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Regeneration niche of whitebark pine in the Canadian Rocky Mountains: the basis to restoring an endangered species

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ABSTRACT

Knowledge of regeneration processes of the endangered whitebark pine (*Pinus albicaulis* Engelm.) is critical for developing approaches for recovery and restoration of the species. We investigated biophysical associates of whitebark pine seedling occurrence and density in different mesohabitats (defined by community type and elevation) within the northern Rocky Mountains of Alberta. We developed candidate linear models to examine factors influencing occurrence and abundance. Occurrence was positively related to bare mineral soil and species richness in forest mesohabitats, while in both open and alpine-treeline environments it was positively related to prostrate shrub cover. Negative associates included tree cover, rocky substrates, and seedling cover of other conifers. Model validation showed a strong correlation between observed and predicted occurrence (correlations of 0.60, 0.56, and 0.56 for forest, open, and alpine-treeline mesohabitats, respectively). Climate models best predicted seedling density; abundance was highest on south-facing slopes in all mesohabitats. Correlations between observed and predicted density were 0.83, 0.92, and 0.72 for forest, open, and alpine-treeline mesohabitats, respectively. Our study identifies biophysical parameters to consider when planting blister rust-resistant seedlings and suggests that open mesohabitats along south-facing slopes may be best for regeneration of whitebark pine, particularly near the northern limits of its range.

INTRODUCTION

Whitebark pine (*Pinus albicaulis*), a keystone (El-lison et al., 2005), subalpine tree species in western North America is declining throughout its range (Tomback and Achuff, 2010). White pine blister rust (Smith et al., 2008; McKinney et al., 2009; Geils et al., 2010) and mountain pine beetle (*Dendroctonus ponderosae*; Logan et al., 2010; Raffa et al., 2013) have drastically increased mortality and lowered reproduction of this species. In addition, increased fire return intervals have resulted in a reduction in the open sites thought to be necessary for regeneration and a concomitant increase in competition from later-successional conifers (Murray et al.,

1998, 2000; Arno, 2001). Indeed, whitebark pine may have already entered into the spiral of extirpation (Tomback and Achuff, 2010).

Restoration of whitebark pine is ongoing throughout its range (Keane et al., 2012). Actions include thinning competing tree species, developing and planting blister rust-resistant seedlings, and emulating natural disturbance regimes such as fire that are thought to help perpetuate whitebark pine in the lower subalpine (Schwandt et al., 2010). The success of restoration efforts designed to increase the species' recruitment depends upon a good understanding of the regeneration niche (Grubb, 1977). Due to whitebark pine's large geographic range (Weaver, 2001) and wide potential niche (Arno and

Hoff, 1989; Larson and Kipfmüller, 2012), research on the regeneration niche would benefit from targeted sampling in a variety of regions. Indeed, most recovery plans for whitebark pine suggest research be conducted on its regeneration niche (Aubry et al., 2008; Keane et al., 2012; Alberta Whitebark and Limber Pine Recovery Team, 2014).

For successful natural whitebark pine regeneration to occur, seed must be produced, removed from the cone and cached by a Clark's nutcracker, germinate, survive, and grow. Seedling abundance is greatly impacted by proximity to seed source and seed source size (Moody, 2006; McKinney et al., 2009; Larson and Kipfmüller, 2010; Barringer et al., 2012). The impact of slope and aspect varies with latitude, with whitebark pine most prevalent on north-facing slopes in the southern part of its range and on south-facing slopes in the north (Arno and Hoff, 1989). This may be due to the balance between moisture and temperature required for germination and early growth. Germination rates appear to be highest on warm sites (McCaughy and Weaver, 1990; Moody, 2006; Larson and Kipfmüller, 2010) as long as adequate moisture is available (McCaughy and Weaver, 1990; Tomback et al., 1993, 2001; Mellman-Brown, 2005; Moody, 2006).

Recruitment of whitebark pine seedlings occurs in a variety of forest and treeline habitats. Whitebark pine is moderately shade tolerant (Arno and Hoff, 1989) and may persist and grow slowly in the understory of late successional stands (Campbell and Antos, 2003), but it is typically outcompeted by spruce and fir (Campbell and Antos, 2003; Moody, 2006; McCaughy et al., 2009; Larson and Kipfmüller, 2010). Whitebark pine seedlings can escape from competition by occupying more harsh, open environments where competing conifers struggle to survive (Callaway et al., 2002; Maher and Germino, 2006). However, seedlings in open environments still benefit from the presence of vegetation or objects that may provide shelter, helping to alleviate water stress induced by high winds or solar insolation (Tomback et al., 1993; Mellman-Brown, 2005; Resler et al., 2005; Izlar, 2007; McCaughy et al., 2009).

There is a dearth of research on whitebark pine at the northern edge of its distribution where environmentally limiting factors might differ. Re-

search in this region could help to inform larger geographic trends in the distribution of whitebark pine and provide insight into the species' adaptation and survival under a changing climate (McLane and Aitken, 2012). Filling this void is important for defining critical habitat under the Canadian *Species at Risk Act* (SARA) and informing provincial (Alberta and British Columbia) and federal (Canada) recovery plans for whitebark pine by identifying (1) specific microsites where seedlings are favored, (2) forest habitats where disturbance would benefit whitebark pine, and (3) important habitat where development should be avoided.

In this study, we characterized the biophysical associates of whitebark pine regeneration at the northern edge of its distribution in Alberta, Canada, examining environmental factors affecting presence/absence and abundance of whitebark in a variety of mesohabitat types at different elevations. We created statistical candidate models to test competing hypotheses about factors that had the strongest effect. For occurrence we compared between: soil microhabitat, light, and plant community. For density we compared between: soil microhabitat, plant community, and climate and seed source. We predicted that coarser scale variables, such as climate and seed source proximity, would better explain variation in seedling abundance/density, while finer scale factors, such as light, competition, and microsite type, would be best related to occurrence. In addition, we hypothesized that the main drivers of whitebark occupancy would vary among mesohabitats. For example, in forested environments we expected that light availability would drive whitebark pine occurrence, whereas in open and treeline environments we expected occurrence to be impacted mainly by microhabitat factors such as soil and the plant community (which could either have negative effects due to competition or positive effects due to protection from the harsh microclimate).

METHODS

Study Area and Site Selection

The study area was located in Jasper National Park and Willmore Wilderness Parks in Alberta,

Canada (53.7786°N, 119.7167°W to 52.4636°N, 117.4219°W), with an elevation range of 1610–2263 m. Both parks lie within the eastern shadow of the Continental Divide and have similar climatic conditions. Here whitebark pine occupies a seral role in the lower subalpine zone and occurs as a late successional species with subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex. Engelmann) or in pure whitebark pine stands in the upper subalpine.

We used 29 sites, all of which contained permanent health monitoring transects for mature whitebark pine (established by Alberta Parks and Parks Canada); this will allow for future examination of levels of white pine blister rust infection at these sites. These sites were randomly selected and are representative of the whitebark pine populations in the area.

Mesohabitat and Microsite Characterization

At each study site we sampled whitebark pine established in different mesohabitats: (1) mixed conifer or pure whitebark pine forest (hereafter referred to as “forest”); (2) open canopied areas below treeline (hereafter referred to as “open”); and (3) within the transition zone from forest to alpine tundra (hereafter referred to as “alpine-treeline” [AT]). In each mesohabitat at each study site, transects—typically 100 m long—were established within a homogenous area representative of the mesohabitat. The forest transect was selected using the same starting point as the formerly established health transects. Open and alpine-treeline transects were selected based on a brief exploration of the site. At several sites, two transects were established in a given mesohabitat type in order to increase replication and capture additional variation (e.g., we might establish transects in two open mesohabitats that exhibited different slopes or aspects at the same site).

At each transect we recorded slope, aspect, pH of the surface mineral soil at the transect start point, and a qualitative description of soil moisture regime and of nutrient regime. Aspect was changed to heat load index (HLI) by converting degrees to a linear value from 0–1 and transforming the data so the warmest aspect (SW or 225°) equals 1 and coldest

aspect (NE or 45°) equals 0 (Beers et al., 1996; as cited in Moody, 2006). We retrieved several climate variables using a climate model based on elevation, longitude, and latitude developed by Hamann et al. (2013). These variables are accurate to 1 km² and can be used with confidence to predict climatic variation as related to elevation. Further details on each of these climate variables can be found in Table 1. For each transect, we calculated canopy cover, total stand density, whitebark pine stand density (as a proxy for seed production), understory vegetation cover, species richness, and availability of different regeneration substrates by taking the average of data collected in the microsite plots (procedure below). Seedling density was quantified by recording the seedlings within 2 m of either side of each transect. All individual whitebark stems shorter than 1.3 m were included in the count. Transects that had no seedlings within 2 m were eliminated from the analysis of density (one forest, three open, and two alpine-treeline transects).

To examine the associates of whitebark pine seedling occurrence, we compared the biophysical characteristics of microsite plots (1 × 1 m) containing whitebark pine seedlings (hereafter referred to as “occupied plots”) to plots without whitebark pine seedlings (hereafter referred to as “unoccupied plots”). We divided each transect into five 20-m segments and selected an occupied and unoccupied plot in each segment for further characterization. The occupied plot was established at the first whitebark pine seedling found in a transect segment (within 2 m either side). If no seedling was found within this area, we extended our search to within 4 m of the transect line, ensuring that this area still fell within the target mesohabitat. The unoccupied plot was randomly located with the constraint that there should be no whitebark pine seedling within 2 m. In each plot we quantified: organic layer depth, litter depth, canopy cover, and tree basal area for each tree species. We visually estimated percent cover for ground cover types (moss, lichen, rock, mineral soil, downed woody material, and cryptogamic crust) and percent cover to species for vascular plants, separately recording seedlings and trees of the same species (Table 1). Canopy cover was determined using a convex spherical densiometer. Basal area was determined by using a basal area prism (BAF 4). From the plant community data, we derived sev-

TABLE 1

Predictor variables used in linear models, the level (mesohabitat or microsite) at which they were sampled, and the candidate model of which each variable was considered a part.

Variable	Explanation	Level	Candidate
HLI	Heat load index (0–1)	Mesosite	Climate
SLOPE	Slope (°)	Mesosite	Climate
MAT	Mean annual temperature (°C)	Mesosite	Climate
MWMT	Mean warmest month temperature (°C)	Mesosite	Climate
MAP	Mean annual precipitation (mm yr ⁻¹)	Mesosite	Climate
MSP	Mean summer precipitation (mm yr ⁻¹)	Mesosite	Climate
AHM	Annual heat moisture index (degree days >5°C / MAP)	Mesosite	Climate
SHM	Summer heat moisture index (degree days >5°C / MSP)	Mesosite	Climate
PH	pH of mineral soil	Mesosite	Soil microhabitat
BA-PIAL	Basal area of mature <i>Pinus albicaulis</i> (m ² ha ⁻¹)	Microsite*	Seed source
BA-TOT	Total basal area of all mature trees (m ² ha ⁻¹)	Microsite*	Light and seed source
CAN-COV	Canopy cover (%)	Microsite*	Light and seed source
TREE	Total tree cover (branches and stems of saplings and mature trees) in understory plot below 1.4m (%)	Microsite	Light and plant community
FORBS	Total cover of forbs (%)	Microsite	Plant community
PR-SHRUB	Total cover of prostrate shrubs less than 5 cm (%)	Microsite	Plant community
GRAMS	Total cover of all graminoid species (%)	Microsite	Plant community
SEEDLING	Total conifer seedling cover excluding <i>Pinus albicaulis</i> (%)	Microsite	Plant community
UP-SHRUB	Total cover of erect shrubs greater than 5 cm (%)	Microsite	Plant community
VEGCOVER	Sum of understory vegetation cover of all species (%)	Microsite*	Plant community
ORGDEP	Depth of organic matter depth (cm)	Microsite*	Soil microhabitat
LITDEP	Litter depth at plot center (cm)	Microsite	Soil microhabitat
RICHNESS	Species richness (species m ⁻²)	Microsite	Soil microhabitat
BARE	Bare mineral soil cover (%)	Microsite*	Soil microhabitat
LICHEN	Lichen cover (%)	Microsite*	Soil microhabitat
LITTER	Litter cover (%)	Microsite*	Soil microhabitat
MOSS	Moss cover (%)	Microsite*	Soil microhabitat
ROCK	Rock cover (%)	Microsite*	Soil microhabitat
WOOD	Downed and decayed woody material cover (%)	Microsite*	Soil microhabitat

*Microsite variables also used in density model. Plots within each transect treated as subsamples.

eral variables: total vegetation cover (sum of covers for all species); species richness (number of vascular species per plot to use as a proxy for soil productivity; Kirkman et al., 2001); cover by functional group—trees (cover below 1.4 m in microsite plot of branches and stems of saplings and mature trees), seedlings (all trees <1.4 m in height, other than whitebark pine), graminoids (grass, sedge, and rush species), forbs (herbaceous broadleaf vascular spe-

cies), prostrate shrubs (woody vascular species <5 cm in height), and upright shrubs (woody vascular species >5 cm height).

Data Analyses

We compared mixed linear models using the lme4 package (Bates et al., 2015) of the R statistical language (R Core Team, 2013) to test our competing

hypotheses about which candidate models best explained variation in seedling occupancy at the microsite scale and density at the mesohabitat scale for each mesohabitat separately. The candidate models considered for occupancy were: soil microhabitat, light, and plant community. For density we considered: soil microhabitat, plant community, climate, and seed source. These models described the linear effect of independent variables on the log-odds probability of a plot being occupied or on seedling density. Seedling density was \log_2 transformed to improve normality. Random effects included site (for density and occupancy) and transect segment nested within transect (for occupancy). We examined correlations among fixed independent variables; when variables had a correlation coefficient > 0.7 we retained only the variable that was most strongly related to the response variable for consideration for inclusion in the candidate models. The variable total basal area was removed due to its strong correlation with canopy cover (Table A1). In addition, because of strong correlations among the retrieved climate variables, only mean warmest month temperature and annual heat moisture index were retained (Table A2).

Each biophysical variable was assigned to a candidate model (see Table 1) prior to analysis. Then, for each model, independent variables with the least significant effect were iteratively removed one at a time until we arrived at the model with the lowest Akaike Information Criterion (AIC). Subsequently, we constructed a “combined” model that considered for inclusion all variables that were retained in each of the separate models (soil microhabitat, light, etc.); again for the combined model we iteratively removed the least-significant variables until we had produced a model with the lowest AIC. Only interactions of independent variables that improved AIC values for respective models were considered for inclusion. As a validation step for each of the final optimal models, we calculated the correlation between observed and predicted values of the response variable.

RESULTS

Comparisons of the candidate models for seedling occurrence illustrated that the most important factors differed among the forest, open, and AT mesohabitats, although some factors were

important in all mesohabitats (Table 2). Notably, tree cover in the microsite plots was negatively related to occupancy in all three mesohabitats. For occupancy in the forest mesohabitat, the soil microhabitat model was the best, whereas the plant community model was the best in the open mesohabitat; in the AT mesohabitat, the microhabitat and plant community models had very similar AIC values. In all cases, the combined model incorporating variables from the three candidate models had the lowest AIC. The validation showed reasonably good performance of these models with correlation coefficients between observed and predicted values of 0.60, 0.56, and 0.56 for the Forest, Open, Alpine-Treeline mesohabitat models, respectively.

In the forest mesohabitat (Table 2, part A), the soil microhabitat model was the best; it included cover of bare mineral soil and species richness, which were both positively related to whitebark pine seedling occupancy. The combined model included these two variables plus tree cover in the microsite plot, which had a negative association with whitebark pine occupancy.

In the open mesohabitat (Table 2, part B), the plant community model was the best; it included cover of trees and seedlings as having a negative impact, and cover of prostrate shrubs as having a positive impact on the probability of whitebark pine seedling occupancy. The combined model was the best overall and it included these three variables along with a negative impact of the cover of rock.

In the alpine-treeline (AT) mesohabitat (Table 2, part C), the plant community, light, and soil microhabitat models had similar AIC values of 386.2, 387.0, and 387.5, respectively. In the plant community model, occupancy was negatively associated with tree cover and positively associated with cover of prostrate shrubs in the microsite plots, while the light availability model included only the negative association with tree cover. Similar to open mesohabitats, in the soil microhabitat model, cover of rock was negatively associated with whitebark pine occurrence and this model also included a positive effect of litter depth. The combined model incorporated the negative impact of tree and rock cover along with the positive association with litter depth.

TABLE 2

Results for the optimum candidate and combined models for whitebark pine seedling occupancy in: (A) forest; (B) open; and (C) alpine-treeline mesohabitats. For each model the estimate for the intercept, the terms and their coefficients are presented. Akaike's Information Criterion (AIC) for each model is also given and was used to choose among competing models. Coefficients represent the effect (negative or positive) on the probability (log odds) of a plot being occupied by a whitebark pine seedling. Also presented is the correlation between predicted and observed values for the model with the lowest AIC value in each mesohabitat. Explanation of abbreviations for the terms in the models can be found in Table 1.

Candidate	Model	AIC	Correlation (observed and predicted)
(A) Forest			
Plant community	0.203 – 0.0219 * (TREE)	436.0	NA
Light	0.203 – 0.0219 * (TREE)	436.0	NA
Soil microhabitat	–0.738 + 0.0802 * (BARE) + 0.0829 * (RICHNESS)	424.7	NA
Combined	–0.430 + 0.0802 * (BARE) + 0.0829 * (RICHNESS) – 0.0171 * (TREE)	418.8	0.60
(B) Open			
Plant community	–0.251 – 0.0209 * (TREE) – 0.0111 * (SEEDLING) + 0.0176 * (PR-SHRUB)	367.4	NA
Light	0.0267 – 0.0221 * (TREE)	375.4	NA
Soil microhabitat	0.137 – 0.0100 * (ROCK)	370.8	NA
Combined	0.174 + 0.0121 * (PR-SHRUB) – 0.0122 * (ROCK) – 0.0263 * (TREE) – 0.0170 * (SEEDLING)	360.9	0.56
(C) Alpine-Treeline			
Plant community	–0.183 – 0.0294 * (TREE) + 0.00881 * (PR-SHRUB)	386.2	NA
Light	0.0318 – 0.0311 * (TREE)	387.0	NA
Soil microhabitat	0.0179 – 0.00665 * (ROCK) + 0.255 * (LITDEP)	387.5	NA
Combined	0.182 + 0.414 * (LITDEP) – 0.0473 * (TREE) – 0.00895 * (ROCK)	373.1	0.56

For seedling density, the climate model consistently outperformed the seed source, soil microhabitat, or plant community models for all three mesohabitats (Table 3). Indeed, in the forest and open mesohabitats, no additional terms entered into the seed source, microhabitat, or plant community models. Further, for the forest and open mesohabitats, only climate variables entered into the combined model; for the AT mesohabitat the combined model included the climate variables along with pH and had a slightly lower AIC than the climate model. The validation showed good performance of the optimal models with correlation coefficients between observed and predicted values of 0.83, 0.92, and 0.72 for the best forest, open, and alpine-treeline mesohabitat models, respectively.

Heat load index had a strong positive effect in all three mesohabitats, indicating that seedling

density increased as the aspect approached the southwest. Mean warmest month temperature (MWMT) was negatively associated with seedling density in the open mesohabitat but positively associated with density in the AT mesohabitat; further, the models for both these mesohabitats included an interaction between MWMT and heat load index (HLI) (Table 3) (Fig. 1). In open mesohabitats, increasing MWMT was associated with decreased seedling density. This contrasted the effect of MWMT in AT mesohabitats where increased MWMT was associated with increased seedling densities. The interaction between HLI and MWMT was similar in the optimal models for both open and AT mesohabitats (although stronger in the latter). The interaction demonstrated increased MWMT resulted in a decrease in the positive effect of HLI. Only in the AT mesohabitat did any terms other than climate

TABLE 3

Results for the optimum candidate and combined models for whitebark pine seedling density in: (A) forest; (B) open; and (C) alpine-treeline mesohabitats. For each model the estimate for the intercept, the terms, and their coefficients are presented. Akaike's Information Criterion (AIC) is also given and was used to choose among the competing models. Coefficients represent the linear effect (negative or positive) on the density (base-two log) of whitebark pine seedlings (seedlings ha⁻¹). For models that include only the intercept, no variables were found to improve the model (based on AIC). Also presented is the correlation between predicted and observed values for the model with the lowest AIC value in each mesohabitat. Explanation of abbreviations for the terms in the models can be found in Table 1.

Candidate	Model	AIC	Correlation (observed & predicted)
(A) Forest			
Climate	7.7507 + 2.41 * (HLI)	114.2	0.83
Seed source	9.2323	144.7	NA
Microhabitat	9.2323	144.7	NA
Plant community	9.2323	144.7	NA
Combined	7.7507 + 2.41 * (HLI)	114.2	0.83
(B) Open			
Climate	14.938 + 2.34 * (HLI) - 0.56 * (MWMT) - 0.082 * (HLI) * (MWMT)	94.9	0.92
Seed source	10.17	110.2	NA
Microhabitat	10.17	110.2	NA
Plant community	10.17	110.2	NA
Combined	14.938 + 2.34 * (HLI) - 0.56 * (MWMT) - 0.082 * (HLI) * (MWMT)	94.9	0.92
(C) Alpine-Treeline			
Climate	-2.059 - 2.58 * (HLI) + 1.12 * (MWMT) + 0.45 * (HLI) * (MWMT)	81.42	NA
Seed source	9.06 + 0.29 * (BA_PIAL)	120.7	NA
Microhabitat	11.69 - 0.40 * (PH)	108.9	NA
Plant community	9.284	124.2	NA
Combined	-11.23 + 9.38 * (HLI) + 2.45 * (MWMT) - 0.75 * (HLI) * (MWMT) - 0.61 * (PH)	81.21	0.72

variables enter any models. In the seed source model, there was a positive association of the basal area of mature whitebark pine with seedling density, and a small negative effect of pH was observed in the soil microhabitat model.

DISCUSSION

The comparison of candidate models for occupancy of microsite plots by whitebark pine seedlings showed that occupancy is driven by soil microhabitat in forest mesohabitats and by plant community in open mesohabitats below treeline and alpine-treeline mesohabitats. Comparison of candidate models for seedling density, on the oth-

er hand, supported the hypothesis that climate is the driver of density. For seedling occupancy, the combined model that incorporated components of both the plant community and soil microhabitat models was superior to any of the simple candidate models in all mesohabitats. Evaluation of the simple candidate models provided information on how different ecological factors influence occurrence; this will be helpful for determining where to focus resources on conservation efforts. However, ecological systems are complex and the combined model better reflected the complexity of factors influencing whitebark pine occurrence.

For occupancy in the forest mesohabitat, the soil microhabitat was the best model, and this contra-

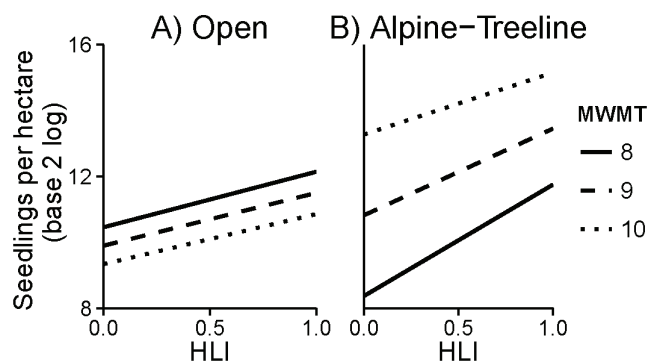


FIGURE 1. Graphical representation of the optimal model predicting seedling density as a function of the interaction between mean warmest month temperature (MWMT) and heat load index (HLI) (see Table 3, parts B and C) for: (A) Open and (B) Alpine-Treeline (AT) mesohabitats. Each line was constructed using a range of values for HLI while holding MWMT at the value shown. The range of MWMT at our sites was 9.1–11.8 °C for open and 8.3–9.9 °C for AT mesohabitats, and the range of HLI at our sites was 0–1 for both mesohabitats. Note that the optimal model for seedling density in alpine-treeline mesohabitats also includes a negative effect of pH, which is not shown here.

dicted our hypothesis. As whitebark pine is considered moderately shade intolerant and isn't known to compete well in understory environments (Arno and Hoff, 1989), we had expected light availability to account for the most variation. It is important to note, however, that we modeled occupancy and not growth. Research has shown that whitebark pine seedlings have the ability to survive suppressed for many years in the understory (Campbell and Antos, 2003). Our results suggest that in these environments availability of appropriate soil microhabitats that facilitate germination and initial growth of seedlings is a key limiting factor, specifically bare mineral soil and areas of high plant species richness. Bare mineral soil is an important substrate for whitebark pine establishment (McCaughey and Schmidt, 1990), while species richness may indicate sufficient moisture availability (Kirkman et al., 2001) or shared mycorrhizae, both of which are vital in early seedling survival and growth (McCaughey and Weaver, 1990; Tomback et al., 1993, 2001; Mellman-Brown, 2005; Moody, 2006). Our results suggest that in areas where appropriate soil microsite conditions exist for whitebark pine ger-

mination and early survival, conservation efforts might be better focused on selective removal of competing tree cover than to employ prescribed fire, because while the latter would destroy existing seedlings the former could allow for their release (Gelderman, 2015).

As hypothesized, occupancy for both the open and AT mesohabitats was best accounted for by the surrounding plant community. This result suggests availability of suitable soil microhabitats for establishment is not a limiting factor in these mesohabitats, while the adverse effects of nearby competition and harsh environmental conditions become more important. Negative impacts included cover of mature trees and seedlings of other species, while cover of prostrate shrubs was positively related to seedling occupancy. While mature trees can play a facilitative role in AT environments (Resler et al., 2014), many studies have demonstrated a negative effect of trees on whitebark pine seedling occurrence (Arno and Hoff, 1989; Campbell and Antos, 2003; Moody, 2006; Larson and Kipfmüller, 2010). The negative impact of nearby mature trees is clear in our study, as occupancy in all three mesohabitats had a significant negative association with tree cover in microsite plots.

Whitebark pine seedlings are noted as having the greatest ability of all subalpine conifer species to survive in open exposed habitats (Callaway et al., 2002; Maher and Germino, 2006), but they still benefit from some protection from wind and solar desiccation (Izlar, 2007; McCaughey et al., 2009). Our results add to the growing literature regarding the benefit of prostrate shrubs in such habitats. Prostrate shrubs do not limit light availability and provide several facilitative effects, such as reducing wind speeds, dampening variation in ground temperature, holding moisture (Körner, 2003), and potentially sharing mycorrhizal associations (Nara and Hogoetsu, 2004). Given the potential benefits, further research should investigate specific effects of prostrate shrubs on whitebark pine seedling survival and growth and determine whether a specific mycorrhizal association exists between these shrubs and whitebark pine.

Contrary to our predictions, climate rather than seed source predominantly drove whitebark pine seedling density. Heat load index (HLI) had a strong positive association with seedling density

across all three mesohabitats, which emphasizes the importance of aspect in whitebark pine regeneration near the northern limits of its distribution. Seedlings on southwest aspects are likely exposed to longer growing seasons and additional heat units in comparison to seedlings on more northeast aspects, both of which could explain increased seedling densities. Another factor causing increased whitebark pine density on southwest slopes is perhaps an increase of Clark's nutcracker seed caching on southwest-facing slopes, where late snow arrival and early snow melt provide access to caching sites; this has been observed in studies in other areas of whitebark pine's range (Tomback, 1978; Lanner, 1982; Lorenz et al., 2011).

We observed a contrasting effect of mean warmest month temperature (MWMT) in open and AT mesohabitats. Increasing MWMT was associated with a decrease in seedling density in open mesohabitats but an increase in density in AT mesohabitats. This contrasting effect may be explained simply by the location of open and AT mesohabitats in relation to each other. Recall that MWMT was largely based off of elevation, and increases or decreases in MWMT likely reflect downward or upward changes in slope position, respectively. Increasing MWMT in open mesohabitats reflects a movement downslope into areas where the climate is too warm to support seedlings. Likewise, decreasing MWMT in AT transects reflects a movement upslope where growth of trees becomes more and more difficult. The interaction of MWMT with HLI in these two mesohabitats also makes intuitive sense. In open mesohabitats, the positive effect of HLI is reduced as you move downslope (where MWMT is higher) because the southwest exposure exacerbates the effect of increased temperature. Further, in AT mesohabitats the positive effect of HLI is increased as you move upslope (to lower MWMT values) where additional heat units are even more important for the survival of whitebark pine seedlings.

Prior to this study, seed availability had been identified as one of the most significant predictors of seedling abundance (Moody, 2006; McKinney et al., 2009; Larson and Kipfmüller, 2010; Barringer et al., 2012). Our seed source candidate model included only percent canopy cover and mature whitebark pine basal area, which likely did a poor

job of representing the seed availability in this region. While whitebark pine basal area did have a small positive effect on seedling density in AT mesohabitats, the lack of seed source impact on forest and open mesohabitats likely reflects our poor characterization of seed source and should not be used as strong evidence that seed source is not important.

MANAGEMENT IMPLICATIONS

Restoration of whitebark pine is ongoing throughout its range (Aubry et al., 2008; Keane and Parsons, 2010; Schwandt et al., 2010; Keane et al., 2012). While most whitebark pine populations in the north aren't under immediate threat of extirpation, white pine blister rust infection rates are increasing (Smith et al., 2013), and proactive measures will be the most effective in reducing future risk. In areas where white pine blister rust is not yet prevalent, increasing natural regeneration may be a proactive means of increasing the likelihood of populations developing natural resistance (Schoettle and Sniezko, 2007), while planting blister rust seedlings will be a likely means of introducing blister rust resistance into declining populations (Sniezko et al., 2014).

McCaughey et al. (2009) provided an excellent seedling planting guide based largely on research done in the core of whitebark pine range. They suggest it is important to provide shade and protection, plant in moist soil, avoid overstory cover, and limit understory competition in general but plant in association with *Vaccinium scoparium*. Similar to McCaughey et al. (2009), we found strong evidence to suggest tree cover should be avoided. *Vaccinium scoparium* was located only in a few of our southern Jasper sites, but we believe there could be a facilitative nurse plant relationship with other prostrate shrubs such as *Vaccinium*, *Dryas*, and *Cassiope* species. Based on our results, whitebark pine seedlings were often found growing in association with species-rich understory plant communities, so we are unable to recommend the removal of understory competition based on our findings. In open and AT mesohabitats, it is likely that these communities provide the shade and protection considered important by McCaughey et al. (2009). Indeed this protection may be even more impor-

tant in the northern portion of the species' range. However, it is important to remember that our study was an investigation of naturally occurring seedlings and not a manipulative test of survivorship and growth.

Prescribed burning in forest environments in the lower subalpine may be an effective way of converting poor habitat into suitable whitebark pine habitat, particularly on southwest-facing slopes, as these supported the highest abundance of whitebark pine seedlings. However, it will be important to conserve mature trees (seed source) as well as to avoid burning in areas that will leave predominantly rocky substrates. In general, we found that the most consistent and predictable regeneration niche for whitebark pine in the north is in open environments below tree-line; our results further suggest that dry forests on southwest-facing slopes and open habitat in close proximity to good seed sources will be important to conserve for the future of whitebark pine populations. Open mesohabitats in mountain areas are often targeted for developments such as buildings, ski hills, or trails. We recommend carefully considering the effect of any such development on the current and future health of whitebark pine populations.

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