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Whitebark pine (*Pinus albicaulis*) assisted migration potential: testing establishment north of the species range

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Abstract. The translocation of species into habitable locations outside of their current ranges, termed assisted migration, has been proposed as a means of saving vulnerable species from extinction as a result of climate change. We explore the use of this controversial technique using a threatened keystone species in western North America, whitebark pine (*Pinus albicaulis*), as a case study. Species distribution models predict that whitebark pine will be extirpated from most of its current range as temperatures rise over the next 70 years. However, the same models indicate that a large area within northwestern British Columbia, Canada, is climatically suitable for the species under current conditions and will remain so throughout the 21st century. To test the capacity of whitebark pine to establish relative to climatic and habitat features within its predicted climatic range, we planted seeds from seven populations in eight locations spanning from 600 km southeast to 800 km northwest of the northern boundary of the current species range. During the first three growing seasons, germination occurred in all locations. Nearly three times as many treated (induced maturation and broken dormancy) than untreated seeds germinated, and most treated seeds germinated a year earlier than the untreated seeds. Germination, survival, and growth were primarily influenced by seed mass, site climate conditions related to the duration of snow cover, and provenance temperature. Our experiment provides a preliminary test of models predicting the existence of climatically suitable whitebark pine habitat north of the current species ranges. More broadly, our techniques and results inform the development of scientific guidelines for assisting the migration of other species that are highly threatened by climate change. Applied case studies of this kind are critical for assessing the utility of species distribution models as conservation planning tools.

Key words: climate change; common garden; managed relocation; quantitative genetics; species distribution model; species range limits.

INTRODUCTION

Species distribution models (SDMs) predict that the climatic niches of trees and other species will shift toward the poles and to higher elevations with climate warming. However, there is considerable uncertainty as to whether trees can migrate fast enough to stay within their moving niches, given the rates at which temperatures are expected to rise (Christensen et al. 2007). Fossil pollen records and molecular data indicate that many tree species migrated 10–50 km per century following the last glacial maximum (Davis and Shaw 2001, McLachlan et al. 2005). However, migration rates up to an order of magnitude higher may be necessary for some trees to stay within their climatic tolerances (Malcolm et al. 2002, Iverson et al. 2004, Hamann and Wang 2006, Loarie et al. 2009). The failure of species to migrate fast enough could lead to population collapses and extinctions. Species with limited ranges, small

population sizes, and major barriers to dispersal are considered most vulnerable (Parmesan 2006).

One way to avert species losses may be to assist the migration of vulnerable organisms in situations where natural migration is implausible (McLachlan et al. 2007, Hoegh-Guldberg et al. 2008, Mueller and Hellmann 2008, Ricciardi and Simberloff 2009). Supporters of assisted migration believe that, under well-researched and ecologically appropriate circumstances, relocating a threatened species can protect it from extinction while minimally impacting the recipient ecological community. Opponents argue that the probability of the new species negatively affecting the biota within its new environment is not worth the risks. Both sides agree that decision-making frameworks based on rigorous ecological risk assessments and economic cost–benefit analyses must be developed prior to taking action.

Whitebark pine (*Pinus albicaulis* Engelm.) is a threatened keystone species that inhabits mountainous regions in western North America. Its nutritious seeds are distributed by Clark's Nutcrackers (*Nucifraga columbiana*) and serve as a critical food source for grizzly bears (*Ursus arctos*) (Mattson et al. 1992). The

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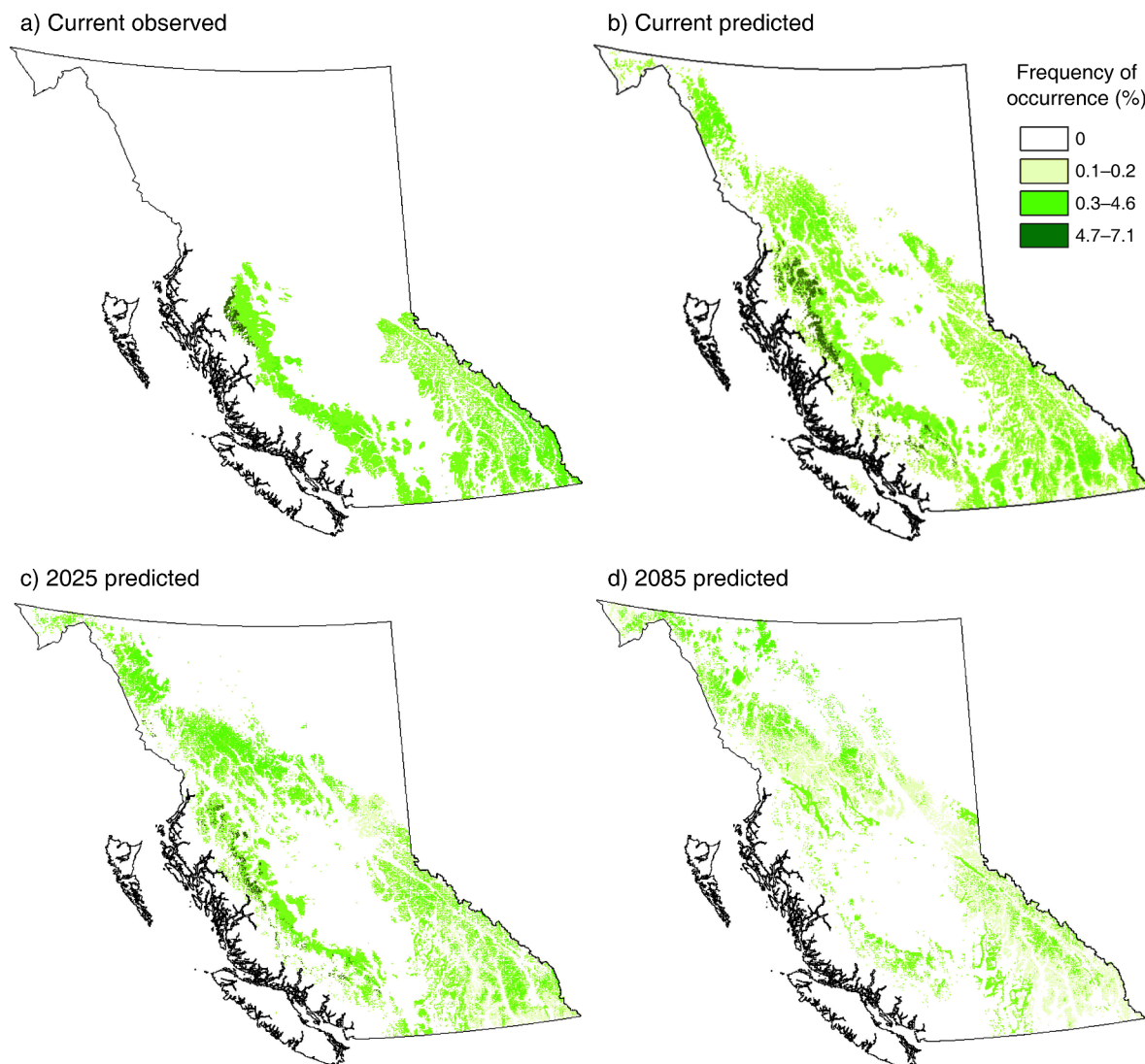


FIG. 1. Species distribution models depicting whitebark pine's (a) current observed range in British Columbia (BC), Canada, (b) current predicted range in BC based on 1961–1990 climate normals, and (c) 2025 and (d) 2085 future predicted ranges in BC based on IS92a CGCM1 GAX future-climate scenarios (Flato et al. 2000). The models were created by T. Wang (*unpublished models*) (University of British Columbia), using methods from Hamann and Wang (2006). See Fig. 2 for the 2055 predicted range, scale, and geographic location. See Appendix A for the model creation methods.

slow-growing tree also creates microhabitats that promote the recruitment of other tree species in high-elevation environments (Callaway 1998).

Over 50% of all whitebark pines in the northern United States and in Canada are dead or dying due to the combined impacts of mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*) (Kendall and Keane 2001, Zeglen 2002, Smith et al. 2008). Logan et al. (2010) (J. Logan, *personal communication*) postulate that nearly all cone-bearing whitebark pine trees in the greater Yellowstone ecosystem will be dead by 2015, primarily due to mountain pine beetle. Because of these severe population declines, the federal governments of the United

States and Canada began evaluating the species for endangered status in 2010.

In addition to the insect- and pathogen-induced declines already experienced by the species, SDMs predict that whitebark pine will need to migrate hundreds of kilometers over the next century in response to climate change (Hamann and Wang 2006). The species is projected to lose 73% of its current climatic range within British Columbia (BC), Canada by 2085, while gaining an equivalent-sized new climatic range northwest of its current northern range limit (Fig. 1). Simultaneously, the species is projected to lose >97% of its current climatic niche within the United States (Warwell et al. 2007).

Interestingly, SDMs show that much of the area in northwestern BC that is predicted to be habitable for whitebark pine in the future is also climatically suitable for the species under current conditions. This implies that whitebark pine does not currently inhabit its full climatic niche. Either nonclimatic factors are restricting recruitment outside of the current range, or SDMs are not accurately predicting the present and future climatic envelopes of the species. The former has important implications for the ability of the species to inhabit its predicted climatic niche in the future, while the latter points to the need for validating and improving SDMs. Bioclimatic conditions in montane habitats are notoriously difficult to predict using regionalized models due to microtopographical features such as slope, aspect, wind, and snow duration (Araújo and Guisan 2006, Dormann 2007). However, SDMs are inexpensive, widely available, and provide broad guidelines for climatic suitability that can be supplemented through knowledge of microclimate and nonclimatic limiting factors (Araújo et al. 2005). Understanding the strengths and shortcomings of these models is important for species that need conservation strategies such as whitebark pine.

Whitebark pine seeds are typically immature at harvest and require a warm, moist maturation period followed by extended chilling to break dormancy. This process occurs naturally during the first summer and second winter following planting by nutcrackers, resulting in most germination occurring two summers after productive cone crops are observed (Tomback et al. 2001). Tree nurseries have established seed-pretreatment protocols to speed up and promote germination (Berdeen et al. 2007, Riley et al. 2007, Bower et al. 2011), but the long-term establishment potential of treated vs. untreated whitebark pine seeds under field conditions has not been previously tested. Likewise, whitebark pine is known to be limited by habitat conditions, particularly those related to snowmelt timing and sun and wind protection (Weaver 1994, Mellmann-Brown 2005, Maher and Germino 2006, McCaughey et al. 2009), and is known to demonstrate population differences corresponding to clines in provenance (place of origin) climate (Mahalovich et al. 2006, Bower and Aitken 2008). These limiting factors have not been tested for trees planted north of the current species range, and must be better understood before managers can consider assisting the migration of whitebark pine. Whitebark is ideal for such trials because of its threatened status, promising future range predictions, restricted ecological niche, and negligible risk of unwanted spread due to slow (30–50+ years) reproductive maturation (McCaughey and Tomback 2001).

In this study, we examined the impacts of seed maturity, habitat quality, and genetics on whitebark pine establishment within the species' realized and predicted climatic range in British Columbia. Seeds from multiple populations were planted in areas

predicted by SDMs to be habitable for whitebark pine under current and 2055 climate conditions, focusing particularly on areas northwest of the current species range. We tested the overall hypothesis that whitebark pine can establish in these model-predicted areas, and furthermore, hypothesized that (a) whitebark pine seeds subjected to screening and induced-maturation treatments prior to planting have greater establishment potential than untreated seeds; (b) establishment is affected by site climate and microsite conditions, particularly those relating to snow duration; and (c) quantitative-trait differences among populations correspond to clines in provenance climate. Our results allowed us to assess the accuracy of SDMs for predicting current range limits for whitebark pine, and inform the creation of assisted migration guidelines for the species. This information is key to understanding the potential for this important threatened species to survive 21st century climate change.

METHODS

Seed collection and treatment

To account for genetic differences among populations, we collected cones from six whitebark pine provenances sampled across a wide geographic and climatic gradient within the northwestern extent of the species range (Fig. 2, Table 1). Cones from 10 trees per provenance were caged using wire exclosures in June and July 2007 to prevent harvesting by Clark's Nutcrackers and rodents. The cones were collected, seeds extracted, and mean family seed masses recorded in August and September 2007. The seeds from each parent tree are considered an open-pollinated family.

To test techniques for promoting germination, we left half of the seeds untreated and treated the remainder using variations on the protocols of Berdeen et al. (2007) and Riley et al. (2007). The treatment protocol comprised numerous steps. In January 2008, the seeds were X-rayed using a Faxitron X-Ray machine (Faxitron Bioptics LLC, Lincolnshire, Illinois, USA) (2-minute exposure, 15 peak kilovolts). Seeds in which the embryo filled <20% of the corrosion cavity were classified as nonviable and discarded. Starting in February 2008, the X-rayed seeds were soaked in warm water for two days to promote imbibition, matured at 15°C for one month, and then stratified at 2°C for three months. Upon termination of stratification in June, the treated seeds were transported to the test sites at 3°C. Prior to planting, 1–2 mm of tissue was clipped from the radical end of each seed coat using a razor blade to promote radical emergence. Nonviable seeds were tallied prior to being discarded at all stages of the treatment process.

Site selection and establishment

We established common gardens in eight locations within the current observed and 2055 projected climatic ranges of whitebark pine. Common gardens are

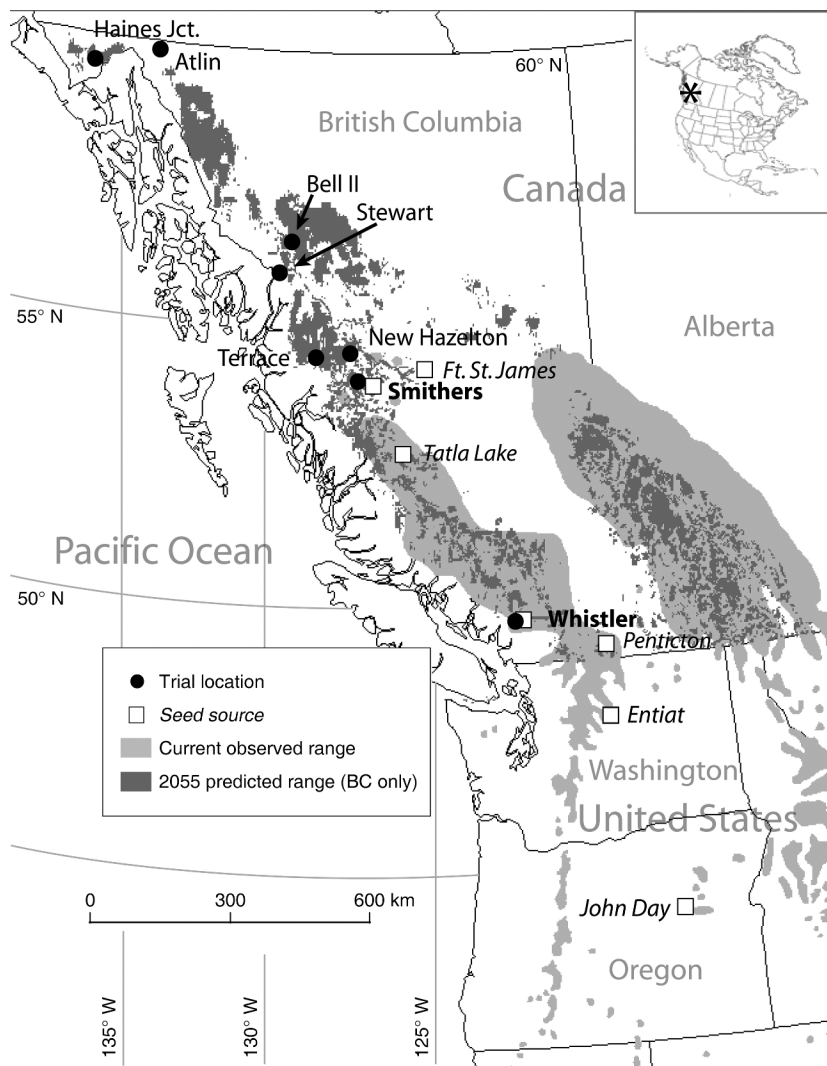


FIG. 2. Trial locations and provenances relative to the 1990s observed and 2055 predicted whitebark pine species range within British Columbia, Canada. Of the eight trial locations, two are within and six are north of the current species range. All trial locations are in areas predicted to be habitable under both present and 2055 climate regimes. The two locations in boldface type, Whistler and Smithers, are both trial locations and provenances. The predicted species range was created by T. Wang (*unpublished model*) (University of British Columbia), using methods from Hamann and Wang (2006), using the IS92a CGCM1 GAX future-climate scenario (Flato et al. 2000). The map scale is accurate in the map center but approximate at the boundaries due to projection skew.

experiments where multiple genetic lineages are grown in common environments to quantify the respective impacts of genetics and site conditions on quantitative-trait differences among individuals. We located the gardens in areas broadly predicted to be climatically suitable according to SDMs created by T. Wang (University of British Columbia) using the protocols of Hamann and Wang (2006) (Appendix A). Two of the gardens are located within the current species range, while six are located north of the range (Fig. 2, Table 1). Collectively, the trial locations span nearly 10° latitude, from 600 km southeast to 800 km northwest of the current northern range margin. A ninth location near Tweedsmuir Park

that was snow-covered at the time of fall planting turned out to have inappropriate substrate (coarse rock) and was abandoned.

Within each trial location, we established two sites with the intention of replicating conditions experienced by whitebark pine within the subalpine extent of its current ecological niche. Sites were located 50–500 m apart, and 100–200 m below the highest tree islands above continuous treeline, on south-facing, 5–20° slopes with coarse, well-drained soils. Areas with evidence of human or animal disturbance were avoided. Maxim iButton temperature data loggers (Maxim, Sunnyvale, California, USA) were installed at each site in Septem-

TABLE 1. Geographic and climatic variables for the two sites in British Columbia (BC) within each of the eight trial locations and the seven sampled whitebark pine provenances (see Fig. 2).

A) Provenance								
Closest town	Latitude (°N)	Longitude (°W)	Elevation (m)	MAT (°C)	PAS (cm)	Seed mass (g per 100 seeds)		
Tatla Lake, BC	52.54	125.81	1541	0.1	524	16.6		
Fort St. James, BC	54.88	125.37	1490	0.2	396	16.9		
Smithers, BC	54.76	127.28	1500	0.5	473	10.2		
Penticton, BC	49.37	119.92	2148	0.7	336	10.2		
Whistler, BC	50.10	122.90	1882	0.8	1290	9.7		
John Day, Oregon	44.28	118.70	2438	3.7	572	12.2		
Entiat, Washington	47.99	120.41	1998	6.5	463	12.7		
B) Trial locations and sites (all in BC)								
Closest town, site	Latitude (°N)	Longitude (°W)	Elevation (m)	MAT (°C)	PAS (cm)	Summer temp. (°C)	Winter temp. (°C)	Day of snowmelt
Atlin, 2	59.7302	133.5177	1368	−2.5	287	11.1	−4.3	n/a
Atlin, 1	59.7292	133.5182	1357	−2.4	287	11.4	−3.8	n/a
Bell II, 2 and 3	56.7627	129.6864	1494	−1.7	628	6.4	−0.1	173
Bell II, 1	56.7627	129.6902	1455	−1.6	628	no data	−0.4	181
Smithers, 2	54.7771	127.3034	1676	0.3	599	9.8	−2.0	149
Smithers, 1	54.7763	127.2957	1650	0.4	594	9.6	−1.2	153
Whistler, 1	50.0899	122.8959	1970	0.5	1430	10.3	0.2	177
Whistler, 2	50.0890	122.8957	1952	0.6	1422	9.5	0.2	186
Haines Junction, 2	59.5669	136.4616	852	0.7	1024	12.1	−0.4	121
Terrace, 2	54.8312	128.7073	1316	0.7	915	13.1	1.2	98
Haines Junction, 1	59.5668	136.4630	842	0.8	1020	12.1	−0.7	135
Stewart, 1	56.1701	130.0434	1274	0.8	1985	10.7	0.4	139
Stewart, 2	56.1692	130.0427	1278	0.8	1989	10.6	0.4	150
New Hazelton, 1	55.3235	127.5239	1543	0.9	427	9.6	−1.8	144
New Hazelton, 2	55.3223	127.5247	1527	0.9	424	10.6	−1.9	143
Terrace, 1	54.8320	128.7047	1319	0.9	943	12.5	0.8	123

Notes: Provenances and sites are ordered from smallest to largest normal mean annual temperature (MAT). MAT and PAS (precipitation as snow) were generated using ClimateWNA (Wang et al. 2006) and represent 1971–2000 normals. Summer and winter temperature and day of snowmelt are averages for the study period (2007–2010), derived from iButton temperature sensors (see *Methods: Data collection*). Key to abbreviations: BC, British Columbia, Canada; WA, Washington, USA; OR, Oregon, USA.

ber 2007, one at ground level and one 10 cm underground, and programmed to record temperatures four times daily.

We planted the seeds in experimental units of two to mimic the multiseed caching behavior of Clark's Nutcrackers (Tomback 2001). Four two-seed caches per family were planted in two blocks per site for replication. Two of the four caches per family and block were planted using untreated seeds in September 2007, and the other two using treated seeds in June 2008. The seeds were planted 2 cm deep in a 0.25 × 0.5 m grid alternating by seed treatment, with vegetation cleared within a 5 cm radius of each cache. A total of 8960 untreated and 6992 treated seeds were planted. Families lacking adequate numbers of treated seeds were not represented in every block. Late snowmelt in 2008 prevented planting the treated seeds in all of Bell II site 2 and half of Blackcomb site 2, so a third site was created at Bell II, very near site 1, and additional rows were added at Blackcomb site 2 (Table 1).

Data collection

To track seedling establishment over time, we recorded germination, survival, health, height, and needle fascicle data in 2008, 2009, and 2010. Germination and survival were recorded as binary variables;

health was ranked as poor, moderate, or good based on foliage and stem appearance; height was measured to the nearest 0.5 cm; and needle fascicles were counted for all buds displaying needle tissue.

We collected microsite data, including slope, convexity, soil type, soil depth, and vegetation height for every seed-cache location in 2008. Slope was estimated in 10° increments; convexity classified as flat, concave, or convex; and soil type classified as pure mineral, mineral topped with organic, or very (>80%) rocky; all of these values represent means for the 10 cm radius surrounding each cache. Soil depth was measured to the nearest centimeter adjacent to each cache, while vegetation height was estimated as mean height outside of the 5-cm cleared area but inside the 10-cm radius around each cache.

We averaged the iButton soil surface temperature data to create mean growing season (June–September) and winter (October–May) temperatures for the duration of the experiment (2007–2010). Most sites were covered in snow, and therefore registered surface and subsurface temperatures near 0°C for the majority of the winter months. Snowmelt dates, determined as the first day of the year that maximum daily temperatures topped 5°C for the proceeding seven days in a row following the winter period of near-freezing tempera-

tures, were also determined from the temperature sensor data. Snowmelt dates could not be determined for the Atlin sites because a snowpack never developed, as indicated by temperatures fluctuating well below 0°C throughout winter, presumably due to wind scouring. A small number of temperature sensors lost functionality or disappeared; when this occurred, we estimated seasonal temperatures and snowmelt dates from below-ground sensors at the same site or from above- and belowground sensors at the other site within the same location. We also obtained normal (1971–2000) mean annual temperature (MAT) and precipitation as snow (PAS) data for each provenance and site using ClimateWNA (an extension of ClimateBC [Wang et al. 2006]) (Table 1).

Statistical analyses

We conducted all statistical analyses using SAS software, version 9.2 (SAS Institute 2008), with seed cache as the experimental unit. Provenance impacts were analyzed with families pooled due to low germination rates. Data from the following sites or populations were excluded from all analyses due to near-zero germination rates: (1) Whistler site 2, treated seeds, attributed to seed-quality deterioration during transport prior to planting; and (2) Smithers provenance, all seeds, attributed to very low seed viability (Fig. 2). Of the 280 seed caches at Smithers site 2, 137 were excluded from the analysis due to obvious signs of seed herbivory by rodents in June 2008. Surprisingly, no signs of seed or seedling herbivory were noted at other sites.

We examined the effects of seed maturity, site conditions, and provenance climate on germination, survival, health, height, and number of needle fascicles using predictive models. Initial regressions were performed for each dependent variable with the explanatory variables separated into four categories: (1) cache microsite (vegetation height, soil type, soil depth, slope, convexity), (2) site climate (normal MAT and PAS, summer temperature, winter temperature, snowmelt date), (3) provenance climate (normal MAT and PAS) and seed mass, and (4) seed treatment. Significant variables from the submodels were pooled and logical interactions added to build a full model for each response variable. Stepwise procedures were used to determine variable significance for all models.

Germination was analyzed using a multinomial logistic model based on cumulative logistic models fitted by SAS PROC LOGISTIC:

$$Y_i = \frac{e^{F(x)}}{1 + e^{F(x)}} + \varepsilon \quad (1)$$

where $Y_i = 1$ or 0 for each cumulative model; $F(x)$ is a linear function of the explanatory variables; and ε represents error. The first model gives the probability of number of germinants = 0 vs. 1 or 2 and the next model gives the probability of germinants = 0 or 1 vs. 2. The probability of each level is then obtained by subtraction.

Model fit was assessed using max-rescaled R^2 values (SAS 9.2 Documentation [SAS Institute 2008]). Germination was modeled separately for treated seeds that germinated in 2008 vs. untreated seeds that germinated in 2009. Total treated-seed germination was also estimated with discarded nonviable seeds accounted for in the calculation. This allowed for a direct evaluation of the impact of seed treatment on germination potential.

As with germination, survival and health were analyzed using multinomial logistic models described by Eq. 1. For survival, the first model gives the probability of survival = 0 (i.e., if no germinants survived) vs. 0.5 (i.e., if 1 of 2 germinants survived) or 1 (i.e., if 1 of 1 or 2 of 2 germinants survived), and the next model gives the probability of survival = 0 or 0.5 vs. 1. Survival was modeled separately for the treated vs. untreated seedlings using the 2010 data set. For health, the first model gives the probability of health = 1 if health was poor vs. 2 or 3 if health was moderate or good, respectively, and the second model gives the probability of health = 1 or 2 vs. 3. The 2010 data set for live seedlings that germinated in 2008 was used for the health analysis. If there were two germinants in a cache, only the health of the larger seedling was analyzed.

Height and number of needle fascicles were analyzed using a general linear model fitted using PROC GLM:

$$Y_i = F(x) + \varepsilon \quad (2)$$

where Y_i is the height or the number of fascicles of the larger seedling in each cache, respectively; $F(x)$ is a linear function of the explanatory variables; and ε represents error. Both variables were analyzed using the 2010 data set for live seedlings that germinated in 2008. Model fit was assessed using variance explained.

RESULTS

Germination occurred and seedlings survived and grew in all 16 common-garden sites (Fig. 3a). By August 2008, 28.5% of the treated and 0.7% of the untreated seeds had germinated (Fig. 3b, Appendices B and C). By July 2009, these numbers had risen to 29.9% of the treated and 9.6% of the untreated seeds. As of 2010, an additional 0.1% of the treated and 0.6% of the untreated seeds had germinated. This translates to 95% of the total treated-seed seedlings germinating in 2008 (two months after planting), and 94% of the total untreated-seed seedlings germinating in 2009 (two years after planting). Total treated-seed germination fell to 20.4%, when seeds discarded during the seed-treatment process were taken into account.

Explained variance was higher for untreated seeds that germinated in 2009 than for treated seeds that germinated in 2008, the primary difference being that site climate influenced the former but not the latter (Table 2). Seed mass was a major explanatory variable for germination of both treated (Fig. 4a), and untreated

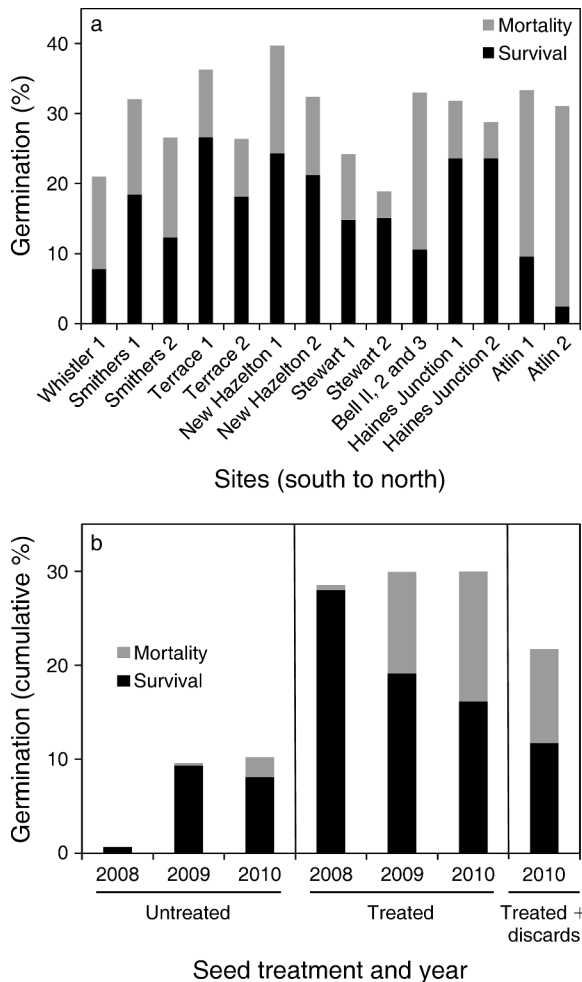


FIG. 3. Whitebark pine germination, survival, and mortality by (a) site (treated-seed data only) and (b) seed treatment and year.

seeds. Germination of treated seeds was higher in microsites with organic soils.

Almost all seedlings survived until assessed during the summer that they germinated (Fig. 3b, Appendices B and C). Survival rates were lower for treated-seed germinants (63.9% in 2009) than untreated-seed germinants (79.2% in 2010) by their respective second summers. Mortality rates leveled off for the treated-seed seedlings after 2009, with 53.9% of the total original treated-seed germinants still alive in 2010. Calculated in terms of total original seeds (i.e., including seeds discarded during the seed-treatment process), 8.1% of the total untreated and 11.7% of the total treated seeds germinated and survived through summer 2010 (Fig. 3b). Survival of the untreated-seed seedlings was primarily negatively associated with colder winters. Survival of treated-seed seedlings was primarily positively associated with seed mass (Fig. 4a) and warmer summers, and negatively associated with later snowmelt dates (Table 2, Fig. 4b).

Seedlings that germinated in 2008 averaged 3.2 cm tall with 6.0 flushed needle fascicles as of 2010 (Appendices B and C). Height, fascicles, and health were primarily positively associated with both provenance and site temperature, and negatively associated with later snowmelt (Table 2). Other than fewer needle fascicles developing on seedlings surrounded by taller vegetation, microsite factors negligibly influenced height, fascicles, and health.

DISCUSSION

Our study demonstrates that whitebark pine is able to germinate and survive in locations hundreds of kilometers north of its current northern range limit. Further monitoring will be necessary to determine if these planted populations will persist. However, our results provide preliminary evidence that whitebark pine can be successfully relocated to model-predicted, climatically suitable environments outside of the current species range. The major factors influencing establishment were seed maturity, growing season length as determined by snow, and provenance temperature.

Seed maturity: the combined effects of treatment and mass

Treating the whitebark pine seeds effectively promoted seed maturation, causing the majority of germination to occur a year earlier and inducing far higher (~3:1) germination rates relative to leaving seeds untreated. However, when nonviable seeds discarded during the treatment process were accounted for, only twice as many treated as untreated seeds germinated overall. Furthermore, survival percentage was lower for treated-seed than untreated-seed seedlings, such that the number of survivors relative to the number of original seeds was not substantially different between seed treatments. We cannot be sure that the mortality rate differences were due to seed treatment rather than weather or other factors, since the major germination and first-year mortality pulses occurred in different years for the two seed treatments. Likewise, the proportion of seeds discarded during the treatment process may have been unusually high due to poor seed development during the year of seed collection. However, our results suggest that practitioners consider whether treating whitebark pine seeds is worth the effort in contexts where space and germination speed are not limiting factors, such as restoration-planting initiatives.

Seed mass was highly variable among the whitebark pine families, and ended up being a primary predictor of establishment potential. We found that heavier seeds had better-developed embryos, germinated and survived in greater numbers, and developed into larger, healthier seedlings. Whitebark pine is an exception to the global trend that seed size decreases with latitude (Moles and Westoby 2003), reflecting the co-evolution between the species and its primary disperser, the Clark's Nutcracker. Whitebark pine seeds must be large in order to provide a net energetic gain for the nutcracker, and yet

TABLE 2. Models to predict whitebark pine germination, survival, health, height, and needle fascicles relative to (1) microsite factors, (2) test site climate, and (3) provenance climate and seed mass.

Dependent variable	Model	Significant variables†	<i>K</i>	<i>N</i>	<i>R</i> ²
Germination of treated seeds in 2008	microsite	soil type (organic)	1	3152	0.03
	test site	sPAS	1	3199	0.02
	provenance	seed mass, pMAT	2	3199	0.13
	full model	seed mass, soil type (organic), pMAT, sPAS	4	3152	0.16
Germination of untreated seeds in 2009	microsite	soil type (organic), soil depth, slope	3	3679	0.07
	test site	sPAS, sMAT, 2009 snowmelt date , 2009 winter temp.	4	2973	0.14
	provenance	pMAT, seed mass	2	3690	0.08
	full model	pMAT, sPAS , seed mass, sMAT, 2009 snowmelt date , 2009 winter temp.	6	3439	0.22
Survival of treated-seed seedlings as of 2010	microsite	vegetation height	1	1425	0.01
	test site	ave. summer temp., ave. snowmelt date , sMAT	3	1224	0.11
	provenance	seed mass, pMAT	2	1428	0.02
	full model	seed mass, ave. summer temp., ave. snowmelt date , sMAT, pMAT, vegetation height	6	1224	0.14
Survival of untreated-seed seedlings as of 2010	microsite	soil depth, vegetation height	2	582	0.05
	test site	ave. winter temp.	1	584	0.10
	provenance	pMAT	1	623	0.03
	full model	ave. winter temp. , vegetation height	2	623	0.09
Fascicles of summer1 germinants in 2010	microsite	vegetation height	1	799	0.05
	test site	ave. summer temp., sMAT	2	758	0.06
	provenance	pMAT, seed mass	2	799	0.07
	full model	pMAT, sMAT, vegetation height , seed mass	4	758	0.17
Height of summer1 germinants in 2010	microsite		0	799	n/a
	test site	ave. snowmelt date , sMAT, ave. summer temp.	3	758	0.11
	provenance	seed mass, pMAT	2	799	0.05
	full model	ave. snowmelt date , pMAT, sMAT, seed mass, ave. summer temp.	5	758	0.16
Health of summer1 germinants in 2010	microsite	vegetation height	1	799	0.03
	test site	ave. snowmelt date , ave. winter temp. , sPAS, sMAT, ave. summer temp.	5	758	0.12
	provenance	pPAS, seed mass, pMAT	3	799	0.07
	full model	ave. snowmelt date , ave. winter temp. , sPAS, pMAT, pPAS, ave. summer temp. , seed mass, sMAT	8	758	0.16

Notes: Full models were built using the significant ($P < 0.05$) variables from the three submodels. Variables with negative slopes are in boldface type. Seed treatment was included for needle fascicles, height, and health, but it was not significant and therefore is not listed. *K* is the number of significant variables; *N* is the number of seed caches observed; *R*² is max-rescaled *R*² for germination, survival, and health. The prefix “p” denotes provenance; “s” denotes site. MAT is normal mean annual temperature; PAS is normal precipitation as snow; ave. stands for average; temp. is temperature; yearly winter temperatures reflect the winter ending in the listed year. Height and seed mass are log transformed.

† $P < 0.05$; deduced using stepwise method, listed in decreasing order of significance.

the short growing-season length in the subalpine environments inhabited by the tree prohibits full seed maturation prior to harvest.

Three of the seven initial populations, Penticton, Whistler, and Smithers, had both low seed masses and poorly developed embryos, and demonstrated far lower germination rates than have been found in previous whitebark pine studies (Appendices B and C) (Berdeen et al. 2007, Riley et al. 2007, Bower et al. 2011). Based on masses and X-rays of seeds collected from the same provenances in earlier years (S. C. McLane, *personal observation*; D. Pigott, *personal observation*), we believe the poor seed quality of these populations results primarily from maternal effects caused by unusually extended snow cover during the second summer of cone development, rather than genetic or normal-climate

factors. These sorts of weather-driven maternal effects are common for plant species inhabiting harsh environments (Moles and Westoby 2003).

Site conditions: the paramount influence of snow cover

Most precipitation in whitebark pine environments falls as snow, accumulating as a snowpack that rarely melts before mid-May (Weaver 2001). This was validated by our ClimateWNA data, where precipitation as snow was 96% correlated with mean annual precipitation for the sites and 86% for the provenances. Between summer rains and melting snow fields, mature whitebark pines rarely experience drought, although it has been hypothesized that strong winds may partially limit the species' altitudinal range by causing foliar desiccation (Weaver 2001).

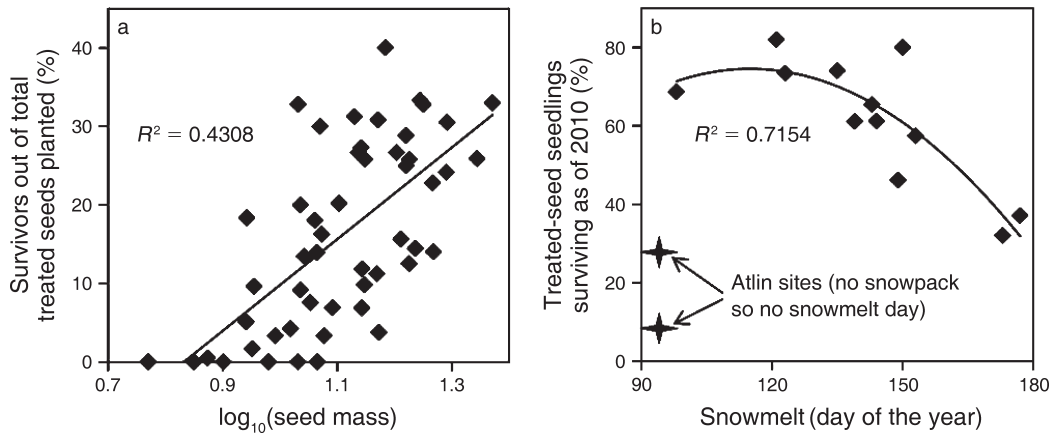


FIG. 4. Whitebark pine treated-seed seedlings that (a) germinated and survived relative to seed mass (originally measured as grams per 100 seeds), and (b) survived relative to snowmelt timing.

Previous researchers have found that snow cover is vital for protecting whitebark pine seeds from cold (Mellmann-Brown 2005), but that survival is poor in areas where the growing season is too short due to snow persistence (Weaver 1994). Indeed, snow has long been recognized for its influence on seedling establishment and survival in subalpine and alpine environments (Germino et al. 2002, Korner 2003). We found snow to play this classic limiting role in our study system. Earlier snowmelt was associated with greater survival rates and better health and growth, and lower amounts of normal precipitation as snow were positively associated with germination. However, extremely low germination of untreated seeds and high mortality of treated-seed seedlings occurred in the Atlin sites, where insulating snowpacks never developed due to wind scouring (Fig. 4). At the same time, mean annual and summer temperatures were positively associated with germination, survival, and growth. Together, these results confirm that a balance between sufficient snow duration and a long-enough growing season are critical for whitebark pine establishment and persistence.

Microsite differences that were not eliminated as a result of our site selection criteria had only a minor influence on whitebark pine establishment. Whitebark pine has previously been found to establish best in proximity to landscape features including trees, herbs, logs, rocks, and stumps, due to the protection these features provide against desiccation by sun and wind (Mellmann-Brown 2002, Maher and Germino 2006, McCaughey et al. 2009). We may have inadvertently decreased seedling establishment by systematically locating our sites away from these sorts of landscape features and by removing vegetation within 5 cm of the seed caches to minimize confounding effects.

Genetic effects follow provenance–temperature clines

Few studies have examined quantitative-trait differences among whitebark pine populations, reflecting the

expense and difficulty of conducting common-garden experiments for such a slow-growing species with difficult-to-procure seeds. However, two such studies indicate that seedlings from milder provenances grow faster and larger but have lower cold tolerance than those from harsher locations (Mahalovich et al. 2006, Bower and Aitken 2008). Our data partially corroborated these trends, with increased germination and survival capacity, growth, and height recorded for populations from warmer provenances. This effect was not an artifact of seed mass, which was only 3% correlated with provenance temperature. Nonetheless, our significant provenance variables should be interpreted cautiously due to the low sample size ($N=6$). We believe that genetic effects and genotype-by-environment interactions may increase with tree age; these effects will be noted during future site visits.

Using SDMs to predict whitebark pine's climatic range

Our demonstration that whitebark pine seedlings can establish in model-predicted areas north of the species range, and that establishment is partially predicted by modeled climate variables including normal precipitation as snow, is preliminary evidence that species distribution models can help to predict climatically suitable habitat for this species. However, annual snowmelt timing, as recorded by iButtons, was an important predictor that is not captured by available climate software, to our knowledge. Despite being temperature and precipitation driven, snow persistence is highly influenced by wind, slope, aspect, local topography, and freeze–thaw cycles. Adding a snow-duration variable to predictive habitat models for whitebark pine and other cold-adapted species could greatly improve their accuracy. Some researchers are generating regional snowmelt-timing models (e.g., Beniston et al. 2003), and satellite-derived snowpack data are available for some portions of the globe (see National Snow and Ice Data Center web site: *available*

online).² We hope to see snow-persistence data such as these incorporated into SDMs in the future.

Should we assist the migration of whitebark pine?

Whitebark is declining precipitously within its current range, and is not expected to adapt nor migrate fast enough to keep pace with climate change. Whitebark pine generations are 30–100 years long, making it highly unlikely that the species can adapt to the ~3°C mean annual temperature increases (Christensen et al. 2007) predicted for northwestern North America by the 22nd century. Natural migration is also unlikely for the species. Numerous biotic and abiotic factors interplay with climate to determine migration potential, including reproductive strategy, recruitment potential, geographic barriers to dispersal, and interactions between species (Davis et al. 1998). For whitebark pine, a major and unusual migration constraint is the species' dependence on the Clark's Nutcracker for seed distribution. Long-distance dispersal could be facilitated if nutcrackers fly seeds to previously uninhabited areas as they become climatically suitable for both species. However, the SDM prediction that much of whitebark pine's potential future range is climatically suitable at present, as well as the successful establishment of seedlings in these areas in our study, calls into question why the nutcrackers have not moved the species northward already.

Whitebark pine and other montane species have the advantage that small uphill migrations yield large temperature reductions relative to migrating across flat terrain (Loarie et al. 2009). However, whitebark pine often lives just below alpine areas in which soils tend to be poorly formed or absent. Given the predicted rate of climate change, it will take centuries for soils adequate for whitebark pine establishment to develop in such environments. The most likely scenario is therefore that whitebark pine will be outcompeted by faster-growing vegetative competitors encroaching from lower elevations (S. C. McLane and S. N. Aitken, *unpublished manuscript*), while remaining unable to migrate far uphill and slow to migrate northward.

The probability of whitebark pine becoming invasive in novel environments is extremely low. Plants in general are at low risk for intracontinental invasions (Mueller and Hellmann 2008), and whitebark pine's slow (30–50+ years) reproductive maturation, infrequent cone crop, poor competitive ability relative to other trees, and habitat-specialist life history strategy make it particularly unlikely to demonstrate uncontrolled population growth (McCaughey and Tomback 2001, Richardson and Rejmánek 2004). However, other ecological and economic factors should be accounted for in assessing whitebark pine's case for assisted migration. Most critical is the continued seeking in nature, or creation, of rust-resistant genetic strains, without which translo-

cating the species could be futile. Fortunately, provenances with higher levels of natural resistance are beginning to be identified (Mahalovich et al. 2006).

While concern for whitebark pine is high, the species is not yet federally legislated as endangered, and as such its migration should not be facilitated at present. Our common gardens are for research only; we will monitor the surviving trees and remove them before they reach reproductive maturity. Current efforts should go instead toward (a) promoting environmental conditions that maximize natural seedling recruitment and minimize losses of reproductive individuals (i.e., through suppressing fire, eliminating competitors, reducing pest populations, and promoting diverse stand age structure) (Schoettle and Sniezko 2007); (b) assessing natural blister rust resistance levels throughout the species range, and propagating and planting rust-resistant stock where appropriate; (c) improving SDMs to more accurately predict the species' future range extent; and (d) evaluating Clark's Nutcracker and whitebark pine dynamics at the current northern edge of the species range to determine the pine's natural dispersal potential. Concurrently, ecological and ethical decision-making frameworks for assisted migration should continue to be developed (Richardson et al. 2009) using whitebark pine as a test case because of its threatened status and noninvasive life history attributes.

CONCLUSION

We found that whitebark pine can establish in model-predicted climate zones north of the current species range limit. The major factors influencing establishment were seed maturity and site conditions, particularly the duration of snow cover. Treating seeds caused germination to occur earlier and boosted germination potential, but the percentage survival of seedlings grown from treated seeds was lower, indicating that treating seeds is a questionable use of resources for restoration planting. The species distribution model that we used was broadly accurate for predicting climatically suitable growing locations for whitebark pine, although it could be improved by adding a snow-duration variable that would help capture the major influence of snow on interannual variability in seedling germination and survival. Further monitoring will be necessary to determine the long-term establishment potential of the whitebark pines in the common gardens. However, current evidence leads us to believe that whitebark pine could eventually benefit from a program of assisted migration.

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² <http://nsidc.org/data/nsidc-0447.html>

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SUPPLEMENTAL MATERIAL

Appendix A

Methods for creating current-observed, current-predicted, and future-predicted species distribution models for whitebark pine within British Columbia, Canada (*Ecological Archives* A022-008-A1).

Appendix B

Whitebark pine germination, survival, and growth summary by population, site, and seed treatment (*Ecological Archives* A022-008-A2).

Appendix C

Whitebark pine germination and survival summary by population \times site and seed treatment (*Ecological Archives* A022-008-A3).