watershed health, and wildlife habitat that was once typical of the region. Whereas western white pine evolved to dominate this landscape and provide all the critical functions of a keystone species, the tree species that now prevail are ill-adapted to be king.

They Called it King Pine

How the range of the western white pine was reduced by over 90% is a story with predictable if not ill-intentioned antiheroes. As the Northern Pacific Railroad laid tracks into northern Idaho in the 1880s, western white pine began to be extolled for its rapid growth and long, straight trunk. The wood was light, clear, straight-grained, and thus easily milled. It was used for everything from window and door frames, shelving, and paneling to furniture and match sticks, and it became the basis for the timber empire of Weyerhaeuser and other timber companies. From 1900 to 1965, mills in Coeur d'Alene, Idaho, produced 17.5 billion board feet of white pine.

Much of this harvesting pre-dated even our most rudimentary understanding of forest management. While high-grading removed the best pines, less vigorous trees were sometimes left on site, thereby diminishing the pine's ability to regenerate while providing an advantage to shade-tolerant grand fir and hemlock. At the same time, many early foresters did not understand the role of fire in the ecosystem and saw it as a threat to both human and ecological health and thus worked to exclude and suppress it. Historical records for this region show an average of 31,000 acres per year burned between 1542 and 1931. In the mid- to late-20th century, an average of 665 acres burned per year as a result of fire exclusion. Such vigorous fire suppression policies all but doomed the natural regeneration of white pine.

Add to this the introduction of the invasive fungal pathogen blister rust pathogen, *Cronartium ribicola*, a species of rust fungus endemic to Asia. The pathogen was introduced to the American West by way of infected western white pine stock grown in France and imported to Vancouver, British Columbia, in 1910. A separate introduction of blister rust in the eastern United States in 1895 contributed to the marked demise of eastern white pine by 1910.



Western white pine can easily live to be 350 years old and grow 150 feet tall, with the oldest specimens reaching 500 years and 200 feet. This photo shows western white pine in northern Idaho, circa 1932.

What made blister rust particularly devastating and intractable is its complex biology and life cycle. The pathogen is also fire-dependent and relies on intermediate hosts of currant and gooseberry (genus Ribes), so eradication measures focused on the elimination of all infected tree species as well as intermediate hosts. Tactics from hand-pulling, spraying, and bulldozing Ribes shrubs to injecting pines with antibiotics were all abandoned, however, as the disease proved too devastating and tenacious, even for entire units of Franklin D. Roosevelt's Civilian Conservation Corps. It was recently found that the blister rust pathogen could also use other (non-Ribes) intermediate hosts to complete its life cycle, which may

"Western white pine still exhibits relatively robust genetic diversity, despite having been subjected to substantial historical pressures from harvesting and blister rust. But, continued studies are needed to assess genetic diversity of western white pine related to adaptation and climate change," said Professor Kim.

partially explain the failure of the Ribes eradication program to control white pine blister rust.

Eventually, when blister rust suppression seemed hopeless, much of what remained of western white pine was harvested in a last ditch effort to salvage what timber could be saved. Scientists and managers look back upon that fateful decision with remorse. We now realize that we harvested and destroyed much of the genetic diversity that may have provided the basis for natural regeneration and disease resistance or may have buttressed future nursery blister-rust resistance programs.

Better Living Through Genetic Diversity

Although many now cringe to think of the genetic diversity and inherent rust resistance that may have been lost when salvage harvesting peaked, research conducted on the remaining natural populations of the Inland Northwest since the 1950s is showing us that all is not lost. Rust-resistant breeding programs have begun to take hold, and recent work done by Kim, Klopfenstein, and others found that these breeding programs have not produced a genetic bottleneck as potentially feared. Nonetheless, the researchers have found that modern day natural populations under lower pressure from blister rust had higher heterozygosity (genetic variation) than populations that had experienced high mortality from blister rust, though this difference was not found to be significant.

The silver lining is that "western white pine still exhibits relatively robust genetic diversity despite having been subjected to substantial historical pressures from harvesting and blister rust. But, continued studies are needed to assess genetic diversity of western white pine related to adaptation and climate change," said Professor Kim.

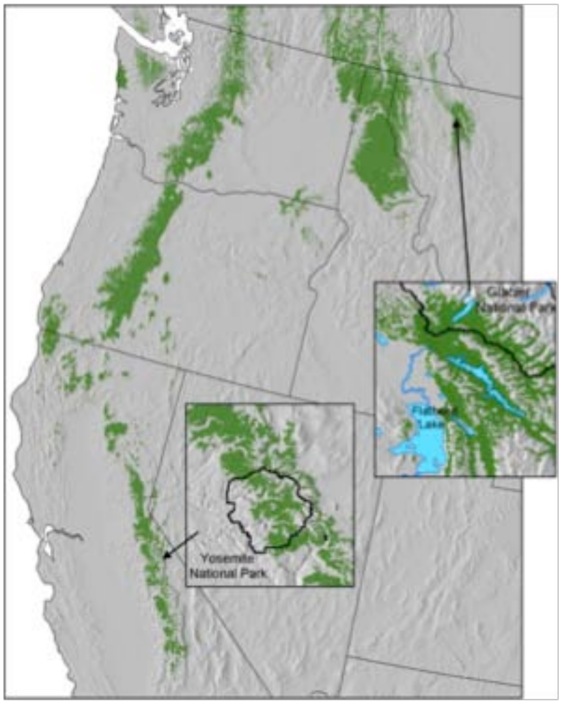
"If you're planting for forest health over the next hundred years and you anticipate an area will undergo changes due to a shifting climate, western white pine has a huge advantage in terms of adaptive structure," said Geneticist Marcus Warwell.

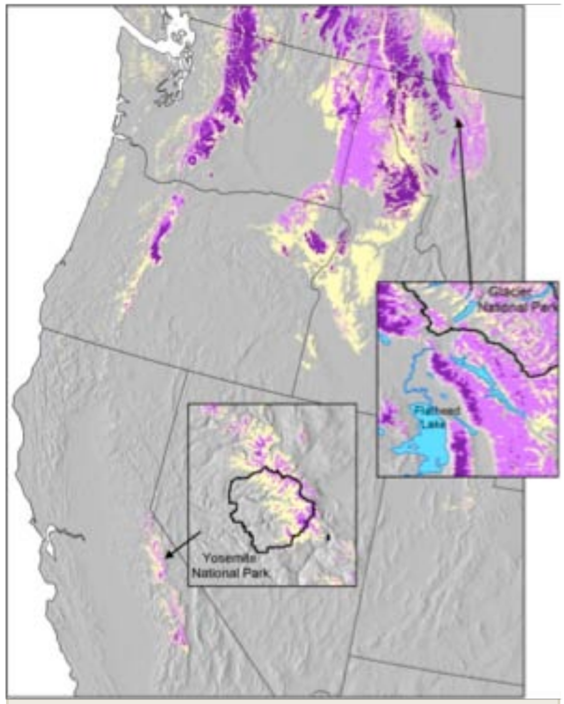
Restoring King Pine in an Uncertain Future

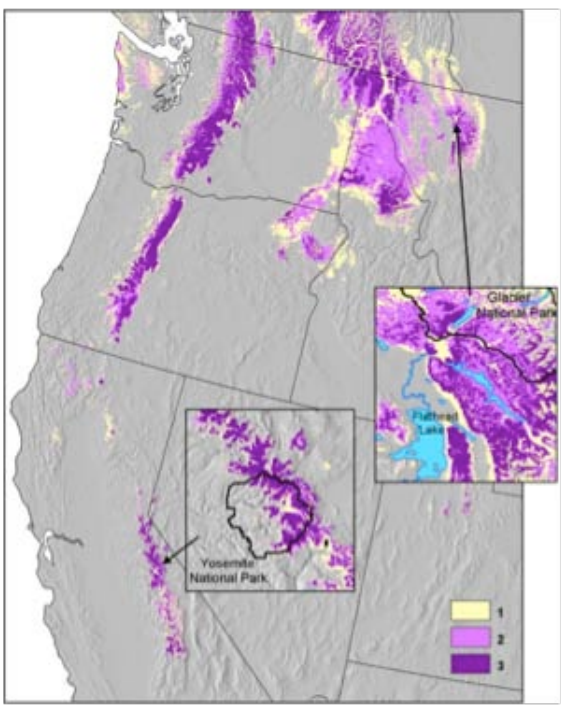
After discovering that all was not lost–in fact, little seems to have been lost–researchers took the next step, using General Circulation Models (GCMs) to predict the future suitable habitat (climate space) for western white pine over the next several decades. GCMs simulate the response of the climate system (including physical processes in the atmosphere, ocean, cryosphere, and land surface) to increases in greenhouse gases. The first step in the modeling process is to "true" the model to the current reality; researchers did this by identifying the approximately half dozen variables that best predict the occurrence of western white pine in climate space. These variables were used as the model predictors. They then ran predicted climate data for about 6 million locations representing all of the western United States through the model. The output matched the geographic distribution where we currently find western white pine–in other words, the model appears to be accurate for current conditions.

A road through a western white pine stand in northern Idaho, circa 1932.

Next, the researchers ran the model for future climate scenarios. The results are promising for western white pine: although suitable habitat will decrease at some southern latitudes, habitat at northern latitudes is predicted to increase. While these results are subject to the accuracy of the model and the GCM, all GCMs show increased precipitation for the area in question during the winter. Summer precipitation predictions, however, remain inconsistent. Recently, the researchers produced an agreement map–a map that identifies where GCMs agree on predicted future occurrence of suitable climate space for western







Mapped climate profile of western white pine (Pinus monticola) projected for contemporary climate (top left), the decade surrounding 2030 (bottom left), and 2060 (above) superimposed for three GCMs (CGCM3 [T63 resolution], HadCM3, and CM2.1) with the SRES A2 emission scenario. Coloring codes indicate the number of projections agreeing that the future climate should be suitable.

"A wealth of studies indicate that restoration of western white pine would help maintain forest resilience and ecosystem services in the face of uncertain climate change in Interior Northwest ecosystems," said Geneticist Marcus Warwell.

white pine. Such tools can help reduce uncertainty for managers by showing the lowest risk areas for white pine restoration in relation to predicted changes in climate.

But, perhaps the biggest challenge for western white pine restoration will be overcoming resistance from the management community. Some commercial timber managers view western white pine as a lost cause—they don't plant it, despite its superior growth and timber quality, because they think it will soon die from white pine blister rust. However, rust-resistant nursery and breeding programs and the inherent adaptability of white pine contradict the assumption. From a timber production perspective, Richardson stated that "if we can address the blister rust issue, the opportunity for economic gain is staring industry in the face, and they're aware of that."

From a forest health perspective, "If you're planting for forest health over the next hundred years and you anticipate an area will undergo changes due to a shifting climate, western white pine has a huge advantage in terms of adaptive structure," said Warwell. "Western white pine is a generalist within its ecotypes. Its populations should physiologically adjust to predicted climate change better than populations that constitute many other species; it's a great species to plant or to attempt to regenerate," he said. Beyond the forest health benefits, because western white pine grows quickly and is extremely long-lived, it has a huge capacity for carbon sequestration. "A wealth of studies indicate that restoration of western white pine would help maintain forest resilience and ecosystem services in the face of

KEY FINDINGS

- Western white pine populations display genetic diversity derived from multiple factors, including migration, adaptation, and multiple glacial refugia.
- Southern-most populations of western white pine, which existed well before northern populations, also contain more genetic variation than northern populations. These southern populations of western white pine that are most at risk from climate change can be prioritized for genetic conservation efforts.
- Conservation efforts must seek to capture the genetic diversity within and among sub-populations of western white pine—in essence, preserving the "entire library" of variation.

uncertain climate change in Interior Northwest ecosystems," said Warwell. Continued research will complement our understanding and refine our ability to implement effective restoration.

Ultimately, the question is: What effect will climate change have on the blister rust pathogen and on its relationship with alternate hosts (Ribes, Castellija, and Pedicularis) and western white pine? It's a complex question playing out on a shifting landscape. All disease results from an interaction of pathogen, host, and environment, and research on the interaction of these three factors overlaid with a shifting climate is nascent. In addition, the white pine blister rust pathogen is an obligate parasite, which means it needs living white pine tissue to survive. In theory, the white pine blister rust pathogen should evolve toward a less aggressive form that does not kill the host on which it depends for survival. The good news is "Western white pine appears to be slowly coming back on several natural sites where it is given an opportunity to regenerate," said Kim. Natural recovery combined with disease management will facilitate the recovery of western white pine.

And in the Meantime?

Climate projections for the Inland Northwest are very favorable to western white pine. The benefits of this species to forest health, watershed health, and aquatic and wildlife communities are substantial. And, armed with knowledge of its genetic diversity and variation within and among sub-populations, we can be sure to preserve the "entire library" when it comes to western white pine genetic diversity. The most important step (and the only thing left to do) is to act on this knowledge.

MANAGEMENT IMPLICATIONS

- Restoration efforts of western white pine must consider climate change in addition to disease resistance, and restoration efforts can be focused on populations that are better adapted to future climate spaces.
- Western white pine has substantial physiological plasticity, and seed from a specific ecotype acts as a generalist within that ecotype; because of this plasticity, western white pine will be better able to adjust to climate change than many other species.
- Western white pine is a great species to plant or to attempt to regenerate from a climate change and forest health perspective. In addition to its physiological plasticity, it is a keystone ecological species that is capable of sequestering large amounts of carbon.
- More information about contributing to western white pine collection and conservation efforts can be found at the National Seed Library (http://www.nsl.fs.fed.us/).

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