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
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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.

BIOTIC AND MICROSITE FACTORS AFFECTING <u>PINUS</u>

<u>ALBICAULIS</u> ESTABLISHMENT AND SURVIVAL

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Ward Wells McCaughey

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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
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Date   Chairperson, Graduate Committee

Approved for the Major Department

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Date   Head, Major Department

Approved for the College of Graduate Studies

June 6, 1990
_____   _____
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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
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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
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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.
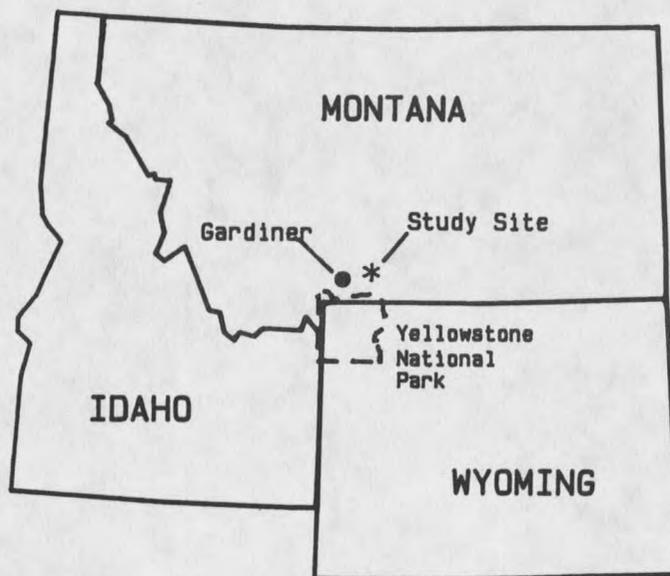
Figure 1. Study site location. Gallatin National Forest.
Section 14, township 9 S, range 9 E, Montana
Principal Meridian.

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

SHADE COVER	Mineral		Litter		Burned	
0%	EA	ER	EA	ER	EA	ER
	EB	EN	EB	EN	EB	EN
25%	EA	ER	EA	ER	EA	ER
	EB	EN	EB	EN	EB	EN
50%	EA	ER	EA	ER	EA	ER
	EB	EN	EB	EN	EB	EN

1 Replication

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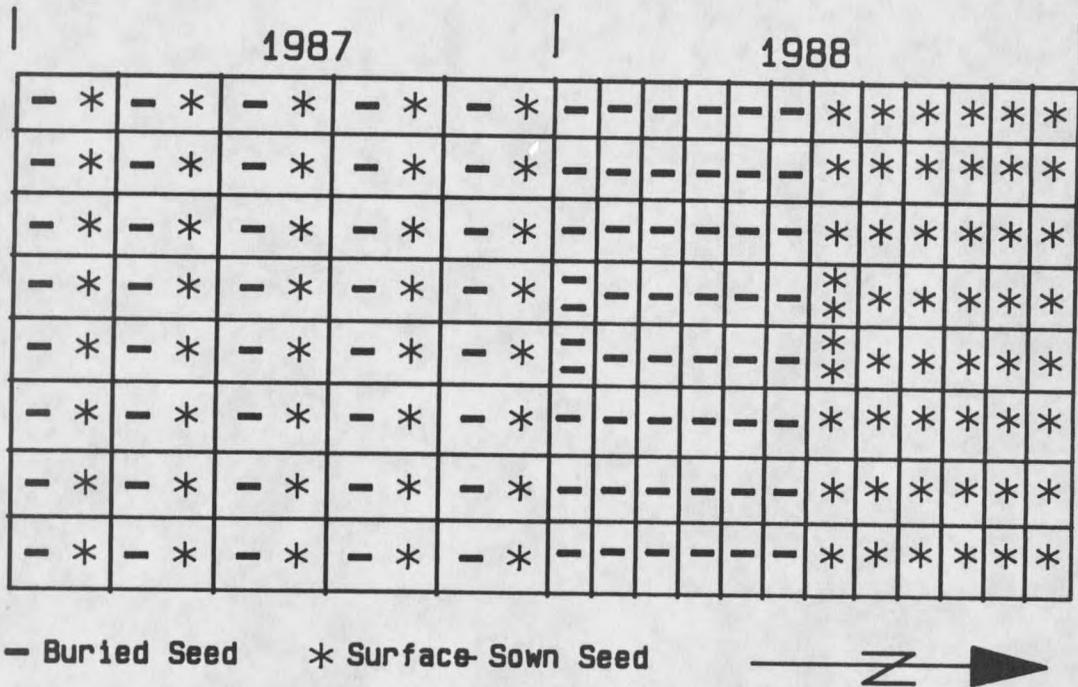
Figure 3. Schematic layout of 1987 and 1988 surface and buried seed locations.

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.

	Treatment	
	Exclude birds	
Year	only	Exclude none
	- - - - - - - 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$\leq$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
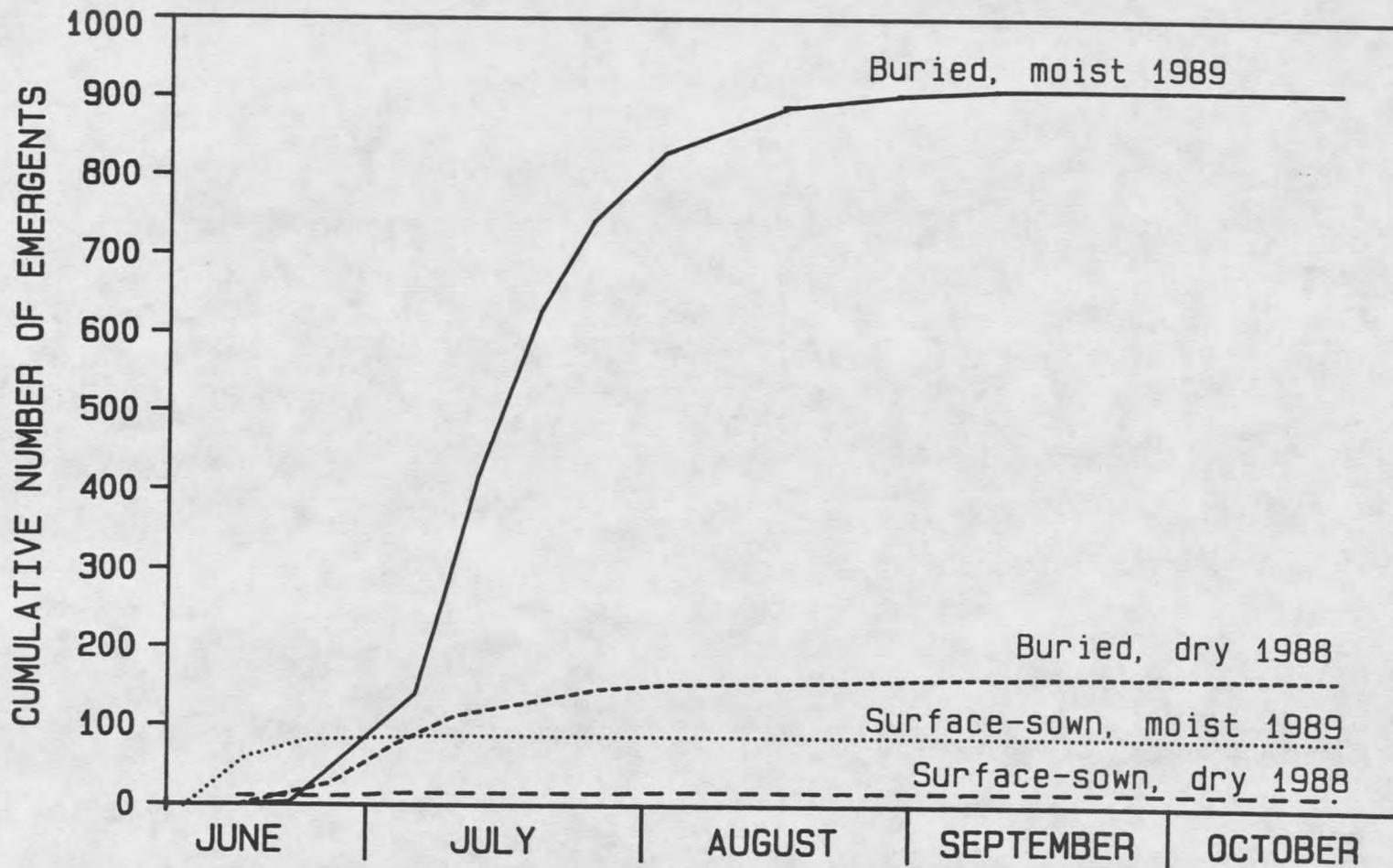
Figure 4. Cumulative number of whitebark pine emergents from buried and surface sown seeds in 2 years.

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Table 7. Percent emergence of whitebark pine as affected by predator exclusion, shade cover, seedbed condition, sowing depth, and replicate on treatments excluding rodents and birds (EA) and excluding rodents only (ER) for 1988 and 1989 first-year and 1989 delayed emergents from the 1987 sowing. Values are not cumulative over years.

| | | First-year | | Delayed |
| | Factor | 1988 | 1989 | 1989 |
Factor	level	mean	mean	mean
		- - - - -[1] - percent - - - - -		
Predator	EA	9.5 (a)	19.3 (c)	20.9 (e)
exclusion	ER	3.8 (b)	17.9 (c)	30.5 (f)
Shade cover	0	5.2 (a)	16.7 (c)	21.3 (e)
(percent)	25	7.9 (a)	18.8 (cd)	28.6 (f)
	50	6.8 (a)	20.4 (d)	27.2 (f)
Seedbed	Mineral	8.2 (a)	26.0 (c)	24.9 (e)
condition	Litter	5.1 (b)	14.5 (d)	26.5 (e)
	Burned	–	15.3 (d)	
Sowing depth	Surface	1.8 (a)	3.5 (c)	6.0 (e)
	Buried	11.5 (b)	33.7 (d)	45.4 (f)
Replicate	1	7.9 (a)	19.3 (c)	20.8 (e)
	2	9.5 (a)	20.2 (c)	29.4 (f)
	3	2.5 (b)	16.4 (d)	26.9 (f)

[1]Similar and dissimilar letters in parentheses within a column for a factor represent nonsignificant and significant differences respectively.

the EA treatment. The EA treatment has hardware cloth, with 0.63 cm-square holes, about 4 inches above the ground level and totally enclosing the plot. The metal cloth may have provided extra shade, reduced daytime temperatures, and increased night temperatures.

Screening method slightly increased emergence of whitebark pine in moist 1989 (Table 6). I attribute the between-year difference to the increased summer rains in

1989 (Tables 12 and 13, Appendix): emergence was enhanced
by screening affects (cooling or reducing evaporation)
provided by the exclude birds and rodents treatments in
dry years. Screening effects disappeared in 1989, when
moisture was not as limiting throughout the growing
season, as it was in 1988.

Shade Cover

In 1989 when water was less limiting, shade
significantly (p=0.008) affected emergence (Table 6).
Percent emergence of whitebark pine in 1989 was
significantly higher (20.4%), under 50% shade than with no
shade (16.7%)(Table 7). The 25% shade treatment was
intermediate (18.8) in percent emergence and did not
significantly differ from 0% or 50% shade cover.
Surprisingly shade did not significantly improve emergence
of whitebark pine seed in dry 1988 (p=0.2483)(Table 6).
The 1988 emergence of whitebark pine appeared higher for
shaded than nonshaded treatments, ranging from 7.9%, 6.8%,
to 5.2% emergence with 25%, 50%, and 0% shade cover,
respectively (Table 7). The snow fence slats caused
alternate strips of shade and full sunlight. Dead shade
may not have been enough to override the effect of drought
on emergence in a dry year, even under 50% shade.

Seedbed Condition

Seedbed condition significantly affected whitebark pine germination in both years (Tables 5 and 6). Emergence of whitebark pine was significantly higher on mineral seedbeds than on litter or burned seedbeds in both years. There was no burned seedbed treatment in 1988.

Most conifers germinate best on mineral seedbeds (Schmidt and Lotan 1980; Seidel 1979; Zasada et al. 1978). The exposure of soil is expected to eliminate competing vegetation, and provide more light, moisture, and nutrients for seedling growth (Schmidt et al. 1976). Although no quantitative measures of competing vegetation were taken, reduction of competition may have been one of the primary reasons for better whitebark emergence on mineral seedbeds. Moisture may have been the factor limiting emergence on litter seedbeds on these high elevation sites. Soil moisture was consistently higher on litter than mineral seedbeds except in the fall (a season of low mortality (Figure 5).

A significantly higher percent of whitebark germinants emerged on mineral (26.0) than on litter (14.5) or burned (15.3) seedbeds in 1989 (Table 7). I expected emergence on the burned seedbeds to be as high as on mineral soil due to the nutrient flush following burning and the reduction in competing vegetation. My burn treatments may have been too light to fully provide these benefits.
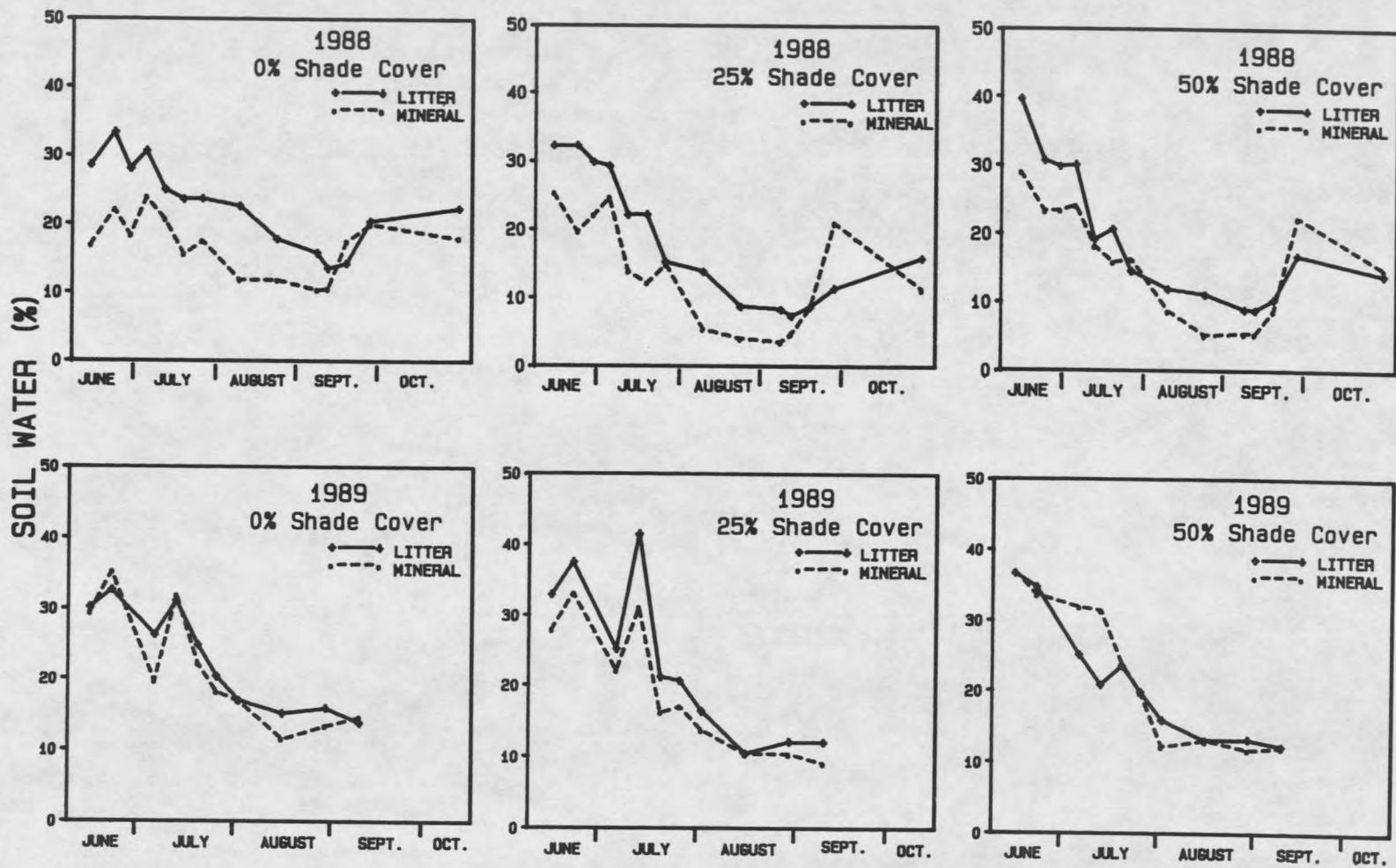
Figure 5.   Soil water in top 5 cm of soil on mineral and litter seedbeds under
0%, 25% and 50% shade cover in 2 years.

Emergence on burned seedbeds in subalpine forests is usually comparable to that on litter initially, it increases rapidly with time, and eventually surpasses emergence on mineral (scarified) seedbeds (Fiedler 1980). Emergence of whitebark on my burned treatments may eventually equal that on mineral seedbeds. Light burning intensities do not have as severe effects on organic matter and soil properties as more intense burns. Hot fires consume most of the organic material, alter soil structure, and create unfavorable conditions for seedling growth (Vogl and Ryder 1969). Hot fires also volatilize nitrogen and result in loss of other nutrients in fly ash (Perry 1979).

Sowing Depth

Even in the absence of predation (EB and ER; discussed above) deep sowing significantly improved emergence of whitebark pine in both measurement years (Tables 5 and 6). Emergence of buried seed was 11.5% and 33.7% compared to 1.8% and 3.5% for surface-sown seed in 1988 and 1989 respectively (Table 7). As previously discussed emergence was significantly lower in dry 1988 for both buried and surface-sown seeds.

The Clark's nutcracker caches whitebark pine seed at a depth of 2 to 4 cm on ground surfaces ranging from mineral, to litter, and gravel (Lanner 1980). Some

factors which may reduce surface germination are lower

water availability and more exposure to solar radiation

(Gorski and Gorska 1979).

Replicate

Whitebark pine emergence was significantly less in

replicate 3 than in replicates 1 or 2 in both 1988 and

1989. Percent emergence for each replicate was 7.9 and

19.3 for replicate 1, 9.5 and 20.2 for replicate 2, and

2.5 and 16.4 for replicate 3 for 1988 and 1989 respectively

(Table 7). The within-year difference may be attributable

to soil differences in the study area. Soils were usually

drier in replicate 3 than in replicates 1 and 2 during the

early summer when emergence was greatest (Figure 6).

The soil on replicate 3 was identified as a Typic

Cryorthent, sandy skeletal with a 6-inch A horizon

containing 54% sand over a C horizon of 60% sand. Soils

on the other replicates had a narrow 4 to 6 cm thick

cambic B horizon between the A and C horizons which

classified them as inceptisols. The deficiency of moisture

likely limiting the emergence of whitebark pine on

replicate 3 is probably due to the high sand content of

the soil profile and the shallow A horizon. The A and

B horizons on replicates 1 and 2 had less sand and more

silts and clays according to hand textural analysis.
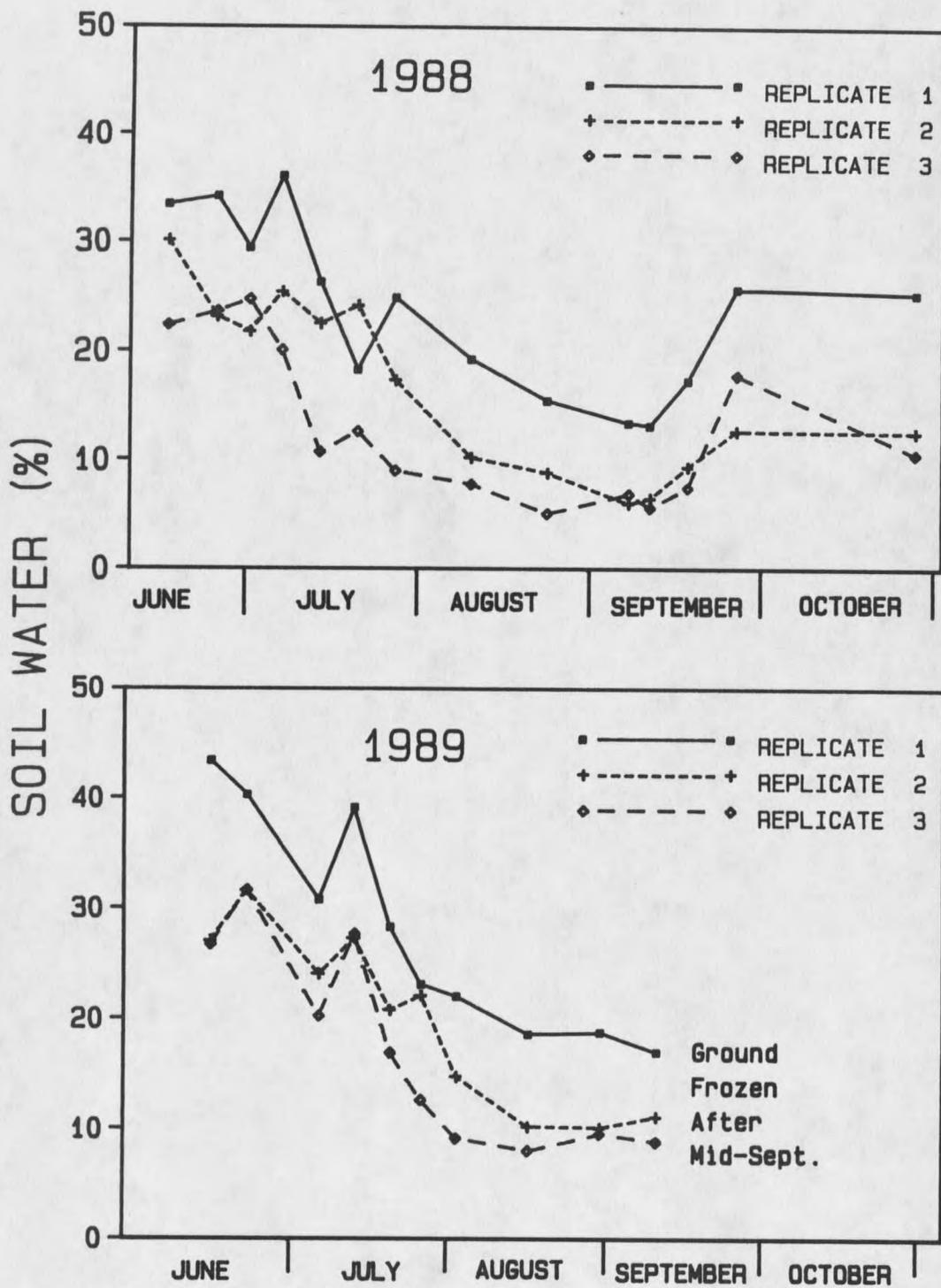
Figure 6.   Percent moisture in top 5 cm of mineral soil by
replicate for 1988 and 1989.

Soils on replicates 1 and 2 would have a higher water-holding capacity than on the sandy soils of replicate 3.

Interactions

Four two-factor interactions of biotic and microsite factors in 1988 and three two-way interactions in 1989 appeared to affect whitebark pine emergence (Tables 5 and 6). No three-way or higher interactions were significant.

1988 Interactions. The 1988 interactions and their significance on emergence of whitebark were: predator exclusion by percent shade cover (A) (p=.1466), seedbed condition (B) (p=.0494), and sowing depth (C) (p=.0144), and percent shade cover by seedbed condition (D) (p=.0544) (Table 5). The interaction of predator exclusion by percent shade cover showed relative differences in mean percent emergence between the 0 (6.3%), 25 (12.1%), and 50 (9.4%) percent shade cover on the exclude birds and rodents (EA) treatment (Figure 7A). A p-value of .1466 is not considered significant at the p<0.1 level but is low enough to indicate that a relationship may exist. There was no difference in mean percent emergence between the three shade levels on the exclude rodents only (ER) treatment.

Figure 7. Two-factor interactions of the 1988 biotic and microsite factors affecting whitebark pine emergence: predator exclusion by shade level (A), seedbed condition (B), sowing depth (C), and percent shade cover by seedbed (D).

Emergence increased considerably when plots were shaded by the EA screen exclosures and shade covers. The change in total numbers may be caused by microclimate differences between predator exclusion treatments due to effects of metal screen exclosures.

The interaction of predator exclusion by seedbed condition showed differences in mean percent emergence of whitebark pine between mineral and litter seedbed under the EA treatment (Figure 7B). The emergence differences ameliorated with the ER treatment. I attribute seedbed treatment differences to microclimate modification from the screening on exclude birds and rodents treatments.

Emergence of buried whitebark seed was greater than surface sown seed and this difference was much larger on EA than on ER treatments (Figure 7C). Emergence differences between predation treatments may again be caused by microclimate effects on EA treatments.

While shading did not (p=0.2483) benefit whitebark pine emergence overall, it did affect it on mineral seedbeds (Figure 7D). Emergence of whitebark on litter seedbeds remained constant under the three shade levels while emergence on mineral seedbeds increased considerably under 25% but only slightly under 50% shade over nonshaded conditions. Emergence between seedbeds was not different on nonshaded conditions but was higher on mineral than on litter under 25% and 50%. Because shading had a negative

effect on soil moisture in the top 5 cm of soil (Figure 5)
I tentatively attribute its positive effects on emergence
to reduction of surface temperature on mineral soils.

   1989 Interactions. The three two-factor interactions
affecting 1989 emergence of whitebark pine are predator
exclusion by shade cover (A) (p=0.1618) and seedbed
condition (B) (p=0.0477) and seedbed condition by sowing
depth (C) (p=0.0015) (Figure 8). Similar to 1988, there
were differences between the three shade levels on exclude
birds and rodents but not on exclude rodents only
treatments (Figure 8A). Explanations were previously
provided for the same 1988 interaction for between- and
within-treatment differences.

   The interaction of predator exclusion by seedbed
condition was significant in both years. In 1989, however,
a burned seedbed treatment was added. Again there was a
high mean difference in the within-treatment emergence of
whitebark pine between mineral and litter on exclude birds
and rodents (EA) treatments in 1989 (Figure 8B). Increased
precipitation is probably why emergence was higher on
mineral seedbeds on both EA and ER treatments in 1989.

   Although there was no significant effect of seedbed
in 1988, emergence differences due to seedbed preparation
increased slightly on the exclude rodents only (ER)
treatments in 1989 (Figures 7B and 8B). Whitebark
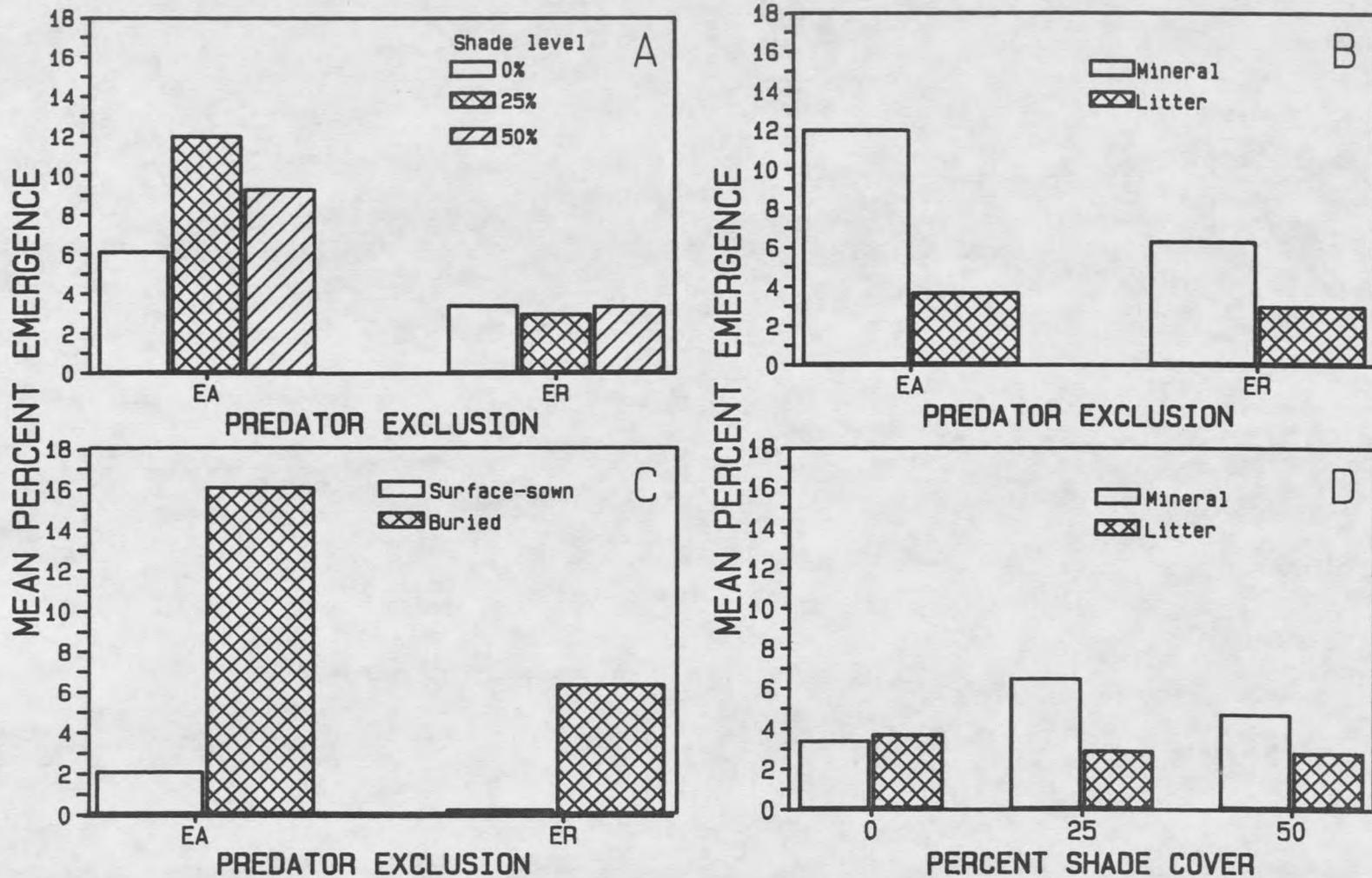emergence on burned and litter treatments remained low in
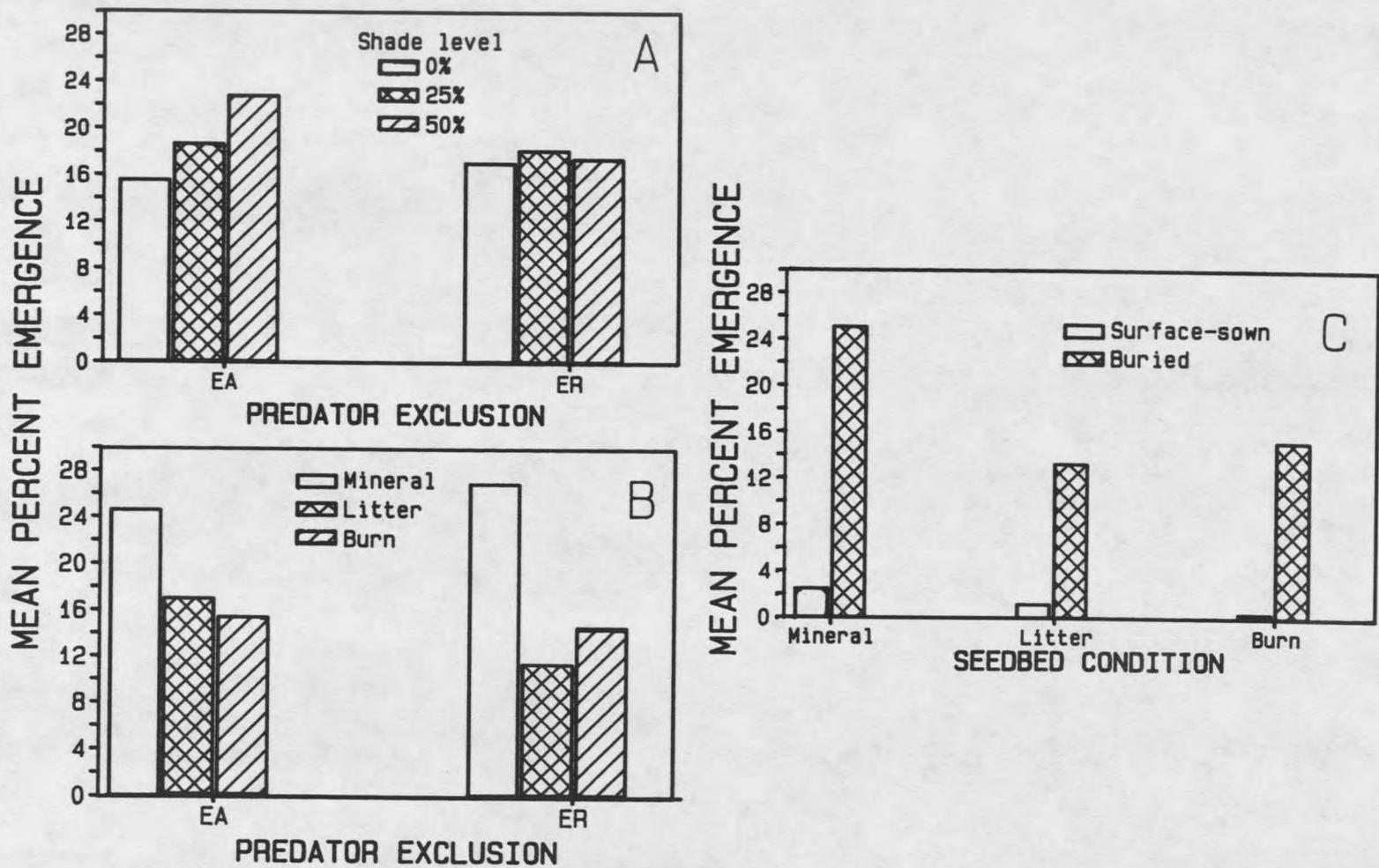
Figure 8. Two-factor interactions of the 1989 biotic and microsite factors affecting whitebark emergence: predator exclusion by shade level (A), seedbed condition (B), and seedbed condition by sowing depth (C).

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1989 on both EA and ER treatments. There was no difference
in emergence between predation treatments in 1989 when
precipitation was near normal and evenly distributed
throughout the growing season.

Seedbed condition by sowing depth was a significant
interaction of emergence of whitebark pine in 1989.
Seedbed condition significantly affected emergence of
buried whitebark seeds and had no affect on surface sown
seeds. Buried whitebark seeds had higher emergence than
did surface sown seeds on mineral, litter, and burned
seedbeds (Figure 8C). Germination of surface-sown seeds
was less than 4% on mineral seedbeds, decreasing slightly
from mineral to litter (2%) to burned seedbeds (1.5%).
Emergence of buried seeds was 26% on mineral seedbeds and
decreased to near 15% for seeds buried on litter and
burned seedbeds.

Delayed Emergence

I call germination in the second or third year
"delayed emergence". Here, delayed emergence is the ratio
of 1989 emergents to the number of seeds that did not
germinate in 1988. Plots seeded in 1987 were examined for
emergence in 1988 and again in 1989 to measure whitebark
pine delayed emergence. Germination of the European

equivalent of whitebark pine (Pinus cembra)(Critchfield
and Little 1966) may be delayed until the second or even
third year after dispersal (Krugman and Jenkinson 1974).

More of the seeds sown in 1987 emerged in 1989 than
in 1988 (Table 7). Of seeds sown in 1987 the 14.6%
emergence in the second summer was significantly more than
first-year emergence in 1988 (4.5%) and in 1989 (10.2%).

The high dormancy rate of 1987 sown seeds in 1988 may
have been due to drought enforcement. High delayed
emergence of 1987 sown seed (higher in relative terms than
first-year emergence in 1989) was observed under most main
factor levels.

The higher delayed emergence of whitebark over
first-year emergence may be due to impermeable seed coat,
the presence of physiological embryo dormancy (Pitel and
Wang 1980), or a combination of these and other unknown
factors. Physiological embryo dormancy is usually overcome
by certain metabolic events resulting in decreased
inhibitor and increased growth promoter content, increased
energy charge, and derepression and activation of the
genome and increased protein synthesis (Kahn 1977). This
study does not evaluate specific reasons for delayed
emergence.

Table 8.   Effects of biotic and microsite factors and
            significant interactions on delayed 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	0.1054	0.0527	2.86	.0650
Predator exclusion	1	0.1666	0.1666	9.05	.0038
Shade	2	0.1439	0.0720	3.91	.0253
Seedbed condition	1	0.0112	0.0112	0.61	.4380
Sowing depth	1	4.9561	4.9561	269.29	.0001
Pred x Shade	2	0.1033	0.0517	2.81	.0683
Pred x Sow	1	0.3514	0.3514	19.09	.0001
Bed x Sow	1	0.4317	0.4317	23.45	.0001
Error	60	1.1043	0.0184		
Total	71	7.3738			

Delayed whitebark emergence varied significantly

between predator exclusion treatments, shade cover, sowing

depth, and replicate (Table 8).   Seedbed condition did not

affect delayed emergence as it did first-year emergence in

both 1988 and 1989.

To determine the natural occurrence of this phenomena

I looked for delayed emergence in the field.   Seedling

clusters on the study site were dug up and intact seeds

were taken to the laboratory.   X-ray analysis showed that

75% (12 seeds) of the intact non-germinated seeds had

fully developed endosperms.   The filled seeds were

cold-moist stratified for 30 days (simulating a second

year of natural stratification) and put in germination

chambers under temperature and moisture conditions

recommended by Jacobs and Weaver (1990).   Germination was

75% for the filled seeds. Rates of delayed whitebark germination appear to be higher than for first-year germination.

Predator Exclusion

Screen design significantly affected delayed germination and emergence as it affected first-year emergence in both 1988 and 1989. Delayed emergence on exclude rodents only treatments (30.5%) was significantly higher than on the exclude birds and rodents treatment (20.9%), the opposite of first-year emergence (Table 7). Delayed emergence rates for both predator treatments were expected to be similar to 1989 first-year emergence because of the moderating effect of higher 1989 precipitation. I can offer no reason why the effect of predator exclusion on emergence in 1988 was reversed for the 1989 delayed emergents.

Shade Cover

Whitebark emergence was significantly higher for shaded than nonshaded treatments for both delayed (Table 8) and first-year emergence in 1989 (Table 7). Increased precipitation in 1989 probably reduced the effect of summer drought on germination, enhancing the effect of shade.

Sowing Depth

Delayed emergence was significantly higher than first-year emergence in both 1988 and 1989 (Table 8) for surface-sown and buried whitebark seeds. Delayed emergence of buried seeds was significantly higher (45.4%) than surface sown seeds (6%)(Table 7).

Replicate

Replicate 1 had significantly less delayed emergence than replicates 2 and 3 (Table 7). While lower first-year emergence in replicate 3 may be explained by textural and soil horizon differences as previously described, I cannot explain why delayed emergence is lowest on replicate 1.

Interactions

Three two-factor interactions of biotic and microsite factors affected delayed emergence of whitebark pine in 1989 (Table 8); predator exclusion by shade level (B) (p=0.0683) and sowing depth (B) (p=0.0001) and seedbed condition by sowing depth (C) (p=0.0001) (Figure 9). The number of delayed emergents was higher on ER than EA treatments for 0% and 25% shade cover and did not change between treatments for 50% shade cover (Figure 9A). Higher delayed emergence on ER treatments was reversed from first-year emergence in 1988 when EA treatments had higher emergence for all three shade treatments.
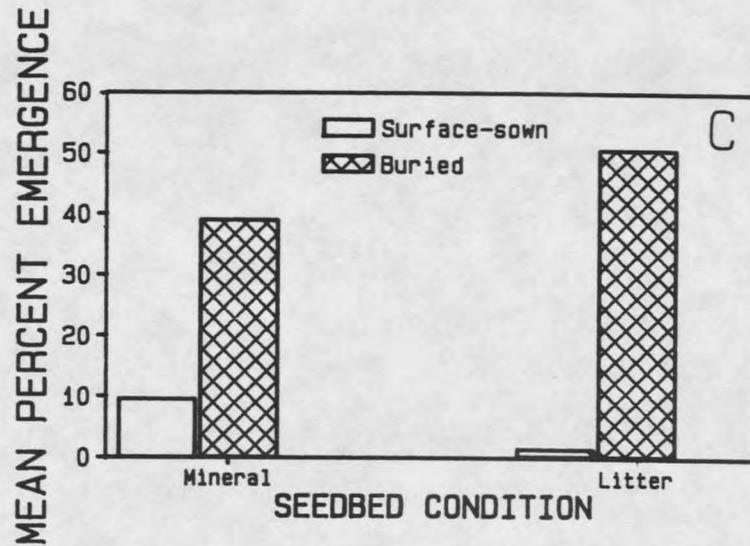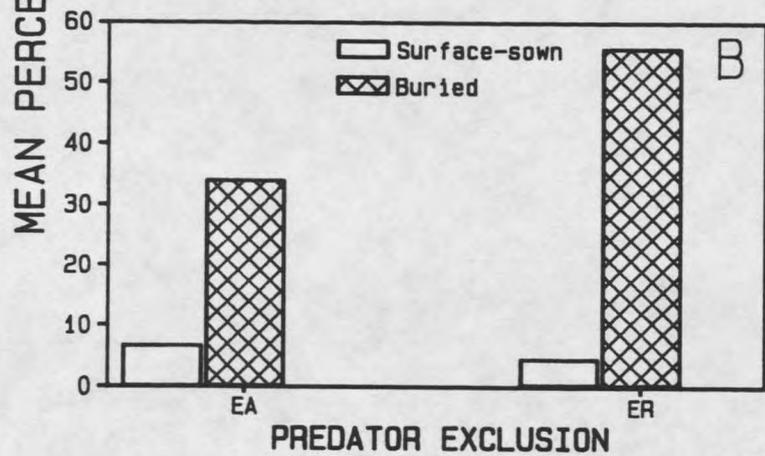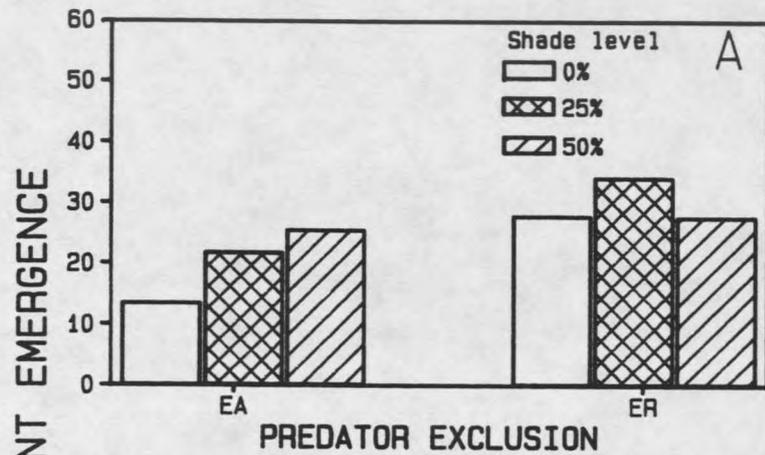
Figure 9. Two-factor interactions of the 1989 biotic and microsite factors affecting delayed emergence of whitebark pine: predator exclusion by shade level (A), and sowing depth (B) and seedbed condition by sowing depth (C).

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First-year emergence in 1989 was the same for 0% and 25% and decreased for 50% shade cover between EA and ER treatments. Precipitation could have caused the between-year differences in emergence but I do not know why 1989 emergence patterns for delayed and first-year emergents were different.

Delayed emergence of whitebark varied significantly within predator exclusion treatment for both buried and surface-sown seeds and between exclusion treatments for buried seeds (Figure 9B). In 1988 first-year emergence was higher on EA treatments. Delayed emergence of buried seeds was significantly higher on ER than EA treatments because more seeds had enforced dormancy in 1988 on the ER treatment.

Buried whitebark seeds had more delayed emergence than surface-sown seeds on mineral and litter seedbeds (Figure 9C). Delayed emergence was 10.2% and 39.7% on mineral and 1.9% and 51.3% on litter seedbeds for surface-sown and buried seeds respectively. Delayed emergence of surface-sown seeds was lower on litter than on mineral seedbeds but the relationship was reversed for buried seeds. The increase in delayed emergence for buried seeds and decrease in surface-sown seeds could be due to a measurement error. The 1987 surface-sown seeds were positioned close to buried seeds (Figure 3). Winter and summer rains moved and partially buried many

surface-sown seeds. When seeds emerged it was difficult
to distinguish if they had originally been a surface-sown
or a buried seed. Sowing depth treatments were separated
in 1988 to eliminate or reduce the overlapping of sowing
types (Figure 3). It was impossible to stop the natural
burying of surface-sown seeds by snow, water, and winds.

Mortality

Whitebark pine emergence rates were high from mid-June
through the end of July, slowed, and were nil in August
(Figure 4). Mortality of first-year whitebark seedlings
followed the same pattern with the highest mortality rates
occurring when emergence was highest (Figure 10). Both
rates decreased after the first of August. Through the
first of August emergence was always greater than mortality
so there was a net accumulation of surviving seedlings.
Germinants continued to emerge from early August until the
first of September but the total numbers of survivors
remained constant because mortality rates equaled emergence
rates.

Mortality began near the end of June and continued at
a low level until early September (Figure 10). Three
causes of mortality were identified: (1) insolation (heat
scorching of seedling stem at ground surface), (2) drought
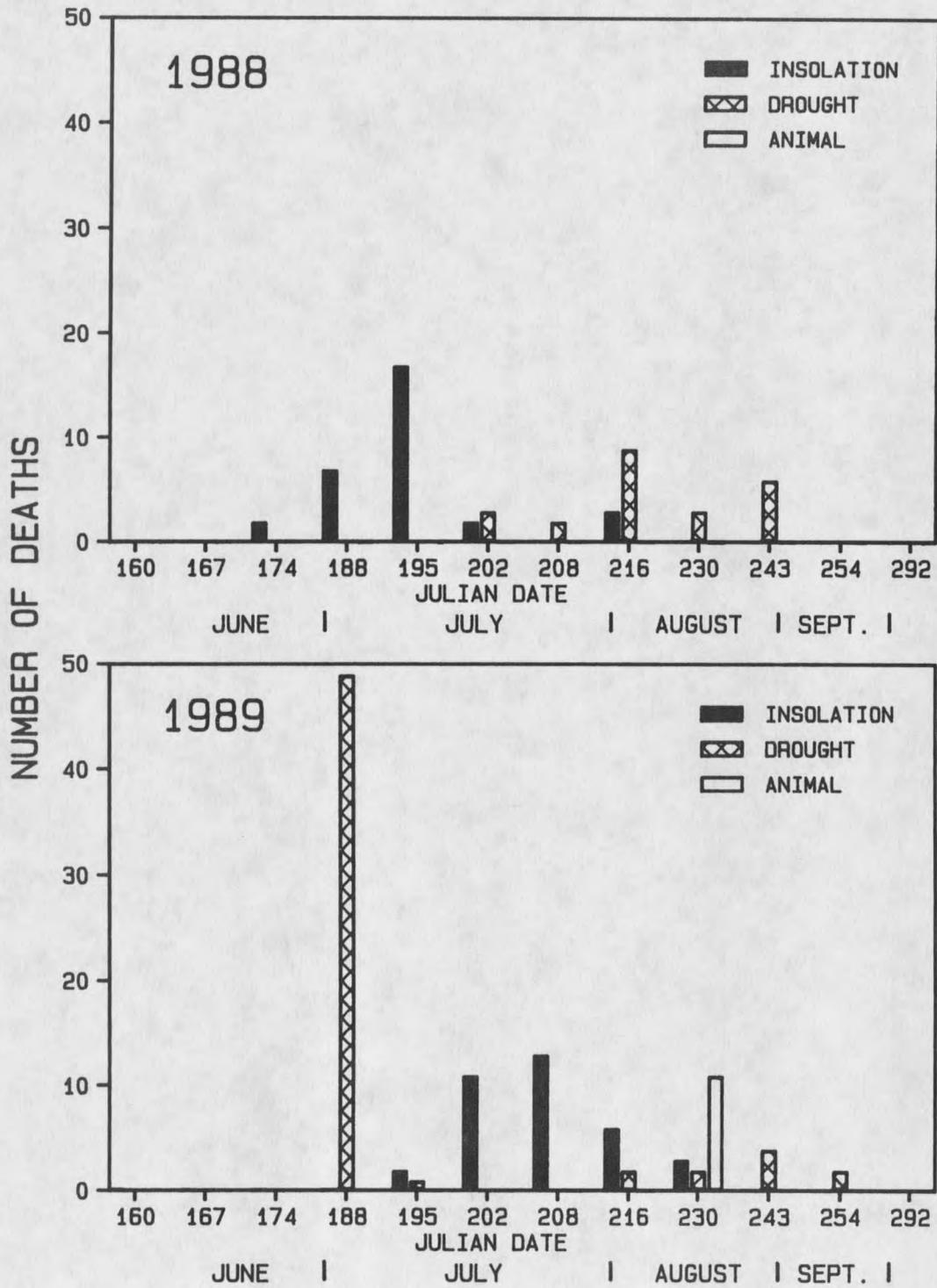
Figure 10.   First-year mortality of whitebark pine
            seedlings by cause over time.

(drying out of seedling), and (3) animal (burial, uprooting, or nipping). Fungi and insect caused mortality were never seen on whitebark seedlings.

Insolation mortality of 1988 emergents began in late June when day lengths were the longest and ended by early August (Figure 10). Insolation mortality slowed during late July and ended around mid-August in 1988 and 1989.

Drought mortality occurred later in the growing season than insolation--except in early July of 1989 when higher numbers of whitebark emergents died from drought than insolation (Figure 10B). Most of the first emergents dying from drought were surface germinated seeds. This was probably due to the fact that roots of surface-sown seeds have a greater distance to reach the more dependable water supplies of mineral soil. Drought mortality of seedlings germinated from buried whitebark seeds began around the third week in July and continued until the first of September.

The only animal caused mortality observed was in 1989 when 11 seedlings were buried by soil brought to the surface by pocket gopher activity. There was no evidence of pocket gophers feeding on seeds or seedlings.

Increased survival of buried seeds compared to surface-sown seeds was evident in both years and more so in moist 1989 than in dry 1988 (Figure 11). Only surface-sown seeds lying on favorable microsites germinated

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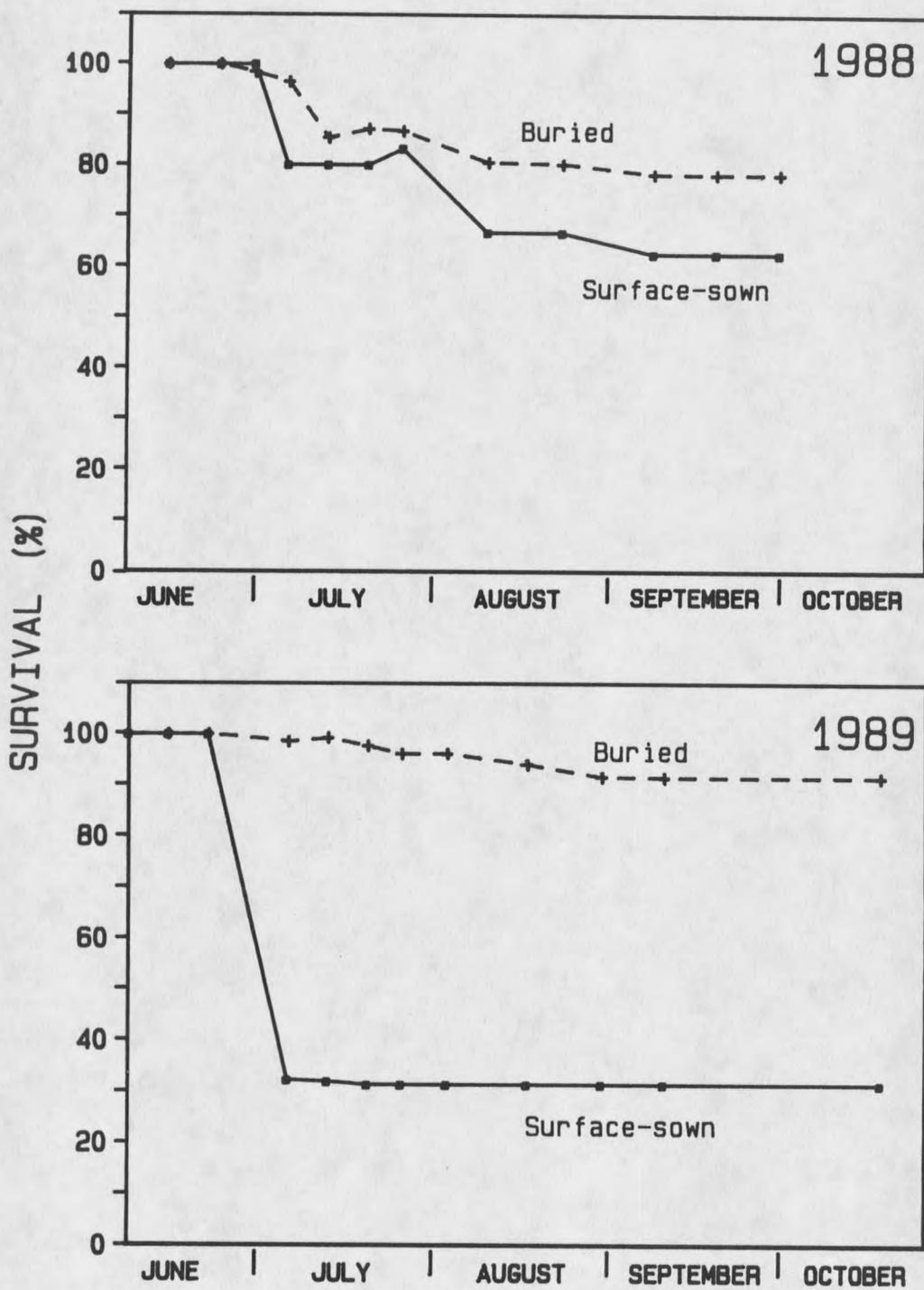
Figure 11. Survival of whitebark pine seedlings germinated from buried and surface sown seeds.

Table 9.   Mortality of 1988 and 1989 whitebark pine
emergents on mineral and litter seedbeds under
0%, 25%, and 50% shade.   Mortality is the
percent of emergents in each category that died.

Year	Percent shade	Seedbed condition	Insolation	Drought	Animal	Total
				percent		
1988	0	Mineral	33	11	0	44
		Litter	23	6	0	29
	25	Mineral	6	8	0	14
		Litter	0	29	0	29
	50	Mineral	5	12	0	17
		Litter	9	22	0	31
1989	0	Mineral	1	2	0	3
		Litter	10	4	0	14
		Burned	14	6	0	19
	25	Mineral	3	5	0	8
		Litter	2	2	0	4
		Burned	6	4	0	10
	50	Mineral	1	4	6	11
		Litter	0	17	0	17
		Burned	0	7	0	7

when moisture was limiting in 1988 and thus many survived.
The high precipitation of 1989 resulted in a four-fold
increase over 1988 in the number of emergents from
surface-sown seed.   Many surface-sown seeds germinated in
1989 because of increased precipitation, but because of
unfavorable microsites most may have succumbed to drought.

Shade helped reduce seedling mortality in 1988 but
not in 1989 (Table 9).   And shading influenced the type of
mortality on mineral, litter, and burned seedbeds.
Insolation mortality of seedlings was highest on seedbeds
with no shade cover in 1988; shading of as little as 25%

Table 10.   Maximum surface temperatures recorded on
             mineral, litter, and burned seedbeds under 0%,
             25%, and 50% shade cover in 1988 and 1989.
             There was no burned treatment in 1988.

Year	Seedbed condition	No. of obs.	Percent shade cover		
			0	25	50
			°C		
1988	Mineral	18	65	59	59
	Litter	18	73	65	73[1]
1989	Mineral	27	59	52	52
	Litter	27	73	65	65
	Burned	27	79	65	73

[1] This high temperature was an anomaly because wax
    temperature pellets were exposed to the sun.

decreased insolation mortality (Table 9).   Insolation

mortality on mineral seedbeds was higher than for litter

seedbeds despite higher surface temperatures on litter

(Table 10).

     In 1989, insolation mortality of whitebark pine

seedlings was highest on burned (14), second highest on

litter (10), and lowest on mineral seedbeds (1) in the

absence of shade cover (Table 9).   Shade reduced surface

temperatures (Table 10) and decreased seedling mortality

due to insolation.   Insolation mortality averaged 8.3%,

3.6%, and 0.3% under 0%, 25%, and 50% shade respectively

(Table 9).

     Drought mortality of whitebark pine seedlings was

lowest on nonshaded plots in 1988.   It was lower on both

0% and 25% shade covered plots in 1989 (Table 9).   As

shade increased drought mortality increased, perhaps

because shading reduced soil moisture under shade coverings by deflecting rain (Figures 12 and 13). This is consistent with the fact that nonshaded plots were moister than shaded plots during the mid-summer weeks when most drought mortality was occurring. No deflection of rain by shade covers may account for higher soil moisture values on open plots.

On non-predation plots (EA and ER) at the end of the second growing season, 81% of the whitebark pine seedlings that had germinated and survived the first growing season were still alive. There were nearly five times more seedlings on EA and ER plots than on EB and EN plots; these seedlings were protected, however, from animal predation thus giving unnaturally low mortality results.

A more realistic picture of natural mortality is obtained from EB and EN treatments allowing both the effects of climate and predation on seedlings. Mortality counts for whitebark pine seedlings were taken in the spring and fall of 1989. Nearly 58% of the seedlings survived the first winter on EB and EN treatments. There was no mortality on these treatments during the 1989 growing season. Of the overwinter mortality, the causes for whitebark seedling loss were: insolation - (0%), drought - (0%), animal - (6%), and unknown - (94%). One seedling was nipped by rodents and five were buried by
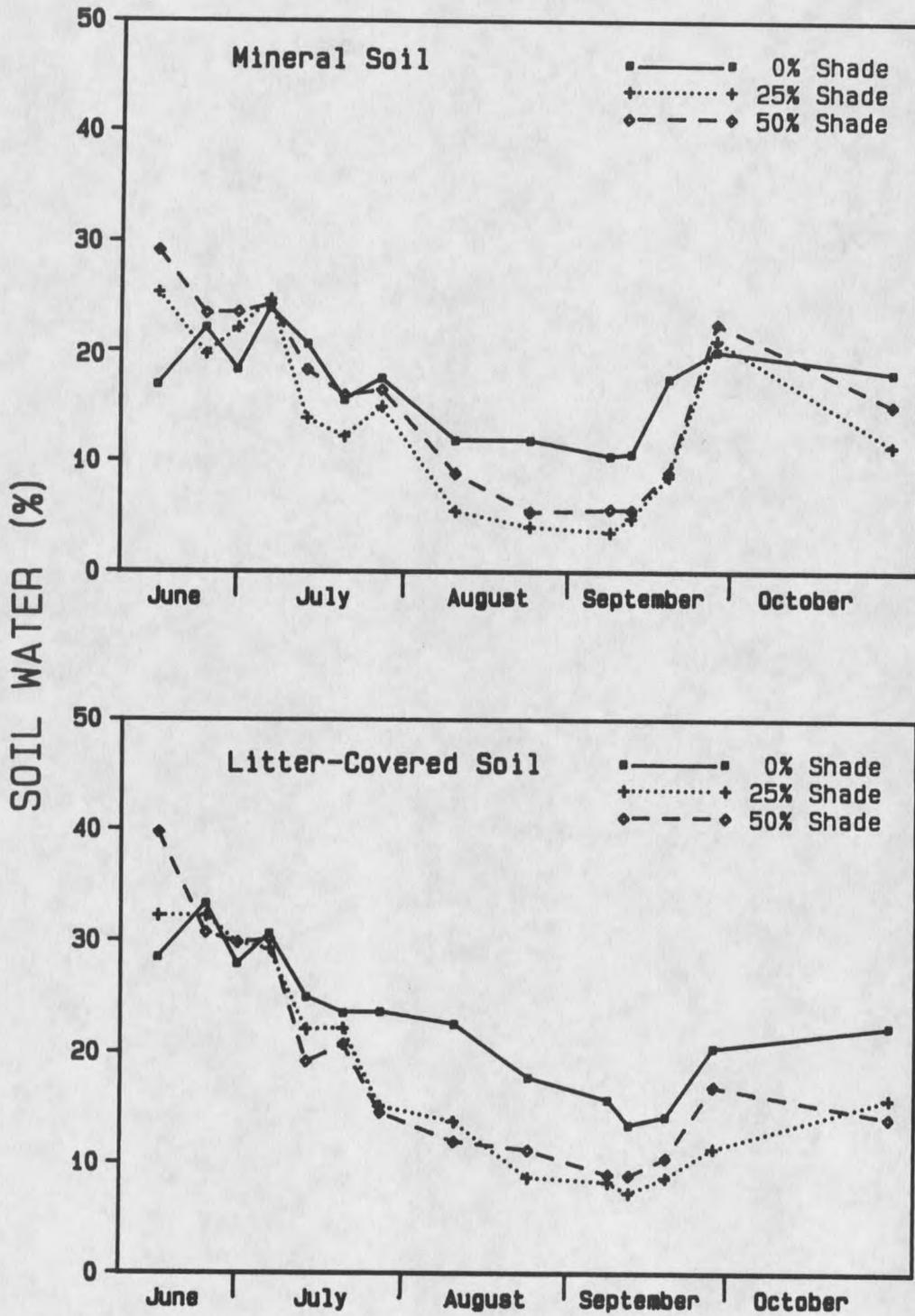
Figure 12. Percent moisture in top 5 cm of soil on
            mineral and litter seedbeds under 0%, 25%, and
            50% shade in 1988.
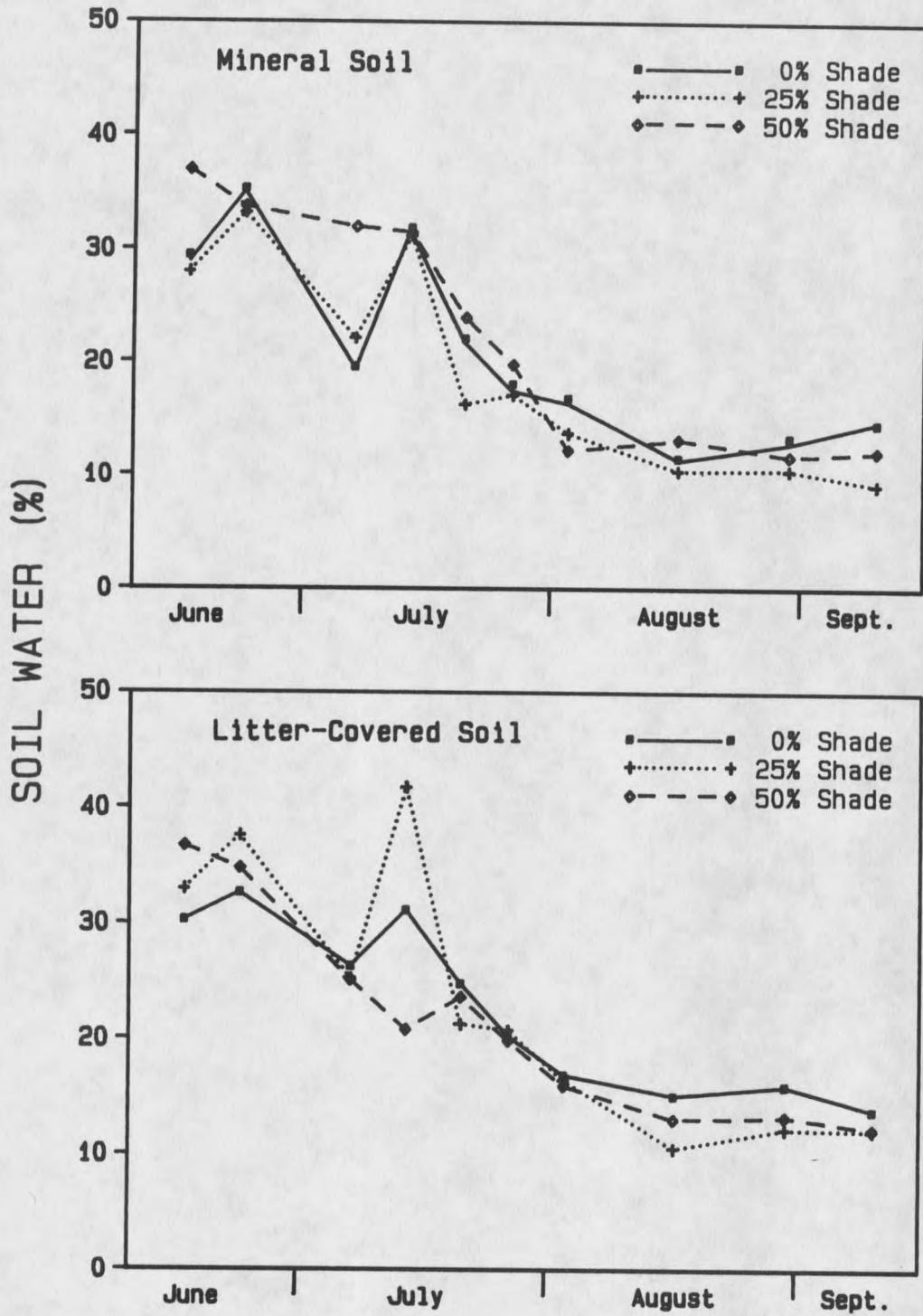
Figure 13.   Percent moisture in top 5 cm of soil on
              mineral and litter seedbeds under 0%, 25%, and
              50% shade in 1989.

pocket gophers. Causes of winter mortality could not be determined because the area is covered by approximately 60 to 150 cm of snow.

Subsurface Soil Temperatures

Germination of seeds depends largely on soil temperature and moisture conditions (Fitter and Hay 1981). Germination of whitebark occurs between 10° and 40°C, has an optimum range for germination enhancement from 15° to 35°C, and peaks at 35°C (Jacobs and Weaver 1990). Moisture is not a limiting factor in laboratory studies; however, when soil temperatures in the field reach 35°C, moisture probably becomes the factor limiting germination.

Minimum subsurface temperatures were generally warmer with increased shade cover, indicating a moderating effect of treatment on soil temperature (Table 11). In general, mineral seedbeds generally had relatively low minimum temperatures and high maximum temperatures; litter mulch moderated soil temperature swings. Temperature variation between shade levels was high for maximum and low for minimum subsurface temperatures throughout the growing season (Figures 14 and 15). Maximum temperatures of around 38°C occurred near the first of August when soil moisture was approximately 50% of field capacity (Figures 12 and 13).

Table 11. Minimum-maximum soil temperatures at a depth of
           2.5 cm on mineral and litter seedbeds under 0%,
           25%, and 50% shade cover--1988 and 1989.
           Values in parentheses are mean minima and
           maxima for the summer.

Year	Seedbed condition	Temperature	Percent shade cover		
			0	25	50
			------- °C -------		
1988	Mineral	Minimum	-12(1)	- 8(3)	- 7(1)
		Maximum	37(26)	28(20)	29(23)
	Litter	Minimum	- 9(2)	- 8(2)	- 7(2)
		Maximum	27(23)	24(19)	28(21)
1989	Mineral	Minimum	-12(-2)	- 8(-1)	- 9(-1)
		Maximum	36(25)	26(22)	29(23)
	Litter	Minimum	- 9(-1)	- 8(-1)	-11(0)
		Maximum	29(23)	30(20)	23(17)
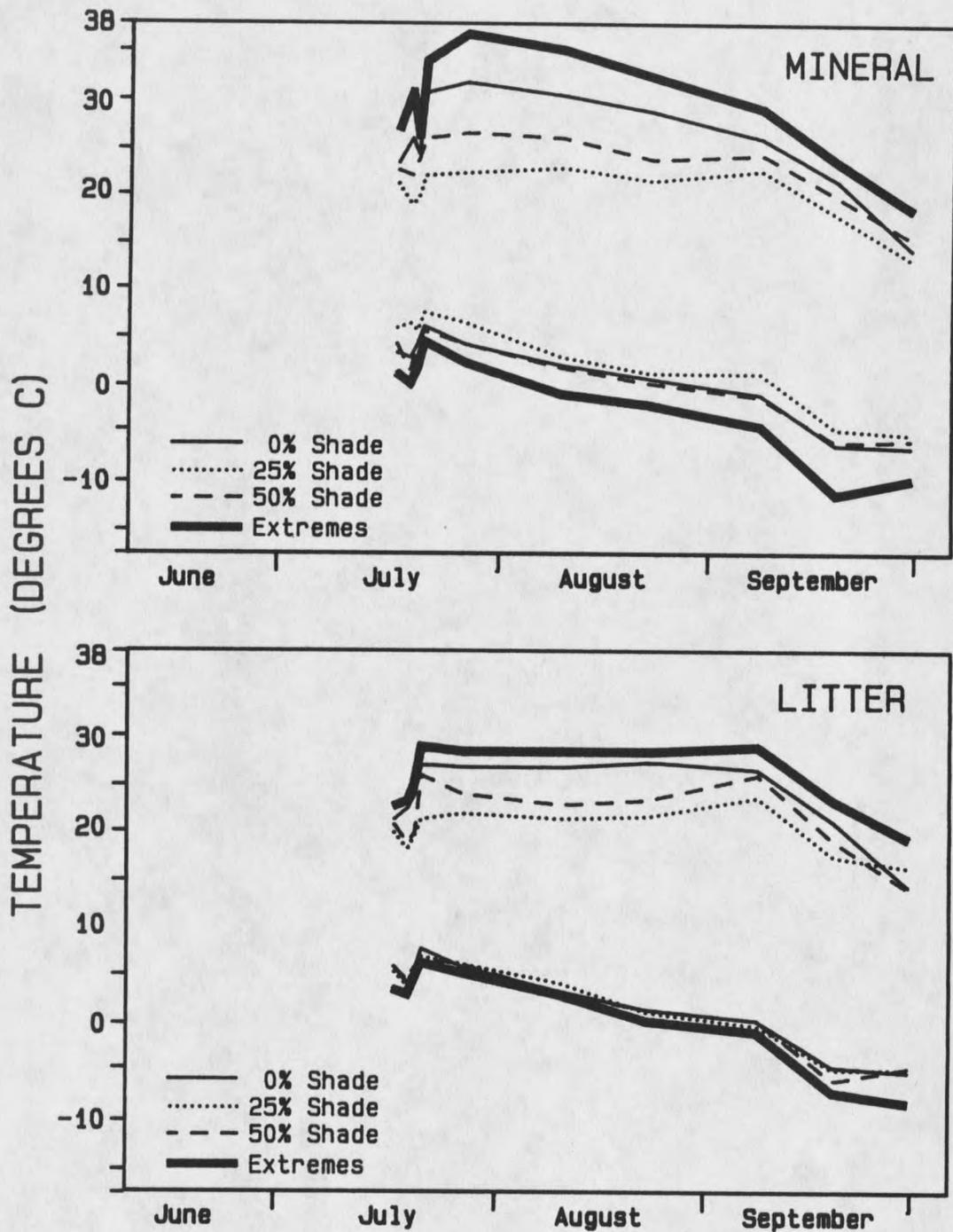
Figure 14. Mean minimum-maximum soil temperatures at a depth of 2.5 cm on mineral and litter seedbeds under 0%, 25%, and 50% shade cover by date for 1988. Bold lines represent the minimum and maximum temperatures recorded.
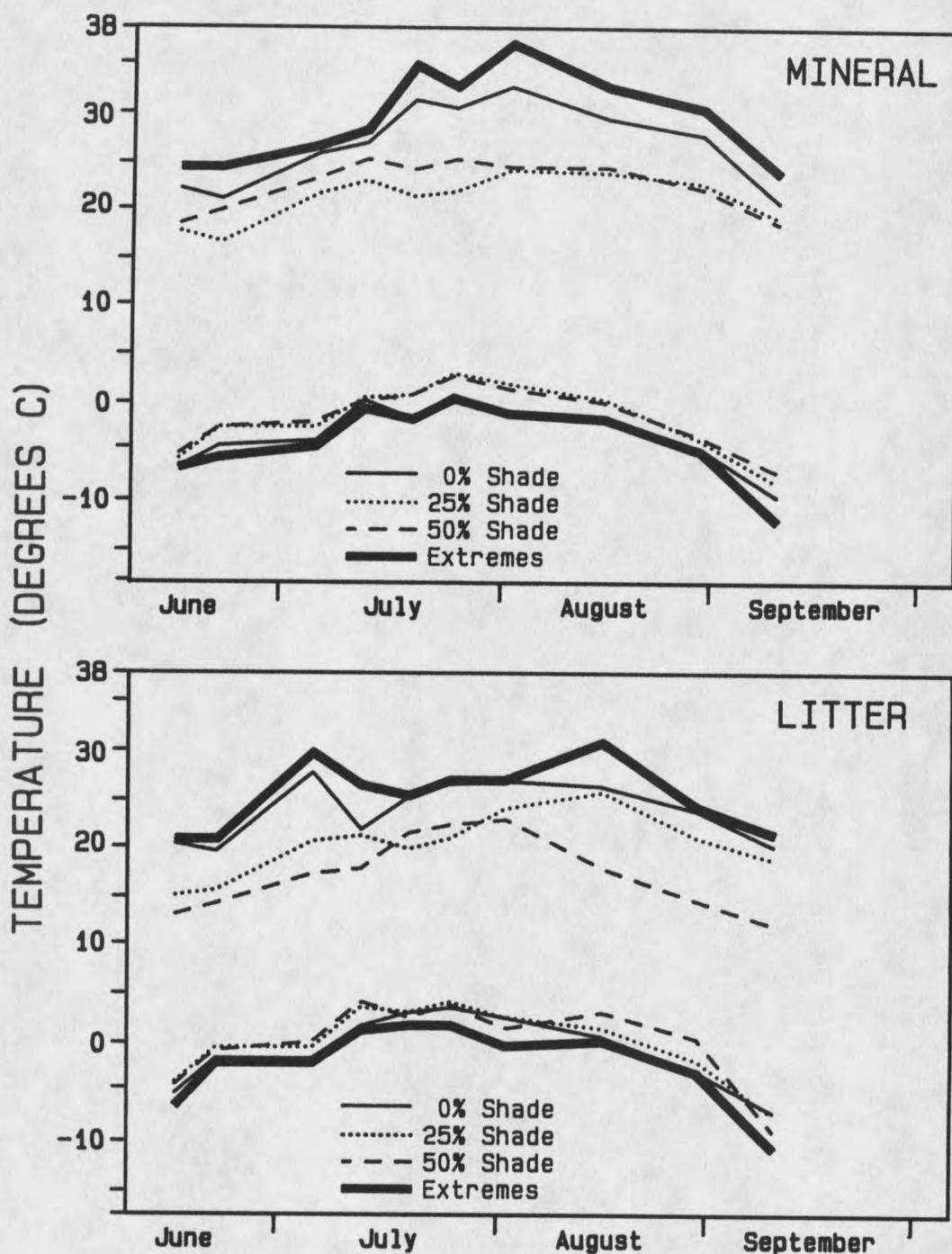
Figure 15. Mean minimum-maximum soil temperatures at a depth of 2.5 cm on mineral and litter seedbeds under 0%, 25%, and 50% shade cover by date for 1989. Bold lines represent the minimum and maximum temperatures recorded.

CHAPTER 4

CONCLUSIONS

Seed survival, germination, and seedling survival of whitebark pine are affected by biotic and microsite factors including predation, shade cover, seedbed, and sowing depth.

Seed Losses

Evaluation of seed losses from predation indicate that:

1. Where it is accessible to them rodents removed essentially all surface-sown and most buried seeds. Survivors germinate the first and second year after planting. Mammals would probably have found fewer buried seeds if nearby surface-sown seeds had not acted as an attractant and, if so, the number of emergents would have been greater.

2. Avian predators did not remove whitebark seeds exposed on the ground. Seed security must have resulted from the inability of the birds to detect the seeds. Clark's

nutcrackers were observed sitting on several exclosures, but none were seen foraging for seed inside exclosures open to birds.

Emergence

Emergence of first-year and delayed whitebark pine is affected by sowing depth, seedbed condition, and shade cover, in decreasing order of significance. The collective effects of those factors were different for seeds that germinated the first summer after seeding than for those that carried over germinated in the second summer (delayed emergence). Results from this study indicate that:

1. Probably due to microclimate effects, emergence rate of whitebark seeds is higher on treatments that exclude birds and rodents than on exclude rodents only treatments. Both these treatments protected all sown seeds from predation. The overtopping screen likely modified the microsite climate on treatments that exclude birds and rodents by retaining heat during the nights and reducing temperatures during the day.

2. More sound whitebark pine seed germinated in the
second (delayed emergence) than in the first spring after
planting. Emergence differences between delayed and
first-year emergence within a year are attributed to a
dormancy delay.

3. First-year emergence was higher in moist 1989 than in
dry 1988. The low germination of 1988 is attributed to
drought enforcement.

4. When predation is eliminated emergence of buried seeds
is significantly higher than that of surface-sown seed.
In the field this effect will be magnified because few
surface-sown seeds escape mammal predation.

5. Emergence of surface-sown seeds occurs immediately
after snow melt and ends by late June. Buried seeds begin
emergence later (late June) and emergence is complete by
the first of August. Most emergence is completed before
optimum soil temperatures are reached in early August.

6. Increased shade cover increases emergence of whitebark
pine seedlings. First-year emergence of whitebark is
slightly higher on shaded plots under low precipitation

conditions (1988) and significantly higher for both
first-year and delayed emergence when precipitation is
near normal (1989).

7. First-year emergence is not different between seedbed
types under non-shaded conditions, but it is significantly
higher on shaded-mineral than on shaded-litter seedbeds.
There was no interaction of shade cover and seedbed
condition for delayed emergents.

8. First-year emergence was affected by soil conditions.
Emergence was lower on sandy soils with only a thin
A horizon than on soils with both A and B horizons.
Delayed emergence was not affected by seedbed condition.

Mortality

Mortality of whitebark pine emergents switches from
insolation to drought to animal causation as the year
progresses. Mortality results indicate that:

1. On nonpredation plots seedling mortality during the
first growing season was due to drought (10% and 6%),
insolation (13% and 3%), and animals (0% and 1%) for 1988
and 1989 respectively. Animals caused mortality by
burying seedlings with soil brought to the surface by
pocket gophers.

2.   Shade cover generally decreased insolation mortality.
Insolation mortality begins in late June when sun angle is
highest, peaks in July and ceased in early August.

3.   Surface germinated seedlings usually died from drought
before the start of insolation mortality. Radicle
extension is apparently too slow to ensure establishment
unless the seed are located on ideal microsites.

4.   Increasing shade cover increased drought mortality.
Shade covers may intercept precipitation, a critical
resource in dry 1988.

5.   Survival of surface-sown seeds is lower than for
buried seeds with most mortality occurring immediately
after germination.

6.   Most first-year mortality occurs during the winter
months but, due to winter inaccessibility of the site, its
cause is unknown.

This study provides information on the regeneration
process of whitebark pine that will help forest managers
and researchers. For example, we now know how much seed
loss is due to predation; when and how much emergence
occurs in dry and near normal precipitation years; how

much shade, which seedbed, and what sowing depth is best for whitebark emergence; that whitebark seeds can delay emergence for at least 2 years; and that several mortality factors affect first-year seedling survival.

Several questions remain: Which habitat type-aspect-elevational combinations are best for whitebark germination, survival, and growth? What are the seed transfer limits for whitebark; longitudinally, latitudinally, and elevational? Will the effect of burning on whitebark emergence be more beneficial over time as it is for other subalpine species (Fiedler 1980)? Will whitebark germinate after 3 or more years of dormancy?

Results from this study are preliminary but begin to explain seed germination and seedling survival characteristics of whitebark pine and also point out the need for additional information. Even though these results are not complete we now know that we can artificially regenerate whitebark pine by placing seeds 5 cm deep in mineral soil seedbeds. Fall planting will provide natural stratification conditions. We also know that to be more successful we should provide 25% to 50% shade to aid seed germination and seedling survival. Shelterwood cuttings could be used to provide these shade conditions. Because seed-eating rodents are attracted to concentrations of seeds, we should sow seeds at least 1 m apart and that we should plant at least 15 times more

seeds than the number of trees we eventually want

established on the area. We should wait at least 2 years

before accessing regeneration results from first-year and

delayed emergence. It should be recognized that these

results are preliminary, that more results will be

forthcoming, and that these recommendations may change to

reflect future results.

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APPENDIX

Table 12. Precipitation based on inches of accumulated water per month for the hydrologic years 1987, 1988, and 1989 at the Canyon weather station in Yellowstone National Park, Wyoming. Data supplied by the Soil Conservation Service.

Year	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total
							— inches$^{1/}$ —						
1987	0.6	3.9	0.3	2.3	1.4	1.5	0.4	4.4	1.6	4.0	1.0	0.2	21.6
	(33)	(155)	(12)	(78)	(65)	(64)	(21)	(167)	(61)	(222)	(47)	(9)	(78)
1988	0.4	1.9	2.6	3.3	2.5	2.5	3.3	2.4	0.5	0.2	0.4	1.2	21.2
	(22)	(76)	(100)	(112)	(116)	(107)	(173)	(91)	(19)	(11)	(19)	(51)	(76)
1989	0.2	4.1	1.7	3.8	2.0	5.7	1.6	3.2	1.3	1.4	2.0	0.7	27.7
	(11)	(163)	(66)	(129)	(93)	(244)	(84)	(121)	(49)	(78)	(94)	(30)	(100)
29 yr Average	1.80	2.51	2.59	2.95	2.16	2.34	1.91	2.64	2.63	1.80	2.13	2.34	27.81

$^{1/}$ Values in parentheses are the percent of accumulated precipitation in relation to the long-term average for that month or total.

Table 13. Precipitation based on inches of accumulated water per month for the hydrologic years 1987, 1988, and 1989 at the Mill Creek weather station on the Gallatin National Forest. Data supplied by the Soil Conservation Service.

Year	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total
	- - - - - - - - - - - - - - - - - - inches[1/] -												
1987	0.5	1.6	0.3	1.1	0.8	2.0	1.2	4.3	1.8	3.9	3.4	0.4	21.3
	(33)	(90)	(15)	(57)	(55)	(79)	(56)	(107)	(70)	(175)	(209)	(18)	
1988	0.5	0.6	1.6	1.9	2.3	2.9	3.4	5.3	1.2	0.9	0.1	0.7	21.4
	(33)	(34)	(78)	(99)	(158)	(114)	(157)	(132)	(47)	(40)	(<1)	(32)	
1989	1.8	2.4	1.0	1.7	1.3	2.8	1.3	6.3	2.9	2.0	1.3	1.8	26.6
	(120)	(135)	(49)	(89)	(89)	(110)	(60)	(156)	(112)	(90)	(80)	(83)	
16 yr Average	1.50	1.78	2.06	1.92	1.46	2.54	2.16	4.03	2.58	2.23	1.63	2.18	26.06

[1/] Values in parentheses are the percent of accumulated precipitation in relation to the long-term average for that month or total.

Table 14. 1988 analysis of variance results showing significance of biotic and microsite factors and two-factor interactions on cumulative percent emergence (arc sine of the square root of proportion transformation) of whitebark pine for each recording date.

Factors and interactions	Probability of 'F' by Date [1]											
	6/16	6/25	7/1	7/7	7/14	7/21	7/28	8/11	8/24	9/9	9/20	10/1
Predator exclusion	.1699	.0035	.0003	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Shade cover	.6063	.3434	.4613	.6064	.4770	.3384	.2901	.2752	.2521	.2483	.2483	.2483
Seedbed condition	.1077	.0102	.0139	.0223	.0190	.0091	.0147	.0199	.0221	.0055	.0055	.0055
Sowing depth	.1077	.1323	.0005	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Replicate	.1298	.0519	.0032	.0022	.0007	.0004	.0002	.0001	.0002	.0001	.0001	.0001
Pred x Shade	.4225	.3660	.2452	.2278	.2090	.1881	.1506	.1431	.1651	.1466	.1466	.1466
Pred x Seed	.1699	.0149	.0308	.1252	.1842	.0763	.0539	.0567	.0599	.0494	.0494	.0494
Pred x Sow	.1699	.1730	.0266	.0048	.0045	.0034	.0042	.0032	.0069	.0144	.0144	.0144
Shade x Seed	.6063	.2516	.2015	.1033	.0602	.0598	.0639	.0733	.0995	.0544	.0544	.0544

[1] The probability values represent the significance probability associated with the F statistic.

Table 15.　　1989 analysis of variance results showing significance of biotic and microsite factors and two-factor interactions on cumulative percent emergence (arc sine of the square root of proportion transformation) of whitebark pine for each recording date.

Factors and interactions	6/9	6/17	6/23	7/7	7/14	7/21	7/27	8/4	8/18	8/31	9/11	10/19
					Probability of 'F' by Date [1]							
Predator exclusion	.0000	.9292	.7793	.0011	.0421	.0743	.0655	.1883	.3825	.3828	.3110	.3110
Shade cover	.0000	.0425	.0047	.3916	.8286	.8192	.5298	.1537	.0679	.0849	.0080	.0080
Seedbed condition	.0000	.2985	.0721	.0101	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Sowing depth	.0000	.0001	.0001	.0296	.0001	.0001	.0001	.0001	.0001	.0001	.0001	.0001
Replicate	.0000	.2090	.1176	.1192	.1216	.0723	.0447	.0651	.0888	.0979	.0736	.0736
Pred x Shade	.0000	.9027	.9481	.7268	.5722	.3875	.2634	.1844	.1749	.1315	.1618	.1618
Pred x Seed	.0000	.6179	.7614	.6825	.7192	.5355	.2600	.1371	.0646	.0690	.0477	.0477
Seed x Sow	.0000	.2985	.0202	.0011	.0001	.0001	.0001	.0001	.0001	.0001	.0015	.0015

[1] The probability values represent the significance probability associated with the F statistic.

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