PROJECT MUSE®

Restoring Whitebark Pine Forests of the Northern Rocky Mountains, USA

Robert E. Keane, Russell A. Parsons

Ecological Restoration, Volume 28, Number 1, March 2010, pp. 56-70
(Article)

Published by University of Wisconsin Press

➔ For additional information about this article

<https://muse.jhu.edu/article/382360>

Restoring Whitebark Pine Forests of the Northern Rocky Mountains, USA

Robert E. Keane and Russell A. Parsons

ABSTRACT

Whitebark pine (*Pinus albicaulis*) has been declining across much of its range in North America because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) epidemics, fire exclusion policies, and widespread exotic blister rust infections. Whitebark pine seed is dispersed by a bird, the Clark's nutcracker (*Nucifraga columbiana*), which caches in open, pattern-rich landscapes created by fire. This study was initiated in 1993 to investigate the effects of various restoration treatments on tree populations, fuel dynamics, and vascular plant cover on five sites in the U.S. northern Rocky Mountains. The objective of this study was to restore whitebark pine ecosystems using treatments that emulate the native fire regime—primarily combinations of prescribed fire, silvicultural cuttings, and fuel enhancement cuttings. The main effects assessed included tree mortality, fuel consumption, and vegetation response measured just prior to the treatment, one year after the treatment(s), and five years posttreatment. While all treatments that included prescribed fire created suitable nutcracker caching habitat, with many birds observed caching seed in the burned areas, there has yet to be significant regeneration in whitebark pine. All burn treatments resulted in high mortality in both whitebark pine and subalpine fir (> 40%). Fine woody fuel loadings marginally decreased after fire, but coarse woody debris more than doubled because of falling snags. Vascular species decreased in cover by 20% to 80% and remained low for five years. While the treatments were successful in creating conditions that favor whitebark pine regeneration, the high level of blister rust mortality in surrounding seed sources has reduced available seed, which then forced the nutcracker to reclaim most of the cached seed. Manual planting of whitebark pine seedlings is required to adequately restore these sites. A set of management guidelines is presented to guide restoration efforts.

Keywords: ecosystem restoration, fire regime, postfire vegetation response, tree mortality, whitebark pine (*Pinus albicaulis*)

Whitebark pine (*Pinus albicaulis*) forests are declining across most of its range in North America because of the combined effects of three factors (Arno 1986, Kendall and Keane 2001). This species is found in the high elevations of the Rocky Mountains from Banff National Park in central Alberta to the Wind River Range in Wyoming, and along the spine of the Cascades and Sierra Nevada mountains of the Pacific Northwest. First, there have been several major mountain pine beetle (*Dendroctonus ponderosae*) outbreaks that have killed many cone-bearing whitebark pine trees over 20 cm in diameter at breast

height (Arno 1986, Waring and Six 2005). The effects of an extensive and successful fire-exclusion management policy since the 1930s have also reduced the area burned in whitebark pine forests, resulting in a decrease of suitable conditions for whitebark pine regeneration (Keane and Arno 1993, Kendall and Keane 2001). Finally, the introduction of the exotic fungus white pine blister rust (*Cronarium ribicola*) to the western United States circa 1910 has killed many five-needle pine trees, and whitebark pine is one of the most susceptible to the disease (Hoff et al. 1980, Keane and Arno 1993, Murray et al. 1995, Kendall and Keane 2001). The cumulative effects of these three agents have resulted in a rapid decrease in mature whitebark pine over the last 20 years, especially in the more mesic parts of its range

(Keane and Arno 1993). What's more, predicted changes in northern Rocky Mountain climate brought about by global warming could further exacerbate whitebark pine decline by increasing the frequency and duration of beetle epidemics, blister rust infections, and severe wildfires (Logan and Powell 2001, Blaustein and Dobson 2006, Running 2006).

The loss of whitebark pine could have serious consequences for upper subalpine ecosystems of the northern Rocky Mountains and Cascades of the United States because it is considered a keystone species (Mills et al. 1993, Tomback et al. 2001). Whitebark pine forests cover a major portion (approximately 10%–15%) of the northern Rocky Mountain forested landscape (Keane 2000, Tomback et al. 2001). This "stone" pine

produces large, wingless seeds that are an important food source for over 110 animal species (Kendall and Arno 1990, Hutchins 1994). In the Yellowstone ecosystem, the endangered grizzly bear (*Ursus arctos horribilis*) depends on whitebark pine seeds as a major food source (Mattson and Reinhart 1990, Mattson et al. 1991, Mattson and Reinhart 1997), which it raids from red squirrel (*Tamiasciurus hudsonicus*) middens (Ferner 1974). Whitebark pine inhabits severe high-elevation environments where it is the only tree species that can exist—thereby protecting snowpack and delaying snowmelt, which reduces the potential for flooding and provides high-quality water into the summer (Hann 1990). While whitebark pine is not highly valued as a timber species because of its diminutive size and its remote locations (Chew 1990, Eggers 1990), it has great value as a recreational resource because of its pleasing aesthetic qualities such as twisted growth forms and open, park-like forests (Cole 1990). The restoration of the dwindling whitebark pine is critically important to high-elevation ecosystems and the numerous species that depend on it for existence (Tomback et al. 2001, Aubry et al. 2008).

In this paper, we present the results of an extensive, long-term study called “Restoring Whitebark Pine Ecosystems,” in which we investigated the effects of several types of ecosystem restoration treatments implemented on five high-elevation sites in the northern Rocky Mountains of the United States. These treatments were primarily combinations of prescribed fire and silvicultural cuttings implemented across 20 treatment units (Keane et al. 2000, Keane and Arno 2001). The main effects assessed included fuel consumption, tree mortality, and vegetation measured at three times: pretreatment, and one and five years posttreatment.

Detailed pictorial, anecdotal, and statistical summaries of measurements and observations for each treatment unit over time have been

recently published (Keane and Parsons 2010). In this article, we present a comprehensive comparison of treatment effects for seven major treatment types across the five sites, which is not presented in the Keane and Parsons (2010) report. Results from this study can be used to plan, design, and implement treatments to restore this keystone ecosystem. To our knowledge, this is the only research study concerning restoration in whitebark pine forests in North America to date.

Whitebark Pine Ecology

It is important to have a general knowledge of whitebark pine ecology to understand the purpose of our restoration treatments and to interpret the effects. Whitebark pine is a long-lived, seral tree of moderate shade tolerance (Minore 1979). It can live well over 400 years (one tree is more than 1,300 years old), but in the northern areas of its range (Arno and Hoff 1990, Keane 2001) it is often eventually replaced, in the absence of fire, mainly by the shade-tolerant subalpine fir (*Abies lasiocarpa*), but also by Engelmann spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*). Lodgepole pine (*Pinus contorta*) can outcompete whitebark pine during early successional stages in some subalpine forests, but both species often share dominance in upper subalpine forests (Day 1967, Mattson and Reinhart 1990, Arno et al. 1993). It can take approximately 50 to 250 years for subalpine fir to replace whitebark pine in the overstory, depending on tree densities, local environment, and previous fire history (Arno and Weaver 1990, Keane 2001).

The Clark’s nutcracker (*Nucifraga columbiana*) plays a critical role in the dispersal of whitebark pine’s heavy, wingless seed (Tomback 1982, Tomback et al. 1990, Tomback 1998, Lorenz et al. 2008). The bird harvests seed from purple cones during late summer and early fall. It carries up to 100 of the seeds in a sublingual pouch up to 10 km away, where

it buries up to 15 seeds in a cache 2–3 cm below the ground (Tomback 1998, Lorenz et al. 2008). Many of the 8,000–20,000 caches that the bird creates each year are reclaimed during the following months, but those seeds that remain unclaimed eventually germinate (Tomback 2005). Nutcrackers often cache in open areas where the ground surface is visible from above, and often near objects on the ground, such as rocks, logs, and snags, because it reclaims seed from caches by pattern recognition (Hutchins and Lanner 1982, Tomback et al. 1993, Lanner 1996). In high-mountain settings, open areas with a high degree of pattern are often created by wildland fire (Morgan and Bunting 1989).

Three types of fires describe the diverse fire regimes in whitebark pine forests (Arno and Hoff 1990, Morgan and Bunting 1990, Morgan et al. 1994). Some high-elevation stands experience nonlethal surface fires (called underburns in this study) because sparse fuel loadings foster low-intensity fires (Keane et al. 1994). The more common fire regime is characterized by fires of mixed severities in space and time that create complex mosaics of tree survival and mortality on the landscape. Mixed-severity fires can occur at 60- to 300-year intervals (Morgan and Bunting 1989, Arno et al. 2000, Murray 2008). Burned patches are often 1 to 100 ha in size, depending on topography and fuels, and these openings provide important caching habitat for the Clark’s nutcracker (Tomback et al. 1990, Norment 1991). Many whitebark pine forests in northwestern Montana, northern Idaho, and the Cascades originated from large, stand-replacement fires that occurred at time intervals greater than 250 years (Keane et al. 1994, Murray 1996). These fires are usually wind driven and often originate in lower-elevation stands (Murray et al. 1998).

Whitebark pine benefits from wildland fire because it is better adapted to surviving and regenerating after fire than associated shade-tolerant trees

(Arno and Hoff 1990). Whitebark pine can survive low-severity fires better than its competitors because it has thicker bark, thinner crowns, and deeper roots (Arno and Hoff 1990). It also readily colonizes large, stand-replacement burns because nutcrackers transport the seed great distances (Tomback 2005, Lorenz et al. 2008). Nutcrackers can disperse whitebark pine seeds up to 100 times farther (over 10 km) than wind can disperse seeds of its competitors (McCaughy et al. 1985, Tomback et al. 1990, 1993). On open, burned sites, whitebark pine can successfully grow and mature to healthy cone-producing trees in the absence of competition (Arno and Hoff 1990).

Our primary assumption is that whitebark pine ecosystems can be restored from the damaging effects

of blister rust, mountain pine beetles, and fire exclusion through treatments that emulate wildland fire regimes to remove competitors and create habitat suitable for nutcracker caching. The primary objective of these treatments was to increase whitebark pine regeneration. We assumed that living, cone-producing whitebark pine seed sources at or near restoration sites possess some degree of blister rust resistance, since they have already survived decades of rust infection (Arno et al. 2001). These potentially rust-resistant whitebark pine trees would provide the seed for the nutcrackers to plant in the treated units and, hopefully, the subsequent regeneration would be somewhat resistant to the rust (Hoff et al. 2001).

Study Sites

We implemented this study in the northern Rocky Mountains of the United States (Figure 1). Five sites were selected that were close to roads or trails, were in the later stages of succession, and where we had support from the Ranger Districts for implementing the planned treatments. Whitebark pine is experiencing heavy rust mortality throughout this area except for the site at Blackbird Mountain, where there are few rust infections and no observed rust-caused mortality. Prior to treatment, the overstory of most sites consisted of 200- to 400-year-old overstory whitebark pine and lodgepole pine with encroaching subalpine fir and scattered large Engelmann spruce (Table 1). The understory was composed mostly

Table 1. Description of the five sites included in the study "Restoring Whitebark Pine Ecosystems." All sites experienced a 1930–1934 mountain pine beetle epidemic and all but Blackbird Mountain had evidence of the 1910 fire. All infection and mortality levels were estimated from the tree data collected on the plots. The habitat type is taken from Pfister et al. (1977): ABLA is *Abies lasiocarpa*, LUHI is *Luzula hitchcockii*, and MEFE is *Menziesia ferruginea*. Cover type acronyms are WP-whitebark pine, SF-subalpine fir, and LP-lodgepole pine. Treatment unit codes are defined in Table 3. The final row indicates the number of sites that experienced unplanned wildfires, with the number of control plots lost in parenthesis.

Study Site Attribute	Smith Creek (SC)	Bear Overlook (BO)	Coyote Meadows (CM)	Blackbird Mountain (BM)	Beaver Ridge (BR)
National Forest	Bitterroot	Bitterroot	Bitterroot	Salmon	Clearwater
Elevation (m ASL)	2,100–2,250	2,070–2,250	2,340–2,425	2,400–2,460	2,010–2,250
Aspect	Southeast	Southeast	Northwest	South	South
Habitat type	ABLA/LUHI	ABLA/LUHI	ABLA/LUHI, ABLA/MEFE	ABLA/LUHI	ABLA/LUHI
Cover type	WP-LP	WP-LP	WP-SF	WP-SF	WP-LP
Overstory whitebark pine density (stems/ha)	158	96	47	115	30
Overstory subalpine fir density (stems/ha)	195	80	93	337	156
Historical fire regime	Mixed severity	Mixed severity	Mixed severity	Stand replacement	Stand replacement
Rust infection (%)	85	70	90	<1	51
Rust mortality (%)	95	93	91	<1	88
Number and type of treatment units	3 MO, MN, LO	2 LO, LF	5 LO, MO, MF, HO, HF	2 HO, HF	6 LO, MO, MF, MN, HO, HF
Pretreatment measurement year(s)	1995	1996	1993, 1996	1997	1997
Prescribed burn year(s)	1996	1999	2000	1999	1999, 2000, 2002
Plots compromised by wildfire	20 (5)	0 (0)	44 (30)	6 (6)	28 (0)

Figure 1. Study sites in the "Restoring Whitebark Pine Ecosystems" study.

Figure 2. Treatment unit design for the Beaver Ridge study site where 1A is the control; 2A and 2B are nutcracker openings and no burning, with and without tree planting; 3A and 3B are nutcracker openings with prescribed burning, with and without tree planting; 4A and 4B are low-severity prescribed burns, with and without fuel enhancement; and 5A and 5B are high-severity prescribed burns, with and without fuel enhancement.

of seedling and sapling subalpine fir with occasional stagnated whitebark pine saplings. Grouse whortleberry (*Vaccinium scoparium*), woodrush (*Luzula hitchcockii*), and beargrass (*Xerophyllum tenax*) were the primary plant species dominating the undergrowth. Sampling of fire scars at the Coyote Meadows site revealed a history of mixed-severity fire with burns in 1933, 1780, and approximately 1390 A.D. Most of the other sites had trees with scars from the 1889 and 1910 burns.

Treatment Summary

Each site was divided into treatment areas, and each treatment area was further divided into treatment units (Figure 2). The treatment area is described by the major treatment implemented within the area, and the treatment unit defined a subarea within which a secondary or minor treatment was implemented. We tried to replicate treatment units within a site to satisfy statistical requirements for analysis of variance, but found that replication was nearly impossible due to the limited extent of most study sites (most were confined by ridgetop settings), diversity of biophysical characteristics within each site (complex aspect, slope, drainage, and species composition conditions), pseudoreplication issues (Hurlbert 1984), and lack of accessible homogeneous areas.

We also attempted to make each site its own replicate, but we found that it was impossible to replicate homogeneous treatments across sites because of disparate stand conditions and inconsistent treatment implementation. As a result, we took a "demonstration" approach to designing this study, where we implemented feasible, operational treatments crafted to restore whitebark pine. Each study site always included a control unit adjacent to the treatment units.

The primary treatment was prescribed fire (Table 2) implemented at three levels of intensity to mimic the three types of fire regimes mentioned above. A high-intensity prescribed fire mimicked stand-replacement fire where more than 90% of the overstory was anticipated to be killed, while the moderate-severity prescribed fire simulated effects from a mixed-severity fire where patches of stand-replacement fire are mixed with varying severities of nonlethal surface fires (10%–90% overstory mortality). The underburn fire was emulated with a low-intensity prescribed fire. We managed prescribed fire intensity levels through a combination of wind speed, fuel moisture, and fuel loadings. Most prescribed burns were ignited using strip-headfires of about 3–6 m wide, but we used a heli-torch on two sites to simulate stand-replacement fire and a terra-torch (flame thrower mounted on a truck) at the Beaver Ridge site to

initiate the prescribed stand-replacement fire (Keane and Parsons 2010).

The second treatment, silvicultural tree cuttings, was implemented at various levels of species selection and intensity (Table 2). We first created "nutcracker openings," where all trees except whitebark pine trees were cut within near-circular areas of 0.4 to 2 ha to entice the nutcrackers to cache seeds there (Figure 3). These openings were designed to mimic the effect of patchy mixed-severity burns based on the findings of Normont (1991), who found that nutcrackers were most abundant in 0.1 to 15 ha disturbed or nonforest patches. Between the nutcracker openings, but within the major treatment unit, we removed all subalpine fir and spruce and left all lodgepole and whitebark pine. Lodgepole pine trees were left because we felt their density did not adversely affect whitebark pine seedling survival (Keane et al. 2007). All silvicultural treatments were noncommercial except for the Smith Creek treatments, where cut trees were whole-tree skidded to landings where they were transported and sold to local mills for minimal profit. We piled and burned the slash on two Beaver Ridge (Figure 2, units 2B and 3B) treatment units. A cutting treatment called "fuel enhancement" was also used to augment the surface fuelbed to enhance prescribed burning by cutting small and large fir and spruce trees and placing them in areas

Table 2. A general summary of treatments and their combinations used in the study. See Table 1 for the study site acronym definitions and Keane and Parsons (2010) for full details on treatment descriptions. Results of the planting are not summarized in this paper.

Prescribed Fire	Cutting	Planting
None	None	None
<i>Underburn</i> —low intensity to consume fuels and kill shade-tolerant competition (BR, CM, BO)	<i>Nutcracker openings</i> —cut small (0.2–2 ha) clearcuts, leaving all healthy whitebark pine trees and thinned shade-tolerant trees between openings (BR, SC)	<i>Planted</i> —areas planted with rust-resistant whitebark pine (BR)
<i>Mixed severity</i> —moderate severity to consume slash and kill subalpine fir regeneration and create patches (BM, BR, CM)	<i>Fuel enhancement</i> —cut subalpine fir and Engelmann spruce to enhance fuel bed (BR, BO, BM, CM)	
<i>Stand replacement</i> —High intensity severe fire that kills over 90% of all trees of all species (BR)

Figure 3. Nutcracker openings at the Beaver Ridge Study site. Nutcracker openings are 0.2–5 ha openings in the canopy where all trees except for whitebark pine are removed. This treatment is designed to emulate the mixed-severity fire regime in whitebark pine forests. Photo by Robert E. Keane

with low fuel loadings (Keane and Arno 1996, Keane et al. 1996). Fuel enhancement increased fuel loadings by 0.3 to 2.8 kg/m², depending on the level and distribution of natural fuels.

Planting was the third major treatment. Owing to the lack of available seed and seedlings, however, we could plant whitebark pine trees on only two Beaver Ridge study sites (2A, 3A). Planting results are not reported for this study but effects can be evaluated in the Keane and Parsons (2010) management guide.

Sampling Methods

We installed ten plots within each treatment unit to record changes in ecological conditions. We systematically located these plots across the treatment units using a random

start because attempts to randomly establish plots failed owing to odd treatment unit shapes, variable fuel conditions, and concerns about finding plots in later years. All plots were mapped using compass bearings and distances from benchmarks (bearing or blazed trees) and GPS.

Plots were circular in shape and 0.04 ha in size (Figure 4) and permanently located using a 1 m rebar. All trees above 12 cm DBH (diameter at breast height) were tagged using numbered aluminum (in the unburned units) or stainless steel casket tags (in the burned units) nailed at the center of the tree bole at DBH facing plot center. We measured species, DBH, tree height, height to crown base, and health (live, sick, dying, or dead) for each tagged tree and also recorded percent crown volume killed by blister rust for all whitebark pine saplings and trees (Lutes et al. 2006). The same measurements were taken on all live trees less than 12 cm DBH and greater than 1.37 m tall (saplings), except DBH was estimated to 2.5 cm diameter classes. Tree seedlings (trees less than 1.37 m tall) were counted by 0.3 m height classes on a 125 m² circular plot nested within the 0.04 ha plot.

Surface fuels were measured on two 15.2 m transects that originated at plot center and extended in opposite directions (Figure 4). Fine woody fuels (1 h, < 1 cm diameter and 10 h, 1 to 2.5 cm

dia.) that intersected the transect were counted along the first 2.0 m of the transects; small branchwood (100 h, 2.5 to 7.5 cm dia.) was counted along the first 3.2 m; and logs (1,000 h, > 7.5 cm diameter) were counted along the entire 15.2 m length. Duff and litter depths were measured at zero, 11.3 m, and 15.2 m distances along each of the two transects. Log diameters were measured in order from the zero end of the tape (plot center) to track newly fallen log material.

Vertically projected foliar cover and heights of each vascular plant species were visually estimated within each of four 1 m² (1.41 m × 0.71 m) microplots at each plot (Figure 4) using the cover classes < 1%, 1%–5%, 5%–15%, 15%–25%, and up to 95%–100% (see Lutes et al. 2006). We also recorded heights and perpendicular crown widths of individual shrubs over 1 m tall. Ground covers for rock, bare soil, wood, duff/litter, and moss were also estimated in each microplot using the same cover class categories.

Tree, fuel, and undergrowth plant species measurements were taken before treatment (1–3 years), then one year and five years after treatment. Some units received two or more treatments (cutting and prescribed burn, for example; Table 2) and we measured after each treatment type, but this report only summarizes the measurements after the last treatment was implemented. We also estimated the

Figure 4. Diagram of the sample plot design used in the study for estimating tree height and health, surface fuels, and foliar cover and height of each vascular plant species. Two fuel transects were oriented north and south for plots 1, 4, 7, and 10, at azimuths 60 and 240 degrees for plots 2, 5, and 8 and at azimuths 120 and 300 degrees for plots 3, 6, and 9 to minimize orientation effects (Brown 1974, Brown and Roussopoulos 1974). Ends of all fuel transects were permanently established using 25 cm nails driven into the ground and marked with wire orange flags to help in relocation. Microplots for estimating vascular plant cover were permanently established with 20 cm stainless steel nails that were relocated using a metal detector.

percentage of the plot burned by the prescribed fire using the mentioned cover classes, and we documented any other disturbances observed at the plot (for example, mountain pine beetles, *Ips* spp.). We always took photographs of the plot in two directions, looking north and east from plot center, at each of the measurement times.

Analysis

Tree mortality was computed for each species as a percentage of individuals killed for three size classes: seedlings, saplings, and overstory trees. All ten plots within each treatment unit were used in the tree mortality calculations. We also included an assessment of snags (dead trees above 11 cm DBH) by comparing pre- and postdisturbance densities. Downed woody fuel

loadings were computed from planar intercept counts using the protocols described by Brown (1974) and implemented in FIREMON (Lutes et al. 2006). Fuel consumption was computed as the difference in loading from pretreatment and posttreatment measurements calculated as an average across all 20 transects in the treatment unit. We used the 60 observations of duff plus litter depth (three measurements on each of two transects for 10 plots) to calculate duff and litter consumption. Depth was converted to loading using a bulk density of 31 kg/m³ (Brown 1981). We used all 40 microplots (4 at each of 10 plots) within each treatment unit as observations in the calculation of plant species cover response and ground cover changes (wood, rock, bare soil, duff/litter, and moss).

We present results for seven major treatment combinations. For brevity, we combined treatment units into similar groups across sites based on the prescribed burn intensity and the secondary cutting treatment (Table 3). Detailed results for all 21 treatment units are presented by Keane and Parsons (2010). We used standard *t*-tests (MATLAB 7.9.0.529 R2009B, Mathworks, Natick MA) to detect statistically significant differences between pretreatment conditions and each of the one- and five-year remeasurements for each treatment combination. We also performed *t*-tests for the control to detect any significance in the change in conditions from the pretreatment conditions to the five-year remeasurement conditions, and also significant differences from the control year-five measurements and the year-five measurements for all treatment units. The pretreatment conditions for the treatment combination with nutcracker openings were taken after the initial cutting but before the prescribed burn to isolate fire-caused tree mortality. Because of the unbalanced plot numbers across the seven treatment combinations (Table 3), we could not perform advanced ANOVA analysis to determine differences across the combinations and across sites.

Results

The length of this study (started in 1993) meant that some treatment combinations were compromised by unplanned circumstances. Four of the five study sites were partially burned in unexpected wildfires that occurred after their last treatment (Keane and Parsons 2010) (Table 1). All no-burn treatment units in this study (nutcracker opening cutting treatments with no prescribed burning, Table 3) were eventually burned in subsequent wildfires. The no-burn units at Beaver Ridge (Figure 2, 2A, 3A) burned when spotting from the 2001 prescribed burn lit portions of these units, and then the 2003 wildfires burned the remaining portions. The same treatment combination at

Smith Creek burned in the 2006 Gash Creek wildfire. We also lost a number of control plots on three sites to unplanned wildfires. The 2000 fires on the Bitterroot National Forest burned the entire Coyote Meadows study site, thereby rendering all 30 control plots ineffective. The 2001 Dry Fork fire on the Salmon-Challis National Forest consumed four of ten control plots on the Blackbird Mountain site, and embers from the prescribed burn started ground fires in two of ten control plots. The Gash Creek wildfire in 2006 burned five of ten control plots on the Smith Creek site and part of the Bear Overlook site (no control plots were burned) (Table 1).

A few trees may have been killed by the mountain pine beetle at the Beaver Ridge site, but overall, beetle mortality was low at the five-year measurement. Statistical analysis (*t*-tests) of the tree, fuel, and undergrowth measurements on the unburned control plots found some significant differences between the pretreatment and five-year measurements for these sites (Table 4). Additional statistical results found most treatment units were significantly different from the controls at year five (Table 4).

Summarized study results for the seven treatment type combinations across all sites are presented in Table 5. Tree mortality was highest

(55%–88%) in treatment units with moderate- to high-intensity prescribed burns (Table 5), and on any treatment with a fuel-enhancement cutting. Mortality for whitebark pine was comparable to that for subalpine fir for nearly all treatment combinations. Fire-caused mortality was highest for mature trees of both species on sites with high burn coverage (> 60% of area burned). Moderate-intensity prescribed fire had the greatest range of mortality across all species and size classes (19%–88%) because of the patchy nature of the fires and the great diversity of site conditions across the five sites (Keane and Parsons 2010). Most importantly, there were no detectable increases in seedling whitebark pine or subalpine fir after five years (except for the low-intensity fire treatment; Table 5). Whitebark pine snag densities did not change significantly after five years (except for 78% reduction in moderate-fire treatment) because fallen snags were replaced by fire-killed trees, but the overall trend was a 10% to 40% decrease in number of snags. In contrast, subalpine fir snags increased significantly for most treatments mainly because there were few fir snags prior to treatment.

New whitebark pine regeneration was rarely detected on any of the treatment units, and only one site (Blackbird Mountain) had significant

Table 3. The seven treatment combinations in this study. Not all combinations could be reported because a majority of the study sites were burned in unplanned wildfires and uncontrolled prescribed burns (see Table 1 for details and study site codes).

Prescribed Burn	Tree Cutting	Study Sites	Code
Low intensity, low severity underburn (Low)	None	BR, BO, CM, SC	LO
	Fuel enhancement	BR, BO	LF
Moderate intensity, mixed severity (Moderate)	None	BR, CM	MO
	Nutcracker openings	BR, SC	MN
	Fuel enhancement	BR, CM	MF
High intensity, stand replacement (High)	None	CM, BM	HO
	Fuel enhancement	CM, BM	HF
No fire (None)	Nutcracker openings	BR	Not presented in this study

Table 4. Statistically significant differences (*t*-test; $p < 0.05$) for seven important response variables. Control plots before treatment and at year five were compared to detect any nontreatment changes (CN). Control plots and treatments units were compared at year five for each treatment combination (see Table 3 for definitions). Wildfires burned control plots on Smith Creek (5 control plots), Coyote Meadows (30), and Blackbird Mountain (4).

Response Variable		Smith Creek	Bear Overlook	Coyote Meadows	Blackbird Mountain	Beaver Ridge
Overstory density (stems/ha)	Whitebark pine	MN, LO	CN, LF, LO	—	CN	MF
	Subalpine fir	CN, LO	CN, LF	LO, HO	—	LO, LF, MO, MF
Log (1,000 h fuel) loading (kg/m ²)		—	CN, LF, LO	LO, MO, MF, HF	—	MN
% Cover	Grouseberry	MN	LF, LO	CN	—	LO, MF, MN
	Beargrass	—	LF, LO	CN	—	LO, MN
	Rock	—	LO	CN, LO, MO, HO	CN, HO, HF	—
	Duff	CN, MN	LF, LO	CN	CN, HO, HF	—
Number and types of treatments						
		3	2	5	2	6
		MO, MN, LO	LO, LF	LO, MO, MF, HO, HF	HO, HF	LO, MO, MF, MN, HO, HF

Table 5. Treatment effects for tree, fuel, and groundcover measurements averaged across all units within each of the seven treatment types expressed as percent change after five years from pretreatment condition. Numbers in bold indicate statistically significant differences ($p < 0.05$). The last row indicates the average area burned within the plot by the prescribed fire.

Fire Severity:	Low			Moderate		High	
Cutting:	None	Fuel enhance	None	Nutcracker opening	Fuel enhance	None	Fuel enhance
Code:	LO	LF	MO	MN	MF	HO	HF
Whitebark pine (<i>Pinus albicaulis</i>) tree density							
Seedling	-41.21	-54.35	-82.87	-79.00	-70.34	29.17	-40.69
Sapling	-31.03	-29.26	-19.44	-88.52	-47.85	-63.39	-61.13
Trees	-47.20	-37.84	-88.37	-68.00	-56.00	-80.00	-86.15
Snags	16.28	-17.28	-36.00	-8.94	-78.26	-25.29	10.00
Subalpine fir (<i>Abies lasiocarpa</i>) tree density							
Seedling	10.98	16.15	-34.08	-87.37	-18.79	-46.55	-84.31
Sapling	-17.62	-40.71	-40.52	-43.57	-84.70	-32.30	-69.92
Tree	-58.05	-47.06	-40.83	-40.63	-75.00	-84.85	-84.73
Snags	188.10	-33.33	19.18	20.69	126.32	276.92	29.73
Fuel loading							
Duff + Litter	868.97	241.29	119.44	-27.13	138.64	-40.25	-23.81
1 h	102.92	-12.94	49.79	-65.13	218.44	-50.40	-18.42
10 h	-16.97	-36.74	-49.76	-72.07	42.06	-10.77	-36.83
100 h	-39.43	-12.00	-39.79	-68.30	45.80	-27.55	-49.63
1,000 h sound	-17.02	-12.34	62.30	-45.29	97.08	11.12	-22.30
1,000 h rotted	173.82	143.35	414.27	-30.95	778.00	342.74	398.90
Groundcover							
Wood	5.70	4.44	13.73	-1.81	12.61	-1.17	-1.09
Rock	2.64	0.84	3.25	2.00	2.78	11.06	17.66
Soil	5.72	7.60	6.74	8.37	5.98	19.24	22.65
Duff + Litter	39.32	17.63	19.69	-5.85	16.93	8.96	-3.96
Burn cover (%)	31	54	56	91	81	61	90

whitebark seedlings, probably because this site had little blister rust infection in the cone-producing whitebark pine (Keane and Parsons 2010). Some whitebark pine seedlings were survivors of the cutting and burning treatments and had marginal vigor. It is unknown whether the residual regeneration will have the capacity to be released from competition and grow into mature trees (Figure 5) (Keane et al. 2007). Subalpine fir trees were twice as plentiful as whitebark pine trees before and after all treatments for both trees and seedlings (Figure 5). Post-treatment fir densities are highest on sites that were burned without fuel enhancement and tended to decrease over the five years.

Major changes in fuel loadings were detected in nearly all treatments, but the direction of this change differed by woody size class (Table 5). Fine woody fuels marginally decreased in

all treatment combinations except for the low-intensity burn because of extensive fuel consumption by the prescribed fires. Fine fuels were mostly unconsumed in the low intensity burn treatment because of the low coverage of the prescribed burn ($< 31\%$ of area burned). However, coarse woody debris increased significantly in all seven treatment combinations, and, in some cases, this increase was striking (two to eight times greater) (Tables 5 and 6). Even though there was significant log consumption (10%–50%) for most fires, especially in rotten logs, the extensive log load increases were a result of prescribed fires weakening the plentiful standing dead whitebark pine snags, causing them to fall (Table 5). Nearly all fallen whitebark pine snags were trees that had been previously killed by mountain pine beetle or blister rust. Duff and litter increased after low-intensity prescribed burns

(241%–868%) because of the contribution of scorched needles from standing trees. Higher severity burns, especially when there was a fuel enhancement cutting, usually reduced duff and litter loads by consuming most canopy fuels (Table 6).

Prescribed fires tended to increase bare soil and rock cover while decreasing duff/litter and woody cover (Table 5), but the magnitude and variability of these changes were entirely dictated by the intensity and coverage of the fire. Woody cover increased in some units because of the fallen snags, whereas duff/litter cover increased because of fallen scorched foliage. Rock and soil cover, however, increased in nearly all treatment combinations, with the most significant increases in fuel-enhanced units with high burn cover and intensity. We feel that an increase in rock and bare soil cover creates more fine-scale pattern within the

Figure 5. Tree density by species (WP, whitebark pine and SF, subalpine fir) and size class for each of the treatment combinations before treatment (PRE) and one year (POST-1) and five years (POST-5) after treatment. Treatment combination codes are described in Table 3. The symbol + represents standard error of the mean.

unit, thereby improving nutcracker caching potential (McCaughey and Weaver 1990, Tomback et al. 1993, Tomback 2005).

Most treatment units in this study had low vascular plant diversity with microplots averaging only five species and the sites having only 20–25 species (Keane and Parsons 2010). We selected four common undergrowth plant species that were dominant across all sites and treatment unit combinations and found, as expected, that these species declined in cover after treatment (20%–100%) (Figure 6). Elk sedge (*Carex geyeri*, CAGE)

increased in cover after five years for all but the most severe burn treatments. Grouse whortleberry (*Vaccinium scoparium*, VASC) cover declined the most after nearly all treatments, but most sites recovered at least half pre-burn cover by the fifth year.

Discussion

All high- and moderate-intensity prescribed fire–cutting treatment combinations were effective at creating desirable nutcracker caching habitat, as evidenced by the abundant nutcracker caching observed on nearly

all sites (Keane and Arno 2000, 2001, Keane and Parsons 2010). These treatments were also successful at removing subalpine fir competition, thereby creating desirable growing conditions for surviving and newly regenerating whitebark pine. However, the expected whitebark pine regeneration from the observed caching has not yet materialized, as nearly all sites have few or no new whitebark pine seedlings (Table 5). This is a result of many factors. First, we believe that many of the cached seeds were reclaimed by the nutcrackers during the following years. Seed sources around most study sites were limited due to extensive mountain pine beetle and blister rust mortality. Even the one treatment site with adjacent abundant healthy seed sources, Blackbird Mountain, contained scattered whitebark pine regeneration.

We suggest that the populations of cone-producing whitebark pine at or near our study areas may be so low that the nutcrackers consume too many seeds during caching and by reclaiming caches later for there to be sufficient seed to provide for adequate tree regeneration (McKinney and Tomback 2007). In addition, the severe site conditions may have killed many emerging seedlings. These steep, high-mountain sites experience deep snowpack, especially the Beaver Ridge site, which had over 15 m in 1997, and the heavy snow tended to creep down slope and pull young seedlings out of the ground. Moreover, most soils on our study sites are highly erosive, and spring snowmelts generate abundant water that usually scoured the topsoil away from seedlings, especially in recently burned sites. It might also be possible that our five-year evaluation period was too short to effectively evaluate regeneration dynamics in these severe sites, and that a 10- or 20-year measurement might be more appropriate to describe the success of our treatments. Some researchers have identified a lag period of up to 40 years for whitebark pine to become established in upper subalpine zones

Table 6. Fuelbed characteristics at pretreatment (Pre), one year after treatment (1 y), and five years after treatment (5 y). Bold numbers indicate statistically significant differences ($p < 0.05$) from pretreatment conditions.

Fire Severity:	Low			Moderate		High	
	Cutting:	None	Fuel enhance	None	Nutcracker opening	Fuel enhance	None
	Code:	LO	LF	MO	MN	MF	HO
Fine fuel loading (kg/m²)							
Pre		0.65	0.76	1.05	0.97	0.37	0.71
1 y		0.39	0.76	0.70	0.37	0.47	0.52
5 y		0.46	0.63	0.64	0.30	0.57	0.53
Sound log loading (kg/m²)							
Pre		2.64	3.94	3.75	11.71	1.72	4.35
1 y		7.34	8.81	21.80	7.37	16.77	13.40
5 y		7.22	9.58	19.30	8.09	15.08	19.24
Duff and litter loading (kg/m²)							
Pre		0.12	0.34	0.55	0.61	0.31	1.04
1 y		0.37	0.68	0.33	0.07	0.35	0.75
5 y		1.13	1.15	1.21	0.45	0.74	0.62
Bare soil cover (%)							
Pre		2.38	4.98	1.68	5.01	6.03	4.50
1 y		14.40	16.08	19.62	38.51	17.69	29.59
5 y		8.09	12.58	8.41	13.38	12.00	23.74

due to severity of the disturbance and the site (Agee and Smith 1984, Arno and Hoff 1990).

We found that it was difficult to implement low-severity prescribed fires to mimic nonlethal surface and mixed-severity fires for a number of reasons. First, the shrub and herbaceous fuels on most sites were rarely dry enough to sufficiently carry a fire under our desired conditions of burning, resulting in a light fire with low tree mortality and low burn coverage. In contrast, fire intensities on fuel-enhanced sites were sometimes too high, resulting in unwanted high whitebark pine mortality and extensive reductions in the stabilizing undergrowth plant community (Table 5, Figure 6). It takes a delicate balance of sufficient fuels and dry fuel moistures to implement an effective prescribed burn that reduces subalpine fir overstory and understory while allowing survival of mature whitebark pine trees.

Lack of experience in burning high-elevation ecosystems may have influenced fire crews to implement prescribed burns under wetter than desired conditions, which were outside of the burn prescription, thereby

achieving lower fire intensity and lower burn coverage across the stand (Table 6). Few crew members wanted to risk an uncontrolled wildfire, although nearly all burn crews recognized that they could have easily achieved the higher severities once they were familiar with burning in this high-elevation system. This may mean that fire crews will need extensive experience in these high-elevation forests to implement successful prescribed burns. Multiple burn treatments might be warranted when burning experience is low, providing there are sufficient fine fuels to realize burn plan objectives.

Contrary to the restoration objective, the level of subalpine fir mortality was nearly the same as whitebark pine mortality, and many fir trees remained after treatment (Table 5, Figure 5). Our objective was to kill the majority of subalpine fir (> 80%) and leave whitebark pine (> 80%), yet we seemed to kill both tree species at the same rate regardless of diameter. This could be due to burn crew inexperience but is more likely a result of the fact that whitebark pine is not as fire tolerant as the literature would suggest (Reinhardt and Ryan 1988, Ryan and Reinhardt 1988). We often

found subalpine fir “skirts” surrounding many mature whitebark pine trees that tended to facilitate ignition of whitebark pine canopies, especially when there are sap-filled wounds on the branches and boles caused by blister rust cankers, animal chewing, and tree rubs (Keane and Parsons 2010). These skirts could be removed to increase whitebark pine survival.

We also found that many whitebark pine trees were killed by *Ips* beetles (originating from populations in unburned slash) and mountain pine beetles after burning (Baker and Six 2001). Because of this, it may be difficult to keep whitebark pines alive in units treated with prescribed burns so alternative nonburn treatments may be warranted, especially in years with high beetle populations. In our study, however, treatments without prescribed fire did not create optimal caching habitat because the slash impeded nutcrackers’ access to the ground, so whitebark pine planting may be needed. Whitebark pine survival on treated sites is most important when off-site seed sources are distant (> 10 km).

Most treatments actually increased fuel loadings (Tables 5 and 6),

Figure 6. Canopy cover of the four dominant undergrowth plant species across each of the treatment combinations before treatment (PRE) and one year (POST-1) and five years (POST-5) after treatment: a) *Vaccinium scoparium* (VASC); b) *Xerophyllum tenax* (XETE); c) *Carex geyeri* (CAGE); and d) *Luzula hitchcockii* (LUHI). Treatment combination codes are described in Table 3. The symbol + represents standard error of the mean.

especially for coarse woody debris (logs > 7.5 cm diameter), because the abundant rust-killed whitebark pine snags were weakened by fire. These newly fallen logs pose a low fuel hazard because of the lack of fine fuels, and their presence might actually improve the potential for whitebark pine regeneration by providing safe sites for cached whitebark pine seed. Managers should inspect the level of whitebark pine snags in potential treatment areas to determine possible safety concerns, evaluate if the restoration treatment could also be a fuel hazard reduction

treatment, and ascertain if there will be suitable safe sites for whitebark pine planting.

The planting of whitebark pine seedlings on the Beaver Ridge site (Figure 2, units 2A and 3A) was marginally effective (approximately 20%–40 % survival after five years) because nursery techniques and planting guidelines for whitebark pine at the time of planting were not as extensive as they are today (Scott and McCaughey 2006) and because a wildfire burned a portion of the area. Our seedlings were somewhat small,

and they were planted in midsummer just after snowmelt and had to endure three hot, dry summer months. There is now extensive reference material for growing whitebark pine in nurseries and recommendations for planting whitebark pine (Tomback et al. 2001, Scott and McCaughey 2006), so planting success would be improved using today's technology. Planting should be done in midautumn, and seedlings should be planted near structures that provide stability from snow-pack damage such as stumps, logs, and rocks. Recently, Perkins (2004) found that grouse whortleberry had a positive effect and elk sedge had a negative effect on the growth and survival of planted whitebark pine seedlings (Figures 5 and 6).

The many unplanned wildfires reduced the strength of statistical tests to detect changes in the controls (Table 4). Most of our treated areas were used as "safe zones" for firefighters attempting to suppress the wildfires, so their actions within these areas, such as snag removal, trampling, and backburning, may have also affected study results. Moreover, our grouping of treatment units into the treatment combinations used to summarize this study's results has also introduced greater variance because of disparities between sites and treatment implementations. The detailed summary of treatment unit results by Keane and Parsons (2010) is probably more helpful to the manager, even though results are highly local, because treatments are often implemented at this scale.

While the treatment combinations used in this study appear to increase regeneration opportunities for whitebark pine by creating desirable nutcracker caching habitat and eliminating competition, the increase in whitebark pine regeneration after five years of monitoring has yet to be realized. This indicates that planting potentially rust-resistant seedlings after treatment is critical for the timely and successful restoration of areas with heavy rust and beetle mortality. The success of whitebark pine restoration

treatments depends on a combination of four factors: elimination of competition, creation of desirable nutcracker caching habitat, continued vigor of cone-producing on- and off-site whitebark pine, and the distance of adequate whitebark pine seed sources. Information gained in this study can be used to design effective cutting, burning, and planting treatments that can ensure the continued presence of this valuable species on the mountain landscapes of the northern Rocky Mountains.

Management Implications

Based on the findings of this study, we recommend the following in designing and implementing whitebark pine restoration activities:

- **Emulate historical fire regimes.** Use the observed fire regime for a potential treatment site to guide design of the whitebark pine restoration treatment. Craft treatment specifics around the effects of historical fires.
- **Use prescribed burning.** Implement prescribed burning as one of the restoration tools if economically possible. Prescribed burning can be enhanced by the following:
 - *Augmenting fuelbeds.* Fuel enhancement cuttings should be implemented one year before a prescribed burn to ensure burn objectives are fully realized. The addition of cured slash to discontinuous fuelbeds facilitates burn effectiveness by providing additional fine fuel to aid fire spread into all areas of the stand and to augment quickly drying fine fuel levels so the burn can be implemented in more moist conditions. Fuel-enhanced fuelbeds can generate undesirable high-intensity fires if burned when conditions are too dry.
 - *Burning under appropriate conditions.* Wait until the first hard frost in late summer or early fall before implementing a prescribed

burn. We found shrub and herbaceous fuels were much drier after the frost.

- **Use wildland fires.** Proactive, controlled management ignited prescribed burns, such as those used in this study, may not always be possible owing to access, cost, and risk considerations. Wildland fire use (letting lightning fires burn under acceptable conditions) may have a wider use in restoring whitebark pine forests.
- **Plant, plant, plant.** Sites experiencing high whitebark pine blister rust-caused mortality (above 20%) and high rust infection (above 50%) or those experiencing high beetle mortality should be planted with potentially rust-resistant seedlings after treatment, including wildland fire use. Potentially rust resistant seeds can be collected from surviving whitebark pine trees (Hoff et al. 2001).
- **Monitor results.** There is a lack of comprehensive studies investigating effects of restoration treatment in whitebark pine. It is critical to monitor treatment effects to ensure future restoration success for others.

Acknowledgments

We thank the large number of skilled ecological technicians that participated in this project since 1993: Todd Carlson, Courtney Couch, Daniel Covington, Laura Dickinson, Janice Garner, Myron Holland, Violet Holley, Curtis Johnson, Cat Maxwell, Ben McShan, Jim Menakis, Scott Mincemoyer, Kirsten Schmidt, Virginia Arensberg, Dennis LeMond, Nadev Kaufman, Cassandra Koerner, and Wayne Lyngholm of the USDA Forest Service Rocky Mountain Research Station Missoula Fire Sciences Laboratory. We also thank the people who participated in the study: Joe Scott, Eva Karau, Alisa Keyser, Mick Harrington, Lisa Holsinger, Helen Smith of the Rocky Mountain Research Station Missoula Fire Sciences Laboratory; and we would like to thank the people from the National Forests who made the study possible: Karen Harvey, Steve Munson, Bob Lippincott, Jon Weston, Chris Ourada, Vicki Edwards of the Clearwater National Forest; Barbara Levesque, Breck Hudson, Diana Schuldt, Terry Black

Salmon-Challis National Forest, Leslie Anderson, Cathy Stewart, Bruce "Buster" Windhorst, Bitterroot National Forest. We also thank those who provided excellent reviews. Last, we would like to thank Steve Arno for getting the study started.

References

- Agee, J.K. and L. Smith. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. *Ecology* 65:810–819.
- Arno, S.F. 1986. Whitebark pine cone crops a diminishing source of wildlife food. *Western Journal of Applied Forestry* 9:92–94.
- Arno, S.F. and R. Hoff. 1990. *Pinus alba-caulis* Engelm., whitebark pine. Pages 268–279 in R.M. Burns and B.H. Honkala (tech coords), *Conifers*. Vol. 1 of *Silvics of North America*. USDA Forest Service Agriculture Handbook 654.
- Arno, S.F., D.J. Parsons and R.E. Keane. 2000. Mixed-severity fire regimes in the northern Rocky Mountains: Consequences of fire exclusion and options for the future. Pages 225–232 in D.N. Cole, S.F. McCool, W.T. Borrie and J. O'Loughlin (comps), *Wilderness science in a time of change conference, Volume 5: Wilderness ecosystems, threat, and management*. USDA Forest Service Proceedings RMRS-P-15-VOL-5.
- Arno, S.F., E.D. Reinhardt and J.H. Scott. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine type: A procedure for quantifying past and present conditions. USDA Forest Service Intermountain Research Station General Technical Report INT-294.
- Arno, S.F., D.F. Tomback and R.E. Keane. 2001. Whitebark pine restoration: A model for wildland communities. Pages 416–419 in D.F. Tomback, S.F. Arno and R.E. Keane (eds), *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- Arno, S.F. and T. Weaver. 1990. Whitebark pine community types and their patterns on the landscape. Pages 118–130 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.

- Aubry, C., D. Goheen, R. Shoal, T. Ohlson, T. Lorenz et al. 2008. Whitebark pine restoration strategy for the Pacific Northwest 2009–2013. Portland OR: USDA Forest Service. www.fs.fed.us/r6/genetics/publications/whitebark-pine
- Baker, K.M. and D.L. Six. 2001. Restoring whitebark pine (*Pinus albicaulis*) ecosystems: A look at endemic bark beetle distribution. Pages 501–502 in *Proceedings of the Society of American Foresters 2000 National Convention, Washington DC, November 16–20*. Bethesda MD: Society of American Foresters.
- Blaustein, A.R. and A. Dobson. 2006. Extinctions: A message from the frogs. *Nature* 439:143–144.
- Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report GTR-INT-16.
- _____. 1981. Bulk densities of non-uniform surface fuels and their application to fire modeling. *Forest Science* 27:667–683.
- Brown, J.K. and P.J. Roussopoulos. 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. *Forest Science* 20:350–356.
- Chew, J.D. 1990. Timber management and target stands in the whitebark pine zone. Pages 211–223 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- Cole, D.N. 1990. Recreation in whitebark pine ecosystems: Demand, problems, and management strategies. Pages 305–310 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- Day, R.J. 1967. Whitebark pine in the Rocky Mountains of Alberta. *Forestry Chronicle* 43:278–282.
- Eggers, D.E. 1990. Silvicultural management alternatives for whitebark pine. Pages 324–328 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- Ferner, J.W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. *Southwest Naturalist* 18:470–473.
- Hann, W.J. 1990. Landscape and ecosystem-level management in whitebark pine ecosystems. Pages 290–299 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- Hoff, R., R.T. Bingham and G.I. McDonald. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology* 10:307–316.
- Hoff, R.J., D.E. Ferguson, G.I. McDonald and R.E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. Pages 346–366 in D.F. Tomback, S.F. Arno, and R.E. Keane (eds), *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Hutchins, H.E. 1994. Role of various animals in dispersal and establishment of whitebark pine in the Rocky Mountains, U.S.A. USDA Forest Service General Technical Report INT-GTR-309.
- Hutchins, H.E. and R.M. Lanner. 1982. The central role of Clark's nutcrackers in the dispersal and establishment of whitebark pine. *Oecologia* 55:192–201.
- Keane, R.E. 2000. The importance of wilderness to whitebark pine research and management. Pages 84–93 in S.F. McCool, D.N. Cole, W.T. Borrie and J. O'Loughlin (comps), *Wilderness science in a time of change conference, Volume 3: Wilderness as a Place for Scientific Inquiry*. USDA Forest Service Proceedings RMRS-P-15-VOL-3.
- _____. 2001. Successional dynamics: Modeling an anthropogenic threat. Pages 159–192 in D.F. Tomback, S.F. Arno and R.E. Keane (eds), *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- 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.
- _____. 1996. Whitebark pine ecosystem restoration in western Montana. Pages 51–53 in C.C. Hardy and S.F. Arno (eds), *The use of fire in forest restoration*. USDA Forest Service General Technical Report INT-GTR-341.
- _____. 2000. Restoration of whitebark pine ecosystems in western Montana and central Idaho. Pages 324–330 in *Proceedings of the Society of American Foresters 1999 National Convention, Portland OR, September 11–15, 1999*. Bethesda MD: Society of American Foresters.
- _____. 2001. Restoration concepts and techniques. Pages 367–400 in D.F. Tomback, S.F. Arno and R.E. Keane (eds), *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- Keane, R.E., S.F. Arno and C. Stewart. 1996. Restoration of upper subalpine whitebark pine ecosystems in western Montana. Pages 31–26 in R.L. Mathiasen (comp), *Proceedings of the 43rd Western International Forest Disease Work Conference*. Bethesda MD: Society of American Foresters.
- _____. 2000. Ecosystem-based management in the whitebark pine zone. Pages 36–40 in H.Y. Smith (ed), *The Bitterroot Ecosystem Management Research Project: What we have learned; Symposium proceedings, Missoula MT, May 18–20, 1999*. USDA Forest Service Proceedings RMRS-P-17.
- Keane, R.E., K.L. Gray and L.J. Dickinson. 2007. Whitebark pine diameter growth response to removal of competition. USDA Forest Service Research Note RMRS-RN-32.
- Keane, R.E., P. Morgan and J.P. Menakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science* 68:213–229.
- Keane, R.E. and R.A. Parsons. 2010. A management guide to ecosystem restoration treatments: The whitebark pine forests of the Northern Rocky Mountains. USDA Forest Service General Technical Report RMRS-GTR-232.
- Kendall, K.C. and S.F. Arno. 1990. Whitebark pine: An important but endangered wildlife resource. Pages 29–36 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.

- 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 (eds), *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- Lanner, R.M. 1996. *Made for Each Other: A Symbiosis of Birds and Pines*. New York: Oxford University Press.
- Logan, J.A. and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47:160–173.
- Lorenz, T.J., C. Aubry and R. Shoal. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. USDA Forest Service General Technical Report PNW-GTR-742.
- Lutes, D.C., R.E. Keane, J.F. Caratti, C.H. Key, N.C. Benson et al. 2006. FIREMON: Fire effects monitoring and inventory system. USDA Forest Service General Technical Report RMRS-GTR-164-CD.
- Mattson, D.J., B.M. Blanchard and R.R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69:1619–1629.
- Mattson, D.J. and D.P. Reinhart. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. Pages 106–117 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- _____. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926–940.
- McCaughy, W.W., W.C. Schmidt and R.C. Shearer. 1985. Seed-dispersal characteristics of conifers in the inland mountain west. In R.C. Shearer (comp), *Proceedings—Conifer tree seed in the inland mountain west symposium*. USDA Forest Service General Technical Report INT-203.
- McCaughy, W.W. and T. Weaver. 1990. Biotic and microsite factors affecting whitebark pine establishment. Pages 319–324 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- McKinney, S.T. and D.F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research* 37:1044–1057.
- Mills, L.S., M.E. Soule and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43:219–224.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: A literature review. USDA Forest Service General Technical Report PNW-87.
- Morgan, P. and S.C. Bunting. 1989. Whitebark pine: Fire ecology and management. *Women in Natural Resources* 11:52.
- _____. 1990. Fire effects in whitebark pine forests. Pages 319–324 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- Morgan, P., S.C. Bunting, R.E. Keane and S.F. Arno. 1994. Fire ecology of whitebark pine (*Pinus albicaulis*) forests in the Rocky Mountains, USA. Pages 136–142 in W.C. Schmidt and F.-K. Holtmeier (comps), *Proceedings—International workshop on subalpine stone pines and their environment: The status of our knowledge*. USDA Forest Service General Technical Report INT-309.
- Murray, M.P. 1996. Landscape dynamics of an island range: Interrelationships of fire and whitebark pine (*Pinus albicaulis*). PhD dissertation. University of Idaho.
- _____. 2008. Fires in the high Cascades: New findings for managing whitebark pine. *Fire Management Today* 68:26–29.
- Murray, M.P., S.C. Bunting and P. Morgan. 1995. Whitebark pine and fire suppression in small wilderness areas. USDA Forest Service General Technical Report INT-GTR-320.
- _____. 1998. Fire history of an isolated subalpine mountain range of the intermountain region, United States. *Journal of Biogeography* 25:1071–1080.
- Norment, C.J. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. *Northwest Science* 65:2–9.
- Perkins, J.L. 2004. *Pinus albicaulis* seedling regeneration after fire. PhD dissertation, University of Montana.
- Pfister, R.D., B.L. Kovalchik, S.F. Arno and R.C. Presby. 1977. Forest habitat types of Montana. USDA Forest Service General Technical Report INT-34.
- Reinhardt, E.D. and K.C. Ryan. 1988. How to estimate tree mortality resulting from underburning. *Fire Management Notes* 49:30–36.
- Running, S.W. 2006. Is global warming causing more, larger wildfires? *Science* 313:927–928.
- Ryan, K.C. and E.D. Reinhardt. 1988. Predicting postfire mortality of seven western conifers. *Canadian Journal of Forest Research* 18:1291–1297.
- Scott, G.L. and W.W. McCaughy. 2006. Whitebark pine guidelines for planting prescriptions. Pages 84–90 in L.E. Riley, R.K. Dumroese and T.D. Landis (tech coords), *National proceedings: Forest and Conservation Nursery Associations—2005*. USDA Forest Service Proceedings RMRS-P-43.
- Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. *Journal of Animal Ecology* 51:451–467.
- _____. 1998. Clark's nutcracker. *The Birds of North America* No. 331. Philadelphia PA: The Birds of North America.
- _____. 2005. The impact of seed dispersal by the Clark's nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. Pages 181–201 in G. Broll and B. Keplene (eds), *Mountain Ecosystems: Studies in Treeline Ecology*. Heidelberg DE: Springer.
- Tomback, D.F., S.F. Arno and R.E. Keane. 2001. *Whitebark Pine Communities: Ecology and Restoration*. Washington DC: Island Press.
- Tomback, D. F., L.A. Hoffman and S. K. Sund. 1990. Coevolution of whitebark pine and nutcrackers: Implications for forest regeneration. Pages 118–130 in W.C. Schmidt and K. MacDonald (comps), *Proceedings—Symposium on whitebark pine ecosystems: Ecology and management of a high mountain resource*. USDA Forest Service General Technical Report INT-270.
- 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 Forest Research* 23:113–119.

Waring, K.M. and D.L. Six. 2005. Distribution of bark beetle attacks after whitebark pine restoration treatments: A case study. *Western Journal of Applied Forestry* 20:110–116.

Robert E. Keane is a Research Ecologist with the USDA Forest Service, Rocky Mountain Research Station at the Missoula Fire Sciences Laboratory, 5775 Hwy 10 West, Missoula, MT 59808, 406/329-4846, Fax: 406/329-4877, rkeane@fs.fed.us.

Russell A. Parsons is a Research Ecologist with the USDA Forest Service, Rocky Mountain Research Station at the Missoula Fire Sciences Laboratory, 5775 Hwy 10 West, Missoula, MT 59808, 406/329-4872, Fax: 406/329-4877, rparsons@fs.fed.us.