NRC Research Press

ARTICLE

The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) populations are declining nearly rangewide from a combination of factors, including mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) outbreaks, the exotic pathogen *Cronartium ribicola* J.C. Fisch. 1872, which causes the disease white pine blister rust, and successional replacement due to historical fire exclusion practices. With high mortality in cone-bearing whitebark pine, seed production may not be sufficient to support natural regeneration after disturbance such as wildfire. Our objective was to examine the relationship between whitebark pine seed source health and whitebark pine regeneration density in adjacent burns. We sampled regeneration and seed source health in 15 burns within six national forests and three Wilderness Areas in Montana, ranging from 5 to 23 years old. We found a significant, positive relationship between seed source health and seedling density in adjacent burns. Natural regeneration was sparse when the proportion of damaged or dead whitebark pine in the seed source exceeded 50%. Factors that influenced the presence of whitebark pine regeneration within a burn included both vegetation cover and potential solar radiation. Sites closer to seed sources had higher probabilities of seedling occurrence, but seedlings were present throughout most burns. Our results suggest that managers can prioritize restoration plantings of whitebark pine seedlings after wildfire based on the health status of the nearest seed sources.

Key words: Pinus albicaulis, postfire regeneration, wildfire, white pine blister rust, mountain pine beetle.

Résumé : Les populations de pin à écorce blanche (*Pinus albicaulis* Engelm.) diminuent presque partout dans l'aire de répartition à cause d'une combinaison de facteurs incluant : les épidémies du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins, 1902), le pathogène exotique *Cronartium ribicola* J.C. Fisch. 1872, qui cause la rouille vésiculeuse du pin blanc, et le remplacement successionnel dû aux pratiques historiques d'exclusion du feu. À cause de la mortalité élevée des pins à écorce blanche qui portent des cônes, la production de graines pourrait être insuffisante pour supporter la régénération naturelle après une perturbation telle qu'un feu de forêt. Notre objectif consistait à examiner la relation entre l'état de santé des semenciers et la densité de la régénération de pin à écorce blanche dans les brûlis adjacents. Nous avons échantillonné la régénération et l'état de santé des semenciers dans 15 brûlis âgés de 5 à 23 ans situés dans six forêts nationales et trois réserves intégrales du Montana. Nous avons trouvé une relation positive significative entre l'état de santé des semenciers et la densité des semis dans les brûlis adjacents. La régénération naturelle était clairsemée lorsque la proportion de semenciers infestés ou morts parmi les de pins à écorce blanche dépassait 50 %. Les facteurs qui influençaient la présence de régénération de pin à écorce blanche dans un brûlis incluaient le couvert végétal et le rayonnement solaire potentiel. La probabilité de retrouver des semis était plus forte dans les sites situés plus près des semenciers mais il y avait des semis partout dans la plupart des brûlis. Nos résultats indiquent que les aménagistes peuvent prioriser les plantations de semis de pin à écorce blanche comme moyen de restauration après un feu de forêt sur la base de l'état de santé des semenciers les plus proches. [Traduit par la Rédaction]

Mots-clés : Pinus albicaulis, régénération après feu, feux de forêt, rouille vésiculeuse du pin blanc, dendroctone du pin ponderosa.

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is widely distributed throughout the mountains of the western United States and Canada but restricted to subalpine and treeline elevations (Arno and Hoff 1990). Its seeds are an important food source for Clark's nutcrackers (*Nucifraga columbiana* (A. Wilson, 1811)), which are the pine's primary seed dispersers (Hutchins and Lanner 1982; Tomback 1982), and for other granivorous birds and mammals, including grizzly bears (*Ursus arctos horribilis* Ord, 1815) (Tomback et al. 2001*a*). Whitebark pine serves as a foundation species in subalpine ecosystems by both structuring communities and stabilizing ecosystem functions, as well as acting as a keystone species by fostering biodiversity (Ellison et al. 2005; Tomback and Achuff 2010).

Invasive disease, native pest outbreaks, and fire exclusion practices have resulted in major losses of this keystone subalpine tree species. The exotic pathogen white pine blister rust (WPBR, *Cronartium ribicola* J.C. Fisch. 1872) is present throughout most of the range of whitebark pine, reducing cone production and killing trees (Schwandt et al. 2010; Tomback and Achuff 2010). Estimates of WPBR infection levels are variable but range from a low of 0%–24% in the Sierra Nevada Range (Maloney 2011) to over 73% in the northern US and southern Canadian Rocky Mountains (Smith et al. 2008), with overall mortality doubling over the course of 20 years in the Bob Marshall Wilderness in northwest Montana (Retzlaff et al. 2015). In the Canadian Rocky Mountains, mean WPBR infection levels have risen from 42% in 2003–2004 to

Received 29 January 2015. Accepted 14 July 2015.

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52% in 2009 (Smith et al. 2008, 2013), with mortality increasing from 18% to 28% over the same time period. In the Greater Yellowstone ecosystem, Bockino and Tinker (2012) found infection rates of over 80% in stands where WPBR was present. In addition, current climate-driven mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) outbreaks have killed cone-bearing whitebark pine at unprecedented rates that could severely depress the regeneration potential of the species (Schwandt et al. 2010; Macfarlane et al. 2013). Finally, fire exclusion policies over the past 100 years are leading to successional replacement of whitebark pine by shade-tolerant conifers in many areas (Keane et al. 1994; Murray et al. 2000). These threats were cited in whitebark pine's recent listing as a candidate species under the United States Endangered Species Act (U.S. Fish and Wildlife Service (USFWS) 2011) and as endangered in Canada under the Species at Risk Act (Government of Canada 2012).

The upper subalpine forests of the northern Rocky Mountains are generally fire prone, with long fire return intervals of 50–400 years for mixed severity fires (Arno and Hoff 1990; Morgan et al. 1994). Despite widespread fire exclusion practices, some fires are allowed to burn on federal lands as "fire for resource benefit", whereas other wildfires burn in whitebark pine forests in spite of suppression efforts (Parsons and Landres 1998). In many parts of the northern Rocky Mountains, the effects of multiple stressors on whitebark pine stands raise several important questions: (*i*) given the widespread declining condition of the whitebark pine seed source, can whitebark pine effectively regenerate in these burns? and (*ii*) is there a measure of seed source health that managers can use to decide which burned areas will need to be planted because of the loss of nearby seed sources?

Whitebark pine regeneration depends on where Clark's nutcrackers cache seeds and the suitability of the cache site for seed germination and seedling establishment (Tomback 2001). Because nutcrackers often cache seeds several kilometers away from a seed source, whitebark pine is often one of the first trees to colonize large, stand-replacing burns (Tomback et al. 1990, 1993, 2001*b*). Additionally, burned areas tend to promote conditions favorable for whitebark pine germination and establishment by providing many ground features, i.e., "nurse objects", that provide protection from environmental exposure (Tomback et al. 1993; Lonergan et al. 2014), reduced litter cover (McCaughey and Weaver 1990), higher levels of soil nutrients (Perkins 2015), and reduced competition from other conifer species that are physiologically less tolerant of environmental exposure (Maher and Germino 2006; Bansal et al. 2011). Evidence suggests that whitebark pine seedlings growing in burns are more robust and have a greater chance to reach cone-producing maturity. Perkins (2015) and Tomback et al. (2011) found higher growth rates of whitebark pine seedlings that had established in burned areas as opposed to closed-canopy forests, whereas Izlar (2007) and Lonergan et al. (2014) found higher survival of planted seedlings on burned sites vs. unburned sites. In summary, fire is often favorable and, in most cases, necessary for the long-term development of whitebark pine forest communities (Keane et al. 2012).

Recently, there has been concern among land managers that high-elevation burns may actually be detrimental to certain populations of whitebark pine (Keane et al. 2012). If a seed source adjacent to a burn produces only a few cones because mature trees are damaged or dead, Clark's nutcrackers may not utilize the seed source or much of the available seed could be consumed by birds and mammals, resulting in low whitebark pine regeneration densities (McKinney and Tomback 2007; McKinney et al. 2009; Barringer et al. 2012). Although some Clark's nutcrackers will transport seeds up to 30 km from a seed source to cache seeds within a defined home range, most caching occurs locally (Lorenz et al. 2011). Managers need to know if sufficient natural regeneration in a burn will occur so they can decide if they need to supplement natural whitebark pine regeneration with planted seedlings (Keane et al. 2012). Regionally coordinated planting of whitebark pine seedlings grown from parents with demonstrated WPBR resistance is a benchmark of the Keane et al. (2012) whitebark pine restoration strategy; implementation of this strategy will be most efficient by considering natural whitebark pine regeneration potential.

In this study, we evaluate natural whitebark pine regeneration patterns following wildfire in areas in the US northern Rocky Mountains, given varying levels of damage and mortality in nearby seed sources. It builds on preliminary work completed by Tomback et al. (2008) in four burns in or near the Bob Marshall Wilderness Complex, Montana. The central objective of this study was to examine effects of seed source health (considering factors such as WPBR infection and outbreaks of mountain pine beetle) on natural regeneration density in large, stand-replacing burns (>100 ha). We hypothesized that there may be a threshold in the relationship between regeneration density and seed source health that would result from a level of seed production that both attracts nutcrackers to a stand and provides sufficient seed for caching (e.g., McKinney et al. 2009; Barringer et al. 2012). In addition, we evaluated site conditions within the burns that may have influenced whitebark pine seedling establishment and described the health and age characteristics of whitebark pine seedlings within burns.

Methods

Study areas

Study areas were identified using extensive GIS analysis and the expertise of local land managers; we analyzed fire histories using MTBS (Monitoring Trends in Burn Severity) data (Eidenshenk et al. 2007) and LANDFIRE vegetation data (LANDFIRE 1.1.0 (U.S. Department of the Interior 2011)) to find burned areas that met the following criteria: (*a*) burned terrain within the elevational range of whitebark pine, (*b*) burns that were at least 5 years old to accommodate delayed germination, (*c*) terrain burned by a stand replacement fire greater than 100 ha, and (*d*) burned area adjacent to at least 100 ha of unburned forest that contained seed-producing whitebark pine trees at the time of the fire. After identifying possible study areas, we prioritized sites that were accessible by foot or vehicle. We attempted to sample across a broad range of seed source health conditions, from relatively intact stands with little whitebark pine mortality to highly impacted stands with extensive mortality. All study areas were located in Montana and ranged geographically from the Flathead National Forest in the north to the Gallatin National Forest in the south–central part of the state, and included three large Wilderness Areas (Fig. 1; Table 1).

Each study area had two distinct sampling components with different sampling objectives. The "seed source" component refers to a patch or stand of mature trees adjacent to or within each sampled burn. Seed sources contained at least 2.0 $m^2 \cdot ha^{-1}$ basal area of mature, live whitebark pine (Barringer et al. 2012) (Table 1). Seed source boundaries generally followed the burn perimeter, but we included patches of unburned, mature trees > 1 ha within the burn as potential seed sources. In these cases, we only sampled seed source characteristics in the largest patch. We used GIS data including aerial photos, elevation data, and LANDFIRE vegetation data and field notes to delineate seed source boundaries for sampling and analysis purposes. The "burned area" component refers to the sampled portion of the burn, adjacent to the seed source(s), and meeting the criteria described above (stand-replacing burn within the elevational distribution of whitebark pine).

Seed source sampling

Seed source stands were sampled using fixed-area, circular plots (area, 400 m^2; radius, 11.28 m). Seed source plots were located along a transect parallel to and 100 m from the edge of the burn (Fig. 2). At sites with multiple seed source patches, we sampled in

Fig. 1. Map of study region showing the location of 15 study areas (squares) across Montana, USA. Shaded areas indicate the United States National Forest; the Continental Divide is shown for reference.

the most prominent or largest patch. The first plot center was selected at random, and each subsequent plot center was located 50 m farther along the transect. We sampled four seed source plots at each burn. In the preliminary study, Tomback et al. (2008) used 500 m² belt transects to assess seed source stands; in 2010, we switched to fixed area plots with nested seedling subplots to better assess vegetation and regeneration characteristics in the seed source.

We used FIREMON methods (Lutes et al. 2006) for measuring plot and tree characteristics, recording UTM coordinates for each plot, slope, aspect, elevation, landform, ground cover, and upper (>3 m tall), mid (>1 m and <3 m tall) and lower (<1 m tall) dominant plant species. We also obtained measurements for mature trees following FIREMON protocol, including the diameter at breast height (DBH, 1.37 m), height, height to live crown base, species, and health status (healthy, unhealthy, sick, or dead) for each tree over 11.5 cm DBH in the plot boundary. For each living, mature whitebark pine tree, we recorded the percent of crown killed by WPBR, abiotic factors, or unknown factors. We confirmed mountain pine beetle damage by pitch tubes and (or) frass at the base of the tree. WPBR was confirmed by a combination of three or more indicators, including stem or branch cankers, presence of aecial spore sacs, foliage flagging, and (or) rodent chewing. A tree was deemed healthy if it showed no sign of insect or disease damage, unhealthy if nonlethal insect or disease damage was present (i.e., a branch canker > 0.15 m from the bole or indication of an unsuccessful beetle attack), and sick if the tree was expected to die within 5 years or could no longer produce cones (i.e., active stem cankers, >50% crown kill, top kill, or indication of a successful beetle attack). For dead whitebark pine trees, we attempted to estimate if the trees were dead prior to or after the fire. We also tallied live saplings (trees with DBH < 11.5 cm) by 2.5 cm DBH classes and recorded average height and crown base height. Finally, we tallied seedlings by species and 0.3 m height classes in a nested fixed-area, circular plot (area, 40 m², radius, 3.64 m).

Burned area sampling

Within a burn, we established fixed area, circular plots (area, 15 m², radius, 2.18 m) along a set of parallel transects that ran from the most prominent seed source stand toward the center of the burn (Fig. 2). We sampled between 30 and 80 plots at each burn, with a grid resolution at or near 100 m between both plots and transects. Tomback et al. (2008) sampled between 22 and 48 plots at each burn, with 25 m spacing between plots and transects. In 2010, we increased the distance between plots to sample a larger portion of the burn. The distance and azimuth between plots and transects were measured by cloth tape and compass, respectively. At each plot, we recorded UTM coordinates, elevation, aspect, and slope, and visually estimated percent ground cover and percent vegetation cover (vertically projected) according to FIREMON protocols. We measured whitebark pine seedlings individually and tallied all other conifer seedlings and saplings by 10 cm height class and species. For each whitebark pine seedling or sapling, we sampled the additional variables of microsite (distance in metres to any major ground feature such as a rock, stump, snag, etc.), presence or absence of WPBR symptoms, and seedling age (estimated from branch whorls). If a plot was unburned or topographically inaccessible, we offset the plot location by up to 20 m or skipped the plot entirely. We ran transects as far as possible into each burn but ceased sampling when we reached the lower elevational limits of whitebark pine or where the topography became inaccessible.

Data analysis

To analyze whitebark pine regeneration patterns, we developed two sets of models. One model describes how overall whitebark pine regeneration density varies among sampled burns. Whitebark pine regeneration increases over time following fire (Tomback et al. 2011); therefore, we normalized the overall mean regeneration density at each site by the number of years since fire at the time of sampling. This step was critical in isolating the effects of seed source health on regeneration density. The second model describes microsite or environmental variables within each burn that might influence the presence or absence (as opposed to density) of regeneration at a given plot. As a result of the caching habits of the Clark's nutcracker, whitebark pine seedlings often grow in clusters (Tomback 1982). For our purposes, each seedling cluster was counted as one regeneration site. All data analyses were completed using the software program R version 3.0.1 (R Core Team 2014).

Regeneration density model selection

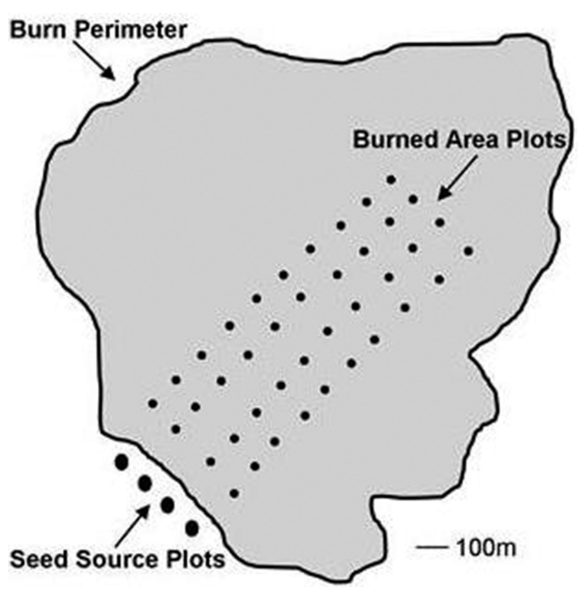
Regeneration densities among burns were compared using simple, multiple, and piecewise linear regression. In using linear regression, we assumed that the response was a linear function of the predictor variables and that errors were normally distributed, independent, and had equal variance. To test these assumptions, we plotted and assessed the residuals from each model. Numerous measures of seed source health were tested as potential predictors of seedling density in the burn (see Table 2). These included (*i*) mature whitebark pine basal area stratified by health class (healthy, unhealthy, or dead), (*ii*) mean percent whitebark pine crown kill, (*iii*) ratio of subalpine fir basal area to whitebark pine basal area, (*iv*) whitebark pine regeneration density in the seed source, and (*v*) proportion of mature whitebark pine in each health class. Measures of overall site severity (mean heatload, potential solar radiation, and burn severity; see description below) were tested but thrown out due to the geographic variation among study areas that confounded the results. We used piecewise regression to test

Table 1. Summary of subalpine burns in Montana, USA, sampled for this study, in order of decreasing seed source health.

Burn name	Year burned	Size of burn (ha)	WBP basal area in seed source ($m^2 \cdot ha^{-1}$)	Healthy WBP in seed source (%)	Mean WBP seedling density in seed source ($clusters \cdot ha^{-1}$)	SD WBP seedling density in seed source ($clusters \cdot ha^{-1}$)	Study location
Pettengill	2007	6192	12.3	65.1	1174	738	Beaverhead-Deerlodge NF
Mussigbrod	2000	11 178	20.5	62.2	185	371	Anaconda-Pintler Wilderness, Beaverhead-Deerlodge NF
Fall Fork	2000	850	44.4	60.5	124	143	Anaconda-Pintler Wilderness, Beaverhead-Deerlodge NF
Red Owl	1984	591	NA	43.3	NA	NA	Flathead NF
Charlotte Pk	1985	2385	23.8	40.9	NA	NA	Bob Marshall Wilderness, Flathead NF
Beaver Creek	2000	4323	5.5	26.7	1297	865	Gallatin NF
Wyman	2007	14 374	4.6	26.7	988	1159	Beaverhead-Deerlodge NF
Bighorn Lk	1988	80 961	3.6	22.5	2224	1555	Scapegoat Wilderness, Helena NF
Skalkaho	2000	3027	16.5	20.3	432	371	Bitterroot NF
Monitor Mtn	1988	80 961	2.8	16.7	3645	3991	Scapegoat Wilderness, Lewis and Clark NF
Gates Park	1988	22 093	10	14	0	0	Bob Marshall Wilderness, Lewis and Clark NF
Challenge	1998	3846	3.9	13.3	NA	NA	Flathead NF
Ann	1994	1265	3.1	7.7	556	816	Bitterroot NF
Monture	2000	9624	5.2	2.7	1977	2917	Bob Marshall Wilderness, Flathead NF
Helen Creek	1994	2846	19.6	1.6	NA	NA	Bob Marshall Wilderness, Flathead NF

Note: The WBP basal area in seed source is the basal area of mature whitebark pine trees with the potential to produce cones (i.e., not damaged or dead). WBP, whitebark pine; SD, standard deviation; NF, National Forest; NA, not available.

Fig. 2. Study area layout. All plots were sampled at or above the lower elevational limit of whitebark pine.



for a statistical threshold in the relationship between regeneration density and seed source health and tested quadratic forms of predictor variables to look for curvilinear relationships. Predictor variables and interaction terms were eliminated using *t* tests; nested models were compared using *F* tests in an analysis of variance (ANOVA). We also used Spearman's rank order correlation (r_s) to test whether whitebark pine regeneration density in each burn was related to regeneration density in the adjacent seed source.

Seedling probability model selection

Because many of our burned area plots had no seedlings, we used nonparametric analysis methods in evaluating site conditions within burns that might influence the occurrence of whitebark pine seedlings at the plot level. Nearly all burned area plots had fewer than five regeneration sites; therefore, we were unable to model relative differences in seedling density within a burn. Instead, we built a logistic regression model to assess factors that influenced seedling presence or absence at each plot. We used a generalized additive mixed model (GAMM) to gain a visual understanding of the relationships between explanatory variables and the probability of seedling occurrence. Then we used generalized linear mixed models (GLMM; binomial family and logit link (R Core Team 2014)) to further assess and refine the relationships (Table 3). We did not include data from Tomback et al. (2008) in the seedling probability model due to sampling resolution and protocol differences.

For both the GAMM and GLMM models, the burn study area was included as a random effect to reflect coarse-scale site differences, including time since fire. We included potential solar radiation, topographic convergence index (TCI), distance to seed source, percent vegetation cover, heatload, and relative differenced normalized burn ratio (RdNBR) (i.e., burn severity) as fixed effects (Table 3). Radiation, TCI, and distance to seed source were all obtained using ArcGIS (v.10.1). To calculate radiation and TCI, we used the Solar Radiation and Flow Accumulation tools within the Spatial Analyst toolset on a digital elevation model of each burn. For the Solar Radiation tool, we updated the slope and aspect to reflect field measurements, which more accurately depicted plot-level characteristics; we used the default inputs in ArcGIS for sampling frequency and calculated total solar radiation ($Wh \cdot m^{-2}$) for an approximate growing season (1 May – 31 October). TCI was calculated using the equation TCI = ln(flow accumulation/tan(slope)). Distance to nearest seed source was calculated using the Near tool, under the Proximity toolset. Seed sources included both mature whitebark pine forests along the burn perimeter and large patches (>1 ha) of unburned forest within the burn perimeter. Vegetation cover (%) was estimated when plots were sampled. We calculated heatload according to the methods of McCune and Keon (2002), and RdNBR values (Miller and Thode 2009) were extracted from MTBS raster data for each burn.

Table 2. Summary of linear regression models for the mean whitebark pine regeneration density among 15 burn study areas in Montana, USA.

Model predictor variable(s)	Coefficients	SE	R^2	P value
Healthy WBP BA	1.397	0.60	0.25	0.037*
Healthy WBP BA + unhealthy WBP BA	0.998	0.53	0.16	0.085
Dead WBP BA	−1.014	0.86	0.02	0.262
Mean WBP crown kill (%)	−0.889	0.23	0.48	0.002**
Ratio of live SAF BA to live WBP BA	−9.789	7.39	0.07	0.218
WBP regeneration density in seed source (clusters·ha^{-1})	−0.009	0.01	0.07	0.222
%healthy WBP	0.850	0.20	0.54	0.001***
(%healthy WBP)^2	0.013	0.00	0.69	0.0001***
%healthy WBP + unhealthy WBP	0.634	0.23	0.33	0.015*
%dead WBP	−0.520	0.25	0.19	0.060
%healthy WBP + (%healthy WBP)^2	**−0.957+0.026**	**0.66, 0.01**	**0.70**	**<0.001*** **
Correlation between measures of seed source health				
%healthy WBP | healthy WBP BA	1.708	0.41	0.56	0.001**
%healthy WBP | mean WBP crown kill (%)	−1.001	0.13	0.81	<0.001***
Healthy WBP BA | mean WBP crown kill (%)	−0.352	0.10	0.47	0.004**

Note: WBP, whitebark pine; SAF, subalpine fir; BA, basal area (m^2·ha^{-1}); SE, standard error. Final model is in bold; also shown are correlations between measures of seed source health. *, P value significant at 0.05; **, P value significant at 0.01; ***, P value significant at 0.001. The seed source WBP regeneration density data are available for only 11 of 15 study areas.

Table 3. Summary of generalized linear mixed model (GLMM, family = binomial, link = logit) predicting probability of whitebark pine seedling presence at plots located throughout 15 burns in Montana, USA.

Model and fixed effects (study area = random effect)	Coefficients	SE	P value
Full model			
Heatload index	-2.169×10^{-1}	1.390	0.8759
RdNBR	3.543×10^{-4}	5.355×10^{-4}	0.5082
Topographic convergence index (TCI)	-7.475×10^{-2}	8.732×10^{-2}	0.3920
Potential solar radiation (Wh·m^{-2})	-3.942×10^{-6}	1.728×10^{-6}	0.0226*
Distance to seed source (m)	-7.104×10^{-3}	1.867×10^{-3}	0.0001***
Distance to seed source^2	6.316×10^{-6}	1.794×10^{-6}	0.0004***
Vegetation cover (%)	7.486×10^{-2}	2.833×10^{-2}	0.0082**
Vegetation cover^2	-1.085×10^{-3}	3.229×10^{-4}	0.0008***
Final, reduced model			
Potential solar radiation (Wh·m^{-2})	-4.346×10^{-6}	1.337×10^{-6}	0.0012**
Distance to seed source (m)	-5.993×10^{-3}	1.628×10^{-3}	0.0002***
Distance to seed source^2	5.367×10^{-6}	1.626×10^{-6}	0.0097***
Vegetation cover (%)	5.948×10^{-2}	2.548×10^{-2}	0.0196*
Vegetation cover^2	-8.759×10^{-4}	2.786×10^{-4}	0.0017**

Note: *, P value significant at 0.05; **, P value significant at 0.01; ***, P value significant at 0.001. SE, standard error.

We eliminated potential explanatory terms from the model using Wald z tests (α = 0.05) and compared nested models using χ^2 tests in an ANOVA to determine whether progressively simpler models were statistically different from more complex models. We tested the accuracy of the final model with a ten-fold cross-validation of the area under the curve statistic. The threshold for determining whether a predicted probability would revert to seedling presence or absence was 0.32, which was the prevalence of seedlings in the combined dataset.

Results

In total, we sampled 15 burns across Montana, ranging from 5 to 23 years following fire (Fig. 1; Table 1). The basal area of live mature whitebark pine in the seed source ranged from 2.8 to 44.4 m^2·ha^{-1}, which was above the threshold identified for a high likelihood (0.75) of nutcracker visitation, as reported in Barringer et al. (2012). Whitebark pine seedling densities in the burns were highly variable across and within sites (Fig. 3; Table 4). Mean study area level densities ranged from 0 to 783 seedling clusters·ha^{-1} (Table 4), with individual plot level densities ranging from 0 to 6000 seedling clusters·ha^{-1}. When normalized by number of years since fire, mean study area level seedling densities ranged from 0 to 86 seedling clusters·ha^{-1}·year^{-1} (Table 4). The Charlotte Peak burn on the Flathead National Forest had the highest overall seedling density but was also one of the oldest burns. When normalized by years since fire, the Pettengill burn on the Beaverhead-Deerlodge National Forest had the highest seedling density, followed by the Mussigbrod burn, which is also on the Beaverhead-Deerlodge National Forest. Two areas had no regeneration at the time of sampling, namely Challenge and Wyman, but these were relatively recent burns (7 and 5 years old, respectively).

Seed source health vs. regeneration density

We found that the greater the proportion of healthy whitebark pine trees in the seed source, the greater the mean seedling density in the burn (Fig. 4). Although several measures of seed source health were statistically significant predictors of seedling density in individual models (Table 2), these variables were often redundant (Table 2); the best model included only the proportion of mature whitebark pine in the seed source that were healthy (%healthy). Seedling density increased among burns in relation to %healthy (R^2 = 0.54, P = 0.001; Fig. 4a), but the R^2 and the residuals were improved by adding a quadratic term, %healthy^2 (R^2 = 0.70, P = 0.0002; Fig. 4b, residuals shown in Fig. 5). In a piecewise regression model, we identified a potential threshold of 50% healthy trees, above which seedling density increased at a higher rate (Fig. 4c). However, there were too few data points at high values of %healthy to determine the robustness of this threshold. We found no significant correlation between normalized whitebark pine regeneration density in burned areas and regeneration density in adjacent seed sources ($r_s(11) = -0.38$, p = 0.25).

Seedling occurrence within burns

We built a model that addresses some of the microsite factors that might influence seedling survival and establishment in burns after nutcracker caching (Table 3). We found that potential solar radiation, distance to seed source, and vegetation cover were significant predictors of whitebark pine seedling presence within the burn (Fig. 6; Table 3). The probability of seedling presence decreased with increasing distance to seed source up to about 600 m but then increased between 600 and 1200 m (the limits of the study), although with a high level of uncertainty given sparse sampling at this distance (Fig. 6a). The probability of seedling presence increased up to 30% vegetation cover but decreased above that (Fig. 6b). Finally, the probability of seedling presence decreased with increasing potential solar radiation (Fig. 6c). The

Fig. 3. Boxplots of whitebark pine seedling density by study area in order of decreasing seed source health. Median, solid black line; mean, solid black circle. Seedling density is normalized by number of years since fire.

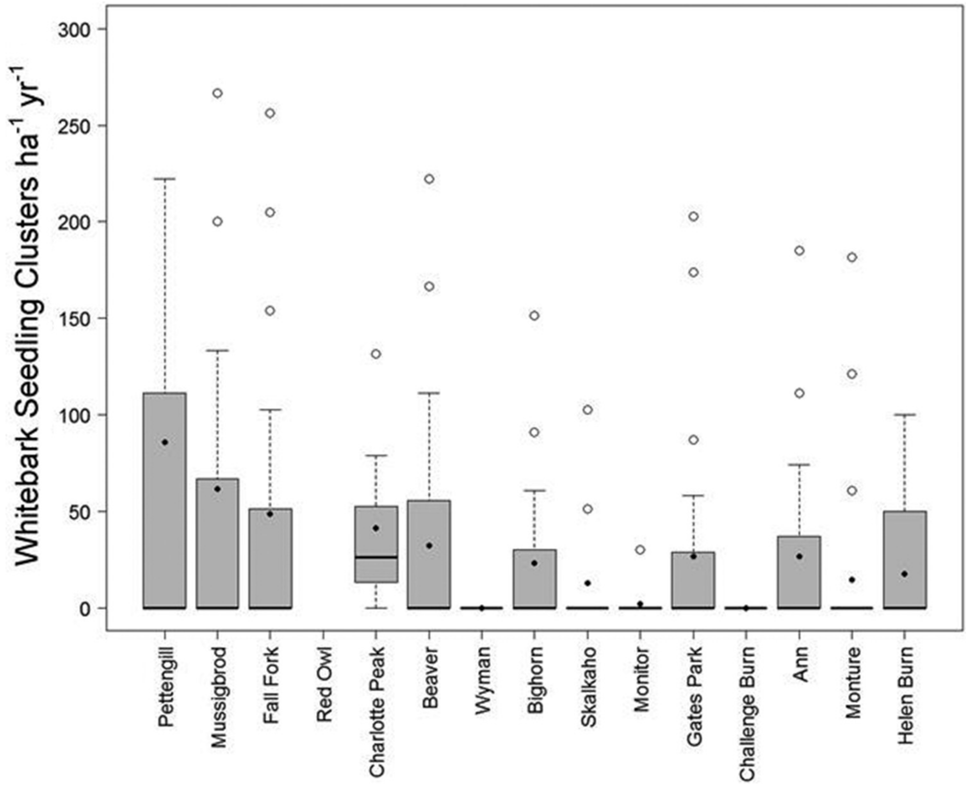


Table 4. Summary of whitebark pine regeneration data from 15 burn study areas in Montana, USA, in order of decreasing seed source health.

Site	n plots	Healthy WBP in seed source (%)	Mean WBP density (clusters·ha^{-1})	WBP SD (clusters·ha^{-1})	WBP SE (clusters·ha^{-1})	Normalized WBP density (clusters·ha^{-1}·year^{-1})	Normalized WBP SD (clusters·ha^{-1}·year^{-1})	Normalized WBP SE (clusters·ha^{-1}·year^{-1})
Pettengill	44	65.1	515	687.5	103.6	85.9	114.6	17.3
Mussigbrod	51	62.2	614	1048.5	146.8	61.4	104.9	14.7
Fall Fork	40	60.5	650	1012.2	160	48.7	77.9	12.3
Red Owl	22	43.3	273	428.9	91.4	13.6	21.4	4.6
Charlotte Pk	23	40.9	783	735.9	153.4	41.2	38.7	8.1
Wyman	30	26.7	0	0	0	0	0	0
Beaver	48	26.7	389	712.4	102.8	32.4	59.4	8.6
Bighorn Lk	80	22.5	508	836.9	93.6	23.1	38	4.3
Skalkaho	40	20.3	167	362	57.2	12.8	27.8	4.4
Monitor	30	16.7	44	169.1	30.9	2	7.7	1.4
Gates Park	39	14.0	615	1063.9	170.4	26.8	46.3	7.4
Challenge	32	13.3	0	0	0	0	0	0
Ann	50	7.7	480	762.4	107.8	26.7	42.4	5.9
Monture	50	2.7	160	394.1	55.7	14.5	35.8	5.1
Helen Creek	48	1.6	177	282.3	40.7	17.7	28.2	4.1

Note: WBP, whitebark pine; SD, standard deviation; SE, standard error.

mean area under the curve of this model was 0.75 (standard deviation, 0.05), indicating that the model had average skill in predicting seedling presence.

Whitebark pine seedling health and age

Out of 376 whitebark pine regeneration sites measured for this study, only 3% showed symptoms of WPBR. About 54% of seedlings were found within 0.5 m of a ground feature such as a rock, log, stump, or snag. Seedlings older than 15 years were difficult to age accurately using branch whorls, so we only analyzed age structure of seedlings in burns that occurred after the year 2000. In these six burns, we found that very few sampled, established seedlings germinated in the first 4 years following fire (Fig. 7). Across the five areas that burned in 2000 (Beaver Creek, Fall Fork, Monture, Mussigbrod, and Skalkaho), we found that only 2% of the sampled, established seedlings germinated in the first 2 years following fire, 11% germinated between 3 and 4 years following fire, 73% of seedlings germinated between 5 and 10 years following fire, and the remaining 14% germinated between 11 and 13 years following fire (the limit of the data). We also evaluated seedling ages within the same five burns to look for regional germination trends that would indicate masting events but did not find any patterns. The Mussigbrod fire had high germination in the year 2009, but this pattern was not evident in the Fall Fork fire, which occurred in the same geographic region. Interestingly, the Monture fire showed almost no germination after the year 2006, which coincides with the start of an observed mountain pine beetle outbreak in the seed source.

Fig. 4. (*a*) Simple linear, (*b*) multiple linear, and (*c*) piecewise models reflecting the relationship between seed source health (percent of mature trees in the seed source that are healthy) and seedling density (seedlings·ha^{-1}·year^{-1}) in the adjacent burn. Standard error bars are shown. The solid vertical line in (*c*) is a potential threshold identified in the piecewise model.

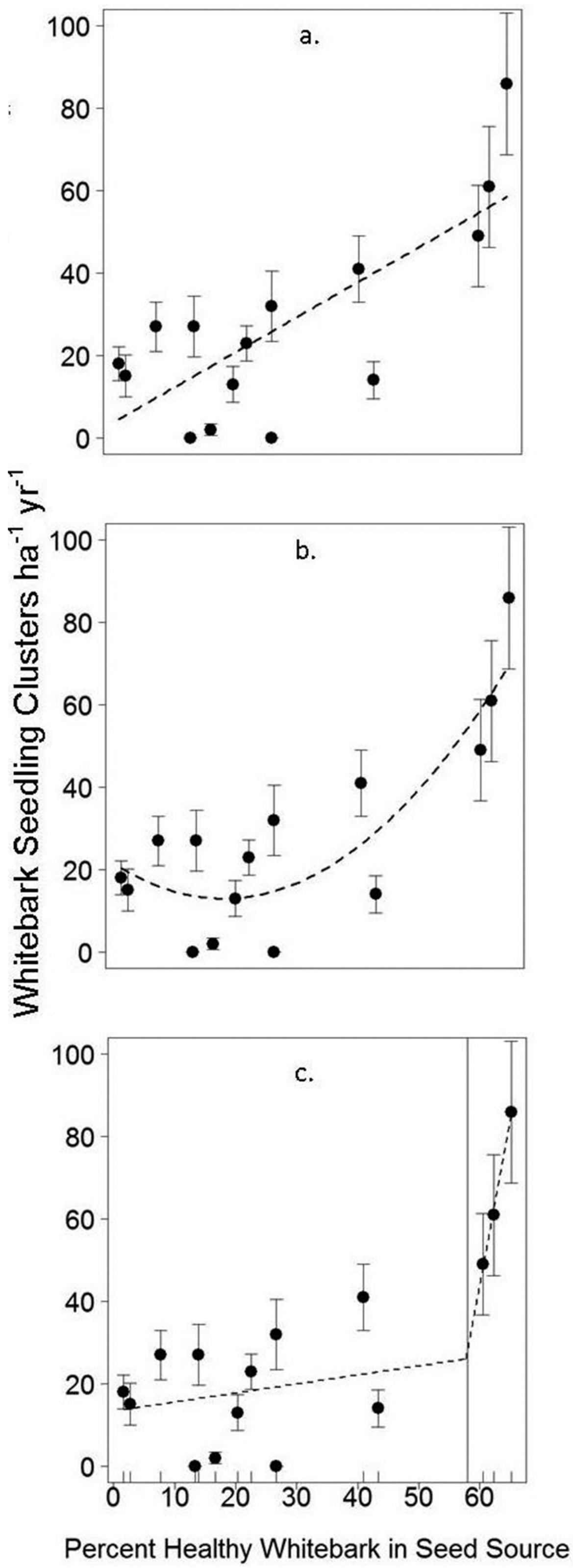
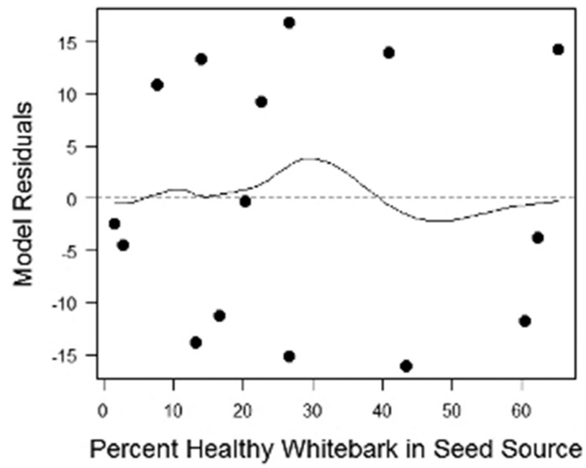


Fig. 5. Residuals with smoother curve from the top multiple linear model (Fig. 4*b*) reflecting the relationship between seed source health (percent of mature trees in the seed source that are healthy) and seedling density in the adjacent burn (seedlings·ha^{-1}·year^{-1}).



Discussion

Given the precipitous decline in whitebark pine in many regions and the importance of fire to successional whitebark pine communities, the question of whether whitebark pine is regenerating at historical rates becomes an important management issue. Several studies have explored whitebark pine regeneration after fire (Tomback et al. 1993, 1995; Perkins 2004; Moody 2006), but none have examined the relationship between whitebark pine seed source health and whitebark pine regeneration density in large burns. Overall, we found that seed source health predicted regeneration density and that distance to seed source, vegetation cover, and potential solar radiation were significant predictors of whitebark pine seedling presence within a burn.

Seed source health vs. regeneration density

Although natural whitebark pine regeneration was present throughout most of the sampled burns, seedling density increased in areas with healthier seed sources, which was likely an indication of greater nutcracker visitation and seed caching. The high variability in regeneration across our study sites (Fig. 3; Table 4) likely reflects bird-mediated seed dispersal and is inherent in this type of data. Barringer et al. (2012) found that regeneration density in unburned stands was related to the health and basal area of mature whitebark pine in the stand, but it was not clear that the relationship would hold for adjacent burned areas, because Clark's nutcrackers could transport seeds into burns from stands as far as 30 km away (Lorenz et al. 2011). Our results suggest that nutcrackers harvest seeds most often from local seed sources for caching in adjacent burns.

The best indicator of seedling density in the adjacent burn was the proportion of mature whitebark pines that were healthy (%healthy). "Healthy" whitebark pine forests are diverse in structure. Open-grown stands might have low basal areas, but cone production (therefore seed availability) might be high in the large, well-spaced crowns. This pattern is evident in a comparison of two of our sampling sites — Mussigbrod and Fall Fork — that burned in the same year, have similarly healthy seed sources (comprised of ~60% healthy whitebark pine), and are relatively close geographically. At Fall Fork, the seed source was dominated by whitebark pine growing in a dense, closed stand, whereas the seed source at Mussigbrod was open grown and park like. The basal area of mature whitebark pine in the Fall Fork seed source was more than twice that of Mussigbrod, but regeneration densities in the burn were essentially the same at both sites (Tables 1 and 4).

Fig. 6. Partial response curves from the generalized additive mixed model (GAMM) that illustrate the influence of (*a*) distance to seed source (DIST, m), (*b*) total vegetation cover (VEG, %) and (*c*) potential solar radiation (RAD, Wh·m^{-2}) on the probability of whitebark pine seedling presence, while holding the other predictor variables at their mean. Gray shading is ±2 standard errors; residuals are shown.

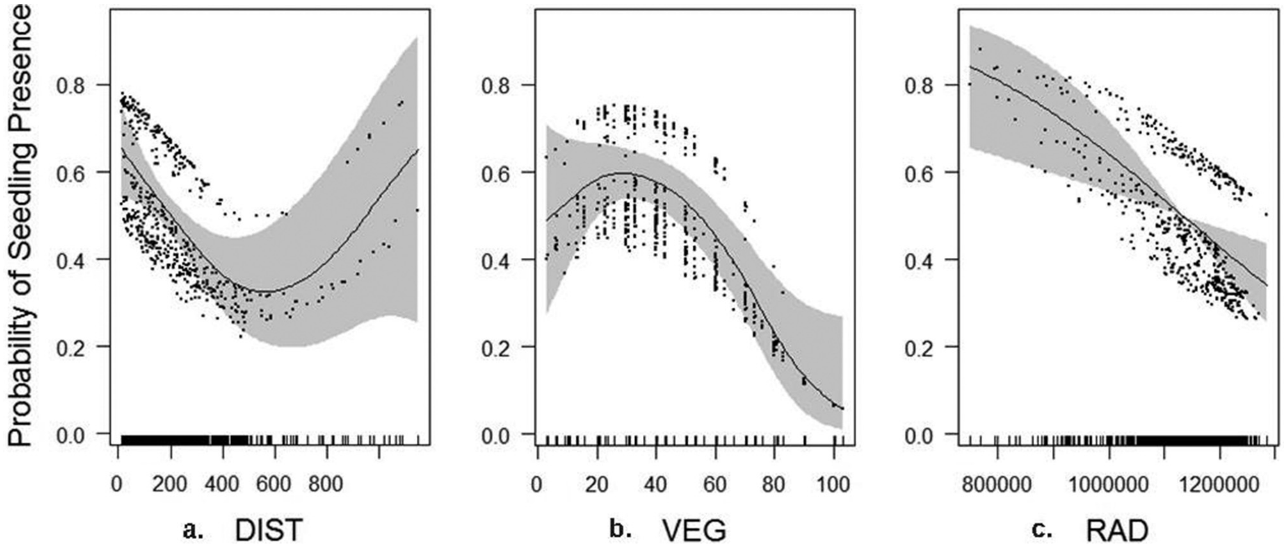
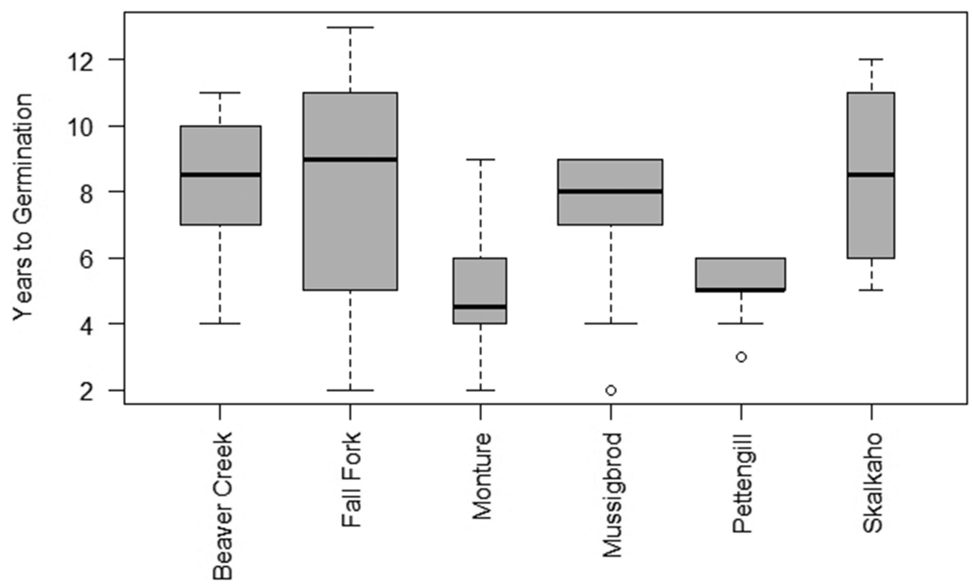


Fig. 7. Boxplots showing number of years following fire until germination of sampled whitebark pine seedlings in the five study areas that burned in the year 2000 and one study area (Pettengill) that burned in 2007. The median is shown by the black line and the width of each boxplot is proportional to the sample size. Note the lag period of at least 4 years until the majority of germination occurs.



Therefore, a qualitative measure such as %healthy may be an appropriate indicator of seedling density across different forest types in the absence of measuring actual cone production.

Factors affecting seedling occurrence

Numerous factors influence whitebark pine seed dispersal and subsequent seedling establishment at a given location. The magnitude and effectiveness of seed dispersal by the Clark's nutcracker are the most important factors and yet the most difficult to measure. Given this caveat, we identified several variables that influence the probability of seedling presence at a given site. Whitebark pine seedling occurrence generally decreased further from seed sources, but this pattern was inconsistent throughout the dataset (Fig. 6*a*). Tomback et al. (1990) found that seedling density declined as distance from the whitebark pine seed source increased (up to 3650 m), but this decline was also associated with an elevational loss of approximately 380 m. Although we intentionally sampled the largest, most continuous stand-replacing burns within our study area, it was a challenge to find portions of a burn that were greater than 600 m from a seed source, especially after accounting for patches of unburned seed source that reside within the burn perimeter. Most subalpine burns are spatially patchy across the landscape, which will result in some spatial heterogeneity in both whitebark pine seed sources and regeneration patterns (see Kolden et al. (2012)).

We found that intermediate amounts of vegetation cover were associated with increased whitebark pine seedling occurrence in sampled burns, but dense vegetation cover decreased the probability of seedling occurrence (Fig. 6*b*). Although we cannot know the percent vegetation cover under which seedlings first germinated in this study, our results suggest that the presence of some cover has facilitated survival. This finding is consistent with previous research

(McCaughey and Weaver 1990; Maher and Germino 2006; Tomback et al. 2011), indicating that although whitebark pine is more tolerant of exposure than other subalpine conifers, it is more likely to establish under partial-shade conditions. Tomback et al. (2011) found that some vegetation cover, in addition to woody debris cover, increased survival of seedlings that germinated after the 1988 Yellowstone Park fires; however, dense residual vegetation in the understory on moderately burned sites limited seedling survival. In addition to reducing competition from other conifers, burns provide an abundance of ground features such as fallen trees, branches, and stumps and low vegetation cover that can help protect new whitebark pine seedlings from desiccation and cold exposure. Seedling establishment is also influenced by changes in topography, which impacts the amount of solar radiation at a given site. Whitebark pine seedling occurrence decreased as potential solar radiation increased; this pattern is not surprising, because higher amounts of solar radiation may lead to lower soil moisture and increased seedling mortality (Maher et al. 2005), especially on an exposed site following fire.

Our results show that whitebark pine establishes for many years following a fire, which is consistent with previous findings (e.g., Tomback et al. 1993, 1995, 2001*b*, 2011). Only 13% of the seedlings that we sampled germinated in the first 4 years following a fire; Tomback et al. (2001*b*) found a similar pattern in a more fine-scale regeneration analysis of the 1988 Yellowstone Park fires. In their study, the first whitebark pine seedlings didn't emerge until 3 years following fire, following a masting event and two winters of seed dormancy. In general, it takes at least 5 years for whitebark pine to begin populating a burn, so immediate post-fire assessments are unnecessary.

Management implications

Our results indicate that in burned areas where more than 50% of the adjacent whitebark pine seed source is damaged or dead, low seed availability may limit natural regeneration potential (<300 seedling clusters·ha^{-1} 10 years following fire). Given that older, taller seedlings are more susceptible to WPBR infection, seedling and sapling mortality will likely increase over time in areas where WPBR is present (Tomback et al. 1995), which may prevent these stands from becoming productive, cone-producing forests. Long-term monitoring of whitebark pine regeneration at these sites is necessary to confirm or refute this trend, as WPBR susceptibility and resistance are highly variable at local and regional scales (Mahalovich et al. 2006).

The Keane et al. (2012) whitebark pine restoration strategy suggests a target density of approximately 250 seedlings·ha^{-1} (6.1 m spacing) for optimal long-term forest structure. This target is based on planted WPBR-resistant seedlings with an assumed survival rate of 50% and will vary based on stand-level forest structure objectives. Target densities for natural regeneration need to be adjusted to local seed source WPBR infection and resistance levels, which will ultimately determine seedling survival. Managers can use WPBR-resistance data from nearby plus trees (trees with demonstrated WPBR resistance, see Mahalovich and Dickerson (2004)) to estimate WPBR resistance in natural regeneration, as it will usually be a mix of putatively resistant and susceptible seedlings. If managers choose to supplement natural regeneration with planted seedlings, they should utilize seedlings grown from screened parents containing multigenic partial WPBR resistance (Keane et al. 2012), because there has been a trend in increased incidence of WPBR infection among trees in all regions (Maloney et al. 2012; Smith et al. 2013). It is also important to note that regeneration rates are but one of the key vital rates that influence population growth rates following wildfire. Although regeneration density and mortality are important indicators of potential forest structure, managers should also consider long-term adult growth rates, fecundity, masting frequency, and mortality rates as WPBR-infection levels stabilize or increase (Maloney et al. 2012). Long-term monitoring of natural regeneration characteristics, planted seedling survivorship, and seed source health is critical in developing effective restoration plans (Keane et al. 2012).

Fire managers are often faced with conflicting issues when determining whether or not to suppress high-elevation fire. On one hand, fire is an integral process in shaping the subalpine landscape. On the other hand, fires that pose a risk to humans, structures and other developments, historical preservation, and other management objectives might preclude "letting it burn". Given that burned areas provide the conditions most favorable for whitebark pine seedling establishment and growth to reproductive maturity, suppressing high-elevation fire for the benefit of whitebark pine could be counterproductive. Patches of burns that are not regenerating will create landscape heterogeneity over time and may help limit the size of future disturbance. Fire suppression on a small scale that leads to the protection of healthy seed source stands and plus trees or small islands of subalpine habitat that hold special recreational or wildlife value comprises the best fire management response in whitebark pine forests (Keane et al. 2012).

Acknowledgements

We are grateful to Steve Wirt, retired Flathead National Forest, and Ward McCaughey, retired USDA Forest Service Rocky Mountain Research Station, for their contributions to the study. For field work in 2004–2005, we thank Deb Mucklow, Larry Schutz, Bob Jeligson, and Tad Wehunt of the Flathead National Forest, Spotted Bear Ranger District, for housing, logistical, and pack support. Dave Warder, Mary Lou Zimmerman, Kate Kendall, Susan Kemper, Marcie Johnson, Jennie Birdsall, and Marcia Youngman provided volunteer field support or logistic support during the study. Students from the University of Colorado Denver — Jennifer Berg, Kara Stevens, David Meyers, Kristen Grompone, Ashley East, Daniel Maddox, David Meyers, and Mario Perez — provided field assistance or help with data analysis in 2004–2006. For field work in 2010–2013, we thank Bob Hutton and Ben Wilson of the Beaverhead-Deerlodge National Forest and Wendel Hann, retired USDA Forest Service, for pack and logistical support. We also thank the Beaverhead-Deerlodge, Flathead, Gallatin, Helena, Lolo and Lewis and Clark National Forests for hosting us in the backcountry. We are grateful to the field crew — Sarah Flanary, Jay Fronden, Violet Holley, Brian Izbicki, Christy Lowney, Aaron Sparks, Greg Cohn, Edith Dooley, and Colin Hunton, all current or former employees of the USDA Forest Service, Rocky Mountain Research Station Fire Sciences Lab. Andrew Larson and Anna Sala of the University of Montana provided helpful reviews of this manuscript, as did two anonymous reviewers. Finally, we are all grateful to the USDA Forest Service, Rocky Mountain Research Station Fire Sciences Lab and Forestry Sciences Lab for funding and logistical support and to the University of Colorado Denver and University of Montana for general project support.

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