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THE EFFECTS OF SEED SOURCE HEALTH ON WHITEBARK PINE
REGENERATION DENSITY AFTER WILDFIRE

By

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2004

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Forestry

The University of Montana
Missoula, MT

December, 2014

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The effects of seed source health on whitebark pine regeneration density after wildfire

Chairperson: Solomon Dobrowski

Whitebark pine (*Pinus albicaulis*) is declining nearly range-wide largely from mountain pine beetle (*Dendroctonus ponderosae*) outbreaks and the exotic pathogen *Cronartium ribicola*, which causes the disease white pine blister rust. With high mortality in cone-bearing whitebark pine, seed production may not be sufficient to support natural regeneration after disturbance such as wildfire. The objective of this study was to examine the relationship between whitebark pine seed source health and whitebark pine regeneration density in adjacent, stand-replacing burns. I sampled regeneration patterns and seed source health and status in 15 burns within four national forests and three Wilderness Areas in Montana, ranging from five to 23 years old. I found a significant, positive relationship between seed source health and seedling density in adjacent burns. Natural regeneration was sparse when the proportion of infested or dead whitebark pine in the seed source exceeded 50%. Fine-scale factors that influenced the presence of whitebark pine regeneration within a burn included both vegetation cover and potential solar radiation. Sites closer to a seed source had higher probabilities of seedling occurrence, but seedlings were present throughout most burns. These results suggest that managers can prioritize where to plant rust-resistant whitebark pine seedlings after wildfire based on the health status of the nearest seed sources.

Keywords: *Pinus albicaulis*; whitebark pine; post-fire regeneration; wildfire; *Cronartium ribicola*; *Dendroctonus ponderosae*; white pine blister rust; mountain pine beetle; wilderness

Acknowledgements

I am grateful for everyone who contributed to the completion of this project. Thanks to my advisor, Solomon Dobrowski, who allowed me to work independently, yet provided academic and project support when I needed it. I appreciate the valuable input and support from my committee: Andrew Larson, Anna Sala and Robert Keane. I am especially grateful to Robert Keane who let me take this project on, found funding, gave me a field crew and served as an excellent supervisor in my years with the Forest Service. Diana Tomback provided helpful reviews of the thesis. Field work in the whitebark pine ecosystem is never dull, and Sarah Flanary, Jay Fronden, Violet Holley, Brian Izbicki, Christy Lowney, Aaron Sparks, Greg Cohn, Edith Dooley and Colin Hunton ensured that the work got done in rain, snow, sleet and sun. The USDA Forest Service Rocky Mountain Research Station Firelab provided financial support, and the Firelab employees provided project support and comic relief. The Whitebark Pine Ecosystem Foundation and a scholarship from Systems for Environmental Management also helped fund this project. Thanks to my professors and peers at the University of Montana College of Forestry and Conservation for providing a rich academic experience. My current employer, the Blackfoot Challenge, provided an immense amount of flexibility in allowing me to complete this project as planned.

I would like to thank my parents, Jarl and Sonja Leirfallom, for showing me the mountains at a young age and always supporting my endeavors. Also, thanks to Kris, Angela, Espen and Eva Leirfallom for their love, laughter and support. Finally, I am grateful to Ben Wilson, Abby-dog and several good friends for putting up with a grumpy, distracted grad student and ensuring that I didn't miss out on the good life.

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Chapter 1: The effects of seed source health on whitebark pine regeneration density after wildfire

Introduction

Whitebark pine (*Pinus albicaulis*) 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*), which are the pine's primary seed dispersers (Hutchins and Lanner 1982; Tomback 1982), and other granivorous birds and mammals including grizzly bears (*Ursus arctos horribilis*) (Tomback et al. 2001a; Tomback and Kendall 2001). Whitebark pine serves as a foundation species in subalpine ecosystems by both structuring communities and stabilizing ecosystem function, and as a keystone species by fostering biodiversity (Ellison et al. 2005; Tomback and Achuff 2010).

Invasive disease, native pest outbreaks, as well as fire suppression practices have resulted in major losses of this keystone subalpine tree species. The exotic pathogen white pine blister rust (*Cronartium ribicola*) 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 blister rust infection levels are variable, but range from a low of 0-24% in the Sierra Nevada Range (Maloney 2011) to 73% in the northern US and southern Canadian Rocky Mountains (Smith et al. 2008). In the Canadian Rockies, mean rust infection levels have risen from 42% in 2003-2004 to 52% in 2009 (Smith et al. 2008; 2013), with mortality increasing from 18% to 28% over the same time period. In addition, current climate-driven mountain pine beetle (*Dendroctonus ponderosae*) outbreaks have killed cone-bearing whitebark pine at

unprecedented rates that could severely depress the regeneration potential of the species (Logan and Powell 2001; 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 (USFWS 2011) and listing as endangered in Canada under the Species at Risk Act (Government of Canada 2012). Current pilot restoration efforts entail planting blister rust-resistant whitebark pine seedlings in suitable seed beds, often following prescribed burns or wildfire (Keane et al. 2012). We anticipate that regionally-coordinated seedling planting will be implemented at larger scales across the West. However, the decision where to plant seedlings needs to consider whether there is potential for natural whitebark pine regeneration. We expected that areas with higher levels of whitebark pine mortality have lower potential for natural regeneration, but this relationship had not been quantified. In this study, we evaluated natural whitebark pine regeneration patterns following wildfire, given varying levels of damage and mortality in nearby seed sources.

The upper subalpine forests of the northern Rockies 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," while other wildfires burn in whitebark pine forests in spite of suppression efforts (Parsons and Landres 1998). In many parts of the northern Rockies, the effects of multiple stressors on whitebark pine stands raises several important questions: (1) Given the widespread declining condition

of the whitebark pine seed source, can whitebark pine effectively regenerate in these burns? (2) 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 upon where Clark's nutcrackers cache seeds and the suitability of the cache site for seed germination and seedling establishment (Tomback 2001). Whitebark pine seeds are morphologically and physiologically adapted for seed caching by nutcrackers, remaining viable in a soil seed bank for several years (Tomback et al. 2001b, Tilman-Sutela et al. 2008). 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; Tomback et al. 1993; 2001b). Clark's nutcrackers may not necessarily prefer to cache seeds in burns (Lorenz et al. 2008), but they do routinely cache in burned areas even years after fire (Lanner and Vander Wall 1980; Tomback et al. 2001b). 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 2004; Certini 2005), and reduced competition from other conifer species that are physiologically less tolerant of environmental exposure (Maher and Germino 2006; Bansal et al. 2011). While Moody (2006) found inconsistent differences in seedling density between burned and unburned sites, there is evidence to suggest that whitebark pine seedlings growing in burns are more robust and have a greater chance to reach cone-producing maturity. Perkins (2004) and Tomback et al. (2011) found higher growth rates of whitebark pine seedlings that had

established in burned areas as opposed to those growing in closed-canopy forests. Both Izlar (2007) and Lonergan et al. (2014) found higher survival of planted seedlings on burned vs. unburned sites. In a study of post-fire whitebark pine regeneration density over 13 years in Yellowstone National Park, Tomback et al. (2001b; 2011) found that whitebark pine regeneration continued to increase over the duration of the study, suggesting that burned areas may provide good regeneration sites for many years following a fire. 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 few cones because mature trees are sick 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 regeneration densities (McKinney and Tomback 2007; McKinney et al. 2009; Barringer et al. 2012). However, Clark's nutcrackers will visit whitebark pine stands with poor cone crops, although at low incidence (Barringer et al. 2012); and some Clark's nutcrackers will transport seeds up to 30 km from a seed source in order to cache seeds within a defined home range (Lorenz et al. 2011). Managers need to know whether or not sufficient natural regeneration in a burn will occur. This information can be used to refine restoration efforts and help managers make decisions about which high-elevation burns should be prioritized for planting rust-resistant seedlings.

Several studies have explored whitebark pine regeneration after fire, but none have quantified a relationship between seed source health and regeneration density in the

adjacent burn. Tomback et al. (1993; 1995) compared whitebark pine regeneration densities in three similarly aged burns in Montana and Idaho, USA (the Sleeping Child, Saddle Mountain and Sundance burns) and found that the regeneration density in the Sundance burn was a fraction of that in the other two burns. They suggested that poor regeneration was a result of the relatively poor condition of whitebark pine seed source adjacent to the Sundance burn, as compared to the healthier condition of the seed source at the Sleeping Child and Saddle Mountain burns, but stand assessments to quantify health status were not conducted. Perkins (2004) found higher densities of whitebark pine seedlings in burns in the Bitterroot Mountains of Montana as opposed to burns in the Swan Range, and suggested poor seed source health in the Swan Range as a possible cause, even though she did not measure seed source stands. In a study comparing whitebark pine regeneration rates on paired burned and unburned sites in the Canadian Rockies and North Cascades, Moody (2006) found that regeneration rates in burns were related to seed source size, regeneration density in the seed source, and distance to seed source, but seed source health was never directly addressed.

This study builds upon preliminary work completed by Tomback et al. (2008) in four burns in or near the Bob Marshall Wilderness Complex, Montana. In 2010-2013, we sampled eleven additional burns. The central objective of this study was to examine the effect of seed source health (considering factors such as white pine blister rust infection and outbreaks of mountain pine beetle) on regeneration density in large burns of the northern Rocky Mountains. We hypothesized that there may be a threshold in the relationship between regeneration density and seed source health; this would result from a magnitude of seed production (cones per ha) that both attracts nutcrackers to a stand

and provides sufficient ripe seeds 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.

Methods

Study Areas

Study areas were identified using GIS analysis and the expertise of local land managers as follows: we analyzed fire histories, MTBS (Monitoring Trends in Burn Severity) data (Eidenshenk et al. 2007) and LANDFIRE vegetation data 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 five years old to accommodate delayed germination, (c) terrain burned by a stand replacement fire greater than 100 ha, and (d) burned area adjacent to an 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 to highly impacted stands. 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 four large Wilderness Areas (Figure 1; Table 1).

Each study area had two distinct sampling components. The “seed source” component refers to a patch or stand of mature trees adjacent to or within each sampled burn. Seed sources had at least $2.0 \text{ m}^2\text{ha}^{-1}$ basal area of mature, live whitebark pine (Barringer et al. 2012). Seed sources were often comprised of multiple patches or

continuous stands – especially when unburned patches of mature trees were present within the burn. We used GIS data including aerial photos, elevation data and LANDFIRE vegetation data and field notes to delineate seed source boundaries for analysis purposes; often, these boundaries varied by species (i.e., a subalpine fir seed source may extend to a lower elevational limit than whitebark pine). 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

Sampling methods were tailored to the unique objectives of each sampling component. Seed source stands were sampled using fixed-area (0.04 ha or 400 m²), circular plots (11.28m radius). Seed source plots were located along a transect parallel to the edge of the burn, and at least 100 m from the edge of the burn (Figure 2). At sites with multiple seed source patches, we sampled in the most prominent or largest patch. We attempted to position seed source plots at approximately the same elevation and aspect as the burn if possible. The first plot center was selected at random and each subsequent plot center was located 50 m farther along the transect. We sampled at least 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), height, height to live crown base, species, and health status (healthy, unhealthy, sick, dead) for each tree over 11.5 cm DBH in the plot boundary. For each living whitebark pine tree we recorded the percent of crown killed by white pine blister rust, abiotic, or unknown factors. We confirmed mountain pine beetle damage by pitch tubes and/or frass at the base of the tree. Blister rust was confirmed by a combination of 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 non-lethal insect or disease damage was present (i.e., a branch canker > 0.15 m from the bole or indication of an unsuccessful beetle attack); sick if the tree was expected to die within five 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 smaller than 11.5 cm DBH) by DBH class and recorded average height and crown base height. Finally, we tallied seedlings by species and height class in a nested fixed area (0.004 ha), circular plot (3.64 m radius).

Burned Area Sampling

Within a burn, we established fixed area (15 m²) circular plots (2.18 m radius) along a set of parallel transects that ran from the most prominent seed source stand

toward the center of the burn (Figure 2). We sampled between 30 and 50 plots at each burn with a grid resolution at or near 100 m between both plots and transects. Tomback et al. (2008) sampled between 20 and 40 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 (2006) protocol. 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 meters to any major ground feature such as a rock, stump, snag, etc.), presence or absence of blister rust 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

As a result of the caching habits of the Clark's nutcracker, whitebark pine seedlings often grow in clusters (Tomback 1978; 1982). For our purposes, each seedling cluster was counted as one regeneration site. Because whitebark pine regeneration increases over time following fire (Tomback et al. 2011), 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.

To analyze whitebark pine regeneration patterns, we developed two sets of models. One model describes how overall whitebark pine regeneration density varies among burns; the second model describes microsite or environmental variables within each burn that might influence the presence or absence of regeneration at a given plot. 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. Numerous measures of seed source health were tested as potential predictors of seedling density in the burn (see Table 2). These included: mature whitebark pine basal area stratified by health class (healthy, unhealthy, sick, dead), proportion of mature whitebark pine in each health class, mean percent whitebark pine crown kill, and the ratio of subalpine fir basal area to whitebark pine basal area. 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 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.

Seedling probability model selection

Because many of our burned area plots had no seedlings, we used non-parametric 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) 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. 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), which were calculated as follows: 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 (DEM) 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/m^2) for an approximate growing season (May 1st – October 31st). TCI was calculated using the equation $tci = \ln(\text{flow accumulation}/\tan(\text{slope}))$. 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 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.

We eliminated potential explanatory terms from the model using Wald z-tests ($\alpha = 0.05$), and compared nested models using chi-squared tests in an analysis of variance 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 (AUC) 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 five to 23 years post-fire. The basal area of live mature whitebark in the seed source ranged from 2.8 to 44 $\text{m}^2 \text{ha}^{-1}$, all above the threshold identified for a high likelihood (0.75) nutcracker visitation in Barringer et al. (2012). Whitebark pine seedling densities in the burns were highly variable across and within sites (Figure 3, Table 4). Mean study area-level densities ranged from 0 to 783 seedling clusters per hectare (Table 4), with individual plot-level

densities ranging from 0 to 6000 seedling clusters per hectare. When normalized by number of years since fire, mean study area-level seedling densities ranged from 0 to 86 seedling clusters $\text{ha}^{-1}\text{year}^{-1}$ (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 Fire on the Beaverhead-Deerlodge National Forest had the highest seedling density, followed by the Mussigbrod burn, also on the Beaverhead-Deerlodge. Two sites had no regeneration at the time of sampling, Challenge and Wyman, but these were relatively recent burns (seven and five years old respectively).

Effects of seed source health on regeneration density

The greater the proportion of healthy whitebark pine in the seed source, the greater the mean seedling density in the burn (Figure 4). While 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 ($R^2 = 0.54$, $P = 0.001$, Figure 4a), but the R^2 and the residuals were improved by adding a quadratic term, %healthy² ($R^2 = 0.70$, $P = 0.0002$, Figure 4b). In a piecewise regression model, we identified a potential threshold of 50% healthy trees, above which, seedling density increased at a higher rate (Figure 4c). However, there were too few data points at high values of %healthy to determine the robustness of this threshold.

Seedling occurrence within burns

There are numerous factors that 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 variables, yet the most difficult to measure. Given this caveat, we attempted to build 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 distance to seed source, vegetation cover, and potential solar radiation were significant predictors of whitebark pine seedling presence within the burn (Figure 5, 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 (Figure 5a). The probability of seedling presence increased up to 30% vegetation cover, but decreased above that (Figure 5b). Finally, probability of seedling presence decreased with increasing potential radiation (Figure 5c). The mean AUC of this model was 0.75 (standard deviation of 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 three percent showed symptoms of blister rust. 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 did not complete a full age-structure analysis for the older burns. For burns that occurred after the year 2000, we

found that only two percent of the sampled, established seedlings germinated in the first two years following fire; 11 percent germinated between three and four years post-fire; 73 percent of seedlings germinated between five and ten years post-fire; and the remaining 14 percent germinated between 11 and 13 years post-fire (the limit of the recent data).

We did not find any regional germination-year trends of sampled seedlings in burns that occurred during or after the year 2000. Given the inaccuracies in aging older seedlings, we did not evaluate germination trends in the older burns. 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 but showed a different pattern of regeneration over time. Interestingly, the Monture fire showed almost no germination after the year 2007, which coincides with the start of an observed mountain pine beetle outbreak in the seed source.

Conifer competition

In most of the sampled burns, whitebark pine seedling densities were higher than that of other conifers. Four of the sampled burns had higher densities of subalpine fir: Challenge, Gates Park, Skalkaho and Wyman (Table 4). Gates Park and Challenge also had higher densities of Engelmann spruce (*Picea engelmannii*).

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. This study is the first to examine the relationship between whitebark pine seed source health and whitebark pine regeneration density in large burns. We sampled regeneration in 15 burns, ranging from five to 23 years old. 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.

The relationship between seed source health and regeneration density

The strongest relationship that we found between regeneration density and seed source health indicated that if at least 50% of the mature whitebark pine are healthy, seedling density in the adjacent burn will increase (Figure 4, Table 2). This effect is likely an indication of greater nutcracker visitation and reliable seed-caching, and might be used as an indicator of natural regeneration potential. For burned areas where more than 50% of the seed source whitebark pine are sick or dead, rates of natural regeneration are likely to be limited (< 40 seedling clusters $\text{ha}^{-1} \text{yr}^{-1}$). Given that older, taller seedlings are more susceptible to blister rust infection (Tomback et al. 1995), seedling mortality is likely to increase over time in these areas. Therefore, while natural whitebark pine regeneration was present throughout most of the burned stands that we sampled, future

seedling and sapling mortality may prevent these stands from becoming productive, cone-producing forests.

The most consistent pattern we found in whitebark pine regeneration across 15 burns was high variability (Figure 3 and Table 4), likely influenced by bird-mediated seed dispersal. Despite this inherent variability, we found a positive relationship between seed source health and burned area regeneration density. This response is intuitive, but up to this point has not been demonstrated. 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 as well for adjacent burned areas, because Clark's nutcrackers could potentially transport seeds into burns from stands as far as 30 km away (Lorenz et al. 2011). These results suggest that nutcrackers harvest seeds most often from local seed sources for caching in adjacent burns.

In analyzing various measures of seed source health, we found that the proportion of mature whitebark pine that was healthy (%healthy) was the best indicator of seedling density in the adjacent burn. "Healthy" whitebark pine forests are diverse – from nearly pure stands of mature, cone-bearing trees, to mixed conifer stands with interspersed whitebark. Additionally, the basal area of open-grown stands might be low, but cone production (therefore seed availability) might be high as a result of the large, well-spaced crowns. This pattern is evident in a comparison of two of our sampling sites – Mussigbrod and Fall Fork – which burned in the same year and are relatively close geographically. At Fall Fork, the seed source stand was predominantly whitebark pine, growing in a dense, closed stand, while the seed source at Mussigbrod was open-grown

and park-like. The basal area of whitebark pine in the Fall Fork stand was more than twice that of Mussigbrod, but Mussigbrod had a higher seedling density in the burn. 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 within burns

Three important variables that influence the probability of seedling presence at a given site were identified: distance to seed source, total vegetation cover, and potential amount of solar radiation. In general, there was a significant decline in whitebark pine seedling occurrence as distance from seed source increased, but this pattern was not consistent throughout the dataset (Figure 5a). Tomback et al. (1990) found a decline in seedling density 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. While 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 600m 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).

From our models, we determined an optimum amount of vegetation cover (30%) that coincided with the highest probability of seedling occurrence on a given plot (Figure 5b). Previous studies indicate that sites with less vegetation cover may be too exposed to

facilitate seedling establishment, while dense vegetation cover may outcompete young seedlings. Although we cannot know the vegetation cover under which seedlings first germinated in this study, the results suggest that the presence of cover has facilitated survival. This finding is consistent with previous research (McCaughey and Weaver 1990; Maher and Germino 2006), indicating that while 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 seedlings from desiccation and cold exposure.

The probability of whitebark pine seedling occurrence had a statistically significant negative relationship with potential solar radiation (Figure 5c). This pattern is not surprising, because increased solar radiation may lead to lower soil moisture and higher levels of seedling mortality (Maher et al. 2005), especially on an exposed site post-fire.

Management implications

Our results indicate that in burned areas where more than 50% of the seed source whitebark pine are sick or dead, natural regeneration may be limited. Without restoration planting of seedlings, these burned stands are less likely to regenerate over time to

produce cone-bearing whitebark pine forests (Keane and Parsons 2010). All planting should be with seedlings from screened, blister rust-resistant parent trees (Keane et al. 2012), because there has been a trend in increased incidence of blister rust infection among trees in all regions (Maloney et al. 2012; Smith et al. 2013). Increased infection incidence increases local spore loads and the chance of regeneration becoming infected (e.g., Tomback et al. 1995). Natural regeneration will usually be a mix of rust-resistant and susceptible seedlings, but high levels of naturally resistant young whitebark pine, even adjacent to relatively healthy stands, is unlikely. It is also important to note that regeneration rates are but one of the key vital rates which influence population growth rates following wildfire. While regeneration density and mortality are important indicators of potential forest structure, managers should also consider long-term adult growth rates, fecundity, and mortality rates as blister rust infection levels stabilize or increase (Maloney et al. 2012). Regardless, 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).

In protected areas, such as Wilderness Areas in the United States, planting seedlings post-fire may be viewed as “trammeling” or a human-caused disturbance, therefore precluded by management policy in those areas (Keane et al. 2012). However, if there is little expectation for natural regeneration as a result of an anthropogenic disturbance such as blister rust, planting seedlings may be a means to help maintain whitebark pine and associated ecosystem function on the landscape. In either case, monitoring of restoration plantings in burns outside of protected areas will provide

managers with valuable insight as to whether planting rust-resistant seedlings following fire is an effective or appropriate means of restoration within protected areas.

Our study shows that whitebark pine establishes for many years following a fire, which is consistent with previous findings (e.g. Tomback et al. 1993; 1995; 2001b, and 2011). Only 13% of the seedlings we sampled germinated in the first four years following a fire; Tomback et al. (2001b) 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 three years post-fire, following a good cone crop and two winters of seed dormancy. This is an important consideration for managers; in general, it takes at least five years for whitebark pine to begin populating a burn, so immediate post-fire assessments of regeneration might be misleading. In the interim, managers might use seed source health as a surrogate indicator of whitebark pine regeneration potential in prioritizing planting prescriptions.

Fire managers are often faced with conflicting values in determining whether or not to suppress high elevation fire. On one hand, fire is an integral process in shaping the subalpine landscape. While many ignitions may occur, fire spread is usually limited by moisture, weather, and/or topography (Fischer and Bradley 1987; Arno and Hoff 1990; Bessie and Johnson 1995). In hot, dry years, fire spread is more contagious, resulting in larger fires and larger patches of high severity or stand-replacing fire, though this effect is reduced in cool, wet subalpine forest types (Cansler and McKenzie 2014). Fires that pose a risk to humans, structures and other development, historical preservation and other management objectives might preclude "letting it burn." Often, fire managers do not have a choice in whether to allow high-elevation fires to burn, since the remote nature

and rugged topography of these burns severely limit suppression activities. 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 counter-productive. While many of the burns we sampled may not meet seedling density objectives for future desired forest structure, natural regeneration can be supplemented with planted seedlings where appropriate (Keane and Parsons 2010), which will also hasten the spread of blister rust resistance. 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 (trees that have been identified as sources for rust-resistant seeds, see Mahalovich and Dickerson (2004)) or small islands of subalpine habitat that hold special recreational or wildlife value comprises the best fire management response in whitebark pine forests.

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. For field work in 2010-2013, we thank Bob Hutton and Ben Wilson of the Beaverhead-Deerlodge National Forest, Wisdom District and Wendel Hann, retired USDA Forest Service, for pack support. We also thank the Beaverhead-Deerlodge, Flathead, Gallatin, Helena, Lewis and Clark and Lolo 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. Finally, we thank the USDA Forest Service, Rocky Mountain Research Station Fire Sciences Lab and Forestry Sciences Lab for funding and logistical support, the Whitebark Pine Ecosystem Foundation for funding and the University of Montana for general project support.

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Tables

Table 1. Summary of study areas.

Burn Name	Year Burned	Size of Burn (ha)	Study location (Montana, USA)
Ann	1994	1,265	Bitterroot National Forest
Beaver Creek	2000	4,323	Gallatin National Forest
Bighorn Lake	1988	80,961	Scapegoat Wilderness, Helena National Forest
Challenge Creek	1998	3,846	Flathead National Forest
Charlotte Peak	1985	2,385	Bob Marshall Wilderness, Flathead National Forest
Fall Fork	2000	850	Anaconda – Pintler Wilderness, Beaverhead-Deerlodge NF
Gates Park	1988	22,093	Bob Marshall Wilderness, Lewis and Clark National Forest
Helen Creek	1994	2,846	Bob Marshall Wilderness, Flathead National Forest
Monitor Mtn	1988	80,961	Scapegoat Wilderness, Lewis and Clark National Forest
Monture	2000	9,624	Bob Marshall Wilderness, Flathead National Forest
Mussigbrod	2000	11,178	Anaconda - Pintler Wilderness, Beaverhead-Deerlodge NF
Pettengill	2007	6,192	Beaverhead-Deerlodge National Forest
Red Owl	1984	591	Flathead National Forest
Skalkaho	2000	3,027	Bitterroot National Forest
Wyman	2007	14,374	Beaverhead-Deerlodge National Forest

Table 2. Summary of linear regression models for mean whitebark pine regeneration density (seedling clusters $\text{ha}^{-1} \text{yr}^{-1}$) among 15 burn study areas in Montana, USA. WBP refers to whitebark pine, SAF refers to subalpine fir, BA refers to basal area ($\text{m}^2 \text{ha}^{-1}$). Final model is in bold. Correlations between measures of seed source health are shown.

Model Predictor Variable(s)	Coefficients	SE	R²	P-value
Healthy WBP BA ($\text{m}^2 \text{ha}^{-1}$)	1.397	0.60	0.25	0.037*
Healthy+unhealthy WBP BA ($\text{m}^2 \text{ha}^{-1}$)	0.998	0.53	0.16	0.085
Dead WBP BA ($\text{m}^2 \text{ha}^{-1}$)	-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 ($\text{m}^2 \text{ha}^{-1}$)	-9.789	7.39	0.07	0.218
%healthy WBP	0.850	0.20	0.54	0.001***
(%healthy WBP) ²	0.013	0.002	0.69	0.0001***
%healthy+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 ($\text{m}^2 \text{ha}^{-1}$)	1.708	0.41	0.56	0.001**
%healthyWBP mean WBP crown kill (%)	-1.001	0.13	0.81	<0.001***
Healthy WBP BA ($\text{m}^2 \text{ha}^{-1}$) mean WBP crown kill (%)	-0.352	0.10	0.47	0.004**

* = P-value significant at 0.05, ** = P-value significant at 0.01, ***= P-value significant at 0.001

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
<u>Full Model</u>			
Heatload Index	-2.169e-01	1.390e+00	0.8759
RdNBR	3.543e-04	5.355e-04	0.5082
Topographic Convergence Index (TCI)	-7.475e-02	8.732e-02	0.3920
Potential Solar Radiation (Wh/m ²)	-3.942e-06	1.728e-06	0.0226*
Distance to Seed Source (m)	-7.104e-03	1.867e-03	0.0001***
Distance to Seed Source ²	6.316e-06	1.794e-06	0.0004***
Vegetation Cover (%)	7.486e-02	2.833e-02	0.0082**
Vegetation Cover ²	-1.085e-03	3.229e-04	0.0008***
<u>Final, Reduced Model</u>			
Potential Solar Radiation (Wh/m ²)	-4.346e-06	1.337e-06	0.0012**
Distance to Seed Source (m)	-5.993e-03	1.628e-03	0.0002***
Distance to Seed Source ²	5.367e-06	1.626e-06	0.0097***
Vegetation Cover (%)	5.948e-02	2.548e-02	0.0196*
Vegetation Cover ²	-8.759e-04	2.786e-04	0.0017**

* = *P*-value significant at 0.05, ** = *P*-value significant at 0.01, *** = *P*-value significant at 0.001

Table 4. Summary of whitebark pine regeneration data from 15 burn study areas in Montana, USA. WBP refers to whitebark pine, SAF refers to subalpine fir.

Site	<i>n</i> plots	Mean WBP Density (clusters ha⁻¹)	WBP SD (clusters ha⁻¹)	WBP SE (clusters ha⁻¹)	Normalized WBP Density (clusters ha⁻¹ yr⁻¹)	Normalized WBP SD (clusters ha⁻¹ yr⁻¹)	Normalized WBP SE (clusters ha⁻¹ yr⁻¹)	Mean SAF Density (seedlings ha⁻¹)
Ann	50	480	762.4	107.8	26.7	42.4	5.9	307
Beaver	48	389	712.4	102.8	32.4	59.4	8.6	83
Bighorn	80	508	836.9	93.6	23.1	38.0	4.3	325
Challenge	32	0	0.0	0	0.0	0.0	0	375*
Charlotte	23	783	735.9	153.4	41.2	38.7	8.1	174
Fall Fork	40	650	1012.2	160.0	48.7	77.9	12.3	150
Gates Park	39	615	1063.9	170.4	26.8	46.3	7.4	1726*
Helen Crk	48	177	282.3	40.7	17.7	28.2	4.1	146
Monitor	30	44	169.1	30.9	2.0	7.7	1.4	0
Monture	50	160	394.1	55.7	14.5	35.8	5.1	267*
Mussigbrod	51	614	1048.5	146.8	61.4	104.9	14.7	39
Pettengill	44	515	687.5	103.6	85.9	114.6	17.3	0
Red Owl	22	273	428.9	91.4	13.6	21.4	4.6	227
Skalkaho	40	167	362.0	57.2	12.8	27.8	4.4	283*
Wyman	30	0	0.0	0	0.0	0.0	0	44*

* = Site had higher subalpine fir seedling density than whitebark pine

Figure captions

Figure 1. Map of study region showing the location of 15 study areas across Montana, USA. Shaded areas indicate National Forest; the Continental Divide is shown for reference.

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

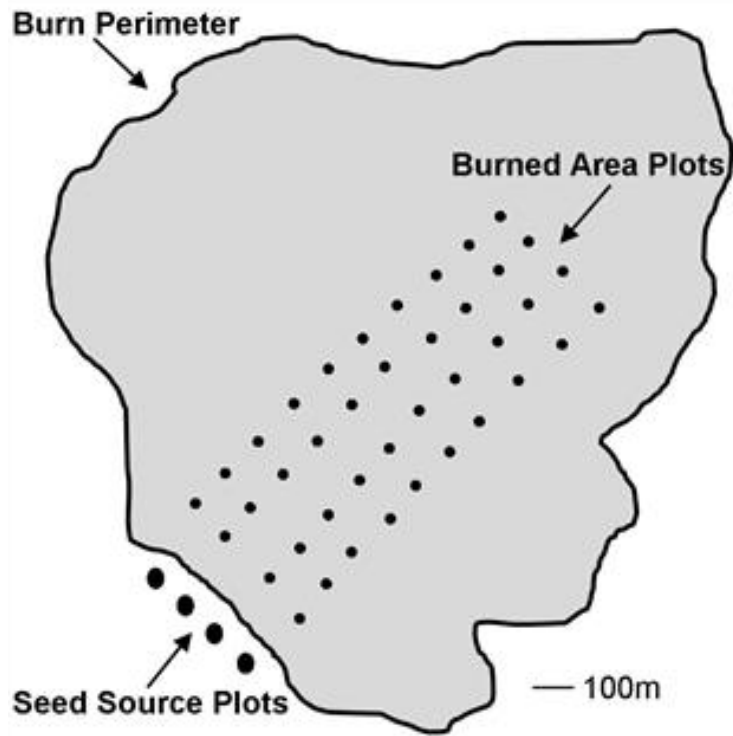
Figure 3. Boxplots of whitebark pine seedling density by study area, where the median is shown by the solid black line and the mean is shown by the solid black circle. Seedling density is normalized by number of years since fire.

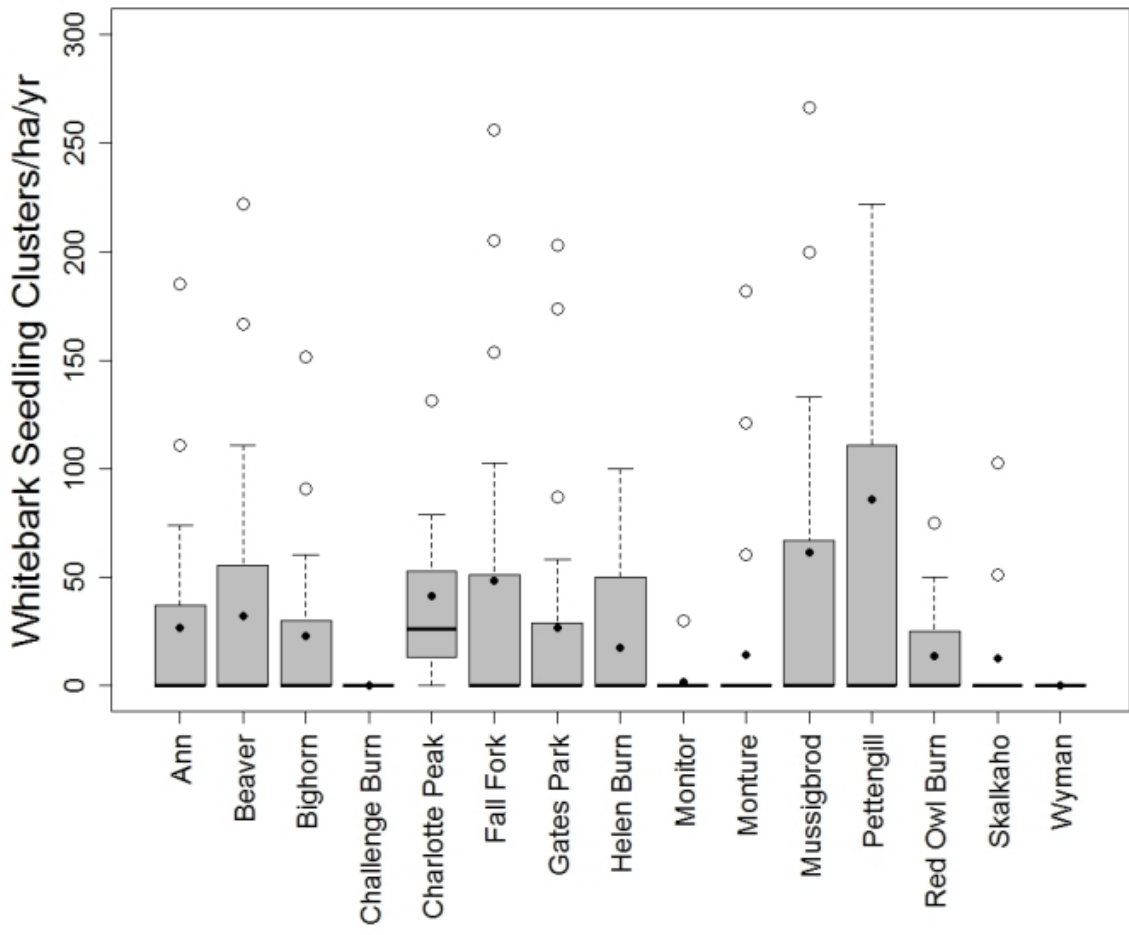
Figure 4. Simple linear (4a), multiple linear (4b) and piecewise (4c) models reflecting the relationship between seed source health (percent of mature trees in the seed source that are healthy) and seedling density (seedlings $\text{ha}^{-1} \text{ year}^{-1}$) in the adjacent burn. Standard error bars are shown.

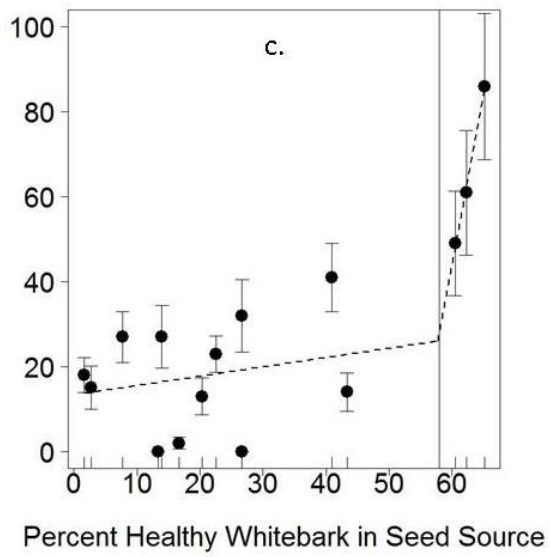
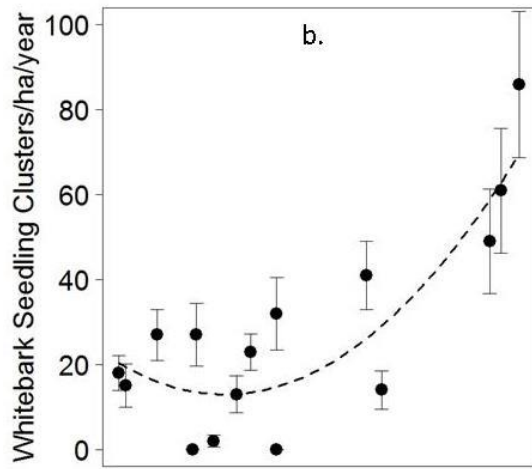
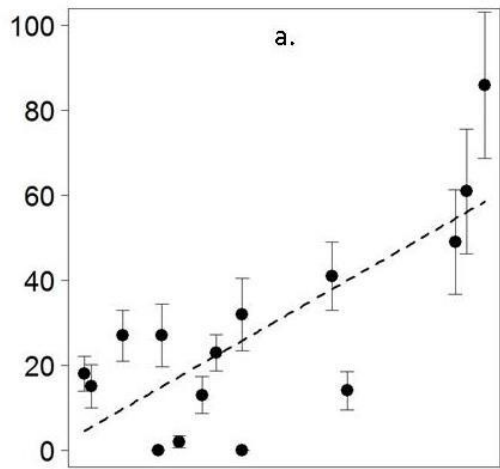
Figure 5. Partial response curves from the GAMM that illustrate the influence of a) distance to seed source (m), b) total vegetation cover (%) and c) potential solar radiation (Wh/m^2) on the probability of whitebark pine seedling presence, while holding the other predictor variables at their mean. Gray shading is ± 2 standard errors; residuals are shown.

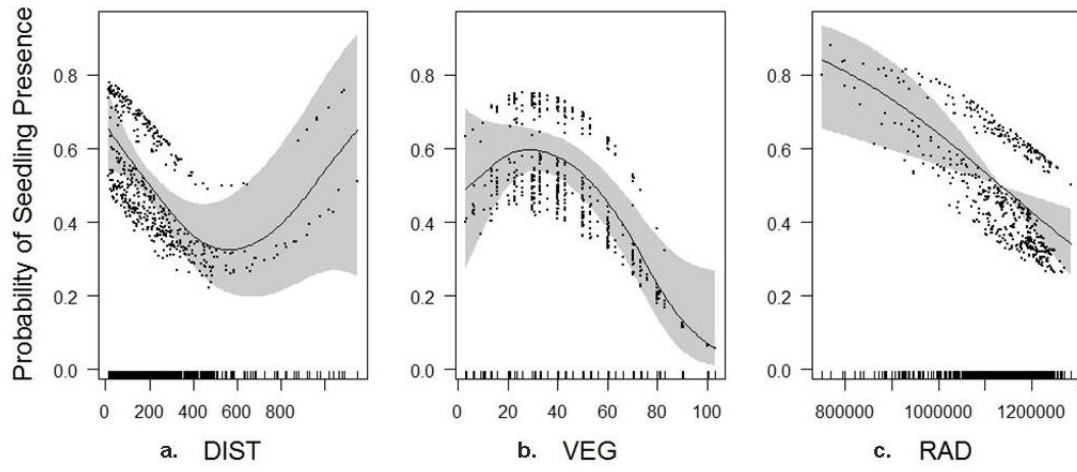
Figures











Chapter 2: Competition and facilitation: a review of interactions between whitebark pine (*Pinus albicaulis*) and other subalpine conifers

Introduction

As a keystone and foundation species (Ellison et al. 2005; Tomback and Achuff 2010), whitebark pine (*Pinus albicaulis*) fills a number of ecological roles across the subalpine landscape (Keane et al. 2012). Its seeds are an important food source for grizzly bears (*Ursus arctos horribilis*), Clark's nutcrackers (*Nucifraga columbiana*) and other animal species (Tomback and Kendall 2001). At high-elevations, whitebark pine forests stabilize and shade the snowpack, tempering snowmelt and spring runoff; the roots of these forests also help stabilize loose soil and reduce erosion (Arno and Hoff 1990; Farnes 1990). Whitebark pine seeds are dispersed by a bird, the Clark's nutcracker (Hutchins and Lanner 1982; Tomback 1982); as a result, the species has long-distance seed dispersal potential relative to wind-dispersed conifers. For this reason, whitebark pine is often the first species to populate sites after disturbance such a wildfire (Arno and Hoff 1990). Whitebark pine may then facilitate the growth and establishment of other conifer species, including subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), especially at higher elevations under increasing environmental stress (Callaway 1998; Resler and Tomback 2008). The objective of this chapter is to describe the physiological traits of whitebark pine that allow for seedling establishment after disturbance and to review the facilitative and competitive interactions between whitebark pine regeneration and other subalpine conifers. These traits and interactions can help inform our understanding of potential forest establishment pathways that may occur (or be disrupted) following disturbance.

Whitebark pine distribution and extent of decline

Whitebark pine occurs in seven western states and two Canadian provinces; it has the broadest distribution of any five-needle white pine in the United States and Canada (Tomback and Achuff 2010). It grows in subalpine or treeline forests throughout the Sierra Nevada and Cascade mountains in California and the Pacific Northwest, and in the Rocky Mountains of Wyoming, Idaho, Montana, Alberta and British Columbia. Small populations occur in the Great Basin of Nevada, and in the mountains of northeast Oregon and Washington (Keane et al. 2012). In the northern Rocky Mountains, whitebark pine communities represent about 10 to 15 percent of the forested landscape (Arno 1986). More than 95 percent of whitebark pine in the U. S. occurs on public lands, including national forests, wilderness areas, and national parks. The three largest wilderness areas in the western U. S. each comprise about 25 to 50 percent whitebark pine forest habitat (Keane 2000). Whitebark pine grows as a seral species in productive subalpine forests, where it is eventually replaced by more shade-tolerant conifers such as subalpine fir or Engelmann spruce (Arno and Weaver 1990). It can also function as a climax species on harsh or dry high-elevation sites where establishment or growth of other conifers is limited by environmental conditions (Arno and Hoff 1990).

As described in the Chapter 1, whitebark pine forests are declining throughout their range as a result of the disease white pine blister rust, caused by the exotic pathogen *Cronartium ribicola* (Schwandt et al. 2010; Tomback and Achuff 2010), extensive climate-driven mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Logan and Powell 2001; Jewett et al. 2011; Macfarlane et al. 2013), and successional replacement by other conifers as a result of fire exclusion over the last century (Keane et al. 1994;

Murray et al. 2000). The most recent data show that blister rust infection levels range from a low of 0-24% in the Sierra Nevada Range (Maloney 2011) to an average of 73% in the northern US and southern Canadian Rocky Mountains (Smith et al. 2008).

Macfarlane et al. (2013) estimated that nearly 95% of whitebark pine forests in the Greater Yellowstone Ecosystem have been impacted by current mountain pine beetle outbreaks. Given the broad distribution of whitebark pine and the functional role of the species across the landscape, the breadth of this decline has the potential to severely impact the structure and processes of subalpine forests as a whole.

Physiological differences among subalpine conifers

It is commonly asserted that whitebark pine can function as a facilitating or colonizing species, but only a few studies describe the underlying physiological traits that allow the species to establish on exposed or disturbed sites. Sala et al. (2001) compared instantaneous gas exchange and water use efficiency between mature subalpine fir and whitebark pine trees to determine whether differences in gas exchange are related to shade tolerance assumptions, and how leaf-area to sapwood ratios influence water use. They found that whitebark pine had higher photosynthetic rates and light saturation points than subalpine fir, which corresponds to decreased shade-tolerance. Long-term water use efficiency was higher in whitebark pine, as evidenced by higher carbon isotope ratios, which allows whitebark pine to grow and establish on drier sites.

Maher et al. (2005) tracked the fate of planted whitebark pine, subalpine fir and Engelmann spruce seedlings across varying levels of tree and herbaceous cover at treeline, and measured differences in physiological traits among species and across levels

of cover. Few subalpine fir seedlings germinated, and none survived. Whitebark pine experienced much higher survival than Engelmann spruce overall, and spruce survival was greatly enhanced by tree and herb cover. Survival of whitebark pine also increased with both tree and herb cover, but this effect was tempered with the addition of supplemental water. Photosynthetic rates in both species increased with cover, indicating that exposure is more of a limiting factor than competition in seedling establishment at treeline.

Similarly, Bansal et al. (2011) compared establishment patterns of whitebark pine and Engelmann spruce to spatial patterns of neighboring vegetation; they also measured physiological traits that might influence seedling survival on exposed sites including gas exchange, specific leaf area, chlorophyll fluorescence, and nonstructural carbohydrate content. They found that whitebark pine experienced much greater survival than Engelmann spruce on exposed sites. While photosynthetic rates were similar in both species, whitebark pine had higher water use efficiency, chlorophyll fluorescence, and soluble sugar concentrations, and lower specific leaf area (SLA) than Engelmann spruce. Whitebark pine seedlings maintained relatively constant respiration rates with increased exposure, resulting in greater carbon use efficiency, while spruce seedlings increased respiration rates in response to exposure. The authors state that higher water and carbon use efficiency allowed whitebark pine to establish on more exposed sites. Higher chlorophyll fluorescence helps whitebark pine resist photoinhibition, and greater soluble sugar concentration increases freeze tolerance. Lower SLA in whitebark pine might increase survival on exposed sites, while higher SLA in Engelmann spruce may have allowed the species to establish under more shaded conditions.

In summary, these studies indicate that whitebark pine is host to several physiological traits that allow seedling establishment on exposed, harsh sites. While tree and herb cover can enhance survival of whitebark pine seedlings at or near treeline, the species is capable of establishing on a greater range of site types than subalpine fir or Engelmann spruce. Both fir and spruce appear to be adapted to establishment under or near existing vegetation cover, especially on sites with high levels of environmental stress.

Whitebark pine as a facilitating species

Under harsh environmental conditions commonly found in subalpine forests, facilitative, or positive, interactions among plants can be important for the establishment and/or growth of certain species (Bertness and Callaway 1994). Competitive interactions may replace facilitation in subalpine species under conditions that are less severe (Callaway 1998). As a result of the physiological characteristics discussed in the previous section, whitebark pine may effectively facilitate the establishment of other conifer species in subalpine or treeline environments.

Studies that explore subalpine conifer interaction suggest that whitebark pine does function as a facilitating species both as a seedling and mature tree in upper subalpine forests and at treeline, but the function may become competitive at lower elevations. Callaway (1998) compared tree spacing and growth rates of subalpine fir and whitebark pine in both upper and lower subalpine forests in western Montana. He found that the effects of whitebark pine on subalpine fir growth and spacing were neutral to competitive at low elevation, yet facilitative at higher elevations. In lower subalpine forests,

subalpine fir spacing was no different than random, while at higher elevations, subalpine fir tended to aggregate around mature whitebark pine. This effect was reduced or non-existent among smaller size classes of subalpine fir, possibly because the winter snowpack protects young trees from wind and extreme temperatures. Callaway (1998) also measured the effects of mature whitebark pine death on adjacent subalpine fir growth across upper and lower elevation forests. At high elevation, growth rates of mature subalpine fir diminished by 24% after the adjacent whitebark pine had died. This effect did not hold at low elevations, where growth rates of fir actually increased by 7% after the adjacent whitebark pine died. These results show that interactions between conifer species can shift from facilitative to competitive across a gradient of site types.

Several studies have addressed conifer interactions at treeline. Based on observations from a vegetation analysis across the treeline gradient, Habeck (1969) suggested that subalpine fir usually followed whitebark pine in tree island formation. Resler and Tomback (2008) examined this relationship, measuring the function of whitebark pine as a facilitator of tree island establishment at two sites near the Continental Divide in northwest Montana. They found whitebark pine to be the primary initial colonizer of tree islands; usually facilitated by the presence of topographic features or other vegetation that provided protection from prevailing winds. Tomback et al. (2014) further examined the function of whitebark pine as a tree island initiator at four additional locations both north and south of the Resler and Tomback (2008) study sites. Overall, whitebark pine was the most frequent tree island initiator, and the most frequently occurring solitary tree species, but with variability between study sites. In the southern study area, Engelmann spruce replaced whitebark pine as the prevalent tree

island initiator, and subalpine fir assumed this role in one of the northern study sites. Concurrent with the findings of Callaway (1998), it is possible that abiotic differences between these sites may have neutralized the facilitative role of whitebark pine. As in Resler and Tomback (2008), Tomback et al. (2014) also found that rocky topographic features were the most frequent facilitators of tree island formation, highlighting the consistent role of topography in treeline establishment and expansion.

Maher and Germino (2006) evaluated the effects of vegetation cover on the establishment of whitebark pine, subalpine fir and Engelmann spruce at or near treeline in Wyoming. Specifically, they addressed the influence of neighboring vegetation on regeneration patterns of these conifers, and whether or not there were interspecific differences in seedling requirements that might contribute to functional relationships between species. They found no relationship between vegetation cover and emergence patterns in all three species, but seedling survival was influenced by both tree and herb cover, as measured by percent exposure to the sky and herbaceous vegetation density, respectively. Tree cover (reduced sky exposure) promoted seedling establishment for all species, but whitebark pine seedlings established in the greatest range of sky exposure, and experienced three times greater survival than subalpine fir or spruce overall. Herb cover also promoted seedling survival, but more so when tree cover was limited, suggesting that seedlings might experience more competition with herbaceous plants than overstory trees. Based on these findings, the authors suggest that exposure, rather than competition, is a limiting factor in the establishment of conifers at or near treeline. In addition, of the three common subalpine conifer species, whitebark pine appears to be the most capable colonizer of open meadows or disturbed areas at high elevations.

Discussion and implications

It is clear that whitebark pine is physiologically well-adapted to function as a colonizing or facilitating species on open, exposed sites, at high elevations, or following a large disturbance. Sala et al. (2001) reported higher photosynthetic rates, light saturation points and water use efficiency in mature whitebark pine, indicating relative shade intolerance and higher drought tolerance relative to subalpine fir. Bansal et al. (2011) found higher water use efficiency, chlorophyll fluorescence and soluble sugar concentrations in whitebark pine seedlings at treeline, as compared to Engelmann spruce. Bansal et al. (2011) found photosynthetic rates to be similar between species (also see Maher et al. 2005), but whitebark pine seedlings were able to maintain a constant rate of respiration across an exposure gradient, leading to higher carbon use efficiency relative to Engelmann spruce.

Given this physiological advantage, and evidence of whitebark pine facilitating growth and establishment of other conifers (Callaway 1998; Resler and Tomback 2008), the loss of whitebark pine has the potential to alter forest establishment pathways following disturbance, but this assertion needs to be made cautiously. Physiologically, whitebark pine is a relative generalist capable of establishing across a range of site types (Arno and Hoff 1990; Maher et al. 2006); also, bird-mediated seed dispersal allows seed delivery across large areas. It appears, then, that whitebark pine establishment is seed source limited (see Chapter 1), especially given the breadth of current seed source decline. Disturbed areas, such as stand replacing burns, may be slow to regenerate with other conifer species without the facilitative effects of whitebark pine. However, this speculation is not entirely clear. Callaway (1998) found that the facilitative effects of

whitebark pine were reduced in lower elevation forests, and among smaller size classes of trees. Disturbance that occurs in lower subalpine forests may very well regenerate into spruce and fir without whitebark pine as a facilitator. Engelmann spruce and subalpine fir are both wind-dispersed species, so the size of disturbance may limit their regeneration potential. At higher elevations, conifer regeneration may be severely impacted by the loss of whitebark pine. Maher et al. (2005; 2006) presented evidence that trees and herbs are important in facilitating establishment of conifers at treeline, and whitebark pine is most capable of establishing on exposed sites. Resler and Tomback (2008) showed that whitebark pine is an important tree island initiator. Therefore, a loss of the species at these elevations could impede regeneration of other conifers.

While there does not appear to be published data measuring physiological differences in whitebark pine along elevational or life stage gradients, several studies confirm physiological plasticity in other subalpine conifers across these gradients (Hultine and Marshall 2000; Bansal and Germino 2009; Reinhardt et al. 2011). These differences illustrate the need to fully understand the physiological mechanisms that limit or promote conifer establishment or growth at a particular elevation or zone (i.e. subalpine vs. treeline) and life stage (i.e. seedling vs. mature). Disturbance size, location, and site type, and seed source characteristics all have the potential to influence forest establishment pathways and the role (or lack thereof) of whitebark pine as a facilitating species.

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