

POST-FIRE REGENERATION OF Pinus albicaulis

IN WESTERN MONTANA:

PATTERNS OF OCCURRENCE

AND SITE CHARACTERISTICS

by

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Post-Fire Regeneration of Pinus albicaulis in Western Montana: Patterns of Occurrence and Site Characteristics

Thesis directed by Associate Professor Diana F. Tomback.

In 1961, a severe fire in the Bitterroot National Forest, western Montana, destroyed about 11,350 hectares of subalpine forest, which included Pinus albicaulis (whitebark pine). The devastated area became known as the Sleeping Child Burn. Because of the recent decline of populations of P. albicaulis, a major subalpine component throughout the northern Rocky Mountains (Arno 1986), regeneration of P. albicaulis in the burn is a general concern. Unlike most pines, P. albicaulis relies on a bird, Clark's nutcracker (Nucifraga columbiana), for seed dispersal. In 1987, forest regeneration within the Sleeping Child Burn was studied on 77 plots along two transects: 1) an east-west ridge exhibiting a gradient for both elevation (range 2148 m to 2182 m) and distance from a P. albicaulis seed source (range 50 m to 3650 m) (n = 63 plots), and 2) a north-south transect of greater distance from a seed source but relatively constant elevation (n = 14 plots).

Results indicated that nutcrackers have dispersed clusters of P. albicaulis seeds up to 8 km into the burn. On the ridge transect, a significant

negative correlation was found between P. albicaulis regeneration density and distance from seed source. A significant positive correlation was also found between density and elevation; it was not possible to separate the effects of elevation and distance. Neither of these correlations were significant on the north-south transect.

Regeneration patterns show that Pinus albicaulis and Pinus contorta are dominating the post-fire succession on the east-west ridge. The regeneration status of P. albicaulis in the Sleeping Child Burn indicates an advantage over its associates, Abies lasiocarpa and Picea engelmannii, and perhaps a return to the successional upper subalpine forest communities that were widespread prior to the fire suppression policies of this century.

The form and content of this abstract are approved. I recommend its publication.

Signed



Diana F. Tomback

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CHAPTER I

INTRODUCTION

Recently, there is concern that Pinus albicaulis (whitebark pine) a major component of subalpine forests in the northern Rocky Mountains, is declining in some regions (Arno 1986). Reduction of the species results from a combination of fire suppression policy, insects, and disease. While not an important timber species, P. albicaulis is now recognized as a valuable food source for wildlife because of its nutritious seeds (Tomback 1978; Kendall 1980a,b; Hutchins and Lanner 1982; Arno 1986). Also, it is the only North American member of the Cembrae subsection of the Strobus pines; species of this subsection are characterized by indehiscent cones and large, wingless seeds (Mirov 1967; Mirov and Hasbrouck 1976). All Cembrae pines are dependent upon birds of the genus Nucifraga ("nutcrackers") for seed dispersal (Lanner 1980; Tomback 1983; Tomback and Linhart, in prep.).

Arno (1986) describes the effect of fire policies on P. albicaulis. Large fires have played an important ecological role in the perpetuation of P.

albicaulis, with surface fires allowing the tree to regenerate in small openings within mixed coniferous forest and severe, stand-replacing fires giving P. albicaulis regrowth an initial advantage over more shade-tolerant species such as Abies lasiocarpa. Fire suppression beginning in the early 1900's has severely limited the size of wildfires and lengthened their intervals, thus reducing the rate at which P. albicaulis is rejuvenated. Two additional factors exacerbate the problem: insects and disease. Infestations of mountain pine beetle (Dendroctonus ponderosae) have destroyed hundreds of thousands of hectares of P. albicaulis forests in the northern Rockies since 1904. Older stands of P. albicaulis and its associate Pinus contorta are favored by mountain pine beetles, and older stands become widespread with longer fire intervals. A disease introduced from Europe, white pine blister rust (Cronartium ribicola), is also a serious threat to P. albicaulis in cool, moist mountain regions such as in western Montana, Idaho, and Washington (Arno 1986, Arno and Hoff 1989).

This study investigated the regeneration of P. albicaulis after a severe fire in 1961 that resulted in the devastation of over 11,000 hectares of subalpine forest in the Sapphire Range, Bitterroot National Forest, western Montana. The patterns of P. albicaulis

regeneration and competition from forest associates are of interest to forest managers who are concerned about losses of successional communities of P. albicaulis, once abundant in this area.

Pinus albicaulis

The following information is summarized from Arno (1986) and Arno and Hoff (1989). P. albicaulis is a haploxylon (soft) pine that ranges from British Columbia south to central California and east to western Wyoming, occurring on exposed slopes and ridges of high mountains. Found only at timberline in the north end of its distribution, P. albicaulis increases in abundance at both timberline and upper subalpine as latitude decreases. In west-central Montana, it is a major component of high elevation forests and the timberline zone between 2130 and 2830 meters. The boundary between the lower and upper subalpine is considered to be the lower limit of P. albicaulis as a major forest species (Pfister et al. 1977). This slow growing, long-lived (as much as 1000 years) conifer reaches heights of 5 - 15 meters and often exhibits a multi-trunk growth form. P. albicaulis occurs on coarse, rocky soils in climatic zones characterized by short, cool summers and cold, snowy winters. In mesic mountain ranges it favors warm dry exposures, while in semi-arid mountains it is more

abundant on cool, moist slopes.

Principally a seral component of mixed coniferous forest in the upper subalpine, and a pioneer on recently burned or disturbed sites, P. albicaulis is also a climax species on xeric sites and in severe timberline zones (Fischer and Bradley 1987). However, in the Rocky Mountains Pinus albicaulis usually associates with Picea engelmannii, Tsuga mertensiana, and Larix lyalli at high elevations bordering timberline (Wright and Bailey 1982), and with Picea engelmannii, Abies lasiocarpa, and Pinus contorta at lower elevations. On some sites bordering timberline, P. albicaulis, P. engelmannii, and A. lasiocarpa may end up as climax co-dominants (Arno and Hoff 1989). But in most subalpine areas, P. albicaulis is eventually replaced by A. lasiocarpa with P. engelmannii and P. contorta as minor components. P. albicaulis is considered to be moderately shade-tolerant. It is less tolerant than A. lasiocarpa or P. engelmannii but more tolerant than P. contorta (Arno and Hoff 1989).

As a successional species in subalpine communities, P. albicaulis is periodically regenerated by fire. The order of fire-resistance or tolerance is P. contorta > P. albicaulis > P. engelmannii > A. lasiocarpa (Fischer and Bradley 1987). Dry exposed sites and open stands offer P. albicaulis more

protection from fire than does its moderately thin bark (Mirov 1967; Mirov and Hasbrouck 1976). P. albicaulis trees shed their lower branches as they grow, preventing vertical fuel continuity that can cause surface fires to become crown fires (Romme 1982).

Fire History in the Northern Rocky Mountains

In coniferous forests of the northern Rocky Mountains, fire regimes vary from relatively frequent, light surface fires that are localized in effect, to severe crown and surface fires that burn large areas at 100 to 300 year intervals (Arno 1976, Heinselman 1978, Romme 1982, Wright and Bailey 1982, Arno and Petersen 1983). Although the calculated lengths of fire intervals vary somewhat with the method used to determine them, researchers agree that major changes have occurred in natural fire regimes due to human intervention.

Fire history in the Bitterroot National Forest is summarized by Arno and Petersen (1983). Depending upon the severity of fire and the sample size unit, estimates of fire recurrence intervals in the Bitterroot National Forest during the 300 years prior to 1910 range from a mean of 20 to 60 years on lower subalpine slopes, and 40 to 100+ years on upper subalpine. In contrast,

the approximate present fire cycle may be greater than 1000 years in both zones. The longer fire intervals are causing the dominant overstory tree species to be affected. Prior to 1900, the dominant overstory in the upper subalpine was Pinus albicaulis, followed by Pinus contorta. However, with continued fire exclusion, Abies lasiocarpa is predicted to dominate. In the lower subalpine, P. contorta and Pseudotsuga menziesii are being replaced by A. lasiocarpa.

Seed Dispersal Mechanisms

Several seed-dispersal mechanisms are found among conifers. Some cones of Pinus contorta release seeds upon ripening, while other cones are serotinous and adhere to the tree for several years, until the heat of fire opens cones and broadcasts seeds (Lotan 1975, 1976). All the cones of Abies lasiocarpa and Picea engelmannii open when ripe, disseminating seeds. Pinus contorta, Abies lasiocarpa, and Picea engelmannii are anemochores, or wind-dispersed species. These three species generally exhibit a U-shaped seed dispersal distribution across forest openings, with the quantity of seeds dispersed being greatest at the windward and leeward edges of clearings and decreasing towards the center. The dispersal curve shape for these three species is a negative exponential curve (McCaughey et

al. 1986).

Pinus albicaulis, in contrast, is one of about eight pines in the world known to be dependent upon nutcrackers and their relatives (family, Corvidae) for dissemination (Lanner 1980; Tomback 1983). The indehiscent cones, i.e., cones that do not open upon ripening, contain large, wingless seeds. Clark's nutcracker (Nucifraga columbiana) is the primary dispersal agent of P. albicaulis (Tomback 1982, 1983; Hutchins & Lanner 1982). Other western pines, P. flexilis and the pinyon pines (P. monophylla and P. edulis), are also dependent on nutcracker dispersal (Vander Wall & Balda 1977; Lanner & Vander Wall 1980). The pinyon pines (Pinus edulis) are also dispersed by pinyon jays (Gymnorhinus cyanocephalus) (Ligon 1978). This relationship has a European counterpart; four species of Cembrae pines of Eurasia are disseminated by the Eurasian nutcracker (Nucifraga caryocatactes) (Turcek and Kelso 1968). Tomback (1983) emphasizes how closely the ecology of the Eurasian Cembrae pines and P. albicaulis are tied to the two species of nutcrackers; these mutualistic associations are most likely co-evolved.

After Pinus albicaulis seeds have ripened and hardened, nutcrackers pry whole seeds from the cones with their bills and transport the seeds in a sublingual

pouch for distances of up to 12.5 km (Tomback 1982). Pouch contents can average 77 P. albicaulis seeds (Tomback 1982). Vander Wall and Balda (1977) report nutcrackers carrying pinyon seed distances of 22 km. Nutcrackers disperse pine seeds by burying clusters or "caches" of seeds in the soil, from 1 - 15 seeds per site with a mean of 3.7; many of these seeds are retrieved by nutcrackers during winter and spring when other foods are scarce (Tomback 1982). Bird dispersal affects the growth form of the trees and genetic structure of P. albicaulis populations (Linhart and Tomback 1985, Furnier et al. 1987). A multi-trunk or clustered growth form is common in P. albicaulis and a few other species dispersed by nutcrackers. Electrophoresis shows multiple trunks in adult P. albicaulis often to be composed of > 1 genotype, the result of germination from seed caches (Linhart and Tomback 1985; Furnier et al. 1987). Nutcrackers usually harvest seeds from only few trees before caching, so several of the seeds in a cache may be full or half-siblings. Even though stems within a cluster may be genetically distinct individuals, the degree of relatedness within a cluster is greater than between neighboring clusters, as caches in one area may be the result of more than one bird caching (Furnier et al. 1987).

Sleeping Child Burn

In August 1961, a lightning-strike fire burned about 11,350 hectares in the Sapphire Range of the Bitterroot National Forest in western Montana. Within a few days plant crowns were totally destroyed and the organic layer reduced to mineral ash. The devastated area became known as the Sleeping Child Burn (Lyon and Stickney 1976). The Bitterroot National Forest, on the eastern boundary of the Selway-Bitterroot Wilderness, is divided by the Bitterroot Valley into the Sapphire Range on the east and the Bitterroot Range on the west. It is an area of steep, rugged mountains with dense forest. Upper subalpine forest grows above 2130 m (Arno et al. 1985). Surface geologic formation is of granitic origin, with medium to coarse-textured, shallow, rocky soils; ancient wind-deposited ash and loess have resulted in the leeward slopes (north and east aspects) having deeper soil mantles (Arno et al. 1985).

The primary elevational range for Pinus albicaulis in the Bitterroot National Forest is within the upper subalpine forests from 2290 to 2620 m (Arno and Petersen 1983). Forest composition at lower subalpine elevations (from 2130 m up to 2290 m) is mixed-conifer species, with occasional islands of P. albicaulis. The nearest P. albicaulis seed source for

the Sleeping Child Burn is considered to be the continuous stands of cone-bearing P. albicaulis that occur primarily at elevations above 2257 m, since forest composition at lower elevations is mixed conifers with relatively few islands of P. albicaulis (Arno, personal communication). The habitat type groups for potential climax on upper subalpine slopes are: 1) Abies lasiocarpa-P. albicaulis/Vaccinium scoparium, 2) A. lasiocarpa/Luzula hitchcockii and 3) P. albicaulis-A. lasiocarpa (Pfister et al. 1977).

Hypotheses

1) Because Pinus albicaulis is a pioneer species and because of the 26 year time period following the fire, regeneration of this conifer should be advanced in the Sleeping Child Burn. 2) The patterns of P. albicaulis regeneration should be consistent with patterns of avian seed dispersal.

CHAPTER II

METHODS

Study Area

The Sleeping Child Burn covers an area about 14.5 km by 8 km in Ravalli County, approximately 80 km south-southeast of Missoula, Montana. From Hamilton, the burn is reached by travelling east on state highway 38 to Skalkahoe Rye Road. The northern boundary of the burn extends to Township 4 N and the southern boundary extends into the north half of Township 2 N. On the east and west the boundaries extend, respectively, from Range 18 W into Range 19 W. Located west of the Continental Divide, this area has an inland maritime climate. As elevation increases from valley (1220 - 1525 m) to mountaintop (2135 - 2745 m), the precipitation increases, and temperatures become cooler. Distinct differences occur between south and north aspects (Pfister et al. 1977). The south slopes are much warmer and drier, whereas north slopes experience less solar insolation, greater snow accumulations and deeper soils - resulting in cooler, moister conditions.

Annual precipitation averages 33 cm and varies with elevation and topography (Lyon 1976). Seventy percent of the precipitation above 2135 m is from snowfall. Early winter and late spring are the wettest seasons; lightning activity and low relative humidity occur in July and August, resulting in a fire season. Daily temperature ranges are greatest at low elevations and least on mountaintops. Monthly mean temperatures in the area show a slight decrease on a south-north gradient. Winds are predominantly from the west or southwest (Finklin 1983).

Field work was conducted from 3 to 26 August on two study sites in the burn. The first study was located along an east-west ridge transect, 3.65 km long, from Lost Tooth Cabin at the edge of the burn heading west to Two Meadows, approximately in the northern center of the burn. The second site was a 20.6 km north-south road transect following Skalkahoe Rye Road from the northern edge of the burn, south and then southwest on Paint Creek Road approximately through the center of the burn to its southern edge.

Study Site #1 - Ridge

The first site (Figure 1) was selected to gather data on forest regeneration patterns in the northern center of the burn. Plots were sampled along a straight

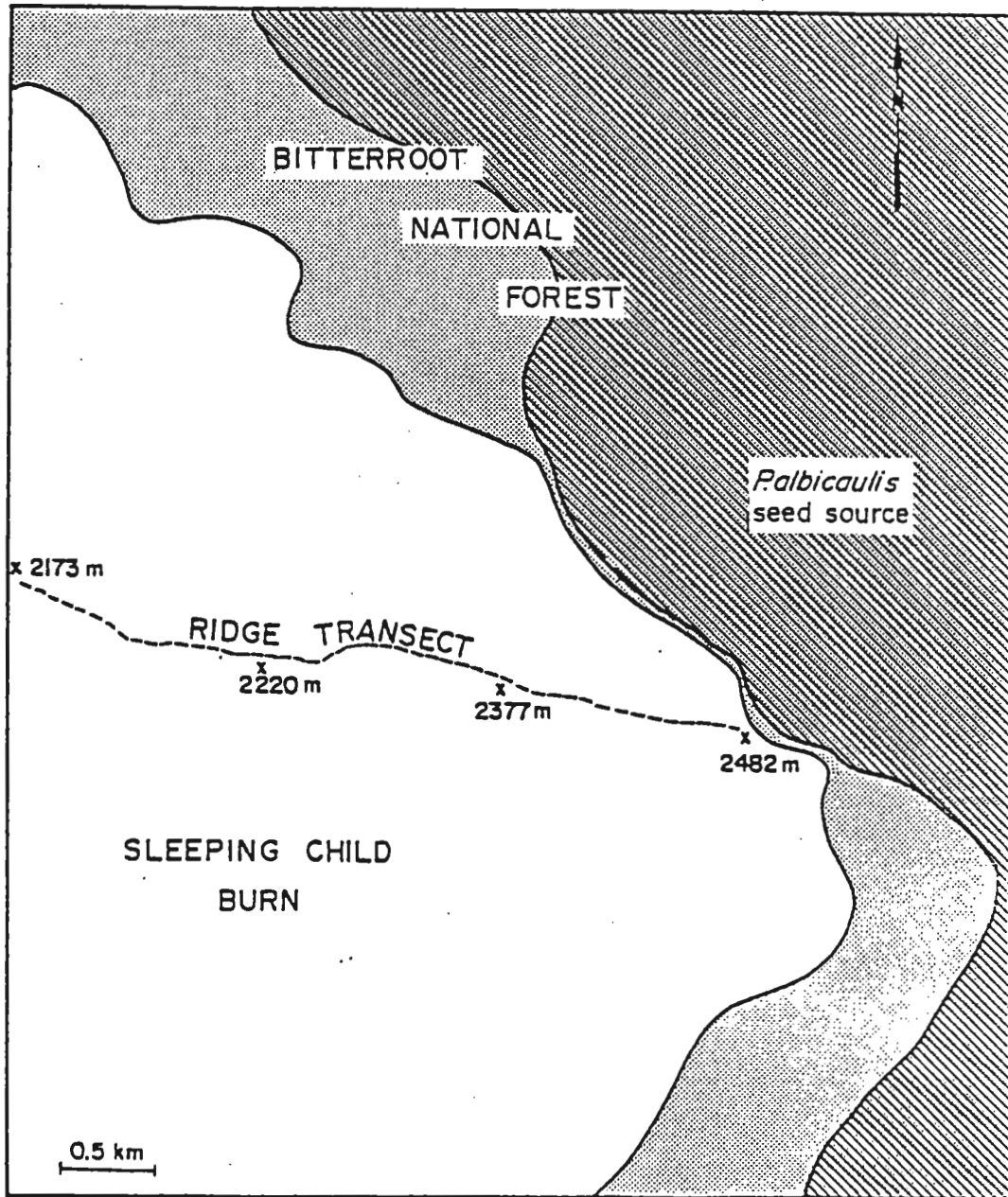


Fig. 1. Study site #1: Sleeping Child Burn, Ridge Transect. The stippled area is the subalpine forest bordering the burn. The hatchmarked area indicates a subsection of the forest with elevations above 2257 m where continuous stands of *P. albicaulis* provide the seed source for regeneration.

ridge of gradually decreasing elevation and increasing distance from the unburned forest at the eastern edge of the burn.

Plots were established 150 m apart on a 3.65 km east-west transect. Each ridge plot was paralleled by plots on the north- and south-facing slopes of the ridge, thus creating three parallel series of plots: north, south, and ridge. In some instances, a representative north or south aspect was not available or could only be obtained by walking several meters east or west. A total of 63 plots were studied: 21 north, 19 south, and 23 ridge. All plots were oriented east-west longitudinally, with belt width measured south from the transect line. Size of the plots ranged from 50 x 1.25 m to 50 x 12 m. Belt width varied for purposes of efficiency. It was important to avoid zero densities of Pinus albicaulis regeneration and yet quickly process plots where densities were high. On the west end of the ridge, P. albicaulis regeneration was sparse, so belt width was increased to 10 m or 12 m. Narrower widths were used on the east end of the ridge where P. albicaulis densities were much higher.

Belt widths were identical for all other species, but were chosen according to density.

Study Site #2 - Road

This second site was selected to measure forest regeneration at fairly constant elevation and aspect but increasingly greater distances from the Pinus albicaulis seed source. A total of 14 plots were studied on north-facing aspects along the Skalkahoe Rye Road and Paint Creek Road (Figure 2). The plots were separated by road distances of 644 m to 2574 m, and their locations corresponded to aerial distances of 900 m to 7950 m from the unburned forest. Plot sizes ranged from 30 x 1.5 m to 30 x 10 m. Plot width was determined by both the density of the vegetation and an effort to include at least one P. albicaulis seedling per plot.

Unburned Forest

For comparison with the burned area on the ridge study site, two plots in the adjacent unburned forest were located on north and south aspects at a distance of 150 m east of the first ridge plot. The north and south forest plots were at elevations of 2440 m and 2420 m, respectively, and each plot was 500 m² in area. All trees within these plots were noted.

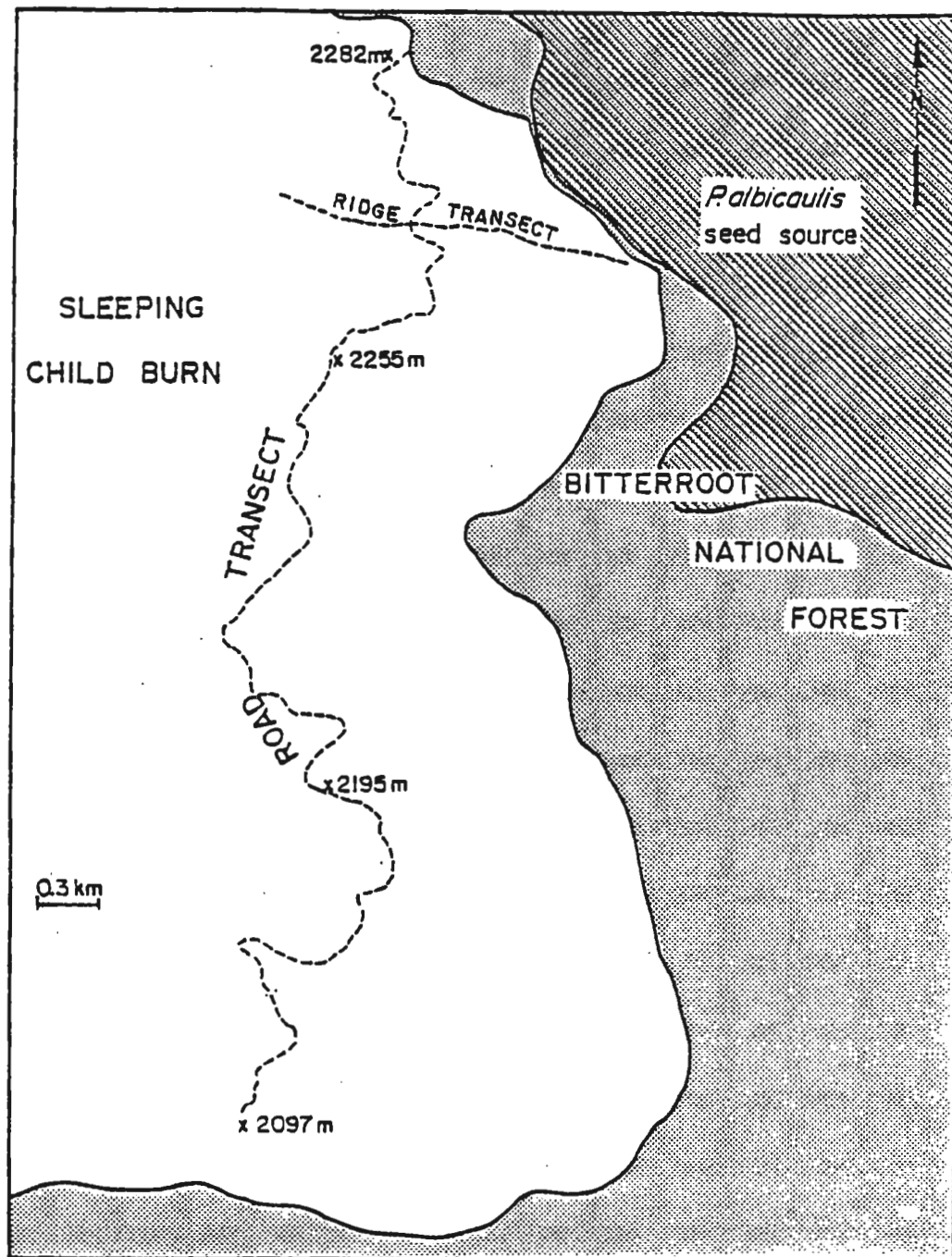


Fig. 2. Study site #2: Sleeping Child Burn, Road Transect. The stippled area is the subalpine forest bordering the burn. The hatchmarked area indicates a subsection of the forest with elevations above 2257 m where continuous stands of *P. albicaulis* provide the seed source for regeneration.

Field Methods

On each plot a list of up to 10 understory plant species, following the checklist of Hitchcock and Cronquist (1973) and Dorn (1984), was compiled by inspection. The purpose was not necessarily to indicate dominance but to list plants representative of the habitat on each plot. In August when field work was conducted, annuals and early-blooming perennials were past flowering, and thus identification of flowering plants was difficult. The percentage occurrence among all plots in a series was calculated for the most common plant species. Evidence of post-fire disturbance such as grazing, thinning, woodcutting, etc. was noted.

Plot measurements included: elevation, slope, aerial distance from Pinus albicaulis seed source, aspect, and number of regeneration sites. Elevation was measured by altimeter and USGS 7.5 minute series topographic map (Kent Peak, and Jennings Camp Creek) readings rounded to the nearest 5 meters. An estimate of slope was made to the nearest 10 degrees, and aerial distance from the boundary of the P. albicaulis seed source was measured on the topographic map to the nearest 10 meters. The seed source is considered to be the continuous stands of P. albicaulis at elevations above 2257 m within the forest; only isolated islands of

P. albicaulis are found in the mixed conifer forest below this elevation. A compass was used to determine aspect. Post-fire regeneration, which ranged in age from recent germinants to saplings and young trees, is collectively referred to as 'trees'. The number of P. albicaulis sites on each plot were recorded. The term 'site' is used to refer to any location with either two trees or a cluster of one or more P. albicaulis trees. At each P. albicaulis site the following data were gathered: slope, aspect, identification of 1 to 4 vascular plant species found within 15 cm of the site, and the nearest object (rock, wood pieces or fallen snag, etc.) located within 15 cm. Cluster size was recorded as the number of individual trunks at a single site and was determined by separating trunks to or below ground level. Although we looked for evidence of blister rust on the trees, none was seen.

The height of each individual tree was recorded, and a number of trees of every representative height category were aged. On the four plot series within the burn, tree age was determined by severing the trunk at ground level and counting tree rings with a hand lens. Newly germinated trees were given a 0.5 year age value; all other ages were in whole years. Tree age on the unburned plots was determined by coring at ground level and counting tree rings.

Statistical Methods

Although a ratio scale of measurement was used for distance, elevation, and tree density data, non-parametric statistics were used in some analyses because underlying parametric assumptions concerning random sampling, normal population distributions, and homogeneity of variance were not always met. Our transects were systematically laid out to obtain plots at pre-determined orientations (east-west along an elevational gradient from center of burn to edge of burn, and north-south along a distance gradient from edge of burn). Normal population distributions were not indicated for P. albicaulis tree or site density on any transect, or for elevation on the north, ridge or south transects. Heterogeneity of variance was also found for P. albicaulis site density on the ridge, north and south plot series (F-max = 19.8). In addition to descriptive statistics for all plot series, Kruskal-Wallis ANOVA was used to compare results among the three ridge plot series (north, ridge, south). Further comparisons were made with Wilcoxon Rank Sum tests. The non-parametric statistical tests were selected in accordance with Seigel (1956).

The independent sampling, ratio measurement scale, and sample sizes were considered adequate to

justify use of parametric analyses for correlation and regression. Pearson Product Moment Correlation analyses (Bailey 1981) were used for testing the following: distance (aerial distance from seed source) vs. tree density; distance vs. site density (a site may be one tree or multiple trees in a single cluster); distance vs. tree age; tree height vs. tree age; elevation vs. site density, and elevation vs. tree density for all plot series. North, south and ridge plot series were combined, and scatterplots with simple linear regression lines were calculated for tree density vs. distance, site density vs. distance, \log_{10} of tree density vs. distance, and \log_{10} of site density vs. distance. The \log_{10} of the density was plotted to see if linearity would result. The regression formula was:

$$Y = bX + a$$

where, Y = dependent variable, b = slope, a = y intercept, X = independent variable (Gravetter and Wallnau 1985). The statistical significance of regression coefficient r was determined from Appendix 4 in Bailey (1981). Analyses were run on an IBM-compatible microcomputer with Microstat (version 4.1, Ecosoft, Inc., Indianapolis, IN). In all tests, results were considered significant only if $P \leq 0.05$.

CHAPTER III

RESULTS

Plot Descriptions (Elevation, Distance, Slope, Area)

For the ridge study site, there were a total of 63 plots; 21 on the north series; 23 on the ridge, and 19 on the south. The general aspect of plots on each plot series was: north - north aspect, range 290 - 20°; ridge - west aspect, range 90 - 330°; south - south aspect, range 170 - 230°; road - north aspect, range 330 - 90° (Table 1). All three ridge plot series were similar in their ranges of elevation and distance to the P. albicaulis seed source (Table 1). Elevation on the north, south and ridge plots ranged from 2105 m to 2480 m with means respectively of 2305 m, 2295 m, and 2305 m. The straight line distance from the eastern edge of individual plots to the seed source ranged from 50 m to 3650 m. Mean distance for north plots was 1680 m, for south, 1810 m, and for ridge, 1790 m. The steepest slopes were on the north aspect (range 0 to 50°, mean = 30°), the south was moderately steep (range 0 to 40°, mean 20°), and the ridge averaged much flatter (range 0

TABLE 1. Plot series characteristics: aspect, elevation, distance, slope, area.

| | PLOT SERIES | | | |
|--|--------------|--------------|--------------|-------------|
| | <u>NORTH</u> | <u>RIDGE</u> | <u>SOUTH</u> | <u>ROAD</u> |
| Aspect | north | west | south | north |
| Range (deg) | 290-20 | 90-330 | 170-230 | 330-90 |
| No. of plots | 21 | 23 | 19 | 14 |
| Elevation (m) | | | | |
| Mean | 2305 | 2305 | 2295 | 2200 |
| Range | 2150-2475 | 2175-2480 | 2165-2465 | 2105-2290 |
| Distance from seed source (m) | | | | |
| Mean | 1680 | 1790 | 1810 | 3860 |
| Range | 50-3500 | 50-3650 | 50-3450 | 900-7950 |
| Slope (deg) | | | | |
| Mean | 30 | 10 | 20 | 20 |
| Range | 0-50 | 0-40 | 0-40 | 0-30 |
| Area (m ²) | | | | |
| Mean | 154.8 | 201.1 | 228.9 | 84 |
| Range | 62.5-500 | 62.5-500 | 62.5-750 | 12.5-500 |
| No. of sites | | | | |
| <u>P. albicaulis</u> | 271 | 119 | 65 | 45 |
| <u>P. contorta</u> | 115 | 186 | 135 | 80 |
| <u>A. lasiocarpa</u> | 33 | 21 | 6 | 123 |
| <u>P. engelmannii</u> | 19 | 16 | 2 | 38 |
| Total sampling area (m ²) | | | | |
| <u>P. albicaulis</u> | 3500 | 5750 | 6225 | 2975 |
| Other (<u>P. contorta</u> , <u>A. lasiocarpa</u> , <u>P. engelmannii</u>) | 3250 | 4625 | 4350 | 1176 |

to 30°, plus one uncharacteristic plot with 40° slope, mean = 10°). For both the ridge and north series, plot sizes ranged from 62.5 m² to 500 m², with a mean of 201.1 m² and 154.8 m², respectively. South series plots had a wider size range (62.5 to 750 m²) and a mean of 228.9 m².

For the 14 plots on the road transect, elevation was generally lower than on the ridge series of plots, between 2105 and 2290 m (mean = 2200 m) (Table 1). The distances to seed source were much greater, with a range of 900 to 7950 m, and a mean of 3860 m, over twice that of the ridge series of plots. The slope on road plots averaged 20°. Road plots were smaller in area than the ridge series because of shorter plot length and ranged from 12.5 to 500 m², averaging 84 m².

Conifer Species and Site Counts

Four species of conifers were found on each plot series (north, south, ridge, road) (Table 1). The number of sites for P. albicaulis was: north - 271, ridge - 119, south - 65, road - 45. The number of sites of P. contorta was higher than that of P. albicaulis on every plot series but the north, despite the smaller P. contorta sampling area; P. contorta site counts on the ridge, south, north, and road were 186, 135, 115, and

80, respectively. In addition, the total number of sites of P. contorta (n = 516) was greater than that for each of the other conifers. The following comparison of total sites per species is based on sampling areas of the same size: Pinus contorta > Abies lasiocarpa > Picea engelmannii. Only on the road plot series were A. lasiocarpa site counts (n = 123) higher than counts of P. contorta. P. engelmannii had the lowest number of sites on every transect (ridge - 16, north - 19, south - 2, road - 38) relative to A. lasiocarpa and P. contorta.

A single Pinus ponderosa was found on a south plot, and one Pseudotsuga menziesii was found on a north plot.

The two unburned forest plots supported predominantly P. albicaulis (north - 44, south - 19) and A. lasiocarpa (north - 38, south - 11), with a few Pinus contorta and Picea engelmannii on the south.

Understory Plant Species Occurrence on Plots

A comparison of understory plant composition among plot series shows the north and south plot series to be very different, reflecting relative occurrence of xeric and mesic species, and the ridge to be intermediate between north and south. Figure 3 shows

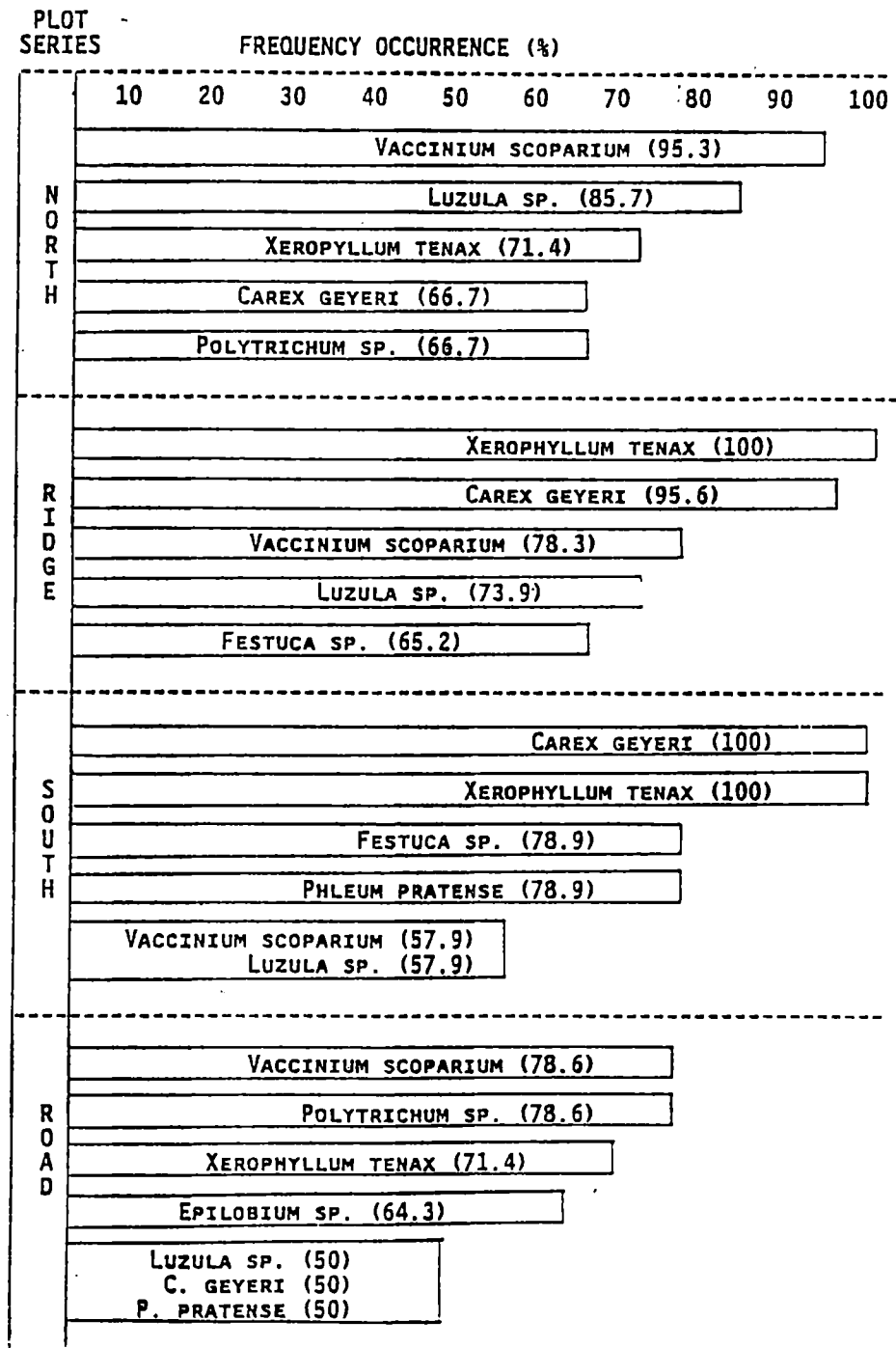


Fig. 3. Five most frequently occurring plant species on plots, by plot series.

the five most frequently occurring plant species by plot series. These species are dominant species for the Bitterroot region, and are classified as mesic or meso-xeric (Lackschewitz 1986). The major vegetation differences between aspects are the result of differences in occurrence of common species (Figure 3): Vaccinium scoparium (north - 95.3%, ridge - 78.3%, south - 57.9%); Luzula sp., north - 85.7%, ridge - 73.9%, and south - 57.9%); Polytrichum sp. (north - 66.7%, ridge - 21.7%, south - 5.3%); Carex rossii, (north - 61.9%, ridge - 52.2%, south - 26.3%).

Grasses and other xeric vegetation were more frequent on the south plot series, less on the ridge, and even less on the north. Xerophyllum tenax occurred on all plots on both south and ridge plot series, and on 71.4% of north plots. Carex geyeri occurred 100% frequency on south plots, 95.6% on ridge and 66.7% on the north; Phleum pratense frequency occurrence was: north - 42.9%, ridge - 43.5%, south - 78.9%; Dactylis glomerata occurred on 4.8% of the north plot series, 19.9% of the ridge, and 52.6% of the south.

Road plots showed some similarities to both the north and ridge plot series. The road plots resembled the north in order of species frequencies on plots: Vaccinium scoparium (78.6%) > Xerophyllum tenax (71.4%) > Carex geyeri (50%) > Anaphalis margaritacea (35.7%) >

Salix sp. (28.6%). Frequency values for the road, V. scoparium (78.6%), P. pratense (50%) and A. margaritacea (35.7%), were similar to the ridge.

The two unburned forest plots exhibited understory occurrences of X. tenax, V. scoparium, and C. geyeri.

P. albicaulis Clusters and Microsite Vegetation

Cluster sizes (number of individual trees per P. albicaulis site) ranged overall from 1 to 9 (Table 2). The ridge and north plot series showed a range of 1 to 8, the south 1 to 5, and the road 1 to 9. Mean cluster size, respectively, was 2.06, 1.92, 1.57, and 2.49. Kruskal-Wallis ANOVA indicated a significant difference in cluster size among the three ridge plot series ($H = 6.475$, $df = 2$, $P = 0.039$). Further analysis with the Wilcoxon Rank Sum test showed south plots differing significantly both from the north ($Z = 1.951$, $P = 0.026$) and the ridge ($Z = -2.543$, $P = 0.006$).

On every transect, the largest percentage of sites were solitary trees (south - 66.2%, north - 52%, road - 51.1%, ridge - 45.4%). As cluster size increased, the percentage of clusters in each size category decreased. One exception was on the road plot series, where clusters of 3 trees accounted for 22.2% of

TABLE 2. Pinus albicaulis clusters: size and frequency.

| | PLOT SERIES | | | |
|--------------------------|-----------------|--------------|--------------|-------------|
| | <u>NORTH</u> | <u>RIDGE</u> | <u>SOUTH</u> | <u>ROAD</u> |
| Number of sites | 271 | 119 | 65 | 45 |
| Number of trees per site | | | | |
| Mean | 1.92 | 2.06 | 1.57 | 2.49 |
| Range | 1-8 | 1-8 | 1-5 | 1-9 |
| Cluster size | Frequencies (%) | | | |
| 1 | 52.0 | 45.4 | 66.2 | 51.1 |
| 2 | 26.6 | 28.6 | 21.5 | 6.7 |
| 3 | 8.5 | 12.6 | 4.6 | 22.2 |
| 4 | 6.3 | 6.7 | 4.6 | 6.1 |
| 5 | 4.8 | 4.2 | 3.1 | 2.2 |
| 6 | 1.1 | 0.8 | -- | 4.4 |
| 7 | 0.4 | 0.8 | -- | 2.2 |
| 8 | 0.4 | 0.8 | -- | 2.2 |
| 9 | -- | -- | -- | 2.2 |

all sites, and clusters of 2 trees accounted for only 6.7%. A cluster of 17 trees was found near a road plot; this is larger than the cluster size range of 1 to 15 previously reported by Tomback (1982).

Pinus albicaulis sites on the three different ridge plot series showed dissimilar frequencies of microsite vegetation species. Vaccinium scoparium was most frequent on all plot series, and Polytrichum sp. or Carex rossii was the second most frequent. Many P. albicaulis trees were growing in the middle of a clump of C. rossii. On north and ridge sites, V. scoparium frequency was 86% and 69.7%, respectively; and all other species accounted for 25% or less of occurrences. South plot series P. albicaulis sites showed no microsite plant species frequency greater than 25% (Figure 4). Despite the frequent occurrence of Xerophyllum tenax on many plots, no P. albicaulis trees were actually growing within these formidable clumps.

On the road transect, V. scoparium and Polytrichum sp. each occurred on more than 50% of the P. albicaulis sites. The species richness was lower on road plots, but this is probably due to the smaller plot size and thus smaller number of P. albicaulis sites.

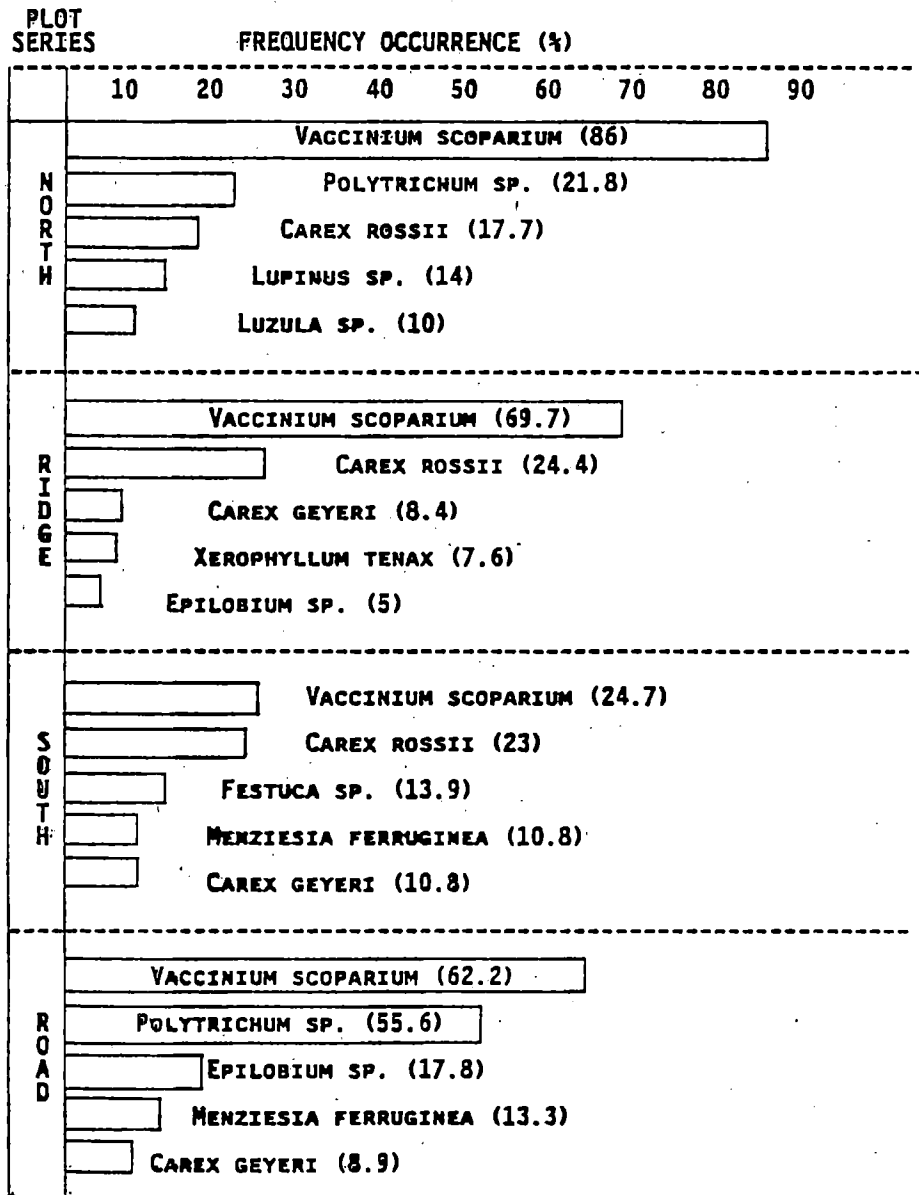


Fig. 4. Five most frequently occurring plant species on P. albicaulis microsites, by plot series.

Nearest Objects on P. albicaulis
Microsites

The total number of P. albicaulis microsites on all four plot series combined (ridge, north, south, road) was 500. Five categories of objects were noted on P. albicaulis microsites within 15 cm of the tree trunk(s). Wood pieces were the nearest object on 122 sites (24.4%), a log or single large branch on 112 (22.4%), a fallen snag on 69 (13.8%), rocks on 68 (13.6%), and a standing snag or stump on 34 (6.8%). Ninety-five (19%) of the microsites were categorized as 'open', because no object was present.

Vegetation Comparisons Between Plot Series
and P. albicaulis Microsites

Analysis of vegetation near P. albicaulis sites shows some similarities to the vegetation frequencies on plot series. Vaccinium scoparium was the most frequently occurring species on tree microsites on all plot series, with a frequency on ridge microsites intermediate between north and south, and a frequency on the road microsites most resembling that of the north. Vaccinium scoparium showed the same frequency pattern on plots, with the exception that the road plots mostly resembled the ridge plots. Polytrichum, a mesic species, was the second most frequently occurring

species on north and road microsities and showed high occurrences on north and road plots.

Distinct differences between microsite vegetation and plot vegetation are reflected in the frequencies of C. rossii and X. tenax. Although C. rossii is the second most frequently occurring species on ridge and south microsities, it ranks much lower in occurrence on ridge and south plots. Conversely, X. tenax was present on all south and ridge plots and over 70% of the road and north plots but occurred on no north microsities and on fewer than 8% of microsities on the other three plot series.

P. albicaulis Site Density,
Elevation, and Distance

The total number and range per plot of P. albicaulis sites on each plot series were: ridge - total 119, range 0 to 24; north - total 271, range 1 to 32; and south - total 65, range 1 to 11 (Table 3). The ranges of P. albicaulis site density per m² per plot for the ridge, north and south plot series, respectively, were: 0 to 0.192, 0.006 to 0.512, and 0.001 to 0.11. Mean site density per plot (defined as P. albicaulis sites per m²) were: north - 0.14, ridge - 0.04, south - 0.02. Road plots had a total of 45 P. albicaulis sites, with a range of 0 to 10 per plot, a mean density of 0.02

TABLE 3. Pinus albicaulis regeneration by plot series: density (sites or trees per m²), age (yrs), height (cm). N = total number.

| | PLOT SERIES | | | |
|----------------|--------------|--------------|--------------|-------------|
| | <u>NORTH</u> | <u>RIDGE</u> | <u>SOUTH</u> | <u>ROAD</u> |
| Sites | | | | |
| N | 271 | 119 | 65 | 45 |
| Range per plot | 1-32 | 0-24 | 1-11 | 0-10 |
| Density | | | | |
| Mean | 0.14 | 0.04 | 0.02 | 0.02 |
| Range | 0.006-0.512 | 0-0.192 | 0.001-0.11 | 0-0.007 |
| Trees | | | | |
| N | 520 | 245 | 102 | 112 |
| Range per plot | 1-61 | 0-56 | 1-13 | 0-22 |
| Density | | | | |
| Mean | 0.275 | 0.099 | 0.035 | 0.051 |
| Range | 0.006-0.976 | 0-0.448 | 0.001-0.13 | 0-0.127 |
| Age | | | | |
| N | 334 | 149 | 79 | 47 |
| Mean | 7.7 | 8.3 | 8.1 | 6 |
| Range | 1-21 | 0.5-20 | 1-21 | 0.5-19 |
| Height | | | | |
| Mean | 29.7 | 36.2 | 30.6 | 19.2 |
| Range | 1.5-234 | 3-238 | 3-202.3 | 1-186 |

per m², and a density range of 0 to 0.067 per m².

Site densities for the north, ridge and south plot series showed differences of high statistical significance (Kruskal-Wallis ANOVA, $H = 10.614$, $df = 2$, $P < 0.005$). North plot series site densities differed significantly from the ridge plot densities (Wilcoxon Rank Sum, $Z = 2.758$, $P < 0.003$) and from the south plot densities ($Z = -3.521$, $P < 0.001$).

Whether a significant relationship occurred between P. albicaulis site density (sites per m²) and elevation, and site density and distance from seed source, was determined for each plot series (Pearson correlation, Table 4). Significant negative correlations with $P < 0.01$ between site density (sites per m²) and distance occurred on all series of plots except the road: north, $r = -0.832$; ridge, $r = -0.618$; south, $r = -0.714$ (Table 4). Site density and elevation were significantly correlated for the three ridge plot series with $P < 0.01$, but not for the road series: north, $r = 0.982$; ridge, $r = 0.632$; south, $r = 0.682$ (Table 4).

Regression Model for Site Density
vs. Distance

Data from the north, south and ridge plot series were combined in a scatterplot of Pinus albicaulis site density (dependent variable) vs. distance from seed

Table 4. Pearson correlation analysis: Pinus albicaulis density (sites or trees per m²) vs. elevation, density vs. distance from seed source, age vs. height. (NS = not significant, P >0.05). Log = Log₁₀. In all cases, df = no. of plots minus two.

| | Plot series | No. of plots | Correlation coefficient(r) | P |
|-------------------------------|-------------|--------------|----------------------------|--------|
| Site density vs. elevation | North | 21 | 0.982 | <0.001 |
| | Ridge | 22 | 0.632 | <0.01 |
| | South | 19 | 0.682 | <0.01 |
| | Road | 13 | 0.428 | NS |
| Tree density vs. elevation | North | 21 | 0.877 | <0.001 |
| | Ridge | 22 | 0.647 | <0.01 |
| | South | 19 | 0.682 | <0.01 |
| | Road | 13 | 0.194 | NS |
| Site density vs. distance | North | 21 | -0.832 | <0.001 |
| | Ridge | 22 | -0.618 | <0.01 |
| | South | 19 | -0.714 | <0.001 |
| | Road | 13 | -0.374 | NS |
| Log site density vs. distance | North | 21 | -0.820 | <0.001 |
| | Ridge | 22 | -0.733 | <0.001 |
| | South | 19 | -0.779 | <0.001 |
| | Road | 13 | -0.500 | NS |
| Tree density vs. distance | North | 21 | -0.822 | <0.001 |
| | Ridge | 22 | -0.627 | <0.01 |
| | South | 19 | -0.703 | <0.001 |
| | Road | 13 | -0.207 | NS |
| Log tree density vs. distance | North | 21 | -0.788 | <0.001 |
| | Ridge | 22 | -0.751 | <0.001 |
| | South | 19 | -0.678 | <0.01 |
| | Road | 13 | -0.334 | NS |
| Tree age vs. height | North | 334 | 0.818 | <0.001 |
| | Ridge | 149 | 0.783 | <0.001 |
| | South | 79 | 0.827 | <0.001 |
| | Road | 47 | 0.742 | <0.001 |

source (independent variable). The plot produced a negative exponential curve with the following regression equation:

$$Y = -0.00006(X) + 0.175$$

(Df = 60, $r = -0.590$, $P < 0.001$). When \log_{10} density was used, the scatterplot produced a straight line and the regression equation was:

$$Y = -0.0005(X) - 0.806,$$

with $r = -0.692$ and $P < 0.001$.

Regression analysis of the road plots indicated no correlations between P. albicaulis site density and distance from seed source. Even when the \log_{10} density was used, the regression was not significant.

P. albicaulis Tree Density,
Elevation and Distance

A total of 1029 Pinus albicaulis trees (more than one tree may occur at a site) were found on the two study sites: 917 on the ridge (includes ridge, north and south plot series) and 112 on the road plot series (Table 3). Total P. albicaulis tree counts on the north plot series were twice as large as on the other two ridge plot series (520 versus 245 for the ridge series and 102 for the south series), although area sampled on the ridge was 1.64 times larger than on the north, and the south was 1.78 times larger. Tree densities,

measured as trees per m^2 , ranged as follows: north (0.006 to 0.976), ridge (0 to 0.448), south (0.001 to 0.13) (Table 3). Mean tree densities per m^2 were: north - 0.275, ridge - 0.099, and south - 0.035. Kruskal-Wallis ANOVA showed P. albicaulis tree densities per plot were significantly different among the north, ridge, and south plot series ($H = 14.191$, $df = 2$, $P < 0.001$). Wilcoxon Rank Sum results were significant for comparisons of the north series vs. both the ridge series ($Z = 2.478$, $P < 0.007$) and the south series ($Z = 3.616$, $P < 0.001$). Thus P. albicaulis is significantly greater on the north than on the other two aspects.

The mean tree density for road plots (0.051 trees per m^2) was intermediate between south and ridge values, and the density range per plot was 0 to 0.127 trees per m^2 (Table 3).

Significant negative correlations ($P < 0.01$) were found for tree density vs. distance from seed source for all three ridge plot series with r values as follows: north, $r = -.822$; ridge, $r = -.627$; and south, $r = -.703$ (Table 4). The correlation was not significant for the road.

Regression Model for Tree Density vs
Distance

Combining north, ridge and south plot series, the scatterplot for tree density against distance also assumed a negative exponential curve (Figure 5). The regression equation was:

$$Y = -0.0001(X) + 0.344,$$

with $df = 60$, $r = -0.571$, and $P < 0.001$. With \log_{10} of tree density (Figure 6), the plot became linear and the equation became

$$Y = -0.0005(X) - 0.542$$

with $r = -0.666$ and $P < 0.001$.

The same analysis for P. albicaulis trees on the road plots failed to produce a significant correlation between density and distance.

P. albicaulis Tree Age, Height,
Distance

Each separate stem within a Pinus albicaulis cluster was considered a tree for aging purposes; the number of trees aged on north plots was 334; on the ridge, 149; and on the south, 79 (Table 3). Field data show that the ages of trees within an individual cluster were the same or similar, usually differing by only 1 or 2 years, but in no case more than 4 years. In virtually all cases no stems were fused at the base, thus it must

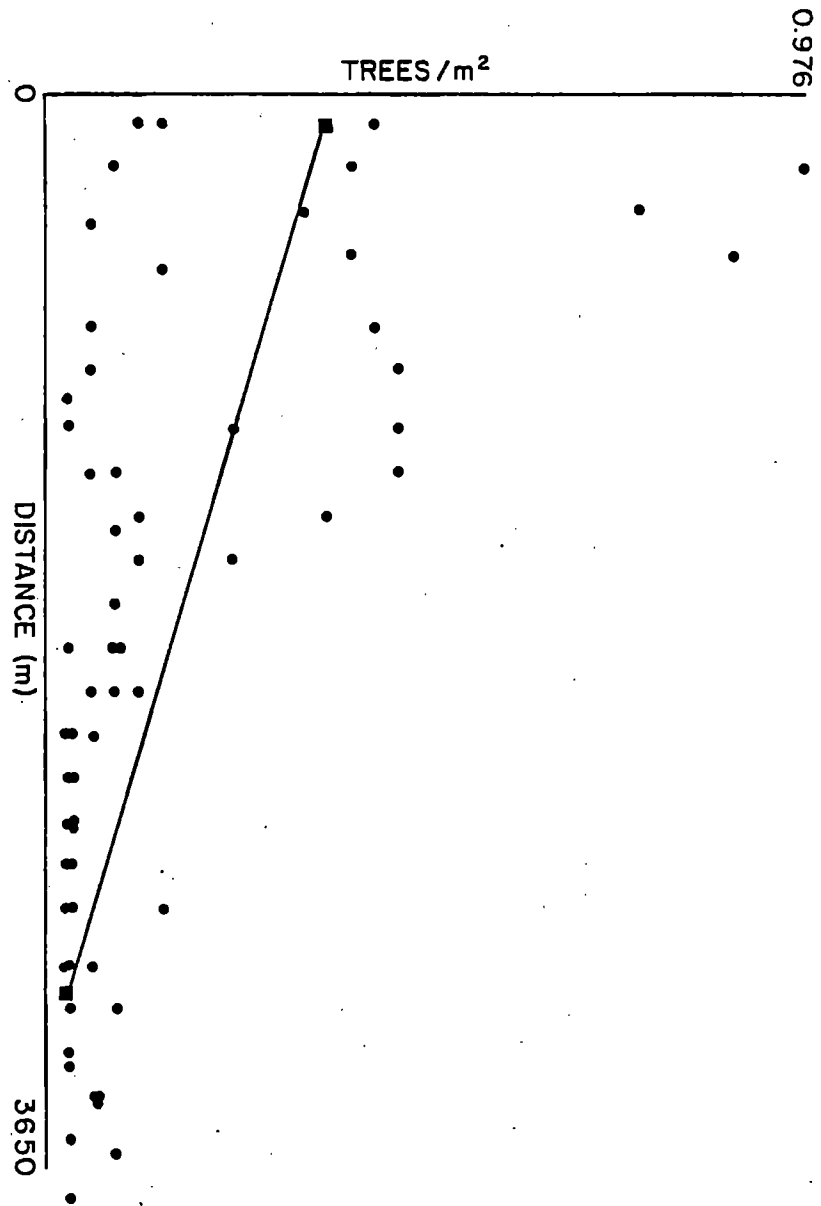


Fig. 5. Scatterplot of *P. albicaulis* tree density vs. distance, for three ridge plot series combined.

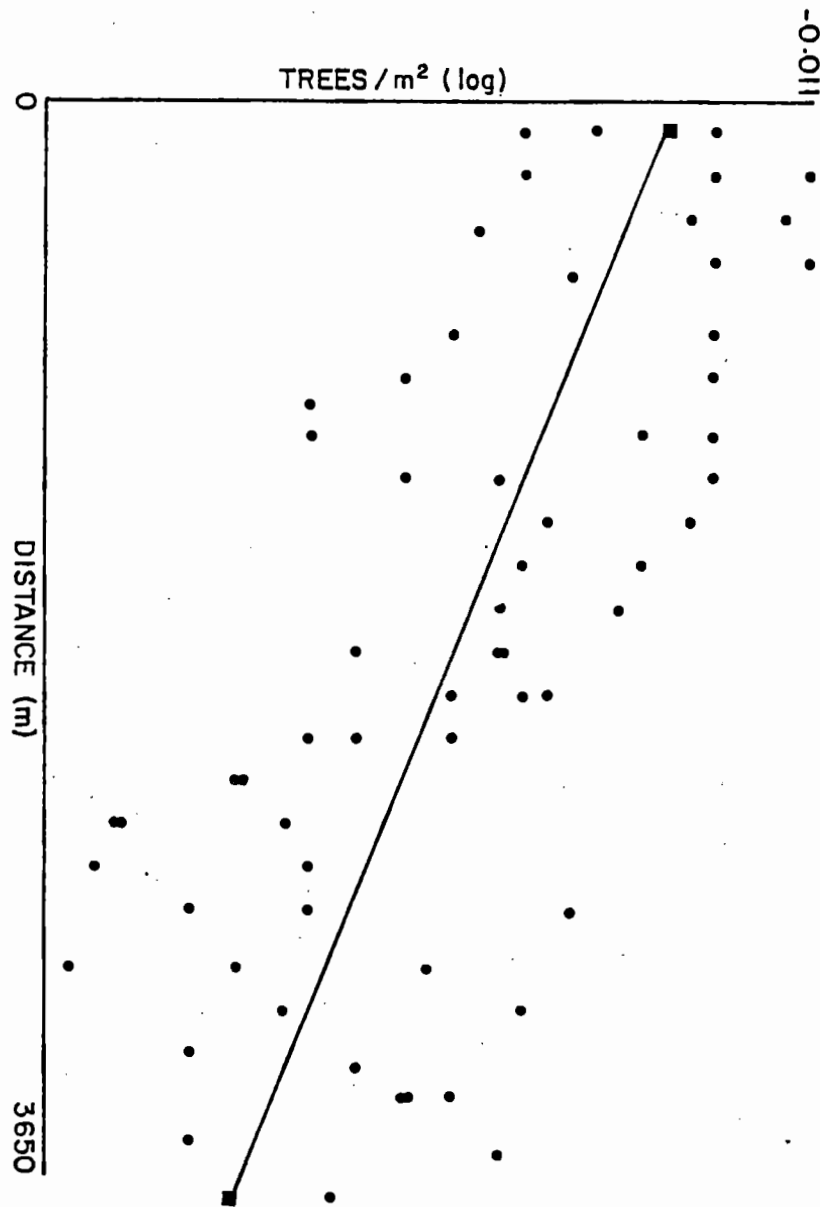


Fig. 6. Scatterplot of *P. albicaulis* log₁₀ tree density vs. distance, for three ridge plot series combined.

be emphasized that each member of a cluster appeared to be a distinct individual. The age differences observed were probably the result of counting error or later germination. Age ranges of trees were nearly identical for the three ridge plot series: north and south, 1 to 21 yr; ridge 0.5 to 20 yr. Compared to the ridge plots and south plots, the north trees had a slightly lower mean (7.7 yr vs. 8.3 yr, and 7.7 yr vs. 8.1 yr). Forty-seven trees were aged on road plots, with a range of 0.5 to 19 yr and a lower mean (6 yr) than any of the ridge plot series. P. albicaulis trees on the two unburned forest plots showed a mean age of 127.7 yr and a range of 76 to 202 yr.

Tree heights ranged from 1 to 238 cm (Table 3). The range and mean for the ridge plot series was the highest (3 to 238 cm, 36.2 cm), followed by the north (1.5 to 234 cm, 29.7 cm), south (3 to 202.3 cm, 30.6 cm) and road (1 to 186 cm, 19.2 cm), the lowest of all. Highly significant Pearson correlations ($P < 0.001$) were found for tree age vs. tree height for all plot series: north ($r = 0.818$, $df = 332$), ridge ($r = 0.783$, $df = 147$), south ($r = 0.827$, $df = 77$), and road ($r = 0.742$, $df = 45$).

CHAPTER IV

DISCUSSION

Regeneration: Consequences of Seed Dispersal by Nutcrackers

Regeneration patterns of Pinus albicaulis in the Sleeping Child Burn demonstrate the importance of nutcrackers as seed dispersers. A few nutcrackers were seen in the study site during field work in 1987, but the lack of a P. albicaulis cone crop that year prevented direct observation of foraging or caching behavior. However, the occurrence of tree clusters and the great distances from regeneration to seed source confirm previous suggestions that nutcrackers are the primary dispersers of P. albicaulis and that their caching behaviors effect establishment of the conifer (Lanner 1980; Hutchins and Lanner 1982; Tomback 1982). This study also confirms that squirrels and other rodents play a very minor role at best in the dissemination of Pinus albicaulis. As reported by Hutchins and Lanner (1982), red squirrels (Tamiasciurus hudsonicus), chipmunks and other mammals are not reliable dispersers compared to nutcrackers. Their limited home ranges indicate that a more mobile

disperser has buried seeds to account for the observed distances between seed source and regeneration. Although Stellar's jays (Cyanocitta stelleri) were seen in the study area, they also establish small territories, damage seeds upon removal from the cone, and bury one-seed caches (Vander Wall and Balda 1981).

Nearly half of all Pinus albicaulis sites were composed of two or more trees, with clusters of up to 9 trees observed on the road plot series, and a cluster of 17 trees observed near that transect. The distinct multiple stems and the similarity in tree ages within a cluster are evidence of germination from buried seed caches.

Interestingly, no P. albicaulis older than 21 yr was found on the plots, even though the burn occurred 26 years prior. This may indicate a lack of regeneration during the five years immediately following the burn, either because of no cone crops or unfavorable conditions for seed germination.

Dispersal distances of P. albicaulis in the Sleeping Child Burn are similar to the distances noted by Tomback (1978) and Hutchins and Lanner (1982), although their studies occurred in California and Wyoming, respectively. Regeneration from the seed source in the adjacent forest extended into the burn westward for 3.65 km and southward nearly 8 km. Because

P. albicaulis trees were found on the study plots furthest from the seed source, we assume regeneration has occurred beyond these distances also. These patterns lead us to conclude that nutcrackers are responsible for nearly 100% of the observed P. albicaulis regeneration in the burn.

An interesting pattern with potential application was the significant linear relationship observed between the density of regenerating P. albicaulis on the three ridge plot series and the aerial distance from the seed source (Figures 5 and 6). This correlation reflects the dispersal pattern generated by the nutcracker, but at this time it is not possible statistically to separate the effect of elevation on density from the effect of distance on density. Elevation also correlated significantly with distance from seed source on the three ridge plot series, and the change in environmental conditions (moisture, temperature) that accompany changes in elevation conceivably may have an effect on seed germination and seedling survival. However, P. albicaulis grows well in western Montana from elevations of 2290 - 2620 m and grows as far down as 2130 meters (Arno and Petersen 1983). All plots on the three ridge plot series were above 2130 m and nearly half of the plots on each series were within the 2290 - 2620 m range. Thus, the pattern

generated should primarily reflect differences in distance and not elevation effects.

The regeneration patterns that result from nutcracker seed dispersal along a distance gradient from a known seed source suggest that the birds cache relatively more seeds close to the parent trees and make fewer caches per m^2 at increasing distances. The result is a negative exponential curve (tree density vs. distance) (Figure 6), a shape similar to the seed shadow curves generated by individual wind-dispersed conifers (McCaughey et al. 1986), but the P. albicaulis regeneration extended over much greater distances. As discussed by Tomback et al. (in preparation), the dispersal distances for P. albicaulis may typically be greater than that for Abies lasiocarpa, a competitor in succession, giving P. albicaulis the edge because of nutcracker-mediated dispersal.

The negative exponential curve was confirmed as well for P. albicaulis regeneration in the Saddle Mountain Burn to the south of the Sleeping Child Burn (Tomback et al. in prep.). For management purposes, this curve may be useful for its predictive value (e.g., Keane et al. 1989). Potential application includes models of P. albicaulis regeneration for prescribed fires or for past fires such as suitable areas of Yellowstone National Park burned in 1988.

The correlation between density and distance did not hold for the road plot series. This could be due to the effects of elevation on P. albicaulis seed germination and seeding survival. All of the road series plots were at elevations of 2290 m or less, and thus were below the range within which P. albicaulis grows well in this region. The forest bordering the southern part of the burn is composed of mixed conifers, and thus may be a better source of regeneration for Abies lasiocarpa, Picea engelmannii, and Pinus contorta than for P. albicaulis.

Variation in Density and Cluster Size

The data show significantly higher densities of both Pinus albicaulis sites and trees on the north aspect of the ridge than on the ridge or south (at least 7 times greater mean density on the north). This is consistent with the prevalence of P. albicaulis on cool exposures and moist sites in semiarid ranges (Arno and Hoff 1987). North slopes, with deeper soil mantles, more moisture and cooler temperatures, may provide more suitable germination conditions. Leadem (1986) examined the dormancy-breaking mechanisms of P. albicaulis seeds, and found that cold temperatures were necessary to overcome physiological barriers to growth. Alternatively, nutcrackers may cache more on north

slopes, but Tomback (1978, 1982) and Vander Wall and Balda (1977) suggest that south slopes are preferred. Regeneration density must be a result of both 1) nutcracker caching preferences, and 2) site quality. Competition from other plant species could also be a factor in density variation among plot series. Xerophyllum tenax tufts were widespread on south slopes, as were grass species; both are potential competitors for young trees.

Another interesting pattern was the relatively large cluster sizes found on the road plot series, where the largest percentages of cluster sizes greater than 5 occurred, and a 17-stem cluster was found nearby. Distances from road plots to the seed source averaged over twice as far as ridge plots. This poses an interesting question: do nutcrackers bury larger clusters of seeds when they fly greater distances? Or perhaps germination and seedling survival conditions were better on the road plot series despite the lower elevations. Although highly tolerant of crowding, P. albicaulis seedlings within a cluster may compete to some degree as they mature. The lower height values observed for trees on the road plot series could be indicative of intra-cluster competition.

Post-Fire Disturbance

Successional processes have been complicated by a history of disturbances in the study area. Lyon (1976) summarized several years of post-fire management activities in the Sleeping Child burn, including chemical thinning of lodgepole pine, pole cutting, cattle grazing, Christmas tree cutting, firewood gathering, road building, aerial sowing of annual grasses, and recreational uses such as hunting and camping. He estimates little long-term effect from these management activities, since competition would have produced substantial losses in dense stands anyhow. However, some of these activities, especially chemical thinning of Pinus contorta, grazing, and sowing of grasses, may affect the type and density of regrowth within some areas of the burn. A case in point is the road plot series, with an elevation range stated to be dominated by P. contorta prior to the fire (Lyon and Stickney 1976), but with regeneration density of P. contorta lower than Abies lasiocarpa. Evidence of grazing and browsing was seen often on south slopes, which tended to be less steep in both study sites. Range cattle were encountered during field work on south aspects as well as on the dirt roads that access the burn.

Vegetation Comparisons Between Plots and Microsites

Much consistency was seen in the understory species on P. albicaulis microsites overall, despite differences in characteristic vegetation found on the four plot series. The predominance of species such as Vaccinium scoparium, Polytrichum sp., and Carex rossii at tree sites reflects the preference of P. albicaulis for mesic to meso-xeric habitat in these mountains (Lackschewitz 1986). This contrasts with the high frequency of X. tenax which grew as large, dense clumps on all the plot series. The growth form of X. tenax undoubtedly makes it a superior competitor compared to young P. albicaulis, and nutcrackers probably do not cache seeds near these plants.

Fire and P. albicaulis Regeneration

Twenty-six years after a severe fire, the Sleeping Child Burn shows regeneration of Pinus albicaulis to be well under way. Tree counts of the four conifer species on the higher elevation study site (the three ridge plot series) support the observation that stand-replacing fires favor P. albicaulis in relation to its more shade-tolerant subalpine associates, Abies lasiocarpa and Picea engelmannii (Arno 1986, Arno and Hoff 1987). This pattern is complicated

by a higher density of Pinus contorta on the plots with south exposures and on the few plots at the west end of the ridge that are within lower subalpine elevations. Our two plots in the unburned forest at the upper edge of the burn show species composition dominated by P. albicaulis and A. lasiocarpa, the potential climax species for the upper subalpine habitat type (Pfister et. al 1977). The striking abundance of P. contorta regeneration on the lower subalpine road plots may be due to the seral P. contorta forest existing at the time of the fire. Large numbers of seeds were probably released as the serotinous cones opened from the heat (Fischer and Bradley 1987).

Tree counts for the road plot series show Pinus albicaulis regeneration to be a relatively minor component in relation to Abies lasiocarpa and Pinus contorta. Regeneration patterns along this plot series, which extends into the upper limits of the lower subalpine, is most likely the consequence of the great distance from P. albicaulis seed crops, lower elevation, and closer proximity to seed crops of the other conifers.

Clearly, the result of severe fire in the Sleeping Child Burn is regeneration of P. albicaulis at higher elevations. The post-fire dominance of this species is typical of the forest overstory composition

for much of the northern Rocky Mountains that existed prior to 20th century fire suppression policies.

CHAPTER V

CONCLUSIONS

Regeneration of Pinus albicaulis, a major component of northern Rocky Mountain subalpine forests and an important wildlife food source, is well underway in an area where it had been declining. Clark's nutcrackers are responsible for the Pinus albicaulis regeneration patterns observed in the Sleeping Child Burn. This severely burned area now has P. albicaulis trees growing at distances of at least 8 km from the nearest seed source, distances that can only be accounted for by the seed caching behavior of the birds. The even-aged tree clusters that were present on both study sites are evidence of seed caches buried by nutcrackers. P. albicaulis regrowth on the ridge study site along a distance gradient from a known seed source corresponds to a linear relationship between regeneration density and distance. This indicates that nutcracker caching behavior is most concentrated nearest the seed source but extends for distances of several kilometers. Birds may also bury larger numbers of seeds per cache when they fly greater distances from the harvest site.

The regeneration densities for four conifer species indicate that avian dispersal results in earlier establishment of P. albicaulis during post-fire succession, compared to its upper subalpine associates Abies lasiocarpa and Picea engelmannii. The regeneration species composition at high subalpine elevations resembles that of regional forests prior to the fire suppression policies initiated in the early 1900's.

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APPENDIX A.

Plant Species List for Sleeping
Child Burn

| COMMON NAME | SCIENTIFIC NAME |
|---------------------|--|
| Subalpine fir | <i>Abies lasiocarpa</i> |
| Yarrow | <i>Achilles millefolium</i> v. <i>alpicola</i> |
| Pearly-everlasting | <i>Anaphalis margaritacea</i> |
| Pussytoes | <i>Antennaria</i> |
| Sandwort | <i>Arenaria aculeata</i> |
| Arnica | <i>Arnica cordifolia</i> |
| Mountain arnica | <i>Arnica latifolia</i> v. <i>latifolia</i> |
| Aster | Family Asteraceae |
| Smooth brome-grass | <i>Bromus inermis</i> ssp. <i>inermis</i> |
| Elk sedge | <i>Carex geyeri</i> |
| Ross sedge | <i>Carex rossii</i> |
| Composite (unknown) | Unknown composite |
| Orchard-grass | <i>Dactylis glomerata</i> |
| Fireweed | <i>Epilobium</i> sp. |
| Buckwheat | <i>Eriogonum</i> sp. |
| Fleabane | <i>Erigeron</i> sp. |
| Forb (unknown) | Unknown forb |
| White hawkweed | <i>Hierachium albiflorum</i> |
| Western hawkweed | <i>Hierachium albertinum</i> |
| Labrador tea | <i>Ledum glandulosum</i> |
| Partridge foot | <i>Leutkea pectinata</i> |
| Lichen (unknown) | Unknown lichen |
| Honeysuckle | <i>Lonicera utahensis</i> |
| Lupine | <i>Lupinus</i> sp. |
| Woodrush | <i>Luzula</i> sp. |
| Fools huckleberry | <i>Mensiesia ferruginea</i> v. <i>glabella</i> |
| Alpine fernleaf | <i>Pedicularis contorta</i> |
| Penstemon | <i>Penstemon procerus</i> |
| Common timothy | <i>Phleum pratense</i> |
| Engelmann spruce | <i>Picea engelmannii</i> |
| Whitebark pine | <i>Pinus albicaulis</i> |
| Lodgepole pine | <i>Pinus contorta</i> v. <i>latifolia</i> |
| Ponderosa pine | <i>Pinus ponderosa</i> v. <i>scopulorum</i> |
| Bluegrass | <i>Poa</i> sp. |
| Bistort | <i>Polygonum bistortoides</i> |
| Moss | <i>Polytrichum</i> sp. |
| Jacobs ladder | <i>Polemonium</i> sp. |

APPENDIX A. (cont.)

| COMMON NAME | SCIENTIFIC NAME |
|-------------------|------------------------------|
| Douglas-fir | <i>Pseudotsuga menziesii</i> |
| Gooseberry | <i>Ribes</i> sp. |
| Sheepsorrel | <i>Rumex acetosella</i> |
| Catchfly | <i>Silene spaldingi</i> |
| Green needlegrass | <i>Stipa nelsonii</i> |
| Needlegrass | <i>Stipa occidentalis</i> |
| Snowberry | <i>Symphoricarpos</i> sp. |
| Dandelion | <i>Taraxacum officinale</i> |
| Downy oatgrass | <i>Trisetum spicatum</i> |
| Huckleberry | <i>Vaccinium globulare</i> |
| Grouseberry | <i>Vaccinium scoparium</i> |
| False hellebore | <i>Veratrum viride</i> |
| Beargrass | <i>Xerophyllum tenax</i> |