Limber Pine Seed and Seedling Planting Experiment in Waterton Lakes National Park, Canada

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Abstract—Limber pine plays an important role in the harsh environments in which it lives, providing numerous ecological services, especially because its large, wingless seeds serve as a high energy food source for many animals. Limber pine populations are declining due to a combination of white pine blister rust, mountain pine beetle, drought, and fire suppression. Outplanting of seedlings is a common strategy to aid in restoration efforts, but the success of revegetation methods in limber pine habitats is little known. To aid in restoration efforts in Waterton Lakes National Park, in southwestern Alberta, and other impacted areas, we studied the survival of limber pine planted as seeds and those planted as seedlings. At our experimental site, 11 percent of the seeds had germinated and seedlings were still alive after three years, while 72 percent of the seedlings that were planted directly survived. Restoration efforts are likely to have greater success when limber pine is planted in groups of five as seedlings rather than as seeds and there may be benefit to planting seedlings in burned areas near cover such as rocks or stumps.

Introduction

Limber pine (*Pinus flexilis*) is a distinctive five-needled white pine that grows as individual trees (up to 12 m), in clusters of trees, or in krummholz form. These trees sometimes reach ages of 1000 years or more (Schoettle 2004a). Its range extends from southwestern Alberta and southeastern British Columbia to New Mexico, Arizona and eastern California, with notable outliers in the Dakotas, Nebraska, eastern Oregon and southwestern California (Steele 1990). It generally occurs on exposed ridges across a wider range of elevations, from 870 m to 3810 m, than any other tree in its range.

While limber pine is not economically important for timber, the species is ecologically vital. In the harsh environments where it grows, limber pine provides wind amelioration, shade and snowdrift accumulation to facilitate other species (Baumeister and Callaway 2006). Limber pine is an effective pioneer species, colonising disturbed areas after fires or avalanches (Donnegan and Rebertus 1999). Once established, it serves as a nurse tree for a variety of shade-tolerant tree species, which eventually out-compete the shade-intolerant limber pine as the habitat nears successional maturity (Baumeister and Callaway 2006, Donnegan and Rebertus 1999).

The large, wingless seeds of limber pine serve as a high energy food source for a variety of animals, including red squirrels (*Tamiasciurus hudsonicus*) (Hutchins and Lanner 1982), grizzly bears (*Ursus arctos*) (Kendall 1983), black bears (*U. americanus*) (McCutchen 1996), and a host of bird species, such as Clark's nutcrackers (*Nucifraga columbiana*) (Benkman and others 1984, Schoettle 2004a, Schoettle and Negron 2001). Limber pine cones open when mature (Benkman and others 1984), providing birds and mammals with easy access to large seeds. Clark's nutcrackers, in particular, store seeds for later use in caches of from 1-5 seeds each (Lanner and Vander Wall 1980), buried 2-3 cm in the ground. Many buried seeds that remain uncollected germinate and grow into trees. Propagation of the species in this manner is one of the few ways in which limber pine is disseminated, and accounts for its having evolved with cones that expose seeds upon maturity (Tomback and others 1990).

Limber pine forests, particularly in the central and northern parts of the species range, are declining due to a combination of white pine blister rust (*Cronartium ribicola*), a non-native fungus that severely affects all five-needled pines (Gautreau 1963, Kearns and Jacobi 2007, Schoettle and others 2008), mountain pine beetle (*Dendroctonus ponderosae*) (Kearns and Jacobi 2007, ASRD and ACA 2007), drought (Kendall and others 1996, Achuff 1997), and fire suppression (Schoettle 2004a, 2004b). In Montana, considerable mortality has also been associated with the needle pathogen *Dothistroma septospora* (Jackson and Lockman 2003).

In Waterton Lakes National Park (WLNP), in southwestern Alberta, 78 percent of limber pine trees surveyed in 1995-96 were infected, and rust had already killed at least 45 percent of surveyed trees (Kendall and others 1996, Kendall 2003). Regeneration in most stands was poor, and many seedlings were already infected with the rust fungus and they probably will never reach maturity. Based on these and other surveys, limber pine was listed as an Endangered species under *The Wildlife Act* in Alberta in 2008 (Government of Alberta 2010).

As limber pine populations decline in health and size, a range of restoration options have been proposed, which include proactive (before rust arrives) and reactive (after rust arrival). Proactive actions include creating regeneration opportunities by maintaining a mosaic of mixed age classes across the landscape (Schoettle and Sniezko 2007); increasing the frequency of rust-resistant traits in the population (Schoettle and others 2009); and reducing pest populations

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(Schoettle and Sniezko 2007). Active management such as protecting putatively resistant trees from mountain pine beetle attack (Schoettle and others 2008); testing these trees for genetic resistance; collecting seed, and; outplanting seedlings (Burns and others 2008) have also been proposed.

Outplanting of two- or three-year old seedlings has been generally recommended as being more desirable than planting seeds but the potential survivorship and long-term success rate of either revegetation method has largely been untested for the high elevation 5-needle pines (see Schwandt and others, this proceedings, for recent experiments with whitebark pine, *Pinus albicaulis*). Collecting limber pine seed is a labour-intensive process (Ward and others 2006), and thus expensive, making seeds precious. Growing seedlings is also an expensive and complex process (Burr and others 2001). The primary argument in favor of planting seeds is that it is more cost effective: less technical expertise and fewer facilities are required, and there is no two-to-three year delay waiting for seedlings to germinate and grow in the nursery. Planted seeds may be susceptible to predation by small rodents or birds.

Our objective was to compare the survivorship and health of limber pine planted as seeds and as seedlings under an array of microsite conditions. We hypothesized that the planted seedlings would have better survival and health than sown seeds.

Methods

Study Site Description

The study site was located in WLNP (49°3'N, 113°47'W) on a morainal ridge at an elevation of 1650 m. The area is moderately well drained with an Orthic Black Chernozemic soil. The slope was negligible. Prior to a wildfire in 1998, limber pine was the dominant tree species on the ridge. The stand was determined to be approximately 90 years of age and was rated as mature prior to the fire (Achuff and others 2002). The fire killed the majority of the limber pine trees, and now the site is dominated by early successional, post-disturbance vegetation.

The site had both burned and unburned areas. Several young limber pine trees were very small and growing only in the unburned area. The ground cover consisted of common juniper (*Juniperus communis*) and bearberry (*Arctostaphylos uva-ursi*), with several other grass and forb species. The burned area had less ground cover, with bearberry and small junipers growing sparsely. There was more grass growing on the burned area than on the unburned area, but total cover was less than the unburned area. The site was exposed to full sun with no shade being cast by anything other than a few limber pine snags and rocks.

Material

The limber pine seeds were collected in September 1999, in Glacier National Park, Montana, approximately 50 km southeast of the planting site, and sent to the U.S. Forest Service Tree Nursery in Coeur d'Alene, ID. The seeds were sown in 2000 and propagated following techniques outlined in Landis and others (1999). Prior to sowing, the seeds were x-rayed and the fill rate was 60 percent, which is analogous to the expected germination rate (McLaughlin, personal communication). The seedlings were three years old when planted. Seedlings were stored at 0°C until one month prior to planting.

Planting and Monitoring Protocol

In 2003, we planted 3-yr seedlings and sowed seeds at the site. A total of 345 seedlings were planted in 101 clusters in October, 2003. A total of 340 seeds were also planted in 100 caches in October of 2003. Seeds and seedlings were planted under the following paired treatments: (1) burned vs. unburned, (2) protected vs. unprotected, (3) near vegetation vs. in the open, and (4) 1, 3 or 5 seeds per cache or seedlings per cluster (table 1). Five replicates of each treatment combination were planned, however, due to a lack of enough seedlings and sufficient unburned area, several treatments were not completed (table 1).

Table 1. Matrix of treatment type and number of seeds/seedlings planted. The total sample size was 340 seeds and 345 seedlings. Number of replicates of each treatment is in parentheses. Zeros indicate that there were no plantings of that particular combination.

		Burned		Unburned	
Cluster/cache size	Open/near vegetation	Protected	Unprotected	Protected	Unprotected
1 seed	Near veg.	5 (5)	5 (5)	0	0
1 seed	Open	5 (5)	5 (5)	0	0
3 seeds	Near veg.	15 (5)	15 (5)	15 (5)	15 (5)
3 seeds	Open	15 (5)	15 (5)	15 (5)	15 (5)
5 seeds	Near veg.	20 (4)	25 (5)	25 (5)	20 (4)
5 seeds	Open	30 (6)	25 (5)	25 (5)	30 (6)
1 seedling	Near veg.	5 (5)	5 (5)	0	0
1 seedling	Open	5 (5)	5 (5)	0	0
3 seedlings	Near veg.	3 (1)	21 (7)	0	18 (6)
3 seedlings	Open	21 (7)	21 (7)	15 (5)	21 (7)
5 seedlings	Near veg.	5 (1)	50 (10)	5 (1)	25 (5)
5 seedlings	Open	35 (7)	35 (7)	25 (5)	25 (5)

Figure 1. Photo-degradable netting used to protect seedlings from herbivory.

Figure 2. Hardware cloth used to protect seeds from herbivory and pilfering.

Plantings were within 1-m^2 plots within the sites to aid in re-locating them during monitoring. Each cache or cluster was marked with a numbered tag. Maps of the planting area were made, with codes for each treatment type. Seedlings were planted by digging a hole that was deep enough (approximately 20-25 cm) to allow the top of the soil plug to be flush with the surrounding soil level, while ensuring that roots were not bent or "j-rooted." The root balls were loosened by hand before planting, and were tamped in carefully with excavated soil to ensure that no air pockets were next to the roots. Seeds were planted at a depth of approximately 3 cm to mimic the depth of a typical Clark's nutcracker cache (Lanner and Vander Wall 1980). Seeds were then covered with soil so that no mounding was visible.

Fifty-three seed caches and 37 seedling clusters were physically protected from herbivory and pilfering with photo-biodegradable plastic netting for seedlings (figure 1) and with steel wire mesh with 0.64-mm grid, called "hardware cloth," for seeds (figure 2). The netting was cut into 15-cm lengths and stretched over the top of the seedlings to completely cover them. The hardware cloth was cut into 20-cm x 20-cm squares with the edges bent approximately 2 cm into the ground to prevent small mammals from digging under the cloth and pilfering seeds. The square was affixed to the ground using 6-cm long aluminum fence staples. In two instances large sheets of hardware cloth, measuring approximately 1 m x 60 cm, were also used to protect six caches together.

Seeds were cached and seedlings planted in either an open, exposed location or near natural objects (either existing rocks or vegetation, or rocks and downed woody debris were placed in their vicinity). Natural objects were positioned within 5-10 cm of the seedlings or seeds and were approximately the same height as the seedlings. Rocks and vegetation were situated to protect the seeds and seedlings from the prevailing southwest wind.

Seeds and seedlings were planted in groups of 1, 3 or 5, mimicking the natural caching behaviour of Clark's nutcracker (Lanner and Vander Wall 1980). The numbers of seeds (caches) and seedlings (clusters) planted were randomly assigned.

The site was monitored weekly from May 7 to August 31 in 2004, and May 18 to August 31 in 2005. In 2006, monitoring occurred bimonthly, starting on May 17 and ending on August 31. Data were not collected for each individual seed or seedling, but rather for each cache or cluster. The emergence of seedlings and the number of seedlings emerged was noted for each seed cache. Then seedlings, whether planted as seeds or seedlings, were monitored for growth and survivorship. The number of seedlings in each cluster was counted and the height of the tallest seedling in the cluster was measured in centimetres. The measurement was made from the ground surface to the tip of the upper bud, needles extending past the bud were not included in the measurement. The overall health and vigor of the majority of the seedlings in each cluster was rated by assigning each cluster to one of the following two categories: healthy (only green needles present) or unhealthy (dead with no needles or only brown needles present, or alive with high number of brown needles or flagging). From these categories, dead vs. live and healthy vs. unhealthy were used in subsequent analyses, described below.

Statistical Analyses

We analyzed seedling survival or seed germination data using logistic regression. Our binomial response variables were (a) seedling survival to the end of monitoring and (b) seed germination. Because the pattern of germination was non-linear in relation to cache size, we treated cache size as a categorical variable.

We analyzed the survival of individuals, but we expected the survival of individuals in the same cache or cluster would be correlated. To account for this correlation in the analyses, we included a random intercept (Breslow and Clayton 1993) using *xtlogit* with a random intercept in Stata 8.2 (StataCorp 2003). In 11 cases seeds germinated, but there was no follow-up information to indicate when the seedling subsequently died. These cases were excluded from the survival analysis, but included in the germination analysis.

Seedling health was assessed for each cluster of seedlings based on whether the seedlings were healthy (0) or unhealthy (1). The health rating at the end of 2006 was used to assess the effects of the covariates (planted as seed or seedling, number planted, burned or unburned, protected or unprotected, exposed or near objects) on seedling health. We used the 2006 data because it was at the end of monitoring. All of the clusters with seedlings had a rating of 0 or 1 so logistic regression was used in the analysis. Because clusters were planted in smaller plots within the site (plots were sometimes separated by many meters) the clusters were not necessarily independent, so we used plot as a grouping variable (random intercept) in *xtlogit* (StataCorp 2003).

The height of the tallest seedling in each cluster was measured regularly through each year. We used the growth during 2006 (final measurement minus the first measurement). The data were not normally distributed because many values were close to zero. Data were analysed with Poisson, using *poisson* and *xtpoisson* (StataCorp 2003).

Results

Seed emergence was first observed on June 10, 2004, eight months after planting. Of the 338 seeds that were planted, 144 (43 percent) germinated by the end of 2006. Of these, 136 seeds had germinated in 2004, eight germinated in 2005, and no seeds germinated in 2006. There were no significant differences in germination among the different cache sizes (table 2), but the trend was that a greater proportion of the seeds in three-seeded caches germinated than in one- or five-seeded caches (figure 3). The measure of correlation within clusters (*Rho*) was significant, indicating there is significant correlation of the response within clusters.

Of the 354 seedlings planted, over 28 percent (100 seedlings) had died by the end of monitoring in 2006 (table 3). In contrast, of the 133 seeds that germinated for which we had information about their longevity, 96 (72 percent) had died by the end of monitoring in 2006. Data on seedlings from both origins (seed or seedling) were combined in the first analysis, then seedlings from the two origins were analysed separately (table 4). The strongest effect on seedling survival was their origin (sown as a seed or planted as a seedling). Seedlings showed first-year survival of 85 percent when planted as seedlings as compared to 65 percent when planted as seeds. The only other significant variable was the number of seeds/seedlings planted. Survival increased with the number of seeds/seedlings in the cluster (figure 3). When the data were split by origin, the number planted was only significant for the seedling data. There was a trend towards an effect of exposure on survival of the combined data; seedlings in the open had a greater probability of dying than those near cover.

Analysis of the seedling health initially combined seedlings sown as seeds and those planted as seedlings before analysing these separately (table 5). Seedlings generated from field-sown seed had a better health rating than those planted as seedlings (origin variable in table 5). The results from both the combined data and the seedling data suggest that seedlings are healthier in larger clusters and in burned sites (figure 4). There were no significant effects in the analysis of seedlings from seeds, suggesting that the significant effects seen in the combined data (number planted and burned) are the result of effects on the individuals planted as seedlings. In contrast to the seedling data, there was no effect of the number of seeds planted on health of the seed

Table 2. Seed germination analysis using logistic regression. The table includes coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (shared frailty) is appropriate.

Covariate	Percent mean germination [b]	Coefficient	SE	*p*
No. planted 3 vs. 1 [a]	0.50/0.25	1.12	0.67	0.073
No. planted 5 vs. 1 [a]	0.39/0.25	0.62	0.66	0.350
Burned	0.38/0.48	0.30	0.32	0.347
Protection	0.39/0.46	0.45	0.32	0.154
Exposure	0.40/0.45	0.28	0.31	0.367
Constant		-1.68	0.66	0.011
Rho		0.20	0.08	χ^2_{01}=9.23, p=0.001

[a] Post-hoc comparison of 3 vs. 5, χ^2=3.13, p=0.077.
[b] First number is for first covariate in pair; second number is for second covariate or opposite.

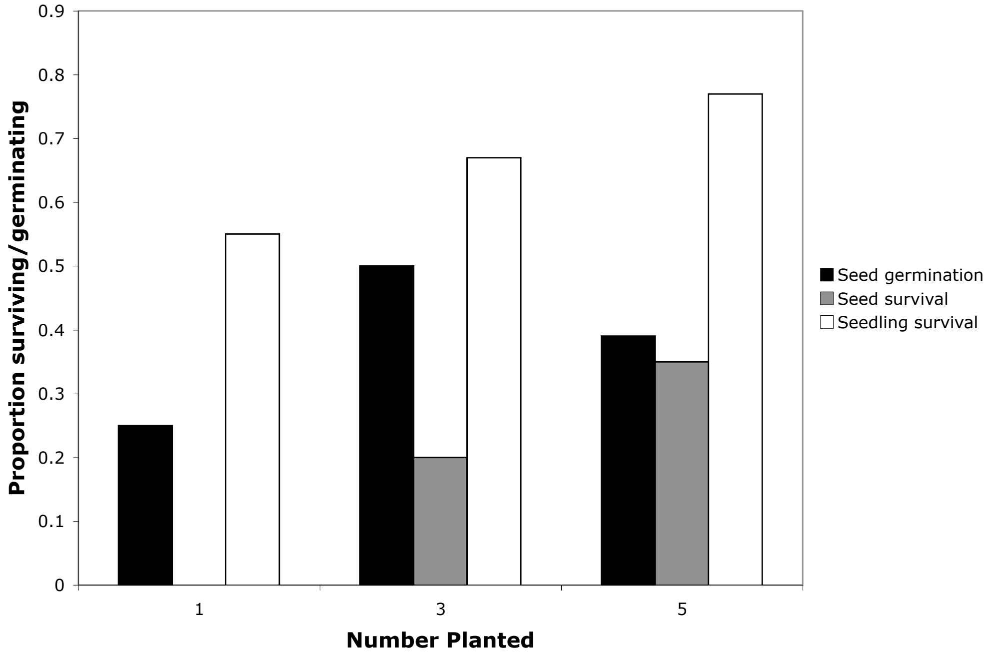

Figure 3. Seed germination and seedling survival as a function of the number that were planted in each cluster. Seed survival is the proportion of seedlings surviving of those seeds that germinated. Seedling survival is the survival of individuals planted as seedlings.

Table 3. Annual and cumulative mortality of seedlings that germinated from seeds and those planted as seedlings. Number of seedlings that died each year are shown with annual percent mortality in parentheses, and cumulative mortality as of the end of monitoring in 2006.

	Annual mortality[a] of seedlings planted	
Year	**(*n*=133)**	**(*n*=354)**
2004	47 (35%)	54 (15%)
2005	29 (22%)	32 (9%)
2006	20 (15%)	14 (4%)
Total dead (cumulative mortality)	96 (72%)	100 (28%)

[a] Annual percent mortality = number of trees that died in that year/number of seedlings at the end of year 1.

origin data. This is likely because there were no seedlings surviving at the end of 2006 that originated from caches of a single seed (figure 3) so the comparison is over a narrower range between caches with three or five seeds, which limits the potential to see an effect with this small sample size. There was significant correlation of clusters which warranted a random intercept for both the combined and seedling-only data.

Growth of the seedlings appeared independent of most of the covariates measured. The exception was the origin variable; individuals planted as seedlings grew faster than those from seeds. This is expected because they are also much taller (mean=16.33 cm vs. mean=3.25, respectively). When we corrected the growth for the final height of the seedling, analysing cm of growth/cm of final height rather than just cm of growth, this effect was no longer significant in the model (Coef.=-0.99, SE=0.65, p=0.129) and the other conclusions were unchanged (unreported results). Protected seedlings were 1.58 cm taller than unprotected seedlings in the seedling-only data.

Discussion

In our experiment, only 11 percent of the seeds that germinated were still alive after three years, while 72 percent of the seedlings that were planted directly survived. All seedlings were healthier in larger clusters and in burned plots.

Of 338 seeds planted, 144 (43 percent) germinated during our study, most of them in the first season after planting. This is lower than in a field experiment (buried in pots) in Kananaskis Country, Alberta, which reported 64.2 percent germination for one-year-old protected (wire mesh) seeds, but higher than the 2.4 percent reported for unprotected seeds (Webster 1998). Glacier National Park nursery reported germination rates of 68-80 percent (Evans and others 2001), while seeds sown at the Couer d'Alene nursery had germination rates of 88-95 percent (Carolin, personal communication).

While the percent of viable seeds can be expected to decline over time, and we do not know the rate of that decline, the seeds had only been stored for three years before planting, a length of time which likely would not have significant effects on germination (Evans and others 2001). Seed survival and germination success are dependent upon factors such as temperature and moisture (Carolin 2006). de Chantal and others (2003) observed that seeds sown earlier in the spring had higher rates of emergence and survival than from summer sowings due to more moisture and cooler temperatures. During the three years of our study (2004-06), the monthly average temperatures during growing season (May through September) was very similar to that of the 12-year average (table 6), at an Environment Canada weather station

Table 4. Seedling survival analysis results using logistic regression. The table includes the mean percentages for the groups, the coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (random effect) is appropriate.

Origin [a]	**Covariate**	**Percent mean survival**[b]	**Coefficient**	**SE**	***p***
	Origin (seed/seedling)	0.72/0.28	-2.95	0.48	<0.001
Seeds & seedlings combined	No. planted (1, 3 or 5)	0.54/0.47/0.35	-0.43	0.15	0.005
	Burned/unburned	0.37/0.44	0.23	0.39	0.566
	Protected/unprotected	0.39/0.41	0.59	0.41	0.148
	Near/exposed	0.37/0.42	0.70	0.40	0.080
	Constant		2.39	0.78	0.002
	Rho		0.45	0.09	χ^2_{01}=36.56, p<0.001
	No. planted (1, 3 or 5)	0.45/0.33/0.23	-0.39	0.17	0.020
From seedlings	Burned/unburned	0.26/0.32	0.43	0.45	0.336
	Protected/unprotected	0.26/0.29	0.56	0.49	0.253
	Near/exposed	0.25/0.31	0.63	0.47	0.183
	Constant		-0.69	0.78	0.373
	Rho		0.41	0.10	χ^2_{01}=25.3, p<0.001
	No. planted (1, 3 or 5)	1/0.80/0.65	-0.66	0.44	0.139
From seeds	Burned/unburned	0.78/0.67	-0.21	0.84	0.807
	Protected/unprotected	0.65/0.77	0.55	0.80	0.492
	Near/exposed	0.68/0.75	0.95	0.83	0.255
	Constant		3.68	2.00	0.066
	Rho		0.60	0.21	χ^2_{01}=9.70, p=0.001

[a] Seedlings from germinated seeds or from planted seedlings.
[b] First number is for first covariate in pair; second number is for second covariate or opposite.

Table 5. Seedling health results from logistic regression. The table includes mean percentages for each group, the coefficient for each covariate, their standard errors, and the probability that the coefficients differ from 0. The reference categories (dummy variable=0) were seeds, burned, protected, and near vegetation. *Rho* is the proportion of the total variance contributed by within-group (cluster) correlation. The *p* value for *Rho* is a test of whether *Rho* differs from zero, suggesting that including the grouping (shared frailty) is appropriate. Because the response is 0= healthy and 1=unhealthy, the negative coefficient for number planted indicates that health improves with an increase in the number of seeds/seedlings planted.

Origin [a]	**Covariate**	**Percent mean health** [c]	**Coefficient**	**SE**	***p***
	Origin (seed/seedling)	0.18/0.31	1.78	0.88	0.043
Seeds & seedlings combined (*n*=112)	No. planted (1, 3 or 5)	0.85/0.38/0.18	-0.60	0.24	0.012
	Burned/unburned	0.30/0.27	1.77	0.81	0.028
	Protected/unprotected	0.23/0.32	-0.64	0.57	0.258
	Near/exposed	0.20/0.35	-0.75	0.68	0.271
	Constant		0.96	1.24	0.438
	Rho		0.36	0.16	χ^2_{01}=8.79, p=0.002
	No. planted (1, 3 or 5)	0.85/0.40/0.20	-0.72	0.29	0.013
From seedlings (*n*=89)	Burned/unburned	0.29/0.33	3.48	1.49	0.020
	Protected/unprotected	0.25/0.33	-0.79	0.73	0.279
	Near/exposed	0.21/0.37	-1.28	1.00	0.201
	Constant		3.09	1.30	0.018
	Rho		0.45	0.18	χ^2_{01}=10.65, p=0.001
	No. planted (1, 3 or 5)	n/a /0.30/0.11	0.044	0.657	0.947
From seeds (*n*=23)	Burned/unburned	0.38/0.06	-1.18	1.22	0.334
	Protected/unprotected	0.15/0.21	-0.50	1.12	0.654
	Near/exposed	0.16/0.20	0.027	1.03	0.979
	Constant		-0.42	2.79	0.881
	Rho [b]				

[a] Seedlings from germinated seeds or from planted seedlings.
[b] A random effect did not improve model fit so was not included.
[c] First number is for first covariate in pair; second number is for second covariate or opposite.

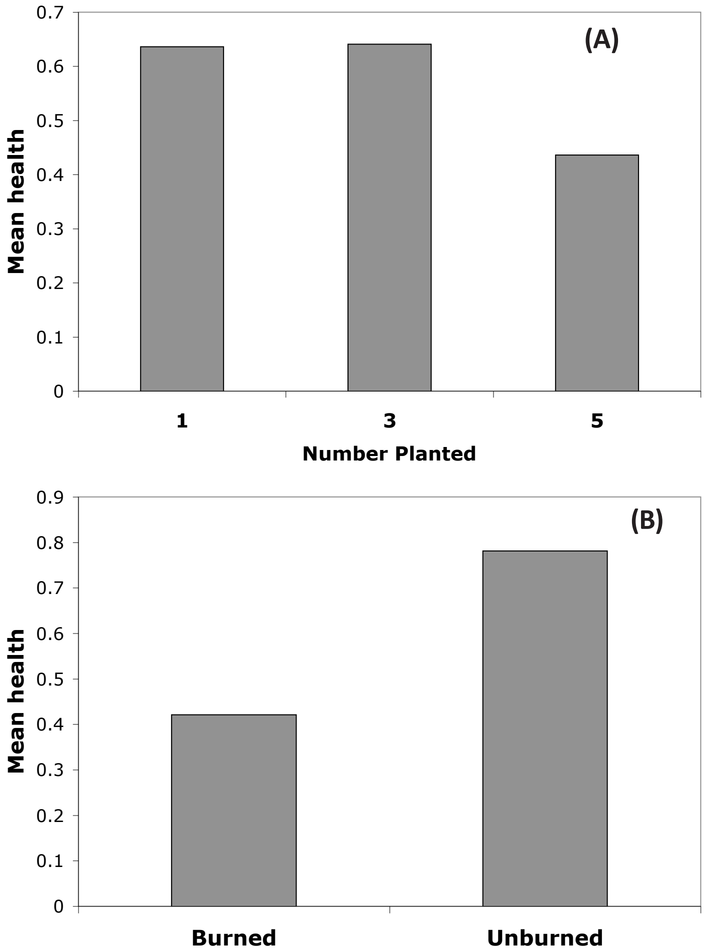

Figure 4. Mean health measures for the two significant covariates from the logistic regression of the seedling only data. Health improved (lower values) with an increase in the number of seedlings planted (A) and seedling health was better in burned than unburned areas (B).

approximately 10 km away. Precipitation was higher during the study than during the 12-year average (table 7). Thus, temperature and moisture did not appear to be limiting factors for germination. In other environments, unpredictable summer precipitation leads to fall planting, which is followed by more predictable winter moisture (Carolin 2006).

Schwandt and others (2007) and McLane (2010) observed significantly greater first-year germination in whitebark pine (*Pinus albicaulis*) seeds after stratification. McLane (2010) also noted that seeds with heavier initial weights were more likely to germinate and survive. Of those seeds that germinated most did so after the first winter but some continued to germinate after the second winter. This result demonstrates that limber pine, similar to whitebark pine (Tomback and others 2001), can have delayed germination and a small, short-duration soil seed bank.

Survival was much higher for individuals that were planted as seedlings (85 percent) than when planted as seeds (65 percent). This was higher than first-year survival (average 51 percent) at 13 different sites in Glacier National Park, MT (Carolin 2006).

Seedling survival after three years was substantially higher when planted as seedlings (72 percent) rather than as seeds (28 percent). This may be explained by the difference in ages at the end of monitoring; by 2006 those planted as seedlings were six years old, and may have passed a critical threshold for survival. Environmental conditions may affect seedlings differently at different stages of growth (Chambers and MacMahon 1994).

Survival and seedling health were improved when more seedlings were planted together in a cluster. Singly-planted seedlings had the lowest survival rate at the end of three monitoring seasons while three- and five-clustered seedlings had higher survival rates. Once emerged, seedling growth and survivorship are enhanced by the presence of other vegetation or seedlings (de Chantal and others 2003, Feldman and others 1999, Powell 1996, Coop and Schoettle 2009) that may alleviate the abiotic effects of the surrounding environment, thus making the microclimate more suitable. The presence of other vegetation may promote growth since soil nutrients, density and moisture are retained, due to an established root system from the other plants, rather than being leached during periods of higher precipitation (Coop and Schoettle 2009).

During the initial stages of seedling growth, high rates of emergence from seed clusters serve as protection against harsh environments for other seedlings in the cluster. In turn, survival increases (Donnegan and Rebertus 1999, Schoettle 2004a). The benefit of being in a larger cluster may not be a long-term effect. It is conceivable that the increased competition from being surrounded by more seedlings may result in lower survival once the seedlings are large enough to compete with one another. As the seedlings progress to later life stages, the requirements for survival and growth change. When root systems become established, competition for resources becomes evident (Powell 1996). Direct sunlight may become limited due to shade from other seedlings. The factors that once maintained the fitness level of the young tree could now contribute to the reduced survival, growth, health and reproductive output of clustered individuals (Powell 1996).

Seedling health was marginally better in burned areas than unburned areas. Burned soils have a higher mineral concentration than unburned soils, offering more nutrients for individuals with growing root systems, thus having a positive effect on the growth of seedlings (Coop and Schoettle 2009). Protection of seedlings appeared to increase seedling height slightly. Baumeister and Callaway (2006) found that the effects of protective covering had a negligible effect on seedling survivorship in their study. Microsites created by downed logs, stumps and and rocks significantly increased whitebark pine seedling survival, height and growth during their first year after planting (Izlar 2007).

Conclusions

Restoration of limber pine is time-consuming and expensive, so determining the appropriate methods of revegetation

Table 6. Monthly and annual average temperature (^{o}C) at Waterton Park Gate, Alberta, 1996-2007 (Environment Canada 2011). Empty cells denote no data available for that month.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	AVE
1996	-12.9	-4.2	-5.9	5.7	6.3	13.4	15.8	16.9	9.6	4.7	-7.3	-10.6	2.6
1997	-8.3	-1.1	-2.0	1.4	9.0	12.9	15.4	15.7	13.6	5.8	0.2	-0.9	5.2
1998	-6.7	0.0	-2.2	6.0	10.2	11.5	18.1	17.3	13.5	7.6	0.2	-6.0	5.8
1999	-4.1	-0.1	1.0	4.2	8.0	11.7	13.8	16.4	10.0	7.0	4.9	0.8	6.1
2000	-5.9	-3.6	0.9	4.7	8.8	12.1	16.1	15.6	10.0	5.7	-3.7	-7.3	4.5
2001	-0.6	-9.1	0.1	2.2	10.9	12.1	15.8	16.4	12.7	5.9	3.0	-4.1	5.5
2002	-4.6	-2.6	-11.4	-0.1	6.6	12.8	17.8	13.6	10.0	1.6	3.6	-0.8	3.9
2003	-1.8	-4.3	-1.8	5.0	8.6	13.5	17.5	17.6	11.0	8.1	-3.1	-1.3	5.8
2004	-6.7	-1.1	2.6	6.3	7.2	11.8	16.5	15.7	11.0	5.4	2.1	-2.7	5.7
2005	-5.3	-1.0	0.4	4.6	8.8	11.8	16.6	14.1	10.3	7.4	1.5	-3.7	5.5
2006	1.4	-4.6	-2.6	6.6	11.1	13.9	18.3	15.7	12.2	4.4	-2.7	-0.1	6.1
2007	-3.7	-52.0	3.5	3.8	9.8	12.7	19.3	14.9	10.3	7.0	0.1		2.3
Average 2004-06													
	-3.5	-2.2	0.1	5.8	9.0	12.5	17.1	15.2	11.2	5.7	0.3	-2.2	5.8
Average 1996-2007													
	-4.9	-7.0	-1.5	4.2	8.8	12.5	16.8	15.8	11.2	5.9	-0.1	-3.3	4.9

Table 7. Total monthly and annual precipitation (mm) at Waterton Park Gate, Alberta, 1996-2007 (Environment Canada 2011). Empty cells denote no data available for that month.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	TOTAL
1996	60.8	38.9	42.2	26.3	121.7	68.2	10.4	27.4	77.8	23.5	79.1	62.0	638.3
1997	44.6	25.9	36.2	43.1	128.0	135.6	13.4	61.2	17.8	42.2	36.8	10.7	595.5
1998	39.5			61.1	92.8	171.6	13.6	14.4	39.0	3.4	52.7	44.4	532.5
1999	23.2	5.8	10.0	53.8	43.6	60.2	48.0	26.2	50.4	53.0	74.0	19.3	467.5
2000	31.8	22.0	32.8	42.0	25.8	55.2	12.2	24.0	67.0	6.4	15.0	22.5	356.7
2001	17.8	32.3	28.0	116.4	6.8	153.4	25.2	4.8	18.0	19.3	28.7	10.2	460.9
2002	37.4	39.6	53.3	52.3	125.3	157.2	16.0	68.6	77.1	31.1			657.9
2003	11.0	13.3	50.3	46.9	54.0	32.8	10.8	3.6	41.4	125.0	73.9	43.5	516.5
2004	94.3	12.2	33.9	36.6	85.7	132.6	29.6	100.6	35.6	50.2	24.4	41.5	687.2
2005	202.4	44.2	41.6	42.6	29.2	260.4	26.0	138.0	129.0	41.0	41.2	26.3	1021.9
2006	28.6	90.1	52.8	54.3	48.2	114.0	17.8	16.4	62.1	56.3	67.5	22.8	630.9
2007	14.3	28.1	21.6	53.6	81.8	32.8	1.8	12.0	78.8	38.6	18.5		381.9
Average 2004-06													
	108.4	48.8	42.8	44.5	54.4	169.0	24.5	85.0	75.6	49.2	44.4	30.2	780.0
Average 1996-2007													
	50.5	32.0	36.6	52.4	70.2	114.5	18.7	41.4	57.8	40.8	46.5	30.3	579.0

is important to success. While the results of our study should be considered preliminary, pending confirmation by other field experiments, we draw the following conclusions from our three seasons of monitoring:

- seedling survival was significantly higher when planted as seedlings rather than grown from field-sown seeds;
- survival was significantly improved, and seedling health somewhat improved, when more seedlings were planted together in a cluster;
- survival was marginally better in seedlings planted near cover;
- seedling health was marginally better in burned areas than unburned areas; and
- protection of seedlings appeared to increase seedling height slightly.

In areas where mortality of limber pine is high, and white pine blister rust is reducing natural regeneration, resource managers are considering revegetating suitable sites. Restoration efforts are likely to have greater success when limber pine is planted in groups of five as seedlings rather than as seeds and there may be benefit to planting them with cover. The benefit of larger clusters may wane, however, if a greater number of seedlings produces greater competition and higher mortality over the long-term. Seedlings are likely to survive well in both burned and unburned areas and the overall effect of seedling protection showed little widespread benefit.

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