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Impacts of White Pine Blister Rust and Competition on Natural Whitebark Pine Regeneration in Northern Idaho 1995–2012

John W. Schwandt, Ph.D., Plant Pathologist
USDA Forest Service Northern Region, Forest Health Protection

Holly S.J. Kearns Ph.D., Plant Pathologist
USDA Forest Service Pacific Northwest Region, Forest Health Protection

James W. Byler, Ph.D., Plant Pathologist
USDA Forest Service Northern Region, Forest Health Protection, Retired

Abstract

The impacts of white pine blister rust (WPBR) on whitebark pine (Pinus albicaulis) *natural regeneration were monitored for 17 years on five sites in northern Idaho. A total of 3,649 trees were tagged in 1995 and remeasured in 2001, 2007, and 2012; 1,898 were whitebark pine, and 80% of the remainder were subalpine fir (*Abies lasiocarpa*). Over 70% of the whitebark pine were less than one inch in diameter in 1995, and less than eight percent were five inches and greater in diameter. In 1995, approximately half (51.0%) of all live whitebark pine were not infected by WPBR (range 14.4 to 67.9%), and nearly 12% were dead (range 6.6 to 15.5%). By 2012 the number of uninfected trees dropped to 12% (range 2.0 to 21.4%), and average mortality increased to 59.5% (range 47.4 to 69.4%). Almost 90% of all mortality was caused by WPBR.*

During the 17-year monitoring period over 75% of whitebark pines originally uninfected by WPBR became infected, a 4.3% average annual rate of infection (range 1.8–5.4%), and 51% of live trees died, an average annual rate of 3.0% (range 2.3–3.8%). Small trees were killed more quickly than larger ones. Almost all WPBR infections on small trees were lethal, whereas 30% of infections on trees five inches and greater in diameter were either safe or prunable. After 17 years only 2.4% of whitebark pine five inches and greater in diameter were not infected by WPBR, and 15% of the trees less than one inch in diameter were uninfected. More than 85% of the remaining live, infected trees are expected to die or be top-killed by existing WPBR infections.

In spite of a 27% increase in the total number of whitebark pine due to ingrowth, the number of live whitebark pine dropped by 26.3%. The number of live, uninfected whitebark pine per acre is now less than the number of subalpine fir in all areas. These results indicate the condition of whitebark pine in northern Idaho stands is in serious decline, and survival of natural regeneration is in jeopardy due to impacts from WPBR.

Introduction

Whitebark pine (*Pinus albicaulis*) is a keystone species in high-elevation forests across the Rocky Mountains and Inland Northwest (Tomback et al. 2001, Tomback and Kendall 2001). It occurs in many upper subalpine and timberline zones in the western United States, southern Alberta, and British Columbia (McCaughey and Schmidt 2001). It is a slow growing species that is moderately shade intolerant. Whitebark pine occurs both as a climax species on harsh sites where competition is limited and as a seral species on more temperate sites where it often facilitates succession of other tree species (Figure 1). In mixed-conifer communities its common associates are subalpine fir (*Abies lasiocarpa)*, lodgepole pine (*Pinus contorta)*, mountain hemlock (*Tsuga mertensiana)*, Engelmann spruce (*Picea engelmannii)* and alpine larch (*Larix lyallii)*. Whitebark pine produces large, wingless seeds in indehiscent cones at the tops of mature trees. The highly nutritional seeds are a favorite food for many animals from squirrels to grizzly bears, but it is the caching behavior of the Clark's nutcracker that assures seed dissemination over wide areas (Tomback 2001).

Figure 1. *Islands of vegetation that have grown up under the protection of mature whitebark pine in northwestern Montana.*

Whitebark pine populations and health have declined dramatically across most of its range during the past century and particularly during recent decades (Tomback et al. 2001). This decline is attributed to four interrelated causes: outbreaks of mountain pine beetle (*Dendroctonus ponderosae)* (MPB); wildfires and wildfire suppression; competition from other vegetation; and white pine blister rust (*Cronartium ribicola)* (WPBR), a fungal pathogen that was introduced into western North America a century ago (Figure 2).

Figure 2. *Natural whitebark pine regeneration infected with WPBR and MPB killed mature trees in the background.*

Throughout history, extensive outbreaks of MPB, a native bark beetle, have periodically occurred in mature whitebark pine forests (Figure 3). The most recent outbreak began in the late 1990s and by 2007 had caused mortality of whitebark pine on nearly half a million acres in the western United States (Gibson et al. 2008). Recent surveys found that MPB killed 30–97 percent of the whitebark pine basal area in affected stands during this outbreak (Kegley et al. 2011).

Figure 3. *Severe whitebark pine mortality caused by MPB. (photo by K. Gibson)*

While high intensity wildfires may kill entire populations of whitebark pine, wildfires in high elevation forests are often mixed severity fires with highly variable fire return intervals. Mixed severity fires can be beneficial for whitebark pine regeneration by creating openings and killing competing vegetation while leaving some mature whitebark pine as a seed source. Wildfire suppression may reduce regeneration opportunities for whitebark pine while increasing competition from shade tolerant tree species (Keane et al. 2002). Whitebark pine is also relatively well adapted to severe, stand-replacing fires as Clark's nutcrackers can disperse seeds up to one hundred times farther than wind disperses its competitors. However, Clark's nutcrackers may not be attracted to sites where most of the cone producing trees have been lost due to fires, competition, WPBR, or MPB (McKinney et al. 2009).

The introduction of *Cronartium ribicola* to western North America altered the historic successional pathways of five-needled pines (McDonald and Hoff 2001). *Cronartium ribicola* has a complicated life cycle involving five spore stages on two different hosts. Five-needled pines can only be infected through live needles under favorable environmental conditions by spores produced on the alternate host (primarily *Ribes spp.*). Once established, the fungus grows into the adjacent branch or bole where it causes a characteristic canker (Figure 4). A branch canker typically continues to expand until it reaches the bole where it girdles and kills the tree above the point of branch origin. Small trees can be girdled and killed within a few years. Mature whitebark

***Figure 4**. Characteristic sporulating WPBR canker girdling a small whitebark pine stem.*

pines are rarely killed by WPBR, but tops and upper branches are often killed resulting in a loss of cone production and therefore the potential for regeneration (Hoff et al. 2001, McKinney and Tomback 2007, McKinney et al. 2009).

All North American five-needled pines have proven to be highly susceptible to WPBR, and early assessments ranked whitebark as one of the most susceptible pines (Lachmund 1926, Childs et al. 1938, Bedwell and Childs 1943). More recently Hoff et al. (2001) concluded that whitebark pine and western white pine (*Pinus monticola)* were both very susceptible, but the level of resistance depended on where the seed was collected. Based on artificial inoculations at the Coeur d'Alene Nursery in Idaho, it appears that whitebark pine contains more genetic resistance to WPBR than western white pine, limber pine (*P. flexilis*), or southwestern white pine (*P. strobiformis*), but it takes fewer cankers to kill whitebark pine than the other species (Mahalovich and Dickerson 2004). The proportion of whitebark pines that are infected or killed by WPBR varies widely by geographic area, but the highest incidence occurs in the northern Rockies where infection levels are often over 70% (Keane and Arno 1993, Schwandt 2006, Kendall and Keane 2001, Kegley et al. 2004).

The ongoing decline of whitebark pine has led to its loss as a functional ecosystem component in many high-elevation ecosystems (Lantz 2010, Schwandt 2006, Tomback et al. 2001). As a result, whitebark pine has been classified as an endangered species in Canada, a species of concern in the state of Washington, and a sensitive species in the Northern Region (Region 1) of the U.S. Forest Service. In 2011, the U.S. Fish and Wildlife Service concluded that listing the species as threatened or endangered in the U.S. is warranted but precluded by higher priority actions, and it is currently a "Candidate Species" for Threatened and Endangered Species listing. Many authors have called for restoration of whitebark pine (Hoff et al. 2001, Keane and Parsons 2010, Lantz 2010, Schwandt 2006, Tomback et al. 2001). Restoration strategies include the development of WPBR resistant whitebark pine, whitebark pine planting or direct seeding, thinning to reduce competition, prescribed fire to encourage natural regeneration, and strategies to reduce losses of mature trees to MPB.

Purpose

Most of the interest in the past has been focused on the loss of mature whitebark, but the future of the species depends on the fate of the regeneration. This project was initiated to monitor impacts from WPBR and competing vegetation on naturally occurring whitebark pine regeneration in northern Idaho over time. This monitoring study was designed to determine if natural regeneration of whitebark pine will lead to mature stands with a significant whitebark pine component.

Specifically, the goals of the study were to determine:

1) the condition of natural whitebark pine regeneration in northern Idaho stands.
2) if the incidence of WPBR infection and mortality varies with tree size.

3) if the severity of infection and mortality varies with sample location.
4) the rates of WPBR infection and tree mortality over time.
5) if whitebark pine regeneration is a significant component in mixed species stands, and if it is declining in abundance relative to other tree species.
6) if suppression of whitebark pine by other tree species is a major concern that might be addressed by silvicultural treatments.

Materials and Methods

In 1995, as part of the U.S. Forest Service Northern Region (Region 1) Permanent Plot Program, a series of permanent monitoring plots were established in five high-elevation, mixed conifer forests in northern Idaho where whitebark pine had historically been a major component. Although there were still some live remnant mature whitebark pine near each area, most of the mature trees had been lost to fires or MPB, but there was an abundance of whitebark pine natural regeneration (Figure 5). The plots were evaluated periodically to document conditions over time. To date, the plots have been re-measured three times: 2001, 2007, and 2012.

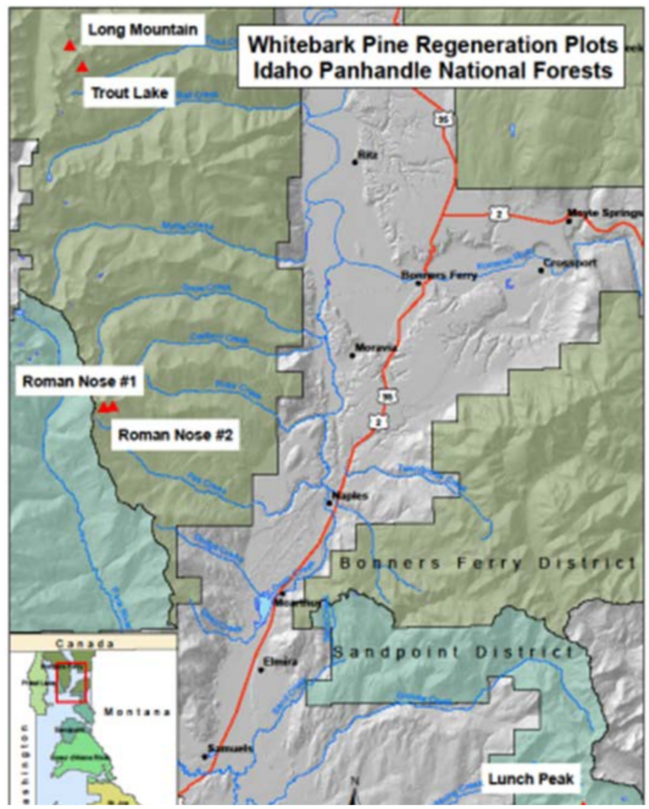


Figure 5. *Whitebark pine regeneration monitoring sites in northern Idaho.*

Sampling Design

The basic sampling design used the Region 1 Permanent Plot Protocols (*Chapter 600),* but instead of small square plots, long, narrow rectangular transects were used to more efficiently sample variable whitebark pine density across the landscape. Transects were 20 feet wide (10 feet on each side of a center line) and 100–500 feet long depending on the density of whitebark pine (Figure 6). Four to seven transects were established at each site and each tree greater than six inches in height was given an x,y coordinate based on distance along the transect and left or right of the center line. The goal was to individually map and monitor at least 400 whitebark pine per site, with approximately 100 whitebark per transect.

Data Collection

Transects were monumented with carsonite or metal stakes, and GPS locations at the start, middle, and end points were recorded. All information was originally taken using the R1-EDIT Stand Exam protocols in use by Region 1 in 1995. Since then the Region switched to the Common Stand Exam System (Anonymous 2012), and all subsequent re-measurements have been taken in accordance with those protocols. Site information recorded for each transect included slope, aspect, elevation, habitat type, and abundance of alternate hosts for WPBR *(Ribes spp., Pedicularis spp.,* and *Castilleja miniata).*

Figure 6. *Typical transect at Long Mtn. site.*

All live and dead trees greater than six inches tall were individually tagged and the following information recorded: tree species, tree status (live or dead), height, live crown ratio, crown class, and diameter at breast height (DBH) for trees ≥ 4.5 feet tall. Tree damage data included agent and severity, as described in the Region 1 protocols (Anonymous 2012). In all cases throughout this report, the terms "infected" and "uninfected" refer solely to the presence or absence of WPBR. Severity rating for WPBR was based on location of the WPBR canker closest to the bole (Schwandt et al. 2013a). WPBR cankers were categorized as lethal if they occurred on the bole or on a branch within six inches of the bole. Infected trees that had at least one branch canker between six and 24 inches from the bole and less than eight feet from the ground were classified as prunable. Trees with WPBR branch cankers more than 24 inches from the bole were classified as safe, but the tree was categorized as infected. Trees top-killed by WPBR (Figure 7) were put in a separate category. In addition, the numbers of branch and bole cankers and percent girdle for bole cankers were recorded. All trees were categorized as live infected, live uninfected, or dead (regardless of cause). Trees that were dead at the time of plot establishment were not evaluated for cause of death, but

Figure 7*. Whitebark pine top-killed by WPBR.*

cause of death was determined when possible for all trees that died between measurement periods. Trees less than six inches tall were tallied by species on 1/300 acre subplots established at the start, midpoint and end of each transect.

In the 2012 re-measurement, all data continued to be recorded for all whitebark pine greater than six inches tall, and competing trees greater than three inches DBH as specified above. However, to reduce sampling time, all competing tree species less than three inches DBH were grouped by species and size class, and recorded on 1/200th acre plots centered on the strip transect center lines and located every 20 feet of transect length (starting with the center of the first plot at 10 feet from the start and continuing plot centers at 30, 50, 70, etc. to the end of the transect).

Data Analysis

Data were summarized by species, tree status, and diameter class for each area based on the 1995 data. This set of originally tagged trees was then re-classified at each measurement period, allowing the amount of new infection and mortality to be calculated for each measurement interval. Trees per acre (TPA) was calculated based on the transect or plot size and number of trees tallied.

Trees that grew to be taller than six inches after 1995 are called "ingrowth." Ingrowth was added to the original trees to determine population trends for whitebark pine that could be compared with trends in competing species over time. Data analysis was complicated by the changing protocols and difficulty with the Regional database, which is not set up for remeasurements of permanent plots. As a result, each measurement was stored separately and analyses required the consolidation of multiple records for each tree.

Results and Discussion

The five survey areas ranged in elevation from 6,377 feet to 7,024 feet and were relatively open sites resulting from fires 40-50 years ago (Table 1, Figures 8 and 9). Over 15,000 total records were created for 3,649 trees; 7,592 records were associated with 1,898 whitebark pine.

***Table 1**. Site information for sampled stands.*

Area	Transect		Habitat Type[1]	Elevation (ft)	Fire History
	#	Total Length (ft)			
Roman Nose #1	4	1814	730 ABLA/VASC	6,496	Stand replacement in 1967
Roman Nose #2	4	1970	730 ABLA/VASC	6,447	Stand replacement in 1967
Trout Lake	5	1124	672 ABLA/MEFE	6,515	Mixed severity in 1967
Lunch Peak	5	1570	694 ABLA/XETE	6,377	Unknown
Long Mountain	7	759	694 ABLA/XETE	7,024	Stand replacement in 1967

[1]See R-1 Common Stand Exam Field Guide Appendix G for details.

Figure 8. *Roman Nose #2 site in 2012.*

Figure 9. *Ridge with Long Mountain transects in 2007.*

Initial Condition (1995)

The percentage of live, WPBR-infected whitebark pine at the time of plot establishment in 1995 ranged from 25.5% at Trout Lake to 70.6% at Lunch Peak, and the amount of dead whitebark pine ranged from 6.6% at Trout Lake to 15.5% at Long Mountain (Table 2 and Figure 10). The average condition of whitebark pine across the five sites was: 47.6% live and uninfected by WPBR, 40.6% live and infected by WPBR, and 11.8% dead. The incidence of WPBR infection at Lunch Peak was nearly twice that of the other areas, but the amount of mortality was similar (Table 2, Figure 10). High infection and low mortality in small trees likely means much of the infection was recent, as small trees are usually killed quickly.

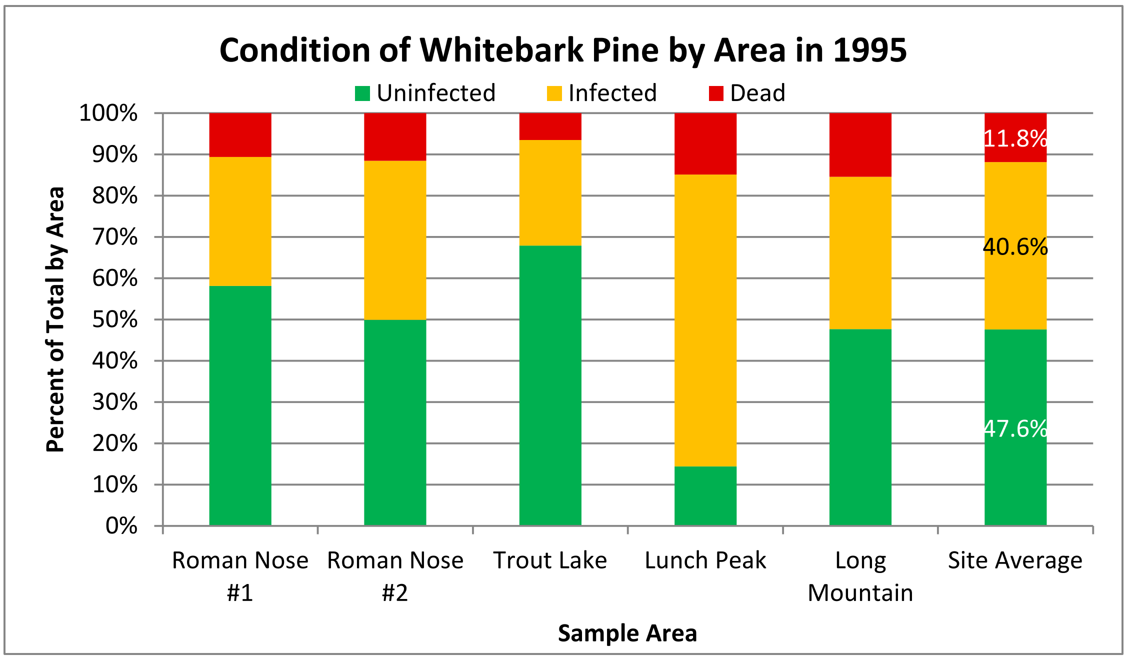


Figure 10. *Condition of whitebark pine at the time of plot establishment (1995).*

Table 2. Condition of whitebark pine at each area at the time of plot establishment in 1995.

Area	Live, Uninfected by WPBR		Live, Infected by WPBR		Dead		Total
	#	%	#	%	#	%	#
Roman Nose #1	158	58.1	85	31.3	29	10.7	272
Roman Nose #2	202	49.9	156	38.5	47	11.6	405
Trout Lake	311	67.9	117	25.5	30	6.6	458
Lunch Peak	29	14.4	142	70.6	30	14.9	201
Long Mountain	268	47.7	207	36.8	87	15.5	562
Total / Ave%	**968**	**47.6**	**707**	**40.6**	**223**	**11.8**	**1898**
of all whitebark pine		51.0		37.2		11.7	

Infection and mortality by WPBR varied greatly by DBH class. Although over 70% of the trees were in the smallest diameter class, the proportion of uninfected whitebark pine declined as tree diameter increased (Figure 11). Schwandt and Kegley (2004) also observed a greater proportion of large trees with WPBR infections, and Tomback et al. (1995) found that age and height were important predictors of incidence of infection. Higher rust incidence in larger trees is probably because they present a larger "target" for the rust spores. Larger trees also may be older and thus have been exposed to the rust for a longer period of time. Since WPBR kills small trees rapidly, the high proportion of dead larger trees seems surprising. But this is likely related to the longevity of larger dead trees as snags compared to the relatively rapid loss of smaller trees due to snow breakage and/or decay.

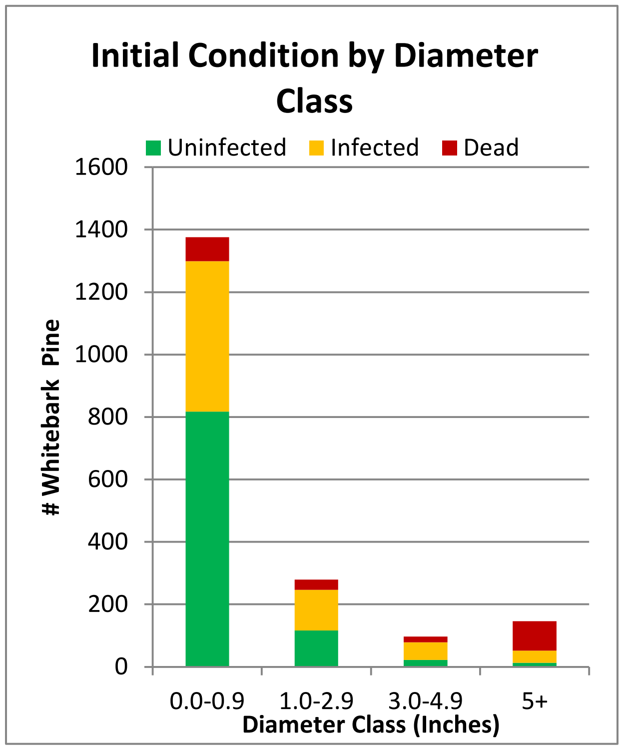


***Figure 11**. Condition of whitebark pine at plot establishment in 1995 by diameter class.*

Cause of Mortality

Of the 1,675 whitebark pine that were alive at the beginning of this study, 847 (50.6%) died during the 17-year monitoring period. WPBR was the cause of death for 87% of the whitebark pine < 1.0 inch in diameter and 92% of whitebark ≥ 1.0 inch in diameter (Table 3, Figure 12). No mortality attributed to MPB was noted as even the large diameter whitebark pine in these areas were too small to be attractive to MPB. Mortality due to WPBR was likely even higher since it was often difficult to identify cankers on small weather-beaten trees. More small trees may have died from other causes than larger trees because they were more susceptible to weather events or

Table 3. Cause of death for trees that were alive in 1995 and died during the study.

	Cause of Death			
DBH Class	WPBR	Other	Total	% Rust
Trees <1" DBH	546	83	629	87%
Trees ≥1" DBH	200	18	218	92%
Total/Average%	746	101	847	88%

***Figure 12**. Typical WPBR caused mortality of small whitebark pine.*

animal damage. However, since the mortality was almost exclusively due to WPBR, we lumped all mortality in the discussions that follow.

Trends Over 17 Years

The total number of live, uninfected whitebark pine decreased while mortality increased greatly over 17 years of monitoring (Figure 13). The percentage of trees that were uninfected was initially 51.0% but decreased to 12.8% by 2012, while the amount of mortality increased from 11.7% to 56.6%. Percent mortality after 17 years exceeds the initial level of infection, which indicates that not only did most trees that were initially infected die but also many trees died that became infected after 1995.

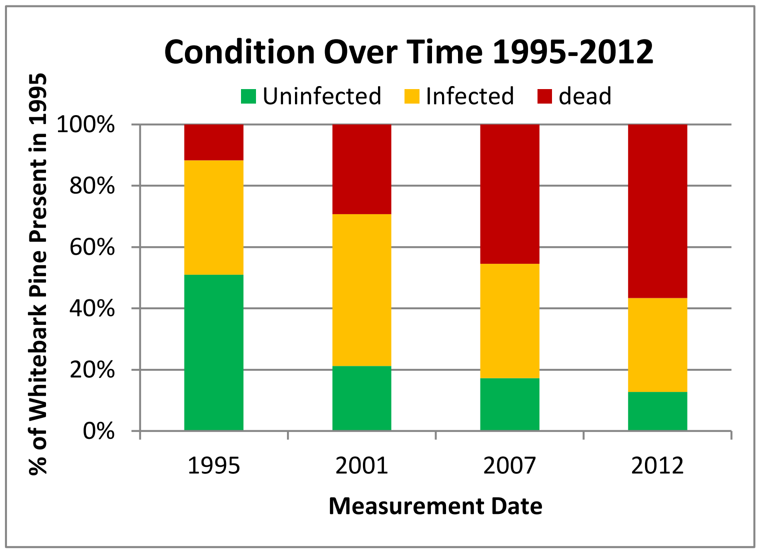


***Figure 13**. Condition of original whitebark pine averaged across all sites from 1995-2012.*

The high level of infection recorded in 2001 may have been the result of one (or more) "wave years" of especially favorable environmental conditions for WPBR infection. A wave year occurred in western white pine during 1995-1996 (Schwandt et al. 2013b) and perhaps the same wave year took place in whitebark pine. Kearns et al. (2012) also found a large increase in the incidence of infection and mortality of planted western white pine between 1995 and 2000. The high initial infection level at Lunch Peak but moderate mortality may indicate a wave year just prior to plot establishment at that location (Table 2).

Between 1995 and 2012, the percent of uninfected whitebark pine in each area declined while the percent mortality increased (Figures 14 and 15). After 17 years, less than 25% of the trees remained free of WPBR infections in any study area, and at Lunch Peak only 2% of the 201 original whitebark pines were not infected. All areas had a low percentage of dead whitebark pine in 1995, but cumulative mortality increased substantially in all five study areas (Figure 15). After 17 years, the average mortality of the original whitebark pine among the five areas was 59%; mortality varied from 47.4% at Trout Lake to 69.4% at Roman Nose #2.

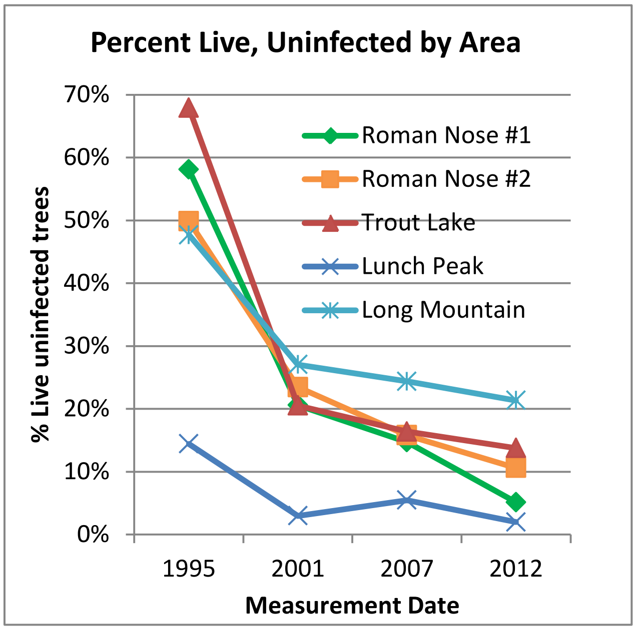


***Figure 14**. Percent of original whitebark pine that remained alive and uninfected during the 17-year monitoring period.*

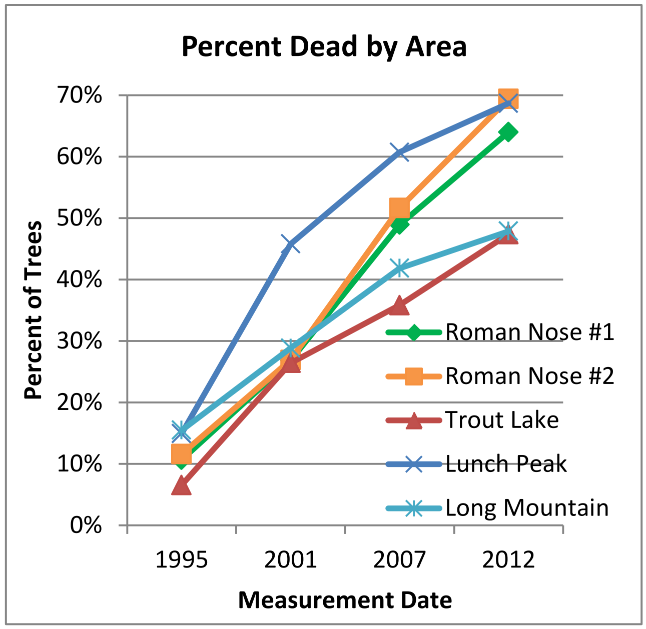


***Figure15**. Cumulative mortality of original whitebark pine at each area during the 17-year monitoring period.*

Of the whitebark pine that were uninfected in 1995, an average of 78% became infected across the five areas during the 17-year monitoring period; an average annual rate of infection of 4.3% (range 1.8 to 5.4%) (Table 4). An average of 51% of the whitebark pine that were alive in 1995 died during the same period, or 3.0% per year (range 3.8 to 6.5%). The relatively high rates of infection and mortality at these whitebark pine sites may indicate highly favorable conditions for WPBR infection across a large portion of the Idaho Panhandle acting on a very susceptible population. These annual rates of infection and mortality in natural whitebark pine regeneration are twice as high as those observed in western white pine stock with improved rust resistance (F_2) over the same time period. Schwandt et al. (2013c) found an average annual rate of new infections in F_2 western white pine stock of 2.3% and average annual mortality rate of 1.1%. Although a larger sample and more monitoring are needed, these differences indicate that whitebark pine may be more susceptible to WPBR than F_2 western white pine. More than 100 natural western white pine were monitored in this study, so it may be possible to make some direct comparisons between these species on sites where they co-exist.

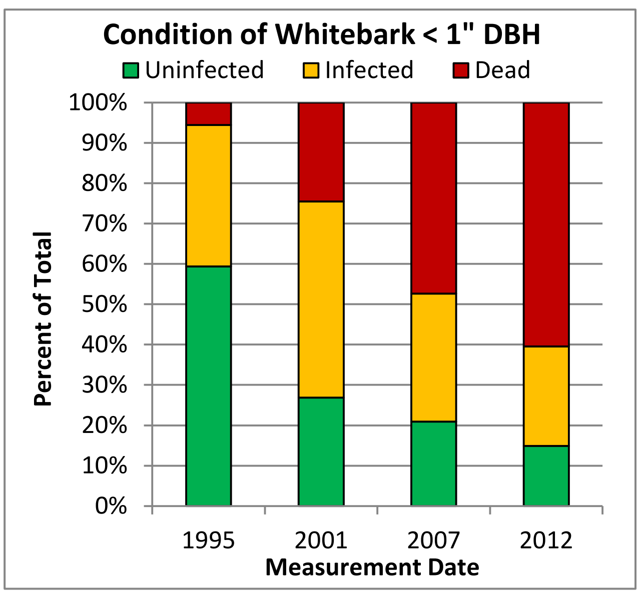
Table 4. *Cumulative increase in new infection and mortality and annual rates of infection and mortality in whitebark pine that occurred between 1995 and 2012.*[1]

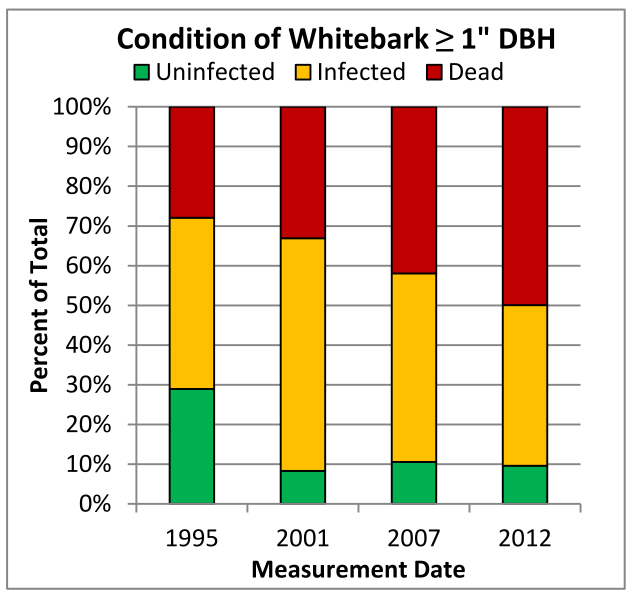
Location	Cumulative New Infection	Annual Infection Rate	Cumulative New Mortality	Annual Mortality Rate
Roman Nose #1	91%	5.4%	60%	3.5%
Roman Nose #2	79%	4.6%	65%	3.8%
Trout Lake	80%	4.7%	44%	2.6%
Lunch Peak	83%	4.9%	63%	3.7%
Long Mountain	55%	1.8%	38%	2.3%
Average	78%	4.3%	51%	3.0%

[1] Increase in percent WPBR infection was based on trees that were uninfected in 1995, and increase in mortality was based on trees that were alive in 1995, regardless of infection.

Trends by Size Class

Trees ≥ 1.0 inch DBH averaged 71.1% infected or dead in 1995 compared to 40.6% of the smaller trees (Figures 16 and 17). The percentage of uninfected trees decreased over the 17-year period until only 14.9% of the trees < 1.0 inch DBH and 9.6% of the trees ≥ 1.0 inch in DBH remained alive and uninfected. The cumulative mortality for trees < 1.0 inch DBH increased from 5.6% to 60.4% during the 17 years of monitoring while mortality of larger trees increased from 27.9% to 49.9%. As trees grew during the 17-year monitoring period, the number of whitebark pine ≥ 1.0 inch DBH increased from 522 in 1995 to 729 in 2012. Mortality in the smaller trees increased more rapidly than mortality in the larger trees, indicating that small trees are killed quickly once they become infected.





Figures 16 *(left) and* ***17*** *(right). WPBR impacts over time for all whitebark pine < 1.0 inch DBH (left) compared with trees ≥ 1.0 inch DBH (right) averaged over the five study areas.*

The total number and percentage of uninfected trees declined as tree size increased (Figure 18). Only four of 168 (2.4%) whitebark pine ≥ 5.0 inches DBH were uninfected at the last remeasurement in 2012, while 15% of the smallest diameter class was uninfected. Since most trees in this study were open-grown, size is considered to be a surrogate for age. However, even small trees 5–10 feet tall may be 50–90 years old especially if growing under an overstory (Schwandt 2014), and large, WPBR-infected trees often survive a long time and continue to produce at least some cones. As a result, the amount of selection pressure for WPBR resistance in these areas may be minimal so far, and the relatively high proportion (15%) of uninfected small trees may simply be due to their small target size and reduced time of exposure.

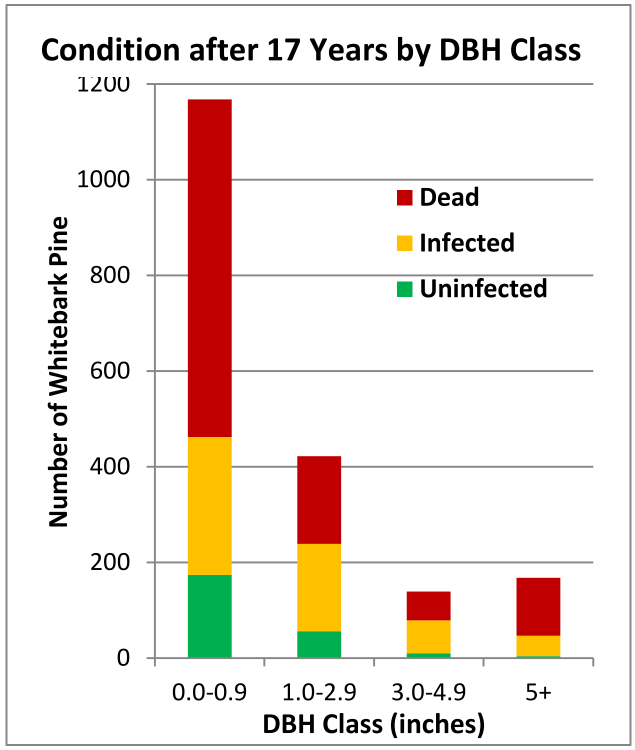


Figure 18. *Condition of original 1,898 whitebark pine after 17 years by DBH class.*

WPBR Severity

Since infections tend start closer to the bole on small trees, rust severity is often higher on small trees and this helps explain why WPBR kills small trees quicker than larger trees. More than 80% of infected whitebark pine < 5.0 inches DBH were classified as lethal or top-kill, and the number of safe or prunable trees declined with decreasing DBH class (Figure 19). Only 2.2% of the infected trees < 1.0 inch DBH were classified as safe compared to approximately 10% of

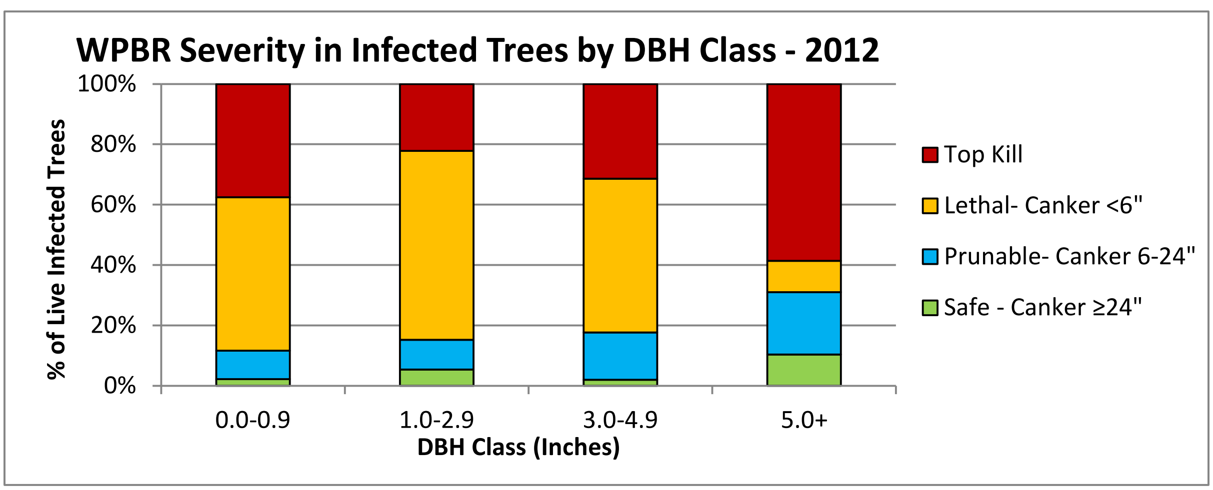


Figure 19. *WPBR severity rating of WPBR infected live whitebark pine in 2012, by DBH class.*

the infected trees ≥ 5.0 inches DBH. Most of the infected trees < 5.0 inches DBH were already lethally infected, but nearly 60% of the infected trees ≥ 5.0 inches DBH were surviving in spite of some top-kill. Some of these top-killed trees may live for many years and may produce new tops from live branches below the canker (Figure 20). However, they will have limited ability to compete and produce cones, and most are expected to eventually die from current or new infections.

Figure 20. *Live branches below a WPBR canker causing top-kill on a small whitebark pine.*

Pruning in western white pine has proven to be successful at increasing survival for many years (Schwandt and Marsden 2000, Schwandt et al. 2013a), but pruning success in whitebark pine has not been tested. Although 21% of the ≥ 5.0 inch DBH class were rated prunable, finding the few prunable trees in young whitebark pine stands in remote areas would be very challenging. In addition, pruning infected trees might only increase survival marginally as these long-lived trees are susceptible to future infections that might be lethal.

In a study of nearly 200 WPBR infections in F_2 western white pine, Schwandt et al. (2013b) found that nearly all cankers originating within six inches of the stem eventually reached the stem, but the probability of reaching the bole declined with distance from the bole. Cankers originating more than 24 inches from the stem never reached the main stem. Less is known about the progression of WPBR cankers in whitebark pine. If whitebark pine behaves similarly to western white pine, more than 90% of infected trees in our sample would be expected to die or be top-killed from existing infections, as only those rated as safe are likely to survive current infections.

Ingrowth

A total of 513 whitebark pine grew to be ≥ 6 inches tall and were added as ingrowth during the 17-year monitoring period (Table 5). Nearly half of all the ingrowth occurred at Long Mountain, and most occurred between 2007 and 2012 (Figure 21). Overall mortality exceeded ingrowth resulting in a 26.3% average loss in number of whitebark pine ≥ 6 inches tall over the 17-year period (Table 6). Long Mountain was the only area where ingrowth outpaced mortality; it had an

Figure 21. *Abundant whitebark pine ingrowth at Long Mountain.*

Table 5. Number of whitebark pine ingrowth recorded at each measurement in the five study areas.

	1995-2001	2001-2007	2007-2012	Total
Roman Nose #1	36	39	32	107
Roman Nose #2	47	30	13	90
Trout Lake	16	11	16	43
Lunch Peak	15	20	0	35
Long Mountain	80	46	112	238
Total	194	146	173	513

11.8% increase in the number of live whitebark pine ≥ 6 inches tall. The number of whitebark pine declined an average 42% across the remaining four sites. The large amount of ingrowth at Long Mountain may be partially explained by the higher elevation at this site, which may favor whitebark pine over its competitors, a more abundant local seed source, or some other factor that makes Clark's nutcrackers prefer caching seeds at this location.

Table 6. Population trends of whitebark pine due to mortality and ingrowth at five locations in northern Idaho and infection levels of remaining live trees after 17 years of monitoring.

Location	# Alive in 1995	17 Yr. Mortality (#)	17 Yr. Ingrowth (#)	# Alive in 2012	Change %	% Inf. in 2012
Roman Nose #1	243	178	107	172	-29.2%	68.0
Roman Nose #2	358	282	90	166	-53.6%	56.0
Trout Lake	428	192	43	279	-34.8%	65.9
Lunch Peak	171	120	34	85	-50.3%	87.1
Long Mountain	475	182	238	531	11.8%	37.5
Total/Ave%	1,675	954	512	1,233	-26.4%	62.9

Competition

In 1995, whitebark pine was the most abundant species on three sites and was a significant component on the other two (Figure 22). Whitebark pine (*PIAL*) comprised 52.0% of all sampled trees and ranged from 27.0% at Lunch Peak to 74.5% at Long Mountain. Subalpine fir (*ABLA*) was the most common associate and accounted for 38.1% of all trees in 1995 (ranged from 19.8% at Roman Nose #2 to 57.4% at Lunch Peak). These two

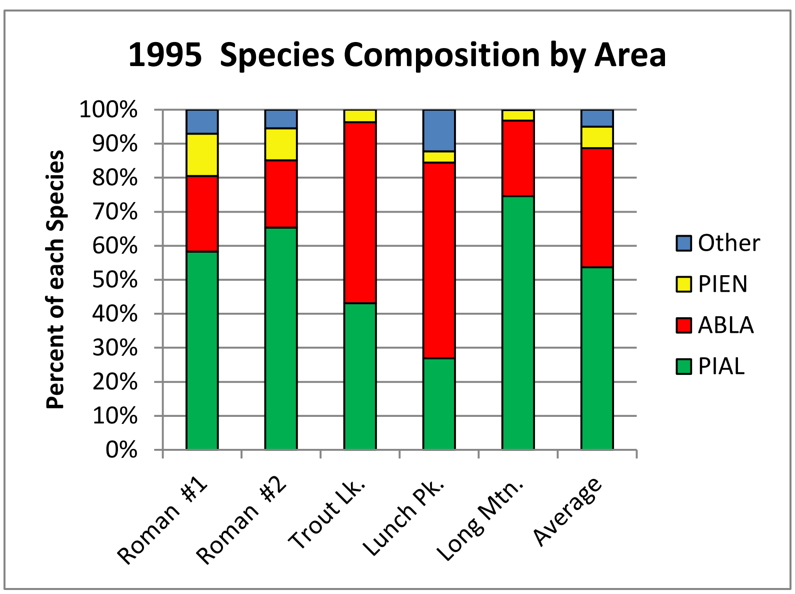


Figure 22. Species composition at each site in 1995.

species comprised 80–96% of the trees at each area. Engelmann spruce (*PIEN*) was the third most common species recorded (3–12% of trees), but many other species were also encountered including: western white pine, alpine larch, lodgepole pine, grand fir (*Abies grandis*), western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosae*), Douglas-fir (*Pseudotsuga menziesii)*, western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*).

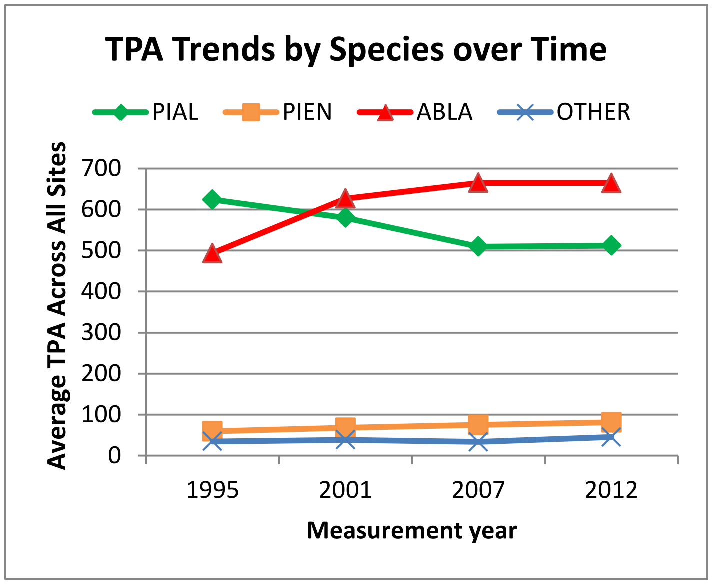


Figure23*. Trends in live tree density (TPA) by species averaged over all areas.*

Initially, the average density in trees per acre (TPA) of whitebark pine across all five sites was 624 TPA while subalpine fir averaged less than 500 TPA (Figure 23). Over the 17-year monitoring period, the average TPA of whitebark pine decreased to 512 TPA while subalpine fir increased to 664 TPA. Long Mountain had the highest TPA of whitebark pine initially and it was the only site where whitebark pine was still the predominant species in 2012 as a result of ingrowth that occurred there. However, a high percentage of whitebark pine on all sites was infected with WPBR in 2012 and most are unlikely to survive: 68.0% at Roman Nose #1, 56.0% at Roman Nose #2, 65.9% at Trout Lake, 87.1% at Lunch Peak, and 37.5% at Long Mountain (Table 6). The lowest infection level of live trees was at Long Mountain, likely due to the amount of recent ingrowth.

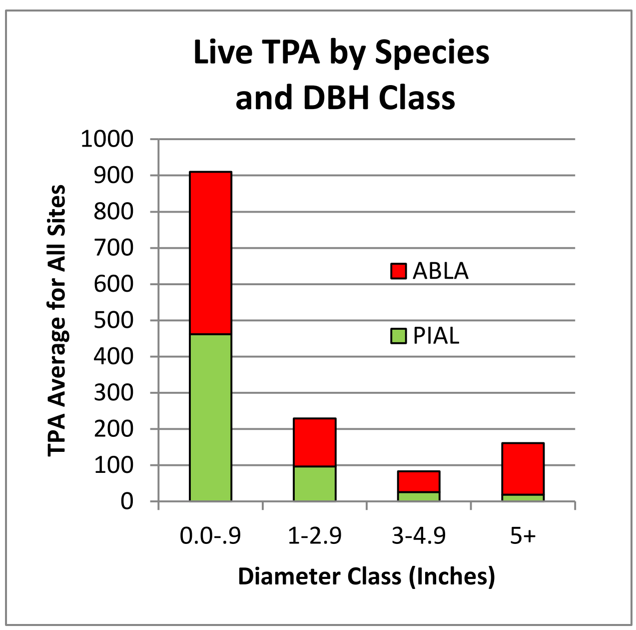


Figure 24. *Comparison of living TPA by DBH class and species averaged across all areas in 2007.*

In all cases, including Long Mountain, the number of uninfected whitebark pine was less than the number of living subalpine fir. When tree size is taken into consideration, the densities of whitebark pine and subalpine fir were similar for the smallest size class in 2007 (Figure 24). But subalpine fir outnumbers whitebark pine in the larger size classes, and outnumbers them by more than 7:1 in the ≥ 5.0 inch size class. If the abundance of shade tolerant subalpine fir combined with high WPBR infection levels threaten the survival of whitebark pine, thinning or “daylighting” (the removal of competing trees around individual high value trees) may eventually be needed to help potentially rust resistant whitebark pine survive to cone-bearing age. Since most of the trees on these sites are still relatively small and open grown (Figures 6, 8, and 12), there is currently little evidence of impacts from competition. Further analysis may find growth impacts on some trees, but additional monitoring will be needed to document long-term impacts from competition.

Summary and Management Implications

While the incidence of WPBR varies widely across the range of whitebark pine, it is generally much lower in drier habitats (Schwandt 2006, Kegley et al. 2011). Prior surveys at some sites in northern Idaho (Kegley et al. 2001, Kegley et al. 2004, Schwandt and Kegley 2004, Tomback et al. 1995) have provided intermittent samples of stand conditions, but do not document the changes that periodic measurements of long-term plots show are occurring. Modeling by Keane (2001) suggests that mortality from both WPBR and MPB will have severe consequences for whitebark pine. Our data indicate that few of the original whitebark pine will survive to maturity due to increasing levels of infection and mortality from WPBR in these naturally regenerated whitebark pine stands in northern Idaho. As a result, the species is unlikely to remain a significant component in these areas that were historically dominated by whitebark pine.

Natural regeneration is occurring on these sites and would be the preferred method of restoration due to the costs and difficulty associated with planting whitebark pine seedlings in high-elevation areas with limited access. But in areas with high levels of WPBR, success of natural regeneration may be limited until the level of rust resistance increases. Using artificial inoculation of seedlings grown from seed collected in natural stands with varying degrees of mortality from WPBR, Hoff et al. (2001) demonstrated that natural section for resistance to WPBR was occurring. Three years after inoculation they found 45% of seedlings not cankered where 90% of the parent stand had been killed; 12% not cankered where 40-60% of the parent stand had been killed; and 1% not cankered where less than 10% of the parent stand had been killed (Hoff et al. 2001). We found higher levels of uninfected trees in the smallest diameter class, but additional monitoring will be needed to determine how much of this is due to increased resistance. Continued WPBR impacts may exert an increasing level of selective pressure for rust resistance in the few surviving mature trees, so the level of resistance may slowly increase. However, losses of mature rust resistant whitebark pine due to MPB and fires may limit the potential production of seed with improved rust resistance in some areas.

The development and planting of seed or seedlings with improved WPBR resistance may be the best solution for whitebark pine restoration on northern Idaho sites severely impacted by WPBR. Efforts to accelerate the development of improved rust resistance in whitebark pine are currently underway (Mahalovich and Dickerson 2004). Since it will be several years before whitebark pine seed orchards start producing seed with improved WPBR resistance, it may be possible to enhance restoration by directly planting seeds from “plus” (uninfected) trees with potential WPBR resistance (Figure 25). A recent study found that direct seeding can greatly reduce

Figure 25. *Whitebark pine seedlings from "plus" trees with little or no WPBR infection.*

Figure 26. *Seedlings from direct seeding trial, Lolo NF 2012.*

planting costs and can be successful on some sites (Figure 26) (DeMastus 2013, Schwandt et al. 2011), but further monitoring will be necessary to determine long-term success.

Silvicultural treatments such as prescribed burns to encourage natural regeneration and promote natural selection should be considered. However, Keane (2011) found little natural regeneration of whitebark pine five years after using prescribed fire and other treatments to create suitable openings. Surveys in seven stands 10–22 years after fires in the Idaho Panhandle found 0.8 to 25.7 TPA of natural whitebark pine regeneration (Art Zack, personal communication). These surveys suggest that it may take many years after fires for natural regeneration to become established, and the amount is likely greatly influenced by fire intensity and proximity to residual cone-bearing trees.

Although there currently appears to be little impact from competing vegetation, the increasing subalpine fir and Engelmann spruce densities observed may become important in the future and should be monitored periodically to document potential impacts. If competition becomes a problem, daylighting to reduce competition and pruning to potentially enhance whitebark pine survival in young stands should also be considered. However, it will be critical to monitor the response of the whitebark pine to these treatments as well as the impacts these treatments may have on the spread and intensification WPBR.

On sites similar to those surveyed in this study, damage from WPBR is the most immediate threat to whitebark pine sustainability, and restoration efforts must address this threat. The ability of WPBR to increase rapidly, as observed during this study, means that current information on WPBR infection and damage plus competing vegetation should be obtained as part of any planning for whitebark pine restoration.

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