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Influence of Site Conditions, Shelter Objects, and Ectomycorrhizal Inoculation on the Early Survival of Whitebark Pine Seedlings Planted in Waterton Lakes National Park

Erin R. Lonergan, Cathy L. Cripps, and Cyndi M. Smith

Whitebark pine (*Pinus albicaulis*) is an endangered five-needle pine limited to high elevations in western North America. Populations are being decimated by white pine blister rust, mountain pine beetles, and fire suppression. Over 200,000 rust-resistant seedlings have been planted for restoration in the western United States, but survival rates are low. Several treatment combinations (planting on burns, in beargrass, near shelter objects, and with mycorrhizal inoculation) intended to enhance the survival of planted nursery seedlings were evaluated. Each of 21 plots contained four site condition combinations (burned/not, beargrass/not). Half of 983 seedlings were inoculated with the native ectomycorrhizal fungus *Suillus sibiricus* in the nursery. Seedlings were planted with/without a shelter object (stumps, logs, rocks). After 2 years, some of the highest seedling survival rates (82%) were in burned areas (prescribed torching) where beargrass mats were absent. In unburned areas with beargrass, mycorrhizal treatment increased survival 17–24% and when combined with shelter objects was 68–84%. Shelter objects increased survival 10–12.5% on burns and 31% on unburned areas without beargrass, where survival was low (42%). Overall, early seedling survival was higher than for other whitebark pine restoration attempts at 95% and 69% for years one and two, likely due to particular treatment combinations possibly helped by favorable spring moisture conditions.

Keywords: high elevation restoration, mycorrhiza, *Pinus albicaulis*, prescribed fire, *Suillus*

Whitebark pine (*Pinus albicaulis* Engelm.) (WBP) is an important tree species limited to upper subalpine and timberline vegetation zones in mountainous areas of western North America (McCaughey and Schmidt 2001). This keystone species is critical to watershed dynamics, environmental stability, and maintenance of biological diversity in high elevation habitats (Farnes 1990, Tomback et al. 2001a, Tomback and Kendall 2001). The high-protein pine nuts are used as food by mammals such as red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), grizzly bears (*Ursus arctos* (Linneaus, 1758)), and black bears (*Ursus americanus* (Pallas, 1790)). Clark's nutcrackers (*Nucifraga columbiana* (Wilson, 1811)) disperse and cache the wingless seeds in a manner that provides the only reliable means of natural regeneration (Tomback 2001). In addition, birds will cache seeds in areas burned by wildfires of varying severity where WBP can grow competition free (Tomback 2001).

Whitebark pine populations are being seriously reduced due to the combined effects of white pine blister rust (*Cronartium ribicola* J.C. Fisch.), mountain pine beetles (*Dendroctonus ponderosae* Hopkins, 1902), successional replacement linked to fire exclusion, and climate change (Schwandt et al. 2010). In 2012, WBP was listed as endangered throughout Canada (Government of Canada 2012) and it is currently judged a candidate for listing in the United States. (Nicholas and Katzenberger 2011). Efforts to maintain and restore this species have had some successes over three decades (Tomback et al. 2001a, Schwandt et al. 2010). Restoration is currently focusing on the planting of nursery-grown potentially rust-resistant WBP seedlings (Keane et al. 2012); over 200,000 nursery have been planted, however, survival rates are low (Izlar 2007).

Several strategies aimed at improving the survival of rust-resistant WBP seedlings have been examined and include planting: on burns (from prescribed fires or wildfires) (Izlar 2007, Perkins 2004, Asebrook et al. 2011), near shelter objects (such as rocks, stumps, or logs, often called "microsites" in WBP restoration) that provide protection (Izlar 2007, McCaughey et al. 2009, Scott et al. 2011), near various understory plants (Perkins 2004, Mellmann-Brown

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2005) and in clusters intended to mimic nutcracker plantings (Smith et al. 2011b, for limber pine). However, results from these studies are inconclusive and statistical evidence that supports the benefits of these strategies is lacking or weak. Several of these restoration treatments such as planting in clusters (Smith et al. 2011b), the use of shelter objects (Krasowski and Elder 2000) and planting in prescribed burns (Sackett et al. 1996) are considered beneficial in restoration of other conifers.

Inoculation of nursery-grown conifer seedlings with ectomycorrhizal fungi is an additional strategy that has been used routinely in reforestation with some success (Steinfeld et al. 2003, Gagne et al. 2006), but this has not been tried with WBP. Inoculation can promote the survival of young seedlings by facilitating access to water and nutrients (Lehto and Zwiazek 2011). A summary on "ectomycorrhizae in forestry" recommends inoculation, particularly in areas devoid of native ectomycorrhizal fungi such as on severe burns (Wiensczyk et al. 2002). However, the benefits of mycorrhizal inoculation depend on a number of factors, including nursery procedures, host-fungus combination (i.e., which fungus is used with a particular host), soil type, planting conditions and climate (Quoreshi et al. 2009).

Whitebark pine is known to associate with at least 50 species of native ectomycorrhizal fungi (Mohatt et al. 2008, Cripps and Antibus 2011). Several, including *Suillus* and *Rhizopogon* species (together called "suilloids"), are specific to pines and most do not form mycorrhizae with other conifers (Bruns et al. 2002). *Rhizopogon* species have been used for nursery inoculation of pine seedlings grown for reforestation in the United States for years (Amaranthus 2002). However, *Suillus sibiricus* (Bonard.) Singer was recently shown to form ectomycorrhizae more efficiently than *Rhizopogon* species on WBP seedlings in greenhouse inoculations (Cripps and Grimme 2011). *Suillus sibiricus* is widespread on WBP and has been found in association with this tree species on a variety of soils types and was selected for further trials. In addition, *Suillus* species have been used successfully to restore the genetically related European stone pine (*Pinus cembra* L.) forests in the Austrian Alps over the last 50 years (Heumader 1992, H. Weisleitner, Federal Nursery of Austria, pers. comm., Apr. 25, 2008).

Whitebark pine is in serious decline in the northern Rocky Mountain region in both the United States and Canada (Keane and Arno 1993, Smith et al. 2011a, Smith et al. 2012). The mortality of WBP increased dramatically in this region from 1996 to 2009 from an estimated 26% to 61% overall and white pine blister rust infection levels rose from 43% to 71% over this time period (Smith et al. 2011a, Smith et al. 2012). Restoration of WBP in Waterton Lakes National Park (WLNP) began in 2006 (Smith 2009) and a field study was initiated there in 2009 to evaluate the effects of various treatments that include the planting of nursery-grown seedlings. The primary method by which whitebark pine will be restored throughout its range is by planting rust-resistant seedlings (Keane et al. 2012). Given the high cost of producing these seedlings from collected cones, it is important to evaluate any strategy that can enhance the survival of these seedlings. In this study, the effects of planting on small prescribed burns, planting in thick understory (beargrass), planting near shelter objects (microsite), and inoculation with native ectomycorrhizal fungi were examined. The effects of treatment combinations on the early survival of WBP seedlings planted in WLNP were assessed one and 2 years after planting.

Methods

Study Area

The study area is located near Summit Lake in WLNP, Alberta Canada (49° 0′N, 114° 1′W) (Figure 1). The site is on a saddle at elevations of 1,950 m to 2,000 m and is relatively flat with a few gentle slopes. The climate is characterized by deep, persistent snow packs and short summers. The average temperature in summer is 14° C and in winter −4° C. Average annual precipitation in the area is around 152 cm. However, in 2011 and 2012 when WBP seedlings were monitored, the snow equivalent at Akamina Pass (< 3 km from the site) had spring snow water equivalent totals 30–40 cm above the normal range, as shown in Figure 2 (Government of Alberta 2012). Melt out was late in 2011, not occurring until late June and in 2012 it occurred in early June (Figure 2). This was followed by summer temperatures in 2011 and 2012 that were near the long-term average (16° C and 15.5° C) (Government of Alberta 2012). Winds are frequent and strong, averaging 30km/hr (20 mph) and gusts over 100km/hr (75 mph) are common in fall and winter (Government of Alberta 2012, Parks Canada 2012). The soil composition is an orthic humo-ferric podzol derived from glacial till and the texture is loam to gravelly loam with 10–70% coarse fragments (Coen and Holland 1976).

The overstory vegetation is mixed coniferous forest comprised of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm) with scattered WBP trees. The understory vegetation consists mostly of thick mats of beargrass (*Xerophyllum tenax* (Pursh) Nutt.) with scattered rusty menziesia (*Menziesia ferruginea* Sm.) and huckleberry shrubs (*Vaccinium membranaceum* Douglas ex Torr.) (Achuff et al. 2002). White pine blister rust infection has caused a higher level of mortality in the mature WBP trees at the site and many of the naturally regenerating WBP seedlings are also dying from rust infection and competitive exclusion from faster-growing, shade-tolerant conifers.

Nursery Seedlings

Seedlings for this study were grown from potentially rust-resistant seeds (entered in the USDA Forest Service genetic testing program) collected at Preston Park (48°34′45"N, 113°39′03"W, 2719 m) in Glacier National Park (GNP) approximately 40 km away from the test plots. The seeds were sown in February 2009 and seedlings were grown under standard nursery conditions (21° C day/night, 18-hour photoperiod) at the Forest Service Coeur d'Alene nursery (Burr et al. 2001) in a substrate mix of 70% Canadian *Sphagnum* peat moss and 30% composted bark in long Ray Leach cone-tainers (3.8–21 cm). Seedlings were fertilized every 8–12 days with a 20–7-10 NPK fertilizer with soluble trace element mix (STEM) micronutrients. In Apr. 2010 (5 months prior to outplanting), 983 14-month-old seedlings were transferred to an outdoor site at the GNP Native Plant Nursery, where fertilization was stopped to allow conditions for mycorrhizal colonization to develop. Seedlings were irrigated as needed with a Rainbird automatic irrigation system until containers were thoroughly leached; seedlings were allowed to dry out between irrigations. Seedlings were transported to WLNP on Sept. 27, 2010 by the GNP revegetation crew. For ease of transport, seedlings were removed from their containers with intact soil plugs, laid on plastic bubble wrap, and bundled into groups of 10 before transportation to

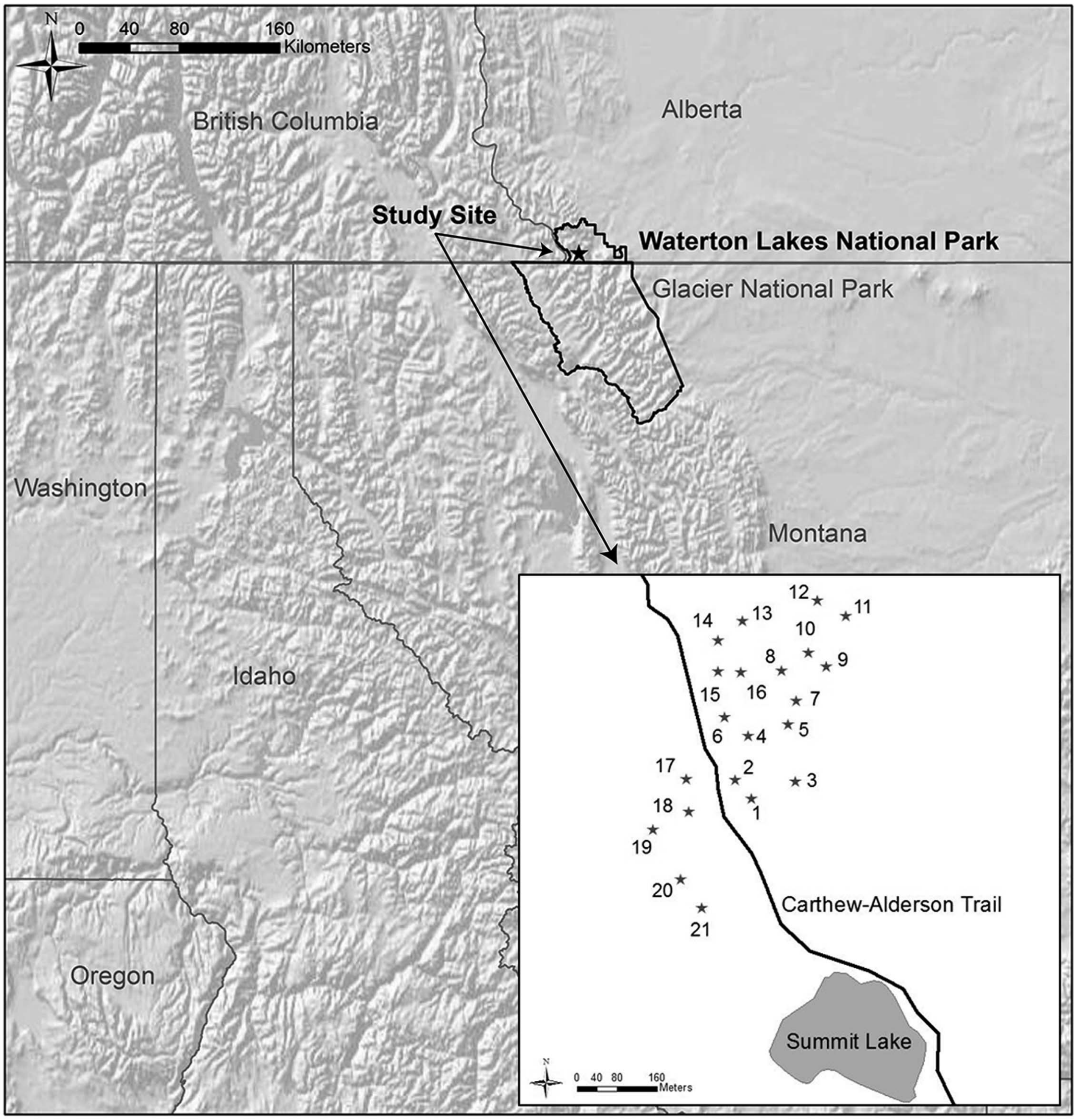

Figure 1. Location of the Summit Lake study site in Waterton Lakes National Park located in southern Alberta, Canada at 49°0′N, 114°1′W. Inset: Field study site showing the locations of each plot within WLNP. Plots are located between 1,950 and 2,000 meters in elevation.

WLNP. Inoculated and uninoculated seedlings were bundled separately to avoid exposing uninoculated seedlings to mycorrhizal treatment.

Spore Slurry and Ectomycorrhizal Inoculation

Spore slurry was made from cleaned fresh sporocarps of the native ectomycorrhizal fungus *Suillus sibiricus* (CLC 2640) collected in 2010. The hymenium was removed, cut into small pieces, and ground for approximately one minute in a coffee grinder with 10 ml of sterile distilled water. The ground-up material was strained through a mesh cloth into 400 ml of sterile distilled water and stored in glass bottles at 4° C. The spore content was counted using a hemocytometer and the slurry was diluted to a spore count of approximately 1×10^6 spores/ml. (Lonergan and Cripps 2013).

On Aug. 19, 2010, 478 seedlings were randomly selected and inoculated at the GNP Native Plant Nursery. Spore slurry was injected directly onto the soil substrate of containerized seedlings using an Allflex 50 ml repeat syringe. Each seedling received approximately 3 ml of slurry with a spore count of 1×10^6 spores/ml for a total of three million spores/seedling. These seedlings were tagged as "inoculated" and 505 uninoculated seedlings were used as "controls."

Site Preparation

Twenty-one plots were established at the Summit Lake study area by randomly generating global positioning systems (GPS) points (Figure 1) and using each point to mark the center of a 50 m diameter circle. A custom-built terrestrial torch was used to burn approximately half of each plot (25 m diameter) mainly to reduce living Engelmann spruce, subalpine fir, and understory vegetation (Schwanke and Smith 2010). Effort was taken to avoid burning young and mature WBP trees. Areas burned by the terrestrial torch were small and patchy and the burns were of a mixed severity ranging from "no lethal fire" to greater than 50% consumption of mature trees and surface fuels such as grasses, juvenile trees, and dead and downed material. Prescribed burning could only be conducted during periods of low fire danger; Plots 1–12 were burned in 2009

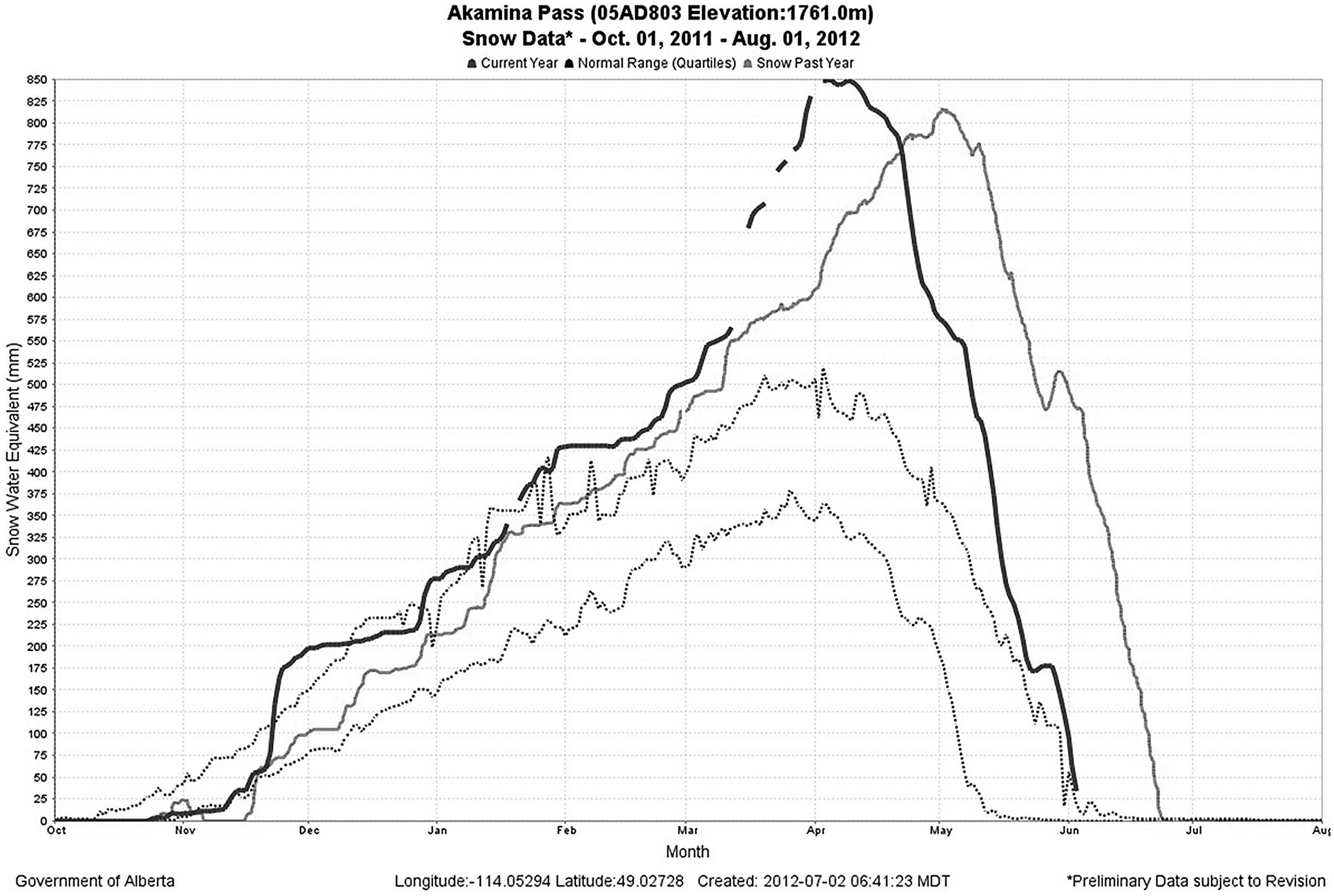

Figure 2. Snow water equivalent data from the Akamina weather station 3 km from the Summit Lake study site. Normal quartile range is bounded by dotted lines; gray solid line is for 2011 and black solid line is for 2012.[1]

and plots 13–21 in 2010. When present, beargrass was lush in unburned areas and remained as a thick root mat in burned areas. Each plot typically contained four site condition combinations: burned without beargrass, burned with beargrass root mats, unburned with beargrass, and unburned without beargrass (Lonergan 2012).

Planting Strategy and Treatments

On Sept. 28, 2010, 983 WBP seedlings were planted in clusters within the 21 plots. Seedlings were planted in clusters of three because previous research found that the survival of the ecologically similar limber pine (*Pinus flexilis* James) was improved when seedlings were planted in clusters (Smith et al. 2011b). The distance and azimuth from the center stake of the plot to each individual cluster was recorded using a meter tape and compass to aid in relocating seedlings. Seedlings in each cluster were designated as either A, B, or C to ensure individual seedling recognition during monitoring.

None, one, two, or three inoculated seedlings were included in each cluster to determine the minimum number of inoculated seedlings needed to improve survival. Individual seedlings were considered "inoculated" if they had initially received spore slurry at the GNP nursery. Uninoculated seedlings placed in clusters containing inoculated seedlings were considered "exposed" to mycorrhizal treatment. Seedlings placed in clusters without any inoculated seedlings were in the "uninoculated" (and unexposed) group. Approximately 16 seedling clusters were planted in each plot, with four replicate clusters on each site condition combination. Clusters were planted near shelter objects (microsites) when possible although this varied somewhat by availability and site condition type (Scott et al. 2011). Clusters planted within 30 cm of a standing tree, stump, large rock, snag, or large log were considered positive for the presence of a shelter object (Lonergan 2012). The final design consisted of two burn treatments (burn/no burn) × two beargrass treatments (XETE/no XETE) × two microsite treatments (yes/no) × three inoculation treatments (inoculated, exposed, not inoculated).

Monitoring and Analysis

All of the WBP seedlings were monitored for survival in August 2011 and 2012. Individual seedlings were assessed as "dead" if all needles were brown or "alive" if some portion of the needles were green. Seedlings were recorded as missing when no trace of the seedling could be found, typically due to frost heaving or rodent activity.

A binary logistic regression model was created in the program R (R Development Core Team 2008) to estimate the odds of WBP seedling survival as a function of burn (Y/N), beargrass (Y/N), microsite (Y/N), and mycorrhizal inoculation treatment (inoculated, uninoculated, uninoculated but exposed). A binary regression model was selected for this analysis because seedling survival (Y/N) is a binary response variable and all explanatory variables were categorical; analysis of variance (ANOVA) was not applicable for this study because the assumptions of this analysis could not be adequately met. Visual exploration of the data suggested varying

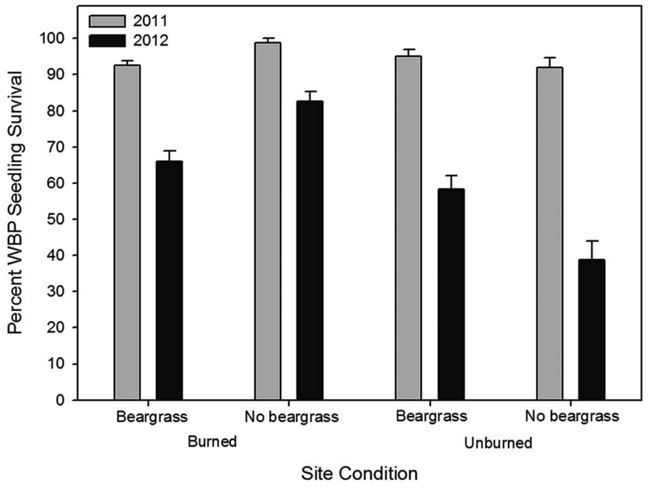

Figure 3. Average percent WBP seedling survival for the first (2011) and second (2012) year after out-planting as a function of site condition at the Summit Lake study site, WLNP. Graph includes 95% confidence bars.

relationships between the binary response variable "seedling survival"(Y/N) and explanatory variables, thus interaction terms between all variables were added to the model to further investigate these putative relationships. Backwards elimination of terms using Wald's *z*-test followed by drop-in deviance tests (Ramsey and Schafer 2002) confirmed that in addition to the main predictor variables the following interaction terms were necessary: burn (b) × beargrass (bg), burn × shelter object (so), beargrass × shelter object, burn × inoculation treatment,and beargrass × inoculation treatment. It should be noted for presentation purposes that there was no interaction between shelter object and inoculation. An $\alpha = 0.05$ was chosen as the criteria on which to retain/reject terms for model inclusion. Only the 2012 data set recorded 2 years after planting was used in the analysis.

Results

Survival of the WBP seedlings averaged 95% across all treatments after 1 year and 69% 2 years after out-planting (Figure 3). Survival was high across all four site conditions after 1 year and dropped more on the unburned area without beargrass in year two. The restoration treatments of: planting in prescribed burns, planting in beargrass, planting near shelter objects, and ectomycorrhizal treatment all influenced seedling survival to some extent.

The following model was found to best describe the probability of WBP seedlings survival and was selected for analysis:

logit(odds of survival) $= \beta_0 + \beta_1$ b $+ \beta_2$ bg $+ \beta_3$ so $+ \beta_4$ exposed $+ \beta_5$ inoculated $+ \beta_6$ b*bg $+ \beta_7$ b*so $+ \beta_8$ bg*so $+ \beta_9$ b*exposed $+ \beta_{10}$ bg*exposed $+ \beta_{11}$ b*inoculated $+ \beta_{12}$ bg*inoculated

Use of prescribed burns, shelter objects, and ectomycorrhizal inoculation all had a positive effect (see Table 1 for individual β values) on seedling survival under specific treatment combinations as indicated by survival odds (Exp(β)) greater than 1.0. Conversely, treatment combinations that had a negative effect on seedling survival are indicated by survival odds of less than 1.0 (Table 1).

Overall, the highest survival rates were for WBP seedlings planted in burned areas, away from beargrass and near microsites, whether inoculated (84%), exposed (80%), or not inoculated (86%) (Figure 4). The effect of ectomycorrhizal treatment was site dependent and improved WBP survival 17–23% on the unburned areas where beargrass was present (Figure 5B; Table 2). In general, the presence of shelter objects improved seedling survival on the burned areas (10–12%) and also on the unburned areas where beargrass was lacking (31%); these unburned areas without microsite had some of the lowest survival rates recorded (43%) (Figure 5A, Table 2).

In the burned areas, WBP seedling survival ranged from 54% to 86% depending on the presence of beargrass, use of shelter objects, and type of inoculation treatment (Figure 4). On these sites, seedlings planted away from beargrass had a higher survival rate (82%) than seedlings planted near/in the burned mats of beargrass (66%). However, planting near shelter objects had a positive influence in the burned areas, increasing survival 10% when beargrass was present ($P = 0.046$) and 12.6% when it was not ($P = 0.002$) (Table 1). Ectomycorrhizal inoculation did not appear to influence seedling survival in the burned areas, either in the presence of beargrass ($P = 0.34$ for exposed, $P = 0.26$ for inoculated) or in areas devoid of beargrass ($P = 0.11$ for exposed, $P = 0.28$ for inoculated), at least at this early stage.

In unburned areas, WBP seedling survival ranged from 19% to 74%, depending on the presence of beargrass, planting near shelter objects, and type of inoculation treatment (Figure 4). In contrast to burned areas, seedlings in unburned areas had a higher survival rate when planted near/in beargrass (62%) rather than in areas where it was lacking (38%), although this was strongly influenced by the presence of shelter objects on areas devoid of beargrass and by ectomycorrhizal inoculation on beargrass sites (Table 2). In unburned areas, planting near a shelter object increased survival 35.1% when beargrass was not present ($P = 0.001$), regardless of ectomycorrhizal treatment; thus the use of shelter objects is important on these exposed sites without vegetation and with rocky soils (unburned, no beargrass), which had low survival rates overall. In the unburned areas where beargrass was present, there was a strong positive effect from ectomycorrhizal treatment that increased seedling survival 23% ($P = 0.03$) in seedlings exposed to ectomycorrhizal inoculum and 17% ($P = 0.07$) in inoculated seedlings in comparison to those without ectomycorrhizal treatment (Table 1). There was also a positive influence (10.7%) from microsite when beargrass was present on these unburned sites ($P = 0.06$).

At this early stage of WBP seedling establishment, no clear, consistent trends were found among cluster ectomycorrhizal treatments (zero, one, two, or three seedlings inoculated per cluster) across the four site conditions (Longergan 2012). However, for applied purposes, it should be noted that for clusters planted in the unburned areas near beargrass (the only site condition with a clear mycorrhizal effect), seedling survival was on average 19.3% higher when clusters contained any number (one, two, or three) of inoculated seedlings in comparison to clusters without any inoculated seedlings.

Discussion

First year survival of the WBP seedlings (95%) planted at Summit Lake is higher than reported by other studies in the Rocky Mountain region. In a much larger study, first year survival rates averaged 74% for over 100,000 nursery-grown WBP seedlings planted across a variety of terrain types at elevations of 1,500 m to 2,900 m (Izlar 2007). In some smaller studies, first year survival rates averaged 68% on Dunraven Pass in Yellowstone National Park (Izlar 2007) and 79% (Red Eagle) and 52% (Flattop Mountain) in GNP (Asebrook et al. 2011). In the second year (2012), WBP

Table 1. Binary logistic regression results for site conditions, shelter object presence, and ectomycorrhizal inoculation treatment on the survival of out-planted whitebark pine seedlings after 2 years. Odds ratio for survival Exp(β) for various treatments is in comparison to a survival of 1.0 for each outgroup.

Model Terms	Estimate (β)[a]	SE	Wald Z[b]	df	Prob.[c]	Exp(β)[d]
Outgroup: Unburned without beargrass, Uninoculated, No shelter object						
Intercept	−1.109	0.387	−2.865	1	0.004	0.330
Burn	2.083	0.434	4.803	1	<0.001	8.029
Beargrass	0.877	0.404	2.168	1	0.030	2.404
Exposed	0.497	0.468	1.062	1	0.288	1.644
Inoculated	−0.042	0.399	−0.105	1	0.917	0.959
Shelter object	1.151	0.359	3.211	1	0.001	3.161
Outgroup: Unburned with beargrass, Uninoculated, No shelter object						
Intercept	−0.233	0.286	−0.814	1	0.415	0.792
Burn	0.572	0.347	1.648	1	0.099	1.773
No Beargrass	−0.877	0.404	−2.168	1	0.030	0.416
Exposed	0.798	0.377	2.114	1	0.035	2.220
Inoculated	0.604	0.331	1.824	1	0.068	1.829
Shelter object	0.551	0.290	1.902	1	0.057	1.735
Outgroup: Burned without beargrass, Uninoculated, No shelter object						
Intercept	0.974	0.384	2.536	1	0.011	2.647
Unburned	−2.083	0.434	−4.803	1	>0.001	0.125
Beargrass	−0.634	0.420	−1.510	1	0.131	0.530
Exposed	−0.583	0.363	−1.608	1	0.108	0.558
Inoculated	−0.359	0.332	−1.082	1	0.279	0.698
Shelter object	1.030	0.328	3.141	1	0.002	2.801
Outgroup: Burned with beargrass, Uninoculated, No shelter object						
Intercept	0.340	0.237	1.435	1	0.151	1.404
Unburned	−0.572	0.347	−1.648	1	0.099	0.564
No Beargrass	0.634	0.420	1.510	1	0.131	1.885
Exposed	−0.283	0.293	−0.964	1	0.335	0.754
Inoculated	0.286	0.253	1.131	1	0.258	1.331
Shelter object	0.429	0.215	1.996	1	0.046	1.536
Interactions						
Burn × beargrasss	−1.511	0.357	−4.229	1	<0.001	0.221
Burn × exposed	−1.080	0.435	−2.483	1	0.013	0.340
Burn × inoculated	−0.318	0.377	−0.843	1	0.399	0.728
Burn × shelter object	−0.121	0.331	−0.366	1	0.714	0.886
Beargrass × exposed	0.301	0.426	0.706	1	0.480	1.351
Beargrass × inoculated	0.645	0.377	1.711	1	0.087	1.906
Beargrass × shelter object	−0.601	0.353	−1.702	1	0.089	0.548

[a] Coeffecient.
[b] Wald chi-square value = (Wald Z value)^2.
[c] Significant values are bolded.
[d] Odds ratio of survival for the predictors.

seedling survival dropped to 69% at Summit Lake and this is consistent with other studies that reported serious declines after the first year (Mellmann-Brown 2005, Izlar 2007, Asebrook et al. 2011); however, survival rates tend to stabilize after 3–4 years (Izlar 2007, Asebrook et al. 2011). For example, the survival rate of WBP seedlings planted in GNP dropped to 38% after 4 years, but subsequent mortality averaged only 1%/yr for the next 3 years (Asebrook et al. 2011). In Izlar's (2007) large study, total survival also averaged 38%, 3–15 years after out-planting.

The high early survival of WBP seedlings at the Summit Lake study site could be a result of particular combinations of strategies and possibly the favorable wet spring conditions in 2011 and 2012 which were followed by mild summers. Higher mortality has been reported on sites with high sun exposure, which suggests that hot, dry spring and summer conditions may not be conducive to establishment of WBP seedlings planted the previous fall (Izlar 2007, Asebrook et al. 2011).

Although a terrestrial torch system has been used previously in WBP restoration to create openings (Keane and Parsons 2010), its use at Summit Lake is unique in that burned patches were typically small, averaging 25 m or less in diameter. Some of the highest survival rates for the WBP seedlings planted at the site were in these small open burned areas where seedlings also benefited by the presence of a shelter object and a lack of beargrass. Seedling survival for this study would be estimated as 70% on burns compared to 51% for the unburned areas if results could be averaged across other variables. Izlar (2007) reported that WBP seedlings planted in mixed severity burns and severe burns to have a higher survival rate (52%, 41%, respectively) than seedlings planted in unburned areas (21%) based on two unburned and 37 burned sites. Direct seeding of WBP seeds has been reported to result in higher germination rates and increased biomass when planted in burned areas (Perkins 2004). Although, McCaughey (1990) found germination rates of directly planted WBP seeds to be similar on litter soils and burns. However, survival rates of seedlings versus direct seeding are not directly comparable. The survival of limber pine seedlings (another five-needle pine) was also higher when planted in burns in WLNP (Smith et al. 2011b). Seedlings may benefit from being planted in burns because mineral nutrition is at least temporarily improved and warmer soil temperatures *in essence* lengthen the growing season (Tomback et al. 2001b). Soils typically experience a pulse of higher mineral concentrations following fire, and higher ammonium, nitrate, and phosphorus levels could benefit developing seedlings (Certini 2005). Also, the lack of shading or root competition from other vegetation could be beneficial, especially given the evidence that seedlings

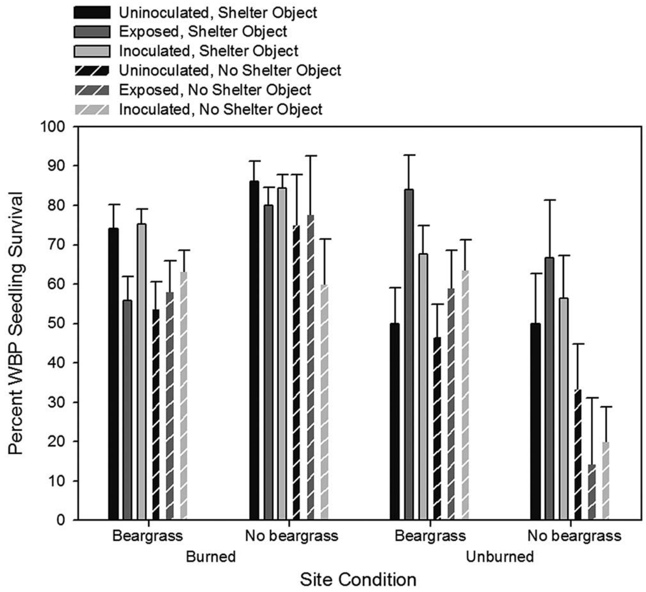

Figure 4. Average percent WBP seedling survival as a function of site condition, presence of shelter object and ectomycorrhizal treatment assessed after 2 years. "Exposed" indicates seedlings planted in clusters next to inoculated seedlings. Graph includes 95% confidence bars.

survived better when not planted in beargrass on burned sites. Although wildfire or prescribed fire creates canopy openings that reduce competition from shade-tolerant conifers and produces space for nutcracker caching, there is evidence to suggest that planting may still be necessary since birds can retrieve a majority of cached seeds for consumption on smaller burns (Keane and Parsons 2010).

Interestingly, several studies have reported no actual difference in the rate of natural regeneration between burned and unburned ground in Montana, Idaho, Oregon, and the Canadian Rockies (Moody 2006, Keane and Parsons 2010, Larson and Kipfmueller 2010). For example, 7 years after the 1988 Yellowstone fires, natural WBP seed germination rates were similar on burned and unburned sites, although germination was lowest on the moist, unburned sites (Tomback et al. 2001b). However, the beneficial effect of fire in killing competing trees also should be taken into account. Successful regeneration of WBP is only effective if seedlings are able to attain maturity and crowding and competition from faster-growing conifers needs to be addressed. Removing competition with prescribed fire or planting after wildfire is one way to ensure regenerated WBP seedlings are not suppressed in future decades. Results could reflect a complicated combination of abiotic and biotic factors at work in natural systems.

The presence of beargrass (or at least its rhizomatous root mass) appeared to reduce the survival of WBP seedlings planted in the burned areas since survival on each comparable treatment combination was lower on burned sites when beargrass was present. Perkins (2004) reported that WBP seedlings had a lower biomass when seeds were planted near beargrass or elk sedge (*Carex geyeri*); both understory types have dense rhizomatous root systems that may be restrictive to conifer establishment. Other herbaceous species and grasses with rhizomatous growth habits have been shown to suppress conifer establishment (Amaranthus et al. 1993). In addition, both beargrass and elk sedge tolerate and quickly resprout after light to moderate severity fire, which could be a concern in WBP restoration when using prescribed burning (Lonergan 2012).

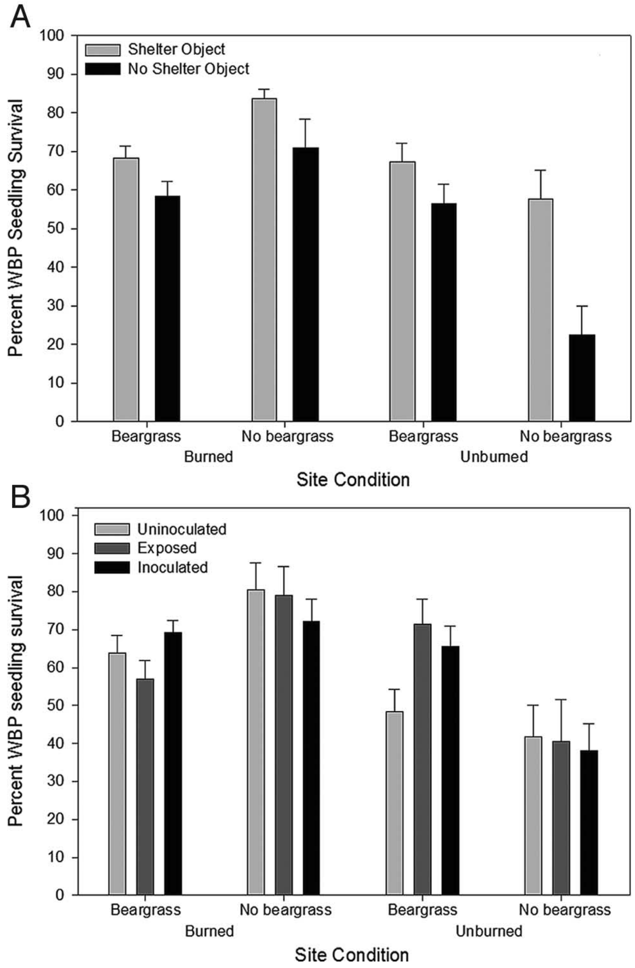

Figure 5. A. Whitebark pine seedling survival as a function of site condition and presence of a shelter object assessed after 2 years. B. Whitebark pine seedling survival as a function of site condition and mycorrhizal treatment assessed after 2 years. "Exposed" indicates seedlings planted in clusters next to inoculated seedlings. Graphs include 95% confidence bars.

In the unburned areas, it is more difficult to tell how beargrass affects seedling survival since it is complicated by a mycorrhizal effect on sites with beargrass and by a strong microsite effect where beargrass is absent. However, survival was generally lower on the exposed, rocky sites lacking beargrass. It is possible that the prolific aboveground vegetation of beargrass benefits early seedling survival by helping to retain moisture or by creating a microclimate suitable for WBP seedlings (Smith et al. 2011b). Protection from harsh environmental conditions, such as heavy creeping snow packs and desiccation from solar radiation and winds during the initial stages of seedling establishment, could be important. If beargrass can be considered *in effect* a type of microsite, this would also dampen any recorded effect from logs, stumps, etc. initially recorded as microsites. However, eventual competition from herbaceous plants for light, water, and nutrients could eventually threaten the survival of young conifer trees (Wagner et al. 1989).

Planting near shelter objects increased seedling survival on burned sites and on the unburned sites with beargrass by 10% and on unburned sites without beargrass by 35% when other variables are averaged. Previously, Izlar (2007) suggested that the presence of shelter objects could improve survival of WBP seedlings but conclusions were based on a sample of 100 seedlings (91 with microsite, 9

Table 2. Sample size and percent survival for out-planted whitebark pine seedlings after 2 years as a function of either ectomycorrhizal treatment or presence of a shelter object.

Site condition	Treatment	Sample size	Survival %
Inoculation Treatment			
Unburned with beargrass	Uninoculated	54	48.3*
	Exposed	47	71.5
	Inoculated	70	65.6
Unburned without beargrass	Uninoculated	27	41.7
	Exposed	16	40.5
	Inoculated	41	38.1
Burned with beargrass	Uninoculated	92	63.9
	Exposed	85	56.9
	Inoculated	191	69.2
Burned without beargrass	Uninoculated	87	80.6
	Exposed	99	78.9
	Inoculated	174	72.1
Presence of a shelter object			
Unburned with Beargrass	Yes	86	67.2[a]
	No	85	56.5
Unburned without beargrass	Yes	37	57.6[b]
	No	47	22.5
Burned with beargrass	Yes	231	68.3[a]
	No	140	58.3
Burned without beargrass	Yes	321	83.5[b]
	No	36	70.9

[a] Significant at 0.05 level.
[b] Significant at 0.01 level.

without). Here we provide clear statistical evidence to support her hypothesis that planting near shelter objects benefits WBP seedlings. Planting near certain types of shelter objects has been hypothesized to increase seedling survival and growth because it protects developing seedlings from wind, soil erosion, snow movement, and the high solar radiation often associated with high elevation sites (Scott et al. 2011). Izlar (2007) suggests that large logs and rocks located uphill or to the side of planted WBP seedlings create the most favorable shelter objects, while live trees and shrubs are the least beneficial. Of the shelter objects used at the Summit Lake site logs, stumps, and snags had a more beneficial effect than rocks on seedling survival for all site conditions except one (Lonergan 2012). On unburned sites without beargrass, only logs and rocks were available and both increased survival. Naturally regenerating WBP seedlings are often associated with a shelter object and a majority has been reported within 15 cm of a shelter object (Tomback et al. 1993). Planting near a shelter object increased seedling survival the most on unburned sites where beargrass was not present; at these sites planting was also difficult because of shallow, rocky exposed soils. Whitebark pine seedling survival was low on these sites, but the use of microsites almost doubled survival in these areas, which should be a consideration in reforestation of similar harsh sites.

The effect of ectomycorrhizal inoculation on WBP seedling survival was dependent on site conditions in this study. The benefits of inoculation are known to be highly variable and site specific (Quoreshi et al. 2009). The mycorrhizal treatment effect was apparent on unburned sites where beargrass was present, and on these sites it increased survival whether shelter objects were present (26%) or not (15%). With mycorrhizal treatment, survival rates on the unburned-beargrass sites (82%) were comparable to some of the high survival rates found on burned areas. The prolific beargrass vegetation could have restricted control seedlings from associating with native fungi and/or the microclimate might have been particularly conducive to the fungi used in inoculation. In a small study in WLNP, few ectomycorrhizae were found on WBP seedlings regenerating naturally in beargrass mats (Cripps et al. 2008), but here inoculation appeared to overcome this limitation.

Mycorrhizal inoculation did not appear to have an effect on WBP seedling survival in unburned areas without beargrass. On these exposed sites with rocky soils, microsite was the dominant factor positively influencing seedling survival. Inoculation might be expected to ameliorate these harsh conditions, however, it is also possible that some harsh abiotic conditions (i.e., xeric soils) are not conducive to maintenance of the inoculated fungus on seedling roots. Inoculation also did not appear to have an effect on seedling survival in burned areas where survival was still high after 2 years. This was surprising since it is generally thought that ectomycorrhizal inoculation might be most important on burns where appropriate fungi are absent (Wiensczyk et al. 2002). However, the influence of fire on ectomycorrhizal communities depends on many factors, including frequency, intensity, severity (Ryan and Noste 1985), and season of burning, as well as climate, soil moisture, fuel load, and forest type (Cairney and Bastias 2007). At Summit Lake, survival on the burned areas was still high after 2 years, and the initial nutrient release typically associated with burned soils could temporarily mask any inoculation effect. Also, inoculation effects may not be apparent early on; longer-term monitoring may be necessary to detect any benefits. An assessment of natural mycorrhizal colonization of planted WBP seedlings on Dunraven Pass in Yellowstone National Park found there was little correlation between survival and mycorrhizal colonization until the third year after out-planting (K. Izlar, University of Montana, pers. comm., Nov. 15, 2009). In addition, native ectomycorrhizal fungi could be available in the soil at Summit Lake since living WBP trees are present that might obscure any potential advantage from nursery inoculation. Areas burned by the terrestrial torch were small and patchy and preexisting mycelial networks and resistant propagules (spores) can remain viable in forest systems after fire (Amaranthus et al. 1993, Baar et al. 2002, Cairney and Bastias 2007). Inoculated and uninoculated seedlings could potentially pick up any native burn-adapted ectomycorrhizal fungi that might be present in the burned areas (Trusty and Cripps 2011).

Results of this study suggest that the combination of terra-torching small areas (in this case where living WBPs were present) prior to planting seedlings is a potentially useful treatment that can enhance at least the early survival of planted WBP seedlings. Planting near microsites is another strategy that can increase seedling survival on both burned and unburned areas. The effect of ectomycorrhizal inoculation is more site dependent but results show it has potential to increase seedling survival in areas where mycorrhizal inoculum may be difficult to access (thick beargrass mats for this study). The value of mycorrhizal inoculation is detailed in Keane et al. (2012). The low survival rates on unburned areas devoid of beargrass suggest that planting in exposed rocky soils without existing vegetation should be avoided, and if it is unavoidable, microsite should certainly be used. This study examined survival during the early acclimation phase of out-planted WBP after 2 years. While valuable insights can be gained on the early establishment of WBP seedlings planted for reforestation purposes, the ultimate impact of these treatments on WBP seedling survival may not be apparent until years later. Whitebark pine is a slow-growing conifer and long-term monitoring will be necessary to assess the ultimate effectiveness of the treatments examined.

Endnote

1. The source of the materials is www.environment.gov.ab.ca/. The use of these materials by the authors is done without any affiliation with or endorsement by the Government of Alberta. Reliance on author's use of these materials is at the risk of the end user.

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