National Park Service
U.S. Department of the Interior

Natural Resource Stewardship and Science

Status of White Pines Across Five Western National Park Units

Initial Assessment of Stand Structure and Condition, Revised October 2021

Natural Resource Report NPS/KLMN/NRR—2022/2342





ON THIS PAGE
Whitebark pine in Crater Lake National Park
Photograph by Erik Jules

ON THE COVER
Whitebark pine below the base of Mount Lassen, Lassen Volcanic National Park
Photograph by Erik Jules

Status of White Pines Across Five Western National Park Units

Initial Assessment of Stand Structure and Condition, Revised October 2021

Natural Resource Report NPS/KLMN/NRR—2022/2342

Matthew J. Reilly[1], Jonathan C. B. Nesmith[2], Sean B. Smith[3], Devin S. Stucki[4], and Erik S. Jules[1]

[1]Humboldt State University
Department of Biological Sciences
1 Harpst St.
Arcata, CA 95521

[2]National Park Service
Sierra Nevada Network Inventory & Monitoring Program
47050 Generals Highway
Three Rivers, CA 93271

[3]National Park Service
Klamath Network Inventory and Monitoring Program
1250 Siskiyou Blvd.
Ashland, OR 97520

[4]National Park Service
497 SW Century Dr., Ste. 105
Bend, Oregon 97702

January 2022

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

This revised report contains the following change:

p. ii, contains a change in the citation, where the first author was initially reported as "Matthew J. R." and has been changed to "Reilly, M. J."

The National Park Service, Natural Resource Stewardship and Science office in Fort Collins, Colorado, publishes a range of reports that address natural resource topics. These reports are of interest and applicability to a broad audience in the National Park Service and others in natural resource management, including scientists, conservation and environmental constituencies, and the public.

The Natural Resource Report Series is used to disseminate comprehensive information and analysis about natural resources and related topics concerning lands managed by the National Park Service. The series supports the advancement of science, informed decision-making, and the achievement of the National Park Service mission. The series also provides a forum for presenting more lengthy results that may not be accepted by publications with page limitations.

All manuscripts in the series receive the appropriate level of peer review to ensure that the information is scientifically credible, technically accurate.

Views, statements, findings, conclusions, recommendations, and data in this report do not necessarily reflect views and policies of the National Park Service, U.S. Department of the Interior. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

This report is available in digital format from the Klamath Inventory and Monitoring Network website and the Natural Resource Publications Management website. If you have difficulty accessing information in this publication, particularly if using assistive technology, please email irma@nps.gov.

Please cite this publication as:

Reilly, M. J., J. C. B. Nesmith, S. B. Smith, D. S. Stucki, and E. S. Jules. 2022. Status of white pines across five western national park units: Initial assessment of stand structure and condition, revised October 2021. Natural Resource Report NPS/KLMN/NRR—2022/2342. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/nrr-2288668.

NPS 963/178192, January 2022

Contents

Page

Figures v

Tables vii

Abstract viii

Acknowledgments x

List of Acronyms xi

Introduction 1

Background 1

Species of Interest 1

Whitebark Pine 1

Limber Pine 3

Foxtail Pine 4

Objectives 5

Methods 6

Study Sites 6

Craters of the Moon 8

Crater Lake 10

Lassen Volcanic 11

Yosemite 13

Sequoia and Kings Canyon 15

Tree Measurements 18

Results 19

Stand Structure 19

Pests and Pathogens 26

Seedlings and cone production 27

Discussion 29

Geographic variability in forest structure 29

Contents (continued)

Page

Patterns of snag density, pathogen and insect infestation, and crown kill 30

Cone production and regeneration patterns 31

Future Directions 31

Conclusions 32

Literature Cited 33

Appendix A: Location Information and Site Characteristics for White Pine Monitoring Plots 39

Figures

Page

Figure 1. Geographic distribution of the ranges of limber pine, white bark pine, and foxtail pine from Little (1971) with locations of five National Park Service units (McKinney et al. 2012). 6

Figure 2. Climatic setting for white pine plot locations in Craters of the Moon National Monument and Preserve (CRMO), Crater Lake National Park (CRLA), Lassen Volcanic National Park (LAVO), Sequoia and Kings Canyon National Parks (SEKI), and Yosemite National Park (YOSE). 7

Figure 3. Limber pine monitoring plot locations (n=93) within Craters of the Moon National Monument and Preserve (CRMO). 9

Figure 4. Whitebark pine monitoring plot locations (n=30) in Crater Lake National Park (CRLA). 11

Figure 5. Whitebark pine monitoring plot locations (n=30) in the northwest corner Lassen Volcanic National Park (LAVO). 12

Figure 6. Whitebark pine monitoring plot locations (n=35) in Yosemite National Park (YOSE). 14

Figure 7. Whitebark pine monitoring plot locations (n=31) in Sequoia and King Canyon National Parks. 16

Figure 8. Foxtail pine monitoring plot locations (n=33) in Sequoia and Kings Canyon National Parks. 17

Figure 9. Pacific West Region Five-Needle Pine Protocol plot design (McKinney et al. 2012). 18

Figure 10. Boxplots of a) total tree density and b) basal area for white pine monitoring plots in five National Park Service units 20

Figure 11. Total live tree density a) and basal area b) per hectare (ha) for individual species in white pine monitoring plots in five National Park Service units 21

Figure 12. Size class distributions of live and dead limber pine from 93 permanent 50 x 50 m plots in Craters of the Moon National Monument and Preserve. 22

Figure 13. Stem size class distributions of whitebark pine populations from permanent 50 x 50 m plots in Crater Lake National Park (n=30), Lassen Volcanic National Park (n=30), Sequoia and Kings Canyon National Parks (n=31), and Yosemite National Park (n=35) 23

Figures (continued)

Page

Figure 14. Size class distributions of foxtail pine from a series of 33 permanent 50 x 50 m plots in Sequoia and Kings Canyon National Parks. 24

Figure 15. Density a) and basal area b) per hectare (ha) for live and dead trees of white pine species in monitoring plots in five National Park Service units. 25

Figure 16. Pattern of crown kill (a), white pine blister rust (WPBR) infestation (b), and c) mountain pine beetle (MBP) infestation in five National Park Service units 27

Tables

Page

Table 1. Climatic and environmental settings of white pine population monitoring plots in five National Park units 7

Table 2. Average and standard deviation of live tree density and live tree basal area in white pine monitoring plots in five National Park Service units 19

Table 3. Dead stand structure, mountain pine beetle (MPB) and white pine blister rust (WPBR) infestation rates means and standard deviations, and mean percent crown kill with standard deviations for white pine populations in five National Park Service units. 26

Table 4. Patterns of white pine seedling regeneration (20 to 136 cm tall) and number of trees with female cones from permanent 50 x 50 m plots in five National Park Service units 28

Abstract

Species of white pine play an essential ecological role in high elevation forests of western North America. These species, particularly whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), and foxtail pine (*P. balfouriana*), are of special concern due to recent declines and mortality associated with native and invasive insects and pathogens and changing climatic conditions. This report synthesizes the results of a monitoring program for these three species of white pines across five national park units in northern and central California, southern Oregon, and central Idaho. This program provides baseline data collected between 2011 and 2017. Whitebark pine, the most geographically widespread of the study species, was sampled in Crater Lake National Park (CRLA) and Lassen Volcanic National Park (LAVO) from 2012 to 2014, and from 2013 to 2017 in Yosemite National Park (YOSE) and Sequoia and Kings Canyon National Parks (SEKI). Limber pine populations were sampled in Craters of the Moon National Monument and Reserve (CRMO) from 2011 to 2013. Foxtail pine populations were sampled in SEKI from 2013 to 2017. Live and dead trees (<1.37 m DBH) of all species were measured and identified in a series of 50 x 50 m plots. Additional observations on cone production, crown kill, regeneration, and the incidence and severity of white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) were recorded for each species. Live and dead structure varied by species and among park units. The structure and composition of whitebark pine habitats were variable and plots often included shade tolerant species at relatively high densities. Limber and foxtail pines were generally found at lower density and with fewer other species, but foxtail pines reached the largest sizes and highest levels of basal area of all three taxa. Whitebark pine snags in CRLA and LAVO were associated with white pine blister rust and mountain pine beetle and occurred at much higher densities than in SEKI or YOSE. Mountain pine beetle was also observed in foxtail and limber pine, but snags of these species were relatively rare and crown kill was generally very low. Regeneration was generally low but varied among species. The findings of this study provide a baseline documenting geographic patterns and condition of three species of high elevation white pines and associated mechanisms for comparison with other studies of these taxa.



Limber pine (*Pinus flexilis* E. James) at Craters of the Moon National Monument and Preserve. Photograph by Devin Stucki, NPS.

Acknowledgments

We are grateful to the following people for help with fieldwork in Crater Lake and Lassen Volcanic National Parks: Alex Borst, Emily DeStigter, Kelsey Guest, Kasey Graue, David McLean, Rachel Patton, and April Sahara. Sean Mohren provided critical database support. Jen Beck and Elena Thomas in Crater Lake National Park, and Mike Magnuson in Lassen Volcanic National Park, helped us understand the whitebark pine system and provided logistical support throughout the study. This work would not have been possible without the amazing contributions of our dedicated field crew members in Yosemite and Sequoia/Kings Canyon National Parks: Sean Auclair, Rosa Cox, Jennifer Cribbs, Pete Del Zotto, Joan Dudney, Dan Esposito, Tressa Gibbard, Sienna Hiebert, Sarah Hoff-Phillips, Roxanne Kessler, Vladimir Kovalenko, Sarah Hendrickson, Allyson Makuch, Hanna Mohr, Matthew Mosher, Matt Nolte, Brianna Permar, Patrick Rizzo, Davis Soderberg, Devin Stucki, Jim Syvertsen, and Sam Zuckerman. Thanks also to the following people for their dedication and assistance in collecting data during fieldwork in Craters of the Moon National Monument and Preserve: Dan Esposito, Jim Syvertsen, Matt Nolte, Gilbert Moreno, Melissa Nicolli, Tiffany Petranek, Cooper Malin, Kevin Mason, and Kraig Esswein. Formatting assistance was provided by Linda Mutch. Project design and logistic support were provided by many I&M as well as Park staff over the years including Tony Caprio, Les Chow, Alice Chung-MacCoubrey, Garrett Dickman, Gordan Dicus, Alex Eddy, Sandy Graban, Sylvia Haultain, Penny Latham, Jeff Lonneker, Shawn T. McKinney, Tom Rodhouse, Daniel Sarr, Gus Smith, and Kristin Weikel.

This report is dedicated to Daniel A. Sarr (1964–2015). Daniel was the first Klamath Network Inventory and Monitoring Program Manager. He served as Manager for 13 years and one of his many contributions was initiating a robust program aimed at assessing threats to five-needle pine.

List of Acronyms

Park acronyms

CRLA: Crater Lake National Park

CRMO: Craters of the Moon National Monument and Preserve

LAVO: Lassen Volcanic National Park

SEKI: Sequoia and Kings Canyon National Parks

YOSE: Yosemite National Park

Other acronyms

DBH: stem diameter at breast height (1.37 m)

MPB: mountain pine beetle

NPS: National Park Service

UCBN: Upper Columbia Basin Network

WPBR: white pine blister rust

Introduction

Background

Five-needled white pines (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*) play an important ecological role in high elevation forests and woodlands of western North America, but are threatened by multiple ongoing stressors (Tomback and Achuff 2010). Limber pine (*P. flexilis* James), foxtail pine (*P. balfouriana* Balf.), and whitebark pine (*P. albicaulis* Engelm.) are foundational species in upper subalpine and treeline environments that occur in several National Park Service (NPS) Pacific West Region parks. White pines are often the dominant species in higher elevation environments and serve key ecosystem functions that include modulating snowmelt and increasing summer water availability, moderating local environments allowing for establishment of shade-tolerant species, and producing large seed crops critical to wildlife (Tomback 1982; Keane et al. 2011). However, these same taxa are currently facing unprecedented challenges from climatic change, insects and pathogens, and changing fire regimes (Keane et al. 2011).

White pine blister rust (WPBR) is caused by an invasive pathogen, *Cronartium ribicola* (Division Basidiomycota, Order Pucciniales), and poses a serious threat to species of white pine in the western United States. WPBR was accidentally introduced into the west coast of North America in 1910 and affects all white pine species (McDonald and Hoff 2001). The fungus exhibits a complex life cycle that includes five different spore types alternating between white pines and plants of the genera *Ribes*, *Pedicularis*, and *Castilleja* (McDonald et al. 2006). WPBR damages and can ultimately kill white pines by girdling branches and boles. White pines are also threatened by a native insect, mountain pine beetle (MPB) (*Dendroctonus ponderosae*), competition with encroaching woody vegetation due to fire exclusion, and increasingly hot and dry drought conditions (Keane et al. 2011; Millar et al. 2012). These factors, acting singly or in combination, are likely to change the structure, function, and composition of high elevation forests.

In 2011, scientists from the Klamath Inventory and Monitoring Network (KLMN), Sierra Nevada Network (SIEN), and Upper Columbia Basin Network (UCBN) began establishing long-term monitoring plots in five western National Park units (Figure 1) using a standardized field methodology following the Pacific West Region Five-Needle Pine Protocol (McKinney et al. 2012). The purpose of the work was to characterize stand structure and composition, determine the extent of mortality and the distribution of causal agents such as WPBR and MPB, and evaluate the patterns of insect and pathogen incidence to inform management of populations of white pines. In addition, the plots were established with the intention of resampling each plot every three years to provide robust estimates of survivorship, growth, and recruitment of whitebark pine, limber pine, and foxtail pine through time.

Species of Interest

Whitebark Pine

Whitebark pine is a long-lived conifer that ranges in structure and size from an upright tree growing up to ~15 m in height (often found in protected sites), to a short and twisted form referred to as *krummholz* found in windy, exposed sites (Weaver 2001). Individuals are generally slow-growing

and may live more than 1,000 years (Perkins and Swetnam 1996). The species has a broad geographic range (Figure 1), extending from northern British Columbia southward in the Rocky Mountains of Idaho and Wyoming, as well as southward along the Cascades in Oregon and Washington and the Sierra Nevada in California (McGaughey and Schmidt 2001). In addition, several isolated regions of Nevada and eastern Oregon also contain whitebark pine. Whitebark pine is generally restricted to high elevation sites, though its elevational distribution varies considerably from north to south. For instance, at the northern edge of its range, whitebark pine is found as low as 900 m (McGaughey and Schmidt 2001), but in the southern Cascades of California it is not found below 2500 m (Jackson et al. 2015). Whitebark pine can occur as the only tree taxa in some habitats such as cold, dry sites near treeline, but commonly occurs in mixed communities with other species (Arno 2001).

Whitebark pine is often described as a keystone or foundation species because of the multiple, critical roles that it plays in subalpine ecosystems (e.g., Ellison et al. 2005; Keane et al. 2012). These roles include the initiation of succession on harsh sites after disturbances such as fire, the reduction in snowmelt rates during the warm season, and the supply of food for wildlife through seed production (Tomback et al. 2001). Seeds of whitebark pine are notable for being large and nutrient-rich relative to most pines and are therefore an important food source for many animals. Across the range of whitebark pine, seeds are utilized by several bird and mammal species, including red squirrels (*Tamiasciurus hudsonicus*), Douglas squirrels (*Tamiasciurus douglasii*), grizzly bears (*Ursus arctos horribilis*), and Clark's nutcracker (*Nucifraga columbiana*; Tomback et al. 2001; Mattson and Haack 1987). The Clark's nutcracker has developed a mutualistic relationship with the whitebark pine. This boisterous, robin-sized bird with flashy black-and-white wings and tail, has a specialized pouch under its tongue for storing seeds, which it caches widely in the soil. The Clark's nutcracker serves as the primary dispersal agent and regeneration from uneaten seeds maintain populations of whitebark pine. McKinney et al. (2009) found that nutcracker visitation decreases in whitebark pine ecosystems as basal area decreases due to high rates of white pine mortality.



Mature female, seed-bearing cones of whitebark pine remain closed (left) unless opened by an animal (right). Seeds have been removed from the cone on the right, either by a Clark's nutcracker or a Douglas squirrel. Photographs by Erik S. Jules.

Numerous studies have assessed the prevalence and impacts of WPBR and MPB on populations of whitebark pine (e.g., Campbell and Antos 2000; Zeglen 2002; Hatala 2010; Smith et al. 2013). The results of this work show that the role of the disease varies considerably across the range of the pine and that the factors controlling its spread probably vary geographically as well. Keane and Arno (1993) found an average of 42% mortality over twenty years (1971–1991) in western Montana. They found that WPBR was the primary agent of mortality, with MPB present only in trees with WPBR. Larson (2011) found geographic differences in WPBR among six mountain ranges from southwest Montana to western Oregon. In his study, average infection rates of trees varied from 5–66% among ranges, and was positively related to several site characteristics, including colder winter temperature and less dense stand structure. Interestingly, Larson (2011) attributed mountain pine beetle as the primary agent of mortality for 83% of the dead trees he observed, while WPBR was not attributed as the cause of any whitebark pine mortality. In California, WPBR incidence varies by region, from 0.0% in the Great Basin to 24.2% in the northern Sierra Nevada (Maloney 2011), though this study does not report on the impacts of mountain pine beetle.

Limber Pine

Limber pine is a widely distributed species that inhabits a variety of landscapes throughout western North America (Steele 1990). This species is found across a wide elevation range (1600–3400 m in the Rocky Mountains, Cleaver et al. 2015), occurring at low elevation sites as well as in alpine and treeline habitats (Webster and Johnson 2000). In these harsh environments, limber pine acts as a foundational species (Tomback and Achuff 2010) and plays an important role in facilitating the establishment of other species (Baumeister and Callaway 2006). Limber pine trees in CRMO are found growing at the lower elevational limits of the range of the species. Limber pine is a long-lived tree species, with an individual aged in CRMO reaching over 1350 years old (Schulman and Ferguson 1956).

Limber pine is susceptible to WPBR, which has caused large scale devastation to five-needle white pines throughout the Pacific Northwest and Intermountain Region (Schoettle et al. 2008; Burns et al. 2011; Klutsch et al. 2011). An additional stressor, dwarf mistletoe (*Arceuthobium cyanocarpum* A.Nelson ex Rydb.), is considered the second most important threat to limber pine (Kearns and Jacobi 2007; Taylor and Mathiasen 1999). Some species of dwarf mistletoe (e.g., *A. cyanocarpum*) are especially virulent and have caused widespread mortality of limber pine in the Rocky Mountains (Mathiasen and Hawksworth 1988). In addition to WPBR, limber pine is also sensitive to MBP, as well as drought (Kendall et al. 1996; Achuff 1997) and fire suppression (Schoettle 2004a, 2004b). Limber pine, like whitebark pine, has large and nutritious seeds, and Clark's nutcracker is an important mechanism of seed dispersal.



Limber pine in Craters of the Moon National Monument and Preserve. Photo taken by Devin Stucki.

Foxtail Pine

Foxtail pine is endemic to two distinct areas in California: the Klamath Mountains in the northwest part of the state and the southern Sierra Nevada (Figure 1). Research on community and population dynamics is lacking for foxtail pine compared to whitebark pine. Foxtail pine occurs in four different forest types: 1) those dominated by foxtail pine, 2) those with foxtail pine and whitebark pine, 3) those with foxtail pine and red fir (*Abies magnifica* A. Murray bis var. *magnifica*), and 4) those with foxtail pine, red fir, and western white pine (*Pinus monticola* Douglas ex D. Don; Eckert and Sawyer 2002). Foxtail and whitebark pine overlap in some portions of their southern Sierra Nevada distribution, however, south of the Kings-Kern divide, foxtail pine is the major (sometimes exclusive) subalpine and treeline tree species (e.g., >3,000 m). Foxtail pine seeds are thought to be dispersed primarily by wind (Lanner 1999), and thus likely have potential to disperse long distances.

The southern population of foxtail (subspecies *austrina*) has provided important data for dendrochronological research on paleoclimate (Lloyd 1997) as a result of its great longevity (>2,000 years) and slow growth. In fact, five-needle pines, in general, have proven valuable in enhancing our understanding of past climates through dendrochronological investigations (Kipfmueller and Salzer 2010; Woodhouse et al. 2011).



Foxtail pine near Rock Creek ranger station, Sequoia National Park. Photo taken by Jenny Cribbs 2017.

Objectives

This report summarizes and synthesizes the initial findings from the collaborative work outlined in the high elevation white pine monitoring protocol (McKinney et al. 2012) conducted by three NPS Inventory and Monitoring Networks in five national park units in northern and central California, southern Oregon, and central Idaho. This report utilizes data from the initial establishment of over 150 long-term demographic plots. The specific objectives for all three species (limber pine, whitebark pine, and foxtail pine) include documenting population structure and its variability among the five park units. Specifically, this report seeks to quantify 1) size structure of living and dead trees, 2) incidence of WPBR and MPB, 3) degree of crown kill, and 4) production of female cones and seedling abundance.

The information gathered from this monitoring project and synthesized in this report will be integral to providing a more comprehensive understanding of the status of high elevation white pine populations and how it varies among species and across a broader geographic area. It will also allow early detection of important changes in populations that may trigger management intervention.

Methods

Study Sites

This study used a probabilistic sampling design (GRTS) to select plot locations within sampling frames of three white pine species found in five national park units in northern and central California, southern Oregon, and central Idaho (Figure 1). Along with the wide geographic distribution of the parks, they also differ in the range of environmental and climatic conditions (Table 1, Figure 2). Climate data are 30-year normals (1981–2010) calculated from interpolated climate grid data (Daly et al. 2002; PRISM Climate Group, available at http://www.prism.oregonstate.edu/normals/).

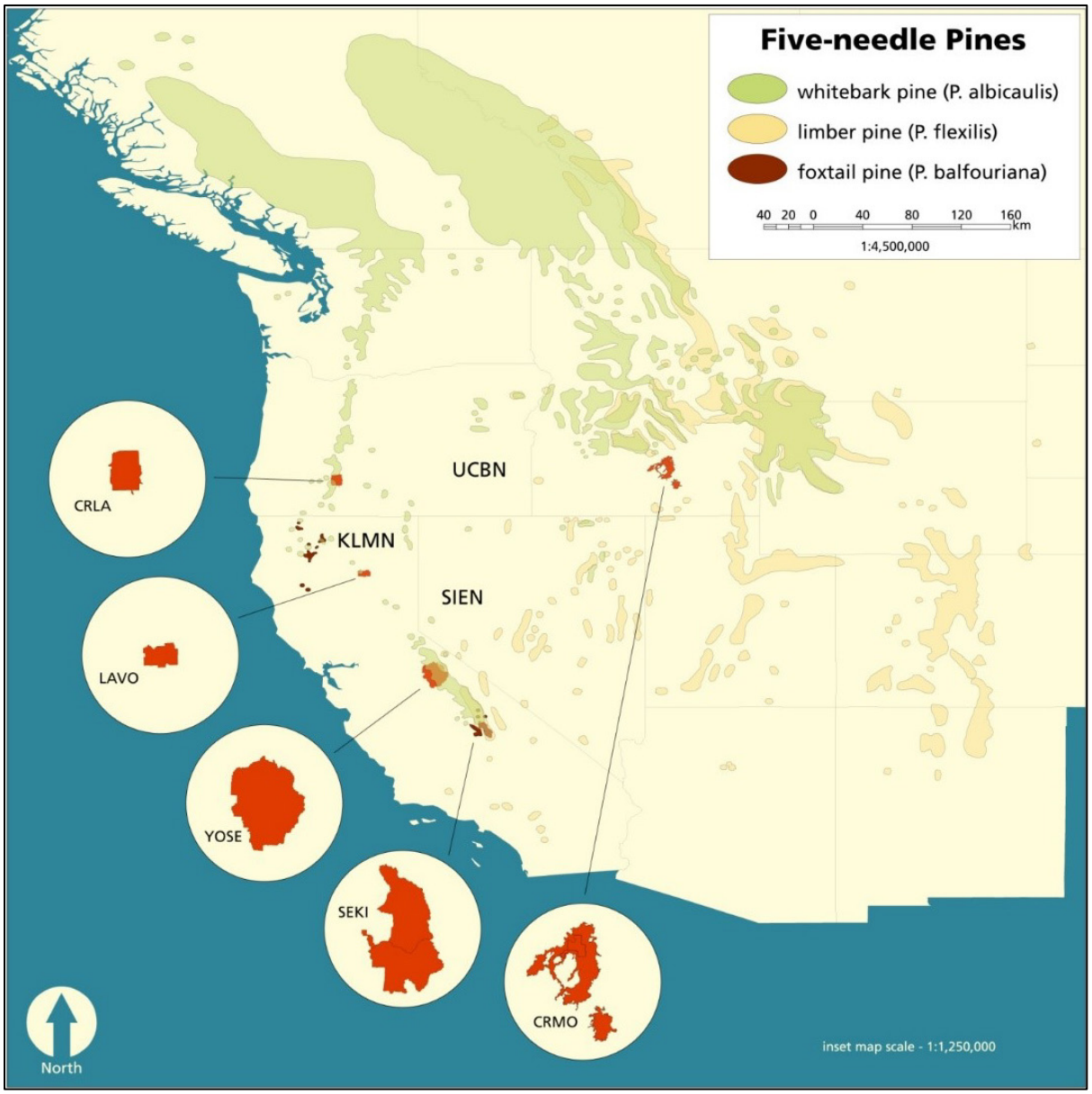


Figure 1. Geographic distribution of the ranges of limber pine, white bark pine, and foxtail pine from Little (1971) with locations of five National Park Service units (McKinney et al. 2012).

Table 1. Climatic and environmental settings of white pine population monitoring plots in five National Park units. Means and standard deviations are included with ranges in parentheses.

Study Site	Elevation (meters)	Slope (degrees)	Aspect (degrees)	Annual Temperature (°C)	Annual Precipitation (mm)
Craters of the Moon (*P. flexilis*)	1,755 ± 76 (1,616 to 1,957)	4 + 6° (0° to 26°)	149 ± 99°* (1° to 358°)	5.8 ± 0.2 (5.3 to 6.4)	356 ± 36 (270 to 388)
Crater Lake (*P. albicaulis*)	2,246 ± 93 (2,077 to 2,408)	9 + 5° (2° to 24°)	217 ± 99° (0° to 343°)	3.1 ± 0.3 (2.7 to 3.9)	1,395 ± 291 (997 to 1809)
Lassen Volcanic (*P. albicaulis*)	2,623 ± 52 (2,528 to 2,782)	13 + 7° (1° to 28°)	143 ± 58° (9° to 252°)	4.3 ± 0.5 (2.3 to 4.8)	2,965 ± 134 (2,731 to 3,173)
Yosemite (*P. albicaulis*)	3,086 ± 161 (2,732 to 3,394)	12 + 5° (3° to 30°)	215 ± 87° (23° to 352°)	1.9 ± 0.5 (0.9 to 3.3)	1254 ± 209 (1,059 to 1,729)
Sequoia & Kings Canyon (*P. albicaulis*)	3,294 ± 133 (3,022 to 3,624)	16 + 7° (4° to 29°)	206 ± 85° (21° to 348°)	1.9 ± 0.9 (-0.1 to 4.4)	1059 ± 166 (717 to 1,394)
Sequoia & Kings Canyon (*P. balfouriana*)	3,233 ± 168 (2,887 to 3,504)	12 + 5° (3° to 30°)	209 + 110° (10° to 354°)	2.4 ± 1.0 (0.9 to 4.5)	744 ± 160 (482 to 1,124)

* In CRMO, 22 of the 93 plots were flat and were not included in the summary statistics for slope or aspect.

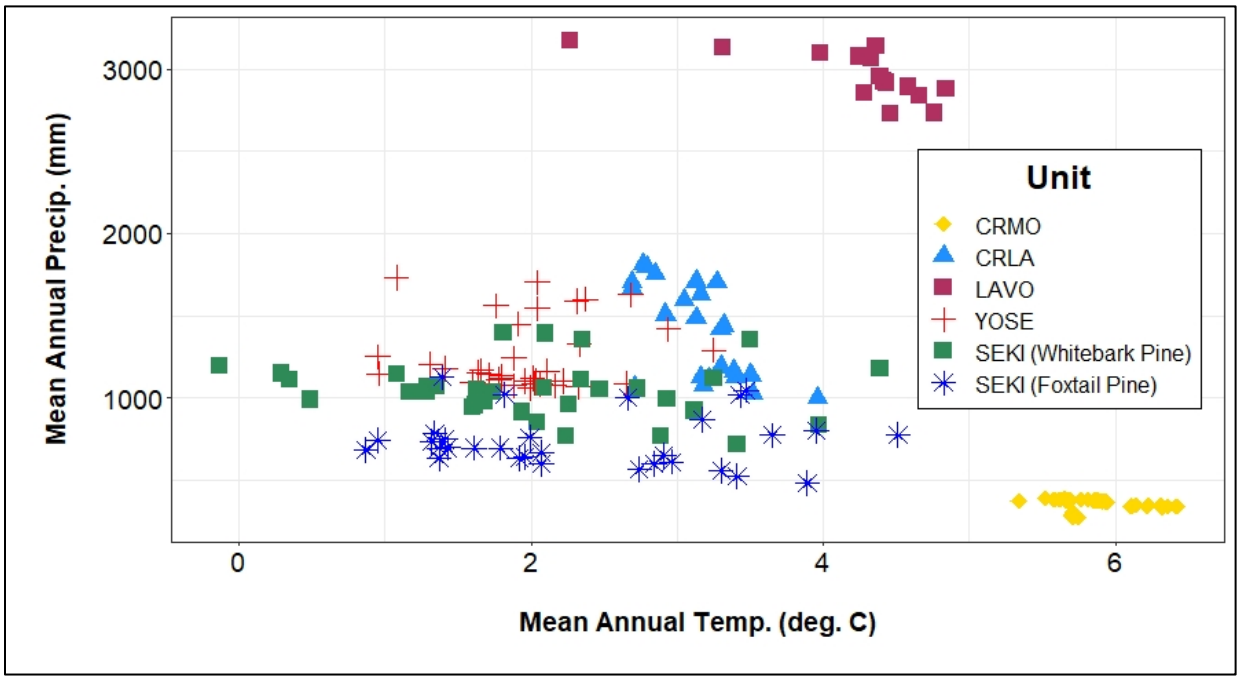


Figure 2. Climatic setting for white pine plot locations in Craters of the Moon National Monument and Preserve (CRMO), Crater Lake National Park (CRLA), Lassen Volcanic National Park (LAVO), Sequoia and Kings Canyon National Parks (SEKI), and Yosemite National Park (YOSE).

CRMO is the warmest and driest of the study units with annual temperature ranging from 5.3 to 6.4 °C and annual precipitation ranging from 270 to 388 mm. Annual temperature in CRLA ranges from 2.7 to 3.9 °C and receives from 997 to 1809 mm of precipitation annually. LAVO receives the most annual precipitation from 2,731 to 3,173 mm/year with average temperature ranging from 2.3 to 4.8 °C. YOSE receives 1,059 to 1,729 mm of precipitation annually and mean annual temperature ranges from 0.9 to 3.3 °C. Annual temperature in the whitebark pine SEKI plots range from -0.1 to 4.4 °C and annual precipitation ranges from 717 to 1,392 mm. Annual temperature in the foxtail pine SEKI plots range from 0.9 to 4.5 °C and annual precipitation ranges from 482 to 1,124 mm.

Plot design and sampling followed the NPS Pacific West Region Five-Needle Pine Protocol (McKinney et al. 2012). The locations for all plots in each unit were generated using the Generalized Random Tessellation Stratified (GRTS) algorithm in GIS (Stevens and Olson 2004). In addition, an oversample of points was also drawn using the GRTS algorithm to support any eventual site rejections.

Sampling frame constraints differed between networks. The sampling frame was generally limited to exclude slopes greater than 35° except in KLMN (30°). The KLMN sampling frame is comprised of whitebark pine habitat that falls within 100 m to 1000 m from a road or trail at LAVO and CRLA. The UCBN sampling frame at CRMO is comprised of limber pine habitat that fall within 2 km of a road or trail. The SIEN sampling frame for YOSE and SEKI are comprised of all habitat within the parks identified as including whitebark pine. The SIEN sampling frame for foxtail pine in SEKI includes all habitat within the parks mapped as including foxtail pine. Sites were rejected if (1) the species of interest was not found, or (2) sampling the area would result in unsafe working conditions (e.g., terrain that was too steep to work on). The GRTS points generated in the GIS were used as the southwest corner (plot origin) of the 50 m x 50 m plots if one or more of the species of interest ≥1.37 m in height were found within the plot boundary. If there were no individuals of the species of interest in a plot, an offset procedure was employed by drawing a random distance (between 5 and 100 m) and azimuth (between 0° to 359°) from a list of random numbers. Lastly, if the offset procedure did not generate a useable plot, a new point was used from the oversample described above. Additional details on plot locations, oversample plots used, and the GRTS algorithm can be found in McKinney et al. (2012).

Craters of the Moon

Craters of the Moon National Monument and Preserve is located along the northern border of the Snake River Plain in southern Idaho (Figure 3). The semi-arid landscape (Table 1) of CRMO is dominated by recent (15,000–2,000 years ago) basalt lava flows, and much of the rugged terrain supports little vascular plant growth. A total of 93 limber pine monitoring plots were established in CRMO during 2011–2013, ranging in elevation from 1,616 to 1,957 m. Limber pine monitoring plots are located in three main clusters along a north to south axis. The northernmost cluster of plots is remote, located within rugged áa lava flows (basaltic lava), and plots typically have low tree density. Terrain, elevation, and stand structure is variable in the central cluster, with terrain ranging from rugged áa to smooth pahoehoe lava types (another basaltic lava), and from steep sided volcanic buttes to relatively flat cinder gardens. The highest elevation plot is found in this cluster, and while

tree density in the central cluster is variable, it contains the highest tree density of the plots. The southern cluster of plots, like the northern, is remote, located mostly within rugged áa lava flows, and plots are characterized as having low tree density. Plots located in the southern cluster are found at the lowest elevations in the sample frame. Other tree species are occasionally found mixed with limber pine at very low densities and include Douglas-fir (*Psuedotsuga menziesii*) and Rocky Mountain Juniper (*Juniperus scopulorum*) (Stucki et al. 2018).

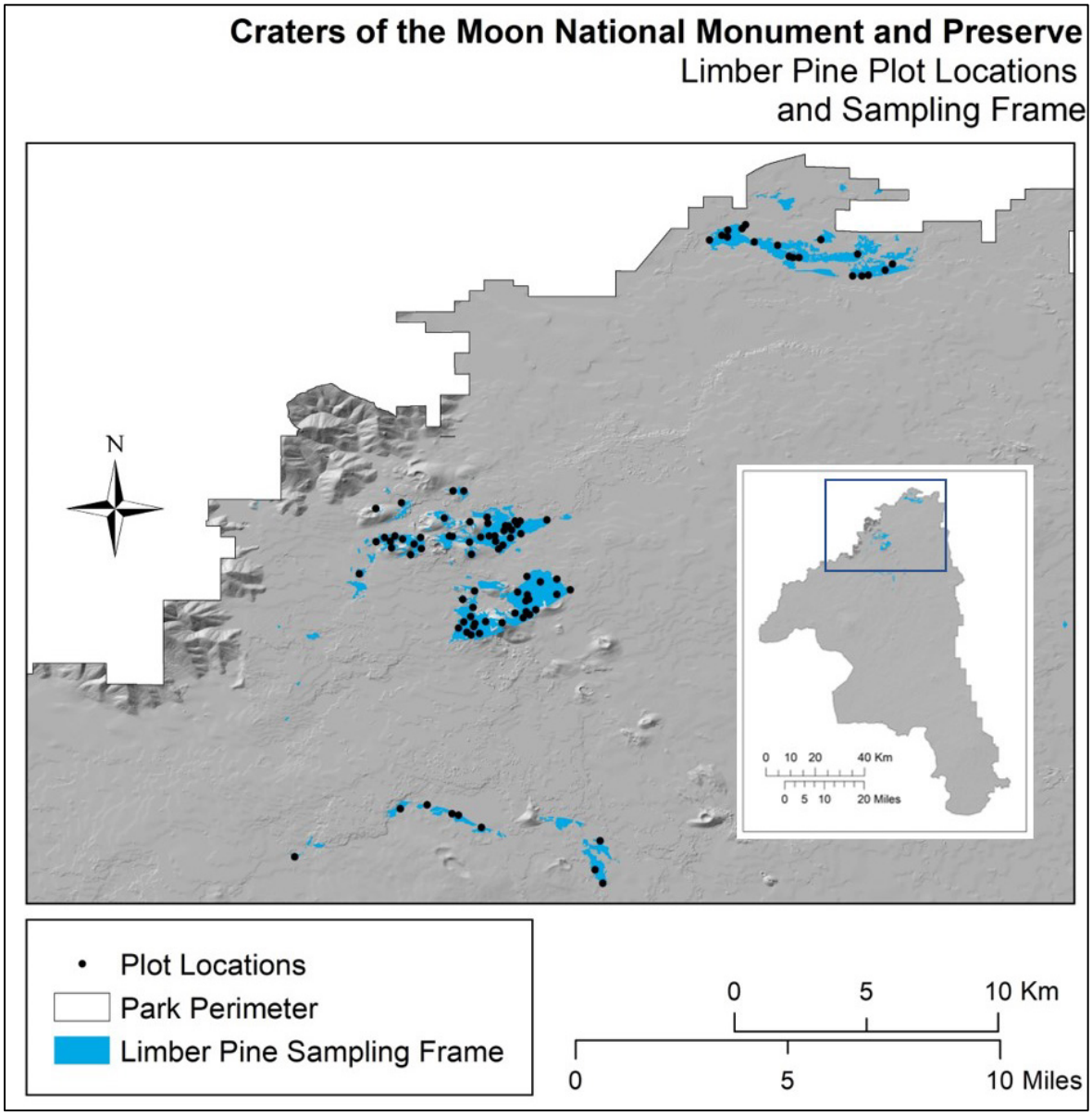


Figure 3. Limber pine monitoring plot locations (n=93) within Craters of the Moon National Monument and Preserve (CRMO).

Crater Lake

Crater Lake National Park (CRLA) is located along the crest of the Cascade Mountains in central Oregon (Figure 4). Higher elevation mixed conifer and subalpine forest dominate this landscape that surrounds a stunning lake in the crater of Mount Mazama, which erupted ~7,700 years ago. The landscape surrounding the crater slopes relatively gently and is covered by volcanic debris. Andesitic and dactic bedrock (both extrusive igneous rock) are exposed in and around the rim of the crater with much of the rest of the landscape covered in deposits of ash, cinder, and pumice. Most of the landscape is currently forested. Populations of whitebark pine are found at elevations ranging from 2,077 to 2,408 m and are distributed in four main clusters around the rim with the largest populations on the northwest and eastern sides of the park. Other species that occur with whitebark pine include mountain hemlock, lodgepole pine, and western white pine.

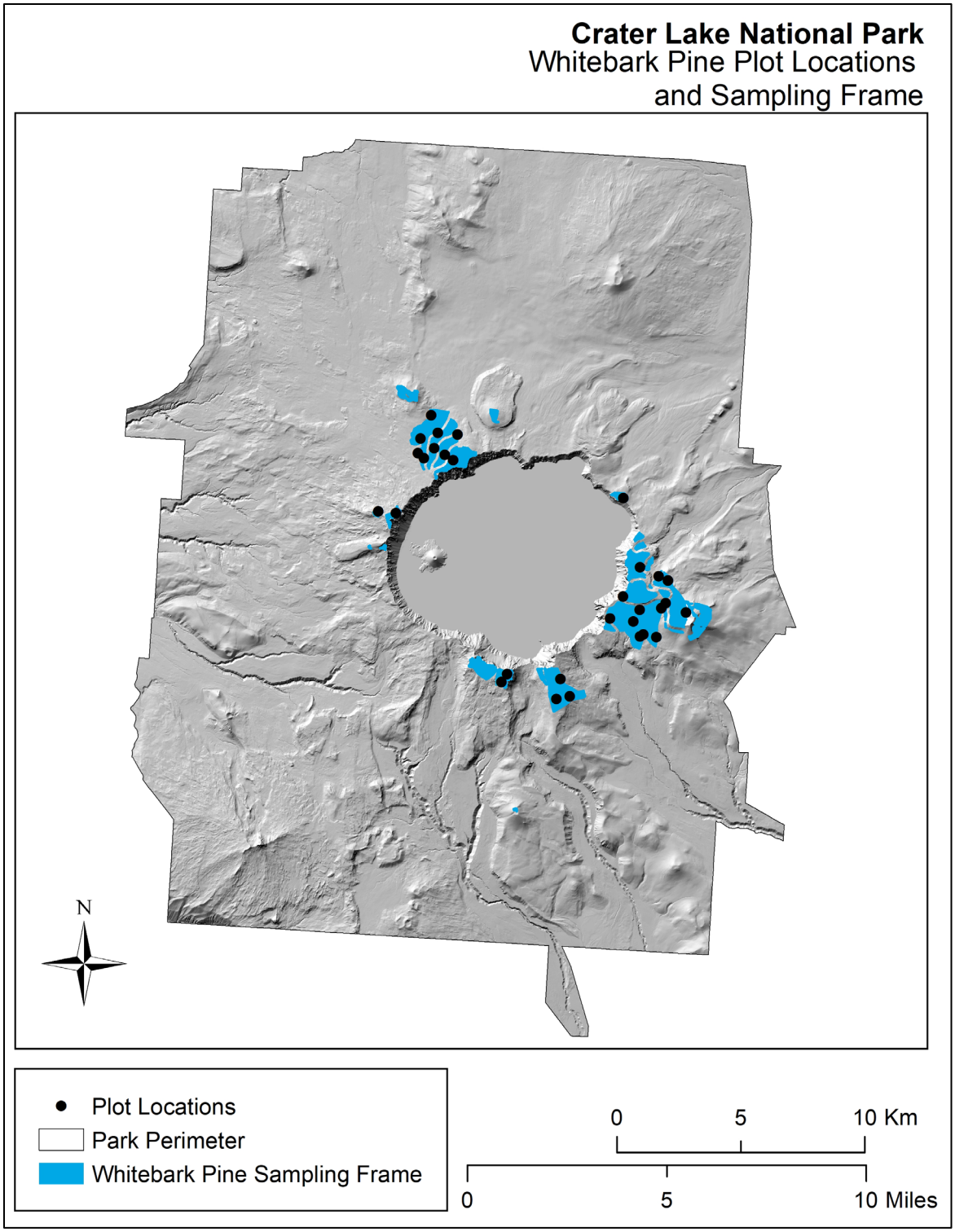


Figure 4. Whitebark pine monitoring plot locations (n=30) in Crater Lake National Park (CRLA).

Lassen Volcanic

Lassen Volcanic National Park (LAVO) is located in the southern most extent of the crest of the Cascade Mountains in northwestern California (Figure 5). The landscape is made up of high

elevation mixed conifer and subalpine forests. The park is a volcanic landscape sculpted by glacial activity and the last eruption of Mount Lassen in 1915. Pyroclastic flows and avalanches from this eruption surround portions of the peak which is also flanked by glacial moraines. Much of the bedrock is composed of basaltic andesite and dacite. Populations of whitebark pine are found at elevations ranging from 2,529 to 2,782 m and are distributed in several large patches that are primarily in close proximity in the northern and western portions of the park. Mountain hemlock and red fir commonly occur with whitebark pine in LAVO. Other infrequent associates include lodgepole pine and western white pine.

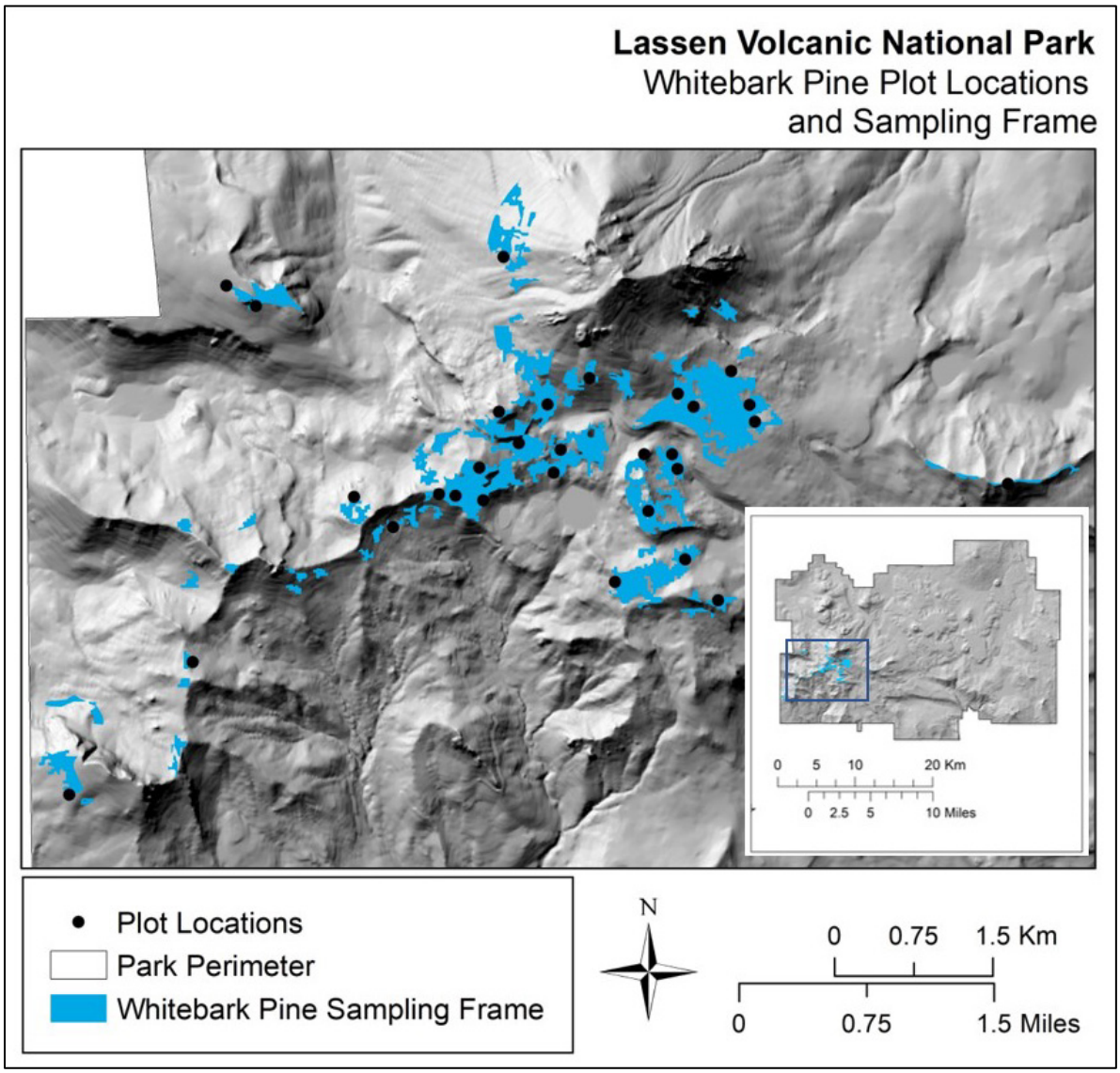


Figure 5. Whitebark pine monitoring plot locations (n=30) in the northwest corner Lassen Volcanic National Park (LAVO).

Yosemite

Yosemite National Park (YOSE) is located in the southcentral Sierra Nevada Mountains of California (Figure 6). The landscape has been sculpted by glaciers and consists of high alpine peaks, large granite domes, high elevation plateaus, and two prominent valleys. Most of the landforms are derived from a granitic batholith. Whitebark pine is primarily distributed along a prominent crest of high elevation environments in the eastern part of the park. Populations of whitebark pine are found at elevations ranging from approximately 2,732 to 3,394 m. Whitebark pine occurs as pure stands as well as in mixed species stands where lodgepole pine and mountain hemlock are common.

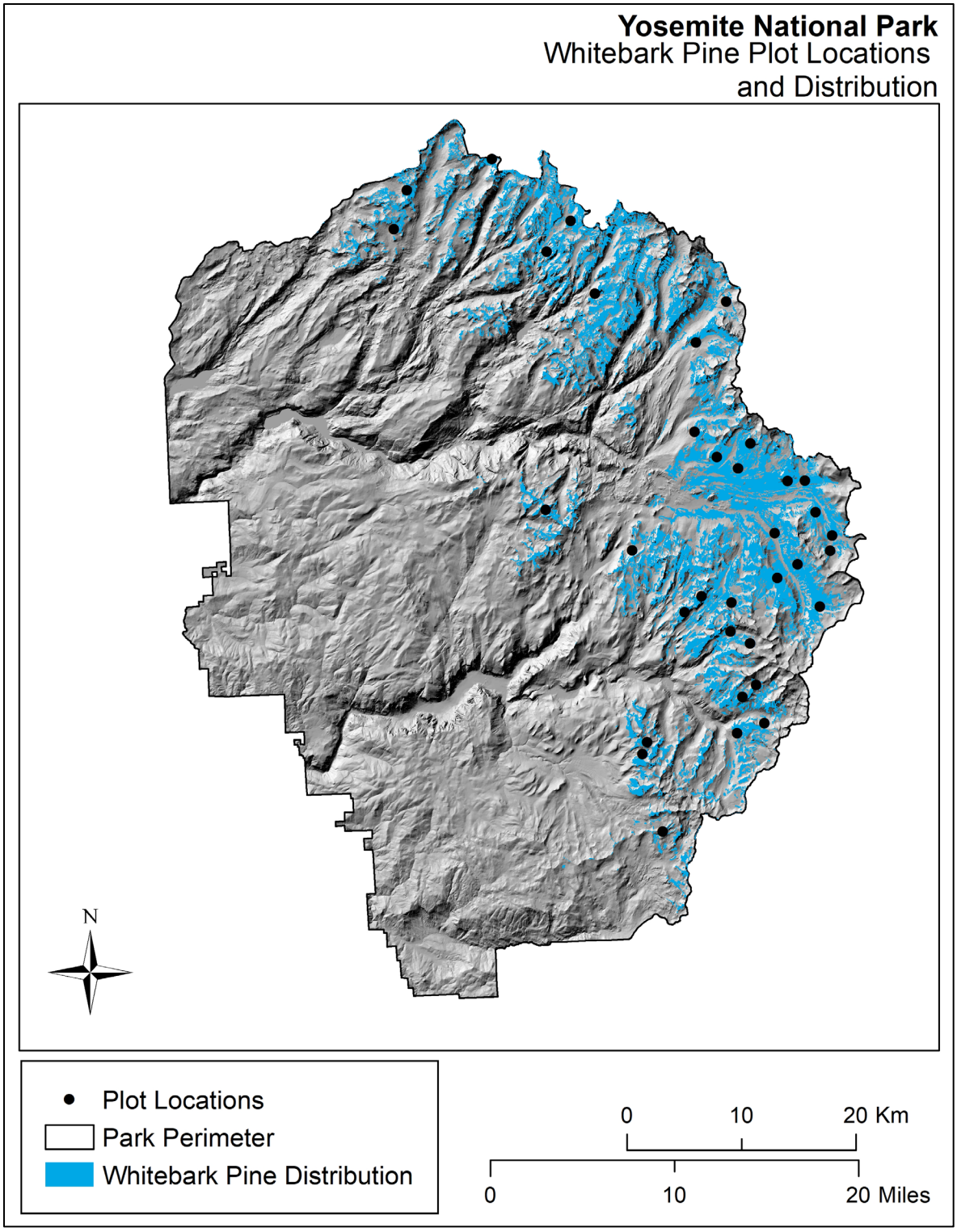


Figure 6. Whitebark pine monitoring plot locations (n=35) in Yosemite National Park (YOSE).

Sequoia and Kings Canyon

Sequoia and Kings Canyon National Parks (SEKI) are also located in the southern Sierra Nevada Mountains of California (Figure 7). The landscape is composed of mid elevation slopes and canyons with a prominent crest of high elevation environments in the eastern part of the park. Most of the landforms are derived from a granitic batholith. Populations of whitebark pine are found at elevations ranging from 3,023 to 3,624 m and are distributed primarily in Kings Canyon National Park, reaching their southern extent in the Mt. Whitney area of Sequoia National Park (Figure 7). Populations of foxtail pine are found at elevations ranging from 2,887 to 3,504 m and are distributed primarily in Sequoia National Park, reaching their northern limit in the Kings River watershed (Figure 8). Lodgepole pine commonly occurs with whitebark pine in SEKI, and common associates of foxtail pine include whitebark pine and lodgepole pine.

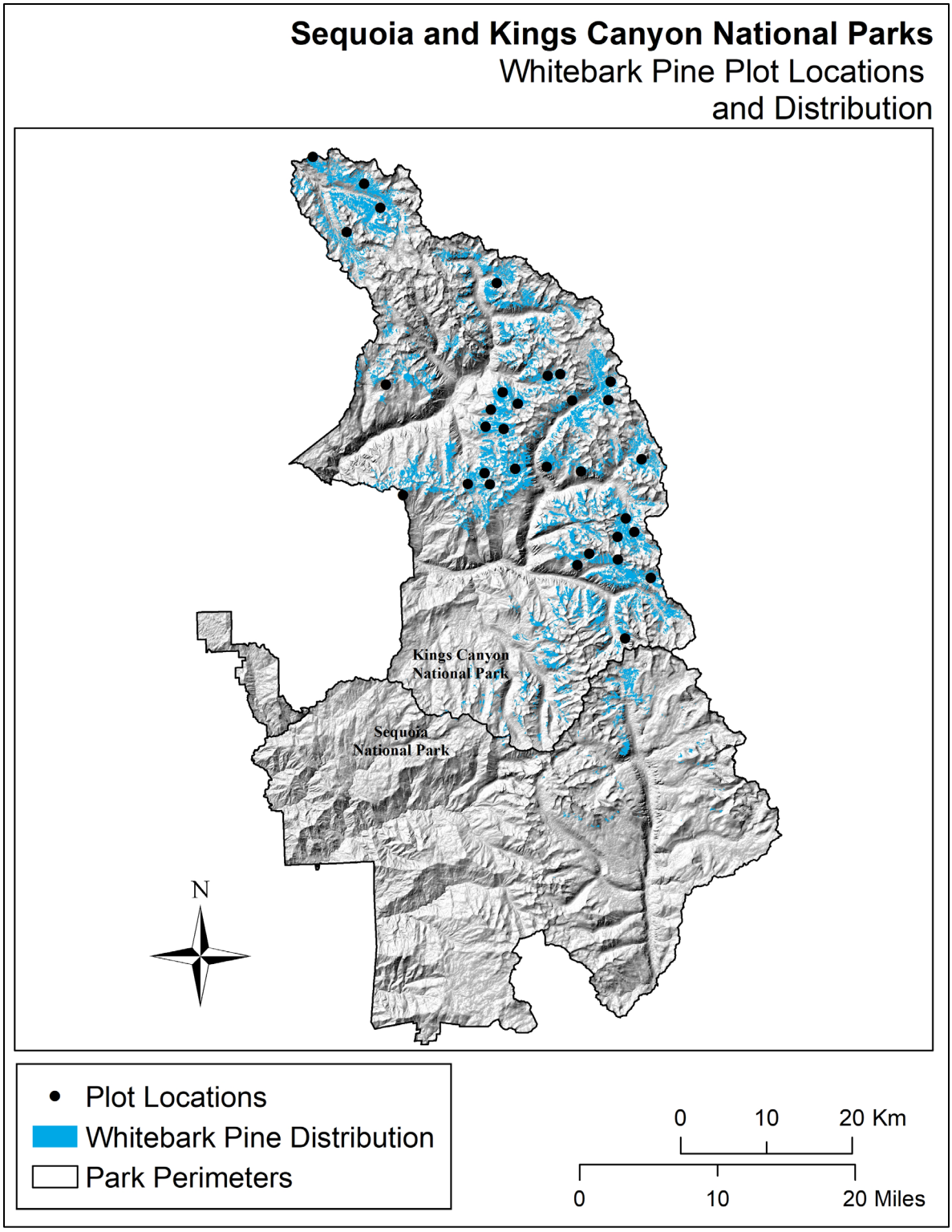


Figure 7. Whitebark pine monitoring plot locations (n=31) in Sequoia and King Canyon National Parks.

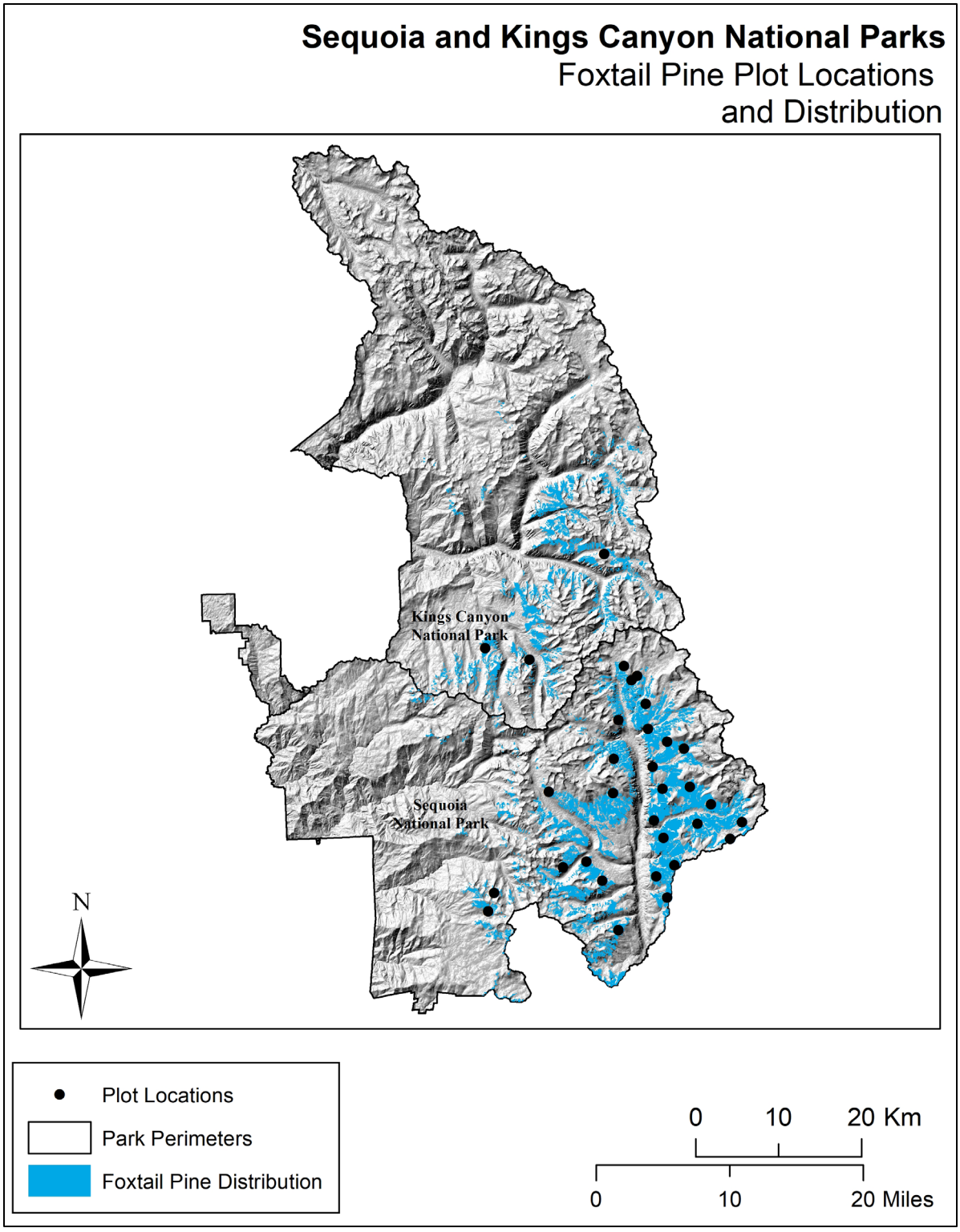


Figure 8. Foxtail pine monitoring plot locations (n=33) in Sequoia and Kings Canyon National Parks.

Tree Measurements

Each 50 x 50 m plot consists of five, 10 x 50 m subplots and nine, 3 x 3 m regeneration plots (Figure 9). Within plots, all trees ≥1.37 m in height were identified to species and tagged with a unique identification number. The diameter at breast height (1.37 m DBH) and height of each tree was recorded. In addition, each species of interest was assessed for signs and symptoms of WPBR, dwarf mistletoe, MPB, and presence of female cones. Dead trees ≥1.37 m in height and ≥5 cm DBH were also tagged with unique identification numbers and their height, DBH, and species (when it could be identified) were measured and recorded. The level of canopy kill in live trees was determined by dividing the tree's canopy (all the main branches, encompassing all foliage and supporting twigs and side branches) into thirds and recording an ocular estimate of the percentage of each third of the canopy that is dead. We did not measure crown kill at CRMO. Seedlings (trees <1.37 m in height) were counted by species and height class (20 to <50 cm; 50 to <100 cm; 100 to <137 cm) in each of the nine regeneration plots.

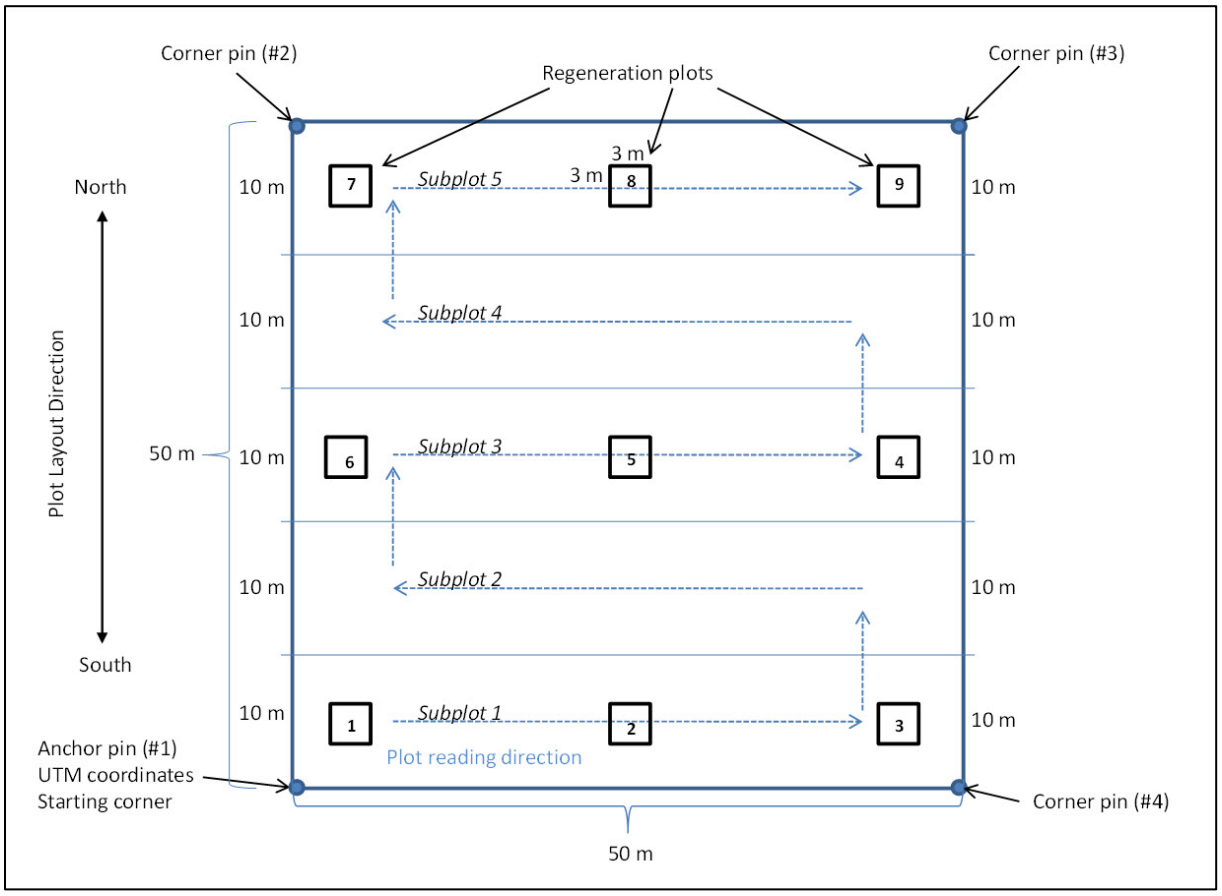


Figure 9. Pacific West Region Five-Needle Pine Protocol plot design (McKinney et al. 2012).

Results

Stand Structure

Structure of live white pines varied among study units. (Table 2, Figure 10). Limber pine in CRMO occurred at the lowest density and basal area of all the study units. Foxtail pine also occurred at relatively low densities, but generally had the highest levels of live basal area of all species in all study units. The highest density of whitebark pine occurred in YOSE and was similar in CRLA, LAVO, and SEKI. The high number of trees/ha in SEKI and YOSE is due in part to several plots dominated by whitebark pine growing with a krummholz growth form, leading to extremely high tree counts, as shown by the large standard deviations. Basal area of live white pines was generally similar among study units with the exceptions of CRMO where it was slightly lower.

Table 2. Average and standard deviation of live tree density and live tree basal area in white pine monitoring plots in five National Park Service units. Other species and other pine species are mutually exclusive.

Study Site	Total live tree density (trees/ha)	White pine (trees/ha)	Other pine species (trees/ha)	Other species (trees/ha)	Total live tree basal area (m^2/ha)	White pine (m^2/ha)	Other pine (m^2/ha)	Other species (m^2/ha)
Craters of the Moon (*P. flexilis*)	89.4 ± 112.6	79 ± 101	–	9.9 ± 50.7	2.74 ± 5.4	2.14 ± 2.47	–	0.59 ± 4.7
Crater Lake (*P. albicaulis*)	483 ± 467	127 ± 217	34.8 ± 56.4	322 ± 446	24.2 ± 25.0	2.61 ± 3.7	1.33 ± 2.46	20.3 ± 25.6
Lassen Volcanic (*P. albicaulis*)	618 ± 510	88 ± 87	0.26 ± 1.01	529 ± 510	17.4 ± 15.8	2.8 ± 3.7	0.001 ± 0.001	14.6 ± 14.6
Yosemite (*P. albicaulis*)	897 ± 543	429 ± 521	317 ± 463	136 ± 337	25.6 ± 23.8	3.7 ± 5.1	18.3 ± 24.3	3.6 ± 8.3
Sequoia & Kings Canyon (*P. albicaulis*)	650 ± 481	459 ± 394	190 ± 355	0.12 ± 71	19.6 ± 17.1	7.7 ± 7.8	11.8 ± 18.5	0.001 ± 0.006
Sequoia & Kings Canyon (*P. balfouriana*)	266 ± 180	130 ± 107	135 ± 185	0.24 ± 1.39	34.0 ± 16.5	26 ± 18.1	8.04 ± 11.5	0.001 ± 0.001

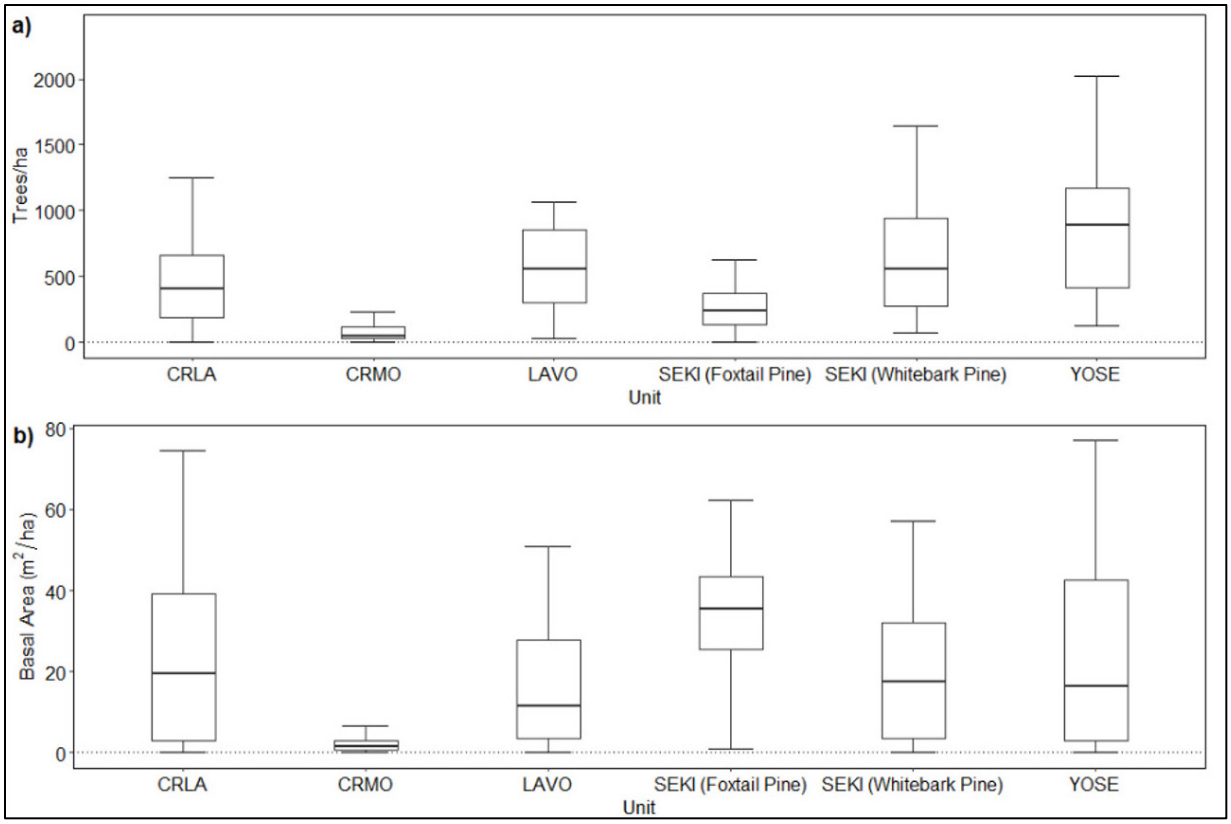


Figure 10. Boxplots of a) total tree density and b) basal area for white pine monitoring plots in five National Park Service units. Upper and lower whiskers represent the 95th and 5th percentiles, respectively. Upper and lower limits of the box represent the 75th and 25th percentiles, respectively, and lines represent medians.

The density and basal area of other species (including other species of white pine) also differed among study units (Table 2, Figure 11). Douglas-fir and Rocky Mountain juniper were present at CRMO at low density, but limber pine made up most of the total density and basal area at this unit. Whitebark pine made up much less of the total density and basal area in CRLA and LAVO where other species including mountain hemlock and lodgepole pine were more abundant. In YOSE, whitebark pine made up much of the density but less of the basal area and was often found with other species including lodgepole pine and mountain hemlock. Whitebark pine made up most of the density but less than half of the basal area in SEKI where lodgepole pine was also often present. Foxtail pine comprised around half of the density in SEKI but made up most of the basal area. Other species that occurred with foxtail pine were whitebark pine and lodgepole pine.

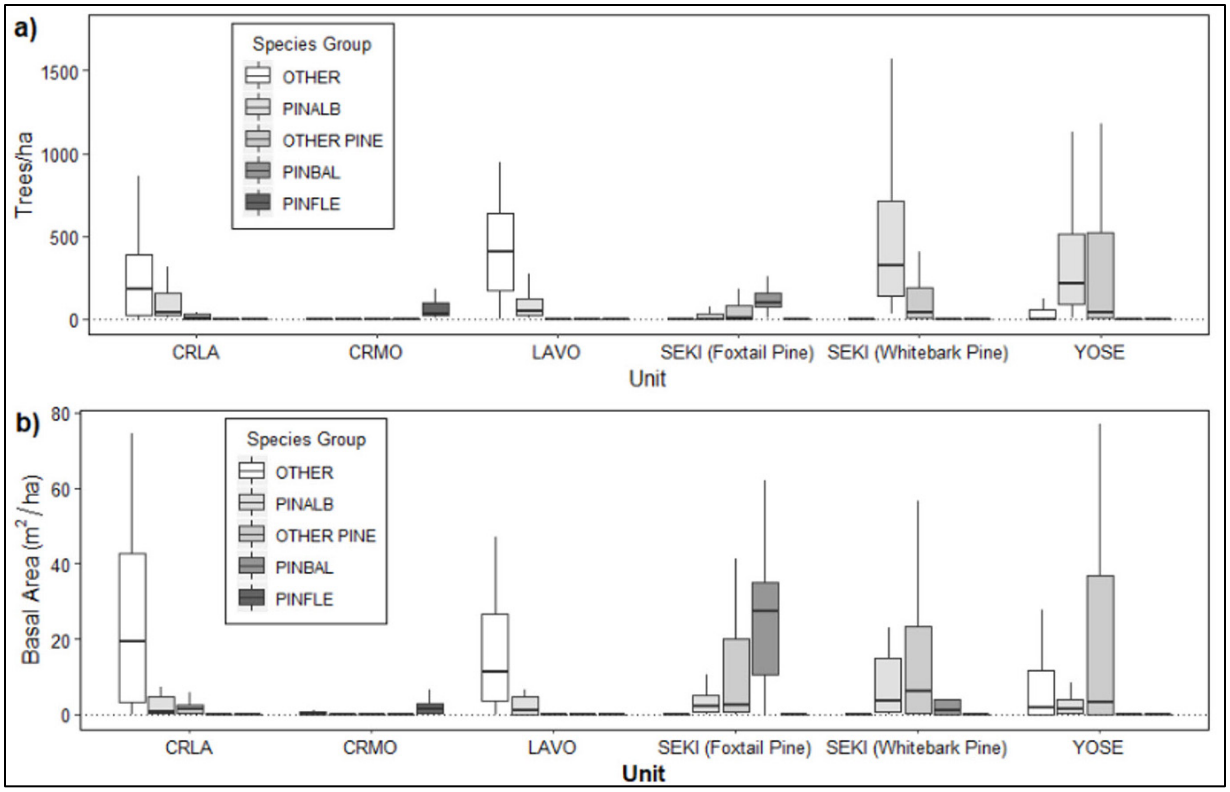


Figure 11. Total live tree density a) and basal area b) per hectare (ha) for individual species in white pine monitoring plots in five National Park Service units. “Other” tree species include white fir, red fir, subalpine fir, mountain hemlock, Rocky Mountain juniper, Douglas-fir, and western juniper; “PINALB” is whitebark pine; “Other pine” includes lodgepole pine, Jeffrey pine, and western white pine; “PINBAL” is foxtail pine; and “PINFLE” is limber pine.

Live size class structure of white pine species varied among parks and by species (Figures 12–14). Size class distributions of live trees generally resembled a typical “reverse-J” distribution with the highest densities of trees occurring in the smallest size classes (e.g., <10 cm DBH, 10 to 20 cm DBH) and decreasing numbers of trees in larger size classes. The biggest trees (>130 cm DBH) were found in SEKI and YOSE and were mostly foxtail pine and a few whitebark pine. Whitebark pine in CRLA and LAVO were smaller and rarely if ever >80 cm DBH. Although a few limber pines in CRMO >100 cm DBH were recorded, live trees were primarily <50 cm.

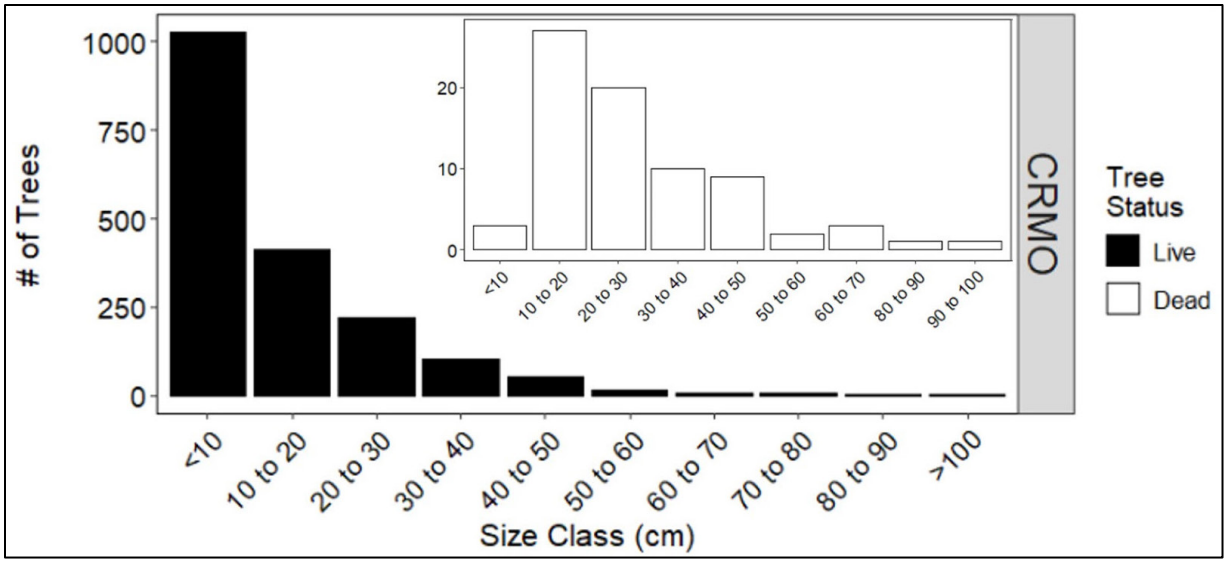


Figure 12. Size class distributions of live and dead limber pine from 93 permanent 50 x 50 m plots in Craters of the Moon National Monument and Preserve.

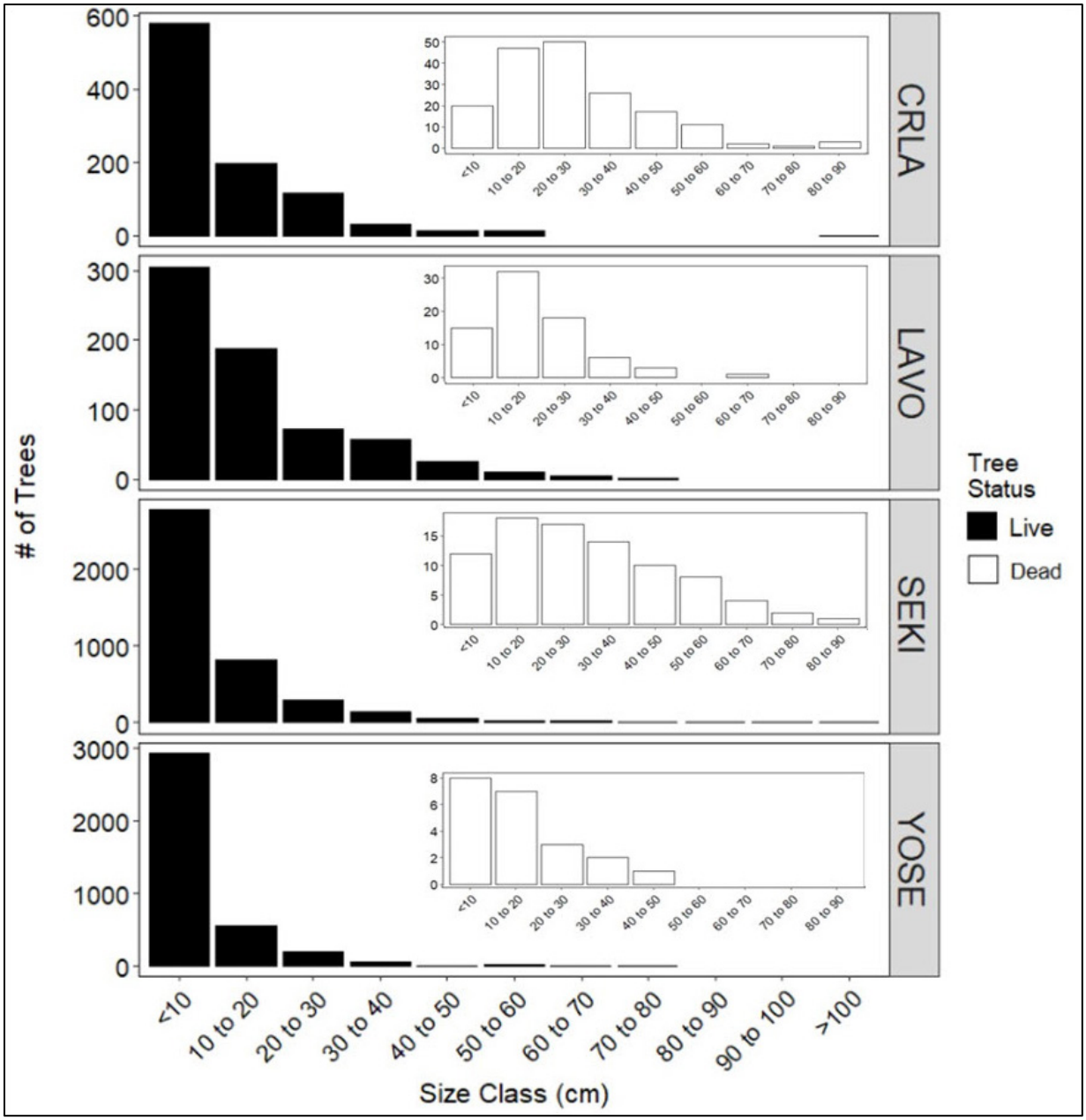


Figure 13. Stem size class distributions of whitebark pine populations from permanent 50 x 50 m plots in Crater Lake National Park (n=30), Lassen Volcanic National Park (n=30), Sequoia and Kings Canyon National Parks (n=31), and Yosemite National Park (n=35).

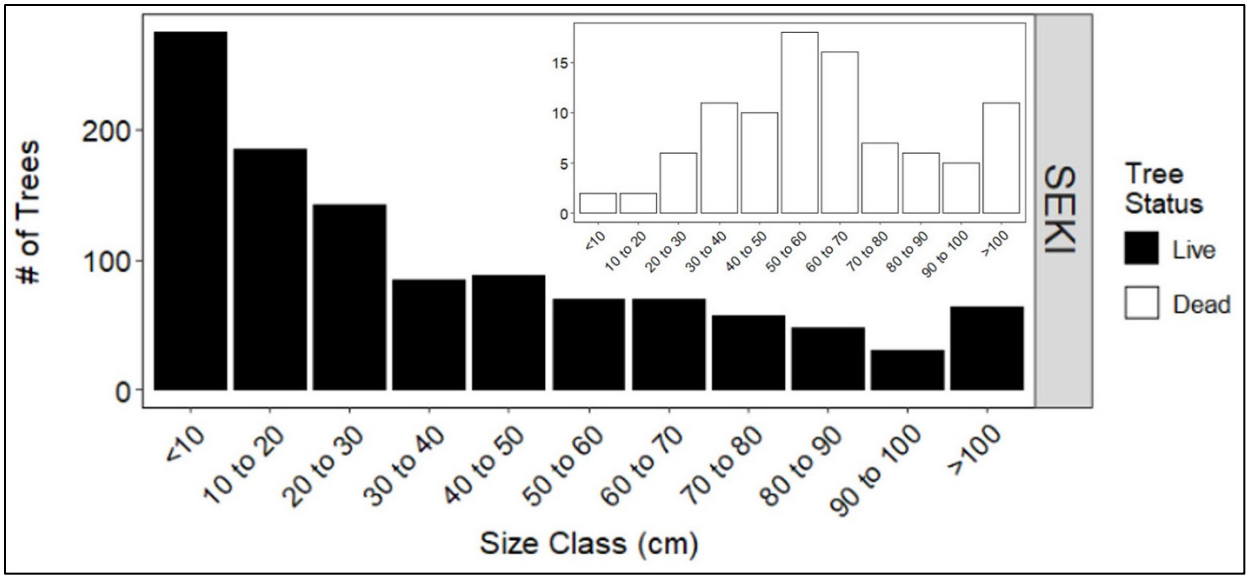


Figure 14. Size class distributions of foxtail pine from a series of 33 permanent 50 x 50 m plots in Sequoia and Kings Canyon National Parks.

Dead size class structure also varied among species of white pine and study units (Figure 15, Table 3). Snag density and basal area varied among parks and species, but was generally low compared to the density of live trees (Figure 15). Total snag density was highest in CRLA (Table 3). SEKI and YOSE had relatively high snag density, but these study units also had the highest density of live trees. Limber pine in CRMO had the lowest density and basal area of snags of all species in all study units (Table 3). The density and basal area of whitebark pine snags varied among units and was highest in CRLA. Foxtail pine in SEKI had the highest basal area of snags, but was still relatively low compared to the basal area of live trees (~25% of total foxtail basal area). Most snags occurred in the small and middle size classes (10 to 50 cm DBH) but varied among species in some parks (Figures 12–14).

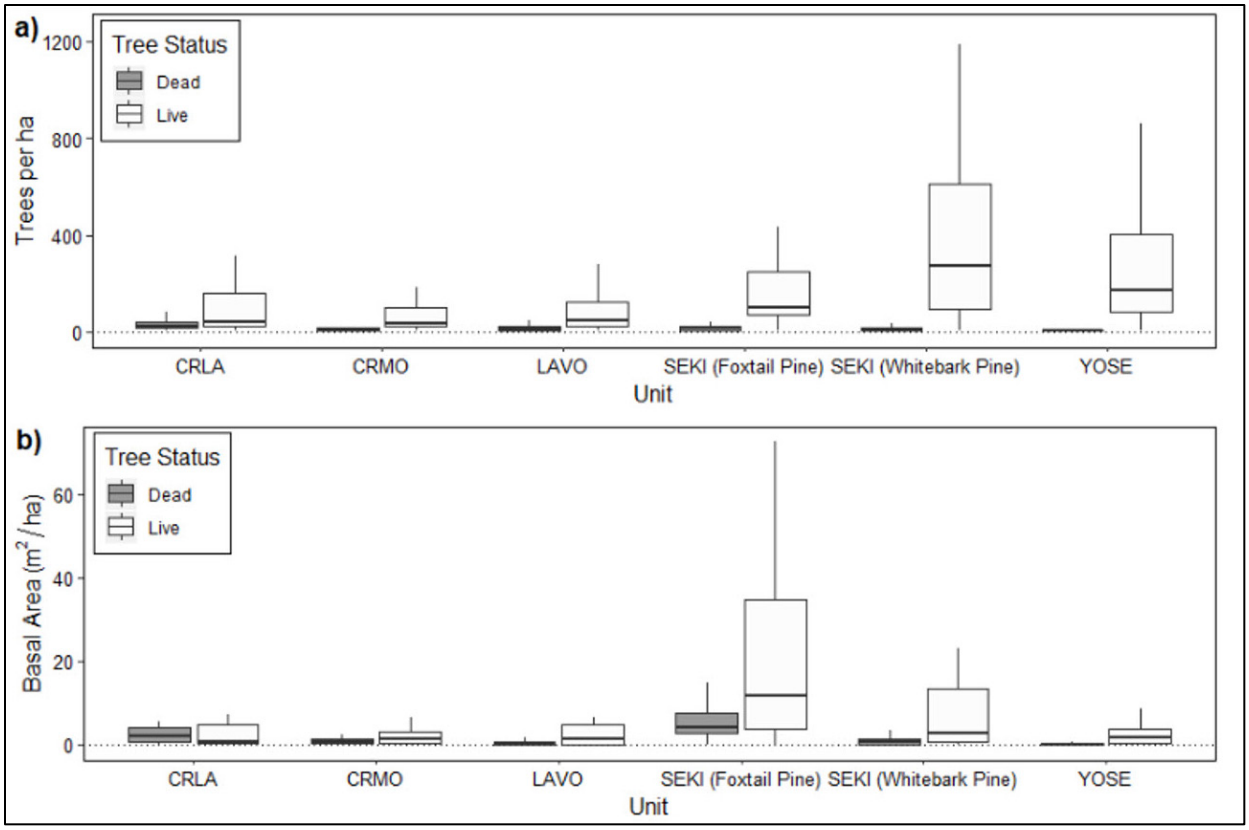


Figure 15. Density a) and basal area b) per hectare (ha) for live and dead trees of white pine species in monitoring plots in five National Park Service units.

Table 3. Dead stand structure, mountain pine beetle (MPB) and white pine blister rust (WPBR) infestation rates means and standard deviations, and mean percent crown kill with standard deviations for white pine populations in five National Park Service units.

Study Site	# of snags/ha	Snag basal area (m^2/ha)	MPB: # of infected trees/ha	WPBR: # of infected trees/ha	Percent crown kill	Dwarf mistletoe: # of infected trees/ha
Craters of the Moon (*P. flexilis*)	12 ± 11.2	1 ± 0.8	0.42 ± 1	0	N/A	7.4 ± 21.6
Crater Lake (*P. albicaulis*)	37.3 ± 37.1	2.9 ± 4.0	3 ± 6	60 ± 90	33 ± 22.7%	–
Lassen Volcanic (*P. albicaulis*)	18.8 ± 22.5	0.75 ± 1.4	1.5 ± 3.2	42 ± 43	31.9 ± 21.3%	–
Yosemite (*P. albicaulis*)	7.4 ± 4.6	0.2 ± 0.21	0.23 ± 0.94	1.3 ± 8.1	8.2 ± 9.0%	–
Sequoia & Kings Canyon (*P. albicaulis*)	18.4 ± 24.4	2.1 ± 4.0	0.51 ± 1.9	0.77 ± 2.2	8.2 ± 7.1%	–
Sequoia & Kings Canyon (*P. balfouriana*)	23.8.4 ± 21.7	8.7 ± 8.6	0.12 ± 0.69	0	6.2 ± 7.0	–

Pests and Pathogens

Dwarf mistletoe was present in 46% of all plots in CRMO with an average of 7.4 infected trees/ha (Table 3). It was not found within the plots in any of the other parks. The presence of MPB and WPBR was wide-spread, but generally at low abundance (<2 trees/ha) with the exception of CRLA and LAVO where an average of 60 and 40 trees/ha, respectively, had signs of symptoms of WPBR. CRLA and LAVO also had a higher mean number of trees/ha with signs of MPB, but infestation was still relatively low compared to the other parks (<3 trees/ha). There was no sign of WPBR in limber pine in CRMO or foxtail pine in SEKI. Percent crown kill was highest in whitebark pine in CRLA (33%) and LAVO (32%). We did not collect crown kill data for limber pine, but found percent crown kill for whitebark pine and foxtail pine in SEKI and YOSE was generally low averaging less than 10% (Table 3, Figure 16).

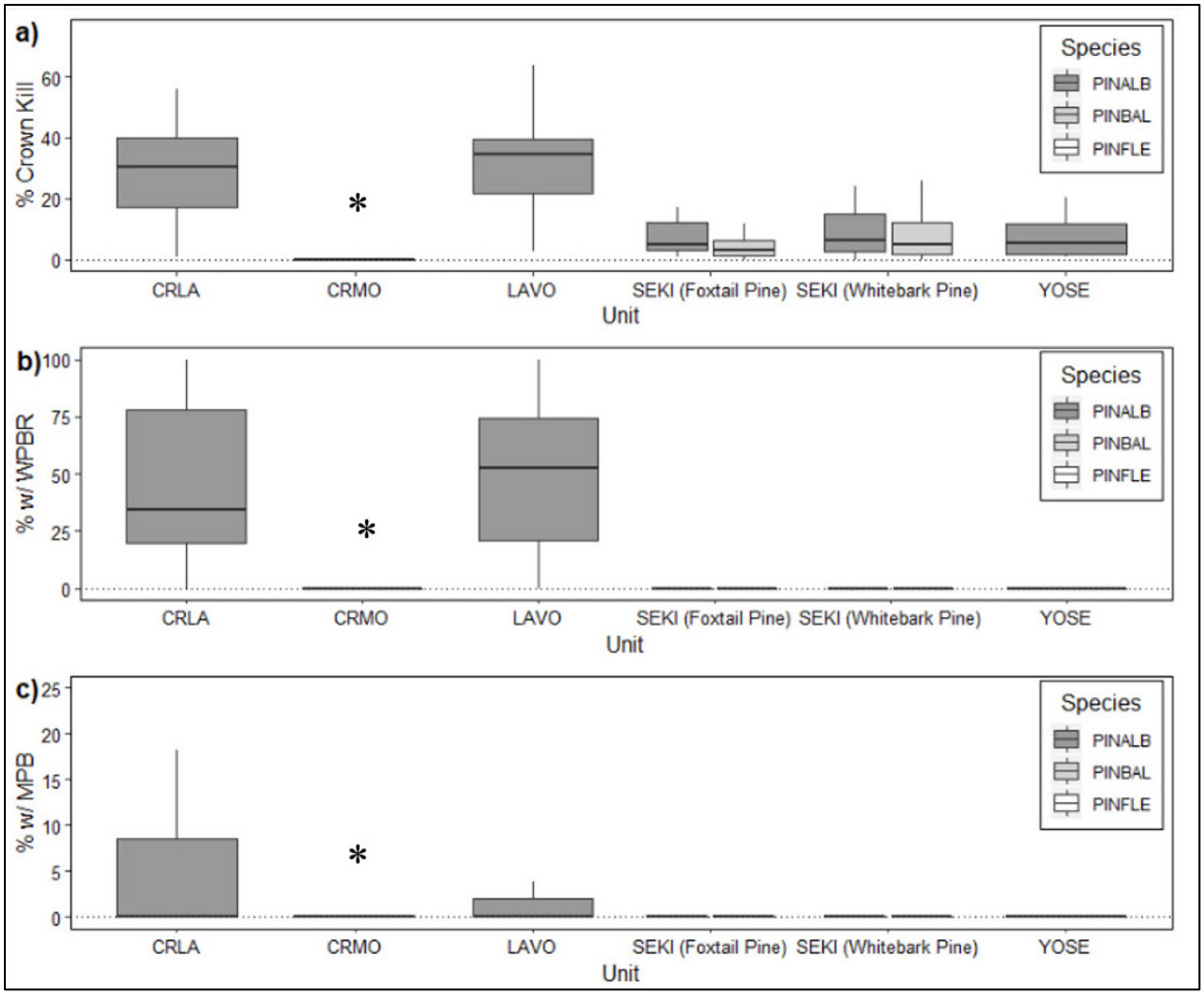


Figure 16. Pattern of crown kill (a), white pine blister rust (WPBR) infestation (b), and c) mountain pine beetle (MBP) infestation in five National Park Service units. "PINALB" is whitebark pine; "PINBAL" is foxtail pine; "PINFLE" is limber pine. **Note*: percent crown kill was only measured in CRMO in 2011.

Seedlings and cone production

Patterns of white pine seedling abundance and the presence of female cones varied among species and park units (Table 4). The frequency (i.e. the percent of plots where seedlings were present) of limber pine seedlings in CRMO was the highest of all species and study units (78%), but the average number of seedlings was only ~1 per plot. Seedlings of other species only occurred in 6% of the plots. Seedling frequency was approximately 40% for whitebark pine in CRLA, YOSE, and SEKI, but the average count of seedlings varied among parks. Whitebark pine seedling frequency in LAVO was relatively low (17%) compared to other parks. The frequency and average seedling count of foxtail pine in SEKI were both low compared to those of other species in other study units. Whitebark pine and foxtail pine in SEKI had the highest presence of female cones. Whitebark pine in CRLA had the lowest abundance of trees with female cones of all species and study units.

Table 4. Patterns of white pine seedling regeneration (20 to 136 cm tall) and number of trees with female cones from permanent 50 x 50 m plots in five National Park Service units. Regeneration sampling consists of nine, 3 x 3 m subplots evenly distributed across a 50 x 50 m plot. Frequency refers to the percent of plots where seedlings were present, followed by the average seedling count. The presence/absence of cones was recorded for all white pines in the 50 x 50 m plot, and are shown as # of trees and percentage of trees with standard deviations.

Study Site	frequency/average seedling count	other species frequency/average seedling count	# of trees with cones/ha	% of trees with cones/ha
Craters of the Moon (*P. flexilis*)	78% / 1.03	6% / 0.6	52.3 ± 63	60 ± 24
Crater Lake (*P. albicaulis*)	40% / 1.1	63% / 5.7	12.8 ± 21.8	7 ± 18
Lassen Volcanic (*P. albicaulis*)	17% / 0.16	60% / 5.2	29.3 ± 41	10 ± 13
Yosemite (*P. albicaulis*)	40% / 4.9	31% / 2.1	29.3 ± 41.3	35 ± 15
Sequoia & Kings Canyon (*P. albicaulis*)	41% / 5.5	29% / 0.88	128 ± 126	32 ± 14
Sequoia & Kings Canyon (*P. balfouriana*)	6% / 0.06	12% / 0.12	90 ± 69	56 ± 20

Discussion

This synthesis of data collected as part of a long-term monitoring protocol established in five national park units provides several insights into the status and conditions of populations of three white pine species across the western United States. We found a wide range of forest structures among the five study areas, with each species present at different density and basal area with varying abundance of other tree species. Our results indicate that whitebark pine health varies considerably across the range of study units, with higher snag density and a higher rate of white pine blister rust infection in CRLA and LAVO. Observations indicate that white pines are relatively healthy in the CRMO, YOSE, and SEKI where WPBR infection and MPB infestation were relatively low.

Geographic variability in forest structure

Stand structure (i.e. tree basal area and density) in these high-elevation woodlands and forests is relatively sparse compared to other warmer and moister forests of the western U.S., particularly in California and the Pacific Northwest where basal area may reach upwards of $\geq$70 m^2/ha with $\geq$3,000 trees per ha (Reilly and Spies 2015). In these high-elevation environments, growth and productivity are limited not only by moisture, but also by the length of the growing season and mechanical damage from wind, snow, and/or frost. The variability in stand structure among study units across moisture and temperature gradients demonstrate the potential diversity of biotic interactions (e.g., inter- and intra-specific competition) and climatic conditions these species can grow in across their ranges. Differences in forest structure among the species and study units are likely related to multiple factors including productivity, abundance of other tree species, longevity, and recent mortality associated with WPBR or MPB.

Structure of limber pine and foxtail pine stands differs considerably from whitebark pine stands in the study units. Despite the relatively cold and dry environment at high elevation in SEKI, the longevity of foxtail pine may contribute to the occurrence of the largest trees and highest levels of basal area of all study units and species. Low seedling density may be the result of moisture limitation, as well as recruitment limitation due to late season snow and other factors. Low levels of recruitment in foxtail pine have been documented in other studies as well (Lloyd 1997) and do not appear to be uncommon. On the contrary, limber pine had the lowest basal area and smallest trees in somewhat similarly dry but much warmer conditions. Limber pine trees in CRMO are growing on the periphery of the species range, found at the lowest elevations recorded for the species in the Rocky Mountains (Cleaver et al. 2015) and growing in a semi-arid environment. Temperatures are higher on average at these low elevation sites, and CRMO was shown to be hotter and drier than the other NPS units (Table 1). Soil can be scarce and trees are routinely found growing from cracks in the lava where surface temperatures can reach over 170° F (pers. communication Todd Stefanic).

Forest structure in whitebark pine plots in CRLA, LAVO, YOSE, and SEKI was relatively similar despite differences in climatic setting, but the relative abundance of whitebark pine compared to other co-occurring species varied considerably among park units. CRLA and LAVO are relatively warmer, and whitebark pine in these parks comprises much less of the total basal area and density, suggesting that these stands may experience greater interspecific competition with more shade

tolerant species (e.g., mountain hemlock). In SEKI and YOSE, in the colder more southern study units at higher elevations, other shade intolerant pine species make up a greater proportion of total basal area and density. Although there may be less intraspecific competition with other pine species in these units, they may act as host species for mountain pine beetle (Meyer et al. 2016).

Patterns of snag density, pathogen and insect infestation, and crown kill

Patterns of snag density, pathogen infection, MPB infestation, and crown kill differ considerably among units and species and are likely related to differences in temperature and precipitation, as well as site and species variability. Whitebark pine in the relatively warm and wetter CRLA and LAVO had more snags, as well as higher rates of infestation of WPBR and associated crown kill. These results are consistent with other studies documenting geographic patterns of WPBR that generally show that infection rates in the Cascade and Sierra Nevada Mountains decreases from north to south (Maloney 2011). Other studies from the northern part of whitebark pines range in Oregon, Idaho, and Wyoming found higher rates of WPBR infection on moist and colder sites (Larson 2011).

Only minor MPB activity was observed in white pines within the study units, as all sites averaged fewer than 3 trees/ha with symptoms of MPB. This is despite a historically severe drought that affected much of California (Griffin et al. 2014). While recent drought has been tied to increased beetle outbreaks and significant forest mortality across the western US (Williams et al. 2013; Anderegg et al. 2015), beetle-caused mortality in these subalpine systems remained low. However, Shanahan et al. (2016) found water deficit to be related to higher MPB kill in whitebark pine and warming temperatures also portend continued shifts in beetle dynamics across the range of whitebark pine (Bentz et al. 2016).

The number of trees infected with WPBR was much higher in CRLA and LAVO than in other study units. Other potential factors affecting whitebark pine in these parks include competition with other more shade tolerant species. Increased interspecific competition with shade tolerant species (e.g., mountain hemlock) may reduce available soil moisture and contribute to mortality. In the absence of biotic disturbance agents, physical factors related to weather (i.e. mechanical damage from wind and snow loading) appear to be the primary mechanism of mortality. The highest densities of snags in CRLA and LAVO occurred in the middle size classes. Higher mortality rates in intermediate size classes may also be related to competition with other species of conifers and larger more dominant whitebark pine.

Fire exclusion during the 20th century may be partially associated with increased density. Although high elevation subalpine forests in this region are primarily associated with a low frequency, high-severity fire regime, there is evidence whitebark pine stands also historically experienced some low severity fires and burned with a mean frequency of 49 years (Murray and Siderius 2018). Interruption of historical fire regimes has resulted in increased stand density in other high-elevation forest where whitebark pine is found (Dolanc et al. 2013), and likely had an even greater effect in more productive environments.

While limber pine and foxtail pine are both susceptible to WPBR and MPB, only MPB was found on these species in this study, and only infrequently. Signs of MPB remain low at CRMO and MPB

contributes minimally to the mortality of limber pine within the monitoring plots. The majority of dead limber pine with a recorded cause of death were killed by dwarf mistletoe, which was present in almost half of the plots. Some snags have been dead for many years and assigning a cause of death to these trees is often difficult or impossible. Limber pine in CRMO had the lowest density of snags, no doubt a direct result of having the lowest tree density and the low presence of other pests and pathogens. The lack of WPBR in CRMO suggests relatively good health of this species in this relatively isolated western part of its range. Foxtail pine snag density and basal area were both high compared to other species in other study units, yet both were low compared to live density and basal area of this species. Given the persistence of snags in cold, dry environments and the lack of WPBR related mortality in these populations of foxtail pine, these snags may be related to past mortality events as opposed to more recent events.

Cone production and regeneration patterns

Results from all sites consistently demonstrate the effects of tree size on the reproductive potential of individual trees. Across all species and studies areas, the production of female cones was significantly related to tree size (Jackson et al. 2015; Stucki et al. 2018; Nesmith et al. 2019). Although the number of trees/ha with cones varied among species and study units, most plots had at least some trees with cones. Despite the abundance of cones across most plots, regeneration appears to be quite variable and particularly sparse is some plots. The presence of cones suggests that seeds may generally be available for regeneration from a local source, but seedling establishment is rare. Recruitment limitation appears to be particularly high for foxtail pine which had the second highest number of trees/ha with cones, but the lowest frequency and count of seedlings. Lack of regeneration may have long-term implications of population structure and persistence, but the seedling densities we found occurred across a similar range as other studies that showed that populations of foxtail appear to be stable and have been over a long period of time. Recruitment is likely episodic and can be associated with mild, wet winters (Lloyd 1997).

Future Directions

The future re-measurements of these monitoring plots will offer great opportunities to further test findings from this synthesis, as well as compare with other studies across the range of white pines. The subsequent sampling events will provide an opportunity for assessment of temporal rates of structural change due specifically to growth, recruitment, and mortality. Thus, re-measurements will be an important component of assessing population health across species and study units through time. A better understanding of how fecundity varies among species and sites as well as over time will help inform modeling efforts. Future re-measures will allow more robust conclusions about associations between environmental changes and forest health and structure and the impact of warming temperatures on crown damage, growth rates, and pest and pathogen dynamics.

Conclusions

This report describes baseline findings of stand structure and composition, incidence of WPBR and MPB, reproduction, and regeneration, among three high-elevation white pine species in five separate national parks in northern and central California, southern Oregon, and central Idaho, and synthesizes these findings to provide comparisons between species and NPS units. Stand structure varied among species and park units. Whitebark pine structure and composition was variable and these plots often included shade tolerant species at relatively high densities. Limber and foxtail pines were generally found at lower density and with fewer other species, but foxtail pine reached the largest sizes and highest levels of basal area of all three taxa. Whitebark pine snags in CRLA and LAVO were associated with higher incidence of WPBR and MPB and occurred at much higher densities than in SEKI or YOSE. MPB was also observed in foxtail pine, but snags of these species were relatively rare and crown kill was generally very low. Neither WPBR nor MPB were observed in limber pine in CRMO. Future monitoring of white pine populations in western National Parks will provide much needed information on how these foundational high elevation ecosystems are changing across their range.

Literature Cited

Achuff, P. I. 1997. Special plant and landscape features of Waterton Lakes National Park. Alberta. Parks Canada, Waterton Lakes National Park.

Anderegg, W. R., J. A Hicke, R. A. Fisher, C. D. Allen, J. Aukema, B. Bentz, S. Hood, J. W. Lichstein, A. K. Macalady, N. McDowell, and Y. Pan. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208(3):674–683.

Arno, S. F. 2001. Community types and natural disturbance processes. Pages 74–88 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

Baumeister, D., and R. M. Callway. 2006. Facilitation by *Pinus flexilis* during succession: A hierarchy of mechanisms benefits other plant species. Ecology 87:1816–1830.

Bentz, B. J., J. P. Duncan, and J. A. Powell. 2016. Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate. Forestry 89(3):271–283.

Burns, K., J. Blodgett, M. Jackson, B. Howell, W. Jacobi, A. Schoettle, A. M. Casper, and J. Klutsch. 2011. Monitoring limber pine health in the Rocky Mountains and North Dakota. Pages 47–50 *in* R. E. Keane, D. F. Tomback, M. Murray, and C. M. Smith, editors. The future of high-elevation, five-needle white pines in western North America. Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, Montana. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. Available from http://www.fs.fed.us/rm/pubs/rmrs_p063.html [accessed 17 August 2016].

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.

Cleaver, C. M., W. R. Jacobi, K. S. Burns, and R. E. Means. 2015. Limber pine in the central and southern Rocky Mountains: stand conditions and interactions with blister rust, mistletoe, and bark beetles. Forest Ecology and Management 358:139–153.

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99–113.

Dolanc, C. R., J. H. Thorne, H. D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography 22: 264–276.

Eckert, A. J., and J. O. Sawyer. 2002. Foxtail pine importance and conifer diversity in the Klamath Mountains and southern Sierra Nevada, California. Madroño 49: 33–45.

Ellison, A. M., M. S. Bank, 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 3:479–486.

Griffin, D. and K. J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? Geophysical Research Letters 41(24):9017–9023.

Hatala, J. A., R. L. Crabtree, K. Q. Halligan, and P. R. Moorcroft. 2010. Landscape-scale patterns of forest pest and pathogen damage in the Greater Yellowstone Ecosystem. Remote Sensing of Environment 114:375–384.

Jackson, J., E. S. Jules, S. B. Smith, E. A. Sahara, and D. A. Sarr. 2015. Whitebark pine monitoring at Crater Lake and Lassen Volcanic National Parks: Fiscal years 2012–2014 project report. Natural Resource Report NPS/KLMN/NRR—2015/1052. National Park Service, Fort Collins, Colorado.

Jules, E. S., J. I. Jackson, S. B. Smith, J. C. B. Nesmith, L. A. Starcevich, and D. A. Sarr. 2017. Whitebark pine in Crater Lake and Lassen Volcanic National Parks: Initial assessment of stand structure and condition. Natural Resource Report NPS/KLMN/NRR—2017/1459. National Park Service, Fort Collins, Colorado.

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.

Keane, R. E., D. F. Tomback, C. A. Aubry, A. D. Bower, E. M. Campbell, C. L. Cripps, M. B. Jenkins, M. F. Mahalovich, M. Manning, S. T. McKinney, M. P. Murray, D. L. Perkins, D. P. Reinhart, C. Ryan, A. W. Schoettle, and C. M. Smith. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). General Technical Report RMRS-GTR-279. Fort Collins, Colorado: USDA, Forest Service, Rocky Mountain Research Station.

Keane, R. E., D. F. Tomback, M. P. Murray, and C. M. Smith, editors. 2011. The future of high-elevation, five-needle white pines in western North America. Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, Montana. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Kearns, H. S. J. 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 Forest Research. 37(2):462–472.

Kendall, K. C., D. Ayers, and D. Schirokauer. 1996. Limber pine status from Alberta to Wyoming. Nutcracker Notes 7:16–18.

Kipfmueller, K. F., and M. W. Salzer. 2010. Linear trend and climate response of five-needle pines in the western United States related to treeline proximity. Canadian Journal of Forest Research 40: 134–142.

Klutsch, J. G., B. A. Goodrich, and A. W. Schoettle. 2011. Limber pine forests on the leading edge of white pine blister rust distribution in northern Colorado. Pages 222–225 *in* R. E. Keane, D. F. Tomback, M. Murray, and C. M. Smith, editors. The future of high-elevation, five-needle white pines in western North America. Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, Montana. Proceedings RMRS-P-63. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. Available from http://www.fs.fed.us/rm/pubs/rmrs_p063.html [accessed 17 August 2016].

Lanner, Ronald M. 1999. Conifers of California. Cachuma Press. Los Olivos, California.

Larson, E. R. 2011. Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. Journal of Biogeography 38: 453–470.

Lloyd, A. H. 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. Canadian Journal of Forest Research 27:936–942.

Maloney, P. E. 2011. Incidence and distribution of white pine blister rust in the high-elevation forests of California. Forest Pathology 41:308–316.

Mathiasen, R. L., and F. G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science 34:429–440.

Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37(2):110–118.

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., B. A. Richardson, P. J. Zambino, N. B. Klopfenstein, and M. S. Kim. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North America: A first report. Forest Pathology 36:73–82.

McGaughey, W., and W. C. Schmidt. 2001. Taxonomy, distribution, and history. Pages 29–40 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, DC.

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: Implications for sustaining a high-elevation ecosystem. Ecological Applications 19:597–607.

McKinney, S. T., T. Rodhouse, L. Chow, A. Chung-MacCoubrey, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, D. Sarr, and L. A. Starcevich. 2012. 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 Resource Report NPS/PWR/NRR—2012/532. National Park Service, Fort Collins, Colorado.

Meyer, M. D., B. Bulaon, M. MacKenzie, and H. D. Safford. 2016. Mortality, structure, and regeneration in whitebark pine stands impacted by mountain pine beetle in the southern Sierra Nevada. Canadian Journal of Forest Research 46(4):572–581.

Millar, C. I., R. D. Westfall, D. L. Delany, M. J. Bokach, A. L. Flint, and L. E. Flint. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA: Influence of environmental context, bark beetles, climatic water deficit, and warming. Canadian Journal of Forest Research 42:749–765.

Murray, M. P., and J. Siderius. 2018. Historic frequency and severity of fire in whitebark pine forests of the Cascade Mountain Range. USA. Forests 9:78: doi:10.3390/f9020078.

Nesmith, J. C. B., M. Wright, E. S. Jules, and S. T. McKinney. 2019. Whitebark and foxtail pines in Yosemite, Sequoia, and Kings Canyon National Parks: Initial assessment of stand structure and condition. Forests 10: 35 doi:10.3390/f10010035.

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

Reilly, M. J. and T. A. Spies. 2015. Regional variation in forest structure and development in Oregon, Washington, and inland northern California, USA. Ecosphere 6(10):1–27. http://dx.doi.org/10.1890/ES14-00469.1

Schoettle, A. W. 2004*a*. Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of non-native pathogen. Pages 146–155 *in* Siilviculture in Special Places: Proceedings of the 2003 National Silviculture Workshop. US For. Serv. Proc. RMRS-P-34. Available from http://www.fs.fed.us/rm/pubs/rmrs_p034.html [accessed 17 August 2016].

Schoettle, A. W. 2004*b*. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. Pages 124–135 *in* Breeding and genetic resources of five-needle pines: Growth, adaptability, and pest resistance. US For. Ser. Proc. RMRS-P-32. Available from http://www.fs.fed.us/rm/pubs/rmrs_p032.html [accessed 17 August 2016].

Schoettle, A. W., K. S. Burns, S. Costello, J. Witcosky, B. Howell, and J. Connor. 2008. A race against beetles: conservation of limber pine. Nutcracker Notes 14:11–12.

Schulman, E. and C. W. Ferguson 1956. Millennia-old pine trees sampled in 1954 and 1955. Pages 136–138 *in* Dendroclimatic Changes in Semiarid America. The University of Arizona Press, Tucson, Arizona.

Shanahan, E., K. M. Irvine, D. Thoma, S. Wilmoth, A. Ray, K. Legg, and H. Shovic. 2016. Whitebark pine mortality related to white pine blister rust, mountain pine beetle outbreak, and water availability. Ecosphere 7(12):e01610. 10.1002/ecs2.1610

Smith, C. M., B. Shepherd, C. Gillies, and J. Stuart-Smith. 2013. Changes in blister rust infection and mortality in whitebark pine over time. Canadian Journal of Forest Research 43:90–96.

Steele, R. 1990. *Pinus flexilis* James. In Silvics of North America. Vol. 1. Conifers. R. M. Burns and B. H. Honkala (*Tech. coords*.). USDA Agric. Handb. No. 654:348–354.

Stevens Jr, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of American Statistical Association 99:262–278.

Stucki, D. S., J. I. Jackson, and E. S. Jules. 2018. Limber pine monitoring at Craters of the Moon National Monument and Preserve: Observations and results from 2011–2013. Natural Resource Report NPS/UCBN/NRR—2018/1823. National Park Service, Fort Collins, Colorado.

Taylor, J. E. and R. L. Mathiasen. 1999. Limber Pine Dwarf Mistletoe. Forest Insect and Disease Leaflet No. 171. USDA Forest Service, Northern Region, Missoula, Montana.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. Journal of Ecology 51: 451–467.

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: ecology and restoration. Island Press, Washington, DC.

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.

Weaver, T. 2001. Whitebark pine and its environment. Pages 41–73 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC.

Webster, K. L. and E. A. Johnson. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecoscience 7:175–182.

Williams, A. P., C. D.Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam, S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and N. G. Mcdowell. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3(3):292.

Woodhouse, C. A., G. T. Pederson, and S. T. Gray. 2011. An 1800-yr record of decadal-scale hydroclimatic variability in the upper Arkansas River basin from bristlecone pine. Quaternary Research 75: 483–490.

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

Appendix A: Location Information and Site Characteristics for White Pine Monitoring Plots

Table A1. Location information and site characteristics for white pine monitoring plots in Craters of the Moon (CRMO), Lassen Volcanic (LAVO), Crater Lake (CRLA), Yosemite (YOSE), and Sequoia & Kings Canyon (SEKI). Plots with recorded aspect and slope values of 0° represent relatively flat or undulating lava flow terrains with no apparent overall slope or aspect. Aspect for these locations are represented with a -1.

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
CRMO	CRMO_North_17	5.7	296.6	1647	-1	0
CRMO	CRMO_North_109	5.7	296.6	1647	-1	0
CRMO	CRMO_North_1	5.7	296.6	1647	-1	0
CRMO	CRMO_North_9	5.7	280.4	1646	210	0
CRMO	CRMO_North_2	5.7	302.9	1647	-1	0
CRMO	CRMO_North_149	5.7	296.6	1647	-1	0
CRMO	CRMO_North_61	5.7	302.9	1647	-1	0
CRMO	CRMO_North_5	5.7	290.0	1647	-1	0
CRMO	CRMO_North_101	5.7	286.2	1647	-1	0
CRMO	CRMO_North_13	5.7	274.6	1641	-1	0
CRMO	CRMO_North_21	5.7	291.2	1647	-1	0
CRMO	CRMO_North_37	5.7	291.2	1647	-1	0
CRMO	CRMO_North_53	5.7	291.2	1647	-1	0
CRMO	CRMO_North_122	5.8	269.2	1641	-1	0
CRMO	CRMO_North_110	5.8	269.2	1641	-1	0
CRMO	CRMO_North_93	5.7	280.3	1641	-1	0
CRMO	CRMO_North_69	5.7	280.3	1641	-1	0
CRMO	CRMO_North_117	5.7	280.3	1641	-1	0
CRMO	CRMO_North_56	5.9	376.8	1773	25	9
CRMO	CRMO_North_79	5.7	376.0	1792	23	9
CRMO	CRMO_North_83	5.7	385.4	1815	231	12
CRMO	CRMO_North_27	5.5	388.4	1876	15	26
CRMO	CRMO_North_104	5.9	372.6	1744	-1	0
CRMO	CRMO_North_151	5.9	378.1	1761	158	3
CRMO	CRMO_North_4	5.8	381.4	1810	358	16
CRMO	CRMO_North_95	5.9	375.6	1749	140	1

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
CRMO	CRMO_North_47	5.7	381.6	1827	32	11
CRMO	CRMO_North_63	5.9	375.6	1750	330	0
CRMO	CRMO_North_20	5.9	375.6	1750	90	0
CRMO	CRMO_North_112	5.9	378.1	1750	225	0
CRMO	CRMO_North_100	5.9	375.6	1751	326	1
CRMO	CRMO_North_8	5.9	378.1	1768	65	9
CRMO	CRMO_North_124	5.9	378.1	1750	70	0
CRMO	CRMO_North_76	5.9	375.6	1751	97	6
CRMO	CRMO_North_52	5.9	375.6	1751	80	0
CRMO	CRMO_North_116	5.9	378.1	1756	240	0
CRMO	CRMO_North_92	5.9	378.1	1758	0	3
CRMO	CRMO_North_59	5.7	381.6	1823	143	9
CRMO	CRMO_North_147	5.6	383.2	1852	2	13
CRMO	CRMO_North_24	5.8	381.4	1768	112	2
CRMO	CRMO_North_43	5.7	381.6	1815	142	2
CRMO	CRMO_North_36	5.9	375.6	1750	69	0
CRMO	CRMO_North_31	5.7	383.8	1817	16	5
CRMO	CRMO_North_40	5.9	377.3	1773	35	4
CRMO	CRMO_North_156	5.7	379.8	1813	21	14
CRMO	CRMO_North_88	5.9	377.3	1764	66	3
CRMO	CRMO_North_71	5.7	383.8	1868	299	16
CRMO	CRMO_North_11	5.7	383.4	1806	147	3
CRMO	CRMO_North_159	5.6	380.8	1811	231	1
CRMO	CRMO_North_67	5.8	379.6	1812	117	1
CRMO	CRMO_North_15	5.6	381.5	1906	103	13
CRMO	CRMO_North_107	5.6	381.5	1843	73	22
CRMO	CRMO_North_119	5.6	380.8	1876	240	6
CRMO	CRMO_North_7	5.6	381.5	1820	193	21
CRMO	CRMO_North_58	5.7	379.8	1835	128	9
CRMO	CRMO_North_42	5.9	374.4	1769	-1	0
CRMO	CRMO_North_6	5.9	369.3	1763	28	3
CRMO	CRMO_North_90	5.9	372.5	1772	142	2
CRMO	CRMO_North_114	5.9	368.0	1752	54	3

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
CRMO	CRMO_North_22	5.9	368.0	1763	76	1
CRMO	CRMO_North_66	5.9	373.1	1775	-1	0
CRMO	CRMO_North_14	5.9	376.2	1786	78	5
CRMO	CRMO_North_78	5.9	373.1	1775	-1	0
CRMO	CRMO_North_35	5.9	373.1	1774	267	0
CRMO	CRMO_North_115	5.9	376.2	1786	11	16
CRMO	CRMO_North_75	5.9	373.1	1775	135	0
CRMO	CRMO_North_123	5.9	371.1	1777	337	11
CRMO	CRMO_North_94	5.9	376.2	1785	67	6
CRMO	CRMO_North_87	5.9	373.1	1796	102	3
CRMO	CRMO_North_19	5.9	373.1	1769	-1	0
CRMO	CRMO_North_99	5.7	371.2	1774	325	2
CRMO	CRMO_North_3	5.7	373.9	1820	341	6
CRMO	CRMO_North_51	5.7	371.2	1797	11	9
CRMO	CRMO_North_103	5.7	373.9	1804	223	5
CRMO	CRMO_North_150	5.3	372.8	1957	5	20
CRMO	CRMO_North_62	5.3	372.8	1854	187	6
CRMO	CRMO_North_111	5.7	373.9	1830	281	6
CRMO	CRMO_North_82	5.7	373.9	1846	317	4
CRMO	CRMO_North_55	5.9	374.3	1780	302	8
CRMO	CRMO_North_91	5.7	373.9	1815	282	7
CRMO	CRMO_North_30	5.7	373.9	1841	220	11
CRMO	CRMO_North_118	5.7	373.9	1871	141	6
CRMO	CRMO_North_64	6.1	345.0	1691	150	0
CRMO	CRMO_North_152	6.1	342.4	1690	219	1
CRMO	CRMO_North_96	6.2	342.6	1695	-1	0
CRMO	CRMO_North_48	6.2	342.6	1695	141	0
CRMO	CRMO_North_60	6.2	346.5	1696	-1	0
CRMO	CRMO_North_16	6.3	346.3	1675	163	2
CRMO	CRMO_North_44	6.3	331.2	1616	325	0
CRMO	CRMO_North_28	6.4	341.3	1665	79	2
CRMO	CRMO_North_12	6.4	337.6	1662	180	3
CRLA	CRLA_Alpine_CRWB25	2.7	1667.3	2157	1	10

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
CRLA	CRLA_Alpine_CRWB41	3.1	1708.3	2096	287	2
CRLA	CRLA_Alpine_CRWB02	3.3	1701.8	2087	295	3
CRLA	CRLA_Alpine_CRWB05	3.1	1708.3	2144	296	9
CRLA	CRLA_Alpine_CRWB45	2.9	1753.1	2117	335	8
CRLA	CRLA_Alpine_CRWB49	2.7	1704.4	2227	289	10
CRLA	CRLA_Alpine_CRWB29	2.9	1753.1	2135	295	7
CRLA	CRLA_Alpine_CRWB21	2.7	1704.4	2370	310	9
CRLA	CRLA_Alpine_CRWB01	4.0	997.7	2077	142	11
CRLA	CRLA_Alpine_CRWB06	2.8	1792.7	2360	60	8
CRLA	CRLA_Alpine_CRWB50	2.8	1809.3	2310	331	17
CRLA	CRLA_Alpine_CRWB23	3.5	1026.0	2296	70	10
CRLA	CRLA_Alpine_CRWB24	3.2	1079.3	2199	335	17
CRLA	CRLA_Alpine_CRWB08	3.2	1079.3	2272	329	3
CRLA	CRLA_Alpine_CRWB51	2.7	1060.2	2408	343	17
CRLA	CRLA_Alpine_CRWB03	3.4	1123.0	2285	198	14
CRLA	CRLA_Alpine_CRWB44	3.2	1123.9	2332	234	13
CRLA	CRLA_Alpine_CRWB28	3.2	1123.9	2293	229	4
CRLA	CRLA_Alpine_CRWB30	3.2	1118.0	2254	161	5
CRLA	CRLA_Alpine_CRWB07	3.3	1187.9	2238	64	5
CRLA	CRLA_Alpine_CRWB46	3.4	1162.6	2202	233	4
CRLA	CRLA_Alpine_CRWB04	3.5	1134.3	2192	343	4
CRLA	CRLA_Alpine_CRWB26	3.5	1136.8	2193	156	4
CRLA	CRLA_Alpine_CRWB42	3.5	1134.3	2199	126	3
CRLA	CRLA_Alpine_CRWB22	3.1	1594.1	2390	211	18
CRLA	CRLA_Alpine_CRWB11	3.1	1486.0	2272	237	13
CRLA	CRLA_Alpine_CRWB47	3.3	1439.8	2367	174	24
CRLA	CRLA_Alpine_CRWB10	3.2	1632.8	2293	223	8
CRLA	CRLA_Alpine_CRWB27	3.3	1418.2	2284	126	12
CRLA	CRLA_Alpine_CRWB43	2.9	1505.2	2319	95	6
LAVO	LAVO_Alpine_LVWB39	4.0	3099.6	2642	247	17
LAVO	LAVO_Alpine_LVWB11	2.3	3172.6	2782	189	28
LAVO	LAVO_Alpine_LVWB31	4.2	3077.6	2697	34	12
LAVO	LAVO_Alpine_LVWB32	3.3	3131.8	2675	178	11

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
LAVO	LAVO_Alpine_LVWB44	4.4	2956.8	2613	53	9
LAVO	LAVO_Alpine_LVWB47	4.2	3077.6	2634	117	6
LAVO	LAVO_Alpine_LVWB48	4.3	3067.7	2671	147	13
LAVO	LAVO_Alpine_LVWB60	4.4	2927.2	2623	185	8
LAVO	LAVO_Alpine_LVWB24	4.4	2927.2	2565	111	11
LAVO	LAVO_Alpine_LVWB28	4.3	3067.7	2648	159	1
LAVO	LAVO_Alpine_LVWB08	4.4	2927.2	2564	9	2
LAVO	LAVO_Alpine_LVWB12	4.4	2927.2	2599	126	6
LAVO	LAVO_Alpine_LVWB22	4.2	3077.6	2647	197	14
LAVO	LAVO_Alpine_LVWB51	4.4	2927.2	2594	118	6
LAVO	LAVO_Alpine_LVWB56	4.4	2927.2	2587	125	4
LAVO	LAVO_Alpine_LVWB59	4.2	3077.6	2716	163	20
LAVO	LAVO_Alpine_LVWB34	4.4	3138.3	2583	179	21
LAVO	LAVO_Alpine_LVWB42	4.4	3138.3	2579	109	14
LAVO	LAVO_Alpine_LVWB07	4.3	3067.7	2568	92	12
LAVO	LAVO_Alpine_LVWB23	4.3	3067.7	2569	95	13
LAVO	LAVO_Alpine_LVWB05	4.8	2732.0	2657	188	15
LAVO	LAVO_Alpine_LVWB10	4.8	2732.0	2627	159	25
LAVO	LAVO_Alpine_LVWB49	4.8	2732.0	2625	157	16
LAVO	LAVO_Alpine_LVWB54	4.7	2838.8	2593	181	26
LAVO	LAVO_Alpine_LVWB06	4.3	2857.1	2647	252	14
LAVO	LAVO_Alpine_LVWB09	4.5	2731.9	2528	113	11
LAVO	LAVO_Alpine_LVWB35	4.3	2857.1	2657	66	14
LAVO	LAVO_Alpine_LVWB14	4.4	2919.1	2607	161	4
LAVO	LAVO_Alpine_LVWB30	4.6	2892.8	2579	230	15
LAVO	LAVO_Alpine_LVWB03	4.8	2878.2	2619	147	15
YOSE_PINALB	YOSE_PINALB_44	1.1	1730.0	3112	244	9
YOSE_PINALB	YOSE_PINALB_16	2.0	1702.3	3022	279	9
YOSE_PINALB	YOSE_PINALB_32	1.9	1449.1	2907	350	21
YOSE_PINALB	YOSE_PINALB_60	2.7	1628.4	2878	230	11
YOSE_PINALB	YOSE_PINALB_53	2.0	1542.5	2845	346	14
YOSE_PINALB	YOSE_PINALB_21	2.3	1325.2	2880	228	11
YOSE_PINALB	YOSE_PINALB_18	1.8	1133.2	3113	279	17

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
YOSE_PINALB	YOSE_PINALB_25	2.3	1067.3	2899	177	14
YOSE_PINALB	YOSE_PINALB_41	2.1	1082.4	3025	320	17
YOSE_PINALB	YOSE_PINALB_54	1.3	1202.2	3228	130	8
YOSE_PINALB	YOSE_PINALB_55	2.0	1120.4	3033	107	15
YOSE_PINALB	YOSE_PINALB_10	2.0	1058.8	2970	242	6
YOSE_PINALB	YOSE_PINALB_26	1.9	1074.9	2992	170	19
YOSE_PINALB	YOSE_PINALB_42	2.2	1075.2	2958	230	6
YOSE_PINALB	YOSE_PINALB_6	2.4	1600.4	3083	284	12
YOSE_PINALB	YOSE_PINALB_38	2.1	1164.9	3131	41	12
YOSE_PINALB	YOSE_PINALB_14	2.0	1088.2	2732	225	15
YOSE_PINALB	YOSE_PINALB_22	1.7	1166.5	3209	248	9
YOSE_PINALB	YOSE_PINALB_7	3.3	1290.3	2993	283	12
YOSE_PINALB	YOSE_PINALB_19	1.0	1250.0	3394	65	10
YOSE_PINALB	YOSE_PINALB_35	2.0	1103.8	3077	237	15
YOSE_PINALB	YOSE_PINALB_46	1.6	1098.0	2906	352	10
YOSE_PINALB	YOSE_PINALB_31	2.2	1101.6	3279	126	30
YOSE_PINALB	YOSE_PINALB_15	1.8	1113.8	3210	201	3
YOSE_PINALB	YOSE_PINALB_4	2.0	1102.2	3191	235	10
YOSE_PINALB	YOSE_PINALB_51	1.6	1156.6	3166	179	9
YOSE_PINALB	YOSE_PINALB_43	1.8	1119.9	3077	259	12
YOSE_PINALB	YOSE_PINALB_3	1.0	1148.0	3361	274	9
YOSE_PINALB	YOSE_PINALB_40	1.4	1176.1	3353	172	6
YOSE_PINALB	YOSE_PINALB_8	1.7	1141.3	3235	303	11
YOSE_PINALB	YOSE_PINALB_24	1.9	1241.3	3099	23	18
YOSE_PINALB	YOSE_PINALB_52	2.7	1086.3	3026	238	6
YOSE_PINALB	YOSE_PINALB_36	1.8	1560.9	3359	213	17
YOSE_PINALB	YOSE_PINALB_20	2.3	1588.0	3100	39	7
YOSE_PINALB	YOSE_PINALB_56	2.9	1418.7	3168	194	17
SEKI_PINALB	SEKI_PINALB_33	1.4	1069.0	3537	193	15
SEKI_PINALB	SEKI_PINALB_2	0.3	1148.3	3355	248	9
SEKI_PINALB	SEKI_PINALB_45	1.9	914.2	3030	21	20
SEKI_PINALB	SEKI_PINALB_18	-0.1	1195.9	3413	222	22
SEKI_PINALB	SEKI_PINALB_13	1.6	940.4	3357	47	14

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
SEKI_PINALB	SEKI_PINALB_25	1.2	1037.1	3287	188	10
SEKI_PINALB	SEKI_PINALB_49	1.1	1144.1	3379	265	4
SEKI_PINALB	SEKI_PINALB_38	3.5	1351.3	3261	183	29
SEKI_PINALB	SEKI_PINALB_5	1.3	1069.6	3373	159	13
SEKI_PINALB	SEKI_PINALB_73	2.9	991.7	3160	58	22
SEKI_PINALB	SEKI_PINALB_15	2.0	850.8	3272	116	19
SEKI_PINALB	SEKI_PINALB_28	2.3	961.1	3161	291	14
SEKI_PINALB	SEKI_PINALB_59	1.3	1037.3	3382	187	23
SEKI_PINALB	SEKI_PINALB_66	2.7	1055.7	3182	328	12
SEKI_PINALB	SEKI_PINALB_24	3.3	1117.8	3023	348	9
SEKI_PINALB	SEKI_PINALB_44	1.7	1035.8	3257	287	8
SEKI_PINALB	SEKI_PINALB_4	1.6	956.7	3286	253	9
SEKI_PINALB	SEKI_PINALB_20	2.3	1111.3	3254	124	13
SEKI_PINALB	SEKI_PINALB_52	2.9	766.1	3159	259	22
SEKI_PINALB	SEKI_PINALB_12	2.4	1352.7	3228	220	12
SEKI_PINALB	SEKI_PINALB_31	3.4	717.9	3212	320	22
SEKI_PINALB	SEKI_PINALB_78	2.1	1391.5	3334	250	9
SEKI_PINALB	SEKI_PINALB_68	1.8	1393.8	3343	236	15
SEKI_PINALB	SEKI_PINALB_48	4.4	1177.6	3140	154	24
SEKI_PINBAL	SEKI_PINBAL_44	3.1	921.3	3129	53	37
SEKI_PINALB	SEKI_PINALB_3	2.5	1052.8	3240	250	13
SEKI_PINALB	SEKI_PINALB_11	2.1	1059.2	3327	102	29
SEKI_PINALB	SEKI_PINALB_74	0.5	989.2	3570	215	25
SEKI_PINALB	SEKI_PINALB_43	0.4	1111.7	3625	206	23
SEKI_PINALB	SEKI_PINALB_27	2.2	764.6	3269	85	23
SEKI_PINBAL	SEKI_PINBAL_40	2.7	999.1	3160	10	14
SEKI_PINALB	SEKI_PINALB_51	1.6	1051.6	3336	219	12
SEKI_PINALB	SEKI_PINALB_51	1.6	1051.6	3336	219	12
SEKI_PINALB	SEKI_PINALB_58	1.7	973.7	3338	347	13
SEKI_PINBAL	SEKI_PINBAL_16	4.0	832.0	3038	97	6
SEKI_PINBAL	SEKI_PINBAL_24	3.2	866.7	3020	272	23
SEKI_PINBAL	SEKI_PINBAL_36	1.0	743.4	3504	273	14
SEKI_PINBAL	SEKI_PINBAL_7	1.3	734.9	3452	179	11

Site	Location_Name	Annual Temp. (°F)	Annual Precip. (mm)	Elevation (meters)	Aspect (degrees)	Slope (degrees)
SEKI_PINBAL	SEKI_PINBAL_23	1.4	695.8	3483	115	3
SEKI_PINBAL	SEKI_PINBAL_39	1.6	694.4	3445	247	8
SEKI_PINBAL	SEKI_PINBAL_27	2.9	648.6	3320	40	18
SEKI_PINBAL	SEKI_PINBAL_11	2.1	597.5	3080	336	28
SEKI_PINBAL	SEKI_PINBAL_35	1.8	694.7	3388	213	23
SEKI_PINBAL	SEKI_PINBAL_19	2.0	759.6	3300	335	8
SEKI_PINBAL	SEKI_PINBAL_26	2.1	668.0	3347	333	1
SEKI_PINBAL	SEKI_PINBAL_18	2.7	564.1	3059	325	19
SEKI_PINBAL	SEKI_PINBAL_3	1.8	1019.8	3257	246	23
SEKI_PINBAL	SEKI_PINBAL_22	1.3	785.8	3384	108	2
SEKI_PINBAL	SEKI_PINBAL_6	3.0	609.4	3061	213	19
SEKI_PINBAL	SEKI_PINBAL_30	1.4	746.2	3387	145	12
SEKI_PINBAL	SEKI_PINBAL_43	1.4	692.4	3412	295	20
SEKI_PINBAL	SEKI_PINBAL_2	3.4	521.9	3020	182	5
SEKI_PINBAL	SEKI_PINBAL_10	1.9	632.7	3222	271	3
SEKI_PINBAL	SEKI_PINBAL_31	0.9	682.6	3404	312	8
SEKI_PINBAL	SEKI_PINBAL_38	2.8	598.0	3088	355	20
SEKI_PINBAL	SEKI_PINBAL_33	1.4	633.2	3400	312	22
SEKI_PINBAL	SEKI_PINBAL_41	4.5	773.9	2887	153	6
SEKI_PINBAL	SEKI_PINBAL_29	1.4	1124.7	3257	167	20
SEKI_PINBAL	SEKI_PINBAL_9	2.0	640.8	3347	24	19
SEKI_PINBAL	SEKI_PINBAL_21	3.9	482.5	3067	309	19
SEKI_PINBAL	SEKI_PINBAL_25	3.7	773.0	3121	22	23
SEKI_PINBAL	SEKI_PINBAL_17	3.4	1015.6	3097	101	14
SEKI_PINBAL	SEKI_PINBAL_37	3.3	557.7	3235	329	24
SEKI_PINBAL	SEKI_PINBAL_1	3.5	1046.3	3091	320	18

The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

NPS 963/178192, January 2022



Natural Resource Stewardship and Science
1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525