

**The influence of microsite characteristics on whitebark pine
(*Pinus albicaulis*) germination and early survival**

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Abstract

Whitebark pine, a hardy high-elevation species distributed throughout northwestern North America, is a keystone species for alpine ecosystems for its seeds, a food source for many wildlife species. It defines the community structure of alpine ecosystems, moderates the harsh climate, and increases ecosystem stability. As it is threatened by many factors, including climate change, facilitated migration may be needed to ensure the species' survival. Outplanting will rely upon knowledge of the specific environmental microsite characteristics that may support successful germination and survival of the species. A common garden experiment to test emergence rates according to variable site conditions was conducted across northern BC. Seed was collected from 7 source populations, stratified for 4 months, and planted in 8 common garden provenance trials distributed across northern British Columbia. Within-site conditions at the microsite level, including soil type, depth, vegetation influence, and topography, were assessed and related to seedling emergence. Convex microsites were positively related to emergence at a coastal, damp site. Surrounding vegetation with lower height seemed to support higher emergence. Organic soils were related to higher emergence rates at that same site. Microsites with shallow soils also had higher emergence rates. Seed source quality, such as seed maturity and development, as well as stratification techniques, may have a greater effect on the germination and first-year survival of whitebark pine seedlings. If facilitated migration supports whitebark pine growth at increasing latitudes, as climate change scenarios suggest may be necessary for species survival, these results may be used for successful outplanting.

Key Words

Whitebark pine, alpine ecosystems, germination, microsite, treeline, emergence, common garden trial, climate change, facilitated migration.

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Introduction

High elevation environments contain many unique and hardy species that have specifically evolved to occupy their specific environmental niches. Whitebark pine (*Pinus albicaulis* Engelm.) is a keystone high-elevation tree species scattered throughout western North American mountain ranges including the US and Canadian Rocky Mountains, coastal ranges, and high-elevation portions of the western US interior (Tomback 1982, Tomback *et al.* 1995, Scott and McCaughey 2006). It is part of the unique ‘stone pine’ (*Cembrae*) subsection of the genus *Pinus*, the members of which rely heavily on active dispersal by avian species, specifically members of the nutcracker genus (*Nucifraga* spp.) (Hutchins and Lanner 1982, Jorgensen and Hamrick 1997). Whitebark pine is considered a keystone species because its seeds are an important source of food to many wildlife species, including the Clark’s nutcracker (*Nucifraga columbiana* Wilson), grizzly bear, black bear, and other small rodent species (Tomback 1982, Tomback and Kendall 2001, Zeglen 2002). It is also ecologically critical to high elevation ecosystems where it is important as a pioneer species, often being the first to establish on exposed, harsh locations (Zeglen 2002).

The species range of whitebark pine has been shrinking over the last half-century due to the combined impacts of disease, competition, mismanagement, and climate change (Scott and McCaughey 2006). A recent increase in white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) attacks on whitebark pine has resulted in the rapid decline of the species over the last 60 to 80 years (Tomback *et al.* 1995, Keane and Arno 1996, Zeglen 2002, Mahalovitch *et al.* 2005). Fire suppression policies are also leading to incursion of shade-tolerant species, especially subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), and the competitive exclusion of whitebark pine in some

areas (Tomback *et al.* 1995, Keane and Arno 1996, Keane 2001, Zeglen 2002, Moody 2006). With such trends occurring across its range, a petition was recently put forth by the NRDC (National Resource Defense Council) requesting whitebark pine be federally listed through the Endangered Species Act in the United States (NRDC 2008). Within Canada, it is acknowledged as threatened in the provinces of British Columbia and Alberta, and may soon be recognized under the federal species at risk act (SARA) (Wilson and Stewart-Smith 2002, Alberta SRDACA 2007, BC Conservation Data Centre 2009). Internationally, it is red-listed by the IUCN as a threatened species with a decreasing overall population trend (IUCN 2008).

The treeline environments where whitebark pine grows are exposed to harsh conditions and any vegetation that exists there is subject to high environmental stress. A delicate dynamic equilibrium exists between influential climatic conditions and growth of mediating vegetation, a balance that is easily affected by minute changes in temperature or moisture levels (Shrag *et al.* 2008). The establishment of whitebark pine stands in harsh environments may moderate local climate enough to allow other species to subsequently establish (Tomback and Kendall 2001). Groups of whitebark pines growing at high elevation may also affect snow accumulation dynamics and moisture conditions of the surrounding area (Zeglen 2002). For example, upper tree islands may delay the average snowmelt in spring by reducing incident solar radiation, increasing water availability, and affecting runoff patterns (Farnes 1990). In this way the presence or absence of whitebark pine stands may explain aspects of spatial and species dynamics at the treeline ecotone (Zeng and Malanson 2006). It is considered a critical foundation species for such ecosystems, as it defines the community structure of high elevation areas by increasing the stability of local environmental conditions and ecosystem processes (Tomback 2007, Ellison *et al.* 2005).

The range and spatial distribution of whitebark pine is closely tied to that of the Clark's nutcracker (Krakowski *et al.* 2003). The ecological relationship between the two species is mutually beneficial and they are thought to have co-evolved to the point where they now rely upon each other (Tomback 1982). Seeds are harvested by the nutcracker, cached for food storage throughout the year, and may later germinate from caches left untouched (Tomback 1982). In this way distribution of whitebark pine relies almost entirely on the seed caching behavior of the nutcracker. Uneaten seeds may not germinate in the year after caching due to embryo immaturity; a year delay in germination is most common but seeds have been found to germinate up to 3 years after planting (Tomback *et al.* 2001). Many aspects of the tree's biology serve to improve avian-assisted dispersal by the nutcracker and to minimize passive dispersal (Jorgensen and Hamrick 1997). These traits, such as wingless seeds, sharp seed cones and the tendency for cones to grow atop tall branches, closely ties seed dispersal with seed-collecting and -caching species such as the nutcracker, as well as, to a lesser degree, many rodent species (Tomback 1982). In this way, the establishment and expansion of unique high-elevation whitebark pine ecosystems is highly dependent on the nutcracker (Tomback 1982).

Warming trends related to anthropogenic climate change (IPCC 2007) are predicted to decrease the quality and quantity of whitebark pine habitat in the long term as high elevation environments become less harsh (Aitken *et al.* 2008). A warming climate in British Columbia specifically (BC MOWLAP 2002) may make the current ranges of many cold adapted species inhospitable. Climate models by Hamann and Wang (2006) suggest that climatically suitable whitebark pine habitat will decrease in B.C. by 73% by 2085, a shift that would result in a 98% decrease in the species' frequency within its current range. While its occurrence currently decreases with increasing latitude (Klinka *et al.* 1989), warming climate trends may affect

whitebark pine's frequency and survivorship throughout its range, and perhaps lead to increasing abundance at higher latitudes (Aitken *et al.* 2008). Slow growing, high-elevation species such as whitebark pine are among the most sensitive to a warming climate (Aitken *et al.* 2008), and facilitated migration may therefore be necessary for conservation of the species. The whitebark pine range may have tracked previous climate changes as the species evolved (Richardson *et al.* 2002), and the potential to assist the tree's spatial movement now may be one way to conserve it. Outplanting, especially of tested superior provenances, may also support the species where its demographics, including natural seed sources, may be inadequate for population persistence due to blister rust or mountain pine beetle (Scott and McCaughey 2007). However, much of the species' range occurs in remote, inaccessible areas where facilitated regeneration may be difficult or unfeasible (Keane 2000, McCaughey and Schmidt 2001). Planting would require an in-depth knowledge of provenance quality, local environmental adaptations, seed treatment schemes, and microsite characteristics that may encourage high rates of establishment for planted *in situ* communities (*e.g.* Scott and McCaughey 2007).

While seed quality may outweigh environmental factors in some cases when it comes to conifer germination, and while genetics certainly affect germination in controlled *ex-situ* trials (*e.g.* El-Kassaby *et al.* 1992), microsite characteristics can affect emergence and survival rates in field *in-situ* studies (*e.g.* McCaughey 1990, McCaughey and Weaver 1990, Mellmann-Brown 2005). Microsite conditions are known to affect germination and establishment of other conifer tree species (*e.g.* Gray and Spies 1997). The Clark's nutcracker's habit of caching seed can create confusion for determining ecological site requirements for the species, as most trees result from the germination of uneaten seed caches (Tomback 1982, Tomback *et al.* 2001, Mellmann-Brown 2005). Arno and Hoff (1990) suggested that while most whitebark pine occurs on south

facing exposed slopes, the most robust and largest trees may be found on slopes with a northern aspect. The pattern may be due to competition from other species, which tend to outcompete whitebark pine on productive and mild sites (Scott and McCaughey 2007). However, on exposed, high-elevation ridgetop sites with shallow soils it will have the competitive advantage (Scott and McCaughey 2006). There is considerable variability amongst whitebark pine site characteristics (Ogilvie 1990), adding complexity to any facilitated planting regime. It commonly grows in subalpine and low-alpine environments with moderately dry to medium moisture regimes and medium nutrient levels, and is an indicator of alpine tundra and subalpine boreal climates (Klinka *et al.* 1989).

The specific seed collection and germination requirements of whitebark pine have been poorly studied until fairly recently (*e.g.* Mellmann-Brown 2005, Maher and Germino 2006, Leslie 2007). McCaughey and Weaver (1990) discuss at length the biological and microsite factors they found to affect success of planted whitebark pine seed within the first three years following germination in an area just north of Yellowstone National Park. They found approximately 150% higher emergence success on mineral seedbeds than on litter substrates, but hypothesized that one reason for this trend may have been lower levels of competition from surrounding vegetation on those areas (McCaughey and Weaver 1990). In the Beartooth Plateau area of Montana and Wyoming, Mellmann-Brown (2005) also found that high seedling survival was associated with low litter coverage. McCaughey and Weaver (1990) also found that sowing seed below the soil surface, rather than surface sowing, was found to support higher germination success on plots where predators (rodents and birds) were excluded. Shade from surrounding vegetation was also assessed, and emergence was higher in shaded microsites versus exposed sites (McCaughey and Weaver 1990). In terms of physical protection, Mellman-Brown (2005)

found that whitebark pine regeneration was commonly associated with tree islands, adult trees, and rocks in that arid, timberline region of the northwestern United States. These features can affect snowmelt patterns and moisture patterns, as well as offer protection from wind and desiccation (Mellmann-Brown 2005). Finally, topography may affect emergence and survival, with depressions and concave microsites supporting whitebark pine recruitment on dry sites, as these microsites retain moisture, provide exposure protection, and may have deeper snow cover in winter (Mellmann-Brown 2005).

The objective of this study was to test the germination and growth potential of whitebark pine seeds, taken from multiple provenances, relative to local environmental characteristics at the planting sites. Specifically we hoped to assess: (1) future potential for facilitated recruitment across the current and predicted species range, (2) environmental limitations for the species in those areas, and (3) optimal abiotic and biotic associations that may support successful emergence and growth of the species.

Methods

Seed Provenance

Seeds were collected in summer 2007 from seven source populations along a latitudinal range from northern Oregon to central British Columbia (Figure 1). Ten trees (whose seeds comprise open-pollinated seed families) per population were chosen based on fecundity and geographical distribution in order to ensure a diverse family structure within population. Cones were caged in June 2008 with small wire enclosures, as suggested by Burr *et al.* (2001), Leslie (2007) and Murray (2007), to prevent predation by the Clark's nutcracker and small rodent species during maturation. The cones were harvested in September 2009 and the seed kept separate by population and family.

QuickTime™ and a
Graphics decompressor
are needed to see this picture.

Figure 1 Seed source locations across British Columbia, Oregon, and Washington.

Common Garden Locations

Planting locations were established according to current and projected whitebark pine range estimates (Hamann and Wang 2006). Sites were distributed across northwestern British Columbia in the Coast, Skeena, Omineca, Hazelton and Babine mountain ranges along a northward latitudinal range (Figure 2, Table 1). Planting locations were established at high elevation, parallel to the highest trees at the transition zone between upper continuous treeline and upper krummholtz tree islands. Seven of the eight sites were established between 1200-2000 metres elevation, while one site was located at just under 1000 metres (Table 1). Sites were chosen that were free of other young seedlings in order to minimize destruction. Aspect was also considered, and south facing slopes were chosen preferentially as south facing slopes may be more hospitable for early seedling growth, with a higher overall temperature and longer growing season (Molgaard 1982). All sites had an average slope of 0-30° and soil with an organic layer of

at least 4cm deep, with good drainage due to moderate levels of coarse rock fragments. Typical of high-elevation locations, soils were relatively undeveloped with little soil horizon differentiation, and were classified to soil order as either Brunosols or Regosols.

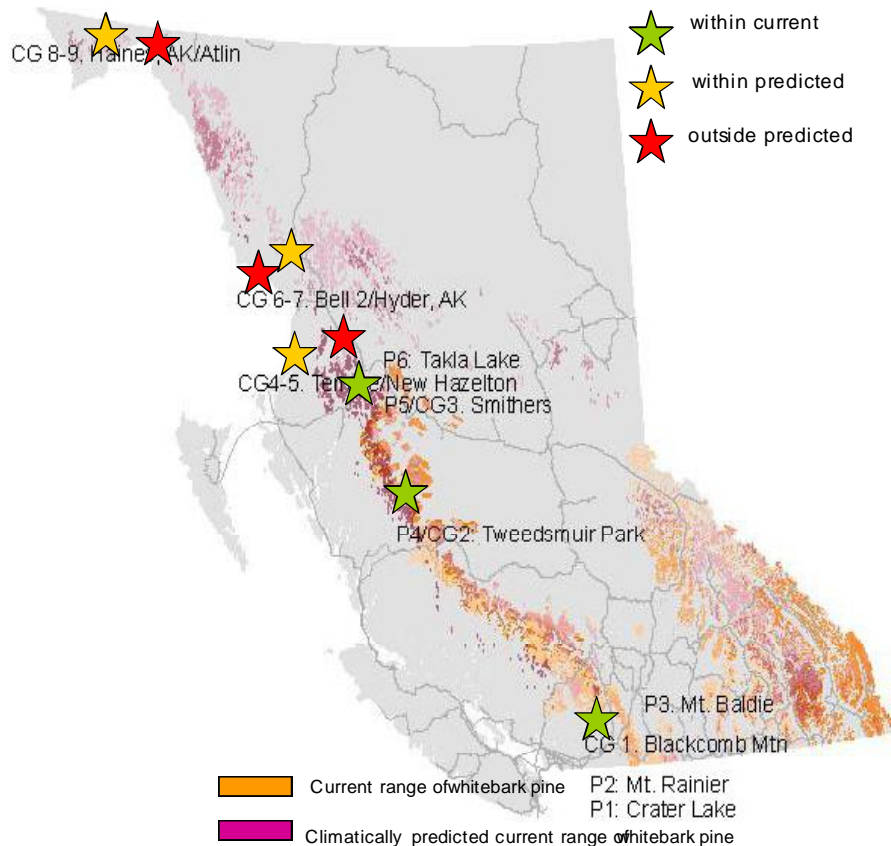


Figure 2 Common garden locations across British Columbia, showing the current and predicted range of whitebark pine.

Table 1 Common garden locations, with latitude, longitude, elevation, and mean temperature during the summer growing season, as determined by temperature data loggers.

Site	Latitude (°N)	Longitude (°W)	Elevation	Temperature (°C)
Blackcomb Mt.	50.089	122.896	1960	11.39
Hudson Bay Mt.	54.776	127.30	1670	7.57
Wesach Mt.	54.832	128.705	1330	11.42
Nine Mile Mt.	55.322	127.524	1540	10.27
Mt. Dilworth	56.169	130.043	1280	11.24
Mt. Tarn	56.763	129.690	1500	9.1
Three Guardsmen Mt.	59.567	136.462	850	10.77
Mt. Vaughan	59.729	133.518	1300	10.46

Seed Stratification

The collected seeds were separated into two groups: one to be stratified, treated and mechanically clipped to increase the likelihood of germination; and the rest to be left untreated and planted immediately. Untreated seeds were planted ($n = 8960$) at the field sites in September and early October 2007, while stratified seeds were planted ($n = 6992$) in June of 2008 with an interlocking block design. Rows of seed caches were set 50 cm apart, with 25 cm left between each cache along each row. The stratified seeds were placed along with the first planting to ensure that the same environmental factors applied to both stratified and untreated seeds. Stratification of whitebark pine seeds is an attempt to meet their dormancy requirement, a period that may last up to three years before successful germination occurs (McCaughey and Tomback 2001, Tomback *et al.* 2001). The stratified seeds were x-rayed and non-viable seeds were culled. Following this, the seeds were subjected to a four-month warm and cold stratification process according to established protocols (Riley *et al.* 2007). Fully stratified seeds were kept chilled during travel to the planting locations, and the tip of their seed coats clipped slightly, a means of scarification to facilitate radical emergence and moisture uptake during germination (Pitel and Wang 1980, Burr *et al.* 2001, Bower *et al.* Submitted).

Each location was planted with four replicated blocks (Figure 3). Seeds from all populations were planted in separate caches within each block according to a random block design. Caches were labeled by seed provenance according to the block plan. A 5 cm radius of surrounding vegetation was cleared around each cache to reduce vegetative competition. Each cache was planted with two seeds to increase the chance of overall cache germination, and seeds were planted at a depth of 2-3cm. This was also an attempt to mimic Clark's nutcrackers caches in which 1-15 seeds are planted at an average soil depth of 2-3 cm (Tomback 1982, Tomback *et al.* 2001, McKinney and Tomback 2007).



Figure 3 Representative images of the planting sites, showing rows of seed caches and the ecology of the surrounding area at treeline elevations. Photo on left was taken at the site on Mt. Vaughn, near Atlin, BC; right is of the site on Wesach Mtn. near Terrace, BC (Photos S. Curtis-McLane).

Data Collection

The slope, aspect and vegetative composition of each planting site were determined qualitatively. Temperature data was collected through the growing period from planting to emergence assessment using small temperature loggers. A soil pit was dug for each site near the blocks in a location that was representative of the local ecology. General soil characteristics were then assessed using soil texture, colour, and horizon depth indices. The relative proportion of mineral to organic material, soil type, and the amount of coarse rock fragments were also estimated.

Microsite characteristics were assessed within each seed cache, whether seeds emerged or not. Microsite topography, as convex, flat, or concave, was assessed visually in comparison to the surrounding site and slope. The primary and secondary types of surrounding vegetation were classified to species or genus when known, or to family where there was ambiguity. The height of vegetation surrounding the cache was also measured (to within 1cm). The soil type was classified into three general types: organic, mineral, or rock, based on the most dominant

material. Soil depth (as potential rooting depth for a germinant) was measured to within 1cm, to the left of each seed cache and to a maximum depth of 15cm using a slender marked rod.

In cases where a cache resulted in a successful emergent (or 2 if both of the seeds planted per cache emerged), the health and size characteristics of that seedling were assessed (e.g. Figure 2). The germinant height was measured, and the relative health was qualified using a 3-point scale (Table 2).

Table 2 Relative health classification scheme for the seedlings, by a three point scale (poor, medium, excellent).

Class	Description
1	Poor health: limp; pale green to yellowish in colour, with broken, dry and/or brown cotyledons.
2	Moderate health: pale green to light green colour, small, missing or broken cotyledons, and no browning or severe desiccation.
3	Robust seedling: Dark green colour, often a purple hue due to saturation by anthocyanin, tall, erect and stocky; sometimes bearing a set of true leaves above the whorl of cotyledons.

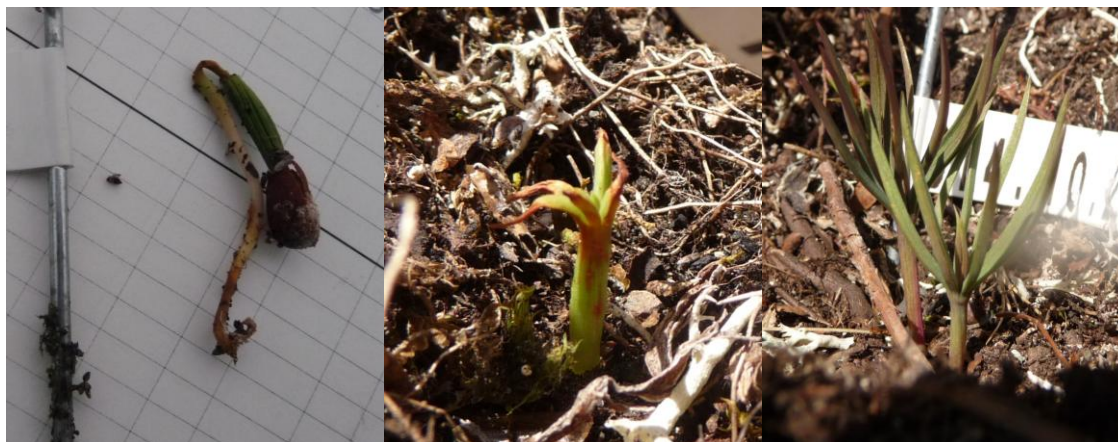


Figure 4 Whitebark pine germinants of varying health, from left to right: dead, due to dessicated stem; poor, with underdeveloped cotyledons; and very healthy, with fully developed cotyledons and robust stem, as observed at the field sites.

Statistical Analysis

To enable biologically relevant comparisons, microsite data were grouped into categories. Soil depths were divided into three classes: shallow (0-5cm), medium (6-10cm), and deep

(>11cm). Likewise, vegetation height measurements were classified as low (0-5cm), medium (6-10cm), and high (>11cm). Surrounding vegetation types, initially recorded in the field by genus and species (where known), were combined into biologically relevant classes including ericaceous ground cover, small shrubs, herbs, grasses, lichens, and mosses.

The data were analyzed using a general liner model (proc GLM) (SAS Version 9.1, SAS Institute 2003, Cary, N.C.). to test the impact of microsite variables on average emergence (as proportion of seed planted in each microsite that emerged) on a site-by-site basis. As the distribution of the emergence data was very non-normal, the data were square root transformed. Least-squared means for all factors were calculated to enable graphical analysis, and the effect of provenance upon average emergence by location was also examined. A p-value of 0.05 was used to assess significance; however, due to the low sample size and variation in germination, p-values of 0.1 were also identified for discussion.

Three sites were chosen for microsite analysis: Hudson Bay Mtn., Three Guardsmen Mtn., and Mt. Dilworth. These sites were chosen because the average growing season temperature and latitude at those locations are representative of the range of all site latitudes and observed growing season mean temperatures (Table 2). Analyses of microsite variables were only conducted on these three sites because testing average emergence rates relative to qualitative microsite conditions is only valid within sites, and the scope of this project did not allow for such analyses across all sites. At all sites, seed sourced from Hudson Bay Mtn. had very low emergence rates and were therefore not assessed further. Additionally, only stratified seed planted in the summer of 2008 were analyzed as the emergence rates of the previously planted, unstratified seed were not possibly analyzed as very few (37) emerged.

Results

Microsite Effects

Microsite variables did not seem to have a large effect on emergence at most sites; however, some interesting trends were evident in certain locations. High variation in emergence and standard error relative to all microsite variables is due in part to differences in seed source quality and maturation.

Table 3 Summary of microsite results by variable within site, showing p-values (bolded where $p < 0.05$)

Variable	Site	DF	F-value	P-value
Topography	Mt. Dilworth	2	4.22	0.0154
	Hudson Bay Mt.	2	1.83	0.1614
Vegetation	Three Guardsmen	1	2.57	0.1100
Height	Mt.			
	Mt. Dilworth	1	3.90	0.0489
Secondary Vegetation	Hudson Bay Mt.	6	1.94	0.0727
Soil Type	Mt. Dilworth	2	9.63	<0.001
	Hudson Bay Mt.	1	1.84	0.1758
Soil Depth	Mt. Dilworth	1	3.89	0.0493

Microsite Topography

Variation in microsite topography was related to emergence at two sites, Hudson Bay Mtn. and Mt. Dilworth, while there was no trend at Three Guardsmen Mtn. At Mt. Dilworth, emergence was significantly higher in convex microsites ($p = 0.0154$) than concave or flat areas (Figure 5). On the other hand, seedlings on Hudson Bay Mtn. seemed to have slightly higher rates of emergence when microsites were flat or slightly concave, although this relation was not significant ($p = 0.1614$, Table 3).

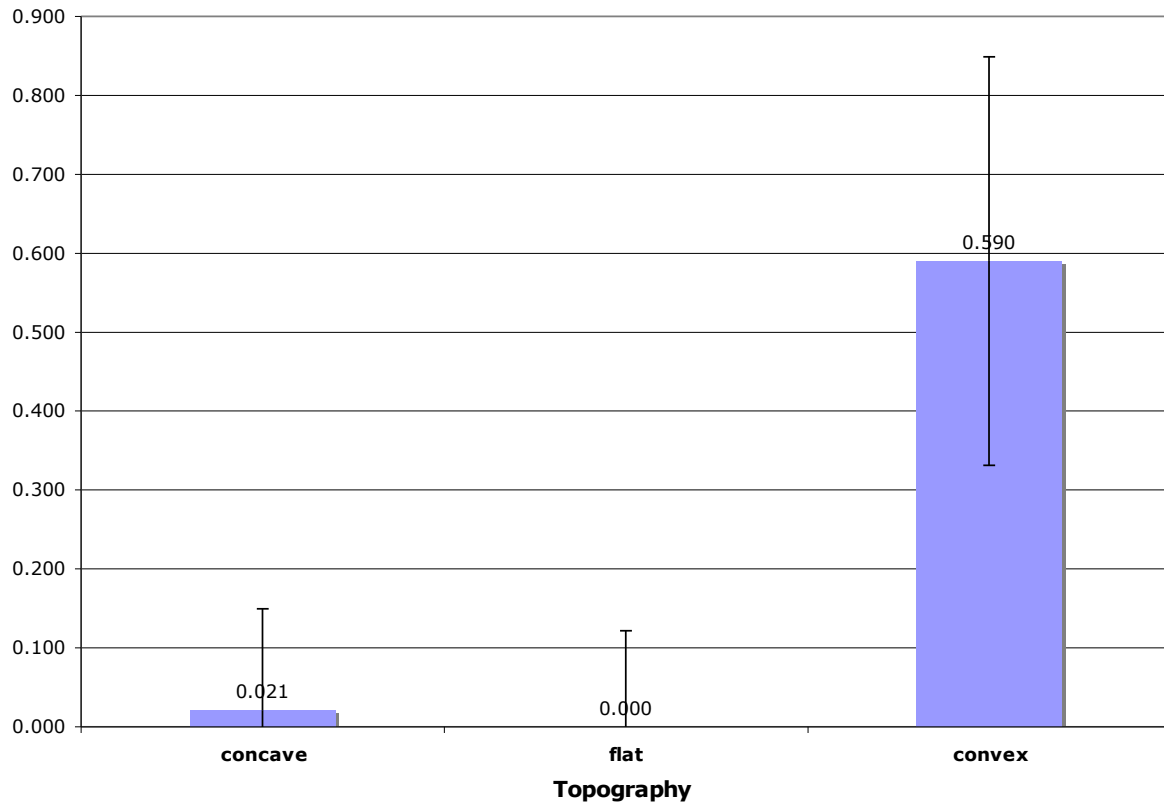


Figure 5 Average proportion of seeds that emerged relative to topographical variation, Mt. Dilworth ($p = 0.0154$), showing standard error bars. Data labels show average emergence values for each microsite type.

Vegetation Effects

Surrounding vegetation appeared to affect average emergence at all three sites, but in variable ways. Vegetation height had a significant effect ($p = 0.0489$) on germination on Mt. Dilworth, with higher emergence observed in microsites surrounded by low-lying vegetation (Figure 6). Emergence at that site was lowest in microsites with vegetation 6-10 cm high. The high standard error in these trends certainly suggests some discrepancy in emergence due to seed source and quality. Additionally, vegetation cover at Mt. Dilworth varied drastically across the experiment site and was difficult to quantify. In contrast, emergence at Three Guardsmen Mt. increased with increasing vegetation height, although this association was not very significant (p

= 0.11, Table 2). However, this trend is worth assessing in future studies using a larger sample size. Finally, it seemed that variation in secondary vegetation type weakly affected emergence on Hudson Bay Mt. in Smithers, with higher levels of emergence in microsites with no vegetation or with just low-lying moss cover (Table 2) ($p = 0.0727$). As vegetation type did not seem to be related to emergence rates at either of Mt. Dilworth or Three Guardsmen Mt, this relationship must be viewed with suspicion.

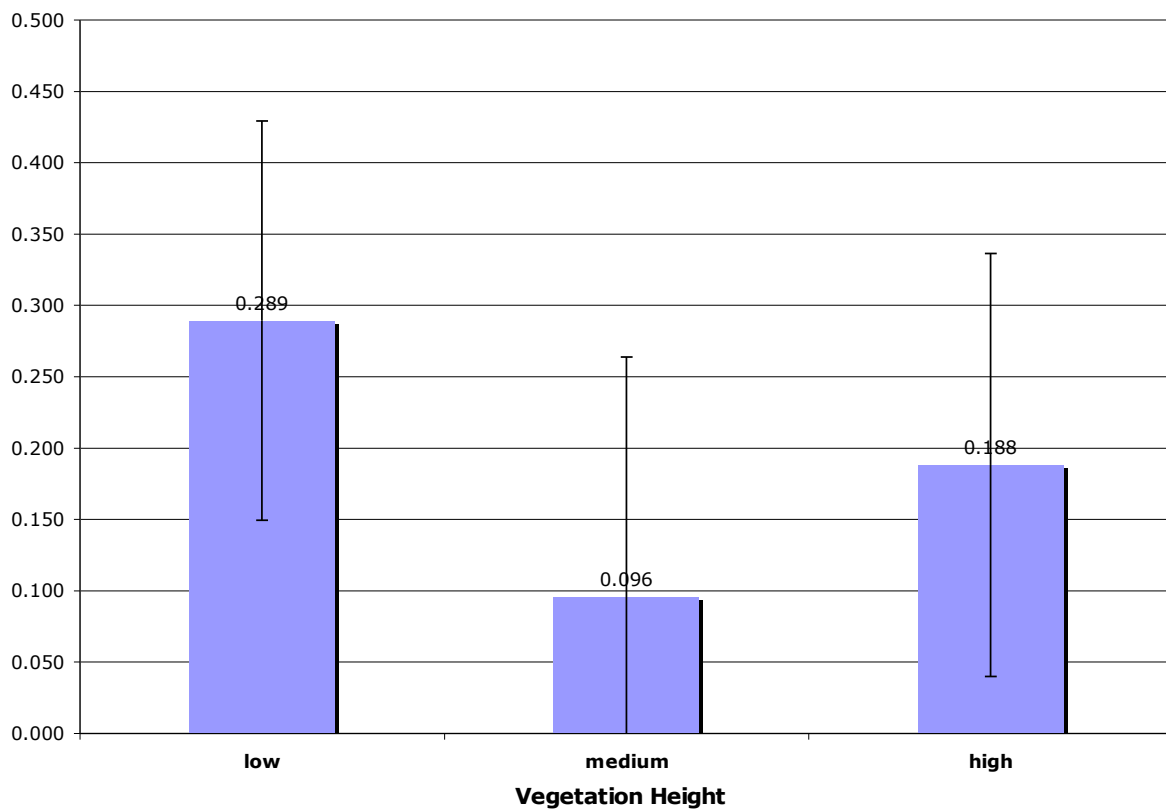


Figure 6 Average emergence by vegetation height, Mt. Dilworth ($p = 0.0489$), showing standard error around the mean. Data labels show average emergence.

Soil Type

Soil type seemed to affect emergence at both Mt. Dilworth and Hudson Bay Mt, with a highly significant trend ($p < 0.001$) at Mt. Dilworth towards higher emergence in organic soils, although the standard error was high (Figure 7). These data should be interpreted with caution, as soil types were difficult to quantify and were based on rapid field assessments of the dominant soil material.

Emergence at Hudson Bay Mt. was much higher in microsites with organic soils (41%) than those with a rocky substrate (14%). However this was a very weak relation ($p = 0.1758$) (Table 3). Soils at this location were quite heterogeneous, with high levels of coarse material, adding complexity to assessing the dominant material. A thick layer of alpine heathers also created a humus layer that varied in thickness over small areas, as this organic material was largely not present where heathers were lacking. Many microsites were therefore largely comprised of litter rather than a recognized soil type.

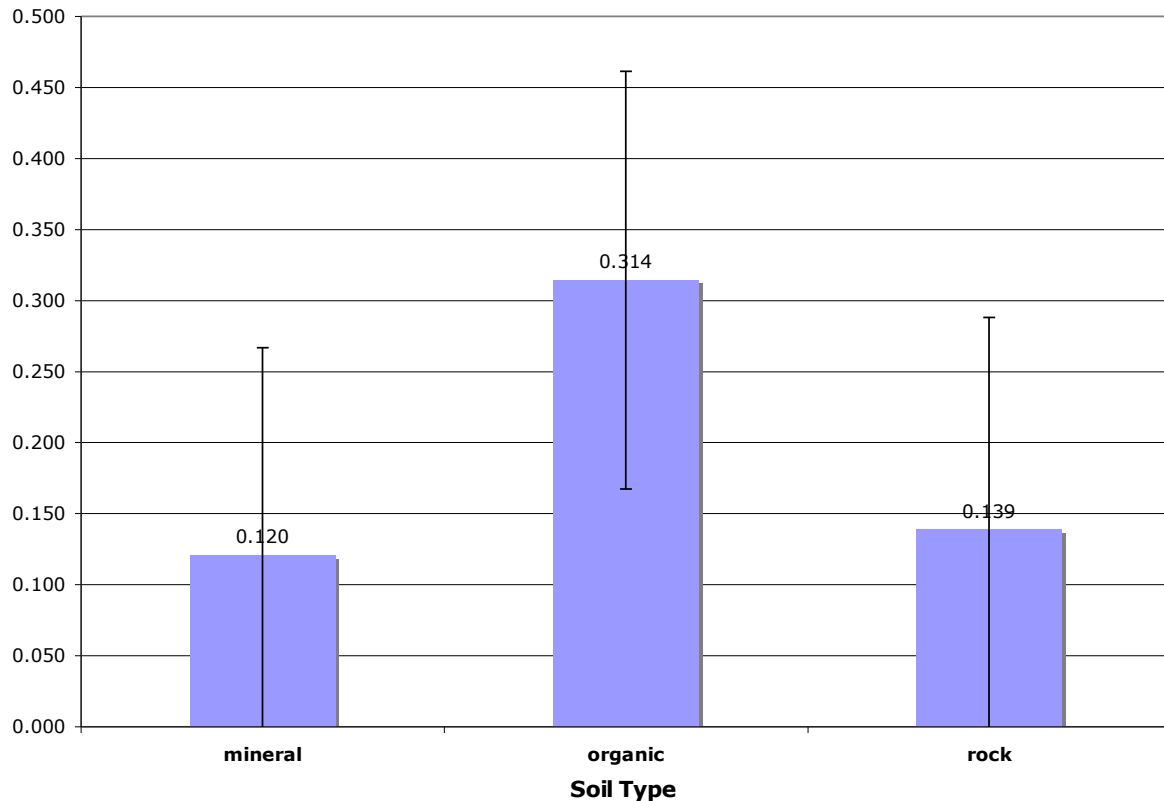


Figure 7 Average emergence by soil type, Mt. Dilworth ($p < 0.001$), showing standard error bars. Data labels show average emergence.

Soil Depth

The depth of soil in a microsite was related to emergence success only at the Mt. Dilworth common garden site, where emergence was higher in microsites with shallow soils, although the standard error of these data is very high (Figure 8). Soil depth was very variable at the Mt. Dilworth location, with one area in particular where soil was consistently shallow for all microsites. This created a situation where soil depth may not have been a controlling factor for those seed caches but instead may have been correlated with other determining factors. Similarly, a different area of the planting location seemed to have consistently deeper soils, which explains the range of higher emergence values for deep soils, and suggests that emergence may be confounded at this site by other microsite factors.

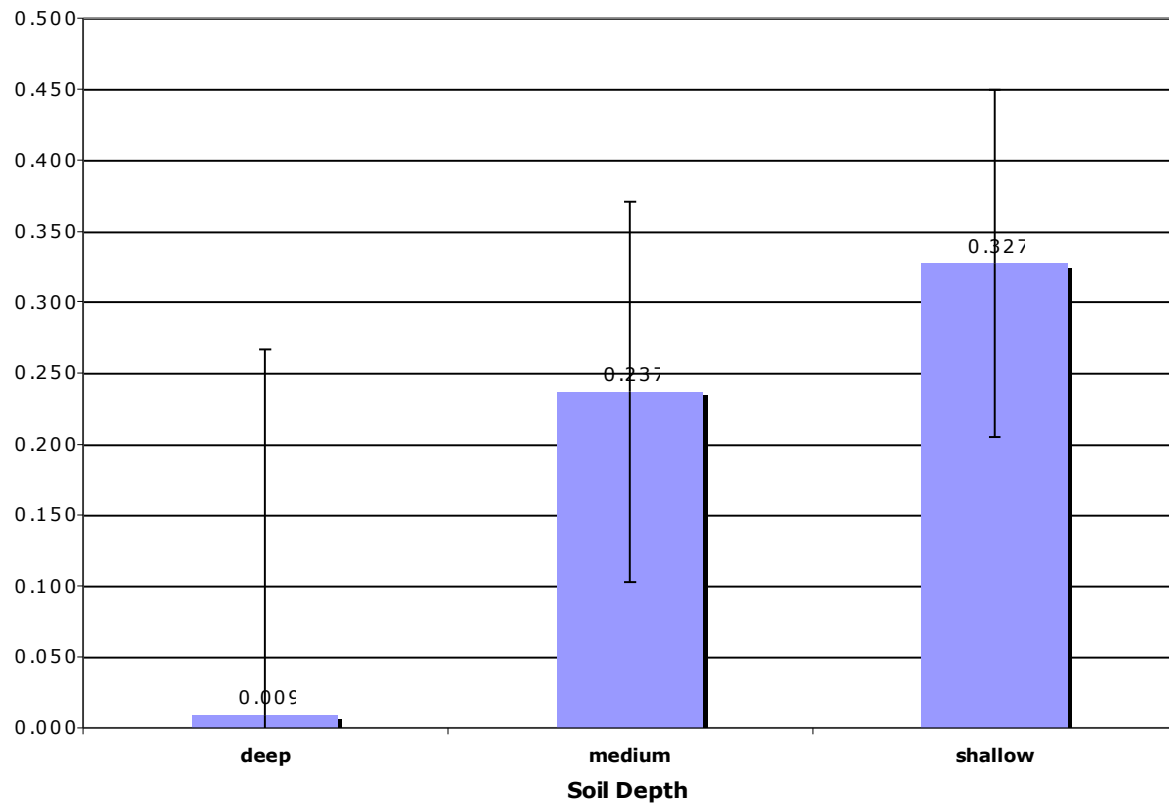


Figure 8 Average emergence by soil depth, Mt. Dilworth ($p = 0.0493$), showing standard error bars. Data labels show average emergence values.

Seed Source Effects

This study only evaluated the first-year emergence of seedlings from difference source location, while the subsequent survival past the first growing season is yet to be studied. Total emergence varied by seed provenance across all planting locations (Figure 9). Emergence was very significantly related to seed provenance at all common garden locations (Table 4).

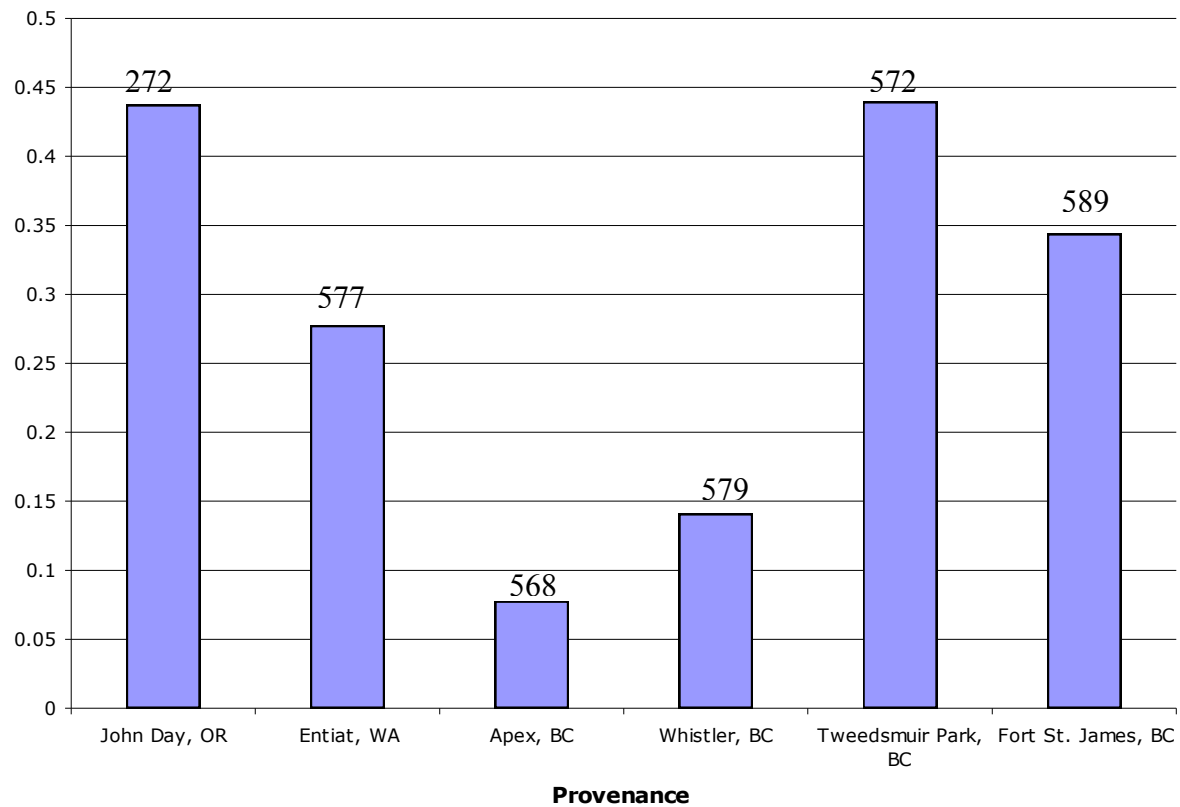


Figure 9 Average emergence at all common garden locations by provenance, arranged latitudinally from Oregon to northern British Columbia. Data labels show total number of emerged seedlings from each seed provenance.

Table 4 Average emergence variation at each discussed location by family provenance.

Site	DF	F-value	P-value
Mt. Dilworth	5	12.64	<0.001
Hudsons Bay Mt.	5	20.08	<0.001
Three Guardsmen Mt.	5	20.18	<0.001

Discussion

Despite the lack of normality in the average emergence data, a GLM method with transformed emergence data was selected as a sufficient, although by no means perfect, method to analyze these types of results. The overall emergence rate was low, as can be expected for whitebark pine trials (*e.g.* Burr *et al.* 2001, McCaughey and Tomback 2001), and emergence data were skewed towards zero. These data can be referred to as zero inflated, due to this skew and high proportion of zero values (Sileshi 2008). However, it may be appropriate and sufficiently accurate in such a situation to continue with a parametric test such as a GLM, given that the scale of the study is appropriate (Sileshi 2008).

While a lengthy dormancy period of up to two years may be an ecological strategy, selected for over time to account for premature collection of seeds by the Clark's nutcracker (Tomback *et al.* 2001), it does not facilitate timely research or restoration. Stratification and laboratory treatment was a critical factor for the emergence rates seen here, as the untreated seeds planted during the previous fall (2007) showed such low emergence rates (37/8960 total planted seeds emerged across all sites) as to be unusable for this analysis (S. Curtis-McLane 2009, pers. comm.), and will be assessed as part of a larger doctoral project over the summer of 2009. Reasons for these rates include poor embryo development, with an insufficient dormancy period to allow for maturation below ground, premature seed collection, and seed coat resistance to water uptake (Tomback *et al.* 2001). Seeds may a cold stratification period of up to 60 days to overcome physiological barriers to germination, a process which seeds need to decrease growth inhibitors, increase growth promoters, and allow the necessary break down of their hard, impermeable seed coats (Pitel and Wang 1980). Even such a lengthy stratification process can be insufficient to create high germination rates, although germination may reach 90% following

laboratory treatment (McCaughey and Tomback 2001). Emergence of stratified seed observed in this study was much lower, ranging from <10% to 44%, depending on the seed source and common garden planting location. This rate is comparable to Schwandt *et al.* (2007), who found 25% - 38% germination of warm stratified seed in an *in situ* trial.

Germination and survival at treeline is heavily dependent on ecological facilitation, whether through abiotic or biotic influences (Smith *et al.* 2003). Microsite characteristics may directly affect the survival and population expansion of high elevation species such as whitebark pine. The variables that may affect the local microclimate can be classified into geophysical (rocks or microtopography), structural (growth form of nearby vegetation), intraspecific interactions, and interspecific effects (after Smith *et al.* 2003). Snow cover is also important for whitebark pine seedlings and seeds as it can act as insulation to prevent freezing, but persistent snow in spring, as seen at the Mt. Dilworth site, can delay emergence and/or growth, as well as affect favorable microsites for germination (Mellmann-Brown 2005). Geomorphological factors such as soil development and general disturbances certainly affect plant growth at treeline (Malanson and Butler 2007). Given that Clark's nutcracker caches control where whitebark pine seeds are able to grow, slope variation and topography can also affect germination success.

Microsite Variables

Topographical Effects

Topographical variation can significantly affect germination and emergence rates of whitebark pine. In timberline areas of Montana and Wyoming, slope depressions and areas to the lee side of tree islands were found to be favorable for germination and survival (Mellmann-Brown 2005). However, these sites were likely much drier than the planting sites in this study, which were all more coastal in terms of continentality, and situated in areas with higher snowpack levels. At the three sites selected for examination of the effects of microsite

characteristics upon emergence, both concave and convex sites had some positive relation to emergence depending on location. A significant trend for higher emergence on convex microsites at the extremely wet Mt. Dilworth location suggests that well-drained microsites may support higher emergence in wet, coastal areas (NRDC 2008). Whitebark pine naturally occurs as a climax species on cold, dry, and exposed sites (Arno and Weaver 1990), and Moody (2006) also found a higher level of recruitment on cooler sites. Planting on damp sites such as Mt. Dilworth may lead to higher emergence on the driest microsites available, those with convexity that allow sufficient water drainage.

Vegetation Effects

Whitebark pine is a shade intolerant species (Arno and Hoff 1989, Klinka *et al.* 1989); however, it may be damaged by direct and intensive solar radiation. Scott and McCaughey (2006) suggest planting whitebark pine in microsites with adequate shade protection. Shade protection up to 50% may reduce seedling mortality following emergence (Maher and Germino 2006), and photosynthetic efficiency of whitebark pine seedlings may be higher with such shade protection as proffered by herbs or small shrubs (Maher *et al.* 2005). Emergence success related to tall surrounding vegetation was seen at Three Guardsmen Mtn., however these trends were counteracted by higher emergence rates in microsites with low vegetation (0-6cm) at both Hudson Bay Mtn. and Mt. Dilworth. Higher overall emergence rates at Mt. Dilworth may be related to a persistent snowpack late in the summer of 2008, meaning that snow in microsites with low-lying vegetation and consequently more exposure to sunlight may have melted sooner, releasing seeds for germination earlier in the year.

A tendency for seedlings to produce anthocyanins as protection against sunshine was observed at all sites, and also in growth chamber experiments (S. Curtis-McLane 2009, pers. comm.), while sun damage was observed on seedlings that failed to adapt to the sunlight. These

pigments are useful for protecting tissue damage from ultraviolet radiation, and may help to prevent photoinhibition, or stress caused by high light levels, which can shut down the process of photosynthesis (Steyn *et al.* 2002). Too much sun may negatively affect germination, as may extremely low levels of sunlight (McCaughey and Weaver 1990). Therefore, it could be expected that exposed seedlings may be more stressed as they are forced to protect themselves against photoinhibition, and could have lower survival rates.

Soil Effects

Within British Columbia's interior Englemann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone, whitebark pine is most common on particularly dry and rocky exposed sites (Yole *et al.* 1989). Whitebark pine communities in Montana and Idaho also grow in rocky, poorly developed soil types (McKinney and Tomback 2007). Emergence at the analyzed common garden sites varied with soil type, with higher emergence occurring in microsites with organic type soils at two of the locations. While this was a purely qualitative measure, it does suggest that organic soils may encourage emergence or at least allow for successful radical emergence. This tendency makes sense according to Clark's nutcracker caching ability, as they tend to make seed caches under the ground at depths of up to 3cm and often in soft soils (Tomback 1982). As all soils at high elevation are low in nutrients and poorly developed with low levels of decomposition, any marginal improvement in organic matter proportion is likely to encourage growth relative to nutrient poor, rocky soils (Hansen-Bristow *et al.* 1990). This is opposed to the findings of McCaughey and Weaver (1990), who observed higher rates of emergence on mineral soils. However, that trend may have been due to reduced vegetative competition on mineral seedbeds (McCaughey and Weaver 1990), while in this study any competing vegetation within a 5cm radius of every microsite, regardless of the substrate, was removed. Additionally, substrate was not a factor under open (i.e. non-shaded) conditions

(McCaughey and Weaver 1990), which is comparable to this study, where all common garden plots were established in open areas.

Influence of Herbivory

Some evidence of seed herbivory was noticed at two sites, although the percentage of caches that appeared to have been affected was low and difficult to quantify. Seed predation can affect treeline species distribution patterns (Malanson and Butler 2007), and could certainly affect the germination rates of planted seeds (Schwandt *et al.* 2007). Small mammals removed many buried seeds in a planting trial by McCaughey and Weaver (1990). Due to the scale of this study, the total number of seeds planted (8,960 unstratified, 6,992 stratified, 15,952 altogether), and the number of planting sites across such a large geographic area, no efforts were made to prevent herbivory, and while this may appear to be a shortcoming, only nominal effects were seen in the first year following planting. Ideally, as predation can vary by microsite, wire cages can be used to physically protect seeds, and rodent repellants may also be used in an effort to minimize predation (Schwandt *et al.* 2007).

Seed Source Effects

Overall, emergence varied by seed provenance at all sites. While germination potential may be affected by genetic factors in the absence of environmental variation, and while site conditions affect seedling success most in the time following emergence (*e.g.* El-Kassaby *et al.* 1992), the seed provenance germination variation observed in this study is likely related to seed maturity and quality. This study only evaluated emergence of seedlings, while the subsequent survival past the first year is yet to be studied. Seed development in the collection year seemed to vary drastically among provenances, as the spring climate was abnormally harsh at three sites. Corresponding emergence of seed from those sites was the lowest at all planting locations. In addition to seed quality and maturity, sheer seed abundance may vary by population and

production year. The species produces large seed crops on an infrequent basis, with low production years in between substantial crops (known as seed mastings) (Siepielski and Benkman 2007). More recently, average cone crops have also declined due to the combined effects of fire suppression, mountain pine beetles, and white pine blister rust (Ellison *et al.* 2005).

While the results noted in this study may suggest that microsite variation is not a limiting factor for whitebark pine germination success, it should be noted that the microsite data can, at this stage in the project, only be related to emergence in the first year of growth. It remains to be seen whether seedling survival and growth varies with these microsite variables, as suggested by previous work examining naturally established seedlings (*e.g.* McCaughey and Weaver 1990, Mellmann-Brown 2005, Maher and Germino 2006).

Conclusions

The spatial extent and population health of whitebark pine is showing a rapidly declining trend across its range. Facilitated planting of seed or seedlings could be instrumental for future species viability, especially where environmental conditions support successful establishment (Krakowski *et al.* 2003). The results of this *in situ* study suggest that successful planting strategies should concentrate more on seed quality and provenance than specific microsite conditions at the planting site. While it seems that vegetation type and height may play a role in protecting emergent seedlings, this may be only at extreme sites where conditions vary drastically across the landscape and exposure may be high. However, planting may be more successful in the long-term when competitive exclusion is limited through allowing wildfires to burn (Krakowski *et al.* 2003, Moody 2006). While fire is not a requirement for its recruitment, whitebark pine is a fire-associated species, and fire suppression policies may be resulting in some competitive exclusion by more competitive, lower-elevation species (Moody 2006).

Implementing adaptive management techniques should be a high priority, with appropriate integration of regeneration and fire management methods (McDonald and Hoff 2001).

Changing temperatures are also likely to affect the range of this slow-growing species, but its response will be limited by its dispersal ability. Its response to warming climatic conditions may be delayed (Korner 1998) due to typically slow growth, slow development of reproductive maturity, and its reliance upon the Clark's nutcracker for dispersed regeneration (Tomback 1982). Several climate models suggest that the species range is likely to shrink drastically, to less than 3% of its current area, with increasing temperatures (Hamann and Wang 2006, Warwell *et al.* 2007, Shrag *et al.* 2008). More immediate threats such as white pine blister rust and mountain pine beetle infections also suggest propagation as a means of maintaining or restoring populations of this critical component of high-elevation ecosystems. Facilitated migration may be a viable conservation solution for relatively stationary species such as whitebark pine, but such a method should be used in combination with other adaptive management techniques and be implemented with effective monitoring for the species' viability (Logan *et al.* 2009). It is imperative that facilitated migration and planting are considered as means to support the species viability of whitebark pine before this critical high-elevation foundation species is reduced to just another victim of our changing climate. Management of this critical alpine resource should be a priority for conservation. Both *in-situ* means of maintaining the species, as described here, and *ex-situ* methods such as seed bank preservation, used to complement outplanting techniques, should be used to ensure that the genetic and population base of whitebark pine is sustained for the long-term.

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