TRENDS IN WHITEBARK PINE HEALTH IN THE GREATER YELLOWSTONE ECOSYSTEM

by

Erin Kathleen Shanahan

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

of

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 2015

©COPYRIGHT

by

Erin Kathleen Shanahan

2015

All Rights Reserved

DEDICATION

To my mother, Martha T. Shanahan, who has supported and encouraged me through all of my various careers and misadventures. As a loving mother of four children, the sacrifices she has and continues to make are too numerous to count. My siblings and I truly won the "Mom" lottery!

To my family, Marcus, Brynn, and Macrae, your support and understanding has been monumental throughout this journey! Do not fret; I have no designs on pursuing a PhD!

ACKNOWLEDGEMENTS

Thank you to all of the people who have supported this effort over the past 12 years. Working with seasonal employees and agency collaborators, has been a joy.

TABLE OF CONTENTS

1. WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM.....1

General Introduction 1
Literature Cited 7

2. STATUS OF WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM; A STEP-TREND ANALYSIS COMPARING 2004-2007 TO 2008-2011.....11

Contribution of Authors and Co-Authors 11
Manuscript Information 12
Executive Summary 13
Introduction.....18
Report Objectives.....23
Study Area 24
Methods.....26
Sampling Design.....26
Field Methodology and Data Collection.....27
Temporal Revisit Design 29
Data Management and Statistical Analyses.....30
Results.....33
Objective 1: Blister Rust Infection Proportions.....34
Objective 2: Blister Rust Infection Severity 36
Infection Transition from Initial Time-step to Revisit Time-step.....36
Objective 3: Whitebark Pine Mortality.....37
Objective 4: Recruitment 39
Cone-producing Trees.....40
Understory Seedlings and Saplings 40
Discussion.....41
Conclusions.....49
Supplemental Information for Chapter 2: Field Form 52
Literature Cited 53

3. WHITE PINE BLISTER RUST IN WHITEBARK PINE STANDS: INFECTION AND INFECTION TRANSITION PROBABILITY 60

Contribution of Authors and Co-Authors 60
Manuscript Information 61
Abstract.....62
Introduction.....63

TABLE OF CONTENTS-CONTINUED

Methods: Study Area 68
Stand and Transect Selection 70
Transect Establishment and Data Collection 71
Statistical Analyses 72
Results: Summary of Data 75
Model Results 76
Discussion 79
Conclusions and Management Implications 83
Literature Cited 85

4. OBJECTIVE 4 OF THE INTERAGENCY WHITEBARK PINE PROTOCOL: ASSESSMENT OF REGENERATION/RECRUITMENT PROTOCOL 91

Contribution of Authors and Co-Authors 91
Manuscript Information 92
Abstract 93
Introduction 94
Specific Objective 4 Goals: 96
Methods: Study Area 97
Sampling Design 97
Response Design Rationale 98
Sample Frame and Sample Units 100
Subplot Size 101
Subplot Data Collection 101
Recruitment into the Whitebark Pine Monitoring Transect 104
Data Handling, Analysis, and Reporting Data 105
Results: Pilot Data 106
Discussion 106
Supplemental Information for Chapter 4: Assessment of Regeneration/Recruitment Subplot Pilot Monitoring 108
Literature Cited 111

5. GENERAL CONCLUSION 113

Conclusion 113

LITERATURE CITED 116

LIST OF TABLES

Table Page

1. Summary of climatic indicators (i.e. annual precipitation, mean annual temperature, total annual rain, total annual snow) from 1980-2011 and stand-level physical attributes for the 176 monitoring transects. 25

2. Design-based ratio estimates for the proportion of blister..... 34

3. Infection transition status for the total number of trees tagged in the initial time-step (T0) that remained alive at the end of the revisit time-step (T1). 37

4. Canker location transitions from live tagged trees in the initial time-step that remained live by the end of the revisit time-step and their canker positions following resurvey in the revisit time-step. 37

5. Panel schedule layout over the three time-step periods. *Panel 4 trees are scheduled to be surveyed in 2015 and therefore were not included as part of the modeling exercise for time-step T2. 72

6. Proportion of trees by size class that were initially uninfected and that remained uninfected into the next time-step. The total number of trees (denominator) is displayed within the parenthesis for each size class..... 75

7. Proportion of trees that had a canopy infection in the initial time-step (either T0 or T1) that transitioned to a bole infection at the end time-step (either T1 or T2). The total number of trees (denominator) is displayed within the parenthesis for each size class. 76

8. Ranking for the probability of infection model based on AIC values with inclusion of fixed effects and GLMM marginal and conditional R^2 estimates. Marginal and conditional R^2 are reported on a scale of 0 to 1 and support the inclusion of transect random effects..... 77

9. Estimates and other associated values for the probability of infection for both time-steps. 77

10. Estimates and other associated values for the probability of infection t ransition from canopy to bole for both time-steps. Marginal and conditional R^2 are reported on a scale of 0 to 1 and support the inclusion of transect random effects. 78

LIST OF FIGURES

Figure Page

1. Whitebark Pine Monitoring Program study area in the GYE. 25

2. Belt transect layout. Permanent markers were placed at the two end points and the center point. 27

3. Panel sampling revisit schedule (br=blister rust, mpb=mountain pine beetle). 30

4. The change in the proportion of trees infected within each stand between the initial and revisit time-steps (↑ =increase, ↓ =decrease, "-" no change). 35

5. Mortality of tagged trees on all four panels by size class and indicators such as fire, mountain pine beetle, and blister rust. 38

6. Mortality estimates of whitebark pine trees >1.4 m tall in the GYE at two-year intervals based on pooled data that ignores strata membership. We surveyed panels 1 and 3 in 2008 and 2010 and panels 2 and 4 in 2009 and 2011. The directional arrows indicate the comparisons between years when the same panels were visited. 39

7. Reproducing tagged trees (996) in the belt transect population at the end of the revisit time-step differentiated by size class 40

8. Variability in the distribution of tagged trees across the monitoring belt transects at the end of 2011 41

9. Maximum count of ≤1.4 m tall whitebark pine trees (per 500 m2) in monitored stands from surveys 2004 through 2011 44

10. Distribution of blister rust-infected trees in sampled transects in the GYE at the end of 2011. 51

11. Whitebark Pine Monitoring Program study area in the Greater Yellowstone Ecosystem. 69

12. To investigate the probability of infection, the data were subset to include trees that remained alive from T0 to T1 or from T1 to T2, had a 4-year revisit interval, and were uninfected in either T0 or T1. The response was infection stat us in T1 or T2. 73

LIST OF FIGURES-CONTINUED

Figure Page

13. To investigate the probability of infection transition, the data were subset to include trees that remained alive from T0 to T1 or from T1 to T2, had a 4-year revisit interval, and were canopy infected in either T0 or T1. The response was infection l ocation status in T1 or T2..... 73

14. The probability of initial infection is positively correlated to DBH over a 4-year interval.Therefore, as DBH increases, so does the chance of infection. Smaller size class trees were more abundant in the sample than larger trees for this analysis. Confidence intervals (95%) were estimated with the Workman-Hotelling procedure and are likely conservative..... 78

15. The probability of infection transition from canopy to bole does not appear to be influenced by tree size in either time-step. Confidence intervals (95%) were estimated with the Workman-Hotelling procedure and are likely conservative. 79

16.Recruitment subplot layout within established whitebark pine monitoring transect where the red dots represents the beginning, center, and end monument spikes. The radius of the circular subplot is 2.08-meters. 100

17. Species and height class bins as presented on field data sheet. 103

18. Data field requirements for understory tree tag number and infection status..... 104

ABSTRACT

Whitebark pine (*Pinus albicaulis*) occurs at high elevations and in subalpine communities in the Pacific Northwest and Northern Rocky Mountains. It is a key component in the upper ranges of these ecosystems where it provides a variety of ecological roles, including regulating snowpack and providing high-energy food sources to birds and mammals. As a stone pine species, it produces indehiscent cones and relies primarily on birds for seed dispersal.

In mixed and dominant stands, whitebark pine occurs in over two million acres within the six national forests and two national parks that comprise the Greater Yellowstone Ecosystem (GYE). Currently, whitebark pine is impacted by multiple ecological disturbances. White pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), wildfires, and warming temperature all pose significant threats to the persistence of healthy whitebark pine populations on the landscape. Substantial declines in whitebark pine populations have been documented throughout its range. In 2004, an interagency whitebark pine long-term monitoring program was established. The objectives of the whitebark pine monitoring program are to detect and monitor changes in the health and status of whitebark pine populations across the GYE due to infection by white pine blister rust, attack by mountain pine beetle, and damage by other environmental and anthropogenic agents.

Here we present work done in three areas of whitebark pine ecology; trends in white pine blister rust infection and overall health status, infection and infection transition probability, and methods for monitoring understory (≤ 1.4-m tall) populations of whitebark pine.

CHAPTER 1

WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM

General Introduction

Whitebark pine (*Pinus albicaulis*) occurs in the interior Pacific Northwest, northern Sierra Nevadas, and northern Rocky Mountains where it is a foundation and keystone species in high-elevation forests and alpine communities. Whitebark pine plays a critical role in ecosystem dynamics by regulating a multitude of ecological processes and influencing biodiversity (Tomback and Kendall 2001, Ellison et al. 2005). It is considered a "pioneer" species due to its tolerance of harsh environmental conditions and ability to establish and persist where other species cannot. In doing so, whitebark pine can alter the microclimate and enable species such as subalpine fir (*Abies lasiocarpa*) to establish in these otherwise inhospitable and harsh environments (Tomback et al. 1993). Although whitebark pine has very little commercial value, its seeds provide seasonal forage for a variety of wildlife and its aesthetic qualities and sheer perseverance inspire awe in recreationists.

Whitebark pine, in mixed and dominant stands, occurs in over two million acres within the six national forests and two national parks that comprise the Greater Yellowstone Ecosystem (GYCCWPS 2010). Currently, whitebark pine is being impacted by multiple ecological disturbances. Substantial declines in whitebark pine populations have been documented throughout its historic range for many decades (Kendall and Keane 2001). The loss of a foundation tree species such as whitebark pine has the

potential to cause major secondary losses, changes in biological diversity, and critical and possibly irreversible changes in community composition and structure (Ebenman and Jonsson 2005). Most of these decreases in whitebark pine have been attributed to white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), wildfires, and climate change (Keane and Arno 1993, Kendall and Keane 2001, Zeglen 2002, Smith et al. 2008, Tomback and Achuff 2010, MacFarlane et al. 2013, Shanahan et al. 2014).

White pine blister rust (blister rust) is an exotic fungal pathogen with a propensity for infecting white pine species (whitebark pine, limber pine; *Pinus flexilis*, and western white pine; *Pinus monticola*). Blister rust is ubiquitous throughout the Greater Yellowstone Ecosystem although the level and magnitude of infection vary geographically (GYWPMWG 2012). Introduced into Vancouver, Canada, around 1910, blister rust thrived in the maritime climate (Kendall and Arno 1990, Keane and Arno 1993). From its coastal landing, blister rust successfully dispersed inland and was first discovered in the Greater Yellowstone Ecosystem in 1937 (Kendall and Asebrook 1998). To complete its life cycle, blister rust requires primary and secondary host species. Originally, white pines and species of the genus *Ribes*, such as currant and gooseberry, were thought to be the primary and alternate telial hosts for blister rust (Smith and Hoffman 2000, Zambino et al. 2007). However, two other species, elephanthead lousewort (*Pedicularis racemosa*) and giant red Indian paintbrush (*Castilleja miniata*), both common flora of whitebark pine communities, were recently identified as successful intermediary hosts as well (McDonald et al. 2006, Shanahan et al. 2014).

The infection process of blister rust is well understood. Basidiospores released from an intermediary host species enter a tree through the needles, ultimately reaching the stemwood of an adjacent branch over a period of several months to form a canker (McDonald and Hoff 2001). After successful infection, it takes approximately two to four years for aecia-filled cankers (the fruiting body of blister rust) to fully erupt on infected tree branches and subsequently release aeciospores that re-infect other alternate host species perpetuating the disease (McDonald and Hoff 2001). With the majority of primary infections initiating in the crown of a tree, canopy branches tend to be affected in the early stages of disease development.

Aecia can structurally damage a tree both directly and indirectly. Spore growth patterns lead to swelling and bark girdling over time (McDonald and Hoff 2001). This occludes nutrient accessibility to healthy tissue distal to the canker causing the branch to eventually die (Tainter and Baker 1996, Smith et al. 2000). Indirectly, aeciospores and associated tree sap act as attractants for rodents and various insects; consumption of sap can cause extensive girdling on affected branches and boles (Zeglen 2002, Schwandt and Kearns 2011, Shanahan et al. 2014). Cone producing branches are typically located on the outermost portions of upper canopy limbs in whitebark pine. Therefore, any significant girdling of cone-bearing branches can have a tremendous impact on reproductive potential (Maloney et al. 2012). A tree may experience reduced cone production resulting from a decrease in the number of cone-bearing branches, or in severe cases, the total loss of reproductive capability following top kill (Shanahan et al. 2014). As the infection continues to mature within an infected tree, the location of an original

infection can change significantly over time (Newcomb 2003, Schwandt et al. 2013). Infections that initiate in the canopy have the potential to spread or transition to the bole of the infected tree under optimal growing conditions. In general, bole cankers are considered to be more severe than are canopy infections, and reduce the longevity of the infected tree (Kendall and Arno 1990, Campbell and Antos 2000, McDonald and Hoff 2001, Schwandt and Kegley 2004). Although a tree can persist for decades after becoming infected, cankers situated on the lower portions of the bole will eventually lead to the death of the tree. Blister rust infection is also thought to have a higher probability of killing smaller trees in a shorter period of time due to their physical stature. Smaller trees tend to have fewer branches and the distance an infection has to travel from the branch to the main bole is typically shorter than in larger-diameter trees (Koteen 2002, Newcomb 2003). Thus, in addition to losing future reproductive potential, smaller trees may die from blister rust infection more rapidly than their larger infected cohorts (Smith and Hoffman 2000, Schwandt et al. 2013).

In the Greater Yellowstone Ecosystem, a bird's eye view presents a striking panorama of mortality in the overstory population of whitebark pine. Mass mortality of whitebark pine has occurred at a landscape level largely attributable to the recent mountain pine beetle outbreak (Logan et al. 2009, MacFarlane et al. 2013). Mountain pine beetle are one of the many species of endemic bark beetles that are present in the western U.S. (Logan and Powell 2001). Mountain pine beetle typically attack lodgepole pine (*Pinus contorta* var. latifolia), but will also attack whitebark pine trees that are 10-cm at diameter breast height (DBH) or greater (Furniss and Carolin 1977). Trees that are

less than 10-cm DBH generally are not large enough to successfully support mountain pine beetle brood. Variations in climate are largely responsible for the success of mountain pine beetle outbreaks. Mild summers and winters tend to favor outbreaks, while cold winters and hot summers tend to decrease beetle activity and increase brood mortality (Kipfmueller and Swetnam 2002). Evidence has shown that mountain pine beetles tend to attack and are more successful when attacking trees that are already weakened by some other process, such as moisture stress or pathogens (Kipfmueller and Swetnam 2002).

In an effort to understand the many challenges faced by whitebark pine and to track its health status in the Greater Yellowstone Ecosystem, a long-term monitoring program was initiated in 2003 by multiple, collaborating agencies (Shanahan et al. 2014). Since its inception, the Interagency Whitebark Pine Monitoring Program (hereafter referred to as Monitoring Program) has documented changes in the overall health of whitebark pine in the Greater Yellowstone Ecosystem. This includes tracking fluctuations in blister rust infection rates and chronicling the ensuing mortality within the whitebark pine population following the recent mountain pine beetle outbreak in the region.

Utilizing the Interagency Monitoring Program data, this thesis explores key aspects of whitebark pine ecology. Each of the three chapters (Chaps. 2, 3, and 4) were written as stand-alone publications. The first chapter describes trends in whitebark pine health from 2004 to 2011. This chapter was published in 2014 through the National Park Service, National Resource Technical Report series. Building upon baseline data

compiled from the first chapter, the second chapter explores whitebark pine blister rust susceptibility and infection severity. This chapter will be submitted for publication in manuscript form. As directed from the information gleaned from chapters 1 and 2, and the third chapter was developed as an addendum to the Interagency Greater Yellowstone Whitebark Pine Monitoring Protocol (Monitoring Protocol), and fulfills the final objective (Objective 4) for the current Monitoring Protocol. Objective 4 describes and details specific field collection methodologies and analysis techniques that will be used to track understory populations on whitebark pine on permanent monitoring transects over the life of the Monitoring Program.

Literature Cited

Campbell, E. M. and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Ebenman, B. and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20:568-575.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swans, J. Thomspon, B. Von Holle and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 39:479-486.

Furniss, R. L. and V. M. Carolyn. 1977. Western forest insects. Misc. Publ. 1339. Washington, D.C.: USDA Forest Service. 654 p.

Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (GYCCWPS). 2011. Whitebark pine strategy for the Greater Yellowstone Area. Greater Yellowstone Coordinating Committee, Bozeman, Montana.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, Montana, USA.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2012. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2011 annual report. pages 56-65 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2011. U.S. Geological Survey, Bozeman, Montana, USA.

Kearns, H. S., W. R. Jacobi and B. W. Geils. 2009. A method for estimating white pine blister rust canker age on limber pine. Forest Pathology 29:177-191.

Keane, R. E. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Kendall, K. C. and J. M. Asebrook. (1998). The war against blister rust in Yellowstone National Park, 1945–1978. In *George Wright Forum* (Vol. 15, No. 4, pp. 36-49).

Kendall, K. C. and R. E. Keane. 2001. Whitebark pine decline: Infection, mortality, and population trends. Pages 221-242 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC.

Kendall, K. C. and S. F. Arno. 1990. Whitebark pine: An important but endangered wildlife resources. pages 264-273 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Kipfmueller KF and Swetnam TW. 2002. Climate and mountain pine beetle-induced tree mortality in the Selway-Bitterroot Wilderness Area. Final Report to the USFS Research Joint Venture Agreement #RMRS-99611-RJVA. http://www.ltrr.arizona.edu/~kurt/research/kkipf_beetles.pdf>.

Koteen, L. 2002. Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. pages 343-414 in S. H. Schneider and T. L. Root, editors. Wildlife responses to climate change: North American case studies. Island Press, Washington, D.C., USA.

Logan, J. and J. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleptera:Scolytidae). American Entomologist, 47:

Logan, J. A., W. W. Macfarlane and L. Willcox. 2009. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2: 19-22 [online: 2009-01-21] URL: http://www.sisef.it/iforest/show.php?id=477

MacFarlane, W. W., J. A. Logan and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications 23:421-437.

Mahalovich, M. F. 2013. Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem. Future status of whitebark pine: blister rust resistance, mountain pine beetle, and climate change. Report 2470 RRM-NR-WP-13-01, U.S. Department of Agriculture Forest Service, Northern Region, Missoula, MT.

Maloney, P. E., D. R. Volger, C. E. Jensen and A. D. Mix. 2012. Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests

of Lake Tahoe Basin, USA: Implications for restoration. Forest Ecology and Management 280:166-175.

McDonald, G. I., B. A. Richardson, P. J. Zambino, N. B. Klopfenstein and M. S. Kem. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North American: A first report. *Forest Pathology* 36:73-82.

McDonald, G. I. and R. J. Hoff. 2001. Blister rust: an introduced plague. pages 193-220 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark Pine Communities Ecology and Restoration. Island Press,Washington, DC.

Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. M.S. Thesis. The University of Montana, Missoula, MT.

Schwandt, J. and H. Kearns. 2011. White pine blister rust: General ecology and management. Insect and Disease Management Series 14:2.

Schwandt, J. W., H. S. J. Kearns and J. W. Byler. 2013. Impacts of white pine blister rust and competition on natural whitebark pine regeneration in Northern Idaho 1995-2012. USDA Forest Service Northern Region, Forest Health Protection Report 13-09. 22p.

Schwandt, J. W. and S. Kegley. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. R1-04-9. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA.

Shanahan, E., K. M. Irvine, D. Roberts, A. R. Litt, K. Legg and R. Daley. 2014. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis comparing 2004-2007 to 2008-2011. Natural Resource Technical Report NPS/GRYN/NRTR—2014/917. National Park Service, Fort Collins, Colorado.

Smith, C. M., B. Wilson, S. Rasheed, R. Walker, T. Carolin and B. Sheppard. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forestry Research 38:982-995.

Smith, J. P. and J. T. Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60:165-179.

Smith, J. P., J. T. Hoffman, K. F. Sullivan, E. P Van Arsdel and D. Vogler. 2000. First report of white pine blister rust in Nevada. Plant Disease 84:594.

Tainter, F. H. and F. A. Baker. 1996. Principals of Forest Pathology. John Wiley & Sons, Inc., New York. 805 p.

Tomback, D. F. and K. C. Kendall. 2001. Biodiversity losses: the downward spiral. Pages 243-262 in D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, D.C.

Tomback, D. F. and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186-225.

Tomback, D. F., S. K. Sund and L. A. Hoffman. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forestry Research 23:113-119.

Zambino, P. J., B. A. Richardson and G. I. McDonalt. 2007. First report of white pine blister rust fungus, *Cronartium ribicola*, on *Pedicularis bracteosa*. Plant Disease 91:467.37

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forestry Research 32:1265-1274.

CHAPTER 2

STATUS OF WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM; A STEP-TREND ANALYSIS COMPARING 2004-2007 TO 2008-2011

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: Erin K. Shanahan

Contributions: Assisted in overall Monitoring Protocol study design. Implemented the study, supervised field crews, collected and analyzed data. Wrote first draft of the technical report.

Co-Author: Kathryn M. Irvine

Contributions: Provided statistical analysis and consultation on many aspects of Monitoring Protocol and Trend report.

Co-Author: David W. Roberts

Contributions: Provided feedback on Trend report drafts

Co-Author: Andrea R. Litt

Contributions: Provided feedback on Trend report drafts

Co-Author: Kristin Legg

Contributions: Guidance and feedback on Trend report drafts

Co-Author: Rob Daley

Contributions: Technical support and verification of data for Trend report analysis

Manuscript Information

Erin K. Shanahan, Kathryn M. Irvine, Dave Roberts, Andrea R. Litt, Kristin Legg, and Rob Daley
Natural Resource Technical Report NPS/GRYN/NRTR—2014/917
Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
_X_ Published in a peer-reviewed journal

National Park Service
2014
No. 917

STATUS OF WHITEBARK PINE IN THE GREATER YELLOWSTONE ECOSYSTEM: A STEP-TREND ANALYSIS COMPARING 2004-2007 TO 2008-2011

Previously published as: Shanahan, E., K. M. Irvine, D. Roberts, A. Litt, K. Legg, and R. Daley. 2014. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis comparing 2004-2007 to 2008-2011. Natural Resource Technical Report NPS/GRYN/NRTR—2014/917. National Park Service, Fort Collins, Colorado.

Executive Summary

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species in upper subalpine environments of the northern Rocky Mountains that strongly influences the biodiversity and productivity of high-elevation ecosystems (Tomback et al. 2001; Ellison et al. 2005). Throughout its historic range, whitebark pine has decreased significantly as a major component of high-elevation forests. As a result, it is critical to understand the challenges to whitebark pine—not only at the tree and stand level, but also as these factors influence the distribution of whitebark pine across the Greater Yellowstone Ecosystem (GYE).

In 2003, the National Park Service (NPS) Greater Yellowstone Inventory & Monitoring Network identified whitebark pine as one of twelve significant natural resource indicators or vital signs to monitor (Jean et al. 2005; Fancy et al. 2009) and initiated a long-term, collaborative monitoring program. Partners in this effort include the U.S. Geological Survey, U.S. Forest Service, and Montana State University with representatives from each comprising the Greater Yellowstone Whitebark Pine

Monitoring Working Group. The objectives of the monitoring program are to assess trends in (1) the proportion of live, whitebark pine trees (>1.4 m tall) infected with white pine blister rust (blister rust); (2) to document blister rust infection severity by the occurrence and location of persisting and new infections; (3) to determine mortality of whitebark pine trees and describe potential factors contributing to the death of trees; and (4) to assess the multiple components of the recruitment of understory whitebark pine into the reproductive population. In this report we summarize the past eight years (2004-2011) of whitebark pine status and trend monitoring in the GYE.

Our study area encompasses six national forests (NF), two national parks (NP), as well as state and private lands in portions of Wyoming, Montana, and Idaho; this area is collectively described as the GYE here and in other studies. The sampling design is a probabilistic, two-stage cluster design with stands of whitebark pine as the primary units and 10x50 m belt transects as the secondary units. Primary sampling units (stands) were selected randomly from a sample frame of approximately 10,770 mapped pure and mixed whitebark pine stands ≥2.0 hectares in the GYE (Dixon 1997; Landenburger 2012). From 2004 through 2007 (monitoring transect establishment or initial time-step), we established 176 permanent belt transects (secondary sampling units=176) in 150 whitebark pine stands and permanently marked approximately 4,740 individual trees >1.4 m tall to monitor long-term changes in blister rust infection and survival rates. Between 2008 and 2011 (revisit time-step), these same 176 transects were surveyed and again all previously tagged trees were observed for changes in blister rust infection and survival status.

Objective 1. Using a combined ratio estimator, we estimated the proportion of live trees infected in the GYE in the initial time-step (2004-2007) to be 0.22 (0.031 SE). Following the completion of all surveys in the revisit time-step (2008-2011), we estimated the proportion of live trees infected with white pine blister rust as 0.23 (0.028 SE). We detected no significant change in the proportion of trees infected in the GYE between the two time-steps.

Objective 2. We documented blister rust canker locations as occurring in the canopy or bole. We compared changes in canker position between the initial time-step (2004-2007) and the revisit time-step (2008-2011) in order to assess changes in infection severity. This analysis included the 3,795 trees tagged during the initial time-step that were located and documented as alive at the end of the revisit time-step. At the end of the revisit time-step, we found 1,217 trees infected with blister rust. This includes the 287 newly-tagged trees in the revisit time step of which 14 had documented infections. Of these 1,217 trees, 780 trees were infected with blister rust in both time steps. Trees with only canopy cankers made up approximately 43% (519 trees) of the total number of trees infected with blister rust at the end of the revisit time-step, while trees with only bole cankers comprised 20% (252 trees), and those with both canopy and bole cankers included 37% (446 trees) of the infected sample. A bole infection is considered to be more consequential than a canopy canker, as it compromises not only the overall longevity of the tree, but its functional capacity for reproductive output as well (Kendall and Arno 1990; Campbell and Antos 2000; McDonald and Hoff 2001; Schwandt and Kegley 2004). In addition to infection location, we also documented infection transition

between the canopy and bole. Of the 780 live trees that were infected with blister rust in both time-steps, approximately 31% (242) maintained canopy cankers and 36% (281) retained bole infections at the end of the revisit time-step. Infection transition from canopy to bole occurred in 30% (234) of the revisit time-step trees while 3% (23) transitioned from bole to canopy infections during this period.

Objective 3. To determine whitebark pine mortality, we resurveyed all belt transects to reassess the life status of permanently tagged trees >1.4-m tall. We compared the total number of live tagged trees recorded during monitoring transect establishment to the total number of resurveyed dead tagged trees recorded during the revisit time-step and identified all potential mortality-influencing conditions (blister rust, mountain pine beetle, fire and other). By the end of the revisit time-step, we observed a total of 975 dead tagged whitebark pine trees; using a ratio estimator, this represents a loss of approximately 20% (SE=4.35%) of the original live tagged tree population (GYWPMWG 2012).

Objective 4. To investigate the proportion of live, reproducing tagged trees, we divided the total number of positively identified cone-bearing trees by the total number of live trees in the tagged tree sample at the end of the revisit time-step. To approximate the average density of recruitment trees per stand, trees ≤1.4 m tall were summed by stand (within the 500 m² transect area) and divided by the total number of stands. Reproducing trees made up approximately 24% (996 trees) of the total live tagged population at the end of the revisit time-step. Differentiating between whitebark pine and limber pine seedlings or saplings is problematic given the absence of cones or cone scars. Therefore,

understory summaries as presented in this report may include individuals of both species when they are sympatric in a stand. The average density of small trees ≤1.4 m tall was 53 understory trees per 500 m². Raw counts of these understory individuals ranged from 0-635 small trees per belt transect. In addition, a total of 287 trees were added to the tagged tree population by the end of 2011. These newly tagged trees were individuals that upon subsequent revisits had reached a height of >1.4 m tall and subsequently added to the sample.

Throughout the past decade in the GYE, monitoring has helped document shifts in whitebark pine forests; whitebark pine stands have been impacted by insect, pathogen, wildland fire, and other disturbance events. Blister rust infection is ubiquitous throughout the ecosystem and infection proportions are variable across the region. And while we have documented mortality of whitebark pine, we have also recorded considerable recruitment. We provide this first step-trend report as a quantifiable baseline for understanding the state of whitebark pine in the GYE. Many aspects of whitebark pine health are highly variable across the range of its distribution in the GYE. Through sustained implementation of the monitoring program, we will continue efforts to document and quantify whitebark pine forest dynamics as they arise under periodic upsurges in insect, pathogen, fire episodes, and climatic events in the GYE. Since its inception, this monitoring program perseveres as one of the only sustained long-term efforts conducted in the GYE with a singular purpose to track the health and status of this prominent keystone species.

Introduction

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species in upper subalpine environments of the northern Rocky Mountains that strongly influences the biodiversity and productivity of high-elevation ecosystems (Tomback et al. 2001; Ellison et al. 2005). A member of the subsection Cembrae (stone pines), whitebark pine is the only representative of this group found in North America (Lanner 1990; Lanner 1996). Although commonly encountered in both pure and mixed-species stands from about 2,000 m to treeline, this drought-resistant tree also establishes on exposed ridges at lower elevations (Arno 1986). Whitebark pine occupy dry and rocky habitats that appear to be intolerable for most montane forest species. Ridge and treeline whitebark pine contributions to subalpine environments are numerous, but principal among these are the collection and maintenance of mountain snowpack throughout the fall and winter (Weaver 2001). As warming temperatures arrive in subalpine environments, whitebark pine's wide canopies retain snow and moderate snowmelt rates (Arno and Hoff 1990; Smith et al. 2008; Farnes 1990). Whitebark pine also creates microsites that provide protection and fertile habitat for shade-tolerant species such as subalpine fir (*Abies lasiocarpa*; Tomback et al. 2001; Keane and Arno 1993). In addition, the seeds of whitebark pine are a valuable food source for a variety of wildlife including grizzly bears (*Ursus arctos horribilis),* Clark's nutcrackers *(Nucifraga columbiana),* and red squirrels *(Tamiasciurus hudsonicus*; Tomback et al. 2001).

Throughout its historic range, whitebark pine has decreased significantly as a major component of high-elevation forests. A century's worth of altered fire regimes and

insect and pathogen outbreaks have combined to reduce whitebark pine stands in many regions (Keane and Arno 1993; Kendall and Keane 2001; Zeglen 2002; Smith et al. 2008; Tomback and Achuff 2010; MacFarlane et al. 2013). White pine blister rust (*Cronartium ribicola*; hereafter, blister rust), an exotic fungal pathogen, is considered a principal threat to the long-term survival of whitebark pine across its range. In the early 1900s, blister rust was introduced inadvertently to western North America from imported European nursery stock (Kendall and Arno 1990;Keane and Arno 1993). With a propensity for infecting five-needle pines, this pathogen thrived in the Pacific Northwest climate and dispersed inward from its coastal landing to infect many white pine species (Smith and Hoffman 2000). Blister rust requires a primary and secondary host to complete its complex life cycle. White pines and species of the genus *Ribes*, such as currant and gooseberry, originally were believed to be the primary and alternate telial hosts for blister rust (Smith and Hoffman 2000; Zambino et al. 2007). Efforts to thwart the spread of blister rust began in earnest in the 1930s using widespread *Ribes* spp. eradication programs that employed both physical and chemical means of control (Ketcham et al. 1968). Given the abundance of *Ribes* spp., combined with the extensive dispersal ability of blister rust aeciospores (the fruiting bodies of blister rust), little success resulted from these labors. Consequently, organized endeavors to suppress blister rust were later abandoned (Benedict 1981; Ketcham et al 1968) and this pathogen has continued to impact geographic regions where white pines occur. In addition to whitebark pine and *Ribes* spp., two other species, giant red Indian paintbrush (*Castilleja miniata*) and elephanthead lousewort (*Pedicularis racemosa*), common flora of whitebark pine

communities, also were discovered to function as intermediary hosts in the blister rust cycle (McDonald et al. 2006).

The pathway for infection by blister rust is well understood; basidiospores enter a tree through the needles (McDonald and Hoff 2001). After successful infection, it takes approximately two to four years for aecia (the fruiting body of blister rust) to fully erupt on infected tree branches and release aeciospores (McDonald and Hoff 2001). Because most of these primary infections are located in the crown of a tree, canopy branches tend to be affected in the early stages of the disease process. Aecia can damage tree structure both directly and indirectly. Growth patterns of the spores themselves lead to swelling and subsequent bark girdling, which occludes nutrient accessibility to healthy tissue distal to the canker (Tainter and Baker 1996; Smith et al. 2000). Indirectly, aeciospores and associated tree sap act as attractants for rodents and various insects; consumption of sap can cause extensive girdling on affected branches and boles (Zeglen 2002; Schwandt and Kearns 2011). Because whitebark pine cones grow on the outermost portions of upper-canopy limbs, girdling of cone-bearing branches can have a tremendous impact on reproductive potential (Maloney et al. 2012). A tree may experience diminished cone production due to a decrease in the number of cone-bearing branches, or in extreme cases, the complete loss of reproductive ability following top kill. Although a tree can persist for decades after infection, cankers found on the lower portions of the bole eventually lead to the death of the tree. Bole cankers have a higher probability of killing smaller trees because they have fewer branches and the distance an infection has to travel from the branch to the main bole is typically shorter than in larger-diameter trees (Koteen

2002; Newcomb 2003). Thus, in addition to losing future reproductive potential, smaller trees may die from blister rust infection more rapidly than larger infected cohorts (Smith and Hoffman 2000).

The endemic mountain pine beetle (*Dendroctonus ponderosae*) also influences the health and abundance of whitebark pine (Logan et al. 2010). An aggressive pest of several coniferous species, mountain pine beetle periodically escalates to epidemic levels of outbreak in lodgepole pine (*P. contorta*), ponderosa pine (*P. ponderosa*), and whitebark pine forests (Perkins and Swetnam 1996; Furniss and Renkin 2003; Six et al. 2014). In whitebark pine, trees measuring >10 cm diameter at breast height (DBH) are preferentially selected by mountain pine beetle for infestation (Furniss and Carolin 1977). Many of these larger-DBH individuals also represent the cone-bearing, reproductive segment of the population. Raffa et al. (2013) hypothesized that because mountain pine beetle outbreaks historically occurred intermittently in high-elevation forests, whitebark pine potentially lack defense mechanisms necessary to block an attack. As a result, whitebark pine can be particularly vulnerable to extensive mortality caused by mountain pine beetles (Raffa et al. 2013). As climate conditions become warmer (Pedersen et al. 2011), shorter intervals between epidemic mountain pine beetle cycles are expected (Raffa et al. 2013). At least three outbreaks of mountain pine beetle have occurred in regions within the Greater Yellowstone Ecosystem (GYE) over the last century (1909-1940, 1970-1980s, 2000-present; (Furniss and Carolyn 1977; Furniss and Renkin 2003; Logan et al. 2010). The most recent occurrence began in the early 2000s with peak mortality observed around 2009 (Olliff et al. 2013; Hayes 2013). This latest infestation

has been labeled as “unprecedented” due to the widespread death of multiple forest species, the novel areas in which mortality has occurred, and the fact that whitebark pine has experienced unparalleled losses to the overall population (Logan et al. 2010; Macfarlane et al. 2013). As is evident in the GYE, bark beetles can swiftly cause mass mortality across vast expanses of forest. Although whitebark pine has survived both endemic and epidemic levels of beetle outbreak, the additional stress of climatic conditions presents unprecedented challenges to its long-term survival in the GYE.

It is critical to understand the challenges to whitebark pine—not only at the tree and stand level, but also as these factors influence the distribution of whitebark pine across the GYE. Identifying the multiple stressors to whitebark pine health, and the potential dynamic interactions among stressors, is an important component of this understanding. Acquiring this degree of in-depth knowledge requires a whitebark pine monitoring program that is spatially representative and long term. In 2003, the National Park Service (NPS) Greater Yellowstone Inventory & Monitoring Network identified whitebark pine as one of twelve significant natural resource indicators or vital signs to monitor (Jean et al. 2005; Fancy et al. 2009), and initiated a long-term, collaborative monitoring program. Partners in this effort include the NPS, U.S. Geological Survey, U.S. Forest Service, and Montana State University with representatives from each comprising the Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG; hereafter, monitoring group).

In this report we summarize the past eight years (2004-2011) of whitebark pine status and trend monitoring in the GYE. During this time period, our monitoring not only

captured the change in the status of blister rust infection in the GYE, but also chronicled the transformation of endemic mountain pine beetle to epidemic levels. As well as providing critical baseline information to land managers, continuous documentation of this event has assisted in the development of species recovery plans, enabled investigation into the possible synergistic interaction of blister rust and mountain pine beetle on whitebark pine mortality, and resulted in a collaborative monitoring protocol that can be used across the GYE regardless of landownership (GYCCWPS 2011, GYWPMWG 2011). Perhaps even more relevant to the long-term survival of whitebark pine in the ecosystem, monitoring data will allow the formulation of predictive models on future survival and recruitment potential of whitebark pine in the presence of blister rust infection and other stand-altering phenomena such as beetle, fire, and climate change.

Report Objectives

Following the objectives outlined in the Interagency Whitebark Pine Monitoring Protocol (GYWPMWG 2011), the intent of this trend report is to:

1. Describe the estimated proportion of live whitebark pine trees (>1.4-m tall) infected with white pine blister rust during 2004-2007 (permanent belt transect monitoring establishment period) and 2008-2011 (belt transect revisit period) and assess evidence of blister rust infection change between the two time periods;
2. Document blister rust infection severity by the occurrence and location of persisting and new infection by the end of 2011 and evaluate the rate at which infection transitioned from canopy to bole cankers between time periods 2004-2007 and 2008-2011;
3. Determine mortality of whitebark pine trees between 2004-2007 and 2008-2011 and describe potential factors contributing to death of tagged individuals; and
4. Assess the multiple components of recruitment of understory whitebark pine into the reproductive population.

Study Area

Our study area encompasses six national forests (NF), two national parks (NP), as well as state and private lands in portions of Wyoming, Montana, and Idaho (Figure 1); this area is collectively described as the GYE here and in other studies. The GYE is geographically defined as the Yellowstone Plateau volcanic fields and the 14 surrounding mountain ranges above 2,130 m (Marston and Anderson 1991).

Whitebark pine stands occupy over 800,000 hectares in the high, mountainous zones of the GYE (Marston and Anderson 1991, GYWPMWG 2011, GYCCWPS 2011). This environment is subject to harsh weather including excessive winds, extreme cold temperatures, and significant snow accumulation. Snow collects early and may persist until late spring and occasionally into mid-summer. Summers tend to be warm and dry. Sample sites in the study area range in elevation from 2,400 m to 3,172 m and extend to the boundaries of the ecosystem (GYWPMWG 2011).

To illustrate the conditions of this region, we used DAYMET 1 km grid cell values (Thornton et al. 2014) to describe the annual averaged climate conditions from 1980 to 2011 for the 176 transects (Table 1). Stand-level physical attributes (slope, aspect, elevation) were obtained from a 30 m digital elevation model (GYWPMWG 2011).

Table 1. Summary of climatic indicators (i.e. annual precipitation, mean annual temperature, total annual rain, total annual snow) from 1980-2011 and stand-level physical attributes for the 176 monitoring transects.

Averages for 176 transects	Precipitation (mm)	Temperature (deg C)	Rain (mm)	Snow (mm)	Maximum Snowpack (mm)	Slope (degrees)	Aspect (degrees)	Elevation (m)
Minimum	238	-1	104	112	112	1	0.2	2,401
Maximum	1,636	4	578	1,271	1,243	45	360	3,172
Average	858	1	303	556	465	20	182	2,787
Standard Deviation	227	1	91	180	173	9	91	173

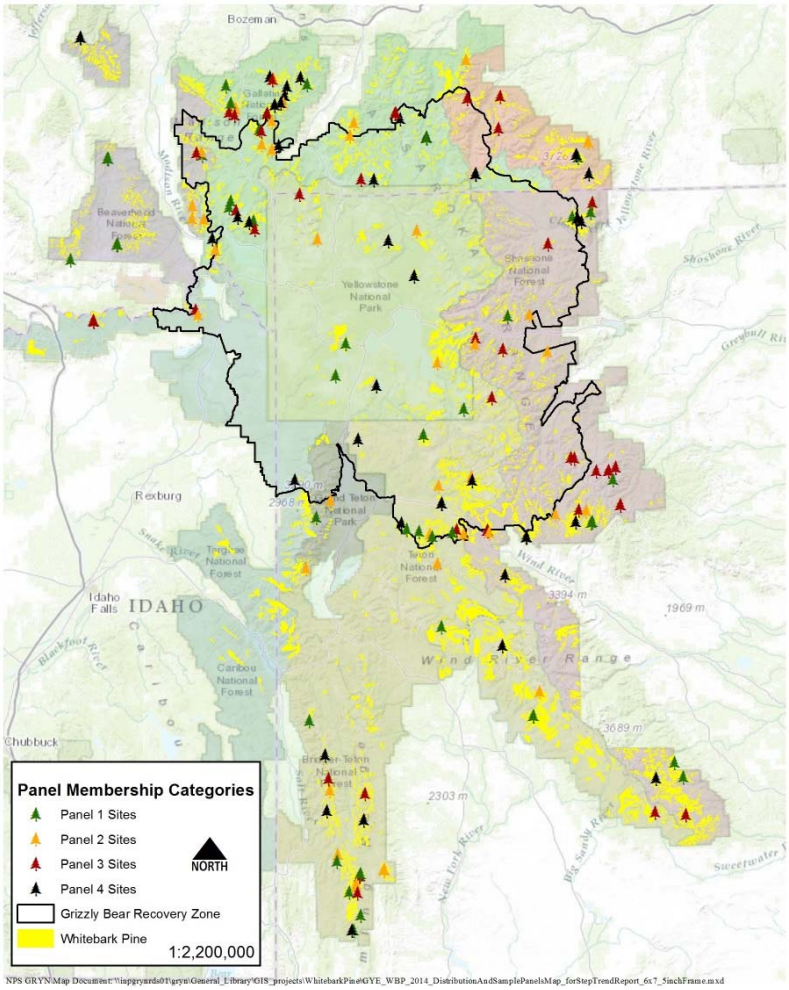

Figure 1. Whitebark Pine Monitoring Program study area in the GYE.

Methods

In this section we describe the methodologies we used in the whitebark pine long-term monitoring program; for more information, refer to the Interagency Whitebark Pine Monitoring Protocol (GYWPMWG 2011).

Sampling Design

The sampling design is a probabilistic, two-stage cluster design with stands of whitebark pine as the primary units and 10x50 m belt transects as the secondary units. Primary sampling units (stands, n=150) were selected randomly from a sample frame of approximately 10,770 mapped pure and mixed whitebark pine stands ≥2.0 hectares in the GYE (Dixon 1997; Landenburger 2012). Stands were stratified according to their location inside or outside of the Grizzly Bear Recovery Zone (an area delineated in the GYE by the U.S Fish and Wildlife Service identified as grizzly bear-sustaining habitat; USFWS 1993) and within an administrative unit boundary (Beaverhead-Deerlodge NF, Bridger-Teton NF, Caribou-Targhee NF, Custer NF, Gallatin NF, Shoshone NF, Grand Teton NP, and Yellowstone NP; Figure 1). Areas that had experienced wildland fire since 1970 were excluded from the sample frame (GYWPMWG 2011). From 2004 through 2007, we established 176 permanent belt transects (secondary sampling units=176) in 150 whitebark pine stands and permanently marked approximately 4,740 individual trees >1.4 m tall to monitor long-term changes in blister rust infection and survival rates. We installed two permanent belt transects in twenty-six of the 150 stands in order to investigate within-stand variability.

Field Methodology and Data Collection

We typically start field sampling the last week in June when snow accumulation is sufficiently depleted to allow access to high-elevation sites and end the last week in September when unpredictable weather may interfere with field work. We established the 10x50 m belt transects within each selected stand using the methodology outlined in the protocol (GYWPMWG 2011); and permanently marked them for future revisits (Figure 2). We tagged all whitebark pine trees >1.4-m tall and examined them for blister rust during full survey visits.

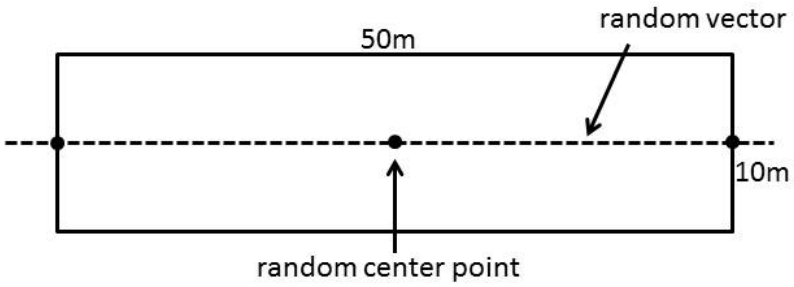

Figure 2. Belt transect layout. Permanent markers were placed at the two end points and the center point.

We recorded the following tree attributes for every tagged tree (see field data form in the Supplemental Information section):

- clump membership (number and letter),
- DBH (measured at 1.4 m from the ground),
- height,
- tree status (live=green needles still present, recently dead=red or brown needles remaining on tree, or dead=tree is completely denuded of needles),
- cone production (Y/N),
- blister rust cankers (number and location in the tree=upper third, middle third, or lower third),
- number of blister rust indicators (flagging, rodent chewing, swelling, roughened bark, and oozing sap),

- upper tree canopy volume (percentage of canopy in the upper one third of the foliage that is alive),
- mountain pine beetle indicators (pitch tubes, frass, or J-shaped galleries), and
- tree health codes (can have multiple per tree such as dead top, fading crown, fire, etc.).

We recorded a tree as reproducing if we observed cones, conelets, or cone scars on the tree. The criteria for inclusion of cankers in the blister rust canker count are based on Hoff's non-aecia blister rust indicators (1992). A complete description of these indicator standards are provided in the monitoring protocol, but in brief, these include branch girdling, flagging, swelling, roughened or split bark, and oozing sap (GYWPMWG 2011). In addition, we assigned canker locations based on tree structure definitions specified in the protocol (GYWPMWG 2011). Instructions for identifying evidence of mountain pine beetle were provided by USFS Forest Health Protection entomologists. We noted additional information including UTM coordinates of beginning, center, and end points of the belt transect (Figure 2), elevation, habitat type (from Steele et al. 1983), and cover type (from Mattson and Despain 1985). We conducted counts and evaluated blister rust infection for all five-needle trees ≤1.4 m tall within the boundaries of the belt transects (snow-free belt transects only). We added new trees to the sample during the first revisit period between 2008 and 2011 when an understory tree on a given belt transect attained a height of >1.4 m tall, in which case we marked it and recorded all attributes for the new individual (as described in the tree tagging process).

Temporal Revisit Design

In 2008, we randomly assigned individual stands to one of four panels. Each panel consisted of approximately 44 belt transects (Figure 3), the number of belt transects that could be visited in a field season by one, two-person field crew. We revisited panels once every four years on a rotating schedule, which was designed to be sufficient to detect change in blister rust infection (McDonald and Hoff 2001). A full panel rotation is completed when all four panels are revisited in a given four-year period; this four-year period is referred to as a time-step.

The first time-step was the initial transect visit period from 2004-2007 (hereafter, initial time-step; in figures and tables also referred to as T0) and the second time-step occurred between 2008 and 2011 after all 176 belt transects were revisited (hereafter, revisit time-step; in figures and tables also referred to as T1). With the increase in whitebark pine mortality due to mountain pine beetle (Gibson 2003), the monitoring group became concerned that a revisit interval of four years might not capture the potentially changing rates of overall mortality of whitebark pine trees >1.4 m tall. In response, the design was temporarily modified to a two-year revisit schedule to detect the dynamic nature of the recent mountain pine beetle epidemic. With this design, we surveyed two of the four panels annually; one panel was subject to the full survey documenting blister rust infection and mountain pine beetle indicators, and the second panel was subject to a partial survey focused on mountain pine beetle indicators (Figure 3). Both surveys recorded tree status as live, dead, or recently dead.

Survey Schedule		Time-step 0	Time-step 1				Time-step 2				
Sample Panel	Sites per panel	2004 thru 2007	2008	2009	2010	2011	2012	2013	2014	2015	Continued Monitoring 2016 forward
1	43	initial surveys for all 176 transects	br & mpb		mpb only		br & mpb				
2	45			br & mpb		mpb only		br & mpb			
3	44		mpb only		br & mpb		mpb only		br & mpb		
4	44			mpb only		br & mpb		mpb only		br & mpb	

Figure 3. Panel sampling revisit schedule (br=blister rust, mpb=mountain pine beetle).

We successfully resurveyed all 176 belt transects for blister rust infection and mortality during the 2008-2011 revisit time-step period. In the case where a belt transect no longer had any live, tagged trees >1.4 m tall, the panel revisit schedule was maintained in order to document potential recruitment of understory individuals into the tagged tree size class and to collect other data on understory cohorts.

Data Management and Statistical Analyses

We trained field observers to carry and use a detailed data recording guide to help ensure legible, valid entries and maximize the quality of recorded values. Network personnel entered data from field data sheets into a Microsoft Access database on a regular basis throughout the field season using a customized data entry form that included a cascading system of data validation controls. We subjected data to rigorous quality assurance and quality control (QA/QC) procedures as outlined in the protocol (GYWPMWG 2011). Due to minor retroactive updates to the master database as part of ongoing quality controls, there may have been an insignificant amount of variability (typically <1% difference) when comparing data reported in previous years.

All analyses and corresponding figures were produced using Microsoft Excel and the statistical computing language R (R Development Core Team 2011) specific to each objective. We have presented some of the results described in this trend narrative as preliminary findings in past versions of the Interagency Whitebark Pine Monitoring Program (monitoring program) annual reports (e.g., GYWPMWG 2012). This document provides results for the full eight years of data collection and analysis in order to present a complete assessment of changes over time across the sample frame. Our results are presented based on the following monitoring objectives.

Objective 1. Investigate changes in blister rust infection between initial transect visit time-step (2004-2007) and revisit time-step (2008- 2011).

We estimated the proportion of trees infected with blister rust in the sampled population of 10,770 whitebark pine stands identified in the GYE. We used a combined ratio estimator for both time-steps separately. A combined ratio estimator is appropriate for estimating a proportion from data collected using a stratified (e.g., Grizzly Bear Recovery Zone and administrative unit) two-stage cluster sample (Lohr 2010). The probabilistic sampling design allows inferences to the entire sampled population of mapped whitebark in the GYE.

To investigate the evidence of a change in the proportion of stands infected with blister rust a nonparametric Wilcoxon signed-ranked test was used (wilcox.test in R). For the 26 double belt transect stands, we calculated the overall average proportion for the stand to account for the potential lack of independence of belt transects nested within stands.

Objective 2. Document blister rust infection severity: new infection and canker transition.

We documented white pine blister rust canker locations as occurring in the canopy or bole. We compared changes in canker position between the initial time-step (2004-2007) and the revisit time-step (2008-2011) in order to assess changes in infection severity. This analysis included the approximately 3,795 trees tagged during the initial time-step that were located and documented as alive at the end of the revisit time-step. We reported canker location summaries as individual categories: branch only, bole only, or branch/bole combination. A more thorough investigation of canker transition is slated for future analysis.

Objective 3. Determine mortality from initial transect visit time-step to revisit time-step.

To determine whitebark pine mortality, we resurveyed all belt transects to reassess the life status of permanently tagged trees >1.4 m tall. We compared the total number of live tagged trees to the total number of dead tagged trees and identified all potential mortality-influencing conditions (blister rust, mountain pine beetle, fire and other). We estimated the proportion of whitebark pine mortality in the GYE using a ratio estimator to determine the cumulative proportion of dead trees within the sample frame based on the original collection of live tagged trees. The revisit schedule for life status (mountain pine beetle only visit) occurred at two-year intervals. For two-year estimates of the proportion of dead trees (mortality), we used a ratio estimator because not all administrative units were visited in a given two-year interval, thus we ignored the

stratification. A stratified ratio estimator (e.g., combined ratio estimator used for blister rust within a four-year window) could not be used because of zero or low sample sizes within the different strata.

We conducted an in-depth examination on the probability of mortality in a separate analysis using a multi-level logistic regression model (Gelman and Hill 2007). Specifically, this evaluation explored the potential synergistic effects of mountain pine beetle and blister rust on whitebark pine mortality.

Objective 4. Investigate recruitment potential.

To investigate the proportion of live reproducing tagged trees, we divided the total number of positively identified live, cone-bearing trees by the total number of live trees remaining in the tagged tree sample at the end of the revisit time-step. To approximate the average density of recruitment trees per stand, we summed trees ≤1.4 m tall by stand (within the 500 m2 transect area) and divided by the total number of stands. Some stands were precluded from the ≤1.4 m tall survey due to lingering snow cover. In the case where there were two belt transects per stand (26 cases), we averaged the count of small trees over the two belt transects for one stand total.

Results

The following results are based on data collected by the monitoring program between the initial and the revisit time-steps.

Objective 1: Blister Rust Infection Proportions

We estimated the proportion of live trees infected in the GYE in the initial time-step (2004-2007) to be 0.22 (0.031 SE). Following the completion of all surveys in the revisit time-step (2008-2011), we estimated the updated proportion of live trees infected with white pine blister rust as 0.23 (0.028 SE; Table 2). There was no significant change in the proportion of trees infected in the GYE between the two time-steps. In addition, the mortality of infected and uninfected trees did not appear to impact these results. Of the 975 tagged trees that died by the end of 2011, 554 were recorded as uninfected while 421 were documented as infected when last observed for the presence of blister rust.

Table 2. Design-based ratio estimates for the proportion of blister

Time-step	**2004-2007 [T0]**	**2008-2011 [T1]**
Number of transects	176	176
Number of stands	150	150
Number of live trees	4,742	3,770
Proportion transects infected	0.812	0.858
Combined Ratio Estimates		
Proportion of live trees infected	0.225	0.231
Proportion of live trees infected standard error (SE)	0.031	0.028
Confidence interval (CI) for proportion of live trees infected	[0.163, 0.287]	[0.175, 0.287]

We estimated a 4% increase in the mean percentage of trees infected with blister rust within a stand from the initial time-step to the revisit time-step (n=150, Wilcoxon signed ranked test, V=2415.5, P-value=0.0049; Figure 4).

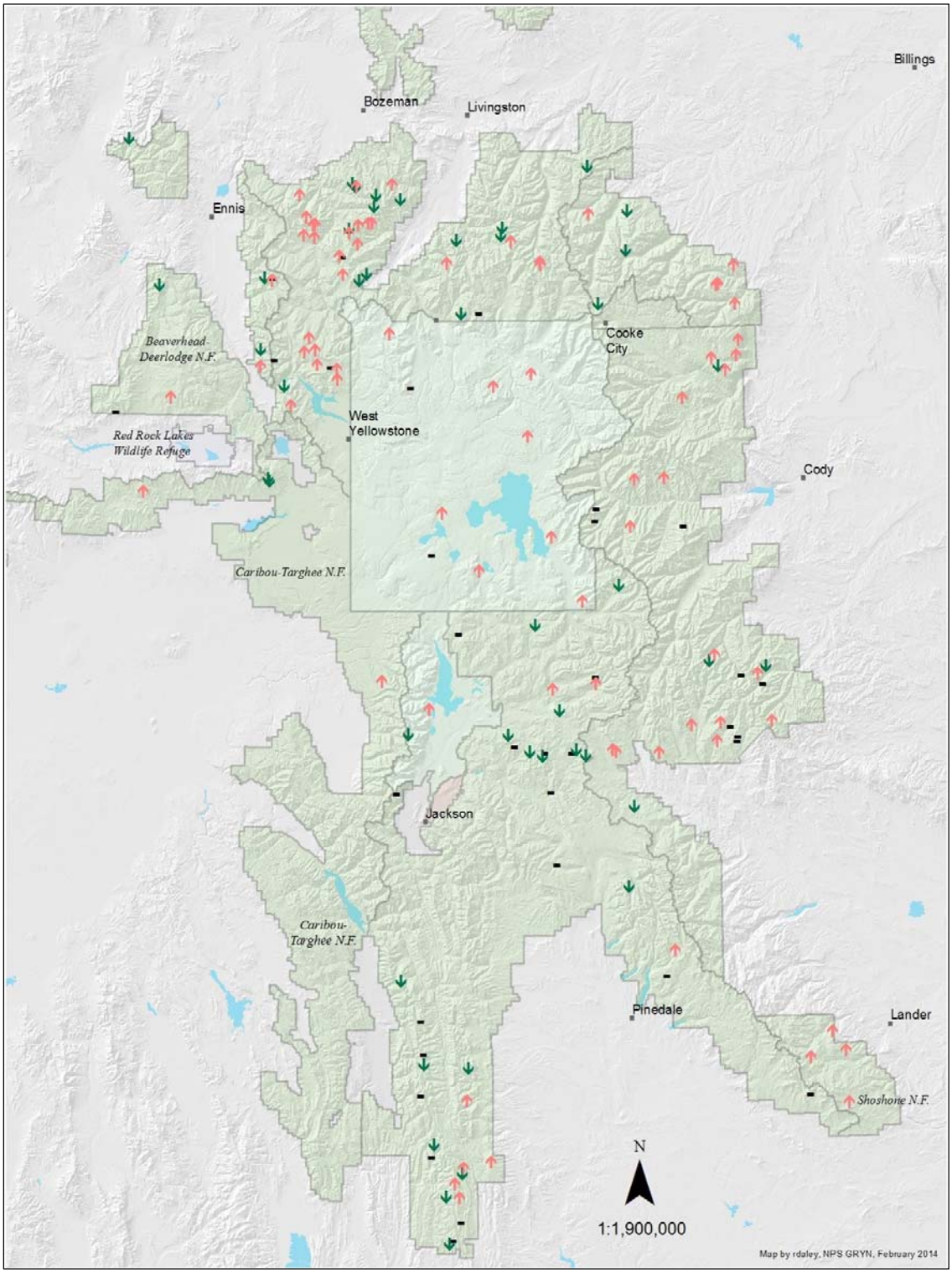

Figure 4. The change in the proportion of trees infected within each stand between the initial and revisit time-steps (↑ =increase, ↓ =decrease, "-" no change).

Objective 2: Blister Rust Infection Severity

At the end of the revisit time-step, we found 1,217 of 4,081 living trees infected with blister rust. This includes the 287 newly tagged trees in the revisit time step of which 14 had documented infections. Trees with only canopy cankers made up approximately 43% (519 trees) of the total number of trees infected with blister rust at the end of the revisit time-step, while trees with only bole cankers comprised 20% (252 trees), and those with both canopy and bole cankers included 37% (446 trees) of the infected sample. Of the documented reproducing trees (996 trees), 45% (444) trees were infected with blister rust and 43% (190) of these infected trees had bole cankers.

Infection Transition from Initial
Time-step to Revisit Time-step

We recorded 174 of the originally tagged trees transitioned from infected to uninfected from the initial time-step to the revisit time-step, whereas 423 previously uninfected in the initial time-step were recorded as infected at the revisit time-step. Positive infection status was static for 780 trees, whereas a total of 2,418 trees remained uninfected between the two time steps (Table 3).

Of the 780 live trees that were infected with blister rust in both time-steps, approximately 31% maintained canopy cankers and 36% maintained bole infections at the end of the revisit time-step. Infection transition from canopy to bole occurred in 30% of the revisit time-step trees while 3% transitioned from bole to canopy infections during this period (Table 4). We assigned trees infected with both canopy and bole cankers to the bole canker category for this analysis.

Table 3. Infection transition status for the total number of trees tagged in the initial time-step (T0) that remained alive at the end of the revisit time-step (T1).

Tree Infection Transition Status T0-T1	
Uninfected to uninfected	2,418
Uninfected to infected	423
Infected to infected	780
Infected to uninfected	174

Table 4. Canker location transitions from live tagged trees in the initial time-step that remained live by the end of the revisit time-step and their canker positions following resurvey in the revisit time-step.

Infected T0	→	**Infected T1**
Canopy only (480)	→	Canopy only (245) Bole (235)
Bole (300)	→	Bole (280) Canopy only (20)

Objective 3: Whitebark Pine Mortality

By the end of the revisit time-step, we observed a total of 975 dead tagged whitebark pine trees; this represents a loss of approximately 20% of the original live tagged tree sample (GYWPMWG 2012). Approximately 40% (395 trees) of the dead trees died with evidence of mountain pine beetle infestation only. The majority of these trees were within the >10-30 cm DBH size class. The remaining 60% (583 trees) of dead

trees died with signs of fire; blister rust; a combination of fire, mountain pine beetle, or blister rust; or with other factors such as structural or animal damage (Figure 5). When considering tree mortality associated with blister rust alone or acting in combination with any of the other health-influencing factors (e.g., mountain pine beetle or fire) we recorded approximately 43% (421 trees) of the dead trees as positive for blister rust, whereas the remaining 57% (554 trees) of dead trees had no signs of infection prior to death.

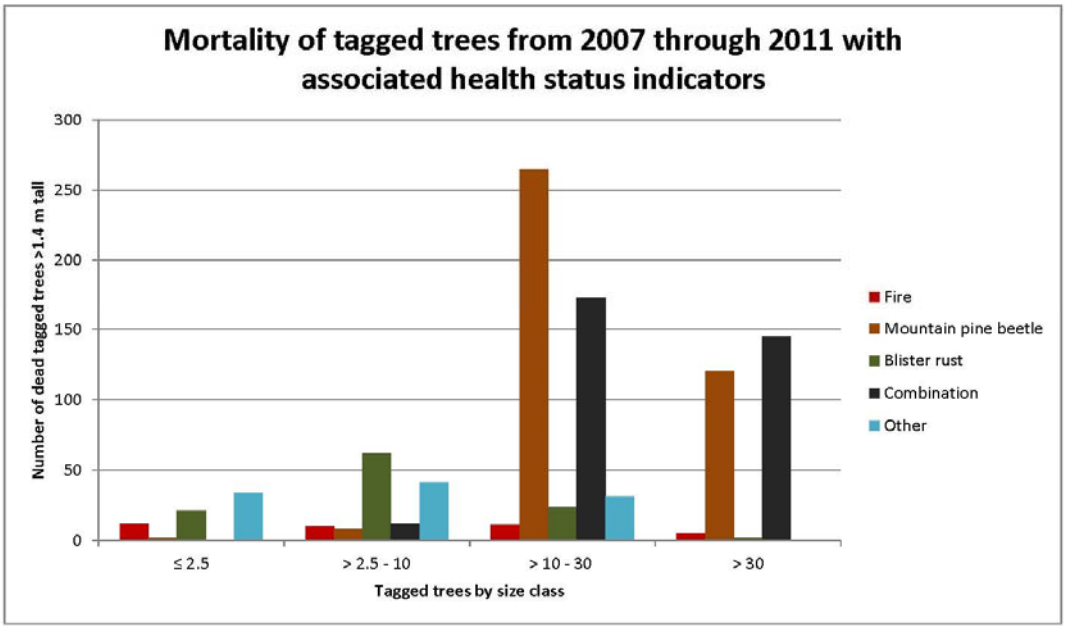

Figure 5. Mortality of tagged trees on all four panels by size class and indicators such as fire, mountain pine beetle, and blister rust.

Documented mortality of tagged trees peaked in 2009 and 2010 with approximately 65% (637 trees) of the dead trees examined recorded as dead within those two years (Figure 6). The estimated overall proportion of recently dead whitebark pine trees was approximately 20% in the GYE (SE=4.35%) at the end of the revisit time-step. The probability of mountain pine beetle-induced mortality increasedas DBH increased.

The generally observed possible synergistic effect of mountain pine beetle and blister rust on whitebark pine mortality was that smaller-DBH trees with evidence of infection on the bole had a higher estimated probability of mortality from mountain pine beetle compared to trees with no or low blister rust infection (<20 cm DBH).

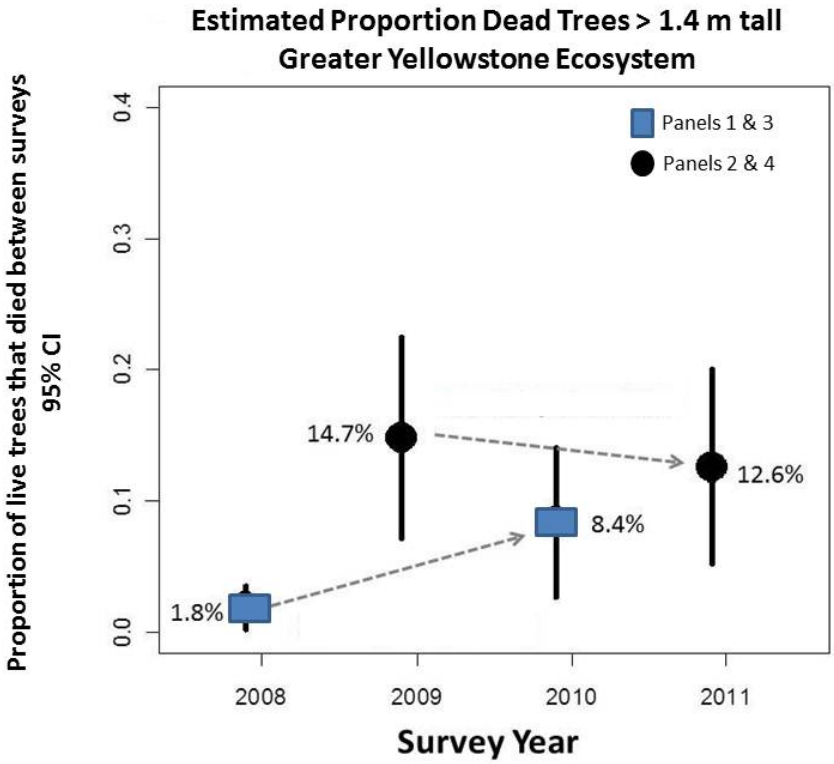

Figure 6. Mortality estimates of whitebark pine trees >1.4 m tall in the GYE at two-year intervals based on pooled data that ignores strata membership.We surveyed panels 1 and 3 in 2008 and 2010 and panels 2 and 4 in 2009 and 2011. The directional arrows indicate the comparisons between years when the same panels were visited.

Objective 4: Recruitment

We assessed recruitment by tracking the number of cone-producing trees and recording new seedlings and saplings in the understory. We tagged 287 trees that grew to >1.4 m tall since the initial time-step.

Cone-producing Trees

Reproducing trees made up approximately 24% (996 trees) of the total live tagged population at the end of the revisit time-step (Figure 7). Although we documented reproduction across all four size classes, the smaller-DBH trees usually did not produce as many cones. These typically younger trees tended to have fewer canopy branches and less overall canopy volume compared to their larger-DBHcounterparts. Seventeen trees were documented with an unknown reproductive status, while 76% (3,085) had no observable signs of past, present, or future cone production.

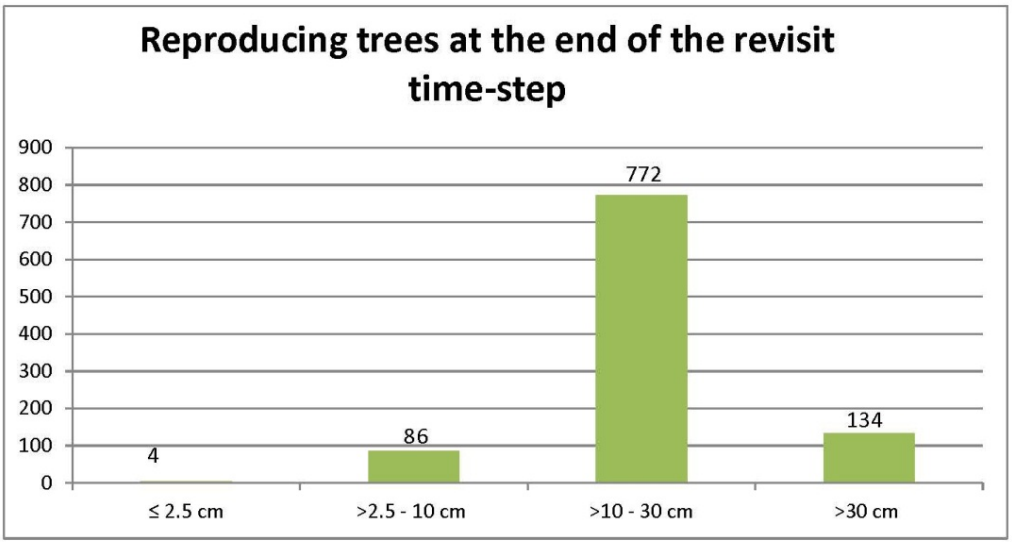

Figure 7. Reproducing tagged trees (996) in the belt transect population at the end of the revisit time-step differentiated by size class

Understory Seedlings and Saplings

Differentiating between whitebark pine and limber pine seedlings or saplings is problematic given the absence of cones or cone scars. Therefore, understory summaries as presented in this report may include individuals of both species when they are

sympatric in a stand. The density of trees ≤1.4 m tall averaged 53 understory trees per 500 m². Raw counts of these understory individuals ranged from 0-635 small trees per belt transect (Figure 8). We documented only 64 of these small trees as having some level of blister rust infection.

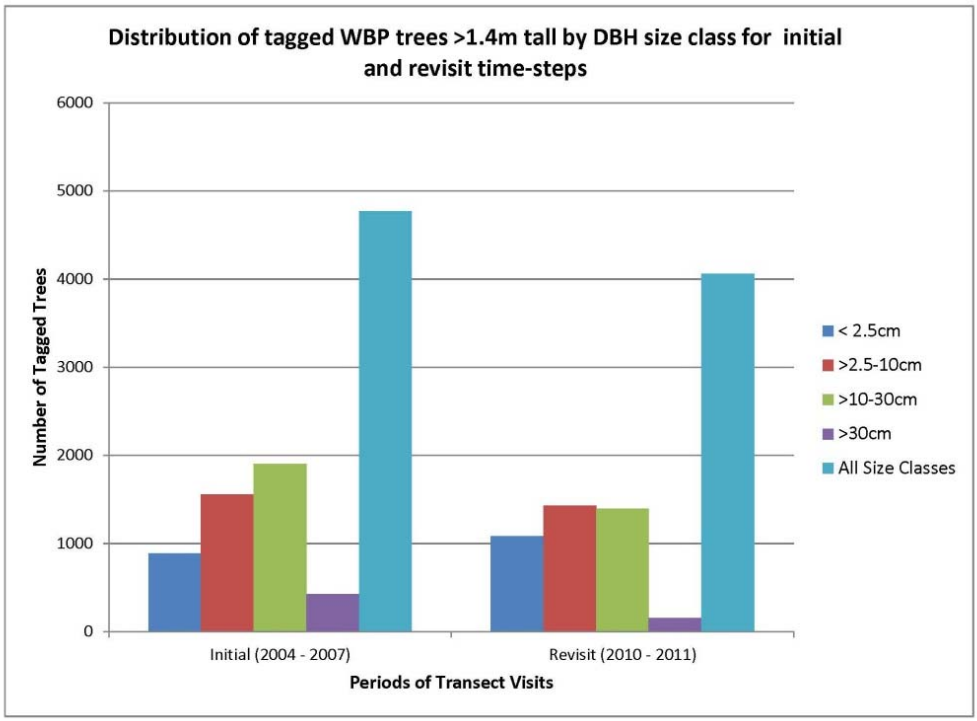

Figure 8. Variability in the distribution of tagged trees across the monitoring belt transects at the end of 2011.

Discussion

The estimated proportion of whitebark pine trees infected with blister rust in the GYE was similar between the two time-steps. The overall percentage of whitebark pine trees >1.4 m tall infected with blister rust in the GYE was estimated to be between 20% and 30%. While variation (increases and decreases) in blister infection occurred across

the 176 monitoring transects and resulted in shifts in the proportion of infection for the majority (77%) of stands, we detected no significant difference between the time-steps on an ecosystem level. From an ecological perspective, we recognize that the mortality event that occurred between the initial time-step and the revisit time-step (influenced by mountain pine beetle, fire, blister rust, and other causes) had the potential to impact the overall infection proportion in the GYE. In our analysis process, we did not find strong evidence to support this notion. We found that mortality decreased the number of trees in the sample with mountain pine beetle and fire acting as the major drivers of mortality. Trees with or without blister rust were attacked or killed by mountain pine beetle and fire in relatively equal numbers.

When we initiated the monitoring program in 2004, mountain pine beetle populations were just beginning to increase in the GYE (Hayes 2013; Olliff et al. 2013). At the time, whitebark pine mortality levels attributable to mountain pine beetle were relatively low and mountain pine beetle was considered a secondary threat to whitebark pine, in contrast to the ubiquitous pathogen, blister rust. As monitoring efforts transitioned from initial transect establishment to revisits, however, field data captured the shift in magnitude from what most observers considered endemic levels of mountain pine beetle infestation to those of epidemic proportions (Logan et al. 2010; Hayes 2013; Olliff et al. 2013). The ensuing mortality within the whitebark pine population was predominantly exhibited by those trees >10 cm DBH and congruent with known mountain pine beetle size preferences (Furniss and Carolin 1977). Within the 176 permanently established belt transects, roughly 50% of the trees initially tagged in the

initial time-step were >10 cm DBH (GYWPMWG 2012; Figure 9). Approximately 36% of the tagged trees in this >10 cm DBH size class had some degree of blister rust infection. Consequently, as the mortality of infected tagged trees occurred on monitored belt transects, the proportion of infection for a given belt transect was affected (following the monitoring protocol, we evaluated only live trees for the presence of blister rust infection). At the same time, we documented 423 tagged trees as transitioning from uninfected in the initial time-step to infected in the revisit time-step. Therefore, it is plausible that mountain pine beetle-caused mortality of infected trees combined with gains in new infections observed in the revisit time-step resulted in neither a net gain nor loss in overall proportion of trees infected with blister rust by the end of the revisit time-step.

The monitoring program is distinguished by the extensive volume of data collected from repeat sampling of tagged whitebark pine trees over an extended period of time. Other accounts of blister rust levels in the GYE are, for the most part, founded on data derived from short-term studies where infection change over time is not measurable (Larson and Kipfmueller 2010; Bockino and Tinker 2012; Kendall et al 1996). In addition, unlike the monitoring program effort, many of these studies and their subsequent reports are centered on specific areas within the GYE. In 2007, Grand Teton NP staff established 26 additional permanent monitoring transects in the park modeled after the Interagency Whitebark Pine Monitoring Protocol (GYWPMWG 2011; in addition to the two established by the monitoring program) and found that the proportion

of trees infected with blister rust fluctuated annually with a range from 34-60% in samples collected from 2007 to 2013 (McCloskey pers. com).

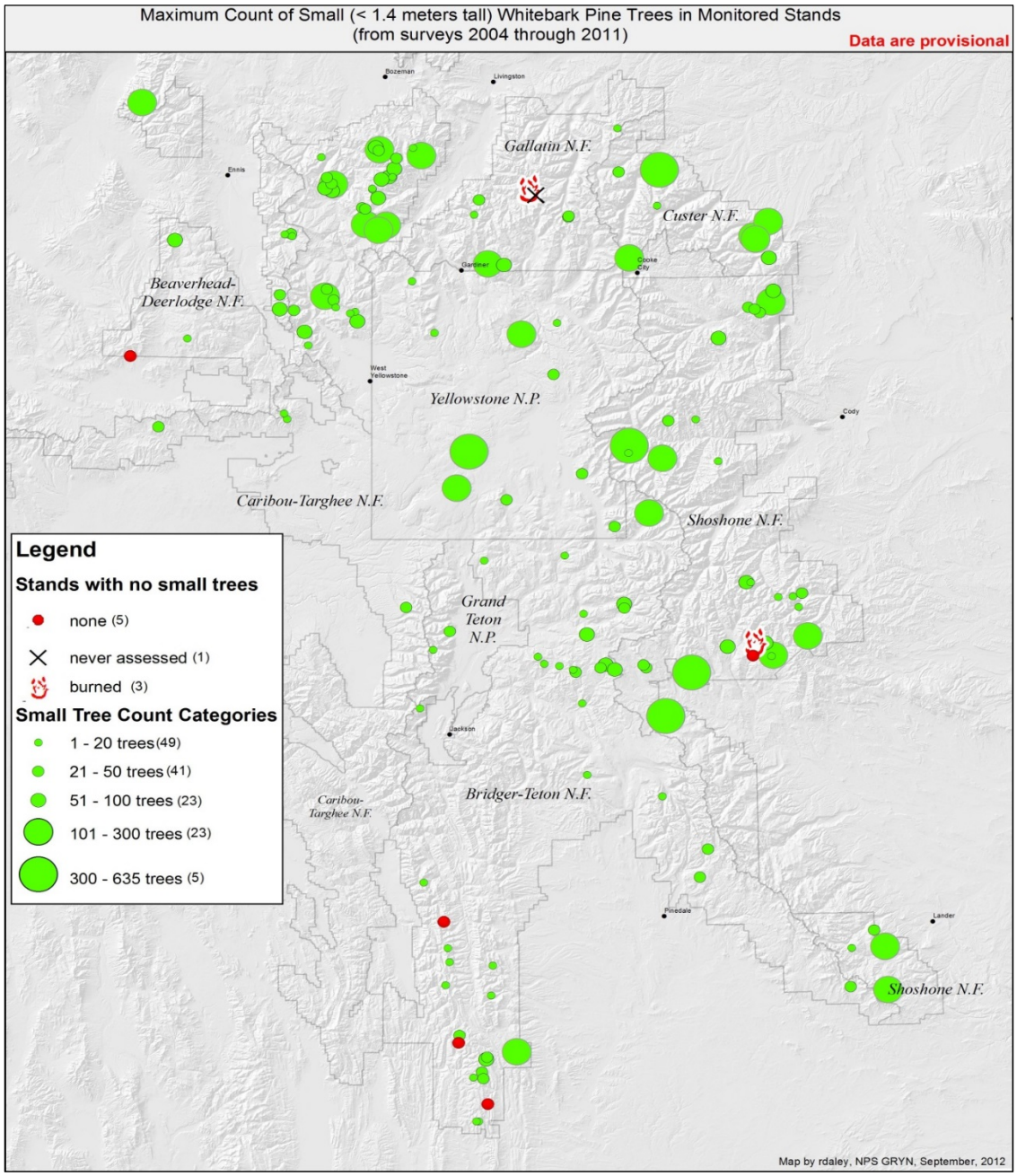

Figure 9. Maximum count of ≤1.4 m tall whitebark pine trees (per 500 m2) in monitored stands from surveys 2004 through 2011.

Infection severity of blister rust has been defined in many ways by multiple studies (Newcomb 2003, Six and Adams 2007, Six and Newcomb 2006). The monitoring program distinguishes infection severity by the specific location of infection on a diseased tree (GYWPMWG 2011). Infection severity fluctuated between the two time-steps. Some trees documented as infected during the initial time-step, no longer exhibited visible signs of infection when surveyed in the revisit time-step. For example, we recorded a total of 174 tagged trees with some level of infection during the initial time-step, but upon revisit were absent of infection. We regarded this as a transition in infection status from infected to non-infected. As observed in several species of white pine, branches with blister rust cankers further than 0.6 m from the main bole of the tree can self-prune (Maloy 2001). With this type of self-pruning, infection may no longer be detectable on a tree that possessed observable cankers when initially inspected.

Another explanation for decreased signs of infection in subsequent revisits is that cankers can change phenotypically as they age and with normal environmental exposure. As outlined in the Greater Yellowstone Whitebark Pine Monitoring Protocol (GYWPMWG 2011), a canker without visible aecia can be recorded as a positive blister rust infection when there is evidence of three of five possible secondary indicators of blister rust infection identified on a tree. These secondary indicators include flagging, swelling, roughened bark, rodent/insect chewing or stripped bark, and oozing sap (Hoff 1992). Over time, due to natural aging and weathering of the tree, it is possible that a canker may no longer meet the established set of indicator standards (see GYWPMWG

2011). If these specifications are not met, then infection criteria may simply not be noted during subsequent examinations, regardless of a previous infection state.

Lastly, although established procedures are implemented to minimize observer variability as a component of the monitoring program, this variability may play a role in both individual tree and proportional changes in infection (Huang 2006). Any of these scenarios may be acting separately or in combination to affect infection rate summaries and are all potential explanations for the shift in infection observed at the stand level. As the monitoring program evolves, we will take steps to quantify the confounding effects of each factor in order to understand how they are influencing recorded rates of infection.

By the end of the revisit time-step, approximately 57% of blister rust infections occurred on the bole of infected trees. This type of blister rust infection is considered to be more consequential than acanopy canker, as it compromises not only the overall longevity of the tree, but its functional capacity for reproductive output as well (Kendall and Arno 1990; Campbell and Antos 2000; McDonald and Hoff 2001; Schwandt and Kegley 2004). Though a tree can live for decades infected with blister rust (Mielke 1937; McDonald et al. 1981), an infected tree may be more vulnerable to other stressors such as mountain pine beetle (Six and Adams 2007; Bockino and Tinker 2012). Results from more recent investigations into this potential interaction indicate an additive pathogen-insect effect on mortality occurred only in smaller-DBH trees.

In addition to potentially increasing the susceptibility to other stressors, blister rust can affect a tree's ability to reproduce (Smith and Hoffman 2000; Maloney et al. 2012). Cones are produced on the outer branches in the upper canopy of whitebark pine;

portions of a branch that are located above an active canker are often precluded from vital nutrients necessary to sustain normal tree function, healthy foliage, and cone production (Maloney et al. 2012). As a result, death of infected upper branches can occur and negatively impact cone production. Although there has been no significant change in the overall proportion of trees infected with blister rust in the GYE, monitoring data indicate that many of the trees that remained alive and infected between the initial time-step and the revisit time-step transitioned from a less lethal (canopy) form of infection to one considered more detrimental (bole) to the health and status of the tree. We plan to evaluate the possible influence of time and DBH on canker transition in future analyses.

Infection by blister rust is a relatively slow process and it can take up to four years before infection is physically apparent to an observer (McDonald and Hoff 2001). Two time-steps comprising only eight years of data collection may not be adequate to fully describe the extent of blister rust infection on the whitebark pine population. As the monitoring program continues, we expect more precise estimates on its overall effects in the GYE.

Mortality of whitebark pine occurred in all DBH size classes since the initial transect establisment. Although no specific cause of mortality is ascribed to dead trees in the monitoring program, we documented conditions that potentially influence the mortality of a given tree. Mountain pine beetle infestation was evident on the majority of recorded dead whitebark pine >10 cm DBH in the belt transect population (Figure 5). Slowly building in the early 2000s, the mountain pine beetle outbreak intensified around 2007 (Hayes 2013; Olliff et al. 2013). The subsequent mortality that followed became

demonstrably evident throughout the GYE and was particularly apparent in and around 2009 and 2010 (Figure 6). Mortality levels in the monitoring belt transects coincided with the period described by others (Hayes 2013, Olliff et al. 2013); though in some cases, documentation of mortality may have been delayed due to the modified two-year revisit timeline. For example, we may have documented a particular tree as live, successfully attacked by mountain pine beetle, and with a fading crown in 2008, but not recorded an actual mortality until 2010 when crews observed that tree during the assigned panel revisit schedule.

White pine blister rust was the sole attribute in 13% of the total number of dead tagged trees by the end of the revisit time-step. Along with mountain pine beetle and blister rust, whitebark stands have also been affected by wildland fires across the ecosystem. Between the two time-steps, six of the 150 monitoring stands had been affected by wildland fire. Under projected climate change conditions, wildland fire events are predicted to increase in the GYE (Westerling et al. 2011). Consequently, we expect an increase in the number of stands affected by fire in the future.

Although approximately 20% of the tagged tree population has died, we observed reproducing trees, regeneration in the understory, and recruitment into the tagged tree population. We documented 26% of the live tree population as producing cones, demonstrating that there is some seed present on the landscape. Regeneration varies dramatically across the 176 belt transects. Counts of whitebark pine trees ≤1.4 m tall ranged from 0 to 635 trees per 500 m2 belt transect (Figure 9). Our estimates suggest that there are about 50 five-needle pines ≤1.4 m tall per 0.04 ha. In addition, by the end

of the revisit time-step, we tagged an additional 287 new trees within the belt transects that had grown into the >1.4-m tall height category.

Conclusions

Throughout the past decade in the GYE, monitoring has helped document shifts in whitebark pine forests; whitebark pine stands have been impacted by insect, pathogen, wildland fire, and other events. Blister rust infection is ubiquitous throughout the ecosystem and infection proportions are variable across the region. For instance, we observed a higher prevalence of blister rust on the monitoring transects in the northwestern portion of the study area compared to transects located in the southeastern part of the Wind River Range (Figure 10). We also observed an estimated loss of approximately 20% of whitebark pine trees >1.4 m tall across the GYE at the end of the revisit time-step in 2011. It is important to note that estimates presented here reflect data collected fromground-based monitoring efforts as opposed to other studies that report higher estimates of mortality based on aerial and remote sensing detection (McFarlane et al. 2013, Logan et al. 2010). Remote sensing tends to focus on canopy-occupying individuals. On the monitoring belt transects, mortality in the overstory constituted approximately 42% (414 trees) of the trees recorded as dead by the end of the revisit time-step. Overstory trees ranged in size from 11.5-122 cm DBH and were recorded as >10 m in height.

Monitoring belt transects reflect the overall trend in whitebark pine stands throughout the GYE. Mortality of overstory cohorts in many stands throughout the GYE

has prompted considerable interest and emphasized the need for investigating the growth of the whitebark pine understory. Due to the potential for observers to miss understory whitebark pine trees within the extensive bounds of a 10x50 m belt transect, we piloted additional efforts in 2010 to more accurately assess recruitment of small trees into the >1.4 m height category. In addition, we consider overall species competition and the effects of canopy openings on whitebark pine understory growth. This aspect is a recent addition to the monitoring program protocol, and we will incorporate our results into future reports.

The monitoring program continues to impart meaningful information to the broader regional assessment of trends in the health and status of whitebark pine. The monitoring program acts as an important resource for a variety of organizations embarking on five-needle pine monitoring and has provided contemporary data to agencies such as the U.S. Fish and Wildlife Service, which listed whitebark pine as warranted but precluded under the Endangered and Threatened Species Act (USFWS 2011).

We provide this step-trend report as a quantifiable baseline for understanding the state of whitebark pine in the GYE. Many aspects of whitebark pine health are highly variable across the range of its distribution in the GYE. Through sustained implementation of the monitoring program, we will continue efforts to document and quantify whitebark pine forest dynamics as they arise under periodic upsurges in insect, pathogen, fire episodes, and other climatic events in the GYE. Since its inception, this monitoring program perseveres as one of the only sustained long-term efforts conducted

in the GYE with a singular purpose to track the health and status of this prominent keystone species.

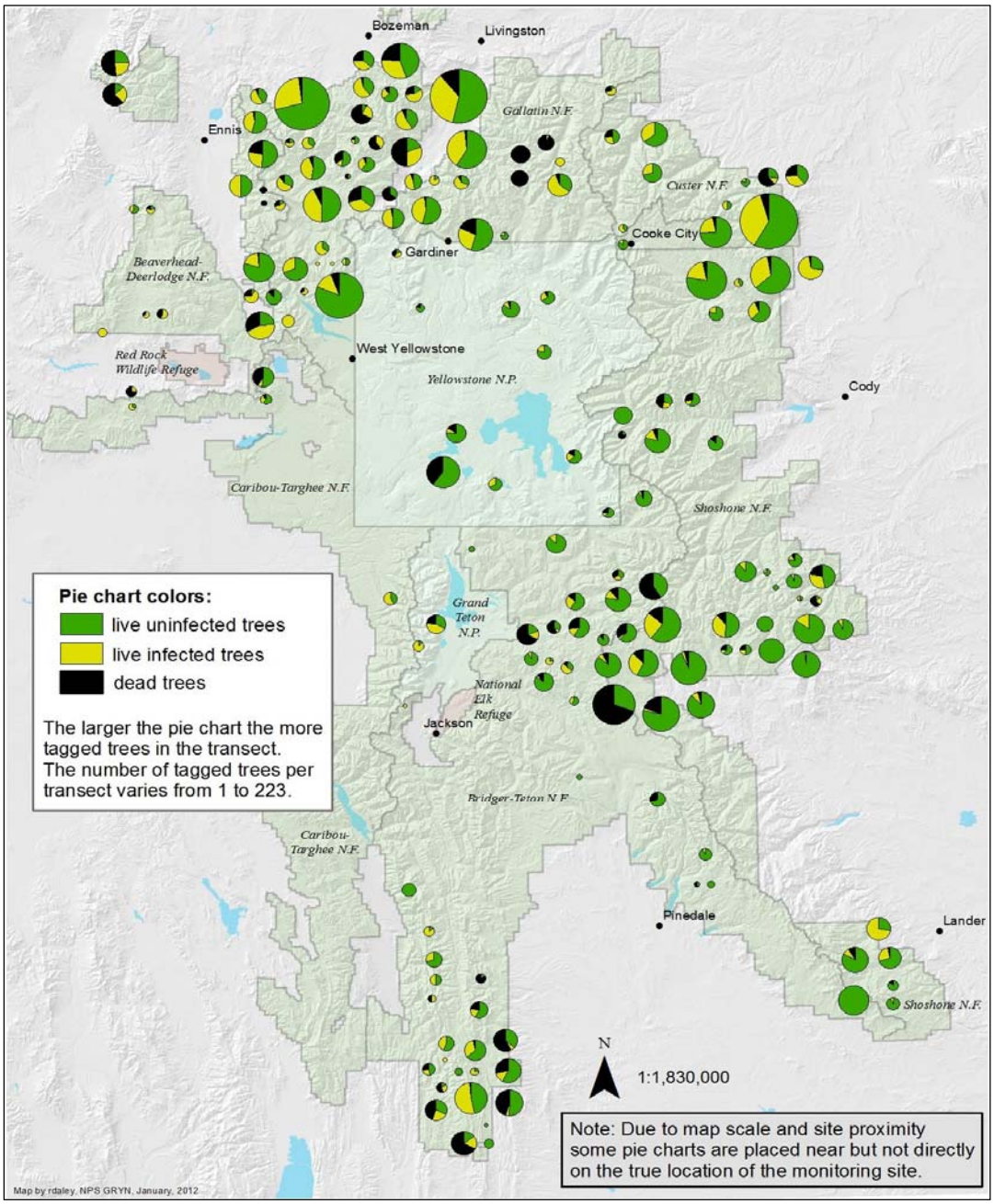

Figure 10. Distribution of blister rust-infected trees in sampled transects in the GYE at the end of 2011.

Supplemental Information for Chapter 2: Field Form

Site 10596-2 | Panel 3 Full Survey | **2014 GYE Interagency WBP Monitoring Program** TREE DATA SHEET | version : 2/3/2014

Please write carefully, neatly, and legibly. **Review and double-check all entries for quality.**

Always enter Tree ID, DBH, and Height Class for new trees

For Independent-observer Surveys, EACH observer records their own values with no interaction with other crew members.

MPB Pitch Tubes	MPB Frass
0 = 0 pitch tubes	0 = no frass
1 = 1-5 pitch tubes	1 = frass less than 30%
2 = > 5 pitch tubes	2 = frass more than 30%

Cone Category
0 - no visible cones
1 - 1 to 5 cones
2 - 6 to 10 cones
3 - more than 10 cones
5 - cone scar(s) but no visible current-year cones

grn = L
red = D
brn=RD

Tree ID (tag no.)	Tree Species	Observer's Initials	Clump Number	Clump Letter	DBH (cm)	Height Class (1-3)	Tree Status (L, RD, D)	Branch Cankers						Bole Cankers						Indicators					Live Canopy Volume (%) (Upper Third)	Mountain Pine Beetle			Cone Category (see above)	Tree Health Code(s) (Use only valid codes from Protocol)
								Upper Third		Middle Third		Bottom Third		Upper Third		Middle Third		Bottom Third		Rodent Chewing	Flagging	Swelling	Roughened Bark	Oozing Sap		Pitch Tube Category(0-2)	MPB-Galleries Present (Y/N)	MPB-Frass Category(0-2)		
								A	I	A	I	A	I	A	I	A	I	A	I											
60	HAL		-	-	1	1																								
61	HAL		1	a	6.5	1																								
62	HAL		1	b	8	2																								
63	HAL		2	a	5	1																								
64	HAL		2	b	3.5	1																								
65	HAL				3.5	1																								
66	HAL		-	-	4	1																								
67	HAL				5	1																								
68	HAL		-	-	2	1																								
69	HAL				5.5	1																								
70	HAL		-	-	1	1																								
173	HAL				3	1																								

Comments on individual trees **(Objective and concise comments only please.)**

Tree ID	Comment

Literature Cited

Arno, S.F. 1986. Whitebark pine cone crops: A diminishing source of wildlife food. Western Journal of Applied Forestry 1:92-94.

Arno, S. F. and R. J. Hoff. 1990. Pinus albicaulis Engelm. Whitebark pine. In: Burns, R. M. and B. H. Honkala, technical coordinators. Silvics of North America, Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 268-279.

Benedict, W. V. 1981. History of white pine blister rust control: A personal account. U.S. Department of Agriculture. Forest Service. FS-355.

Bockino, N. K. and D. B. Tinker. 2012. Interactions of white pine blister rust and mountain pine beetle in whitebark pine ecosystems in the southern Greater Yellowstone Ecosystem. Natural Areas Journal 32:31-40.

Campbell, E. M. and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Dixon, B. G. 1997. Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. Thesis Montana State University. 143 pages plus appendices. Bozeman, Montana, USA.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swans, J. Thomspon, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 39:479-486.

Fancy, S. C., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. Environmental Monitoring and Assessment 151:161-174.

Farnes, P. 1990. SNOTEL and snow course data: Describing the hydrology of whitebark pine ecosystems. page 386 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium 31 on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Furniss, M. M. and R. Renkin. 2003. Forest entomology in Yellowstone National Park, 1923-1957: A time of discovery and learning to let live. American Entomologist 49:198-209.

Furniss, R. L. and V. M. Carolyn. 1977. Western forest insects. Misc. Publ. 1339. Washington, D.C.: USDA Forest Service. 654 p.

Gelman, A. and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.

Gibson, K. 2003. Mountain pine beetle: Conditions and issues in the Western United States. page 298 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Proceedings, Mountain Pine Beetle Symposium: Challenges and Solutions (Kelowna, British Columbia, October 2003). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC.

Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (GYCCWPS). 2011. Whitebark pine strategy for the Greater Yellowstone Area. Greater Yellowstone Coordinating Committee, Bozeman, Montana.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, Montana, USA.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2012. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2011 annual report. pages 56-65 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2011. U.S. Geological Survey, Bozeman, Montana, USA.

Hayes, C. 2013. Montana: Forest insect and disease conditions and program highlights, 2012. Report 13-02. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA. 32

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. USDA Forest Service, Intermountain Research Station, Research Note INT-406, Ogden, Utah., USA.

Huang, M. 2006. A statistical analysis of observer variability in the identification of blister rust infection occurring in whitebark pine monitoring. Unpublished Report

prepared for the Whitebark Pine Monitoring Working Group. Department of Mathematical Sciences, Montana State University, Bozeman.

Jean, C., A. M. Schrage, R. E. Bennetts, R. Daley, E. A. Crowe, and S. O'Ney. 2005. Vital signs monitoring plan for the Greater Yellowstone Network. National Park Service, Greater Yellowstone Network, Bozeman, Montana.

Keane, R. E. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Kendall, K. C., D. Schirokauer, E. Shanahan, R. Watt, D. Reinhart, S. Cain, and G. Green. 1996. Whitebark pine health in northern Rockies national park ecosystems: A preliminary report. Nutcracker Notes 7:16.

Kendall, K. C. and R. E. Keane. 2001. Whitebark pine decline: Infection, mortality, and population trends. pages 221-242 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington DC.

Kendall, K. C. and S. F. Arno. 1990. Whitebark pine: An important but endangered wildlife resources. pages 264-273 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Ketcham, D. E., C. A. Wellner, and S. S. Evans, Jr. 1968. Western white pine management programs realigned on northern Rocky Mountain national forests. Journal of Forestry 66:329-332.

Koteen, L. 2002. Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. pages 343-414 in S. H. Schneider and T. L. Root, editors. Wildlife responses to climate change: North American case studies. Island Press, Washington, D.C., USA.33

Landenburger, L. 2012. Description of whitebark pine primary sampling unit selection. Unpublished.

Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. page 386 in W. C. Schmidt and K .J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Lanner, R. M. 1996. Made for each other, a symbiosis of birds and pines. Oxford Press Inc., New York, New York, USA.

Larson, E. R. and K. F. Kipfmueller. 2010. Patterns in Whitebark pine regeneration and their relationship to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40:476-487.

Logan, J. A., W. W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20:895-902.

Lohr, S. 2010. Sampling: design and analysis, 2nd edition. Brooks/Cole Cengage Learning, Boston, Massachusetts. pp. 145-146.

MacFarlane, W. W., J. A. Logan, and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications 23:421-437.

Maloney, P. E., D. R. Volger, C. E. Jensen, and A. D. Mix. 2012. Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests of Lake Tahoe Basin, USA: Implications for restoration. Forest Ecology and Management 280:166-175.

Maloy, O. C. 2001. White pine blister rust. Online. Plant Health Progress, doi: 10.1094/PHP-2001-0924-01-HM. Available at: https://www.apsnet.org/edcenter/intropp/lessons/fungi/Basidiomycetes/Documents/whitepine_PHP2001_0924_01.pdf (accessed July 10, 2014)

Marston, R. A. and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338-346.34

Mattson, D. J. and D. G. Despain. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Prepared for the Interagency Grizzly Bear Study Area. 37 p.

McDonald, G. I., B. A. Richardson, P. J. Zambino, N. B. Klopfenstein, and M. S. Kem. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North American: A first report. Forest Pathology 36:73-82.

McDonald, G. I. and R. J. Hoff. 2001. Blister rust: An introduced plague. pages 193-220 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark Pine Communities Ecology and Restoration. Island Press,Washington, DC.

McDonald, G. I., R. J. Hoff, and W. R. Wykoff. 1981. Computer simulation of white pine blister rust epidemics I. Model formulation. U.S. Dep. Agric. For. Serv. Res. Pap. INT-258.

Mielke, J. L. 1937. An example of the ability of Ribes lacustre to intensify Cronartium ribicola on Pinus monticola. Journal of Agricultural Research 55:873-882.

Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. M.S. Thesis. The University of Montana, Missoula, MT.

Olliff, S. T., R. A. Renkin, D. P. Reinhart, K. A. Legg, and E. M. Wellington. 2013. Exotic fungus acts with natural disturbance agents to alter whitebark pine communities. pages 236-251 in P. J. White, R. A. Garrott, and G. E. Plumb, editors. Yellowstone's Wildlife in Transition. Harvard University Press, Cambridge, Massachusetts, USA.

Pedersen, G. T., S. T. Grey, C. A. Woodhouse, J. L. Betancourt, D. B. Fagre, J. S. Little, E. Watson, B. H. Luckman, and L. J. Graumlich. 2011. The unusual nature of recent snowpack declines in the North American cordillera. *Science* 333:332-335.

Perkins, D. L. and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal of Forestry Research 26:2123-2133.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raffa, K. F., E. N. Powell, and P. A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. Proceedings of the National Academy of Sciences 110.6:2193-2198.35

Schwandt, J. and H. Kearns. 2011. White pine blister rust: General ecology and management. Insect and Disease Management Series 14:2.

Schwandt, J. W. and S. Kegley. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. R1-04-9. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA.

Six, D. L., E. Biber, and E. Long. 2014. Management for mountain pine beetle outbreak suppression: Does relevant science support current policy? Forests 5:103-133.

Six, D. L. and J. Adams. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). Journal of Entomological Science 42:345-352.

Six, D. L. and M. Newcomb. 2006. A rapid method for rating white pine blister rust incidence, severity, and distribution within individual trees in whitebark pine. Northwest Science 79:189-195.

Smith, C. M., B. Wilson, S. Rasheed, R. Walker, T. Carolin, and B. Sheppard. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forestry Research 38:982-995.

Smith, J. P. and J. T. Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60:165-179.

Smith, J. P., J. T. Hoffman, K. F. Sullivan, E. P Van Arsdel, and D. Vogler. 2000. First report of white pine blister rust in Nevada. Plant Disease 84:594.

Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of eastern Idaho-western Wyoming. USDA Forest Service General Technical Report INT-144. Intermountain Forest and Range Experiment Station, Ogden. Utah.36

Tainter, F. H. and F. A. Baker. 1996. Principals of Forest Pathology. John Wiley & Sons, Inc., New York. 805 p.

Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelmi, Y. Wei, and R. B. Cook. 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. Date accessed: YYYY/MM/DD. Temporal range: YYYY/MM/DD-YYYY/MM/DD. Spatial range: N=DD.DD, S=DD.DD, E=DDD.DD, W=DDD.DD. http://dx.doi.org/10.3334/ORNLDAAC/1219

Tomback, D. F. and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186-225.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention. pages 4-25 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities. Island Press, Washington DC.

U.S. Fish and Wildlife Service (USFWS). 1993. Grizzly bear recovery plan. Missoula, MT 181 pp.

U.S. Fish and Wildlife Service (USFWS). 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. Federal Register 76:42631-42654.

Weaver, T. 2001. Whitebark pine and its environment. pages 41-66 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regime by mid-21st century. Proceedings of the National Academy of Science of the United States of America; 108(32): 3165-13170. Published online 2011 July 25. doi: 10.1073/pnas.1110199108 PMCID: PMC3156206. Available at: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3156206/ (accessed July 10, 2014)

Zambino, P. J., B. A. Richardson, and G. I. McDonalt. 2007. First report of white pine blister rust fungus, *Cronartium ribicola*, on *Pedicularis bracteosa*. Plant Disease 91:467.37

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forestry Research 32:1265-1274.

CHAPTER THREE

WHITE PINE BLISTER RUST IN WHITEBARK PINE STANDS: INFECTION AND INFECTION TRANSITION PROBABILITY

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Erin K. Shanahan

Contributions: Conceived and implemented the modeling effort. Wrote first draft of the manuscript

Co-Author: David W. Roberts

Contributions: Helped conceive the modeling design. Reviewed results and provided feedback on final draft of manuscript.

Co-Author: Kathryn M. Irvine

Contributions: Assisted in study conception, modeling effort, and review of early drafts. Provided feedback on early statistical analysis and final draft of manuscript.

Co-Author: Andrea R. Litt

Contributions: Provided feedback on final draft of manuscript.

Manuscript Information

Erin K. Shanahan, Dave Roberts, Kathryn M. Irvine, Andrea R. Litt, Kristin Legg
Natural Areas Journal
Status of Manuscript:
__X__ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Natural Areas Association

CHAPTER 3

WHITE PINE BLISTER RUST IN WHITEBARK PINE STANDS: INFECTION AND INFECTION TRANSITION PROBABILITY

For submission to *Natural Areas Journal*

Erin K. Shanahan, 2327 University Way, Ste. 2, Bozeman, MT 59715

Dr. David W. Roberts, Ecology Department, Montana State University, 310 Lewis Hall, P.O. Box 173460, Bozeman, MT 59717-3460

Dr. Kathryn Irvine, U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Ste. 2, Bozeman, MT 59715

Dr. Andrea R. Litt, Ecology Department, Montana State University, 310 Lewis Hall, P.O. Box 173460, Bozeman, MT 59717-3460

Abstract

Whitebark pine (*Pinus albicaulis*) contributes to a variety of ecological functions in high-elevation forest communities throughout its range. Recent declines in whitebark pine populations in the Greater Yellowstone Ecosystem have been attributed to a variety of influencing factors including white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), wildfires, and changes in alpine climatic conditions. We employed data collected by the Interagency Whitebark Pine Monitoring Program from 2004 to 2014 to model blister rust infection probability and the probability of infection transition or expansion from canopy to bole as influenced by tree size

(diameter at breast height; DBH) in a tagged population of whitebark pine trees 1 to 20-cm DBH. On average, about 35% of trees became infected over a 4-year period. Using generalized linear mixed modelling techniques, we found that initial blister rust infection was positively correlated with DBH. Fifty percent of canopy infected trees showed infection transition from the, to the bole. However, tree size was surprisingly not an important component of infection. Through this effort we provide contemporary data to managing agencies tasked with the preservation and restoration of whitebark pine throughout the ecosystem.

Index terms: whitebark pine, white pine blister rust, transition, Interagency Whitebark Pine Monitoring Program, bole

Introduction

Whitebark pine (*Pinus albicaulis*) occurs throughout the interior Pacific Northwest, northern Sierra Nevadas, and northern Rocky Mountains where it exerts considerable influence on the biodiversity and productivity of high elevation forests and alpine communities (Tomback et al. 2001, Ellison et al. 2005, Ebenman and Jonsson 2005, Shanahan et al. 2014). This five-needle pine can exist under extreme environmental conditions and, importantly, under conditions that limit the establishment of many heterospecifics. Although its relative inaccessibility and crooked growth form lead to low commercial value, whitebark pine is recognized for its ecological importance to alpine and subalpine environments (GYWPMWG 2011).

At the stand or tree-scale, whitebark pine's canopy structure helps retain snowpacks and moderates snowmelt rates (Weaver 2001). As temperatures increase in alpine and subalpine environments during the spring and summer the maintenance of snowpacks is recognized as an increasingly important function benefiting many species (Arno and Hoff 1990, Smith et al. 2008, Farnes 1990). For example, mature whitebark pine trees produce microclimates in alpine and subalpine locations that facilitate the establishment of other forest species including subalpine fir (*Abies lasiocarpa*; Tomback et al. 1993). Throughout its range, whitebark pine cone seeds are also recognized as an important food source for a variety of wildlife including many granivorous small mammals and birds (Arno and Hoff 1990, Tomback et al. 2001). In the Greater Yellowstone Ecosystem (GYE), whitebark pine has been documented as a critical food source for grizzly bears (*Ursus arctos horribilis*), red squirrels (*Tamiasciurus hudsonicus*), and Clark's nutcrackers (*Nucifraga Columbiana*; Tomback et al. 2001).

For many decades and throughout its range, extensive declines in whitebark pine populations have been documented (Kendall and Keane 2001, Shanahan et al. 2014). Decreases in whitebark pine have been attributed to the incidence of white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*), wildfires, and warming temperatures (Keane and Arno 1993, Kendall and Keane 2001, Zeglen 2002, Smith et al. 2008, Tomback and Achuff 2010, MacFarlane et al. 2013, Shanahan et al. 2014). Acting individually or in concert, these agents have reduced the abundance and distribution of this important conifer in high-elevation forests and

continue to pose a significant threat to the persistence of living whitebark pine populations (Kendall and Keane 2001).

In the GYE, mass mortality of whitebark pine has occurred across the region and is largely attributable to a recent mountain pine beetle outbreak (Logan et al. 2009, MacFarlane et al. 2013). Aerial surveys conducted in the GYE during the height of the mountain pine beetle outbreak reported stand-level mortality rates as high as 82% (MacFarlane et al. 2013). Mortality has been most pronounced within the larger size classes (>10-cm diameter at breast height; DBH), which are typically the mature, cone-producing individuals in the population (GYWPMWG 2012, Shanahan et al. 2014). As a result, significant changes in the demographic properties of many whitebark pine stands have been documented (GYWPMWG 2012). Even though the mountain pine beetle outbreak appears to have waned in most locations in the GYE (Haroldson and Podruzny 2013, Mahalovich 2013, GYWPMWG 2014), surviving whitebark pine are still at risk. White pine blister rust arguably poses the most severe threat to the long-term survival of whitebark pine across its range (Kendall and Keane, 2001).

White pine blister rust (blister rust) is an exotic fungal pathogen with a propensity for infecting white pine species [e.g. whitebark pine, limber pine (*Pinus flexilis)*, and western white pine (*Pinus monticola*)]. Blister rust is ubiquitous throughout the GYE, although the magnitude of infection varies across this geographically diverse region (GYWPMWG 2012). In contrast to rapid mountain pine beetle infestations (Hicke et al. 2006, Safranyik et al. 2010), blister rust infestations are gradual but may have lethal effects (Kendall and Keane, 2001). Blister rust basidiospores released from intermediary

hosts enter whitebark pine trees through the needles and reach the stemwood over a period of several months. Ultimately, infection manifests in the formation of a canker (McDonald and Hoff 2001). After infection, it takes approximately two to four years for aecia-filled cankers (the fruiting body of blister rust) on infected trees to erupt and release aeciospores that perpetuate the disease (McDonald and Hoff 2001).

The majority of primary infections initiate in the crown of a tree and canopy branches are disproportionately affected in early stages of the disease (McDonald and Hoff 2001). Aecia directly and indirectly damage infected trees. Over time, spore growth patterns lead to swelling and bark girdling (McDonald and Hoff 2001) and infected branches eventually die (Tainter and Baker 1996, Smith et al. 2000). Indirectly, aeciospores and associated tree sap attract rodents and various insects that can cause extensive girdling on affected branches and boles through consumption of affected stemwood (Zeglen 2002, Schwandt and Kearns 2011, Shanahan et al. 2014). Any significant girdling of cone-bearing branches can have a tremendous impact on an infected tree's reproductive potential (Maloney et al. 2012). Infections that initiate in the canopy also have the potential to spread or transition to the bole of infected trees. Bole cankers are generally considered to be more severe or lethal to the infected tree (Campbell and Antos 2000, McDonald and Hoff 2001). Although a tree can persist for decades after becoming infected, cankers situated on the lower portions of the bole will eventually lead to tree death (Schwandt and Kegley 2004).

Blister rust infection may represent a more severe threat to smaller trees because rust-related mortality occurs over a shorter time period (Hoff et al. 1980, Schoettle and

Sniezko 2007). Smaller trees are believed to be more susceptible to canker expansion than larger ones because they have fewer branches and the distance an infection has to travel from the branch to the main bole is shorter (Koteen 2002, Newcomb 2003). As a result, infection in smaller trees will not only affect future reproductive potential, but smaller trees may die from blister rust infection more rapidly than larger infected trees (Smith and Hoffman 2000) further diminishing the ecological benefits provided to alpine and subalpine environments.

Numerous, short-term studies have presented summary data on blister rust infection as a function of tree size (Zeglen 2001, Kearns and Jacobi 2007, Schoettle and Sniezko 2007, Smith et al. 2008). Hatala et al. (2011) modeled general blister rust spread and transition in whitebark pine using data collected from five different field protocols with non-overlapping timeframes. However, inconsistencies amongst the study designs and data collection methodologies for the five individual studies on which their models were based is of concern. The use of a probabilistic sampling design on permanently-marked trees provides opportunities to explore the effects of blister rust infection on individual trees and stands and to extrapolate those findings to the broader population of whitebark in the GYE. Here, we investigate whether tree size influences whitebark pine's susceptibility to initial blister rust infection and whether tree size is associated with the probability that an individual tree with an existing canopy infection will expand to a bole infection over time. Our specific objectives were to (*i*) estimate the probability of transition from uninfected to infected with blister rust and (*ii*) to estimate the probability of an existing canopy infection expanding to a bole infection. We selected a 4-year time

span based on the Monitoring Program revisit schedule, and selected trees 1 to 20-cm DBH as this size class range comprised 89% of the Monitoring Program data (3343 out of a total of 3750 live trees; GYWPMWG 2014).

Methods: Study Area

Our study area encompasses six national forests (NF), two national parks (NP), as well as state and private lands in portions of Wyoming, Montana, and Idaho (Figure 11); this area is collectively described as the GYE. The GYE is geographically defined as the Yellowstone Plateau volcanic fields and the 14 surrounding mountain ranges above 2,130 m (Marston and Anderson 1991). Whitebark pine stands occupy over 800,000 hectares in the high, mountainous zones of the GYE (Marston and Anderson 1991, GYWPMWG 2011, GYCCWPS 2011). Sample sites in the study area range in elevation from 2,400 m to 3,172 m and extend to the boundaries of the GYE (Fig 1; GYWPMWG 2011).

These alpine and subalpine environments are subjected to harsh weather including excessive winds, extreme cold temperatures, and significant snow accumulation. Snow collects early and may persist until late spring and occasionally into mid-summer. Summers tend to be warm and dry.

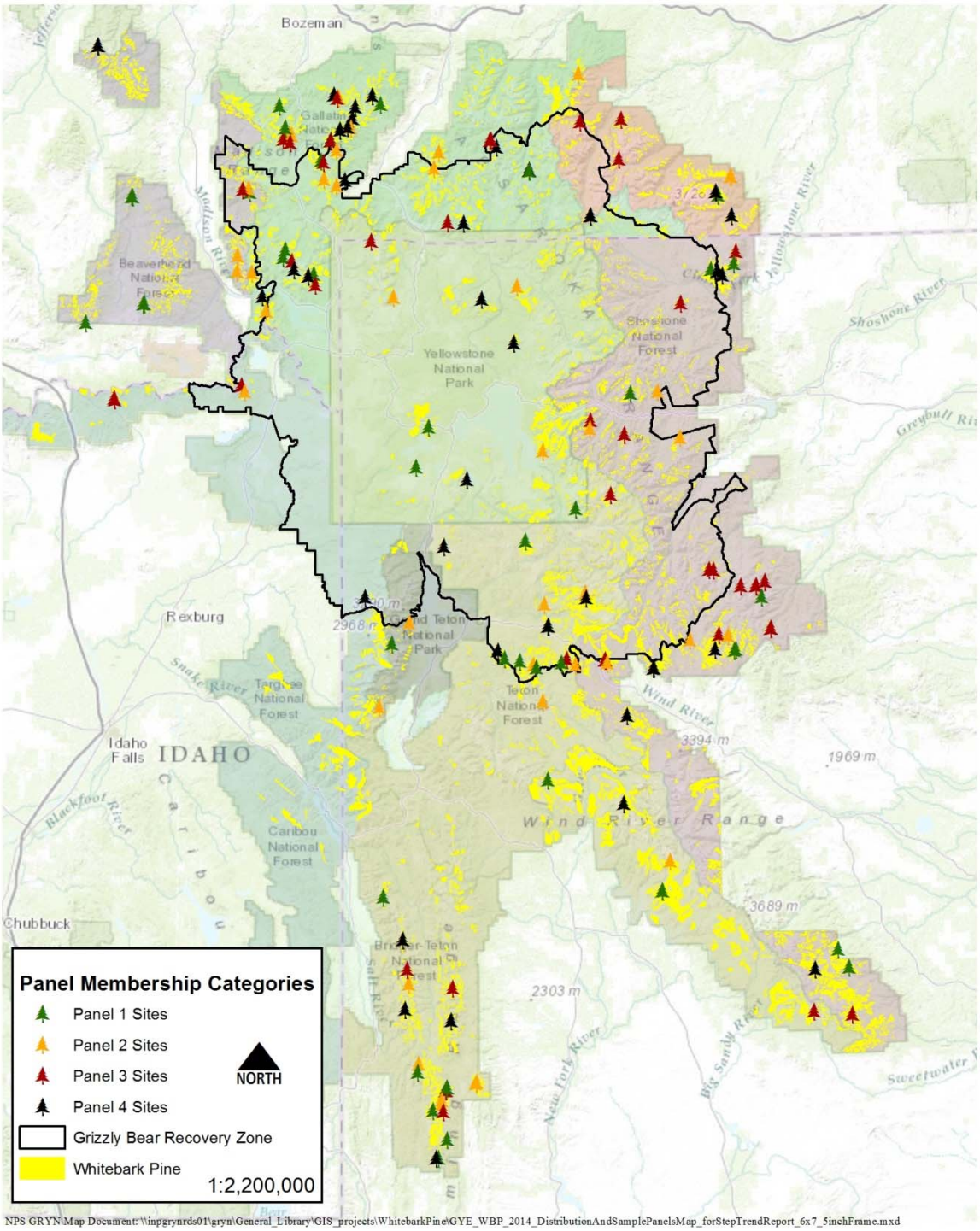

Figure 11. Whitebark Pine Monitoring Program study area in the Greater Yellowstone Ecosystem.

Stand and Transect Selection

For the purposes of this document a whitebark pine stand is defined as a contiguous area of forest of which whitebark pine is a component (e.g. dominant, co-dominant, present). Whitebark pine stands were randomly selected from approximately 10,770 mapped pure and mixed whitebark pine stands (sample frame) located on public lands throughout the GYE, identified from existing GIS vegetation layers (Dixon 1997) and cover maps produced by the individual U.S. Forest Service National Forest units included in the study area (GYWPMWG 2011).

We used a probabilistic, two stage sampling scheme with a two-stage cluster design. Whitebark pine stands were the primary sample units (PSUs) and 10 x 50-m transects were the secondary sample units (SSUs; Lohr 2010). Within each stand, UTM coordinates for five points were randomly generated as potential center points for the establishment of a 10 x 50-m belt transect. Using handheld GPS units, field crews navigated to the first randomly selected point. At this point, a randomly drawn azimuth was used to orient the transect on the landscape (GYWPMWG 2011). If a minimum of one live whitebark pine tree > 1.4-m tall was observed the transect was selected permanently monumented in order to facilitate relocation of the transect for future revisits. If the location did not meet this standard, the closest random point was visited in turn until a location met the criterion. In the rare case that none of the five randomly selected points in a stand exhibited live whitebark pine the randomly-selected stand was removed from the sample frame.

Transect Establishment and Data Collection

All live, whitebark pine trees >1.4-m tall located within the delineated boundaries of the transect (10 x 50-m) were tagged at breast height with an individually numbered aluminum tag. Whitebark pine trees may occur singly, but often occur in clumps. Clumping is associated with the multiple seed caching behavior exhibited by Clark's nutcrackers or squirrels (Tomback et al. 2001). A clump is characterized by multiple smaller boles seemingly emerging from a single, larger bole. When a clump was encountered on a transect, each bole in the clump that separated from the main bole at or below 1.4-m tall was considered to be a distinct tree and received a uniquely numbered tag.

Multiple tree attributes for every tagged tree were documented including tree size (DBH in centimeters), height (binned as < 15-m, 15-30-m, and >30-m), tree status (live; retaining any green needles or dead; all needles have turned brown or have shed), and mountain pine beetle indicators (pitch tubes, frass, or J-shaped galleries). Binoculars were used to examine trees for blister rust infection with the number and location of blister rust infections (canopy or bole) recorded for each tree in the transect. A canopy canker was defined as any infection occurring within the canopy of a tree two or more inches distal from the main bole of the tree. A bole canker is an infection that is situated on the main trunk of the tree or within two inches of the bole along peripheral branches. Canker location was recorded as occurring in the top, middle or bottom of the canopy or bole (GYWPMWG 2011). New trees were added to the sample during the first revisit period between 2008 and 2011 when an understory tree on a given belt transect attained a

height of >1.4-m tall. When trees were added, they were tagged as described above and we recorded all attributes for each new individual (as described in the tree tagging process).

Permanent stand and transect selection occurred from 2004 through 2007 (time-step T0). One hundred seventy-six permanent transects in 150 whitebark pine stands were established and 4,740 individual trees >1.4-m tall were permanently tagged. In 2008, stands were randomly assigned to one of four panels each consisting of approximately forty-four transects with planned revisits to each stand in a panel on a four-year rotating schedule. A four-year interval was selected as the amount of time that it takes to visually detect a new blister rust infection (McDonald and Hoff 2001). Each 4-year period is referred to as a "time-step" (Table 5).

Table 5. Panel schedule layout over the three time-step periods. *Panel 4 trees are scheduled to be surveyed in 2015 and therefore were not included as part of the modeling exercise for time-step T2.

2004 – 2007 Time-step T0				**2008 – 2011 Time-step T1**				**2012 – 2015 Time-step T2**			
2004	2005	2006	2007	2008 Panel 1	2009 Panel 2	2010 Panel 3	2011 Panel 4	2012 Panel 1	2013 Panel 2	2014 Panel 3	2015* Panel 4

Statistical Analyses

Data used for this analysis were collected between 2004 and 2014, and were drawn from transects that were (1) sampled during the initial set-up phase from 2004 and 2007, (2) revisited between 2008 and 2011, and for the three panels (Panels 1, 2, and 3) (3) revisited between 2012 and 2014. Tree data were restricted to trees from 1 to 20-cm DBH to avoid undue influence of size classes with small sample sizes. Probabilities of

infection and canker transition as functions of DBH were estimated separately for two intervals (T0 to T1 and T1 to T2) using all tree observations appropriate for each time-step interval (Figures 12 and 13). For example, all live trees from 1 to 20-cm DBH in T0 that were documented as still alive in T1 were used to predict probabilities for the T0 to T1 time period. To investigate infection location transition from canopy to bole, data were subset to trees with a documented canopy infection in T0 or T1.

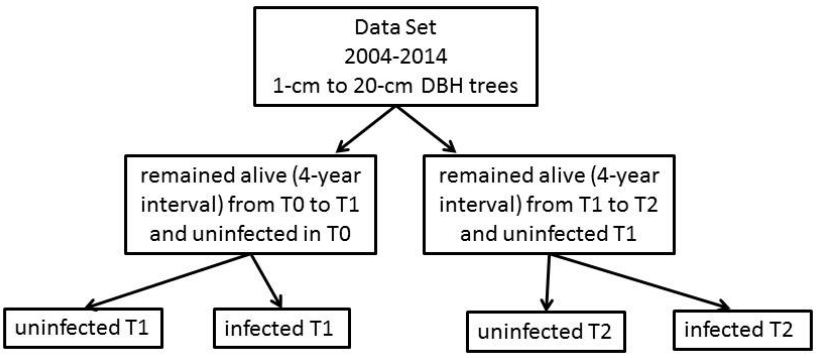

Figure 12. To investigate the probability of infection, the data were subset to include trees that remained alive from T0 to T1 or from T1 to T2, had a 4-year revisit interval, and were uninfected in either T0 or T1. The response was infection stat us in T1 or T2.

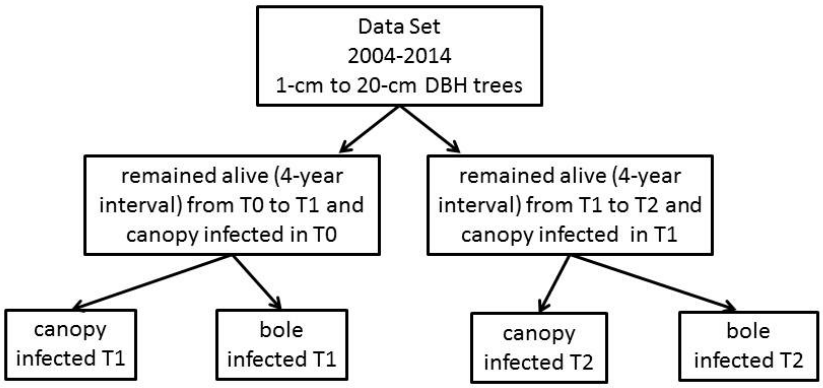

Figure 13. To investigate the probability of infection transition, the data were subset to include trees that remained alive from T0 to T1 or from T1 to T2, had a 4-year revisit interval, and were canopy infected in either T0 or T1. The response was infection l ocation status in T1 or T2.

We assume stands (PSUs) are independent of one another as reflected in the random selection of stands. We used generalized linear mixed modeling (GLMM) procedures which estimate the covariance among trees within a stand by specifying a random intercept for each transect (Bolker et al. 2008). With the GLMM approach, we considered tree DBH and survey year as fixed effects and transects as random effects to model the probability of infection on a 4-year interval for trees 1 to 20-cm DBH. When modeling the probability of canopy to bole canker expansion, we did not include year as trees used for this analysis were already infected and therefore year of initial infection did not apply. We used the function glmmML in the glmmML package to estimate predictor and random effects (R Development Core Team 2011; Brostrom 2013). glmmML uses maximum likelihood to estimate the model parameters and produces AIC values for model comparison (Zuur et al. 2009).

We fitted a full model including the fixed effects DBH and year and reduced models containing DBH or year only. We compared AIC values on the full and reduced models to rank models, with a minimum difference of 4.0 for significance. In place of a traditional R^2 goodness of fit estimate, which is not applicable for GLMM models, we used an adapted marginal and conditional R^2 estimates to measure variation explained and to determine the importance of transect random effects in the model (Nakagawa and Schielzeth 2013; Wilmoth 2015; *unpublished*). The marginal R^2 estimate considers only the influence of the fixed effect(s) when describing the variance in the response explained by the model, whereas the conditional R^2 estimate reflects the proportion of variance explained from both the fixed and random effects (Nakagawa and Schielzeth 2013).

Confidence intervals (95%) for both infection probability and infection transition were estimated using the Workman-Hotelling procedure (Ramsey and Schafer 2002). The Workman-Hotelling procedure produces a confidence interval for the entire line as opposed to point estimates, and is likely a conservative estimate for the range of uncertainty. All analyses and corresponding figures were produced using the statistical computing language R (R Development Core Team 2011).

Results: Summary of Data

From time-step T0 (2004-2007) to time-step T1 (2008-2011) 218 out of 584 trees (0.37) changed health status from uninfected to infected; From time-step T1 to time-step T2 (2012-2015), 528 out of 1665 trees (0.32) from panels 1, 2, and 3 changed infection status. For infection transition from canopy to bole, form T0 to T1, 34 of 114 trees (0.3) had infection expand to the bole whereas 73 out of 256 (0.29) transitioned from T1 to T2.

Generally, the smallest of trees remained uninfected over the two time-steps. For time-step T0 to T1, 91% (228 of 250) of trees in the smallest size class (1.0 to 5.0-cm DBH) remained uninfected and for time-step T1 to T2, a total of 94% (779 of 831) of the 1.0 to 5.0-cm DBH size class remained blister rust-free. (Table 6).

Table 6. Proportion of trees by size class that were initially uninfected and that remained uninfected into the next time-step. The total number of trees (denominator) is displayed within the parenthesis for each size class.

Proportion of trees that remained uninfected in time-steps T0 →T1 & T1→T2		
Size class (cm DBH)	**T0→T1**	**T1→T2**
1.0-5.0	0.91 (250)	0.94 (831)
5.5-10.0	0.82 (128)	0.87 (378)
10.5-15.0	0.76 (125)	0.92 (301)
15.5-20.0	0.80 (81)	0.83 (155)

For trees that had canopy infections that transitioned to the bole, the smallest trees exhibited the least degree of change in infection transition relative to other size classes. Over the range of the size classes from T0 to T1, 34 (0.29) of the trees transitioned from canopy to bole and from T1 to T2, at total of 73 (0.28) canopy infections expanded to the bole (Table 7).

Table 7. Proportion of trees that had a canopy infection in the initial time-step (either T0 or T1) that transitioned to a bole infection at the end time-step (either T1 or T2). The total number of trees (denominator) is displayed within the parenthesis for each size class.

Proportion of trees with initial canopy infection that transitioned to bole infection infected by time-step		
Size class (cm DBH)	**T0→T1**	**T1→T2**
1.0-5.0	0.20(15)	0.21 (48)
5.5-10.0	0.29 (34)	0.29 (73)
10.5-15.0	0.38 (34)	0.31 (70)
15.5-20.0	0.25 (31)	0.31 (65)

Model Results

First we investigated the probability of becoming infected with blister rust for each time-step interval; T0 to T1 and T1 toT2. In both cases the full and DBH-only reduced models produced similar AIC values and we selected the model DBH-only model as more parsimonious. The year-only reduced model ranked last. The stand random effect is important in the model analysis as supported by the marginal and conditional R^2 estimates (Table 8).

Table 8. Ranking for the probability of infection model based on AIC values with inclusion of fixed effects and GLMM marginal and conditional R^2 estimates. Marginal and conditional R^2 are reported on a scale of 0 to 1 and support the inclusion of transect random effects.

Time-step	Rank	DBH	YEAR	AIC	Marginal R^2 (DBH only)	Conditional R^2 (DBH only)
T0→T1	1	√	√	489.3	0.0636	0.1753
	2	√		490		
	3		√	501.4		
T1→T2	1	√		931.2	0.0271	0.3629
	2	√	√	934.4		
	3		√	1373		

Based on the selected model smaller size class trees have a lower probability of becoming infected with blister rust over a 4-year time period (Table 9 and Figure 14). The 95% confidence interval for T0 to T1 was 0.03 to 0.58 and for T1 to T2 it was 0.02 to 0.32.

```
Model1 <- glmmML(canopy.transition ~ DBH, family = binomial,
  cluster = Site.Id)
```

Table 9. Estimates and other associated values for the probability of infection for both time-steps.

		Estimate	SE	z	Pr(>|z|)	CI lower	CI upper
T0 to T1	Intercept	-2.59	0.298	-8.69	0.00E+00	0.03	0.58
	DBH.cm	0.098	0.021	3.959	7.52E-05		
T1 to T2	Intercept	-3.242	0.27	-11.996	0.00E+00	0.02	0.32
	DBH.cm	0.069	0.019	3.667	2.46E-04		

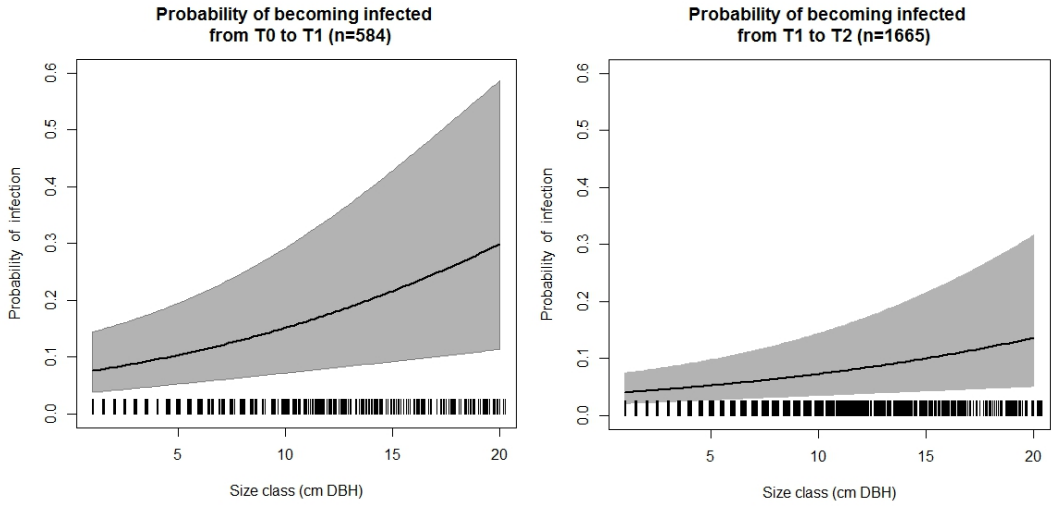

Figure 14. The probability of initial infection is positively correlated to DBH over a 4-year interval.Therefore, as DBH increases, so does the chance of infection. Smaller size class trees were more abundant in the sample than larger trees for this analysis. Confidence intervals (95%) were estimated with the Workman-Hotelling procedure and are likely conservative.

Next we modeled the probability of infection transitioning from the canopy to bole as influenced by DBH (Table 10). In this case, tree size did not appear to influence canker expansion to the bole (Figure 15). The 95% confidence interval for the probability of transition for T0 to T1 was 0.0.11 to 0.0.92 and for T1 to T2 it was 0.0.26 to 0.0.85.

```
Model2 <- glmmML(bole.transition ~ DBH, family = binomial,
    cluster = Site.Id)
```

Table 10. Estimates and other associated values for the probability of infection transition from canopy to bole for both time-steps. Marginal and conditional R^2 are reported on a scale of 0 to 1 and support the inclusion of transect random effects.

		Estimate	SE	z	Pr(>|z|)	CI lower	CI upper	Marginal R^2	Conditional R^2
T0 to T1	Intercept	-0.359	0.674	-0.532	0.594	0.11	0.92	5.56E-05	0.0493
	DBH.cm	-0.003	0.049	-0.058	0.954				
T1 to T2	Intercept	0.251	0.498	0.503	0.615	0.26	0.85	0.006	0.229
	DBH.cm	-0.031	0.037	-0.845	0.398				

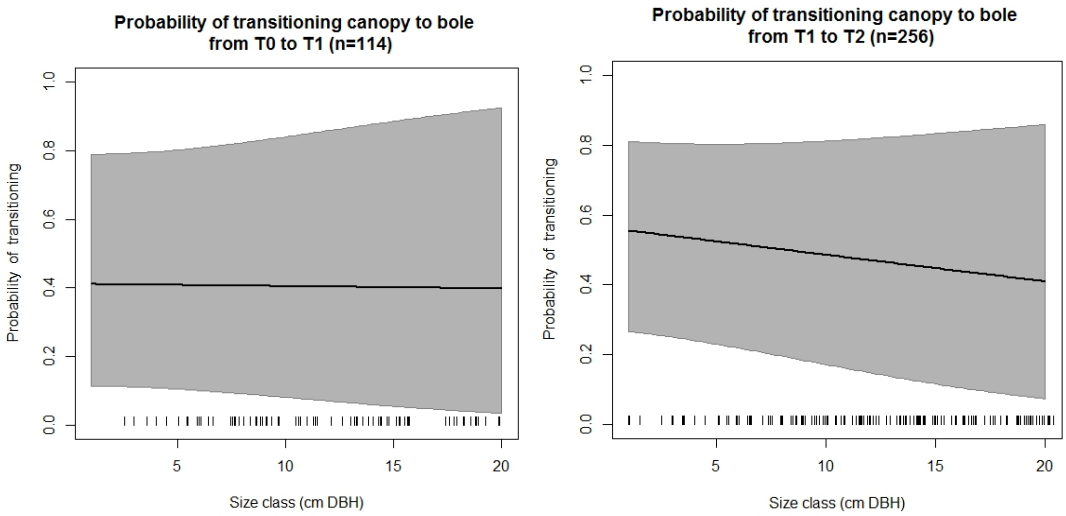

Figure 15. The probability of infection transition from canopy to bole does not appear to be influenced by tree size in either time-step. Confidence intervals (95%) were estimated with the Workman-Hotelling procedure and are likely conservative.

Discussion

Previous studies have reported on the vulnerabilities of understory whitebark pine trees to blister rust exposure and infection, often with contradictory hypotheses (Tomback et al. 1995; Smith et al. 2008; Mahalovich 2013; Campbell and Antos 2000; Smith and Hoffman 2000; Kearns and Jacobi 2007). Some studies hypothesize that due to small stature and microclimate within the understory smaller size class trees are more vulnerable to blister rust (Tomback et al. 1995; Smith et al. 2008; Mahalovich 2013). Other investigators suggest that because small trees represent a smaller target and benefit from protection by the overstory infection is less likely (Campbell and Antos 2000; Smith and Hoffman 2000; Kearns and Jacobi 2007). Although these studies suggest differing mechanisms affecting infection, they draw their conclusions from observations that lack multiple revisits. Here, we modeled the probability of infection and infection transition

using data from repeat observations on the same individual trees over a 4-year time-period.

Schwandt et al. (2013) observed over a 17-year period (1995 to 2012) that infection presence increased with tree size in whitebark pine populations in northern Idaho. In our study tree size was significantly and positively correlated with the probability of infection over a 4-year period. In our sample, smaller size class trees (1 to 5-cm DBH) were considerably more numerous than larger trees, and thus we are more confident in the estimates for smaller size class trees. Over a 4-year period, the probability of acquiring an initial infection was 0.07 [CI 0.038, 0.146] from T0 to T1 and 0.04 [CI 0.021, 0.075] for a 1-cm DBH and increased to approximately 0.29 [CI 0.114, 0.587] from T0 to T1 and 0.14 [CI 0.051, 0.316] from T1 to T2 for a 20 cm DBH tree. Due to environmental variability and different initial conditions we did not expect to see similar probability point estimates between T0 to T1 and T1 to T2. For example, blister rust "wave" years when environmental conditions are thought to be more favorable for the spread of blister rust spores can increase the incidence of blister rust infection (Mahalovich 2013) but effects may not be visible for two to four years post-initial infection (McDonald and Hoff 2001). Under this scenario, a wave year could have occurred toward the latter part of T0 (2006 or 2007) or sometime between 2008 and 2009, with evidence of infection visible toward the end of T1 (2010 or 2011).

We concur with Kearns and Jacobi (2007) that larger trees tend to have more canopy volume than smaller trees, which increases the surface area of susceptible foliage. Conversely, smaller understory trees may be less vulnerable to infection due to sheltering

by overstory trees, as spores may be absorbed by the canopies of larger trees (McDonald and Hoff 2001; Campbell and Antos 2000).

Though associated with the probability of infection, tree size was not a significant factor associated with infection transition. This is somewhat contrary to results reported from previous studies (Hoff 1980; Schoettle and Sniezko 2007). Infections initiate in the canopy of a tree and smaller DBH trees tend to have less canopy volume as compared to their larger cohorts (McDonald and Hoff 2001; Mahalovich 2013, Kearns and Jacobi 2007). Because of this, a canopy infection will have a shorter distance to travel before it reaches the bole of the infected tree, thus transitioning to a more lethal type of infection more rapidly than in larger infected trees (Smith and Hoffman 2000; Koteen 2002; Newcomb 2003). Unfortunately, there is a paucity of studies that repeatedly track disease progression in natural settings. Instead, much of the information referenced on infection transition is based on experimental work (Hoff et al. 1980). In nursery trials, most seedlings inoculated with blister rust infection were dead within a 3-year time frame (Hoff et al. 1980). The trees used in the nursery trials were significantly smaller than the tagged trees observed in our transects which may explain the discrepancy in our study results. It is also believed that previous work may be confounded by tree size and source materials; some whitebark pine populations are more resistant to blister rust infection than others (Mahalovich et al. 2006). For these reasons, employing repeated observations on trees in multiple age cohorts in a large geographic area provides greater insight on the dynamics of infection transition.

While our findings do not lend strong support to the size of a tree acting as a significant influence on the probability of infection transition, other factors may be contributing to the discrepancy in our results with that of other studies. Importantly, we recognize that there are climatic or environmental differences between the GYE and other study areas. Kearns et al. (2009) found that in limber pine, trees located in areas with higher moister retention capacity had measurably greater rates of canker expansion. The drier, continental climate of the Greater Yellowstone Ecosystem could therefore aid in reducing canker expansion rates compared to rates documented for more maritime-influenced or wetter regions. In addition, whitebark pine in our study area typically occur above 2,400-m. The length of the growing season for trees and blister rust in these high elevation sites is most likely shorter than lower elevation sites; this factor could also be affecting proximal canker growth. Finally, studies on canker expansion specifically in whitebark pine are lacking. Canker expansion rates may be species-specific and therefore observed rates in other white pine species (e.g., limber pine) may not be applicable to canker growth in whitebark pine.

Overall, canopy-infected trees transitioned to bole-infected trees at an unexpectedly high rate, regardless of size class in a 4-year time-span. Averaged across all size cohorts, 40% of the trees with canopy infections in T0 transitioned to a more severe state of infection by the end of T1. The average was slightly higher for trees in the T1 to T2 time-step with 48% transitioning to bole cankers. For both time steps, nearly one-half of canopy infected trees became infected at some location on the bole of the tree regardless of size.

We recognize that our sample size and/or time-span may be insufficient to adequately model infection transition as a function of DBH. Admittedly, a wider range of DBH trees would have been more informative in explicitly modeling the effect of DBH on infection dynamics. Unfortunately, very few trees populated the size classes above 20-cm DBH and including those larger trees would potentially skew our results. Finally, we acknowledge that two, 4-year time-step intervals which total a time-span of 8-years may not have been sufficient to fully describe the extent of blister rust infection probability and transition in the whitebark pine population in the GYE. Schwandt et al. (2013) found that only 12% of the tagged whitebark trees from their sample population remained alive and free of blister rust after 17 years.

Conclusions and Management Implications

Throughout the GYE, whitebark pine populations have been adversely impacted by blister rust infection, albeit to varying degrees. As a result of the recent mortality in the GYE, the size class distribution of whitebark has shifted over the last decade to predominately smaller trees (Shanahan et al. 2014) ranging from 1 to 20-cm DBH. Though trees on the lower end of this range are less likely to become infected, their larger cohorts show increasing susceptibility to infection over a 4-year time period. Yet when considering infection transition, all trees from 1 to 20-cm, have a high and relatively fixed rate of transition from canopy to bole infection. In essence, while it may take many years for smaller size class trees to become infected with blister rust, once initially

infected and regardless of size, there is an almost 50% chance that a canopy infection will progress to the bole in a 4-year time span.

Our findings of the dynamics of infection initiation and transition reflect a relatively short time interval. With sustained, repeat monitoring, we are poised to clarify some of the uncertainties by continuing to document the enduring presence of blister rust in whitebark pine population in the GYE. By tracking the impacts of blister rust through stochastic events such as the recent mountain pine beetle outbreak, other stand-altering occurrences, and projected changes in climate, we can identify significant patterns of blister rust infection and communicate the potential consequences of this pathogen on future generations of whitebark pine. Understanding these relationships will provide managers with contemporary data which will enable sound decision making in their efforts to protect and restore whitebark pine on the landscape.

Literature Cited

Arno, S. F. and R. J. Hoff. 1990. *Pinus albicaulis* Engelm.Whitebark pine. In: Burns, R. M. and B. H. Honkala, technical coordinators. Silvics of North America, Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 268-279.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, *24*(3), 127-135.

Broström, G. (2013). glmmML: Generalized linear models with clustering. R package version 1.0. http://CRAN.R-project.org/package=glmmML

Campbell, E. M. and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Dixon, B. G.1997. Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. Thesis Montana State University. 143 pages plus appendices. Bozeman, Montana, USA.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swans, J. Thomspon, B. Von Holle and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 39:479-486.

Ebenman, B. and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20:568-575.

Farnes, P. 1990. SNOTEL and snow course data: Describing the hydrology of whitebark pine ecosystems. page 386 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (GYCCWPS). 2011. Whitebark pine strategy for the Greater Yellowstone Area. Greater Yellowstone Coordinating Committee, Bozeman, Montana.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, Montana, USA.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2012. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2011 annual report. pages 56-65 in C. C. Schwartz, M. A. Haroldson and K. West, editors. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2011. U.S. Geological Survey, Bozeman, Montana, USA.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2014. Summary of preliminary step-trend analysis from the Interagency Whitebark Pine Long-term Monitoring Program—2004-2013: Prepared for the Interagency Grizzly Bear Study Team, Natural Resource Data Series NPS/GRYN/NRDS–2014/600. National Park Service, Fort Collins, CO.

Hatala, J. A., Dietze, M. C., Crabtree, R. L., Kendall, K., Six, D., & Moorcroft, P. R. (2011). An ecosystem-scale model for the spread of a host-specific forest pathogen in the Greater Yellowstone Ecosystem. *Ecological Applications*, *21*(4), 1138-1153.

Haroldson, M. A. and S. Podruzny. 2013. Whitebark pine production. Pp. 43–44. in F. T. van Manen, M. A. Haroldson, K. West, eds. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2012. U.S. Geological Survey, Bozeman, MT.

Hicke, J.A., J.A. Logan, J. Powell and D.S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research 111:pp 12.

Hoff, R.J., R.T. Bingham, and G.I. McDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10:307-316.

Kearns, H.S. and W.R. Jacobi. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forestry Research 37:462-472.

Kearns, H.S., W.R. Jacobi, and B.W. Geils. 2009. A method for estimating white pine blister rust canker age on limber pine. Forest Pathology 29:177-191.

Keane, R. E. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Kendall, K. C. and R. E. Keane. 2001. Whitebark pine decline: Infection, mortality, and population trends. Pages 221-242 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC.

Koteen, L. 2002. Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. pages 343-414 in S. H. Schneider and T. L. Root, editors. Wildlife responses to climate change: North American case studies. Island Press, Washington, D.C., USA.

Logan J. A., W. W. Macfarlane and L. Willcox. 2009. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2: 19-22 [online: 2009-01-21] URL: http://www.sisef.it/iforest/show.php?id=477

Lohr, S. 2010. Sampling: design and analysis, 2nd edition. Brooks/Cole Cengage Learning, Boston, Massachusetts. pp. 145-146.

MacFarlane, W. W., J. A. Logan and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications 23:421-437.

Mahalovich, M. F., K. E. Burr and D. L. Foushee. 2006. Whitebark pine germination, rust resistance and cold hardiness among seed sources in the Inland Northwest: Planting Strategies for Restoration. In: National Proceedings: Forest and Conservation Nursery Association; 2005 July 18-20; Park City, UT, USA. Proc. RMRS-P-43. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 91-101.

Mahalovich, M. F. 2013. Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem. Future status of whitebark pine: blister rust resistance, mountain pine beetle, and climate change. Report 2470 RRM-NR-WP-13-01, U.S. Department of Agriculture Forest Service, Northern Region, Missoula, MT.

Maloney, P. E., D. R. Volger, C. E. Jensen and A. D. Mix. 2012. Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests of Lake Tahoe Basin, USA: Implications for restoration. Forest Ecology and Management 280:166-175.

Marston, R. A. and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338-346.

McDonald, G. I. and R. J. Hoff. 2001. Blister rust: an introduced plague. pages 193-220 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark Pine Communities Ecology and Restoration. Island Press,Washington, DC.

Nakagawa, S. and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133-142.

Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. M.S. Thesis. The University of Montana, Missoula, MT.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ramsey, F. L. and D. W. Schafer. 2002. The Statistical Sleuth. Brooks/Cole, California.

Safranyik, L., A. L. Carroll, J. Regniere, D. W. Langor, W. G. Reil, T. L. Shore, B. Peter, B. J. Coole, V. G. Neialis and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist 142:415-442.

Schoettle, A. W. and R. A. Sniezko. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research 12:327-336.

Schwandt, J. and H. Kearns. 2011. White pine blister rust: General ecology and management. Insect and Disease Management Series 14:2.

Schwandt, J. W., H. S. J. Kearns and J. W. Byler. 2013. Impacts of white pine blister rust and competition on natural whitebark pine regeneration in Northern Idaho 1995-2012. USDA Forest Service Northern Region, Forest Health Protection Report 13-09. 22p.

Schwandt, J. W. and S. Kegley. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. R1-04-9. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA.

Shanahan, E., K. M. Irvine, D. Roberts, A. R. Litt, K. Legg and R. Daley. 2014. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis comparing 2004-2007 to 2008-2011. Natural Resource Technical Report NPS/GRYN/NRTR—2014/917. National Park Service, Fort Collins, Colorado.

Smith, C. M., B. Wilson, S. Rasheed, R. Walker, T. Carolin and B. Sheppard. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forestry Research 38:982-995.

Smith, J. P. and J. T. Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60:165-179.

Smith, J. P., J. T. Hoffman, K. F. Sullivan, E. P Van Arsdel and D. Vogler. 2000. First report of white pine blister rust in Nevada. Plant Disease 84:594.

Tainter, F. H. and F. A. Baker. 1996. Principals of Forest Pathology. John Wiley & Sons, Inc., New York. 805 p.

Tomback, D. F. and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186-225.

Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff and S. F. Arnos. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of northern Idaho (U.S.A.). Conservation Biology 9:654-664.

Tomback, D. F., S. F. Arno and R. E. Keane. 2001. The compelling case for management intervention. Pages 4-25 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark pine communities. Island Press, Washington, DC.

Tomback, D. F., S. K. Sund and L. A. Hoffman. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forestry Research 23:113-119.

Weaver, T. 2001. Whitebark pine and its environment. pages 41-66 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Wilmoth, S. 2015. R code developed specifically for marginal and conditional R^2 for the Interagency Whitebark Pine Monitoring Program; unpublished.

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forestry Research 32:1265-1274.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, New York.

CHAPTER 4

OBJECTIVE 4 OF THE INTERAGENCY WHITEBARK PINE PROTOCOL: ASSESSMENT OF REGENERATION/RECRUITMENT PROTOCOL

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Erin K. Shanahan

Contributions:

Co-Author: Kathryn M. Irvine

Contributions: Review of final draft of protocol

Co-Author: Dave Roberts

Contributions: Review of final draft of protocol

Co-Author: Andrea R. Litt

Contributions: Review of final draft of protocol.

Manuscript Information

Erin K. Shanahan, Kathryn M. Irvine, Dave Roberts, Andrea R. Litt, Kristin Legg, and Rob Daley

This manuscript/protocol will be an addition to the published Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. NPS/GRYN.

Status of Manuscript:

_X_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Abstract

Whitebark pine (*Pinus albicaulis*) is a key component in the upper ranges of the Greater Yellowstone Ecosystem (GYE) where it influences the biodiversity and productivity of these high-elevation areas. It is an important food source for a variety of wildlife including red squirrels (*Tamiasciurus hudsonicus*), Clark's nutcrackers *Nucifraga columbiana*), grizzly bears (*Ursus arctos horribilis*), and other granivorous small mammals. The Clark's nutcracker is the primary seed disperser for whitebark pine.

Whitebark pine is found predominantly on public lands throughout the GYE. Substantial declines in whitebark pine have been attributed to white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and wildfires. In 2004, an interagency whitebark pine long-term monitoring program was established to document monitor whitebark pine populations in the GYE. The objectives of the whitebark pine monitoring program are to detect and monitor changes in the health and status of whitebark pine populations across the GYE due to infection by white pine blister rust, attack by mountain pine beetle, and damage by other environmental and anthropogenic agents.

Objectives 1, 2, and 3 have been developed and implemented since 2004 by the monitoring program. These three objectives are outlined in the Interagency Whitebark Pine Monitoring Protocol Version 1.2, 2012. This regeneration/recruitment protocol addendum has been designed to specifically explain and define Objective 4 which is to assess and monitor recruitment of whitebark pine understory individuals (≤1.4-m tall) into the cone producing population. A pilot effort on this objective was initiated in 2012

and pilot data were examined at the end of 2014. After analysis of this pilot, we found that our nested, circular plot methodologies will specifically meet our objective goals for tracking regeneration/recruitment of the whitebark pine understory. Information from this objective can be used to guide managing agencies in their restoration efforts of whitebark pine.

Introduction

Coniferous forests throughout western North America are currently experiencing unparalleled health challenges. Climate change, upsurges in forest insects and pathogens, and changing disturbance regimes have the potential to alter forest ecosystem structure, function, and species composition (McKinney et al. 2011). Foundation species strongly influence the biodiversity and productivity of high-elevation ecosystems and are of vital importance to fundamental ecosystem processes and are therefore irreplaceable (Tomback et al. 2001; Ellison et al. 2005). The loss of a foundation tree species has the potential to cause major secondary losses, changes in biological diversity, and critical and possibly irreversible community disturbances (Ebenman and Jonsson 2005). Several timberline foundation species have been severely impacted by the prevailing and growing cadre of anthropogenic events that are currently stressing many high-elevation ecosystems (Tomback et al. 2001). Five-needled white pines are considered foundation or keystone species in high elevation forests and alpine communities (Arno and Hoff 1989; Tomback et al. 2001). Whitebark pine (*Pinus albicaulis*) occurs in the Pacific Northwest and northern Rocky

Mountains where it is a foundation species in the subalpine zone. It is considered a "pioneer" species due to its tolerance of harsh environmental conditions and ability to establish and persist where other species cannot. In doing so, whitebark pine can alter the microclimate and enable species such as subalpine fir (*Abies lasiocarpa*) to establish in these otherwise inhospitable and harsh environments (Tomback et al. 1993). Although whitebark pine has very little commercial value, its seeds provide seasonal forage for a variety of wildlife and its aesthetic qualities and sheer perseverance inspire awe in recreationists.

Mass mortality of mature, cone-producing whitebark pine is occurring at a landscape-level across the Greater Yellowstone Ecosystem (GYE; MacFarlane et al. 2013). An aerial view depicts a striking picture of mortality in the whitebark population that occupies the upper canopy (MacFarlane et al. 2013). Although data collected since 2004 from the Greater Yellowstone Interagency Whitebark Pine Monitoring Program (Monitoring Program) provide summary statistics on understory populations, there is a dearth of more in-depth coverage of this cohort. Regeneration and recruitment (herein referred to as "recruitment") of whitebark pine is happening at various levels throughout the GYE. At present, very little is known about the health of the understory population and the general dynamics and trajectory of regenerating whitebark pine communities. By developing and incorporating recruitment monitoring methods into the existing protocol, we will be able to track and assess whitebark pine recruitment into the cone-producing population and to monitor emerging understory

population trends of whitebark pine in the understory in concurrence with overall stand transition.

Monitoring whitebark pine in the understory will fulfill Objective 4 as described in the Interagency Whitebark Pine Monitoring Protocol (Monitoring Protocol) for the Greater Yellowstone Ecosystem, Version 1.1 (GYWPMW 2011). Objective 4 has been developed with relevance to the three central concepts of whitebark pine recruitment: germination, establishment, and survival. This effort will contribute meaningful information to the broader regional assessment of recruitment status and trends, will help management decisions across numerous national forests and several parks, and provide a valuable resource for a variety of agencies embarking on five-needle pine monitoring.

Our specific monitoring objectives are intended to answer the following questions: In the GYE, 1) are understory whitebark pine (≤ 140-cm tall) continuing to emerge and survive into the reproducing population, 2) is white pine blister rust increasing within the understory whitebark pine population, and 3) how is competition from other species influencing whitebark pine understory recruitment? Information gathered from these investigations will help guide management decisions on intervention strategies (e.g., active restoration, propagation of disease resistant trees).

<u>Specific Objective 4 Goals:</u>

1. To estimate the mean density of ≤ 140-cm tall five-needle pine trees and document changes in mean density over time.
2. To measure the change in height of five-needle pines in the understory and track individuals as they survive to be tagged as part of the Interagency Whitebark Pine Program monitoring population.

3. To determine the proportion of five-needle trees (≤ 140-cm tall) that are infected with blister rust and how this is changing over time.
4. To estimate the mean density of competitor species (subalpine fir, Engelmann spruce, and lodgepole pine, ≤ 140-cm tall) and document changes over time.

Methods: Study Area

Our study area encompasses six national forests (NF), two national parks (NP), as well as state and private lands in portions of Wyoming, Montana, and Idaho; this area is collectively described as the GYE. The GYE is geographically defined as the Yellowstone Plateau volcanic fields and the 14 surrounding mountain ranges above 2,130 m (Marston and Anderson 1991). Whitebark pine stands occupy over 800,000 hectares in the high, mountainous zones of the GYE (Marston and Anderson 1991, GYWPMWG 2011, GYCCWPS 2011). Sample sites in the study area range in elevation from 2,400 m to 3,172 m and extend to the boundaries of the GYE (Fig 1; GYWPMWG 2011). These alpine and subalpine environments are subjected to harsh weather including excessive winds, extreme cold temperatures, and significant snow accumulation. Snow collects early and may persist until late spring and occasionally into mid-summer. Summers tend to be warm and dry.

Sampling Design

We will utilize the existing Monitoring Program's 176 transects for investigating the status of understory whitebark pine populations. The recruitment protocol has been developed under the format outlined in the Monitoring Protocol Guidelines (Oakley et al.

2003). This includes institution of a detailed study plan with all aspects of data collection, data management, analysis, and reporting. For data collection, we will follow methods for collecting understory or subplot field data collection methods developed by the Sierra Nevada and Upper Columbia Basin Networks, as well as methods employed in the Forest Inventory and Analysis program which is ubiquitously practiced by the U.S. Forest Service. Methods were piloted from 2012 to 2014 and modified to fit into the ongoing Monitoring Program. Following a review of the pilot data collected between 2012 to 2014, we referenced methods developed on other studies of natural whitebark pine regeneration and direct seeding trials (Schwandt et al., 2013, Schwandt et al., 2011) by John Schwandt (retired U.S. Forest Service) and Holly Kearns (U.S. Forest Service) to further refine the recruitment objectives and data collection methods.

Surveys will be conducted from late June through late September depending on snow levels. Field crews will consist of two people trained to identify white pine blister rust and other pertinent forestry mensuration techniques. Transects will be sampled for understory conditions based upon the existing Monitoring Program's sample panel schedule (GYWPMW 2011). It should be noted that the following methods will not replace the complete belt count of understory constituents but complement these counts. Also, subplot data collection will only occur on snow-free transects.

Response Design Rationale

Field methods for quantifying the abundance and demographic trajectory of whitebark pine trees ≤ 140-cm tall within the dimensions of a 500-m² plot can be difficult, error prone, and time-consuming. Understory vegetative composition and

density, forest floor debris, and micro-topography of a site can create a challenging environment for observers as they attempt to locate and record small and sometimes emerging individuals. Current understory data collection based on the Monitoring Protocol includes a rudimentary tally of all detected whitebark pine trees (or five-needle) trees ≤ 140-cm tall within the boundaries of the transect for each survey event. Studies have shown that plot size can be negatively correlated with both sampling efficiency and detection rates when ground sampling static objects (Smith 1968). We recognize that to successfully track recruitment of the understory whitebark pine population in the GYE, a recruitment response design must minimize observer variability, increase accuracy and proficiency, and ensure that as much as is logistically possible, the same understory whitebark pine individuals are being chronicled during each survey.

Ideally, we would prefer a recruitment study design that incorporates identical tagging methods regardless of tree height. Tagging would allow us to better understand and track the health and life status of each individual five-needle tree within the understory of the monitoring belt transect. Unfortunately, financial constraints and revisit schedules preclude tagging smaller trees. Tagging smaller (<61-cm tall) trees on such a large scale long-term monitoring effort may not be successful due to the dynamics of seedling survival and inability to maintain tags (G. Peterson, pers. com. 2014). Therefore, for this endeavor, we will capture changes in the understory population founded on more broadly based sampling efforts that involve tagging of only a subset of understory trees (those >61.1-cm tall for this effort).

Three recruitment subplots will be permanently established at each of the 176 transects. Recruitment subplots will be circular with a radius of 2.08-m and associated with the beginning, center, and end monument points with a distance of approximately 20.84-m between each subplot edge (2.08-m radius x 2 – 25-m = 20.84-m; Figure 16).

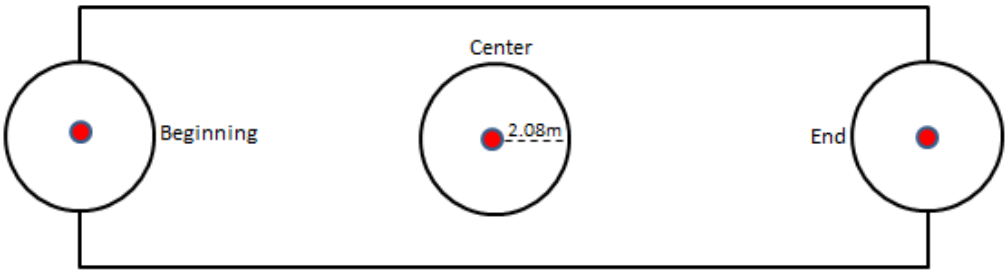

Figure 16.Recruitment subplot layout within established whitebark pine monitoring transect where the red dots represents the beginning, center, and end monument spikes. The radius of the circular subplot is 2.08-meters.

To maintain the 2.08-meter radius, a cord will be attached to the ground monument spike to facilitate movement in a circular fashion about the center point of the circle. Starting at a marked location on the outer limits of the circle, the cord will be moved progressively forward until a complete circle has been surveyed.

Sample Frame and Sample Units

This recruitment monitoring will utilize the sample frame developed for the Monitoring Protocol (GYWPMW 2011). For recruitment monitoring, transects are the primary sampling unit (*psu*) and circular subplots associated with the transects are the secondary sampling units (*ssu*) (Lohr 2010). This is a design-based probabilistic sample,

allowing inference to all mapped polygons of whitebark pine in the GYE from our original sample frame.

Subplot Size

Circular plots with a radius of 2.08-m were chosen for ease of measuring these partially nested subplots. The dimensions of the subplots were chosen so as to minimize observer variability and minimize the chance of missing focal cohorts. In addition, a radius of 2.08-m converts to 0.0012-ha (1/300th acre) which is utilized by the U.S Forest Service for their Forest Inventory and Analysis subplot efforts (Bechtold and Patterson 2005). This data collection scheme can be easily incorporated into the current monitoring sampling effort without significantly increasing survey time on a given transect.

Subplot Data Collection

Data will be recorded for a variety of attributes within each subplot. The date of survey, established monitoring transect ID where the survey is taking place, and observer names will be recorded. Five-needled tree species will be recorded in each subplot in three size classes: < 15-cm, 15-cm – 61-cm tall and 61.1-cm – 140-cm tall (Figure 17). These size classes are based on differences in the main source of mortality. Most mortality amongst trees < 61-cm tall results from environmental stressors or animal damage, whereas mortality in trees > 61-cm tends to be attributed more often to blister rust infection (Schwandt et al. 2011). In addition, five-needle trees that reach a height of approximately 15 cm tall are considered to be 'established', compared to trees that have not attained this height. Trees < 15-cm tall are regarded as somewhat 'ephemeral' and suffer mortality due to any number of causes, including sun damage, animal trampling,

rodent consumption, bark sloughing from adjacent trees, and frost heaves (Schwandt et al 2011). Limiting the number of size classes to three, we aim to significantly minimize the observer variability within this metric (Thoma et al. 2004).

To document the transition of ≤ 140-cm tall five-needle trees as they advance from the understory population into the sample frame of marked trees in the established Monitoring Program we will mark all trees ≥ 61.1-cm and ≤140-cm tall within the subplot boundaries with a recruitment-specific tree tag. The distinct number on tagged understory trees will be recorded by subplot location and an infection status will be documented (Figure 18). These tags will be replaced with a regular monitoring tag (per the Monitoring Protocol) once they have reached a height > 140-cm tall.

When cones are absent, positively discriminating between whitebark pine and limber pine is extremely difficult. Due to this uncertainty, any ≤ 140-cm tall five needle seedling/saplings that are located within the subplot will be categorized as whitebark pine/limber pine species (referred to as five-needle). To document continued seed germination, five-needle trees < 15-cm tall will be tallied. The presence of positively-identified limber pine anywhere in the stand will be documented.

Five-needle trees < 140-cm tall will be examined and documented for blister rust infection based on the presence of aecia and other indicator criteria as described in the GYWPMW Version 1.1 protocol (GYWPMW 2011). New blister rust infection can be difficult to positively identify in understory five-needle trees. New infections often are characterized by the presence of yellow or red spots on a few or several needles of the

tree. These features are shared by a group of fungi that cause needle casts and needle blights or can result from drought, root disease, or winter damage (Allen et al., 2010).

A tree or cluster of trees will be included in a subplot survey so long as the middle of the trunk or cluster of trunks, at ground level, is/are within 2.08-m from the center of the subplot.

Beginning Point	Tree Count by Size Class	
Species	15 cm - 61 cm	61.1 cm - 140 cm
PIAL/PIFL **CLEAN**		
PIAL/PIFL **BR**		
15 cm - 140 cm		
PICO		
FIR		
SPRUCE		
Other (Specify)		
5-needle emergents (< 10 cm) tally		
Limber Pine Present in Stand? Yes / No (circle one)		

Figure 17. Species and height class bins as presented on field data sheet.

Tag #	CLEAN Y/N	BR Y/N

Figure 18. Data field requirements for understory tree tag number and infection status.

Recruitment into the Whitebark Pine Monitoring Transect

Any tree within a recruitment plot that reaches a height of >140-cm tall will be added to the whitebark pine monitoring transect data set if as it is within the boundaries of the regular monitoring plot. These new trees will be tagged and data will be collected following section 3.4.4.2 titled "Identify and tag live whitebark pine trees >1.4-meters tall within transects" in the Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1 (GYWPMW 2011).

Data Handling, Analysis, and Reporting Data

Data will be collected on pre-generated data sheets and entered into the GRYN database as described in the Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1 (GYWPMW 2011).

The mean density of five-needle trees ≤ 140-cm tall per hectare will be determined after completing each full panel rotation (every 4 years; Objective 1). A Wilcoxon Signed-Rank Test (matched pairs) will be used to determine changes in density of five needles between survey intervals (Ramsey et al. 2002). Design-based sampling allows us to draw conclusions on the mean density of five-needle trees ≤ 140-cm tall in our sample frame (10,770). Detailed records will be kept regarding understory tree tag numbers and infection status to determine blister rust presence/absence and changes over time (Objective 2). A combined ratio estimator will be used to determine the proportion of five-needle trees ≤ 140-cm tall infected with blister rust (Objective 3). A combined ratio estimator is appropriate for estimating a proportion from data collected using stratified random sampling (e.g., Grizzly Bear Recovery Zone and administrative unit) in a two-stage cluster sample (Lohr 2010) and is used for similar analysis with trees >140-cm tall. The probabilistic sampling design allows inferences to the entire population of mapped whitebark in the GYE. And finally, an estimate for the density of all other tree species ≤ 140 cm tall that occur within the subplot dimensions will be determined following the completion of each full panel rotation (every 4 years; Objective 4). Changes in species-specific densities over time will be assessed with a Wilcoxon Signed-Rank Test (matched pairs) between survey intervals (Ramsey et al 2002).

Information gleaned from this study will be distributed via the Interagency Whitebark Pine Monitoring Annual Report.

Results: Pilot Data

The sum of all 3 subplots together (each 0.0012 ha) accounts for approximately 8% of the total area of the 500-m² transect. Therefore, we would expect that the sum of the counts of the five-needle trees ≤ 140-cm tall across the 3 subplots should represent 8% of the total count of five-needle trees ≤ 140-cm tall trees recorded on the 500-m² transect. Utilizing pilot data collected from 2012 to 2014 on transects in panels 1, 2, and 3, we found that the sum of the ≤ 140-cm tall, five-needle trees tallied on the 3 subplots (3 x 132 transects) did in fact accounted for 8% (0.079) of the total number of five-needle ≤ 140-cm tall trees documented on the 132 transects surveyed. We did not detect a change in the density of tall five-needles ≤ 140-cm tall or a change in the density of competitor species ≤ 140-cm tall between the two survey periods.

Discussion

Given the short time span between survey events, it is not surprising that we did not detect any significant change in densities for any of the tree species ≤ 140-cm tall or a change in the proportion of five-needle trees infected with blister rust documentation. Blister rust infection was essentially negligible with no trees recorded as infected in 2012 and only one tree with evidence of infection in 2014. In the future, we would expect to

see the greatest change in density within the smaller size class bin (< 15-cm) on the scheduled 4-year revisit interval.

Although analysis of the Panel 3 pilot data was very basic, review of these data provided vital insights for further adjustment in the development the Interagency Monitoring Protocol, Objective 4 addition. This review allowed us to better conceptualize the pitfalls and shortcomings of our original methods design and to refine our overall objectives.

Currently, there is a paucity of information on the proportion of germinants that survive long enough (in a natural setting) to become established. This deficiency is partly due to the onerous and logistically challenging task of tracking these diminutive individuals through time. We recognize that documentation of germinant trajectory could result in science-based management decisions regarding restoration techniques and practices that include efficacy and financial advantages of direct seeding versus nursery stock planting. Germinant survival data collection will also have an explicit role in determining the levels of direct seeding needed to accomplish restoration goals (Schwandt pers. com, 2014). Results from these analyses will inform more complex modeling applications that incorporate other potential covariates such as site specific factors and variable climatic conditions. With these advanced efforts our intent is to gain applicable knowledge on the common drivers of five-needle pine understory dynamics.

We will continue to address this topic as we move forward in our monitoring efforts. In the 2015 monitoring season, we will once again pilot this updated recruitment method design while continuing to improve upon the data collection techniques.

Supplemental Information for Chapter 4: Assessment of
Regeneration/Recruitment Subplot Pilot Monitoring

Analysis of pilot data

Data used in this analysis were collected from subplots measured in 37 Panel 3 transects surveyed initially in 2012 and revisited in 2014.

Objectives:

1. Estimate the change in density of five-needle pine trees ≤ 140-cm tall from 2012 to 2014.
2. Estimate the change in density of competitor species (fir, spruce, lodgepole, other) ≤ 140-cm tall from 2012 to 2014.

Species	2012 subplot totals	2014 subplot totals
5-needle (no rust)	117	162
PICO	2	8
FIR	239	275
SPRUCE	47	47
5-needle (rust)	0	1
other	0	0

Summary of Panel 3 pilot data:

Analysis results of Panel 3 pilot data:

1. Estimating the change in density of five-needles ≤ 140 cm tall:

```
Wilcoxon signed rank test with continuity correction
V = 133, p-value = 0.4309
Warning messages:
1: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with ties
2: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with zeroes
mean(new.diff)
-1.243243
```

We did not detect change in the density of tall five-needles ≤ 140-cm tall between the two survey periods.

2. Estimating the change in density of species specific competitors ≤ 140-cm tall:

Fir

```
Wilcoxon signed rank test with continuity correction
data:  NewDen$T0 and NewDen$T1
V = 81.5, p-value = 0.3878
Warning messages:
1: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with ties
2: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with zeroes
 mean(new.diff) = -0.972973
```

Pico

```
Wilcoxon signed rank test with continuity correction
data:  NewDen$T0 and NewDen$T1
V = 0, p-value = 0.1814
Warning message:
In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with zeroes
mean(new.diff) = -0.1621622
```

Spruce

```
Wilcoxon signed rank test with continuity correction
data:  NewDen$T0 and NewDen$T1
V = 24.5, p-value = 0.7941
Warning messages:
1: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with ties
2: In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with zeroes
mean(new.diff) = 0
```

Other

```
Wilcoxon signed rank test with continuity correction
data:  NewDen$T0 and NewDen$T1
V = 0, p-value = NA
Warning message:
In wilcox.test.default(NewDen$T0, NewDen$T1, paired = TRUE) :
  cannot compute exact p-value with zeroes
mean(new.diff) = 0
```

We did not detect change in the density of competitor species ≤ 140-cm tall between the two survey periods.

Literature Cited

Allen, K. K., J. T. Blodgett, K. S. Burns, R. J. Cain, S. L. Costello, T. J. Eager, J. L. Harris, B. E. Howell, R. A. Mask, W. C. Schaupp, Jr., J. J. Witcosky and J. J. Worrall. 2010. Rocky Mountain Region, Forest Health Protection. Field guide to diseases and insects of the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-241, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 336 p.

Arno, S. F. and R. J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). USDA Forest Service, Intermountain Research Station, General Technical Report INT-253, Ogden, Utah.

Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20:568-575.

Ellison, A. E., M. S. Banks, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment. 3 (9): 479-486.

Greater Yellowstone Whitebark Pine Monitoring Working Group. 2011. Interagency whitebark pine monitoring protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, MT.

Lohr, S. 2010. Sampling: design and analysis, 2nd edition. Brooks/Cole, Cengage Learning, Boston, Massachusetts. pp.145-146.

MacFarlane, W. W., J. A. Logan and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications 23:421-437.

McKinney, S.T., T. Rodhouse, L. Chow, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, D. Sarr, and L.A. Starcevich. 2011. Monitoring white pine (*Pinus albicaulis, P. balfouriana, P. flexilis*) population dynamics in the Pacific West Region: Klamath, Sierra Nevada, and Upper Columbia Basin Networks. Narrative version 1.0. Natural Resouce Report NPS/PWR/NRR-2011/XXX. National Park Service, Fort Collins, Colorado.

Oakley, K. L., L. P. Thomas and S. G. Fancy. 2003. Guidelines for long-term monitoring protocols. Wildlife Society Bulletin 31:1000-1003.

Pederson, G. 2014. Personal comment by Dr. Greg Pederson, Forest Ecologist for the U.S.G.S. on tagging and successful tracking of emergent/germinant five-needle seedling.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http:/*I* www.R- project.org.

Ramsey, F. L. and D. W. Schafer. 2002. The Statistical Sleuth, 2nd edition. Brooks/Cole, Cengage Learning, Belmont, California. pp. 100-101.

Schwandt, J. W., K. Chadwick, H. S. J. Kearns and C. Jensen. 2011. Whitebark pine direct seeding trials in the Pacific Northwest. In: Keane, R.E., D.F. Tomback, M.P. Murray, and C.M. Smith (Eds.). The future of the high-elevation, five-needle white pines in western North America: proceedings of the High Five Symposium. 28-30 June, 2010; Missoula, MT. Proceedings RMSP-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. pp.357-361.

Schwandt, J. W., H. S. J. Kearns and J. W. Byler. 2013. Impacts of white pine blister rust and competition on natural whitebark pine regeneration in Northern Idaho 1995-2012. USDA Forest Service Northern Region, Forest Health Protection Report 13-09. 22p.

Schwandt, J. W. 2014. Personal comment from John W. Schwandt, retired U.S. Forest Service pathologist, on direct impacts on management decisions in regards to direct seeding stocking levels.

Smith, R. H. 1968. A comparison of several sizes of circular plots for estimating deer pellet-group density. Journal of Wildlife Management. 32(3): 585-591.

Thoma, D. P., S. C. Gupta and M. E. Bauer. 2004. Evaluation of optical remote sensing models for crop residue cover assessment. Journal of Soil and Water Conservation. 59(5):224-233.

Tomback, D. E., Holtmeier, F. K., Mattes, H., Carsey and K. S., Powell. 1993. Tree clusters and growth form distribution in Pinus cembra, a bird-dispersed pine. Arctic and Alpine Research. 25:374-381.

Tomback, D. F. and K. C. Kendall. 2001. Biodiversity losses: the downward spiral. Pages 243-262 in D. F. Tomback, S. F. Arno and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, D.C.

CHAPTER 5

GENERAL CONCLUSION

Conclusion

Whitebark pine is a vital component of high-elevation ecosystem in the Greater Yellowstone Ecosystem (GYE). Over the past decade, whitebark pine has been adversely impacted by multiple agents in the GYE. White pine blister rust (blister rust), mountain pine beetle, and other agents that affect whitebark pine health, have been individually and collectively influencing survival of whitebark pine populations throughout the GYE. We found that blister rust infection is ubiquitous through the ecosystem with infection proportions varying across the region. From 2004 to 2011, the proportion of trees infected with blister rust was between 20% to 30% in the GYE. Infection ranged from a single canker on a tree to multiple infections. Mortality from our ground-based monitoring of a tagged tree population indicated that 27% of whitebark pine trees have died in the GYE since 2004 with larger size class trees disproportionately represented in this estimate. Similar to aerial-based surveys, we observed the greatest mortality in trees that formerly occupied the overstory in the forest structure. This is consistent with mountain pine beetle's propensity for attacking trees > 10-cm DBH.

Unlike the rapid mortality observed in whitebark pine infested with mountain pine beetle, blister rust infection is gradual, but potentially just as lethal. In our work presented here, we found that smaller size class trees have a lower probability of becoming infected over a 4-year time-span with the probability of infection increasing as

tree size increases. The probability of infection ranged from 0.04to 0.07 for the 1.0-cm trees to 0.14 to 0.30-cm for 20-cm trees (depending on the time-step considered). Once infected, the chance that a canopy infection will expand to the bole is about 50% over a 4-year period regardless of tree size. While many factors can influence infection susceptibility and transition probabilities, we recognize that environmental conditions many have a substantial role in both of these processes. Climatic conditions influence many aspects of blister rust transmission and within the GYE these conditions can vary greatly not only by geographic location but on a year to year basis (Mahalovich 2013). Seasonal fluctuations in weather patterns can not only enhance or hamper blister rust spore development and dispersal but can also promote or inhibit canker expansion on an infected tree (Kearns et al. 2009).

Over the past decade, the recent mortality of whitebark pine in the GYE has changed the demographic properties of many affected whitebark pine populations (Shanahan et al. 2014). The Interagency Whitebark Pine Monitoring Program data indicate that the majority of surviving whitebark pine in the GYE are somewhere between 1 to 20-cm DBH. In order to monitor the long-term trajectories of regenerating and recruiting whitebark pine population, we developed a protocol specifically designed to track understory stand dynamics. Information collected from this effort will be important for future projections on continued seedling emergence, overall understory survival, impacts of blister rust infection, competition effects and future cone production.

As we persist in monitoring trends in the health of whitebark pine throughout its range in the Greater Yellowstone Ecosystem, we continue to enhance the wealth of

knowledge available on this important species. In order to make sound management decisions it is critical to provide contemporary and regional data. The information we provide on the multiple aspects of whitebark pine health can be used to update managers of blister rust infection rates and changes, mortality estimates and shifts in the dynamics of the influencing agents of mortality, cone production potential and the occurrence of natural regeneration, and other baseline elements of whitebark pine ecology. Managers can use this knowledge to guide management strategies on restoration efforts, to gauge the need for increased development of rust-resistant trees, to make informed decisions on how to distribute financial resources to various whitebark pine endeavors, and as a tool for leveraging policy decisions for the preservation and restoration of whitebark pine.

LITERATURE CITED

Allen, K.K., J.T. Blodgett, K.S. Burns, R.J. Cain, S.L. Costello, T.J. Eager, J.L. Harris, B.E. Howell, R.A. Mask, W.C. Schaupp, Jr., J.J. Witcosky, J.J. Worrall. 2010. Rocky Mountain Region, Forest Health Protection. Field guide to diseases and insects of the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-241, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 336 p.

Arno, S.F. 1986. Whitebark pine cone crops: A diminishing source of wildlife food. *Western Journal of Applied Forestry* 1:92-94.

Arno, S.F. and R.J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). USDA Forest Service, Intermountain Research Station, General Technical Report INT-253, Ogden, Utah.

Arno, S.F. and R.J. Hoff. 1990. P*inus albicaulis* Engelm. Whitebark pine. In: Burns, R. M. and B. H. Honkala, technical coordinators. Silvics of North America, Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 268-279.

Benedict, W.V. 1981. History of white pine blister rust control: A personal account. U.S. Department of Agriculture. Forest Service. FS-355.

Bockino, N. K. and D. B. Tinker. 2012. Interactions of white pine blister rust and mountain pine beetle in whitebark pine ecosystems in the southern Greater Yellowstone Ecosystem. *Natural Areas Journal* 32:31-40.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, *24*(3), 127-135.

Broström, G. (2013). glmmML: Generalized linear models with clustering. R package version 1.0. http://CRAN.R-project.org/package=glmmML

Campbell, E. M. and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Dixon, B. G. 1997. Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. Thesis Montana State University. 143 pages plus appendices. Bozeman, Montana, USA.

Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20:568-575.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliot, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swans, J. Thomspon, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 39:479-486.

Fancy, S. C., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. *Environmental Monitoring and Assessment* 151:161-174.

Farnes, P. 1990. SNOTEL and snow course data: Describing the hydrology of whitebark pine ecosystems. page 386 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Furniss, M. M. and R. Renkin. 2003. Forest entomology in Yellowstone National Park, 1923-1957: A time of discovery and learning to let live. *American Entomologist* 49:198-209.

Furniss, R. L. and V. M. Carolyn. 1977. Western forest insects. Misc. Publ. 1339. Washington, D.C.: USDA Forest Service. 654 p.

Gelman, A. and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.

Gibson, K. 2003. Mountain pine beetle: Conditions and issues in the Western United States. page 298 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Proceedings, Mountain Pine Beetle Symposium: Challenges and Solutions (Kelowna, British Columbia, October 2003). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC.

Greater Yellowstone Coordinating Committee Whitebark Pine Subcommittee (GYCCWPS). 2011. Whitebark pine strategy for the Greater Yellowstone Area. Greater Yellowstone Coordinating Committee, Bozeman, Montana.

Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2011. Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. Greater Yellowstone Coordinating Committee, Bozeman, Montana, USA.

_____. 2012. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2011 annual report. pages 56-65 in C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2011. U.S. Geological Survey, Bozeman, Montana, USA.

_____. 2014. Summary of preliminary step-trend analysis from the Interagency Whitebark Pine Long-term Monitoring Program—2004-2013: Prepared for the Interagency Grizzly Bear Study Team, Natural Resource Data Series NPS/GRYN/NRDS–2014/600. National Park Service, Fort Collins, CO.

Haroldson, M. A., and S. Podruzny. 2013. Whitebark pine production. Pp. 43–44. In F. T. van Manen, M. A. Haroldson, K. West, eds. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2012. U.S. Geological Survey, Bozeman, MT.

Hatala, J. A., Dietze, M. C., Crabtree, R. L., Kendall, K., Six, D., & Moorcroft, P. R. (2011). An ecosystem-scale model for the spread of a host-specific forest pathogen in the Greater Yellowstone Ecosystem. *Ecological Applications*, *21*(4), 1138-1153.

Hayes, C. 2013. Montana: Forest insect and disease conditions and program highlights, 2012. Report 13-02. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA. 32

Hicke, J.A., J.A. Logan, J. Powell, and D.S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research 111:pp 12.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. USDA Forest Service, Intermountain Research Station, Research Note INT-406, Ogden, Utah., USA.

Hoff, R.J., R.T. Bingham, and G.I. McDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10:307-316.

Huang, M. 2006. A statistical analysis of observer variability in the identification of blister rust infection occurring in whitebark pine monitoring. Unpublished Report

prepared for the Whitebark Pine Monitoring Working Group. Department of Mathematical Sciences, Montana State University, Bozeman.

Jean, C., A. M. Schrage, R. E. Bennetts, R. Daley, E. A. Crowe, and S. O'Ney. 2005. Vital signs monitoring plan for the Greater Yellowstone Network. National Park Service, Greater Yellowstone Network, Bozeman, Montana.

Kearns, H.S. and W.R. Jacobi. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forestry Research 37:462-472.

Kearns, H.S., W.R. Jacobi, and B.W. Geils. 2009. A method for estimating white pine blister rust canker age on limber pine. Forest Pathology 29:177-191.

Keane, R. E. and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44-47.

Kendall, K. C., D. Schirokauer, E. Shanahan, R. Watt, D. Reinhart, S. Cain, and G. Green. 1996. Whitebark pine health in northern Rockies national park ecosystems: A preliminary report. *Nutcracker Notes* 7:16.

Kendall, K. C. and J. M. Asebrook. (1998). The war against blister rust in Yellowstone National Park, 1945–1978. In *George Wright Forum* (Vol. 15, No. 4, pp. 36-49).

Kendall, K. C. and R. E. Keane. 2001. Whitebark pine decline: Infection, mortality, and population trends. Pages 221-242 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC.

Kendall, K. C. and S. F. Arno. 1990. Whitebark pine: An important but endangered wildlife resources. pages 264-273 in W. C. Schmidt and K. J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Ketcham, D. E., C. A. Wellner, and S. S. Evans, Jr. 1968. Western white pine management programs realigned on northern Rocky Mountain national forests. *Journal of Forestry* 66:329-332.

Kipfmueller KF and Swetnam TW. 2002. Climate and mountain pine beetle-induced tree mortality in the Selway-Bitterroot Wilderness Area. Final Report to the USFS

Research Joint Venture Agreement #RMRS-99611-RJVA. http://www.ltrr.arizona.edu/~kurt/research/kkipf_beetles.pdf>.

Koteen, L. 2002. Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. pages 343-414 in S. H. Schneider and T. L. Root, editors. Wildlife responses to climate change: North American case studies. Island Press, Washington, D.C., USA.

Landenburger, L. 2012. Description of whitebark pine primary sampling unit selection. Unpublished.

Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. page 386 in W. C. Schmidt and K .J. McDonald, editors. Proceedings, symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource (Bozeman, Montana, March 1989). INT-GTR-270. U.S. Forest Service, Intermountain Research Station, Ogden, Utah, USA.

Lanner, R. M. 1996. Made for each other, a symbiosis of birds and pines. Oxford Press Inc., New York, New York, USA.

Larson, E. R. and K. F. Kipfmueller. 2010. Patterns in Whitebark pine regeneration and their relationship to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Canadian Journal of Forest Research 40:476-487.

Logan, J. and J. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleptera:Scolytidae). American Entomologist, 47:

Logan J.A., W.W. Macfarlane, and L. Willcox. 2009. Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. iForest 2: 19-22 [online: 2009-01-21] URL: http://www.sisef.it/iforest/show.php?id=477

Lohr, S. 2010. Sampling: design and analysis, 2nd edition. Brooks/Cole Cengage Learning, Boston, Massachusetts. pp. 145-146.

MacFarlane, W. W., J. A. Logan, and W. R. Kern. 2013. An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications 23:421-437.

Mahalovich, M. F. 2013. Grizzly bears and whitebark pine in the Greater Yellowstone Ecosystem. Future status of whitebark pine: blister rust resistance, mountain pine beetle, and climate change. Report 2470 RRM-NR-WP-13-01, U.S. Department of Agriculture Forest Service, Northern Region, Missoula, MT.

Mahalovich, M.F., K.E. Burr, and D.L. Foushee. 2006. Whitebark pine germination, rust resistance and cold hardiness among seed sources in the Inland Northwest: Planting Strategies for Restoration. In: National Proceedings: Forest and Conservation Nursery Association; 2005 July 18-20; Park City, UT, USA. Proc. RMRS-P-43. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, pp. 91-101.

Maloney, P. E., D. R. Volger, C. E. Jensen, and A. D. Mix. 2012. Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests of Lake Tahoe Basin, USA: Implications for restoration. Forest Ecology and Management 280:166-175.

Maloy, O. C. 2001. White pine blister rust. Online. Plant Health Progress, doi: 10.1094/PHP-2001-0924-01-HM. Available at: https://www.apsnet.org/edcenter/intropp/lessons/fungi/Basidiomycetes/Documents/whitepine_PHP2001_0924_01.pdf (accessed July 10, 2014)

Marston, R. A. and J. E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338-346.

Mattson, D. J. and D. G. Despain. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone ecosystem. Prepared for the Interagency Grizzly Bear Study Area. 37 p.

McDonald, G. I., B. A. Richardson, P. J. Zambino, N. B. Klopfenstein, and M. S. Kem. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North American: A first report. *Forest Pathology* 36:73-82.

McDonald, G. I. and R. J. Hoff. 2001. Blister rust: An introduced plague. pages 193-220 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark Pine Communities Ecology and Restoration. Island Press,Washington, DC.

McDonald, G. I., R. J. Hoff, and W. R. Wykoff. 1981. Computer simulation of white pine blister rust epidemics I. Model formulation. U.S. Dep. Agric. For. Serv. Res. Pap. INT-258.

McKinney, S.T., T. Rodhouse, L. Chow, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, D. Sarr, and L.A. Starcevich. 2011. Monitoring white pine (*Pinus albicaulis, P. balfouriana, P. flexilis*) population dynamics in the Pacific West Region: Klamath, Sierra Nevada, and Upper Columbia Basin Networks. Narrative version 1.0. Natural Resouce Report NPS/PWR/NRR-2011/XXX. National Park Service, Fort Collins, Colorado.

Mielke, J. L. 1937. An example of the ability of Ribes lacustre to intensify Cronartium ribicola on Pinus monticola. *Journal of Agricultural Research* 55:873-882.

Nakagawa, S. and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133-142.

Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. M.S. Thesis. The University of Montana, Missoula, MT.

Oakley, K.L., L.P. Thomas, and S.G. Fancy. 2003. Guidelines for long-term monitoring protocols. Wildlife Society Bulletin 31:1000-1003.

Olliff, S. T., R. A. Renkin, D. P. Reinhart, K. A. Legg, and E. M. Wellington. 2013. Exotic fungus acts with natural disturbance agents to alter whitebark pine communities. pages 236-251 in P. J. White, R. A. Garrott, and G. E. Plumb, editors. Yellowstone's Wildlife in Transition. Harvard University Press, Cambridge, Massachusetts, USA.

Pederson, G. 2014. Personal comment by Dr. Greg Pederson, Forest Ecologist for the U.S.G.S. on tagging and successful tracking of emergent/germinant five-needle seedling.

Pedersen, G. T., S. T. Grey, C. A. Woodhouse, J. L. Betancourt, D. B. Fagre, J. S. Little, E. Watson, B. H. Luckman, and L. J. Graumlich. 2011. The unusual nature of recent snowpack declines in the North American cordillera. *Science* 333:332-335.

Perkins, D. L. and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. *Canadian Journal of Forestry Research* 26:2123-2133.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raffa, K. F., E. N. Powell, and P. A. Townsend. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences* 110.6:2193-2198.35

Ramsey, F.L. and D.W. Schafer. 2002. The Statistical Sleuth, 2nd edition. Brooks/Cole, Cengage Learning, Belmont, California. pp. 100-101.

Safranyik, L., A.L. Carroll, J. Regniere, D.W. Langor, W.G. Reil, TL. Shore, B. Peter, B.J. Coole, V.G. Neialis, and S.W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist 142:415-442.

Schoettle, A.W. and R.A. Sniezko. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research 12:327-336.

Schwandt, J. and H. Kearns. 2011. White pine blister rust: General ecology and management. Insect and Disease Management Series 14:2.

Schwandt, J.W. 2014. Personal comment from John W. Schwandt, retired U.S. Forest Service pathologist, on direct impacts on management decisions in regards to direct seeding stocking levels.

Schwandt, J.W., H.S.J. Kearns, and J.W. Byler. 2013. Impacts of white pine blister rust and competition on natural whitebark pine regeneration in Northern Idaho 1995-2012. USDA Forest Service Northern Region, Forest Health Protection Report 13-09. 22p.

Schwandt, J.W., K. Chadwick, H.S.J. Kearns, and C. Jensen. 2011. Whitebark pine direct seeding trials in the Pacific Northwest. In: Keane, R.E., D.F. Tomback, M.P. Murray, and C.M. Smith (Eds.). The future of the high-elevation, five-needle white pines in western North America: proceedings of the High Five Symposium. 28-30 June, 2010; Missoula, MT. Proceedings RMSP-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. pp.357-361.

Schwandt, J. W. and S. Kegley. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. R1-04-9. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA.

Shanahan, E.K. 2014. Information derived from tree ring analysis from samples collected from the Gallatin National Forest in 2012.

Shanahan, E., K. M. Irvine, D. Roberts, A. Litt, K. Legg, and R. Daley. 2014. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis comparing 2004-2007 to 2008-2011. Natural Resource Technical Report NPS/GRYN/NRTR—2014/917. National Park Service, Fort Collins, Colorado.

Six, D. L., E. Biber, and E. Long. 2014. Management for mountain pine beetle outbreak suppression: Does relevant science support current policy? *Forests* 5:103-133.

Six, D. L. and J. Adams. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). *Journal of Entomological Science* 42:345-352.

Six, D. L. and M. Newcomb. 2006. A rapid method for rating white pine blister rust incidence, severity, and distribution within individual trees in whitebark pine. *Northwest Science* 79:189-195.

Smith, C. M., B. Wilson, S. Rasheed, R. Walker, T. Carolin, and B. Sheppard. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forestry Research 38:982-995.

Smith, J. P. and J. T. Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60:165-179.

Smith, J. P., J. T. Hoffman, K. F. Sullivan, E. P Van Arsdel, and D. Vogler. 2000. First report of white pine blister rust in Nevada. Plant Disease 84:594.

Smith, R. H. 1968. A comparison of several sizes of circular plots for estimating deer pellet-group density. Journal of Wildlife Management. 32(3): 585-591.

Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of eastern Idaho-western Wyoming. USDA Forest Service General Technical Report INT-144. Intermountain Forest and Range Experiment Station, Ogden. Utah.36

Tainter, F. H. and F. A. Baker. 1996. Principals of Forest Pathology. John Wiley & Sons, Inc., New York. 805 p.

Thoma, D.P., S.C. Gupta, and M.E. Bauer. 2004. Evaluation of optical remote sensing models for crop residue cover assessment. Journal of Soil and Water Conservation. 59(5):224-233.

Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelmi, Y. Wei, and R. B. Cook. 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. Date accessed: YYYY/MM/DD. Temporal range: YYYY/MM/DD-YYYY/MM/DD. Spatial range: N=DD.DD, S=DD.DD, E=DDD.DD, W=DDD.DD. http://dx.doi.org/10.3334/ORNLDAAC/1219

Tomback, D.F., J.K. Clary, J. Koehler, R.J. Hoff, and S.F. Arnos. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of northern Idaho (U.S.A.). Conservation Biology 9:654-664.

Tomback, D.F. and K.C. Kendall. 2001. Biodiversity losses: the downward spiral. Pages 243-262 in D.F. Tomback, S.F. Arno, and R.E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, D.C.

Tomback, D.F. and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186-225.

Tomback, D. F., S.F. Arno, and R. E. Keane. 2001. The compelling case for management intervention. Pages 4-25 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities. Island Press, Washington, DC.

Tomback, D.F., S.K. Sund, and L.A. Hoffman. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. Canadian Journal of Forestry Research 23:113-119.

U.S. Fish and Wildlife Service (USFWS). 1993. Grizzly bear recovery plan. Missoula, MT 181 pp.

_____. 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. *Federal Register* 76:42631-42654.

Weaver, T. 2001. Whitebark pine and its environment. pages 41-66 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regime by mid-21st century. Proceedings of the National Academy of Science of the United States of America; 108(32): 3165-13170. Published online 2011 July 25. doi: 10.1073/pnas.1110199108 PMCID: PMC3156206. Available at: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3156206/ (accessed July 10, 2014)

Wilmoth, S. 2015. R code developed specifically for marginal and conditional R^2 for the Interagency Whitebark Pine Monitoring Program; unpublished.

Zambino, P. J., B. A. Richardson, and G. I. McDonalt. 2007. First report of white pine blister rust fungus, *Cronartium ribicola*, on *Pedicularis bracteosa*. *Plant Disease* 91:467.37

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forestry Research 32:1265-1274.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, New