Biotic and microsite factors affecting Pinus albicaulis establishment and survival
by Ward Wells McCaughey

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
To culture a major high elevation tree, we need information on biotic and microsite factors affecting whitebark pine (Pinus albicaulis) seed survival, emergence, and seedling establishment. This thesis summarizes the results of the first 2 years of a long-term field study designed to evaluate physical and biological factors affecting whitebark pine establishment and survival. Predator effects on seed survival were estimated by recording seedling emergence under four levels of predator exclusion (exclude birds and rodents, exclude rodents only, exclude birds only, and exclude no predators). Microsite effects were evaluated by recording seedling emergence on mineral, litter, and burned seedbeds, under shade cover (0%, 25%, and 50%), and for buried (5 cm) and surface-sown seeds.

Rodents ate or removed all the surface-sown seeds and most of the buried seed they had access to. Birds took neither surface-sown nor buried whitebark pine seeds.

Whitebark pine seeds with delayed germination, those that laid dormant over two winters, had higher emergence rates than seeds that germinated after only one winter stratification period. Emergence rates of buried seeds was significantly greater than for surface-sown seeds. Emergence of surface-sown seeds preceded buried seeds. First-year emergence on mineral soil was higher than on litter or burned seedbeds; however, there was no difference in numbers of second-year emergents among seedbed conditions. Shading improved emergence of both first- and second-year seeds.

Insolation, drought, and rodents were the primary agents affecting survival of whitebark pine seedlings. Insolation mortality occurred in late June and early July of both measurement years. It was followed by drought mortality which ended in late August. Shade cover decreased insolation mortality and increased drought mortality. Drought mortality was higher than insolation mortality. Seedling losses due to animal damage were minimal and sporadic. More seedling mortality occurred during the winter than during the second growing season.

If whitebark seeds are planted, seedling emergence including first-year and delayed emergents, may be highest on shaded mineral seedbeds.

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APPROVAL

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Ward Wells McCaughey

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

17 May 1990 — Date

Chairperson, Graduate Committee

Approved for the Major Department

17 May 1990 — Date

Head, Major Department

Approved for the College of Graduate Studies

June 6, 1990 — Date

Graduate Dean

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This thesis summarizes the results of the first 2 years of a long-term field study designed to evaluate physical and biological factors affecting whitebark pine establishment and survival. Predator effects on seed survival were estimated by recording seedling emergence under four levels of predator exclusion (exclude birds and rodents, exclude rodents only, exclude birds only, and exclude no predators). Microsite effects were evaluated by recording seedling emergence on mineral, litter, and burned seedbeds, under shade cover (0%, 25%, and 50%), and for buried (5 cm) and surface-sown seeds.

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Insolation, drought, and rodents were the primary agents affecting survival of whitebark pine seedlings. Insolation mortality occurred in late June and early July of both measurement years. It was followed by drought mortality which ended in late August. Shade cover decreased insolation mortality and increased drought mortality. Drought mortality was higher than insolation mortality. Seedling losses due to animal damage were minimal and sporadic. More seedling mortality occurred during the winter than during the second growing season.

If whitebark seeds are planted, seedling emergence including first-year and delayed emergents, may be highest on shaded mineral seedbeds.

CHAPTER 1

INTRODUCTION

Whitebark pine (Pinus albicaulis Engelm.) is a high elevation species which ranges from northern British Columbia to south-central California and from the Pacific coast range to the Wind River range in Wyoming (Critchfield and Little 1966). Whitebark pine communities comprise 10% to 15% of the forested landscape (1.2 million hectares) in the Rockies from western Wyoming to the Canadian border (Arno 1986). It forms only a minor component of forest communities which are commercially harvested, but is found in pure stands immediately below timberline. Pure stands may be either woodlands with widely spaced diffuse crowned trees or "krummholz" with a low flagged form (Arno and Weaver 1990).

Whitebark pine is found in a variety of habitats and grows with several tree species including subalpine fir (Abies lasiocarpa), Engelmann spruce (Picea engelmannii), and lodgepole pine (Pinus contorta) in the Yellowstone ecosystem (McCaughey and Schmidt 1990; Pfister et al. 1977; Weaver and Dale 1974). Understory associates are listed by Forcella (1977), Pfister et al. (1977), and Weaver and Dale (1974). Vaccinium scoparium is the most abundant understory species in pure or nearly pure stands of whitebark pine (McCaughey and Schmidt 1990; Weaver and Dale 1974).

Throughout its range whitebark pine is important for esthetics, watershed protection, wildlife food and cover (Eggers 1986; Kendall 1983), and ornamental planting. Whitebark pine stands provide cover for a variety of plants and animals in timberline and subtimberline zones (Arno and Hoff 1989). Its seeds are an important food source for grizzly (*Ursus arctos horribilis*) and black bear (*Ursus americanus*) (Craighead et al. 1982; Kendall 1983; Knight et al. 1987) and a supplemental food source for birds (Tomback 1982; VanderWall and Hutchins 1983) and other small animals (Hutchins and Lanner 1982; McCaughey and Schmidt 1990).

Whitebark pine is threatened by mountain pine beetle (*Dendroctonus ponderosae*), white pine blister rust (*Cronartium ribicola*), and fire suppression (Amman 1982; Arno 1986). Mountain pine beetle and white pine blister rust are direct killers of whitebark pine. Fire suppression reduces available habitat by allowing its replacement more competition-tolerant subalpine fir and Engelmann spruce.

Management for the survival of whitebark pine forests will require management of plant competitors, insects, disease, and the tree itself. For example: 1. Wildfires or prescribed burns may be needed to maintain whitebark in areas where it is seral. 2. Stand conditions in lower lodgepole forests may be manipulated to reduce the effect of beetles on whitebark pine. This is because mountain pine beetle populations build to epidemic proportions in lodgepole forests and sweep up into high elevation whitebark stands (Arno and Hoff 1989) where they are unable to sustain themselves due to severe climatic conditions. 3. Exotic diseases, especially white pine blister rust, must be managed. 4. Where competition or disease mortality cannot be reduced, regeneration must be increased to compensate for losses.

Studies of the regeneration process of whitebark pine will contribute to the long-term survival of the species by improving regeneration. Little is known about seed production (Kendall 1983; Weaver and Forcella 1986) or regeneration processes of whitebark pine under natural or artificial conditions (Eggers 1985). Weaver and Dale (1974) recorded whitebark pine regeneration rates in undisturbed climax communities of whitebark pine. While seedlings germinated in meadows, openings created by disturbances, and closed forests, those not occurring in openings (large or small) rarely produce cones (Weaver et al. 1990). The germination percent of seeds cached by the nutcracker is unknown but of seedlings germinating in nutcracker caches 56% survived the first year but only 25% survived the third year (Tomback 1982). Published information is sparse on later growth autecology of whitebark pine, including mechanisms of flowering and fruiting, cone production (Weaver and Forcella 1986), seed characteristics and dissemination (Lanner 1982; Tomback 1982), vegetative reproduction, growth and morphology, rooting (Jacobs and Weaver 1990), shade tolerance (Arno and Hoff 1989), longevity, and phenology. Whitebark pine has not been considered a timber production species because of its slow growth and generally poor form (Arno and Hoff 1989; Weaver et al. 1990).

This study was designed to determine the effects of biotic and microsite factors on seed survival, germination emergence, and first year survival. The design includes treatments that are directly applicable to silvicultural practices. Five specific objectives of this study were to:

1. Determine differences in seed loss due to bird and small mammal predators when seed are surface sown (simulating unusual but conceivable tree dispersal) and when seed are buried 2 to 4 cm in soil (simulating burial by Clark's nutcracker [*Nucifraga columbiana*]).

2. Compare seedling emergence and establishment from surface-sown seeds and seeds buried 2 to 4 cm in soil.

3. Compare seedling emergence and establishment on mineral, litter, and burned seedbeds.

4. Compare emergence and establishment under 0%, 25%, and 50% shade cover.

5. Record seedling survival rates across seedbeds and shade treatments.

6. Compare between-year differences in emergence across seedbed and shade treatments.

CHAPTER 2

METHODS

Study Area

The experimental site was identified as an *Abies lasiocarpa* - *Pinus albicaulis*/*Vaccinium scoparium* habitat type (Pfister et al. 1977) occupied mainly by lodgepole pine. Most of the area appears to be on an inceptisol. This soil has a 6 to 8 cm thick cambic "B" horizon between the A and C_1 and C_2 horizons. The soils on a small portion of the study area are were identified as Typic Cryorthent, sandy skeletal being well drained (Soil Survey Staff 1975). This soil has a 12 cm thick "A" horizon overlying C_1 and C_2 horizons. Both soil types have a 3 to 5 cm thick "O" horizon. Soil pH values range from 4.7 to 5.5. The elevation is 2,652 m MSL with 0% to 25% slopes and a northeast aspect.

The study area is located in section 14, township 9 south, range 9 east on the Gardiner Ranger District of the Gallatin National Forest. It is north of Yellowstone National Park (Figure 1), and near the southwestern corner of the Absaroka Beartooth Wilderness approximately 8.8 air kilometers east of Gardiner, MT.

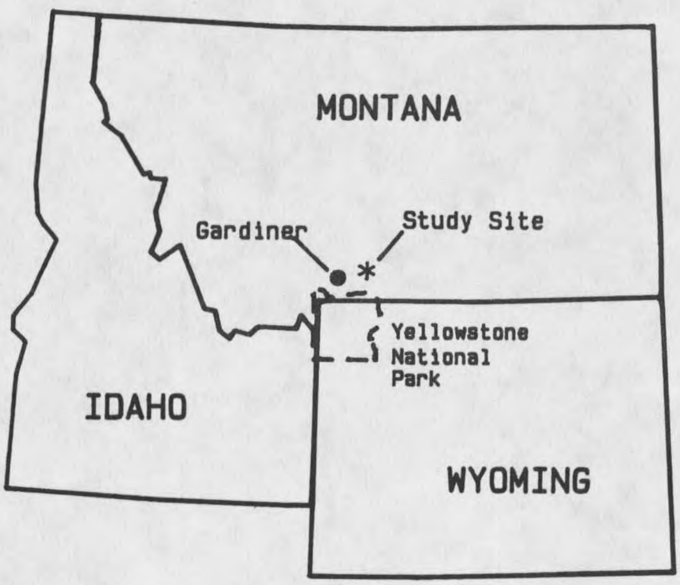

Figure 1. Study site location. Gallatin National Forest. Section 14, township 9 S, range 9 E, Montana Principal Meridian.

Study plots were established on a 6 hectare clearcut which is connected on the east to a large clearcut (20 hectare) called the Palmer Coop timber sale. The entire area was harvested during the winter of 1985-1986. Approximately 305 to 358 m^3/ha of timber were harvested with 22 to 33 metric tons/ha of slash left on the site. The species and volumes harvested were: live lodgepole pine - 75%, dead lodgepole - 13%, Engelmann spruce - 4%, subalpine fir - 4%, and whitebark pine - 4%. The study area is bordered by a mature forest of similar composition on the south and west, and a forest with 20% whitebark pine to the north.

Study Design

A factorial experiment (Table 1) was used to determine the effects of seed predators, light levels, seedbed conditions, and seed sowing depths on the germination and early survival of whitebark pine. Three subsites (replicates) were subjectively chosen within the 6 ha clearcut as representative, similar, and suitable for plot establishment. The subsites had minimal amounts of logging slash, large areas of undisturbed litter, and reasonably represented the overall stand conditions. Figure 2 is a schematic diagram of one replication of each predator exclusion - shade cover - seedbed condition - sowing depth combination. Plots were randomly located in each replicate.

Treatment Descriptions

Predator Exclusion

Four treatments were used to evaluate predation effects on whitebark pine seed: exclude birds and rodents, exclude rodents only, exclude birds only, and exclude none. Wire screen was used to exclude seed predators from the plots while plots exposed to all predators were un-screened. Plots protecting seeds from all predators were completely covered using hardware cloth with 0.63 cm

Table 1. Factors and factor levels.

Factor	Levels
1. Predator exclusion	4
a. Exclude birds and rodents (EA)	
b. Exclude rodents only (ER)	
c. Exclude birds only (EB)	
d. Exclude none (EN)	
2. Shade level	3
a. No shade	
b. 25 percent shade	
c. 50 percent shade	
3. Seedbed condition	3
a. Mineral (1988 analysis)	
b. Litter (1988 analysis)	
c. Burned (1989 analysis)[1]	
4. Sowing depth	2
a. Surface-sown	
b. Seed buried (2 - 4 cm)	
5. Replication	3

[1]First year results did not include a burned seedbed treatment.

square holes. Plots for protecting seed from birds only were covered by screen with 5 by 7.6 cm wide holes. Plots excluding rodents only were enclosed by a 76 cm high fence of 0.63 cm square mesh hardware cloth. The rodent fence was designed to exclude rodents but allow access to avian predators. The top of the fence had a 20 cm lip, bent outward from the plot. A 15 cm piece of tin flashing was attached to the underside of the lip to effectively exclude rodents. The bottom of screens were buried 10 to 15 cm deep on plots excluding both birds and rodents and plots excluding rodents only. The bottom edge of the buried screen had a 5 cm lip bent outward from the plot to minimize the chance of rodents tunneling under the screen. Screening techniques for the control of seed predation were suggested by Curt Halverson, U.S. Fish and Wildlife Service, Fort Collins, CO.

Shade

Three shade treatments were used; no shade, 25%, and 50% shade cover. Shade treatments were imposed with slatted roofs. Four 1.8 m tall steel posts were installed at the corners of an imaginary 1.2 by 2.4 m rectangle overtopping but slightly to the south of each plot to be shaded. A 1.2 by 2.4 m long wood frame was constructed with 5 by 10 cm lumber and attached to the steel posts 100 cm above the ground. A 1.2 x 2.4 m section of wood snow fence was suspended on the wood frame. The 50% and 25% shade levels were simulated by either leaving all the wood slats in the snow fence or by removing alternate slats respectively.

Seedbed

Mineral, litter and burned seedbed treatments were used to examine emergence and survival of whitebark pine. Mineral seedbed treatments were located on scarified skid trails or hand scalped (top 2 to 5 cm of soil) when logging scarified areas did not occur on a mineral treatment location. Litter treatments consisted of areas undisturbed by logging.

Prescribed broadcast burns created the burn seedbed conditions. Because burning was done in confined (15 m^2) areas of the clearcut, burned treatment plots were randomly located within a burned area adjacent to the mineral and litter seedbed plots for that replicate. The burn treatment areas were burned twice in 1987 because high moisture content of litter and other fine fuels created poor burning conditions. The completed treatment resembled scattered spots of a light surface fire even after two burns. Because burning was not completed until late fall of 1987, no plots were seeded until the fall of 1988.

Sowing Depth

Two sowing depth treatments were used; surface-sown and buried. Surface-sown seed were placed on the ground surface and buried seed were buried 2-4 cm below the surface level and covered by the appropriate seedbed material (i.e., covered by mineral soil, litter, or ash).

Plot and Seed Layout

Within each subsite, 36 plots were established to represent all combinations of the four predator exclusion, three shade, three seedbed, and two sowing depth treatments (Figure 2). Plots were rectangular (0.5 x 2.0 m) and

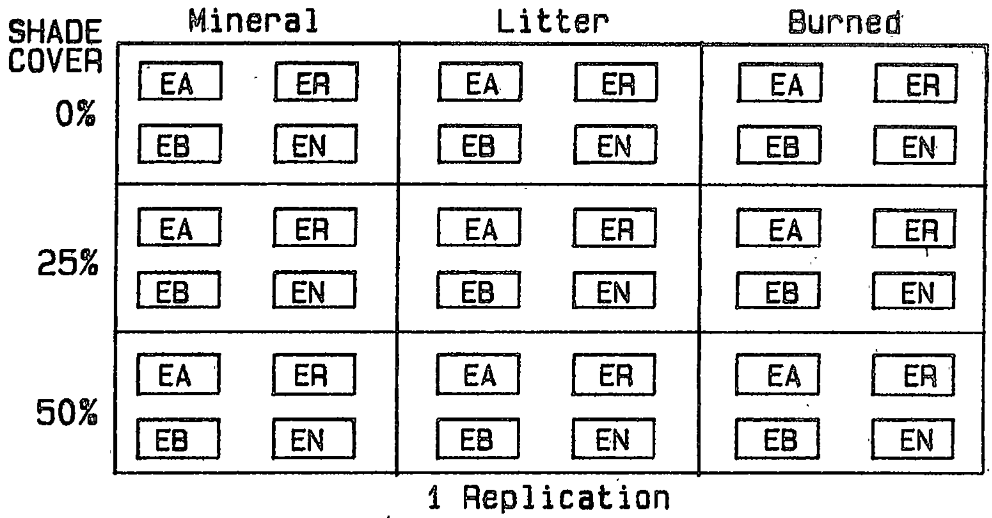

Figure 2. Schematic layout of study design showing all the treatment combinations in one of three replications. In the field, treatment combinations were located randomly. Predator treatments were exclude birds and rodents (EA), exclude rodents only (ER), exclude birds only (EB), and exclude none (EN).

oriented the long direction north-south. The south half (0.5 x 1.0 m) of each plot was seeded in the fall of 1987 and the north half was seeded in the fall of 1988.

In 1987, the south half of each plot was subdivided into 40 subplots measuring 10 by 11 cm (Figure 3). Within each subplot two seeds were planted, one surface-sown and one buried. The surface-sown seed were placed in the north half of each subplot. The buried seed were placed in the south half of each subplot.

In 1988, the north half of each plot was subdivided into two halves, a surface-sown half (north) and a buried half (south), each measuring 49 by 100 cm (Figure 3). The seed sowing design was modified to reduce measurement

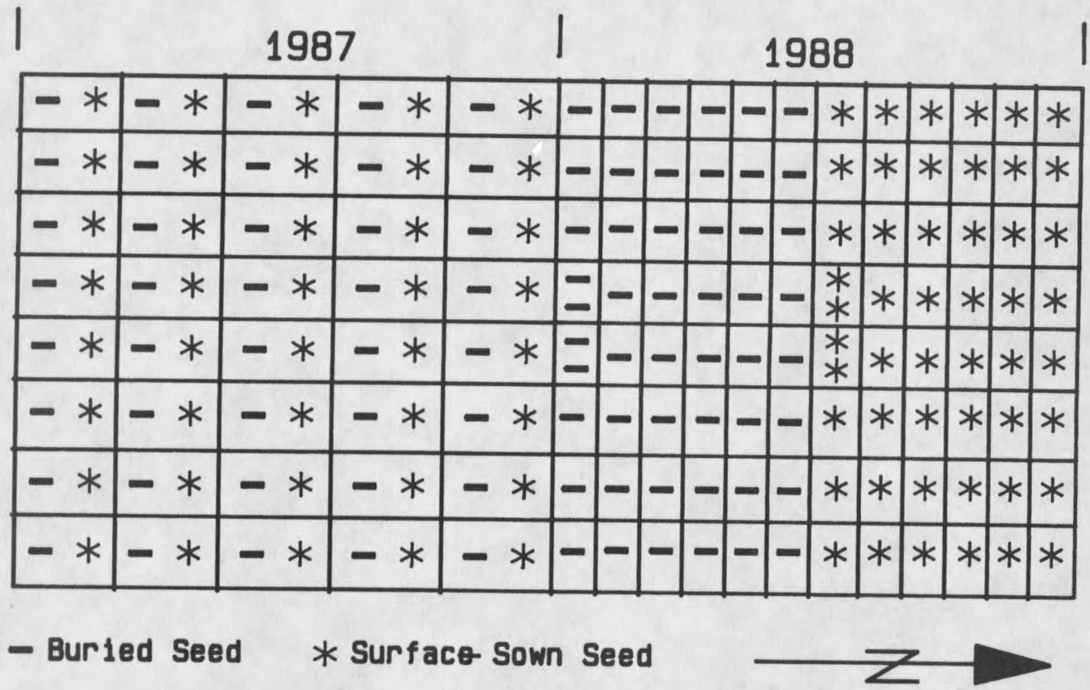

Figure 3. Schematic layout of 1987 and 1988 surface and buried seed locations.

errors since surface-sown seeds were occasionally moved short distances due to natural factors such as wind, rain, and snow and this sometimes made identification of sowing depth type difficult. The surface and buried halves were further subdivided into 48 subplots with each subplot measuring 6 x 8 cm. On the surface half, 50 seeds were sown, one placed on the ground in each of 46 subplots and two seeds in 2 subplots. On the buried half, 50 seeds were placed 2 to 4 cm below the surface level in 46 subplots and two seeds in 2 subplots. Again, the buried seed were covered by the appropriate seedbed material (mineral soil, litter, or burned litter).

Exactly 5,760 whitebark pine seeds were planted in 1987 and 10,800 in 1988. The addition of the burned seedbed condition and an increase from 40 to 50 seeds accounted for the increased seed numbers in 1988. All seeds were x-rayed and only filled seeds were planted. X-rays do not reduce the germinative capacity or initial seedling growth of conifer seeds, however, it is unknown if there are long-term growth effects (Borzan 1973). Seeds planted in 1987 were collected (seedlot 1) in 1985 and stored in sealed plastic bags (relative humidity = 6% to 8% inside bag) for two years under standard external conditions (temperatures = -17 to -20°C; humidity = 30%) until planting. Seeds were collected (seedlot 2) in the fall of 1987 and stored under the same conditions as seedlot 1 until planting in 1988.

Measurements

Whitebark pine seedlings were counted periodically throughout spring and summer on all plots. Counting began on June 16 in 1988 and June 9 in 1989. I could not determine exactly when germination occurred since half the whitebark seeds were buried and continuous monitoring of surface-sown seed was prohibitive. Emergence and emergents are used to describe germination and to quantify resultant seedlings, respectively. Emergents were counted and numbers recorded weekly until the first of August and bimonthly from August to the first of October. Emergents were marked with colored plastic toothpicks of different colors to record the emergence week. The week of mortality and its likely cause was recorded for all dead seedlings.

Soil moisture was measured gravimetrically in 1988 and 1989 on 6 of the 24 germination plots at each of the three replicates. These six plots comprised one plot from each combination of mineral and litter seedbed and 0%, 25%, and 50% shade cover. Soil from the upper 5 cm of the A horizon was collected in soil cans and sealed for transport from the field to the laboratory. Percent soil moisture was determined by comparing wet and dry weights (Soil Survey Staff 1975). Soil moisture was never measured on burned seedbeds due to the limited burned treatment area available.

Subsurface soil temperatures were measured in 1988 and 1989 with Taylor minimum-maximum thermometers at the same seedbed-shade plots where soil moisture collections were taken on replicates 1 and 3. Soil temperatures in replicate 2 were measured with temperature probes connected to electronic microprocessors designed for continuous collection of environmental conditions. Problems with temperature probes caused sporadic and sometimes unreliable data. Minimum and maximum soil temperatures were measured at a soil depth of 2.5 cm (the level where seeds were buried). Temperatures were measured and recorded weekly throughout the 1988 and 1989 summers.

Maximum surface temperatures were measured weekly in 1988 and 1989 with wax (Big Three Industries-tempil) pellets which melt at specific temperatures. Tempils used for this study were designed to melt at 37.7, 41.1, 45.0, 51.7, 58.9, 65.6, 72.8, 79.4, 86.7, and 93.3 degrees Celsius. Tempils were placed on one of the mineral and litter seedbeds on each of the 0%, 25%, and 50% shade plots for a total of six plots on each replicate.

Data Analysis

The whitebark emergents/seed planted ratio on each subplot was used as the dependent variable for analysis of emergence differences between years, predator exclusion levels, shade levels, seedbed conditions, sowing depth, and factor interactions. Proportion of emergence is defined as the number of emergents divided by the number of seeds sown (40 in 1988, 50 in 1989). Empty plots were counted as 1/4n to prevent distortion of the analysis by small numbers (Mosteller and Youtz 1961). A transformation, arc sine of the square root of the proportion of germination, was used to stabilize variation due to proportions (Snedecor and Cochran 1980).

The statistical analysis system (SAS 1987) was used to analyze whitebark pine emergence and seedling survival data. Analysis of variance was used to test for statistical significance of main factors and interactions on seedling emergence and survival. ANOVA was also used for evaluation of soil moisture and temperature data. The "F" statistic was used to determine the significance of factors and their interactions on emergence of whitebark pine. Multiple comparison procedures were used to analyze differences between factor levels. I used the Ryan-Einot-Gabriel-Welsch multiple F test for equal cell sizes and the Tukey-Kramer method for unequal cell sizes (SAS 1987). All significance tests were done at the "$p \leq 0.1$" level. I chose this high p-value level for two reasons: (1) regeneration data typically has a high degree of variation and (2) p-values between 0.05 and 0.1 indicate a strong relationship that might otherwise be overlooked.

Predation on whitebark pine seed was analyzed separately from microsite factors affecting whitebark germination. Seed predation was assessed using results from all four exclusion treatments (EA, ER, EB, and EN). The EA and ER treatments were used in analysis of variance to assess whitebark emergence and survival differences among shade levels, seedbed conditions, and sowing depths.

The fact that no seed were lost to predators in these treatments fully eliminated predation effects and allowed direct comparisons to be made.

CHAPTER 3

RESULTS AND DISCUSSION

Seed Predation

Birds and rodents were the principal potential predators on whitebark seed considered in this study. The Clark's nutcracker, the major bird species consuming whitebark seed, harvests directly from cones (Hutchins and Lanner 1982). In other studies chipmunks (Eutamia spp.), deer mice (Peromyscus maniculatus), and golden-mantled ground squirrels (Spermophilus lateralis) were the principal rodent consumers (Hutchins and Lanner 1982; Lanner 1980; Tomback 1981). I considered insects a minor predator and saw none feeding on or removing whitebark pine seed.

Surface-Sown Seed

In 1987 and 1988, animals removed 100% of surface-sown seeds on exclude birds only (EB) and exclude none (EN) treatments within 5 days after sowing. No seeds were removed from exclude birds and rodents (EA) and exclude rodents only (ER) treatments, indicating that birds were not randomly searching for whitebark pine seeds and these screening methods effectively excluded rodents. Hutchins

(1989) believes that random foraging by Clark's nutcrackers is highly unlikely since their foraging efforts appear to be directed toward finding their own seed caches. The exclosures and shade cover may have discouraged seed foraging by birds; however, birds, including the Clark's nutcracker, were observed sitting on exclosures of both ER treatments and shade structures. No birds were seen foraging for seeds on or in the vicinity of any plots. Birds were observed caching seeds on the study site in 1987 and 1989. It is assumed that surface-sown seeds on EB and EN treatments were eaten or removed by rodents while bird predation was, at most, minimal.

In 1988 and 1989 eight rodent species were trapped on the study area. Deer mice represented 54% and southern red-backed voles 23% of all species caught (Table 2). Squirrels (*Tamiasciurus hudsonicus*) clipped whitebark cones in the adjacent forest but I saw none foraging for seeds on the study area. Because of their high frequency of occurrence and known use of whitebark seeds, deer mice are probably the main consumers of whitebark seed on this area.

Buried Seed

Animal predation on whitebark pine seeds buried in exclude birds only (EB) and exclude none (EN) plots was shown by depressions on mineral soil and litter seedbeds, in 1988 and on all seedbed treatments in 1989. There was

Table 2. Species list of rodents trapped on whitebark pine study area in 1987 and 1988. Percent represents the proportion of total sample size (n=47).

Species	Percent
Deer mouse (*Peromyscus maniculatus*	54
Southern red-backed vole (*Clethrionomys gapperi*)	23
Masked shrew (*Sorex cinereus*)	4
Montane shrew (*Sorex monticolus*)	2
Montane vole (*Microtus montanus*)	2
Long-tailed vole (*Microtus longicaudus*)	9
Heather vole (*Phenacomys intermedius*)	2
Yellow-pine chipmunk (*tamias amoenus*	4

no evidence of disturbance at buried seed locations on exclude rodents only treatments; therefore, it is assumed that there was no seed predation of buried seeds by birds. Seeds were untouched on exclude birds and rodents treatments, indicating that rodent and bird predation was eliminated by screening. Pocket gopher (*Thomomys tolpoides*) activity was noted in all predation treatments in 1989; surface-sown seeds were not disturbed (except by burial with soil brought to the surface) and I have no evidence of disturbance of buried seed.

Rodents foraged for but did not find all available buried seeds. Emergence from buried seeds occurred on exclude birds only treatments with seeds accessible to rodents even though all the planting sites were disturbed.

Loss of buried whitebark seeds may have been higher on predation treatments than under natural bird-cached conditions because surface-sown seeds attracted rodents. To test the hypothesis that surface-sown seeds acted as an attractant, 100 seeds each on mineral and litter were singly buried on sites accessible to rodents. Five areas of 20 seeds each were laid out for each seedbed condition with seeds buried 2 to 4 cm deep in a 1 dm by 1 dm grid pattern. Seed disturbance was 24% on mineral and 40% on litter seedbed. Since disturbance was observed on 100% of the buried seed locations in the predator exclusion treatments allowing access to rodents (EB and EN), it appears that surface-sown seeds did act as a rodent attractant.

Seeds that germinated on the exclude birds only and exclude none treatments were buried seeds that rodents looked for but did not find. There was no significant difference in percent emergence of whitebark seedlings between exclude birds only and exclude none treatments within a year (Table 3).

There were, however, significant (p=0.056) between year differences in the exclude birds only and exclude none treatments. Significant differences between years for percent emergence could have been due to differences in viability between seedlots, predator populations, or climatic factors.

Table 3. Emergence of whitebark pine for exclude birds only and exclude none treatments in 1988 and 1989.

Year	Treatment: Exclude birds only	Treatment: Exclude none
	percent[1/]	percent[1/]
1988	2.1 a	2.5 a
1989	3.6 a	3.5 a

[1/]Percent germination within year, sharing a common letter are not significantly different (p-value≤0.1).

Viability was 95% and 97% respectively for seed planted in 1987 and 1988; thus the probability that emergence differences were due to different seedlots was low. Seeds were x-rayed to ensure that only filled seeds were planted.

It is also unlikely that year to year differences were due to rodent effects. Rodent populations did not appear to vary enough to suggest that they caused between-year emergence differences. Rodent catches were 19 in October of 1987, and 16 in July and 11 in September of 1988.

Precipitation was probably responsible for the between-year differences in seedling emergence. The study site was clear of snow and soils were at field capacity immediately after the first week of June in both measurement years. Emergence was noted from mid-June through the first of September in both years. Precipitation records for two Soil Conservation Service weather stations, Mill Creek to the north and Canyon to the southeast of the study area were obtained to examine area wide moisture patterns (Tables 12 and 13, Appendix). The weather stations demonstrated dry conditions (26% and 17% of normal), in 1988, and near normal (79% and 72% of normal), in 1989, for the months of June through August. The three to four fold difference in precipitation between 1988 and 1989 was distributed evenly throughout the spring and summer months.

Emergence

There was no predation of surface sown or buried whitebark pine seeds on exclude birds and rodents and exclude rodents only treatments. These treatments thus provide an estimate of maximum emergence under field conditions. Analysis of variance was used to evaluate the effects of biotic and microsite factors on whitebark pine emergence.

Years

Analysis of variance showed that emergence varied significantly between planting years (Table 4). Therefore, analysis of biotic and microsite factor affects on emergence and survival of whitebark pine was conducted

Table 4. Effect of year and biotic and microsite factors on emergence of whitebark pine. An ANOVA. Emergence was measured as a proportion and transformed to the arc sine of the square root of the proportion (Snedecor and Cochran 1980).

Factor	df	SS	MS	F	P
Year (1988-1989)	1	1.3381	1.3381	80.52	.0001
Predator exclusion	1	0.1094	0.1094	6.58	.0112
Shade cover	2	0.0881	0.0440	2.65	.0735
Seedbed condition	2	0.4831	0.2415	14.53	.0001
Sowing depth	1	5.6318	5.6318	338.86	.0001
Error	172	2.8586	0.0166		
Total	179	10.5091			

within individual years. Between-year differences in emergence were attributed to precipitation differences (Tables 12 and 13, Appendix).

Seedbed and sowing depth significantly affected total summer emergence in both years, while predator exclusion was significant in 1988 only, and shade was significant in 1989 only (Tables 5 and 6). Significant differences in emergence among replicates occurred in both measurement years.

Significance of all factors varied by measurement date as the summer progressed. Tables 14 and 15 (Appendix) show the 1988 and 1989 analysis of variance results for biotic and microsite factors and two-way interactions as the cumulative percent emergence of whitebark pine for each recording date. Significance of all factors and interactions increased as germination progressed through the summer months.

Table 5. Effect of biotic and microsite factors and their interactions on 1988 emergence of whitebark pine: An ANOVA. Emergence was measured as a proportion and transformed to the arc sine of the square root of the proportion (Snedecor and Cochran 1980).

Factor	df	SS	MS	F	P
Replicate	2	0.2975	0.0487	17.88	.0001
Predator exclusion	1	0.1648	0.1648	19.81	.0001
Shade cover	2	0.0237	0.0119	1.43	.2483
Seedbed condition	1	0.0692	0.0692	8.32	.0055
Sowing depth	2	0.7385	0.7385	88.79	.0001
Pred x Shade	2	0.0330	0.0165	1.99	.1466
Pred x Seed	1	0.0335	0.0335	4.03	.0494
Pred x Sow	1	0.0530	0.0530	6.37	.0144
Shade x Seed	2	0.0509	0.0254	3.06	.0544
Error	58	0.4824	0.0083		
Total	71	1.9466			

Table 6. Effect of biotic and microsite factors and their interactions on 1989 emergence of whitebark pine: AN ANOVA. Emergence was measured as a proportion and transformed to the arc sine of the square root of the proportion (Snedecor and Cochran 1980).

Factor	df	SS	MS	F	P
Replicate	2	0.0472	0.0236	2.68	.0736
Predator exclusion	1	0.0091	0.0091	1.04	.3110
Shade cover	2	0.0895	0.0447	5.09	.0080
Seedbed condition	2	0.4718	0.2359	26.84	.0001
Sowing depth	1	5.5792	5.5792	634.73	.0001
Pred x Shade	2	0.0327	0.0163	1.86	.1618
Pred x Seed	2	0.0553	0.0276	3.14	.0477
Seed x Sow	2	0.1221	0.0611	6.95	.0015
Error	93	0.8175	0.0088		
Total	107	7.2244			

Total numbers of whitebark emergents varied significantly between years but the emergence curves were similarly shaped (Figure 4). Surface-sown seed apparently germinated about 1 week before buried seeds in both years (Figure 4). While seeds buried 2 to 4 cm may have germinated (when radicle first extends through the seed coat) at the same time as surface-sown seed, germination could not be recorded until emergence occurred. There was no germination after the first of July for surface-sown seeds; perhaps surface conditions were too dry to allow germination or all nondormant seeds had germinated by then.

After July emergence from buried seeds was significantly higher than from surface-sown seeds in both years (Figure 4). Emergence from buried seeds was rapid before the first of August and sparse thereafter.

Predator Exclusion

Whitebark pine emergence differed significantly between the exclude birds and rodents (EA) and exclude rodents (ER) only treatments in 1988 but not in 1989 (Tables 5 and 6). Emergence differences were attributed to screen design differences and not bird predation since no seeds were removed from the pests. The percent emergence was 9.5% for EA and 3.8% for ER treatments in 1988 (Table 7). The higher emergence rate in the EA treatment is attributed to the milder plot microclimate of