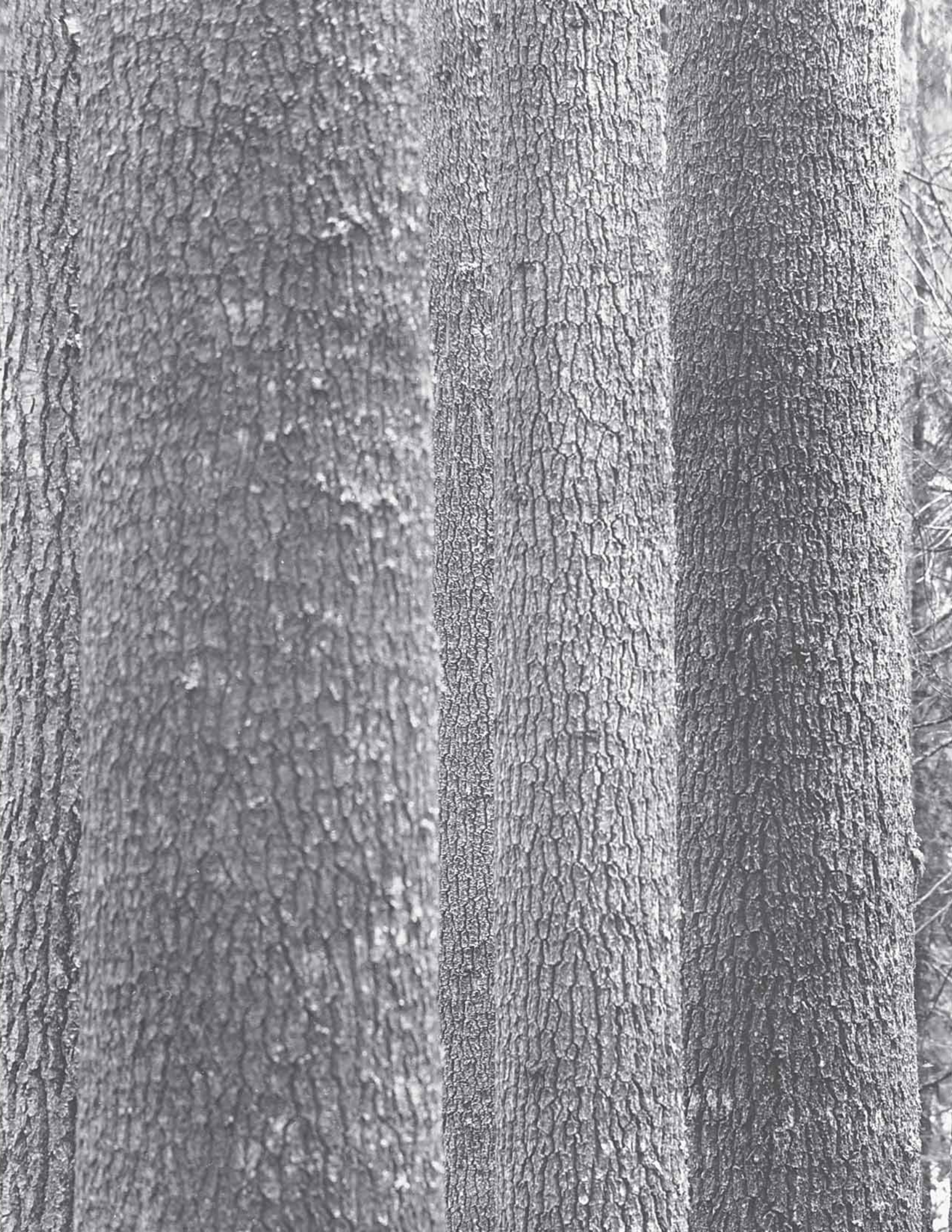




return of the giants

*Restoring White Pine Ecosystems by Breeding and Aggressive Planting
of Blister Rust-Resistant White Pines*

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Mary Frances Mahalovich, GERAL McDonald, Dan Miller, John Schwandt, and Art Zack



RESTORING WHITE PINE

– why should we bother?

In 1883, when the Northern Pacific Railroad made its way through northern Idaho, western white pines dominated the moist, mid-elevation, mixed-species forests of the Inland Northwest between 2,000 and 6,000 feet. These majestic trees often lived to 350 years but could reach the ripe old ages of 400 and even 500 years. They were an integral part of the most productive forests in the region, providing habitat for a highly diverse mixture of organisms, from the smallest microbes to lichens, higher plants, and animals.

On good sites, white pines grew to more than 150 feet tall and 36 inches in diameter. (In 1992, the record-holding western white pine in Idaho was 229 feet tall and 78.7 inches in diameter.) Other species, such as western larch, sometimes grew as large, but there were many more white pines, often outnumbering the other trees in mature forest stands. Inland Northwestern forests held the promise of riches for a timber industry that by 1900 had virtually exhausted the supply of old-growth eastern white pine in New England and was rapidly depleting it in the Lake States.

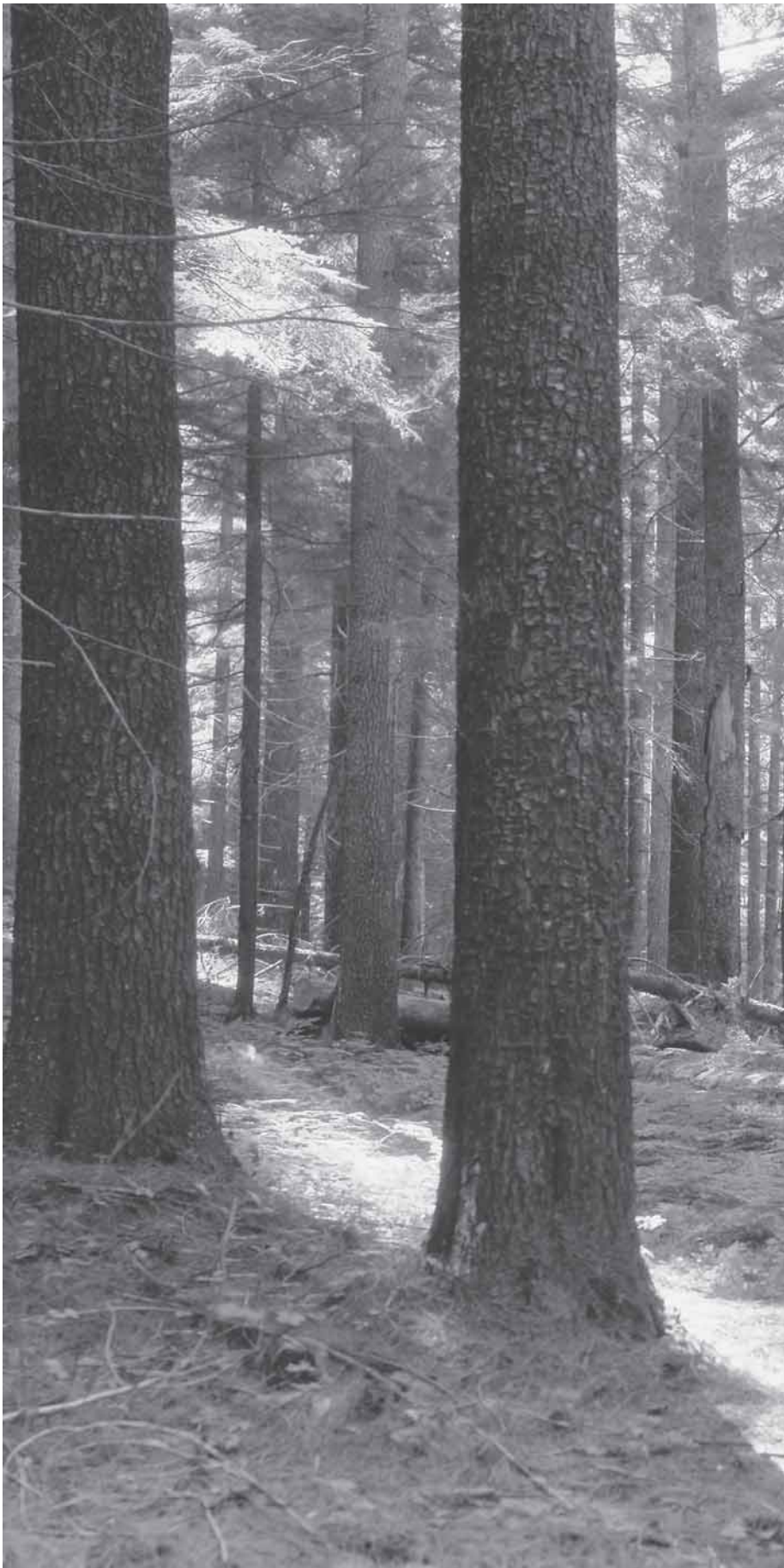
By the late 1960s, our white pine forests in the Inland Northwest were nearly gone, decimated by a combination of white pine blister rust disease, high-grading, overcutting, mountain pine beetle attack, and exclusion of stand-replacing fires. Today, at the turn of a new century, only 5 to 10 percent of the original 5 million acres of white pine cover type in the Inland Northwest still carries a significant component of white pine.

Where white pines used to dominate we now find Douglas-fir, grand fir, and hemlock. Douglas-fir and grand fir are susceptible to a much greater variety of insect and disease problems than is white pine; hemlock is more sensitive to drought and decay. The loss of white pine and the shift in forest tree species has resulted in lower productivity in our forests. Whereas mixed white pine stands commonly produced 50,000 board feet per acre, the best mixed fir stands of today are projected to average only half that much. Loss of white pine also means less large wood for fish and wildlife habitat and for nutrient cycling, less old growth, and an increasing risk of particularly severe wildfires.

If we want to reverse this dismal picture, we must restore white pine to our Inland Northwestern ecosystems. We cannot rely on natural regeneration to do the job because too little of our native white pine remains to provide a reliable seed source. Only an aggressive planting program, using genetically improved, blister rust-resistant stock and appropriate silvicultural techniques, will ensure the “Return of the Giants.”

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WHITE PINE ECOLOGY

– the ideal species

If you tried to design a coniferous forest tree species that was adapted to the moist forest environments of the Inland Northwest (northern Idaho, northeastern Washington, northeastern Oregon, and northwestern Montana), you would probably come up with a tree that is much like the majestic western white pine. White pines grow rapidly when moisture conditions are favorable (average precipitation in the western white pine region ranges from 28 to 60 inches annually), and they tolerate the extremes of winter cold and summer drought that commonly occur in Inland Northwestern forests. They produce seed crops at 3- to 4-year intervals, and under relatively open conditions, compete well with aggressive, shade-intolerant species such as western larch and lodgepole pine.

FRONT COVER PHOTOGRAPH BY: Pam Benham.
INSIDE FRONT COVER PHOTOGRAPH: Potlatch
Historical Society. THIS PAGE: At 160 years old
in 1937, this stand of almost pure white pine
near Coeur d'Alene, Idaho, was a stunning
example of the white pine forest type.
Montford Creek Natural Area, Deception
Creek Experimental Forest. PHOTOGRAPH
COURTESY OF: USDA Forest Service.

– dependence on fire

One reason white pine was so successful and so abundant in the Inland Northwest is because the species is so well-adapted to fire. White pine seedlings can get established initially in moderately shady areas, but once established, white pines grow best in full sunlight. Even moderate amounts of shade will reduce their growth. To persist in this ecosystem, white pines need fire or some other force to create large openings in the forest.

Historically, wildfires were common in Inland Northwestern forests. They were largely responsible for the diverse mosaic of species, age classes, and stand structures that characterized forests in the region. Patchy fires of low and mixed severity averaged 50 to 100 years between occurrences in the same stands. Large, high-intensity, stand-replacing fires occurred at 150- to 250-year intervals.

TO PERSIST IN THIS ECOSYSTEM, WHITE PINES NEED FIRE OR SOME OTHER FORCE TO CREATE LARGE OPENINGS IN THE FOREST.

Fires created open spaces of different sizes where white pines could become established. In the larger openings, white pine seedlings would eventually outgrow competing species and dominate the forest for 200 years or more. Because white pines often lived to 350 years and occasionally to 500, there were plenty of mature trees to provide a seed source when the next stand-replacing wildfire came along.

– resistance to native pests

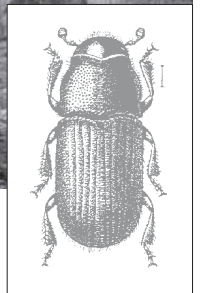
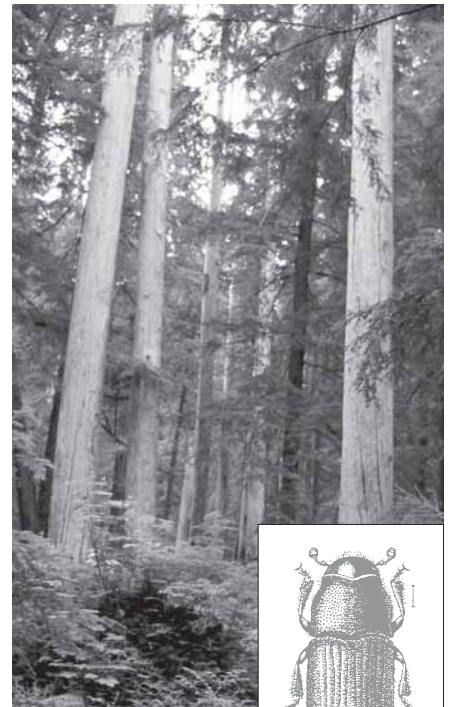
White pine's ecological success was also related to its resistance to most native insects and diseases. As stands aged, insects and diseases thinned out



the more susceptible species, thereby maintaining or increasing white pine's dominance.

White pines did have one primary native foe, however, the mountain pine beetle. While fungal root diseases slowly removed white pines of all sizes, mountain pine beetles could kill their aging hosts in just one year.

TOP: The great fire of 1910 burned across more than 3 million acres of forest in the Inland Northwest, including the Little North Fork of the St. Joe River, St. Joe National Forest, Idaho. Wildfires regularly created large openings in the forest where new white pine seedlings became established and eventually outcompeted other tree species. PHOTOGRAPH BY: J. B. Harm, courtesy of USDA Forest Service. RIGHT: From the mid-1980s and into the 1990s, beetles killed nearly all the white pine in the more than 200-year-old Montford Creek Grove, Montford Creek Natural Area, Deception Creek Experimental Forest, Idaho. PHOTOGRAPH BY: Art Zack.



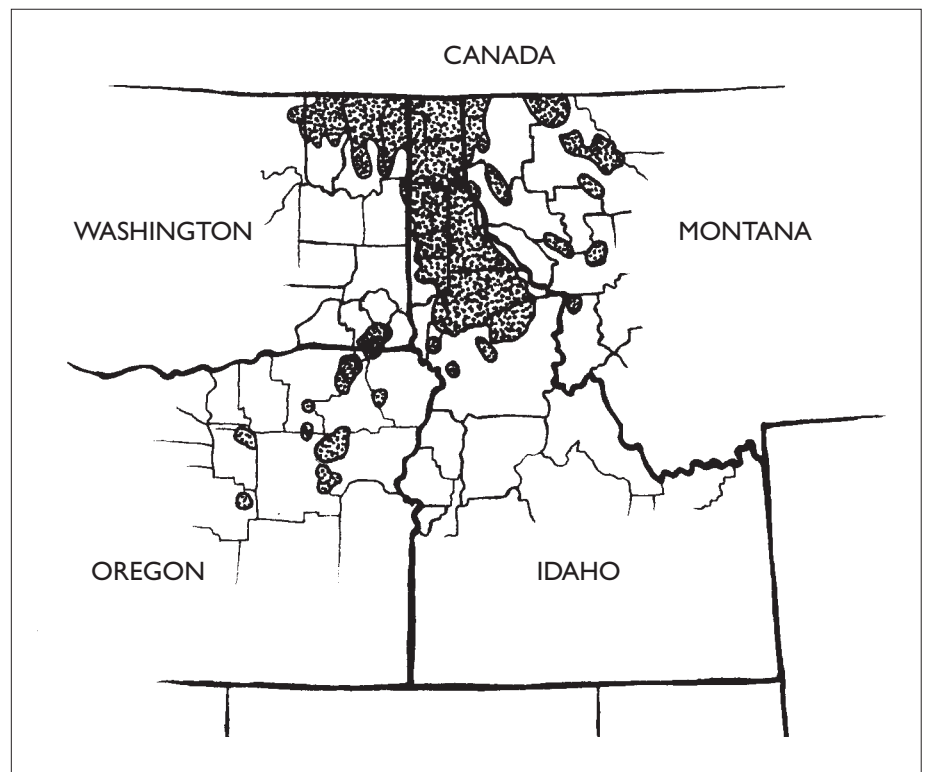
During periods of drought, mountain pine beetles killed thousands of mature white pines over thousands of acres. Heavy fuel loads that resulted from these outbreaks then set the stage for the next stand-replacing fire. Once the fires did their work, they created open growing conditions that were ideal for a new generation of vigorous, fast-growing white pines. Trees in adjacent stands and residual trees whose seeds matured after the fire had passed through provided the seed that became the new young stands of this remarkable species.

– a hub in the wheel of life in the forest

Even dead and dying white pines were critical to the cycles of life in the forest. Their tops provided roosts for large birds such as bald eagles and ospreys that build nests in large, broken-topped trees along lakes and streams. They also attracted woodpeckers that created holes in the tree trunks and nested in large snags. Owls and smaller birds followed—swallows in riparian areas and bluebirds in more open forests.

Chipmunks, raccoons, squirrels, and bats also found shelter in the old veterans. As carpenter ants and wood borers moved in, they helped recycle the wood of the old giants. The insects, in turn, provided an additional food source for bears and many kinds of forest birds.

By the time natural wildfires returned to a stand, the dead giants had little protection against the flames. Eventually, much of their wood burned. Some became soil wood or charcoal and left pools of nutrients in the soil that were (and are) essential to the long-term high productivity of the Inland Northwest's forests.



White pine's native range extends from the northwestern corner of Montana, north into British Columbia, west into Idaho and Washington, and southwest into Oregon and California. But it is in the forests of the Inland Northwest that white pine achieves its best stand development and characteristic large individual tree size. Map modified from *Silvics of North America*, Volume 1, *Conifers*, Agriculture Handbook 654, December 1990.

Fires cranked the wheel of forest life in another way. Large burned white pine snags can stand for decades, and fire-killed logs may persist on the forest floor for more than a century. Whether standing or down, the dead trees provided shelter for an array of forest critters that included mice, foxes, bobcats, martens, skunks, fishers, minks, bears, and other animals who made their dens in the hollowed-out shells that remained after the flames had passed. Eventually the downed trunks were home to more fungi that decomposed the wood, further enriching the forest soils and increasing their ability to hold water.

Native fish also relied on the once-grand white pines. In addition to providing shade directly to streams when they were standing, large trees would sometimes fall into streams,

creating natural deep pools and critical habitat for cutthroat and bull trout.

EVEN DEAD AND DYING WHITE PINES WERE CRITICAL TO THE CYCLES OF LIFE IN THE FOREST.

Today, few forest trees in the Inland Northwest reach the age and size that were common to old-growth white pines. Losing the white pines has ultimately meant losing important habitat for the creatures that traditionally relied on the species for food and shelter. Although we cannot create large trees overnight, planting white pine—and managing at least some of our forests for production of large stems—will go a long way toward restoring these habitats and the natural cycles of life in our Inland Northwestern forests.

THEY CALLED IT “KING PINE”

Dense forests of large white pines provided a critical economic resource for settlers in the late 1800s and early 1900s. With its light, clear, straight-grained, easily milled wood, it was the most valuable tree species in the moist forests of the Inland Northwest. They called it “King Pine.”

IT WAS THE MOST VALUABLE TREE SPECIES IN THE MOIST FORESTS OF THE INLAND NORTHWEST.

White pine dominated the timber industry in the Inland Northwest between 1900 and 1965. Founders of some of the nation’s largest and most successful timber companies, including Frederic Weyerhaeuser, were attracted to the region and built their Inland Northwestern empires on a foundation of white pine. Weyerhaeuser and his associates incorporated seven companies in Idaho, including the three that eventually merged to form Potlatch Forests, Inc. (Rutledge Timber Company, Potlatch Lumber Company, and the Clearwater Timber Company) and the two that eventually merged to become Boise Cascade (Barber Lumber Company and the Payette Lumber and Manufacturing Company).

By 1903, large timber companies owned most of the private timberland in northern Idaho, and by 1910, there were 72 mills operating in Kootenai, Benewah, and Shoshone counties alone. Mills in the Coeur d’Alene region produced more than 17.5 billion board feet of lumber between 1900 and 1965, much of it white pine. Between 1925 and 1934, the average annual cut of white pine was 430 million board feet in northern Idaho, western Montana, and north-eastern Washington. Whereas in 1889



the Inland Northwest had been producing less than 1 percent of U.S. white pine lumber, by 1929, it was producing 43 percent.

White pine wood was used for everything from construction lumber to boxes to match sticks. High quality white pine is still a highly valuable resource, rivaling old-growth ponderosa pine and western redcedar in log prices. Its wood is used for interior and exterior siding and is a choice

TOP: The largest known white pine (“The White Pine King”) was felled on December 12, 1911, on Potlatch Lumber Co. lands near Bovill, Idaho. It was 425 years old. The bole was sawn into magnificent solid boards. PHOTOGRAPH BY: G.B. Joslin, courtesy of Potlatch Corporation.

material for milled products such as window sashes, doors, and blinds. In recent years white pine has also been in high demand for solid-wood home furnishings such as dressers, beds, and tables.



for at least the remaining white pines, but society at large, and even many foresters, did not yet fully understand the role of fire in maintaining these ecosystems. They saw fire as a threat to both forests and humans and began to suppress all wildfires.

IN MANY AREAS THE STANDS WERE HIGH-GRADED.

Fire suppression efforts in the latter half of the 20th century were so successful that the number of acres burning annually in northern Idaho was only a small fraction of the region's historical average. For example, although the number of acres that burned varied widely from year to year, the Idaho Panhandle National Forests averaged 31,000 acres burned per year between 1542 and 1931. The average number of acres burned per year between 1969 and 1998 was only 665. This drastic decline in fire disturbance closed another pathway for white pine regeneration, and fire, at least temporarily, ceased to be a major force in shaping forest vegetation in the Inland Northwest.



WHITE PINE'S DECLINE

– logging and fire suppression take their tolls

Harvesting alone would not have decimated white pine. In fact, logging can create openings large enough to let direct sunlight reach the forest floor where white pine seedlings can become established and grow. In addition, prescribed fire can be used to clean up logging slash, release nutrients, and further reduce shade to create conditions that give white pines a competitive advantage in regeneration.

In many areas, however, the stands were high-graded. The highest-value white pines were removed, the less-valuable, less-vigorous individuals or species were left on-site, and forest succession was dramatically changed. Not only did this type of logging remove the best genetic stock, it gave the more shade-tolerant grand fir and hemlock an overwhelming advantage in regeneration.

Natural wildfires could have provided regeneration opportunities

– blister rust brings King Pine to its knees

High-grading and fire suppression clearly diminished white pine in the Inland Northwest's ecosystems, but it was an exotic disease that, by far, did the most damage. White pine blister rust was inadvertently introduced to North America from Europe as early as 1898 when infected pine seedlings were widely planted in the northeastern United States. In 1910, the rust arrived in Vancouver, British Columbia, on infected seedlings from France, and by 1923, it had begun to infect Idaho's white pines. By the 1940s blister rust was epidemic, and millions of western white pines were

TOP: In the early 1900s, logs were commonly hauled to the mills by rail as on this first log train out of Jaype, Idaho. PHOTOGRAPH COURTESY OF: Potlatch Corporation.

ABOVE: A mistaken view of wildfire as an enemy of forest ecosystems led to one of the most successful ecological/environmental campaigns of a generation. Even lifetime city dwellers recognize the image of Smokey Bear admonishing us to prevent forest fires, as in this 1952 poster. COURTESY OF: USDA Forest Service.

dying throughout the region.

White pine blister rust is caused by a fungus (*Cronartium ribicola*) that lives part of its life on *Ribes* plants (gooseberries and currants) and the other part on white pine trees. This devastating pathogen needs both hosts to complete its life cycle.

In the fall of the year, when temperatures are low and moisture levels are high, fungal spores are produced on *Ribes* plants and dispersed by the wind. When they land on white pine needles, the spores germinate and enter the needles through their stomata. In susceptible white pine trees, the fungus continues growing down the needles and into branches and the main stem, producing stem-girdling cankers and eventually killing the trees.

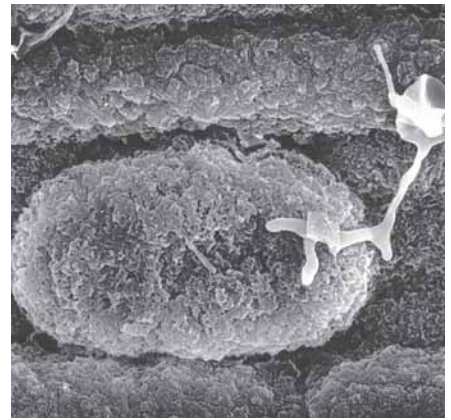
IT WAS AN EXOTIC DISEASE THAT, BY FAR, DID THE MOST DAMAGE.

Blister rust usually spells rapid death for small trees, but infected large trees may live for many years before they finally succumb. Infections in the crowns of large trees may kill only individual branches or cause top-kill above a girdling infection. Large trees will usually die when they have many crown infections or a stem-girdling infection in the lower bole.

EARLY EFFORTS TO SAVE WHITE PINE

– attempts to directly control blister rust fail

The USDA Forest Service and forest industry made valiant efforts to save white pines by attempting to interrupt the life cycle of the rust fungus. Starting in 1909 in the East and later in the West, foresters tried everything, from pulling out every *Ribes* plant in sight to injecting antibiotics into the bark of infected trees.



TOP: In spring, new leaves of *Ribes* species (currants and gooseberries) are infected by blister rust aeciospores released from infected pines. The spore population builds up during the summer months as the infection spreads among *Ribes* plants. Then in late summer/early fall, when temperatures are cool and relative humidity is high, rust infection spreads back to the pines through wind-dispersed basidiospores. PHOTOGRAPH BY: Ray Hoff. TOP RIGHT: When rust spores from *Ribes* leaves land on white pine needles, their germ tubes invade the stomata. The growing fungus eventually causes cankers in branches and stems of susceptible trees. PHOTOGRAPH BY: Kwan-Soo Woo. RIGHT: Classic bole cankers on rust-susceptible white pines are diamond-shaped. The bright yellow-orange margin is especially visible when wet. BELOW: In the 1930s almost 2 million pounds of sodium chlorate were sprayed along streams and riparian areas in the effort to interrupt the



blister rust life cycle by eradicating *Ribes*. PHOTOGRAPHS RIGHT AND BELOW COURTESY OF: USDA Forest Service.





Approximately \$150 million was spent over a period of about 50 years in the effort to control blister rust. But none of the programs worked well enough to rescue white pine. In 1967, efforts to directly control the rust were abandoned. Instead, **harvesting was accelerated to extract the valuable timber before the rust killed it.**

Unfortunately, these pre-emptive harvests removed white pines that could have served as seed sources for natural selection to increase rust resistance in the next generation.

– turning the corner: genetics research provides hope for saving white pine

Although the blister rust epidemic seemed to spell certain death for white pine in the Inland Northwest, Richard T. Bingham, a scientist with the Bureau of Entomology and Plant Quarantine in Spokane, Washington, noticed that in stands otherwise decimated by blister rust, an occa-

sional tree appeared to be perfectly healthy. Could these stalwart few harbor a natural resistance to the rust? Bingham thought so.

THEIR STUDIES DEMONSTRATED
GENETIC CONTROL OF BLISTER
RUST RESISTANCE.

LEFT: The blister rust-resistance breeding program began in the summer of 1950. A.E. Squillace, J.W. Duffield, and R.T. Bingham climbed 25 field-selected white pines and pollinated female strobili that were isolated in about 600 pollination bags. When the cones began to mature, they installed cloth bags to protect cones from insects and to catch seed, as in this 1951 photo of tree 19 near Fernwood, Idaho. PHOTOGRAPH COURTESY OF: USDA Forest Service. NEAR RIGHT: R.T. Bingham, a forest pathologist in Spokane, Washington, suspected that the occasional rust-free white pines he found in the midst of otherwise heavily infected stands were genetically resistant to blister rust. As part of the genetic improvement program, Bingham grafted cuttings from candidate trees in the testing program. PHOTOGRAPH COURTESY OF: Bureau of Entomology and Plant Quarantine.



In the 1950s Bingham and his colleagues J.W. (Jack) Duffield and A.E. (Tony) Squillace embarked on a program to test whether these trees were genetically resistant to the disease. Their hunch was right! When they bred disease-free trees with each other, many of the seedlings resulting from the crosses were resistant to the rust. Their studies demonstrated genetic control of blister rust resistance.

Beginning in 1957, using the most resistant seedlings from their crosses, Bingham and his colleagues established a breeding orchard on the University of Idaho campus in Moscow. When they made controlled crosses between the trees in the orchard and tested their seedlings (the “F₂” generation) for resistance by inoculating them with blister rust, approximately 66 percent of the progeny had no rust cankers after 2 1/2 years.

The breeding orchard in Moscow began producing small seed crops in about 1970. In the 1980s the site was converted to a seed orchard and was managed for high levels of seed production. The orchard produced its first major seed crop in 1985. Since 1970, the white pine seed orchard at Moscow has produced approximately 10,000 pounds of seed (more than 200 million seeds). In 1999, the orchard was dedicated and renamed the R.T. Bingham White Pine Seed Orchard.

The research conducted by Bingham and his colleagues, along with the orchard they planted, provide the foundation for ongoing efforts to increase rust resistance levels in white pine through breeding. By planting genetically improved, rust-resistant seedlings

produced by regional tree improvement programs, and managing those stands to promote high survival and growth, we can restore white pine to Inland Northwestern ecosystems.

TOP RIGHT: Trees in the R.T. Bingham White Pine Seed Orchard in Moscow, Idaho, produce abundant, high-quality, rust-resistant seed. Cones are picked in mid to late August. PHOTOGRAPH BY: Kelly Weaver. MIDDLE: The fleshy green cones are stored on racks in burlap sacks. Because the cones generate heat and release considerable moisture, a sack of cones can provide an ideal growth environment for fungi that destroy cones and seeds. So it is essential to pack the cones loosely and to maintain good air circulation around the sacks. PHOTOGRAPH BY: Michele Kimberling. BOTTOM RIGHT: White pine cones are picked while their scales are green and still closed. As the cones dry, the scales curve outward and open, releasing ripe seeds—the promise of future white pine forests. PHOTOGRAPH BY: Kelly Weaver.



CURRENT STATUS OF WHITE PINE ECOSYSTEMS

To date, only a small fraction of the area suited to white pine has been planted with rust-resistant stock. On public lands, tree planting has actually declined as timber harvests have been reduced in recent years.

One tally estimates that federal, state, private, and other organizations planted Moscow white pine on about 250,000 acres in the Inland Northwest between 1976 and 1996. This may sound like a lot of acres, but 250,000 acres is only 5 percent of the estimated 5 million acres that have the potential to grow white pine in the region.

In addition, current harvest practices generally create only small openings in forest stands. **Without stand-replacing fires or even-aged management systems to create larger forest openings, natural regeneration has tended to favor shade-tolerant species such as hemlock and grand fir.** These species, along with Douglas-fir, have now largely replaced white pine in our Inland Northwestern ecosystems. If current management strategies continue, the future of white pine and of the former white pine ecosystems could be grim.

Western hemlock, a species with very low tolerance to drought, is now growing in historically unprecedented amounts in an ecosystem prone to periodic drought. Douglas-fir and grand fir, both of which are particularly susceptible to root diseases, drought, and bark beetles, are the sources of many forest health problems plaguing the region today. Without long-lived pioneer species such as white pine to replace these species, the insect and disease epidemics that have become common in the region will persist. And ulti-

mately, because periodic drought and fire are parts of the natural cycle, the frequency of major stand-replacing fires will also increase.

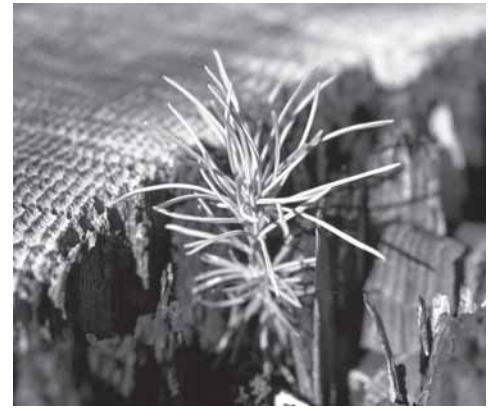
Alternatively, we can seize every opportunity, including those created by wildfires and by the decline of grand fir and Douglas-fir, to reestablish white pine as a significant component of Inland Northwestern forests. Salvage logging may create some opportunities for the return of white pine, but, unfortunately, **salvage logging of individual dead and dying trees usually perpetuates the establishment of shade-tolerant species and rarely creates conditions suitable for successful white pine regeneration.** Regeneration harvests, however, and stand-replacing fires (whether wild or planned) will create openings large enough and with enough light for white pine to thrive.

Our task is to ensure that blister rust-resistant white pines become established on these sites. We need to plant them broadly and aggressively. And we need to manage the resulting stands to support white pine—light shade for 2 to 3 years for good seedling establishment followed by open, full sunlight for optimal growth.

– why we can't expect white pine to come back on its own

One piece of good news is that natural selection has begun to increase rust resistance levels in natural stands, and foresters are finding occasional healthy-looking naturally regenerated white pines in the forest. **These trees can be valuable contributors to genetic diversity and species recovery, so it is important to leave the best of them as a source of seed and seedlings for the continuing process of natural selection for rust resistance.**

But relying exclusively on natural



ABOVE: Natural selection may have increased blister rust resistance in native white pine stands, but too few mature, rust-resistant trees remain to produce sufficient seedlings to restore white pine to its former abundance in Inland Northwestern ecosystems. PHOTOGRAPH BY: Karen Wattenmaker.

processes to restore white pine to its former ecological position will be slow and uncertain at best, especially in areas where only a few remnant white pines remain to provide a seed source. These diminished gene pools are subject to chance occurrences of bark beetles, wildfire, and other disturbances. Where natural regeneration does occur, blister rust mortality in seedlings takes a heavy toll, leaving few white pine seedlings to populate the stands of the next generation. And natural selection cannot work at all where white pine seed sources have already been lost.

Without significant help, white pine is likely to continue its decline for the foreseeable future. If, within the next few human generations, we want to restore white pine to anything like its former role in the ecosystem, we must manage our forests actively, with restoration of white pine ecosystems as a specific and high priority goal. The only way we can achieve this seemingly daunting task on a landscape scale within a reasonable time-frame is to aggressively plant rust-resistant white pines.

WHITE PINE BREEDING PROGRAM

– a tool for ecological restoration

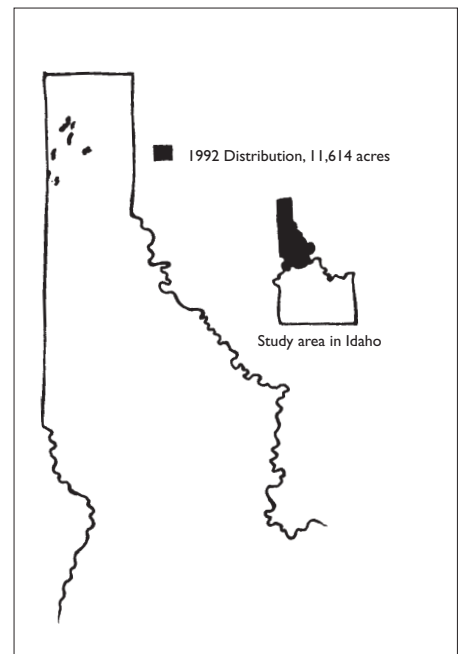
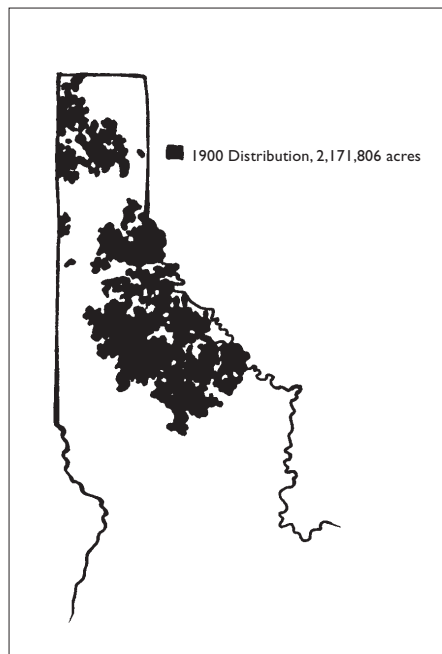
The Inland Empire Tree Improvement Cooperative (IETIC) and the USDA Forest Service have an active program designed to increase and diversify white pine’s genetic resistance to blister rust beyond the levels achieved in the original breeding program. They produce resistant materials, such as pollen, seed, and cuttings, that the IETIC distributes to its members, including nearly all the major public and private forest management organizations in the region (see member list, page 20).

– current status of planted, genetically improved trees

The white pines growing in planted stands today have come from a variety of genetic sources, including early “wild tree” collections, early seed orchards with relatively low levels of blister rust resistance, more advanced seed orchards with higher levels of resistance, and natural regeneration. These different genetic sources, which vary widely in their average levels of rust resistance, are sometimes also combined in planted forest stands.

However, even the genetic sources with the highest levels of resistance are not immune to the rust. In Bingham’s tests in the early 1970s, approximately 34 percent of seedlings from the Moscow seed orchard had either died or developed cankers 2 1/2 years after they were inoculated with rust. So it is no surprise that we see cankers in planted stands and that the amount of cankering varies from site to site.

Although we have been planting rust-resistant white pines in the Inland Northwest since the 1970s, very few



Approximately three quarters of a century after blister rust reached northern Idaho, western white pine cover type (stands with more than 15 percent white pine) has been reduced by more than 90 percent. Maps based on data from Interior Columbia River Basin Ecosystem Assessment Project and modified from map produced by Landscape Dynamics Lab, University of Idaho.

Table 1. Infection levels in planted F₂ western white pine in northern Idaho, 1997.

Site	Age ¹	N ²	Infected (%)
Priest Lake 1	8	83	2.5
Priest Lake 2	8	40	12.5
Palouse 1	8	129	33.3
Powell 1	9	152	21.1
Powell 2	9	109	35.8
Pierce 1	9	104	26.9
Pierce 2	9	116	32.8
Lochsa	9	112	64.3
North Fork 1	10	107	15.9
Palouse 2	11	99	19.2
North Fork 2	12	172	20.9
Fernan 1	13	69	63.8
Fernan 2	13	105	33.3
Avery	13	88	35.2
Mean		106.1	29.8

Source: J. Schwandt, personal communication

Notes: Surveys were conducted using nonpermanent plots. Overall mortality was not assessed.

F₂ refers to seedlings produced from matings between the selected progeny of crosses between the original wild stand parent trees selected by Bingham and his colleagues for the blister rust resistance program.

¹Age is years from planting.

²N refers to the number of trees in the sample.

plantings were designed to test the long-term stability of rust resistance under different environmental conditions. As a first step in gathering this information, we have begun to use genetic field tests and operational field plantings established by members of the Inland Empire Tree

Improvement Cooperative to evaluate the status of planted, genetically improved white pine.

Genetic tests, in which identities of the trees in the tests are known and their planting locations mapped, are inspected at regular intervals and therefore provide excellent opportuni-

Table 2. Rust infection and mortality in six Potlatch Corporation operational field plantings of western white pine; surveys conducted 1992-96.

Site	Stock type ¹	Age ²	N	Infected (%)	Rust killed (%)
French Creek	Moscow improved (F ₂)	11	489	48	13
	Unimproved	11	379	100	77
Camp 43	Moscow improved (F ₂)	11	435	38	9
	Unimproved	11	272	67	52
Robinson Cr. #6	Moscow improved (F ₂)	12	556	26	5
	Unimproved	12	664	100	38
Robinson Cr. #9	Moscow improved (F ₂)	11	400	9	0
	Unimproved	11	500	43	12
Scofield	Moscow improved (F ₂)	11	405	28	5
	Unimproved	11	487	93	33
	Moscow improved (F ₂)	15	150	64	16
	Unimproved	15	137	96	68
W. Fork Strychnine	Moscow improved (F ₂)	12	197	2	1
	Unimproved	12	43	0	0
	Moscow improved (F ₂)	14	150	2	0
	Unimproved	14	150	14	3
Mean ³	Moscow improved (F ₂)		363	31	7
	Unimproved		350	70	42

Notes: Data from these surveys came from nonpermanent plots in six planted stands that contained separate blocks of Moscow F₂ (blister rust-resistant) and unimproved white pine seedlings. All six stands were surveyed first by the Potlatch Corporation. The Scofield and Strychnine stands were re-surveyed several years later by the Inland Empire Tree Improvement Cooperative's White Pine Species Group. (Data on file with the Inland Empire Tree Improvement Cooperative, University of Idaho).

¹F₂ refers to seedlings produced from matings between the selected progeny of crosses between the original wild stand parent trees selected by Bingham and his colleagues for the blister rust resistance program.

²Age is years from planting.

³Mean does not include data from first evaluations at Scofield and Strychnine sites.

Table 3. Rust infection and mortality of western white pine in four genetic field tests, 1996.

Site	Stock type ¹	Age ²	N	Infected (%)	Rust killed (%)
Jackson Mountain	Moscow improved (F ₂)	14	142	60	11
	Unimproved	14	132	98	69
New Scofield	Moscow improved (F ₂)	14	124	68	10
	Unimproved	14	127	91	29
Gletty Creek	Moscow improved (F ₂)	25	163	20	13
	Unimproved	25	216	91	70
Merry Creek	Moscow improved (F ₂)	26	104	93	66
	Unimproved	12	171	100	100
Mean	Moscow improved (F ₂)		133	60	25
	Unimproved		162	95	67
Mean difference between Moscow F ₂ and unimproved				35	42

Note: The Jackson Mountain and New Scofield tests belong to the Potlatch Corporation. Rust surveys were conducted in these tests in 1996 by the Inland Empire Tree Improvement Cooperative White Pine Species Group. The Gletty Creek and Merry Creek sites are U.S. Forest Service tests.

¹F₂ refers to seedlings produced from matings between the selected progeny of crosses between the original wild stand parent trees selected by Bingham and his colleagues for the blister rust resistance program.

²Age is years from planting.

ties to monitor the occurrence and progression of blister rust infections. Paired operational plantings also provide good opportunities to compare the performances of genetically improved and unimproved stocks grown under similar operational reforestation conditions.

The evaluations conducted to date show three important trends. First, even where the same genetic material

was planted across the landscape, infection levels vary considerably from site to site. Infection levels are relatively high at a few sites, but low at most sites (table 1). Of 14 plantations surveyed in 1997, only two had very high infection levels (about 64%). In the remaining 12 locations, infection levels were near or substantially less than expectations that were based on the performance of F₂ seedlings

that had been inoculated only once in nursery tests.

Second, across the landscape, blister rust infection is much lower in the genetically improved white pines than in their unimproved counterparts (tables 2 and 3).

Third, mortality from blister rust is substantially lower in genetically improved white pines compared with their unimproved counterparts (tables 2 and 3).

MORTALITY FROM BLISTER RUST IS SUBSTANTIALLY LOWER IN GENETICALLY IMPROVED WHITE PINES COMPARED WITH THEIR UNIMPROVED COUNTERPARTS.

These differences hold true even at the heavily infected Merry Creek study site. There, by age 12, *all* the unimproved stock had died. But 34 percent of the F₂ trees from the Moscow white pine seed orchard were still alive at age 26, and many of them were already of merchantable size. Furthermore, at the Gletty Creek study site, where the same genetic sources were planted as at the Merry Creek site, only 13 percent of the Moscow (F₂) white pines had died by age 25 compared with 70 percent of unimproved stock of the same age (table 3).

So, although survival percentages of the Moscow (F₂) white pines at a small number of sites are lower than expectations that were based on early nursery tests (which showed 66% canker-free seedlings at 2 1/2 years after inoculation), on most sites, survival is close to or higher than expected. It is clear that genetic resistance to blister rust continues to function, even under a wide variety of environmental conditions.

– could we have a new strain of rust?

Are the higher-than-expected infection levels at a few sites evidence that the rust has mutated and become more virulent? Probably not.

Over the past 10 years or so, geneticists and tree improvement specialists have collected wild rust spores from many areas, including Merry Creek, a site with particularly high levels of rust infection in the white pines planted there. The spores have been used to screen white pine seedlings for rust resistance in nursery tests that included check-lots of seedlings with known levels of resistance. If a new, virulent strain of rust were present, levels of infection in the check-lots should have increased dramatically compared with previous inoculations. But levels of infection have not increased.

In addition, the rates of infection at the Merry Creek site follow a fairly smooth trajectory over time. If a new, virulent strain of rust had developed at Merry Creek, it would have shown up as a sharp increase in the infection rate over a short period of time. But this hasn't happened either.

Mutation in the rust is always a possibility. Two virulent strains of blister rust have been found, one in California and one in Oregon. Both appear to be ecologically restricted and have not spread beyond very limited geographic areas. At this time, we have no evidence of a new, more virulent strain of rust in the Inland Northwest.

– factors affecting rust infection levels in genetically improved trees

It would be useful to understand why the levels and rates of rust infection vary so widely from site to site and be able to predict the risk of



blister rust infection before we plant white pines. One reasonably good predictor of rust infection levels appears to be the abundance and species of *Ribes* plants near the white pines. For example, stinking currant (*Ribes hudsonianum*), which is found in riparian areas, produces about 100 times more inoculum than either prickly currant (*Ribes lacustre*) or sticky currant (*Ribes viscosissimum*), both of which are widely distributed in the upland areas of northern Idaho. So even sites with a low incidence of *Ribes hudsonianum* may promote high levels of infection in susceptible white pines.

Other variables, such as local climate, fire history, soil conditions, availability of soil nutrients, physiological conditions of the rust and the trees, and interactions among them may also affect intensity of rust infection. Once we have a better understanding of how each of these variables, and perhaps others, affects the incidence and severity of blister

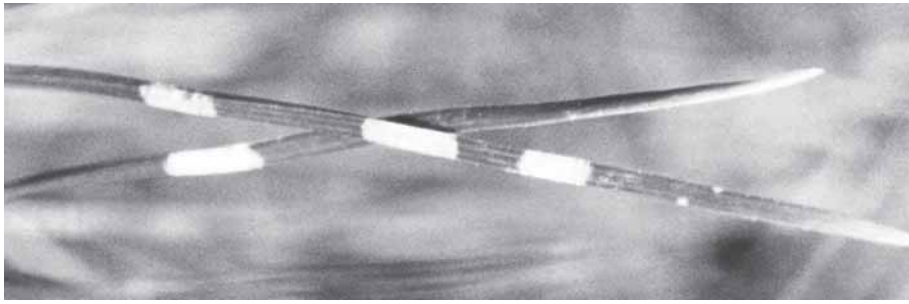
rust, we will be better able to predict the risk of infection and rank sites for probability of success in establishing new stands of planted white pine.

PHOTOGRAPH BY: Karen Wattenmaker.

– how we measure rust resistance and susceptibility

No single measure of rust infection tells the whole story of resistance and susceptibility. The easiest and most direct measure of susceptibility in seedlings is the number that die soon after they become infected.

Another indicator of susceptibility is a high number of rust spots on infected needles. But this indicator can be misleading because some resistant seedlings shed their infected



LEFT: The first measure used to differentiate between rust-resistant and susceptible families in the selection and breeding program is the number of rust spots per unit of needle. PHOTOGRAPH COURTESY OF: USDA Forest Service.

needles before the infection spreads or have a mechanism to stop the infection at the base of the needles or in the branches.

In addition to screenings in nurseries using artificial inoculations with rust spores, one of the most important ways we measure rust resistance is by tracking inoculated seedlings under many different field conditions and documenting the presence or absence of blister rust cankers and seedling growth and survival. On larger, more mature trees, measures of resistance and susceptibility may also include the numbers of rust cankers, their locations and shapes, and their rates of growth on the branches and main stems of infected trees. Trees with only a few cankers in the midst of stands with otherwise heavily cankered trees, or trees with cankers that are slow-growing or oddly shaped, may be resistant to the rust.

– current expectations of rust resistance and white pine mortality

Our expectation that approximately 34 percent of genetically improved trees from the Moscow white pine seed orchard will die from blister rust before they reach maturity is based on Bingham's tests of seedlings that were inoculated once under controlled conditions in forest nurseries in the early 1970s. Some people think we should anticipate higher mortality under field conditions because trees may be exposed repeatedly to rust

spores and because we have found a few highly infected planted stands. Repeated exposure to rust may indeed increase infection and mortality, but we are finding that even in highly infected stands, many of the improved white pines are alive and growing long after they were initially infected with rust. This is a rare phenomenon with unimproved trees.

WE ARE SELECTING AND BREEDING FOR STABILITY OF RUST RESISTANCE, THAT IS, LOW RISK OF LOSING OUR WHITE PINES TO A NEW STRAIN OF RUST.

At this time we do not have sufficient information to revise our long-term expectations of infection and mortality from rust. To get good

data we need well-designed, long-term tests that track the progression of rust infection and the timing of rust-caused mortality in known genetic materials. The USDA Forest Service and the Inland Empire Tree Improvement Cooperative currently have plans to establish and monitor new tests specifically designed for this purpose.

– progress toward highly resistant white pine

The Inland Empire Tree Improvement Cooperative/USDA Forest Service white pine breeding program is designed to increase rust resistance beyond the levels achieved in the early years. But *genetic immunity to rust is not a goal of the program.*

Genetic immunity means that immune trees do not become infected at all. But genetic immunity is usually

TYPES OF RUST RESISTANCE TRAITS IN WESTERN WHITE PINE

Screening for resistance to white pine blister rust is conducted in forest nursery beds. Seedlings are inoculated with rust spores in the fall of their second growing season and are inspected four times over the following three years.

HORIZONTAL Resistance Types (for selecting families)

- **low needle lesion frequency:** Seedlings have a relatively small number of needle lesions, based on number of spots per meter of needle length.
- **early stem symptoms:** Cankers and/or bark reactions take a relatively long time to develop. Selected families exhibit a small number of cankers and/or bark reactions at the second inspection relative to the number at the fourth inspection.
- **canker alive:** A high incidence of live seedlings have active cankers at the fourth inspection.
- **adjusted bark reaction:** High proportion of bark reaction in cankered seedlings at the fourth inspection

VERTICAL Resistance Types (for selecting individuals within families)

- **no spots:** Seedlings appear to be immune to rust infection. No lesions form on the needles after inoculation with rust spores.
- **needle shed:** Seedlings develop needle lesions after inoculation with rust spores, but drop the infected needles the first summer after infection.
- **fungicidal short shoot:** Seedlings develop needle lesions after inoculation with rust spores, but they retain their infected needles and don't develop a canker.
- **bark reaction:** Seedlings develop needle lesions after inoculation with rust spores and they develop a canker, but canker growth is arrested.

controlled by only one or a few genes. Strategies based on immunity can be overcome with relative ease by mutations in the disease organism. (This is one lesson we learned from breeding agricultural crops such as wheat and corn.) So, although it may be technically possible to breed for immunity, we are taking a different approach. **We are selecting and breeding for stability of rust resistance, that is, low risk of losing our white pines to a new strain of rust.**

The white pine blister rust resistance program relies on a variety of rust resistance mechanisms in white pines, many of which appear to be controlled by several genes. With this multi-resistance, multi-gene approach, the rust may infect, and even kill, some of the trees, but we expect *most* of the trees, even if they become infected, to continue to survive and grow, perhaps for centuries.

To be selected for the breeding program, each seedling must display at least two types of rust resistance in nursery trials. Geneticists identify seedling families that display multi-gene, or horizontal, types of resistance and then, within those families, they select a small number of individual seedlings that have superior height growth and display the types of resistance that appear to be controlled by single genes (vertical resistance).

So each seedling selected for the program has good growth potential and is doubly protected against death from blister rust by having both multi-gene *and* single-gene types of resistance. These selected seedlings are planted or grafted into seed orchards and may later be bred with each other in the breeding program.

In the newest seed orchards, we



group the trees by resistance type. Since near-neighbors tend to pollinate each other more frequently than trees farther apart, grouping by resistance type encourages pollination between similarly selected trees. This increases the likelihood that blister rust resistance will be expressed in the offspring.

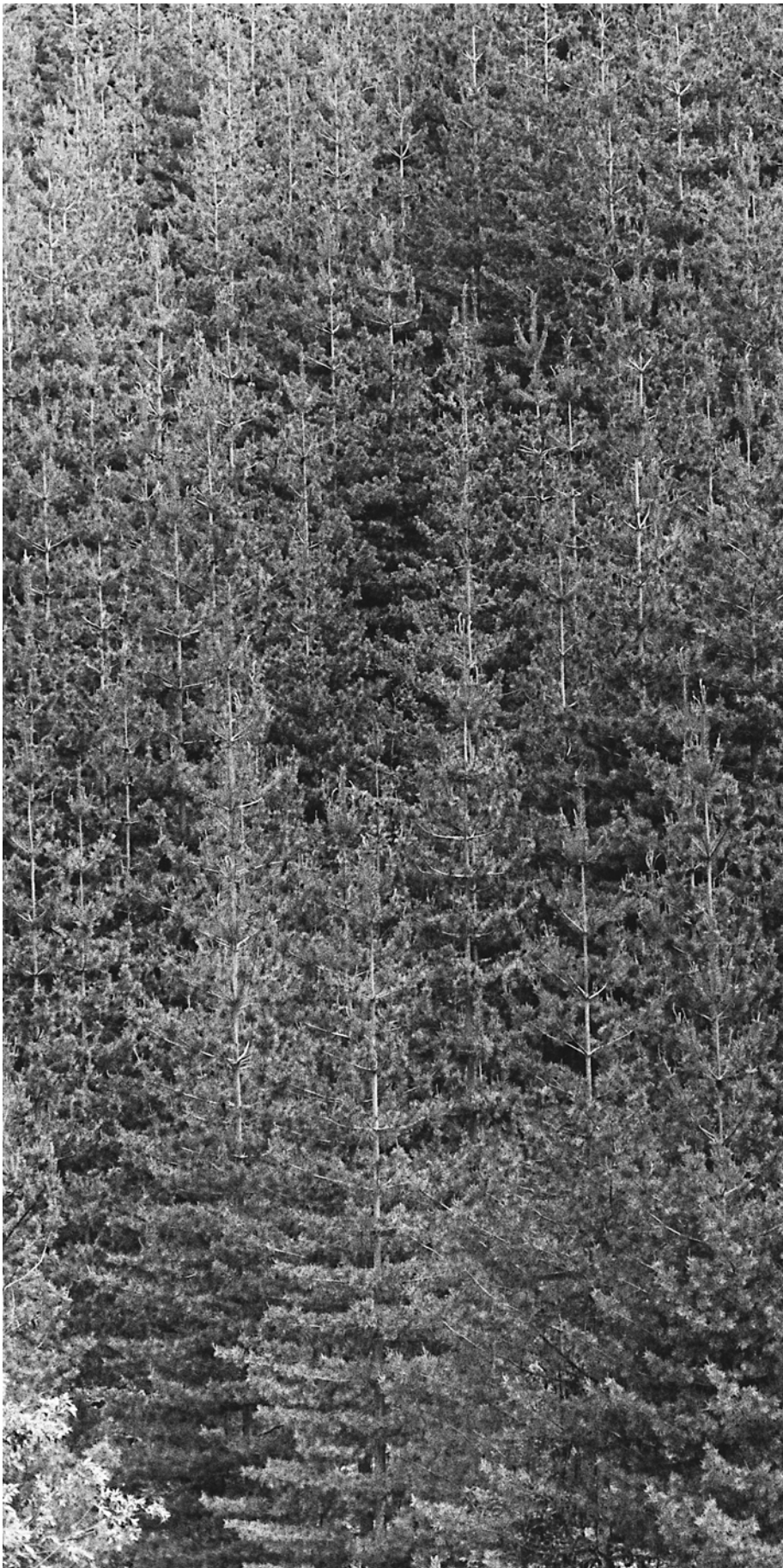
WE EXPECT SEEDLINGS FROM THE NEW ORCHARDS TO HAVE HIGHER LEVELS OF RESISTANCE... AS HIGH AS 90+ PERCENT.

We expect seedlings from the new orchards to have higher levels of rust resistance than those from the older orchards, possibly as high as 90+ percent. Although it will take several years to establish the new orchards, seed production should begin before the year 2010. Once we have enough seed, it will be critical to establish long-term field trials to help quantify the actual gains in resistance over the life of the trees. With stable genetic resistance to blister rust, we can manage stands to favor white pine for long-term ecological and/or economic benefits.



TOP: At the USDA Forest Service Nursery at Coeur d'Alene, Idaho, white pine seedlings are inspected four times over a period of three years after inoculation with blister rust spores. Data from the multiple inspections help researchers and breeders to identify families and individuals that are genetically resistant to rust. BOTTOM: In addition to blister rust resistance, height growth at two and five growing seasons after germination is considered when identifying genotypes for the breeding and/or seed orchard programs.

PHOTOGRAPHS BY: Jesse Tinsley.



A FUTURE FULL OF WHITE PINES

We can restore our white pine ecosystems to health and vigor, but it is going to take a concerted effort among forest managers in the Inland Northwest to do so. To really have an impact, the white pine breeding program must be coupled with a strong delivery system—an aggressive planting program using blister rust-resistant white pines. This will require much larger forest openings than are favored by the strong current emphasis on selection cutting. In addition, silvicultural tools such as pruning can help deal with the wide variation in infection levels across the landscape.

With so much variability in site and stand conditions in the region, it is impossible to provide a comprehensive set of management guidelines in this publication. However, here are some recommendations that will make a difference.

– regeneration

- **plant rust-resistant white pines.** Take every opportunity you can to restore white pine across the estimated 5 million acres of forests in the region that have the potential to grow this valuable and important species. Plant where fires and/or insects and diseases have killed the species that replaced white pine in the Inland Northwest. Make sure those seedlings have full or nearly full sunlight two to three years after planting to promote optimal growth. We have an abundance of improved seed, so resistant stock is readily available.

LEFT: Healthy stands of planted, blister rust-resistant white pine such as the vigor/quality plot at Priest River Experimental Forest in northern Idaho demonstrate the potential for restoring white pine to Inland Northwestern ecosystems. PHOTOGRAPH BY: Michele Kimberling, courtesy of USDA Forest Service.

Plant up to 300 to 400 white pines per acre. (See page 20 for information on who to contact for seed, seedlings, and advice on species mixes, stocking levels, planting techniques, and maintenance of new white pine stands.)

- **retain the best 5 to 10 wild white pines per acre and sufficiently large openings for natural regeneration.**

These trees will help maintain a broad genetic base of white pine in the forest and allow natural selection to gradually increase resistance levels in naturally regenerated stands. We can't rely exclusively on these stands to restore white pine, but they can contribute variation and a source of seed for natural selection in the long term.

- **reduce overstory densities and create relatively large openings in the canopy so sufficient light can reach the forest floor. Don't wait for stand-replacing wildfires to create large openings. Either create openings that are several acres in size or leave scattered seed trees in an overstory that provides less than 20 percent canopy cover.**

In full sunlight white pines can outgrow most of their competitors. Partial shade (30-40% full sunlight) can improve survival of planted or naturally regenerated white pines during their first two to three years, but too much shade greatly reduces their growth and favors the shade-tolerant species.

- **retain and protect the wild white pines that were selected for the blister rust resistance testing and breeding program.** You may come across some large old white pines that are marked with tags or numbers or are painted with stripes. These old veterans are rare and valuable. They represent the foundation of the breeding program and can contribute significantly to naturally regenerated



stands that will gradually increase in resistance through natural selection. Protect these trees from harvest or other people-related damage. Re-tag or remonument them where previous tagging is weathered or otherwise damaged. Flag these trees as "protected" in your stand records and other information systems. Clone them by grafting into gene conservation clone banks.

– pruning

In young white pine stands where infection levels and the risk of losing large numbers of trees to blister rust may be too high, pruning may help to reduce infections and prolong survival. Here are some guidelines:

- **concentrate on stands with infected trees that are between 10 and 25 years old.** In stands of this age with any significant rust, most of the very susceptible trees will already have died or will be clearly declining so your efforts will not be wasted. Stands with little or no blister rust don't need to be pruned.



TOP: Planting genetically improved white pine seedlings is a key strategy in re-establishing healthy ecosystem processes in Inland Northwestern forests. PHOTOGRAPH BY: Pam Benham. BOTTOM: Pruning branches that have non-lethal cankers in the lower crowns of young white pines may prolong survival and increase the numbers of trees that survive to maturity. PHOTOGRAPH BY: John Schwandt.

• **prune branches before infections reach the main stems.**

Once the infection reaches the main stem, it is too late to prune. A canker that is more than 6 inches from the main stem is considered a candidate for pruning. Leave a branch collar (the ringed, slightly swelled base of the branch) when pruning. Make the cut perpendicular to the axis of the branch. This will result in a smaller wound, promote faster healing, and minimize decay.

• **prune branches from ground level up to 8 to 10 feet, but do not reduce live crown ratio to less than 50 percent.**

Branches close to the ground have the highest risk of infection because environmental conditions for rust infection are most favorable there. But the crown is the tree's photosynthetic engine. A crown that is too small will not be able to sustain a tree's vigor. So prune prudently.

Consult your local Idaho Department of Lands forest practices adviser or your local extension forester for more information on pruning tools and techniques.

– **thinning**

Use caution! We usually manage white pine in mixed-species stands, and thinning may be desirable to meet some management objectives. For example, thinning overly dense stands can increase the value of stands by concentrating growth on fewer, better-quality trees. Thinning can help maintain growth of the white pines and survival of the larch and ponderosa pine.

But thinning should be applied with caution where managing white pines.

More than 20 to 30 percent of full sunlight reaching the forest floor will increase *Ribes* populations, leading to an increase in the numbers of rust spores and, potentially, an increase in the levels of rust infection in the pines.

In one study that was established in 1969 in naturally regenerated and planted white pine stands in northern Idaho, at 22 years after treatment, thinned plots had a lower percentage of healthy trees than the control plots (15% versus 21%) and a slightly greater mortality (61% versus 59%).

Similarly, in a study established in a dense stand of naturally regenerated white pines (with about 600 trees per acre) in British Columbia, at 10 years after thinning, the thinned-only treatment (with about 200 trees per acre) had a lower percentage of healthy trees than the controls (54% versus 61%). **It appears that in addition to increasing *Ribes* populations, thinning may also remove infected trees that might otherwise survive a rust infection.**

Where thinning is desirable to meet management objectives, a variety of techniques can mitigate impacts on white pine. For example you can:

- **thin by removing trees of the other species, but not the white pines.** If densities of white pine are not too high, you may ignore white pines in spacing considerations and expect to lose some white pines to blister rust.
- **delay thinning** until most of the *Ribes* has already been shaded out of the stand.
- **thin to tighter spacing** in stands that have a significant white pine component. In a 30-year-old white pine stand, 10-foot spacing would be ideal. Depending on site, stand condition, and objectives, however, spacing may be as tight as 7 feet.
- **thin only around the potential crop trees of shade-intolerant species** (e.g., white pine, larch, and ponderosa pine) and leave the rest of the stand unthinned.

It may also be desirable to couple the thinning operation with pruning in at least part of the white pine stand. In the Idaho study mentioned above,

white pine survival in plots that were pruned as well as thinned was higher (60-65% survival) than in the thinned only and control plots (35-40% survival). In the British Columbia study, however, the percentage of healthy trees was slightly lower in the thinned-and-pruned block (~230 trees per acre) than in either the control block or the pruned-only block (58%, 61%, and 63% healthy trees, respectively). Treatments such as these clearly require additional study to evaluate their effectiveness over time and across a wider array of sites.



PHOTOGRAPH BY: Theresa Jain.

RESEARCH HORIZONS

We do not yet fully understand the genetic basis of blister rust resistance or the interactions among blister rust, its hosts, and their environments. Only through well-planned, long term research will we be able to answer questions such as these: How do natural and genetically improved white pines perform under field conditions over the long term? How can cultural treatments be modified to enhance long-term survival over a variety of environmental conditions? What are the critical points in the disease process? What are the

critical factors in the genetic and physiological conditions of resistance in the host? What factors affect the biology and virulence of the rust?

All of these pieces of the puzzle are needed to support our long-term management strategies to restore healthy white pine ecosystems. Answers to some of these questions will become available as ongoing research studies are completed and as we begin to utilize our genetic tests and new technologies in new ways. What is required is a commitment to allocate the resources to sustain long-term research and application of results.

WORKING TOGETHER

Any broad-based program that produces critical scientific information, as well as trees for planting, requires a strong scientific base and partnerships among federal, state, and private land management, research, and educational institutions in the region. Existing coalitions, such as the Inland Empire Tree Improvement Cooperative, provide the foundation for such partnerships, but it is the long-term support of these programs on the part of member organizations that is the key to success.

Furthermore, on public lands and on many privately owned lands, management programs aimed at restoring western white pine need broader public support. By continuing to breed, plant, and manage white pine, and by continuing to tell the white pine story, we can garner that support and help to restore King Pine to its majestic place in the ecosystems of the Inland Northwest. Our legacy will be the towering and healthy white pine forests of the future. They will remain long after we have gone.

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WHERE TO GO FOR INFORMATION & PLANT MATERIALS

– seed

Tim Greaney
Northwest Management, Inc.
P.O. Box 9748
Moscow, ID 83843
Phone: (208) 883-4488
Fax: (208) 883-1098
email: nwmanage@turbonet.com

– blister rust-resistant white pine seedlings

Clifty View Nursery, Inc.
wholesale only (resale number required);
50 minimum

Route 1, Box 509
Bonners Ferry, ID 83805
Phone: (208) 267-7129
Fax: (208) 267-8559

Coeur d'Alene Nursery
sales to public agencies only (city,
county, federal, etc.); 300 minimum

USDA Forest Service
3600 Nursery Road
Coeur d'Alene, ID 83814
Phone: (208) 765-7375
Fax: (208) 765-7474

Forest Research Nursery
5 minimum for 20 cubic inch containers;
20 minimum for 5 cubic inch containers
University of Idaho
Moscow, ID 83844-1137
Phone: (208) 885-3888
Fax: (208) 885-6226
<http://www.uidaho.edu/seedlings>

North Woods Nursery, Inc.
P.O. Box 149
Elk River, ID 83827-0149
Phone: (208) 826-3408
Fax: (208) 826-3421

Pleasant Hills Nursery
20 minimum
1011 Anderson Road
Troy, ID 83871
Phone: (208) 877-1600
Fax: (208) 877-1356
email: mason@moscow.com

Western Forest Systems, Inc.
10,000 minimum under contract
1509 Ripon
Lewiston, ID 83501
Phone: (208) 743-0147
Fax: (208) 746-0791

– extension and forestry assistance

Extension Forestry
College of Natural Resources
University of Idaho
P.O. Box 441140
Moscow, ID 83844-1140
Phone: (208) 885-6356
email: extfor@uidaho.edu

Montana State University Extension Forestry
32 Campus Drive
Missoula, MT 59812-0606
Phone: (406) 243-2773
email: extfor@selway.umt.net

Extension Forester
Department of Natural Resources
131 Johnson Hall
Washington State University
Pullman, WA 99164-6410
Phone: (509) 335-2963

Idaho Department of Lands
Forestry Assistance Bureau
3780 Industrial Avenue
Coeur d'Alene, ID 83814
Phone: (208) 769-1525
Fax: (208) 769-1524
email: blove@cda.idl.state.id.us
<http://www2.state.id.us/lands/Bureau/forasst.htm>

– rust resistance breeding program

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– blister rust biology

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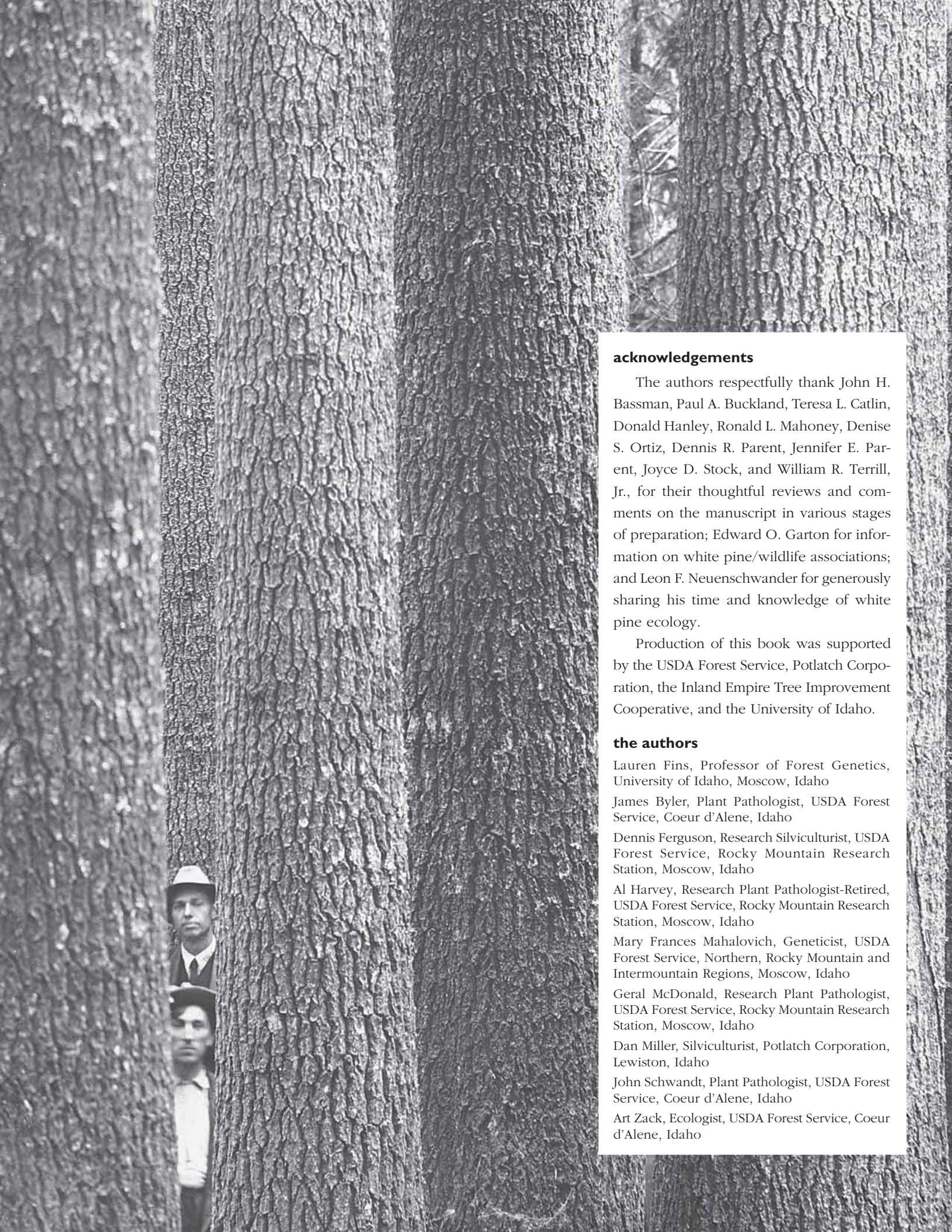
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