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THE INFLUENCE OF SOME ENVIRONMENTAL FACTORS ON INITIAL
ESTABLISHMENT AND GROWTH OF PONDEROSA PINE SEEDLINGS

By

Michael G. Harrington

B.S., University of Montana, 1970


Presented in partial fulfillment of the requirements for the degree of


Master of Arts

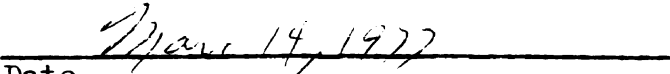
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ABSTRACT

Harrington, Michael G., M.A., March 1977

Botany

The Influence of Some Environmental Factors on Initial Establishment and Growth of Ponderosa Pine Seedlings (107 pp.)

Director: Dr. Mark Behan *M.B.*

Natural regeneration of ponderosa pine occurs infrequently because of its dependence on the coincidence of an abundant seed crop, a mineral soil seedbed, adequate available soil moisture, and a rather low rodent population. This study attempted to disclose additional and more specific information concerning the effects of various environmental parameters on ponderosa pine seed germination and initial seedling establishment and growth.

A series of field study plots were established and divided into two groups. The first group consisted of plots located within a ponderosa pine stand and the second plot group was situated in openings away from the direct influence of the pine stand. A series of treatments were performed on the plots in both groups, each of which was to emphasize the impact of one or more environmental factors. After treatment, an equal number of ponderosa pine seeds were planted in each plot. During the following spring and summer, a record was kept of seed germination and seedling mortality, as well as the measurement of numerous environmental parameters. At the end of the growing season, seedling shoot and root lengths, weights, and numbers were obtained.

Seed germination was significantly greater in the opening plots. The influence of the canopy and the organic layer on precipitation and light reaching the seedbeds seemed to be the greatest germination deterrent. Cutworm and bird or small mammal activity caused the greatest number of seedling mortalities. Poor root development, sun scald, and an unknown agent accounted for additional mortality. The largest seedlings occurred in the fire-treated plots. This was presumed due to an increased nutrient supply and reduction of competition. The seedlings grown in the openings had better growth of shoots and roots than the majority of seedlings grown under the influence of the pine stand. Amount of sunlight, degree of competition, and susceptibility to injury appeared to be the major factors contributing to the seedling size differences.

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I must first express my deepest appreciation to my project cooperator and friend, Dr. Rick Kelsey, from whom and with whom I learned so much. It was my fortune to have been affiliated with the Northern Forest Fire Laboratory and its staff during the extent of this study. Many Fire Lab scientists and technicians gave unselfishly of their time and expertise. Two of these scientists deserve my special gratitude. William Fischer, as project leader, willingly provided material, technical, and moral support. Also Dr. Rodney Norum eagerly furnished technical assistance and encouragement. A special thanks goes to my graduate committee who reviewed this manuscript and provided direction. They are Dr. Mark Behan, Dr. David Bilderback, Dr. James Habeck, Dr. Alan Harvey, and Dr. Fred Shafizadeh. Finally to my parents, special appreciation for their generous domestic support, without which this study would have suffered.

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CHAPTER I

INTRODUCTION

Ponderosa pine (Pinus ponderosa Laws.) is found throughout the western United States, from Mexico to Canada and from Nebraska to the Pacific coast, making it the most widely distributed pine species in North America (Curtis and Lynch, 1965). Although it grows under a variety of environmental conditions and different forest types, it is most commonly associated with sites that are characterized by low soil moistures and high surface temperatures at some time during the growing season (Foiles and Curtis, 1973; Pearson, 1951). Because of its drought resistance, it can survive in areas that are too dry for other conifer species. It is only on these dry sites that ponderosa pine is a climax species; as moisture becomes less prohibitive, it gives way to more competitive conifers such as Douglas-fir (Foiles and Curtis, 1973).

Throughout much of its range, natural regeneration of ponderosa pine is usually slow and frequently uncertain. In addition, obtaining successful artificial regeneration is quite difficult and often accomplished only after rather drastic measures are applied to the stand or to the site (Wellner, 1970). Certain clearcutting, burning, and mechanical site preparation practices that have been quite adequate in obtaining regeneration are increasingly coming under attack by concerned individuals (US Congress, 1970; USDA, Forest Service, 1970). Successful forest management requires either prompt regeneration following harvest cutting or

the establishment of advanced reproduction to prevent the site from lying unproductive, from a timber standpoint, for any length of time. Knowledge of the intricate factors which affect the establishment of ponderosa pine reproduction is vital if a complete understanding of regeneration problems is to be obtained.

This study was an attempt to bring forth additional information concerning the effects of various environmental factors on ponderosa pine seed germination and initial seedling establishment and growth in a western Montana ponderosa pine stand.

CHAPTER II

LITERATURE REVIEW

Ponderosa Pine Regeneration

Natural and artificial attempts at regeneration of ponderosa pine are frequently followed by inconsistent results and failures. Most ponderosa pine sites will regenerate if given enough time, but time is a critical factor in the economics of timber harvesting. Although economics is the main reason for wanting rapid regeneration, social and political pressure for a quality environment and proper management are becoming increasingly important (Stoltenberg, 1970). Therefore, one of the major problems associated with the utilization of ponderosa pine over its entire range is the rapid establishment of reproduction (Adams, 1970; Schubert, 1974; Wellner, 1970).

It appears that desired natural restocking is principally dependent upon a good seed crop, a low rodent population, adequate available moisture, and a bare mineral soil seedbed. A bare mineral soil seedbed is thought to be important because seeds and seedlings are provided with more moisture, nutrients, and sunlight by the reduction of competing vegetation and by the elimination of the dry, dense litter-duff layer (Foiles and Curtis, 1973). Baker (1951) and Fowells and Schubert (1951) observed pine invasions on mineral soil seedbeds in far greater numbers than on any other sites. Fisher (1935) tested the germination of conifer seeds from the western white pine type on a series of seedbeds and found

that ponderosa regenerated best on bare and ash-covered soils and least well on duff-covered soils. In the presence of grass associates, this pine species reproduced at a very low rate as compared to nearby areas lacking grasses (Baron, 1962; Larson and Schubert, 1969; Pearson, 1934).

The artificial preparation of sites is considered an important technique in aiding pine regeneration. Roe and Squillace (1950) found that eight times as many seedlings occurred on scarified mineral soil seedbeds as on duff-covered areas. Foiles and Curtis (1965) determined stocking of ponderosa pine to be 40 percent on artificially prepared sites three years after scarification as compared to 3 percent on sites left natural.

Because mature ponderosa pine stands generally occur as open forest types, understory vegetation is either well established before harvesting or rapidly occupies most sites after cutting. Thus, young pine seedlings may encounter tremendous competition for necessary resources. Many authors advocate scarification of a site to reduce this competition (Fisher, 1935; Foiles and Curtis, 1965; VanSickle and Hickmann, 1959). This, they believe, will increase available moisture, nutrients, and light, which are all essential for growth of young seedlings.

Besides reducing vegetation, litter removal is also thought to be necessary for proper pine restocking. Litter and duff are known to have a lower thermal conductivity and volumetric heat capacity than mineral soil. Thus, higher daytime temperatures and lower nighttime temperatures will occur on the litter-air interface (Cochran, 1970). Furthermore, the pine needles, which make-up most of the litter, are so large that they

compact poorly and dry rapidly allowing little moisture for seedling survival (Biswell, 1973).

In some instances, intraspecific competition, especially between different age classes of ponderosa pine, can have marked effects on a stand. Saplings have been known to reduce the vigor of the overstory enough to cause susceptibility to insect attack (Weaver, 1955). Conversely, overstory pines very often leave understory seedlings and saplings in a stunted and severely weakened condition (Cooper, 1960). Baker (1942) reported that in certain stands of 50-year-old pine, no reproduction existed and, generally, no vegetation whatsoever grew on the needle-strewn ground. He described a grove of pine trees in this intermediate age class which were growing around an old orchard. In the center of the orchard grew 10-year-old pine reproduction that was 12-16 feet high. Proceeding toward the 50-year-old pine grove, these 10-year-old saplings became remarkably smaller until at 15 feet from the grove they were only 2-3 feet high.

Once a seed has germinated and the seedling begins its struggle for survival, other factors can be destructive. Since pine sites are generally areas of high summer temperatures and low precipitation, the young trees, though rather drought resistant, can succumb due to lack of moisture (Wellner, 1970) and to insolation (Foiles and Curtis, 1965). Frost heaving can uproot and kill young trees during their first winter. Livestock, big game, and porcupines feed on and often kill sapling pines (Black, 1970) and trees of nearly all ages can be damaged by disease (Roth, 1970).

Fire Ecology

Harold Weaver (1943), who has extensively studied the ecological role of fire in ponderosa pine, characterized a forest dominated by this species as uneven-aged stands composed of small even-aged units in various stages of maturity. In natural pine forests, mature or overmature trees were killed by insects, disease, windthrow, or fire. This created openings for seedlings to become established. Eventually, a fire swept the area burning snags, fallen debris, and removing small seedlings and saplings. The seedlings that survived grew rapidly, while new openings created by the fire provided seedbeds for new seedlings. The young trees were thinned by repeated fires until they reached an intermediate size that was no longer susceptible to fire. These trees matured and eventually were destroyed by natural causes, allowing the cycle to be repeated (Weaver, 1943). The patches of even-aged trees were produced by a single year of germination in the openings (Weaver, 1951). Larger stands of even-aged trees were accounted for by the occurrence of large epidemics of insects, severe windstorms, or tremendous crown fires which destroyed large tracts of timber that then regenerated as even-aged stands (Weaver, 1943).

Weaver used dendrochronology to obtain evidence of periodic fires in ponderosa pine. In southwestern forests, examination of fire-scarred stumps indicated a fire frequency of 5-12 years, depending on the site (Weaver, 1951). In north central Washington, the frequency was every 8 years (Weaver, 1955), while in Oregon the average interval between fires ranged from 11-47 years (Weaver, 1959).

Weaver (1955) believes that since the settlement of the white man in the West, overgrazing and fire exclusion have brought significant changes to the pine forests. Heavy use by livestock reduced grass competition and soil cover, thereby providing suitable seedbeds for pine seedlings. This often led to large, dense stands of reproduction, which stagnated. Fire exclusion also prevented the natural thinning of these dense stands and allowed more tolerant species, such as Douglas-fir, white fir, and incense-cedar, to invade areas where ponderosa pine was not climax. Lunan and Habeck (1973) found that since fire suppression in Glacier National Park mesophytic conifers, such as Douglas-fir and spruce, were invading old-growth ponderosa pine stands. These stands had been maintained essentially as pure ponderosa pine presumably by fire periodicity. Furthermore, where fire has been suppressed, the fire hazard has been increased because of larger, flammable stands of reproduction and the accumulation of windfalls and litter over the years (Weaver, 1955). Areas where cool, surface fires once occurred now burn very hot and fast, usually through the crowns.

Observations on burned areas previously protected from fire gave further support to Weaver's beliefs. In one example, fire swept a forest characterized by overgrazing and fire exclusion. In this area, thick reproduction was stagnated and the vigor of the overstory was being affected. In addition, a pine beetle epidemic created serious fire hazards. Twenty years after the fire, the conditions were examined in both burned and unburned portions of the forest. The unburned forest was similar to what it had been 20 years earlier. However, the part of the stand that had burned was characterized by well-spaced reproduction with excellent growth.

The overstory was healthy and vigorous with a park-like appearance, relatively free of accumulated fuel and brush (Weaver, 1959).

Cooper (1960) has studied southwestern ponderosa on three areas of east-central Arizona. Intensive field work was conducted in an old-growth forest, a reproduction stand previously logged, and a primitive area. The primitive area had experienced light grazing and periodic fires. The other two had been heavily grazed and free of fire since protection in 1924.

The primitive area was more open than either the old-growth forest or the reproduction stand with more grass covering the ground, and regeneration occurring almost exclusively in these openings. This area also had fewer smaller trees and more large diameter trees than either of the other two areas. The absence of small trees within the stand at the primitive area was attributed to root competition and periodic fires. In the old-growth forest the reproduction occurred under the mature canopy as well as in the sparse openings. The trees in the openings grew more vigorously than those under the canopy.

The evidence suggests that ponderosa pine populations are highly dependent upon frequent fires for stability. They may burn more readily than non-fire dependent communities because of site conditions and a tendency for natural selection to favor the development of characteristics which may make them more flammable but more fire-tolerant (Mutch, 1970). So we have an interesting interaction. "Ponderosa pine-grasslands are dependent on frequent surface fires for their health and stability, and on the other hand, frequent surface fires are dependent on the plant

communities that produce the fuels that carry fire, each being dependent on the other" (Biswell, 1973).

Since natural fire has often been shown to be beneficial, many feel that prescribed fire can likewise be an effective tool in ponderosa pine regeneration. Roe and Squillace (1950) have illustrated that prescribed fire prepared sites well enough to cause marked increases in pine reproduction as compared to unburned sites. Another study in northwestern Montana resulted in similar findings. Broadcast burning helped the establishment of twice as many seedlings as on untreated areas (Shearer and Schmidt, 1970). Schultz and Biswell (1959) performed a study in which the effects of different seedbed preparations on ponderosa pine seedling emergence were investigated. Eight different treatments were applied including burning different plots at different times before seedfall, burning and rototilling, bulldozing, raking, and controls. The total elimination of litter, duff, and vegetation by handraking resulted in highest seedling emergence. An important relationship was found between the time interval from burning until seedfall, and the number of new seedlings established. The sooner the seedfall occurred after burning, the more seedlings appeared. This was attributed to the deterioration of seedbed conditions through time, caused by the gradual build-up of competition, crusting and smoothing of the soil surface by rain and wind, and the accumulation of fallen needles. Schultz and Biswell (1959) concluded their report with three principles they felt were important for ponderosa pine regeneration: "(1) mineral soil should be exposed so that seed and subsequent seedling roots can be in contact with a medium of high moisture-holding capacity; (2) the amount of dead litter which may

shade, smother, or obstruct the emergence of newly germinated seedlings should be reduced, and; (3) since the seedbed deteriorates rapidly, it should be prepared just prior to or during the seedfall from heavy cone crops."

Additional effects of fire upon ponderosa pine regeneration were demonstrated in a number of studies by Vlamis and associates. In the first they showed that fire increased the amount of nitrogen and phosphates in the soil (Vlamis et al., 1955). Later, their experiments revealed that ponderosa pine seedlings responded greatly, by increased growth, to artificially added nitrogen (Vlamis et al., 1957), and to burned soils, presumably because of increased nutrients (Vlamis et al., 1956). Wagle and Kitchen (1972) also showed that the soils in a new wildfire area contained more phosphates and nitrogen than soils in a similar area which was untouched by fire.

Allelopathy

In recent years natural plant chemicals have been shown to influence the ecological relationships of plant-plant, plant-animal, and plant-insect interactions (Rice, 1974). Plant-plant chemical interaction, or allelopathy, is defined by Rice (1974) as, ". . . any direct or indirect harmful effect by one plant (including microorganisms) on another through the production of chemical compounds that escape into the environment." It is important to emphasize that allelopathy is independent of competition. Allelopathy involves the placement of natural chemicals into the environment, whereas competition involves rivalry for environmental factors such as light, moisture, and nutrients (Rice, 1974).

Detailed ecological investigations of conifer trees that conclusively demonstrate the involvement of chemicals in species patterning or succession are very limited. The need for further work along this line has been emphasized by Debell (1970) and Rice (1974). One of the most comprehensive studies was conducted by Lee and Monsi (1963, cited in Rice, 1974) in Japanese red pine forests in Korea and Japan. Bioassay experiments revealed that plant tissues from Japanese red pine and soils from beneath its canopy were toxic to species not common to red pine forests, but nontoxic to those species commonly found within the forest.

In another study, evidence was revealed concerning Scotch pine seedling mortalities in tree nurseries in parts of Germany. The nursery soils had been fertilized for years with a manure and pine needle mixture. Experimentation with this problem revealed the existence of toxic compounds (Hippeli, 1968). These pine needle compounds not only reduced the seed germination of Scotch pine, but also reduced seedling root growth. Hippeli stated that phytotoxins leached by precipitation probably play an important role in seedling establishment in natural Scotch pine forests.

A number of investigations have been conducted dealing with herbage production within and adjacent to ponderosa pine stands. Pase (1958), Moir (1966), and McConnell and Smith (1971) reported a dramatic decrease in herbage within pine stands compared to nearby openings. Reasons for this were thought to be crown cover and resulting shading, low soil nitrogen due to competition, and the physical and possibly chemical influence of pine litter. Eckert (1975) has revealed results which indicate that ponderosa pine needles produce chemical by-products which

adversely affect some understory vegetation creating obvious ecotones in and around ponderosa pine trees.

Rietveld (1975) has shown under laboratory conditions that Arizona fescue extracts reduce ponderosa pine seed germination and initial radicle growth compared to distilled water controls. Also, ponderosa pine litter extracts reduced ponderosa seedling radicle lengths (Jameson, 1968). After many years of observation and experimentation, Hall (1975) stated that he suspects ". . . a selective inhibitory substance in ponderosa pine litter that is destroyed with periodic underburning. Without fire, this substance is free to build up in the soil and reduce pine growth."

Although no toxins have been identified, the above studies point out the possibility that allelopathy, working with the complex of other environmental factors, may have a role in ponderosa pine regeneration. Weaver (1943), Cooper (1960), and Biswell (1973) discussed the poor seedling establishment and growth within mature stands. The best regeneration occurred in the openings, which were created periodically through the death of older trees by insects, disease, or wind, or by the removal of a large stand of trees by fire. Furthermore, investigations concerning regeneration of ponderosa pine after logging have demonstrated the benefits of well-scarified seedbeds, either by burning or mechanical means.

CHAPTER III

GENERAL DESCRIPTIONS AND PROCEDURES

Study Site

The study site was located 40 miles northeast of Missoula on the Blackfoot-Clearwater Game Range (SW $\frac{1}{4}$ sec. 29, T. 15 N., R. 14 W.). The area under investigation was quite small, only 5.7 hectares (14 acres). It was dominated by a ponderosa pine overstory (Table 1) as determined by the quarter method (Cottam and Curtis, 1956), with intermittent openings in the stand where pine regeneration was frequently abundant (Figure 1). Pine regeneration was nearly absent in the understory.

Table 1. Stand inventory for trees over 10.0 cm d.b.h.

Tree Species	Relative Frequency	Relative Density	Relative Dominance	Trees per Hectare	Basal Area per Tree
	- - - - - Percent	- - - - -	- - - - -	No. Trees	Meter ²
Quaking aspen	6.7	2.0	1.0	0.4	0.05
Douglas-fir	10.0	4.0	2.4	0.8	0.06
Ponderosa pine	83.3	94.0	96.6	16.8	0.10

The entire stand was located on valley-bottom alluvial soils (Clapp, 1932), bound by large grass fields on the east and west and foothills on the north and south (Figure 2). The site was excellent for ponderosa pine growth with an index of 95 feet in 100 years (Meyer, 1938). However, close observation indicated that Douglas-fir was invading the understory



Figure 1. Ponderosa pine regeneration prospering in small openings within the pine stand.



Figure 2. Part of the ponderosa pine-grassland in which the study was conducted. Note pine seedlings advancing into grassland.

and would probably dominate eventually, creating a Douglas-fir - pine grass habitat type (Pseudotsuga menziesii-Calamagrostis rubescens) (Pfister et al., 1974).

Festuca scabrella was the dominant vegetative species in the large openings and the intermittent clearings within the stand. This species was also the major component of the understory vegetation beneath the pine as long as the trees did not form a continuous canopy. In heavily forested areas, Calamagrostis rubescens was dominant. Further information regarding understory vegetation will be discussed later.

Because this site is part of the Blackfoot-Clearwater Game Range, livestock grazing is not allowed and has not been a significant factor since the early 1950's. The impact of deer and elk use has been minimal. Some of the largest pine trees were selectively logged in the early 1950's, but their removal did not influence the field studies conducted here.

Field Study Design

The field study was established in the summer of 1974 in an attempt to determine which areas within pine stands and, perhaps, which specific parts of the pine trees are influential in ponderosa seed germination and seedling growth. To accomplish this objective, two major treatment groups were set up at the study site. The first group of treatment plots was situated within a ponderosa pine stand where little or no pine regeneration was present. The second group was located in large openings, near, but not under the direct influence of the ponderosa pine stand (Figure 3). Within both groups a series of treatments were set up. Three



Figure 3. Examples of selected plot placement. Plots within the pine stand (top and middle) and plot in opening (bottom).

separate plots were replicated for each treatment described. Each plot was 16 square meters (4 x 4 m) in size. The entire plot received a specific treatment and was fenced with one-quarter inch hardware cloth. The fence extended 30 inches above and 6 inches below the ground. Before placing the fence into a six-inch trench, the entire length of the trench was lined with plastic to prevent surface roots of outside vegetation from entering the plots. The fence was inserted into the plastic-lined trench which was then filled with soil and packed tightly. A twelve-inch strip of heavy-duty aluminum foil was secured along the top of the fence to discourage rodents from climbing into the plots.

A 3 x 3 meter square was centered and permanently marked within each fenced plot, leaving a one-half meter border between the square and the fence. Each 3 x 3 meter square was planted in November with 400 unstratified ponderosa pine seeds collected on site (details of the planting are discussed in the next chapter). The one-half meter border between the fence and the 3 x 3 meter square allowed investigators to enter the plots during the 1975 growing season without disturbing the planted areas.

Within the pine stand, six different treatments with three replications each were established (Figure 4). In the first treatment, or canopy plots, each replicate was situated directly under a thick tree canopy with all organic matter and vegetation removed. An effort was made to keep soil disturbance at a minimum. This treatment was located to emphasize the physical and perhaps chemical effect of the overstory canopy. The second treatment, called the litter plots, was established by removing all live vegetation and leaving the litter and duff undisturbed. Selected placement helped to minimize the canopy effect and stress the impact of

PINE-INFLUENCED TREATMENTS

Stemflow plots:
S1, S2, S3.

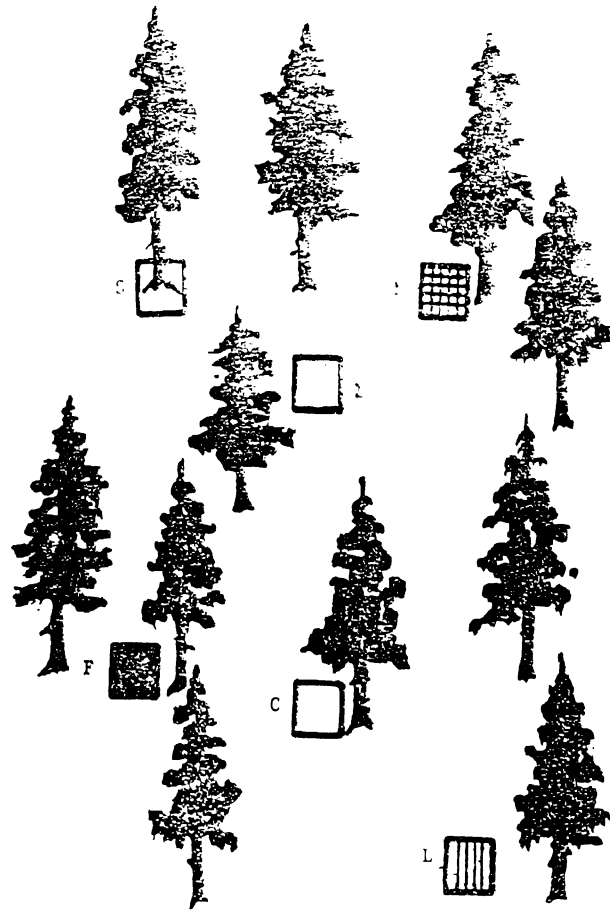
Natural plots:
N1, N2, N3.

Near plots:
Z1, Z2, Z3.


Fire plots:
F1, F2, F3.


Canopy plots:
C1, C2, C3.


Litter plots:
L1, L2, L3.



OPENING TREATMENTS

OC  Opening cleared plots:
OC1, OC2, OC3.

OL  Opening litter plots:
OL1, OL2, OL3.

ON  Opening natural plots:
ON1, ON2, ON3.

Key:





-  Litter, duff, and vegetation removed to mineral soil.
-  Vegetation removed. Litter and duff left or placed on plot.
-  Litter, duff, and vegetation left natural.
-  Burned.

Figure 4. Position and treatment of field study plots.

the organic layer. In the third treatment, all dead organic matter and live vegetation was removed from each plot except for one large ponderosa pine tree located in the center. Trees with small crowns were chosen in an effort to minimize the canopy effect and accentuate the effect of stemflow. It was, of course, impossible to eliminate all canopy and root influences. These are called the stemflow plots. In treatment four, each replicate was located within a group of pine trees but not directly under a canopy. All vegetation and organic matter was removed. These "near" plots, as they are called, were under the general influence of the stand and not subjected to the direct and complete impact of any one part of the pine trees. Treatment five included the natural plots. These were placed under a heavy pine canopy with all vegetation and organic matter left undisturbed. These had the potential for receiving maximum impact from all parts of the pine trees. The burned plots comprised the sixth and last treatment. They were placed under a pine canopy or within the pine stand where regeneration was very sparse or absent (Figure 5). Details of the burning procedure will be discussed later.

A series of three treatments, with three replications each, were established away from the pine trees in the openings dominated by grasses and forbs (Figure 4). The first treatment, the opening-cleared plots, had all the dead organic matter and live vegetation removed. These were set up for comparison with similar treated areas within the pine stand. Treatment two, called the opening-litter plots, had all organic matter and vegetation removed, but replaced with pine litter and duff to cover the topsoil. A layer of humus was placed first, followed by a layer of decomposing duff that was then covered with a layer of recently fallen

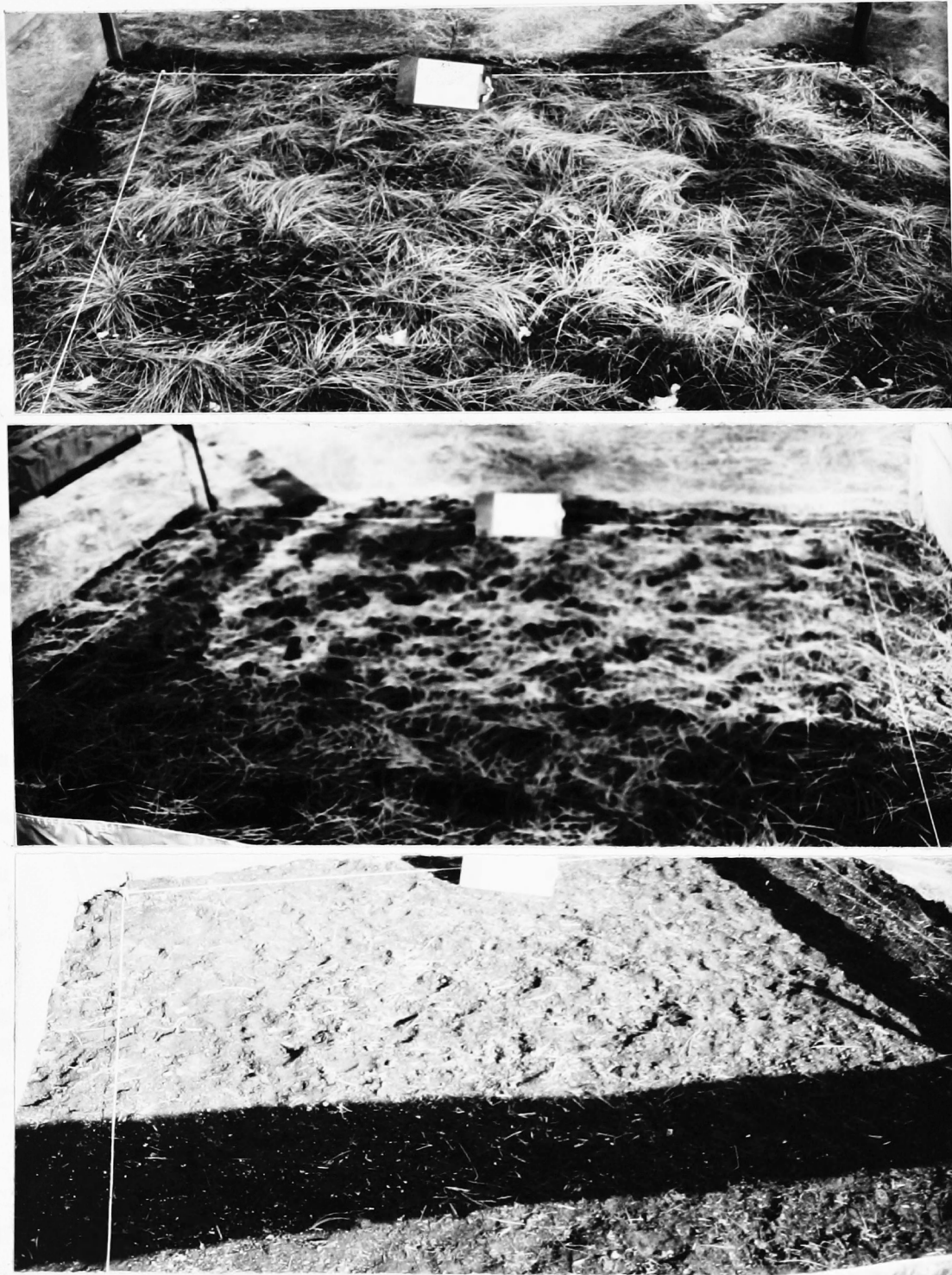


Figure 5. Examples of treatments; top photo shows litter and vegetation undisturbed (natural or opening-natural plots), middle shows litter left or placed on plot (litter or opening-litter plots), and bottom shows bare mineral soil from which all organic matter has been removed (opening-cleared, canopy, stemflow, near plots).

litter. These plots were designed as an additional check on the influence of pine litter and duff. The last treatment consisted of opening plots left untreated and were known as the opening-natural plots (Figure 5).

Burning Procedure

On September 5, 1974, a fireline was built around three, 25-square meter areas, which had been selected for the fire plot locations. Ten heat sensors were systematically placed into each of the plots. Each sensor consisted of an 8 x 15 cm piece of asbestos, painted with 12 heat sensitive lacquers. These lacquers melt when a corresponding temperature is reached. The fusing temperatures ranged from 39°C (103°F) to 343°C (650°F). Four chromal-alumel thermocouples were placed in each plot to monitor soil surface temperatures during the burning. The functioning of these thermocouples was erratic; therefore, their data were not used.

Moisture contents of the litter and duff shortly before burning are shown in Table 2. Plot F1 had the driest conditions and F2, located under the heaviest canopy, had the wettest.

Table 2. Percentage moisture content of the litter and duff on the fire plots prior to burning

	F1	F2	F3
	Percent		
Surface litter	5.7	8.6	7.2
Decomposing duff	11.3	19.4	12.4

After the firelines were constructed and the temperature sensors were placed, the burning began. Ignition was achieved with the use of a

hand-held propane torch. The fires were allowed to spread at will within the plots. Winds were light and variable, but aided the fires with a fanning action.

Plot F1 was ignited first, in the late morning. The ambient temperature was 67°F and the relative humidity was 40 percent. This plot burned "hot," evenly, and completely. Maximum mineral soil surface temperatures throughout the plot ranged from 118°C (244°F) to greater than 343°C (650°F) with the average of ten maximums being 182°C (360°F) (Table 3). Most of the organic layer was consumed, leaving a thin layer of ash (Table 4).

Table 3. Number of heat sensors reaching respective soil surface temperatures

F°	Temperatures										
	103	103	109	119	194	244	300	350	400	500	650
C°	39	39	43	48	90	118	149	177	204	260	343
Plot	Number of Sensors										
F1						2	4	1	1	1	1
F2	3		1	1	1	1		2			1
F3	2	1	2				4		1		

Plot F3 was burned next, in the early afternoon. The ambient temperature was 72°F with a relative humidity of 44 percent. One-half of this plot burned quite well because of an accumulation of pine litter. The rest of the plot, which contained a sparse mixture of pine and grass litter, burned lightly and in patches, leaving a portion of organic layer (Table 4). Soil surface temperatures reached maximums ranging from less

than 39°C (103°F) to greater than 204°C (400°F) with an average of 93°C (200°F) (Table 3).

Table 4. Average litter and duff depths and weights, with standard deviations, before and after burning

Plot	Depth	Depth	Reduction	Weight	Weight	Reduction
	Before	After		Before	After	
	Cm	Cm	Percent	Kg/m ²	Kg/m ²	Percent
F1	7.13 ±2.34	1.13 ±0.83	84.2	5.54 ±1.69	0.47 ±0.40	91.3
F2	7.25 ±1.98	2.44 ±1.57	66.3	5.21 ±1.86	1.82 ±1.41	65.0
F3	3.88 ±1.73	1.38 ±1.03	64.4	3.85 ±2.75	1.32 ±1.20	65.7

In the late afternoon, plot F2 was ignited when the ambient temperature was 76°F and the relative humidity was 25 percent. The fire spread slowly and burning was spotty and incomplete. This was probably due to higher litter and duff moisture contents and shading during burning. Litter and duff were completely consumed in isolated areas, but only lightly scorched in others. Soil surface maximum temperatures ranged from less than 39°C (103°F) to greater than 343°C (650°F) with the average of ten readings being 100°C (230°F) (Table 3). The percentage of litter and duff reduction was similar to F3 but the actual amounts were much greater (Table 4).

Most of the burning was completed within one hour following ignition. However, smoldering and slow consumption of larger materials, such as pine cones, continued for about 24 hours.

Seed Planting Procedure

A 3 x 3 meter square planting frame was constructed with three stationary sides and one movable side (Figure 6). Three sides were marked at 15.0 cm intervals. With the frame in position bordering the plot, seeds were placed on the ground directly beneath each 15.0 cm mark on the movable side. This side was then progressively moved across the plot at 15.0 cm intervals marked on the parallel stationary sides. This allowed 400 seeds to be planted in each plot in a series of 20 rows and 20 columns. Each row and column began and ended 7.5 cm from the plot border. In addition to seed planting, the frame was used throughout the growing season to locate the planted seeds as they germinated. To insure that the frame could be removed and returned to the exact position at a later date, permanent markers were placed in each plot. In the stemflow plots the tree in the center created a situation that required extra rows to be planted to compensate for the area occupied by the tree.



Figure 6. Frame along which ponderosa pine seeds were systematically planted and resulting seedlings were observed.

Planting began on November 1 and ended on November 11, 1974.

The seeds were pushed slightly into the ground, but not covered, to eliminate rolling or blowing out of place. In the natural plots, litter plots, and opening-litter plots, the seeds were placed below the litter and duff layer close to mineral soil. This was done because during the natural seed count (discussed later) it was observed that most seeds filtered down deep into the organic layer after they had lost their wings, and many came to rest very near the mineral soil surface. In all plots the seeds were placed at the exact spot below the mark on the movable bar, regardless of seedbed variation (bare ground, clumps of grass, rotten logs, etc.).

CHAPTER IV

ENVIRONMENTAL CHARACTERISTICS OF THE FIELD PLOTS

Vegetational Analysis

During July, 1974, after the plots had been permanently located but prior to treatment, the understory vegetation was sampled. Four parallel lines, equally spaced from each other and the plot boundaries, were laid out in each plot. A 20 x 50 cm quadrat was then used to estimate canopy cover for the grasses, sedges, forbs, and shrubs at three randomly selected nonoverlapping points on each of the four lines. The canopy cover percentage for each species was estimated to the nearest 5 percent cover class (0-4.9, 5.0-9.9, ..., 95.0-100.0). The midpoint of each class was then used in the final calculations.

In order to simplify the presentation of this information, the total understory canopy cover on each treatment and the canopy cover of the three most influential grasses or sedges and three most influential forbs or shrubs on each treatment are shown in Table 5. Those species with the greatest canopy cover were considered the most influential. Table 6 provides a list of all species encountered during the sampling.

Festuca scabrella was the dominant grass species in the open fields and intermittent openings within the stand. Stipa richardsonii, Danthonia unispicata, and Festuca idahoensis were also important in these areas. When large trees were present but did not form a continuous canopy cover, Festuca scabrella remained the dominant grass with the major

associates being Calamagrostis rubescens, Carex filifolia, Carex rossii, or Carex geyeri. Within the stand where the pine formed a rather continuous canopy, Calamagrostis rubescens was dominant, although Festuca scabrella was usually present.

Table 5. Amounts of understory vegetation on study plots before treatment

Treatment	Total Canopy Cover %	Grasses and Sedges	Canopy Cover %	Forbs and Shrubs	Canopy Cover %
Opening-Cleared	30.4	<i>Festuca scabrella</i>	12.9	<i>Antennaria</i> spp.	2.6
		<i>Stipa richardsonii</i>	6.4	<i>Hieracium albertinum</i>	1.0
		<i>Danthonia unispicata</i>	1.7	<i>Solidago</i> spp.	1.0
Opening-Litter	29.6	<i>Festuca scabrella</i>	11.4	<i>Arctostaphylos uva-ursi</i>	4.8
		<i>Stipa richardsonii</i>	6.4	<i>Antennaria</i> spp.	1.4
		<i>Danthonia unispicata</i>	2.0	<i>Solidago</i> spp.	1.3
Opening-Natural	33.2	<i>Festuca scabrella</i>	16.0	<i>Antennaria</i> spp.	1.4
		<i>Stipa richardsonii</i>	6.2	<i>Solidago</i> spp.	1.0
		<i>Carex geyeri</i>	2.9	<i>Achillea millefolium</i>	1.0
Fire	22.1	<i>Festuca scabrella</i>	8.1	<i>Solidago</i> spp.	4.1
		<i>Carex rossii</i>	3.1	<i>Berberis repens</i>	1.0
		<i>Danthonia unispicata</i>	1.0	<i>Achillea millefolium</i>	1.0
Litter	29.6	<i>Festuca scabrella</i>	19.6	<i>Solidago</i> spp.	1.7
		<i>Carex rossii</i>	1.9	<i>Galium</i> spp.	1.7
		<i>Carex geyeri</i>	1.3	<i>Penstemon</i> spp.	1.0
Stemflow	33.1	<i>Festuca scabrella</i>	21.3	<i>Solidago</i> spp.	2.2
		<i>Carex geyeri</i>	2.9	<i>Berberis repens</i>	1.5
		<i>Carex rossii</i>	1.0	<i>Arctostaphylos uva-ursi</i>	1.0
Near	35.5	<i>Calamagrostis rubescens</i>	15.3	<i>Arctostaphylos uva-ursi</i>	5.3
		<i>Festuca scabrella</i>	6.3	<i>Berberis repens</i>	1.9
		<i>Carex rossii</i>	1.0	<i>Penstemon</i> spp.	1.6
Canopy	36.5	<i>Festuca scabrella</i>	22.8	<i>Heuchera cylindrica</i>	2.6
		<i>Carex filifolia</i>	6.2	<i>Gaura triflorum</i>	1.0
		<i>Calamagrostis rubescens</i>	1.0	<i>Solidago</i> spp.	1.0
Natural	18.5	<i>Festuca scabrella</i>	6.9	<i>Penstemon</i> spp.	3.1
		<i>Calamagrostis rubescens</i>	2.2	<i>Solidago</i> spp.	1.7
		<i>Carex geyeri</i>	1.6	<i>Galium</i> spp.	1.1

The forbs or shrubs present demonstrated greater variability but those most frequently encountered included Solidago spp., Arctostaphylos uva-ursi, Penstemon spp., and Antennaria spp.

Table 6. Species tallied in understory vegetation analysis

Forbs	Shrubs and Trees	Grasses and Sedges
<u>Achillea millefolium</u>	<u>Arctostaphylos uva-ursi</u>	<u>Agropyron spicatum</u>
<u>Anemone spp.</u>	<u>Berberis repens</u>	<u>Calamagrostis rubescens</u>
<u>Antennaria spp.</u>	<u>Eriogonum spp.</u>	<u>Carex filifolia</u>
<u>Chrysopsis villosa</u>	<u>Pinus ponderosa</u>	<u>Carex geyeri</u>
<u>Collinsia parviflora</u>	<u>Pseudotsuga menziesii</u>	<u>Carex rossii</u>
<u>Erigeron compositus</u>	<u>Rosa spp.</u>	<u>Danthonia californica</u>
<u>Erigeron glabellus</u>		<u>Danthonia unispicata</u>
<u>Fragaria virginiana</u>		<u>Festuca idahoensis</u>
<u>Galium spp.</u>		<u>Festuca scabrella</u>
<u>Geranium viscosissimum</u>		<u>Koeleria cristata</u>
<u>Geum triflorum</u>		<u>Poa pratensis</u>
<u>Heuchera cylindrica</u>		<u>Stipa richardsonii</u>
<u>Hieracium albertinum</u>		
<u>Hypericum perforatum</u>		
<u>Lithospermum ruderale</u>		
<u>Orthocarpus tenuifolius</u>		
<u>Penstemon spp.</u>		
<u>Perideridia gairdneri</u>		
<u>Polygonum douglasii</u>		
<u>Potentilla arguta</u>		
<u>Potentilla gracilis</u>		
<u>Solidago spp.</u>		

Organic Layer

The depths and dry weights of the organic layer on each plot were determined for comparison before treatment. No effort was made to separate pine litter from grass and forb litter. The majority of the organic matter in the canopy, litter, and natural treatment plots was pine residue, whereas in the fire, stemflow, and near treatment plots, the organic matter was a mixture of pine and grass residues. All of the organic matter in the opening treatment plots was from grasses and forbs.

Soil samplers, 12.5 cm in diameter, were used to take cores of litter and duff from eight points around every plot; one from each corner and the middle of each side in the one-half meter boundary zone. The samples were placed into paper bags, returned to the laboratory, placed into an oven set at 105°C, dried overnight (15 hours), and weighed.

Naturally, the plots associated with one or more large pine trees had the most litter and duff, both by depth and weight (Figure 7). The stemflow plots had less organic matter than the other pine-associated plots, except for the near plots, because they (stemflow plots) were placed beneath only one small-crowned tree. The near plots, as explained earlier, were placed close to, but not directly under a pine canopy. This explains why the organic accumulation there was light.

Natural Seed Occurrence

During the last week of October, 1974, the number of naturally occurring seeds was determined for each plot by quadrat sampling. Three equally spaced parallel lines were positioned in each plot. The seeds were counted in four randomly-placed 20 x 50 cm quadrats on each line.

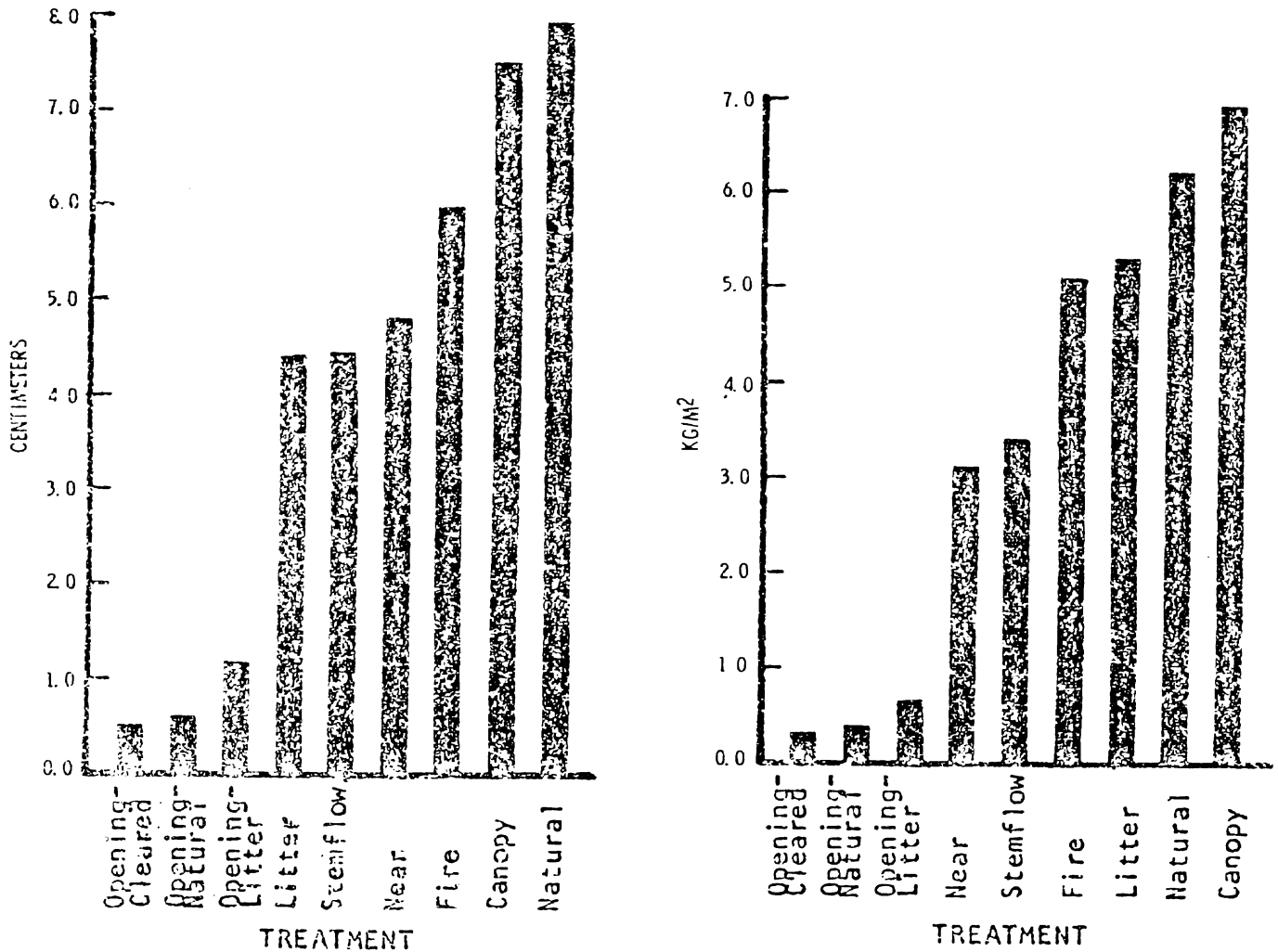


Figure 7. Depths and weights of organic matter on study plots before treatment.

As might be expected, the plots associated with the pine stand had much greater numbers of natural seeds than plots in the openings (Figure 8). The greatest number of seeds ($151/\text{m}^2$) occurred on the canopy plots, and the least ($29/\text{m}^2$) were found on the opening-cleared plots. As a group, the opening treatments averaged only $31.4 \text{ seeds}/\text{m}^2$ compared to $112.3 \text{ seeds}/\text{m}^2$ on the pine-associated plots. Thus, the areas adjacent to seed-producing trees have the greatest potential for seedling occurrence due to greater seed numbers.

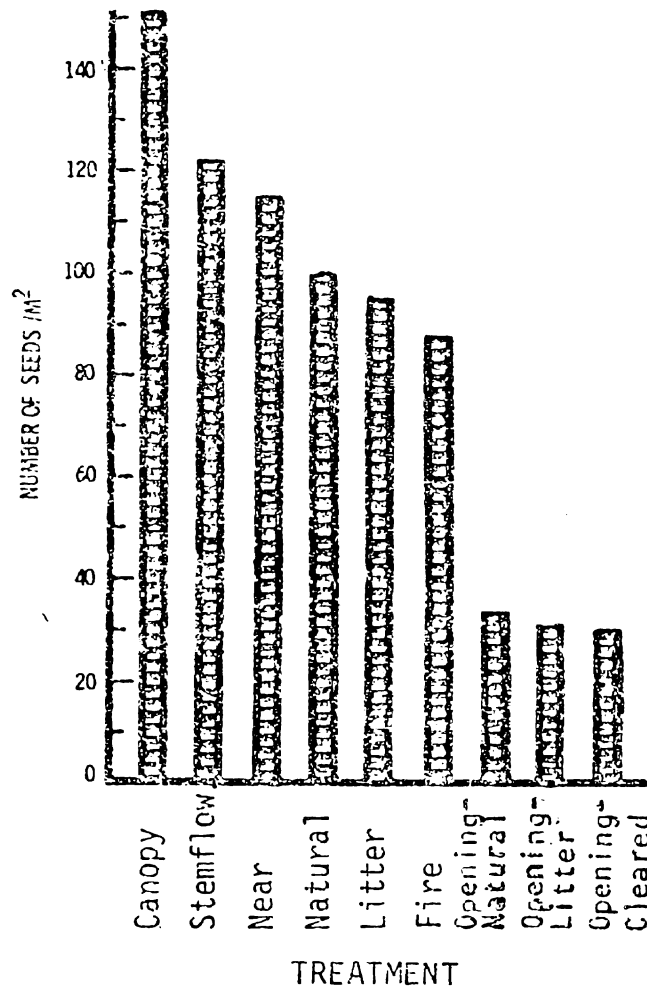


Figure 8. Number of naturally fallen seeds per treatment.

General Weather Conditions

A weather station was established in a small opening near the middle of the study site. The instruments used included a hygrothermograph, maximum-minimum thermometers, and a fan-operated psychrometer, all located inside a Cotton Region weather shelter. A recording rain gauge and a standard rain gauge with measuring stick were placed near the shelter. Weather data were collected from May 14 until November 11, 1975.

The nearest official weather station was located approximately 12 miles due east of the study site near the town of Ovando. This station was situated in a grass prairie with few trees and at some distance from the nearest hills. Since most weather systems move from west to east, it seems likely that the weather systems which influence the study site also pass near Ovando. A comparison of weather data collected during the summer of 1975 confirmed this. Tables 7 and 8 present the average monthly air temperatures and total monthly precipitation occurring on the study site. In addition, these tables include a summary of temperature and precipitation data collected at the Ovando weather station from 1941-1970 (U.S. Dept. Comm., 1973). It was assumed that these data corresponded to "normal" weather conditions encountered near the study site. Obviously, the two locations did not have exactly the same weather, but these comparisons are the best available.

Average monthly temperatures varied little from the approximated normal monthly temperatures. The study site was slightly cooler than normal during the months of June, August, and October and slightly warmer during July and September. The precipitation varied greatly from normal with all but one month receiving excessive amounts of rainfall, resulting in 5.8 inches (147.4 mm) above the normal for the 1975 growing season. The 12.66 inches (321.6 mm) that fell during the five-month period amounts to over 77 percent of the normal yearly precipitation. Obviously, 1975 had a much wetter than average growing season.

Figure 9 represents a weekly precipitation record for the 1975 growing season. The three longest periods without rain were 11 days from

Table 7. Average monthly air temperatures at the study site and normal monthly approximations

Month	Average Temperature				Maximum		Minimum	
	Study Site		Normal (Ovando)		Study Site		Study Site	
	^o F	^o C	^o F	^o C	^o F	^o C	^o F	^o C
June	50.4	10.2	54.3	12.4	66.1	18.9	34.7	1.5
July	64.7	18.2	61.3	16.3	83.5	28.6	45.9	7.7
August	57.3	14.1	59.6	15.3	74.8	23.8	39.7	4.3
September	51.3	10.7	50.7	10.4	72.4	22.4	30.2	-1.0
October	38.8	3.8	41.4	5.2	50.0	10.0	27.2	-2.7
Averages	52.5	11.4	53.5	11.9	69.4	20.7	35.5	1.9

Table 8. Total monthly precipitation at the study site and normal monthly approximations

Month	Study Site		Normal (Ovando)		Difference	
	Inches	Mm	Inches	Mm	Inches	Mm
June	2.69	68.3	2.47	62.7	+0.22	+ 5.6
July	2.81	71.4	1.00	25.4	+1.81	+46.0
August	2.10	53.3	0.99	25.1	+1.11	+28.2
September	1.15	29.2	1.22	31.0	-0.07	- 1.8
October	3.91	99.3	1.18	30.0	+2.73	+69.3
Total	12.66	321.6	6.86	174.2	+5.80	+147.2

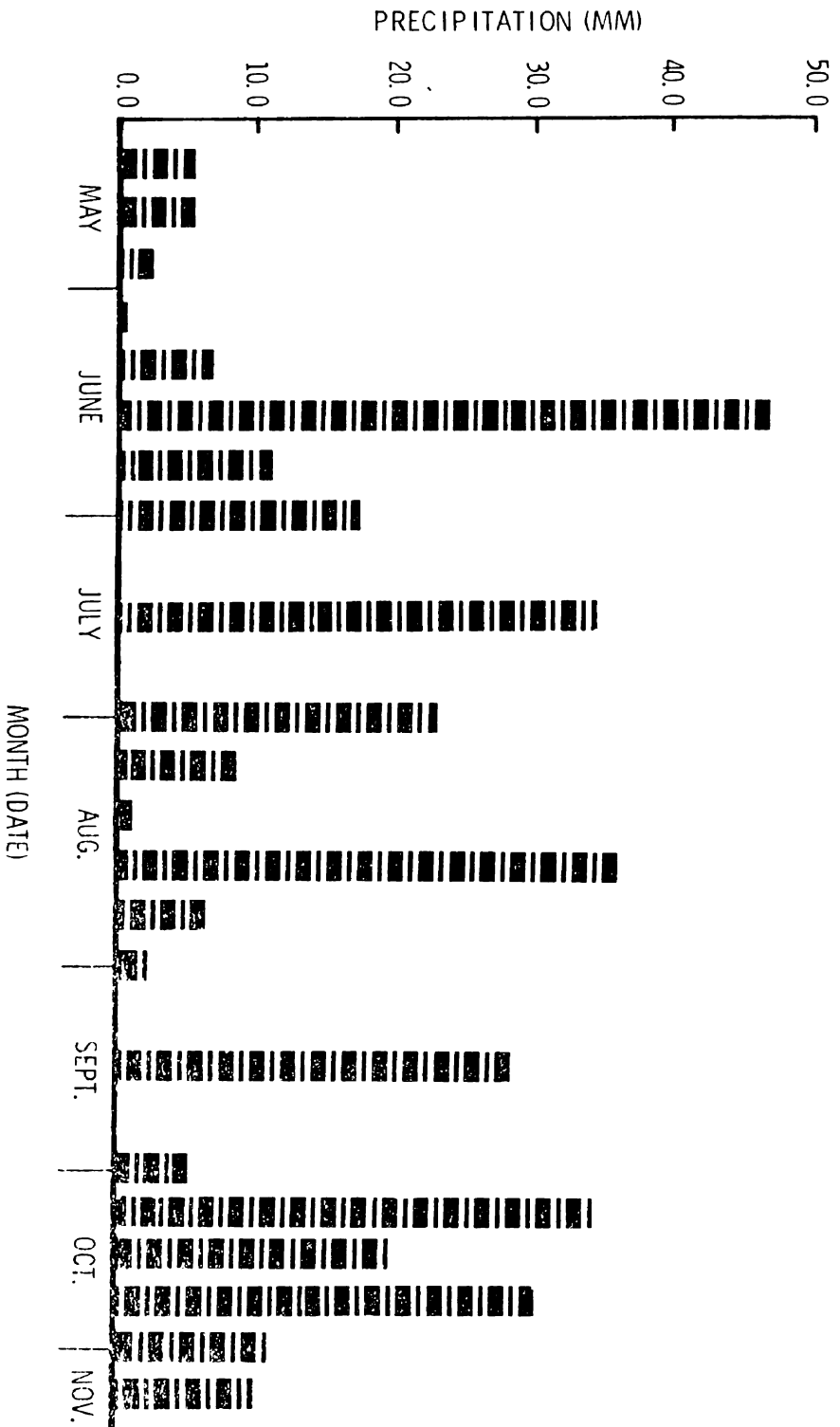


Figure 9. Weekly amounts of precipitation at the study site.

July 18 to July 29, 14 days from September 2 to September 16, and 15 days from September 19 to October 4. The dry periods in September were separated by 1.12 inches (28.4 mm) of rain.

Soils Analyses

Procedures. The soils of each plot were sampled at three to four-week intervals starting June 4 and ending September 3, 1975. The three other collection dates were June 24, July 21, and August 13. At each of these five dates the ammonium and nitrate ion concentrations and pH were measured in addition to the soil moisture content. On three of the sampling dates—June 4, July 21, and September 3—additional analyses were made for phosphates, potassium, magnesium, manganese, calcium, sodium, copper, zinc, and iron. Measurement of sulfate content and particle size distribution were made only on the September 3 sample.

Using a soil auger 2 cm in diameter, six samples of soil were collected within each plot at regular intervals on two lines running parallel to the plot border. These samples were thoroughly mixed in the field, passed through a 2.00 mm soil sieve into a plastic bag that was immediately sealed, and placed into an ice chest. Sampling depth varied between collection dates starting with 7.0 cm on June 4, 11.0 cm on June 24, and 15.0 cm on the three remaining dates. The depths for the June 4 and 24 collections were approximately equal to the longest roots measured by uprooting newly germinated seedlings on several plots. It became impossible to determine root depth for every sampling date, so 15.0 cm was chosen as a depth that would adequately evaluate the moisture and nutrient status of the soil in each plot. The soil samples were returned to the

laboratory where a subsample was immediately prepared for soil moisture analysis by the gravimetric method.

The NO_3^- ion concentration was measured with a specific ion electrode by extracting 25.0 gm of fresh soil with 25.0 ml of distilled water, shaking for 5 minutes, and centrifuging to remove the soil particles (Harvey et al., 1976). The NH_4^+ ion concentration was measured with a NH_3 electrode by extracting 25.0 gm of fresh soil with 25.0 ml of 2N KCl, shaking for one hour, and centrifuging (Harvey et al., 1976). The soil pH was determined using a glass electrode pH meter on the distilled water extract prior to the measurement of the NO_3^- concentration.

Samples of soil were oven dried at 70°C for 48 hours and passed through a 1.0 mm soil sieve. Duplicate 10.0 gm samples from each plot were analyzed for extractable Na, Ca, Mg, K, Cu, Mn, Fe, and Zn. Four 25 ml 1N NH_4OAc extracts were made for each sample by shaking, centrifuging, and filtering. The final volume was brought to 100.0 ml at room temperature. The eight elements were then analyzed on a Techtron AA-5 Atomic Absorption Spectrophotometer. A 1 percent lanthanum (v/v) solution was added to the extracts prior to the Ca measurement to suppress phosphorus interference (Stark, 1975). The soil phosphates were determined by a colorimetric analysis of $\text{NH}_4\text{-HCl}$ extracts (Olsen and Dean, 1965) and sulfates were measured by the barium chloride turbidimetric method (Bardsley and Lancaster, 1965). A mechanical analysis was conducted on the soils collected September 3 by soaking overnight with a Calgon solution and analyzing by the Bouyoucos hydrometer method (Bouyoucos, 1936).

Cation and anion content. In general, the nutrient status of the plots associated with the pine stand was equal to or greater than that found in the opening plots, and the burned soils were consistently high in their nutrient content, as expected (Christenson and Muller, 1975; Viro, 1974). Figures 10-12 show seasonal changes in soil nutrient status in each treatment. When interpreting these results it is important to remember that there are two variables, time and depth. The June 4 samples included the upper 7.0 cm of soil, the June 24 samples (NH_4^+ and NO_3^- analysis only) were collected from the top 11.0 cm, and all remaining samples included the upper 15.0 cm of soil. As stated previously, this provides a more accurate picture of the nutrients available to the seedlings following germination and during early growth.

Three of the eight exchangeable cations—Fe, Cu, and Zn—showed very little variation between treatments throughout the summer and were therefore not graphed. The Fe averaged 2-4 ug/g of soil, the Cu averaged 2-3 ug/g, and the Zn averaged 1-2 ug/g.

The amounts of calcium and sodium showed slightly greater treatment variation, but seemingly not enough to cause growth differences. The calcium content in the opening treatment soils averaged 2300-1800 ug/g of soil throughout the summer, whereas soil from the pine-influenced plots averaged over 2200-1600 ug/g over the same period. Sodium from the pine-influenced plots averaged 11 ug/g of soil throughout the growing season. The opening plots contained 2-3 ug/g less than these.

The remaining three cations—Mn, K, and Mg—were more variable, but it is obvious that those treatments associated with the ponderosa pine stand had equal or greater amounts of these cations than the

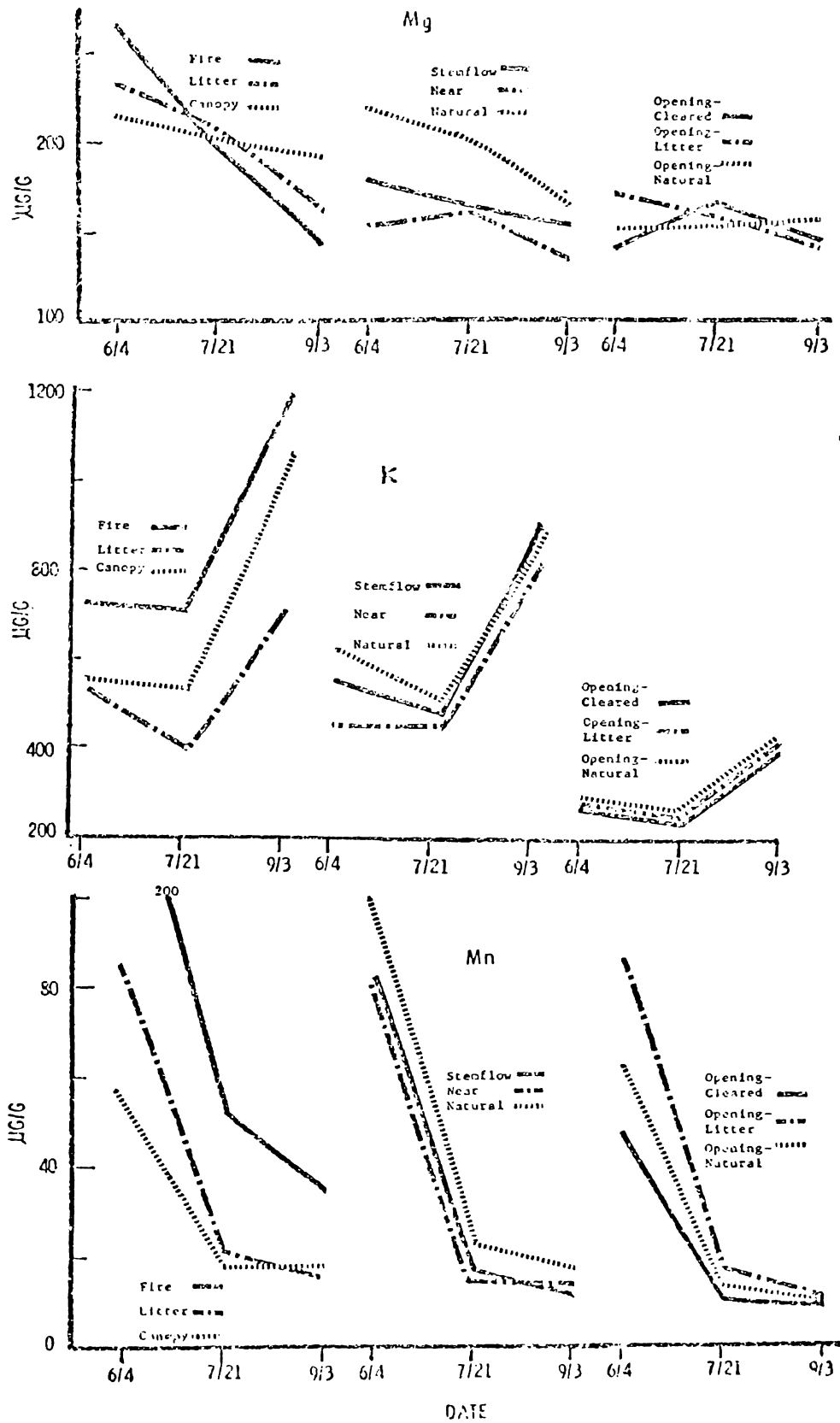


Figure 10. Temporal changes in soil manganese (bottom), potassium (middle), and magnesium (top) per treatment.

opening plots (Figure 10). The fire-treated soil had appreciably greater amounts of extractable potassium and manganese than all other treatment soils during the entire growing season.

The fire-treated soil had an extremely high ammonium ion content that varied with fire intensity. Plot F1, which burned the hottest (Table 3), causing the greatest litter reduction (Table 4), had the highest NH_4^+ concentrations; and plot F3, which burned the coolest and had the poorest litter reduction, had the lowest NH_4^+ concentrations of the fire plots. There was very little difference in NH_4^+ levels between the rest of the pine-associated plots and the opening plots (Figure 11). The opening-litter treatments tended to be slightly higher in NH_4^+ than either the opening-cleared or opening-natural treatment.

Closely associated with NH_4^+ is the NO_3^- content of the soil due to nitrification. In general, the tree-associated sites had lower NO_3^- contents than the opening sites with the exception of the fire and canopy treatments (Figure 11). The canopy treatments had a very high NO_3^- concentration in June but continually dropped throughout the summer, whereas the fire treatments started very low, rose to a peak during the summer, and dropped off again by September. At two of the three opening sites the nitrate content of the opening-cleared and opening-litter treatments rose abruptly during the summer. In the opening-natural plots there was no increase in nitrates at all. The extreme abundance of NH_4^+ in the fire plots did not lead to high NO_3^- concentration. This may have been due in part to extensive leaching resulting from excessive rainfall. The nearby opening plots had nitrate levels similar to the fire plots although these

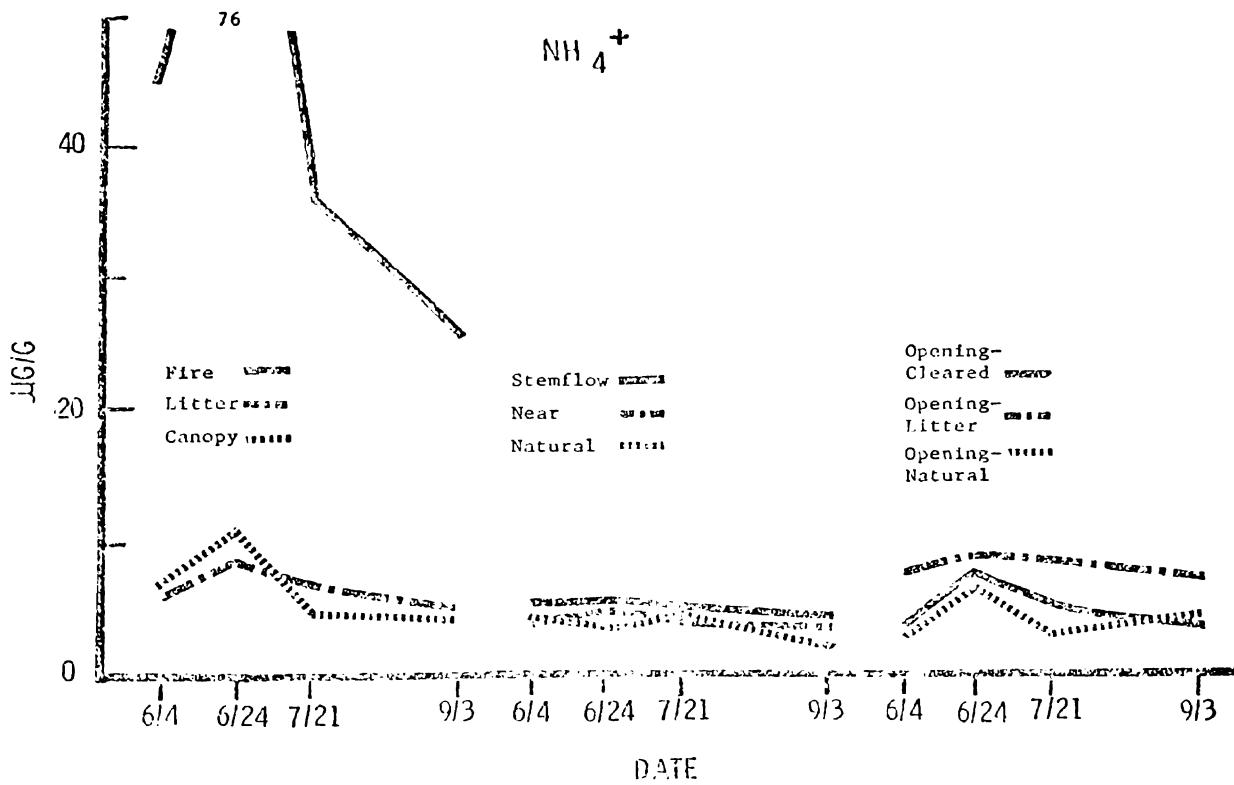
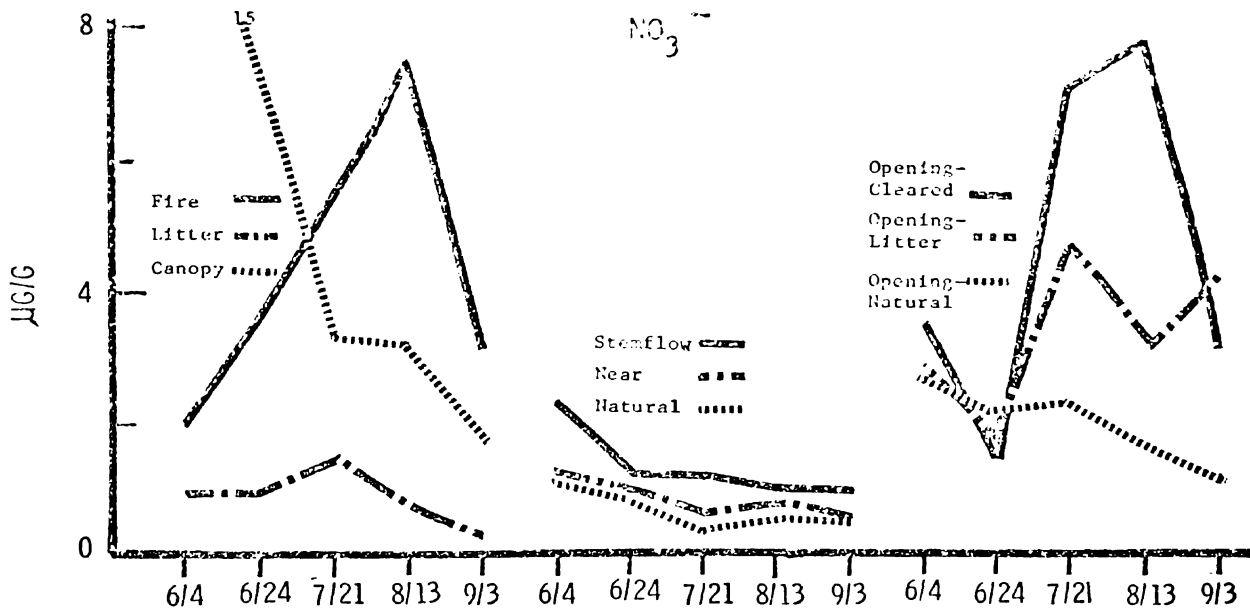


Figure 11. Temporal changes in soil ammonium (bottom) and nitrates (top) per treatment.

opening plots had much lower ammonium levels. The same was true for the comparison of the canopy versus fire treatments.

The phosphate content was noticeably higher on the tree-associated sites than in the openings (Figure 12). The fire treatment appeared to raise the PO_4^{-3} concentration slightly over some treatments and greatly over others.

Sulfate concentrations were measured because Youngberg and Dyrness (1965) found its presence in Oregon soils to be nearly as critical to ponderosa pine growth as nitrogen. The sulfate content was not clearly segregated as was the phosphate content. The canopy, fire, and opening-cleared treatments were highest in sulfates, but there were no consistent trends (Figure 13).

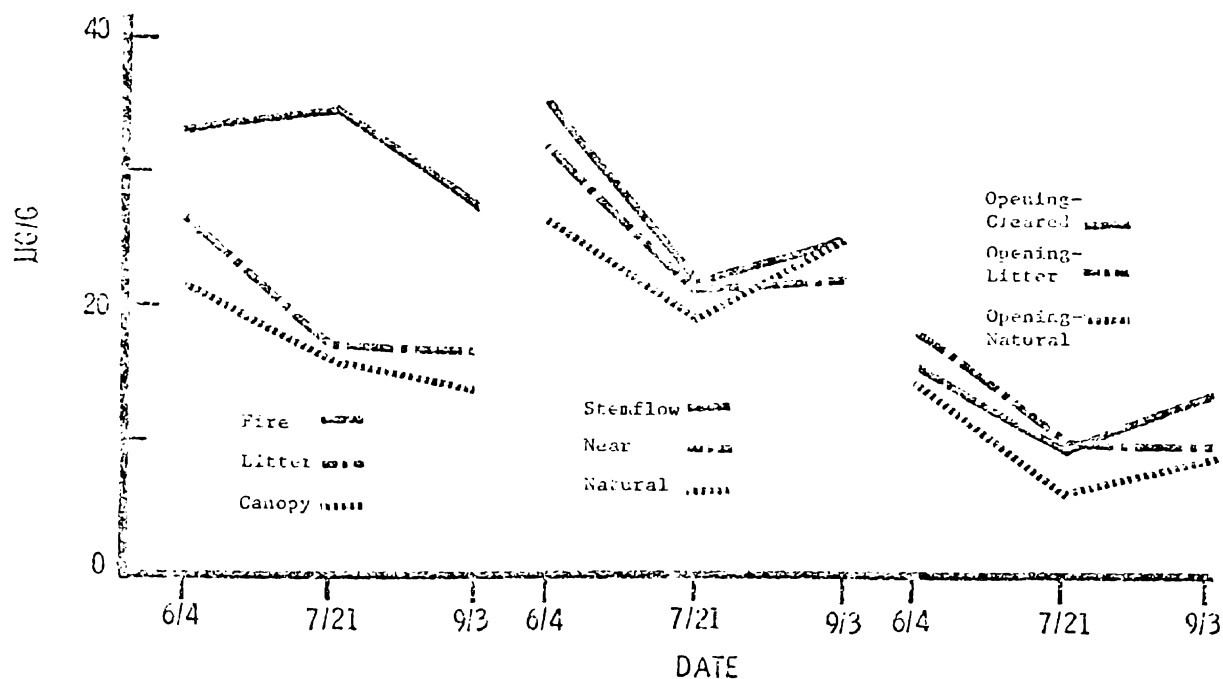


Figure 12. Temporal changes in soil phosphates per treatment.

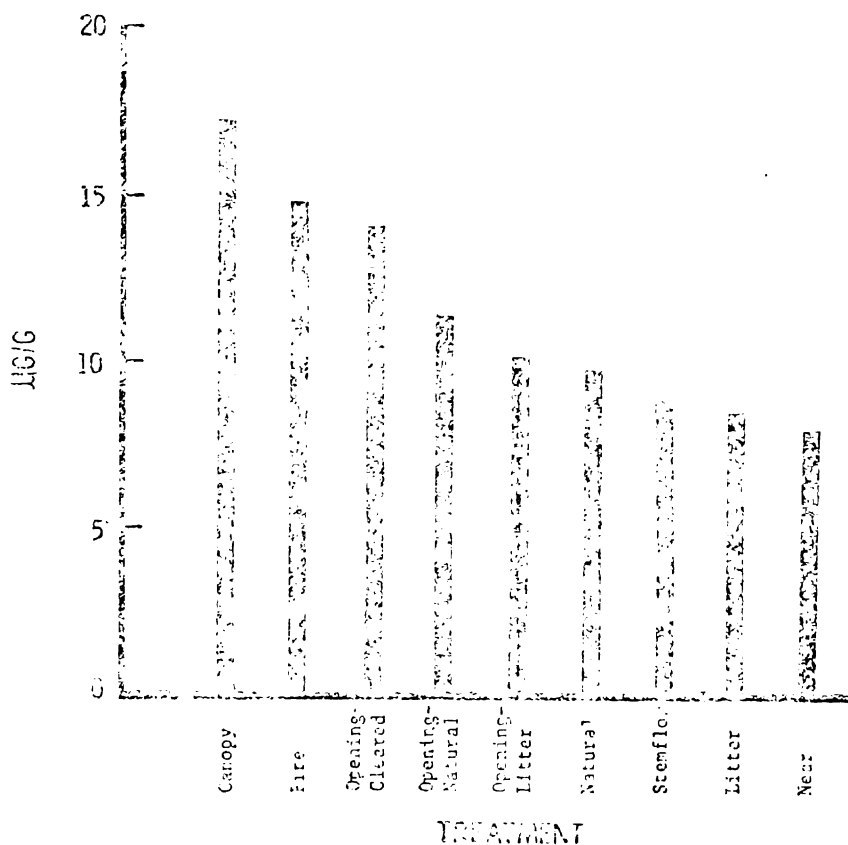


Figure 13. Concentrations of soil sulfates per treatment.

These analyses indicated that the nutrient content of the soils within the pine stand was comparable to that in the openings. In fact, in many instances the nutrients in the pine stand soils exceeded those in the opening soils. Going one step further and rating the treatments in terms of seedling growth potential on the basis of nutrients is very difficult. However, the fire plots do stand out from the other treatments, particularly in regard to the nitrogen content. This is important because the soil nitrogen content, as well as other nutrients, can have a significant influence on the growth of ponderosa pine seedlings (Cochran, 1972; Vlamis *et al.*, 1957). There is also evidence that nitrogen may play a role in the drought resistant capabilities of ponderosa pine, but the evidence is not conclusive (Loewenstein, 1970). The particular form of nitrogen may also be important. Recent studies indicate that NH_4^+ is the preferred source over NO_3^- and urea (Wollum, 1968, 1970).

pH. The soil reaction is very influential in determining the nutrient status of the soil. In general, very acid conditions reduce the availability of most nutrients by affecting their valence and by saturating the exchange sites with hydrogen ions, releasing other cations and allowing them to be leached. pH values approaching neutrality consistently permit higher nutrient availability and tend to stimulate soil microbial activity, thereby producing and releasing more mineral nutrients.

All treatments had similar soil pH values, except for the fire plots which, as expected, had much higher values (Table 9). The average for the three opening groups was about 5.1, compared to just under 5.3 for the pine-influenced treatments. In all cases, pH values were highest in June and continually decreased throughout the summer. The average soil reaction for the opening plots for June 4 was 5.5 compared to 5.6 for the pine-influenced plots. On September 3 the average pH had fallen to 4.7 in the opening treatments compared to 4.9 for the others. Average fire treatment pH dropped from a June 4 high of 6.5 to a September 3 low of 5.5, probably due to leaching of the oxides and carbonates found in the ash. Most temporal changes resulted in a drop in pH of one unit or less. These slight increases in acidity were probably due to increases in acidic compounds that were released during the decomposition of organic matter.

Soil moisture content. The moisture content of the soil was highest in June, decreased through July and August, and started to rise again in early September (Figure 14). For the three opening treatments, the opening-litter plots tended to have a higher soil moisture than the opening-cleared or opening-natural plots. This was likely due to the

Table 9. Temporal changes in soil pH per treatment

Treatment	June 4	June 24	July 21	Aug. 13	Sept. 3	Average
Opening-Cleared	5.4	5.2	5.0	5.1	4.9	<u>5.1</u>
Opening-Litter	5.8	5.3	5.1	4.9	4.5	<u>5.1</u>
Opening-Natural	5.5	5.2	5.0	5.0	4.6	<u>5.1</u>
Fire	6.5	6.1	5.7	5.9	5.5	<u>5.9</u>
Canopy	5.6	5.3	5.2	5.2	4.9	<u>5.2</u>
Stemflow	5.6	5.4	5.4	5.1	5.0	<u>5.3</u>
Litter	5.8	5.5	5.3	5.0	4.8	<u>5.3</u>
Natural	5.6	5.3	5.4	5.2	5.0	<u>5.3</u>
Near	5.5	5.1	5.3	5.1	4.9	<u>5.2</u>

absence of herbaceous vegetation and the presence of the litter layer that helped retain the moisture. For those sites associated with the pine trees, the litter and near plots had the highest soil moisture levels throughout the summer. The natural plots started with high soil moisture in June but dropped to low values in August and September. The lowest soil moistures for the summer were found in the fire and canopy treatments. Most treatments involving the removal of vegetation and litter, including the canopy, stemflow, and the opening-cleared plots, had similar soil moisture levels. The near plots also had the vegetation and litter removed but they started with high soil moistures in June and stayed relatively high throughout the summer. The opening-natural plots, having had no litter or vegetation removed, had soil moisture levels similar to those treatments which had been cleared.

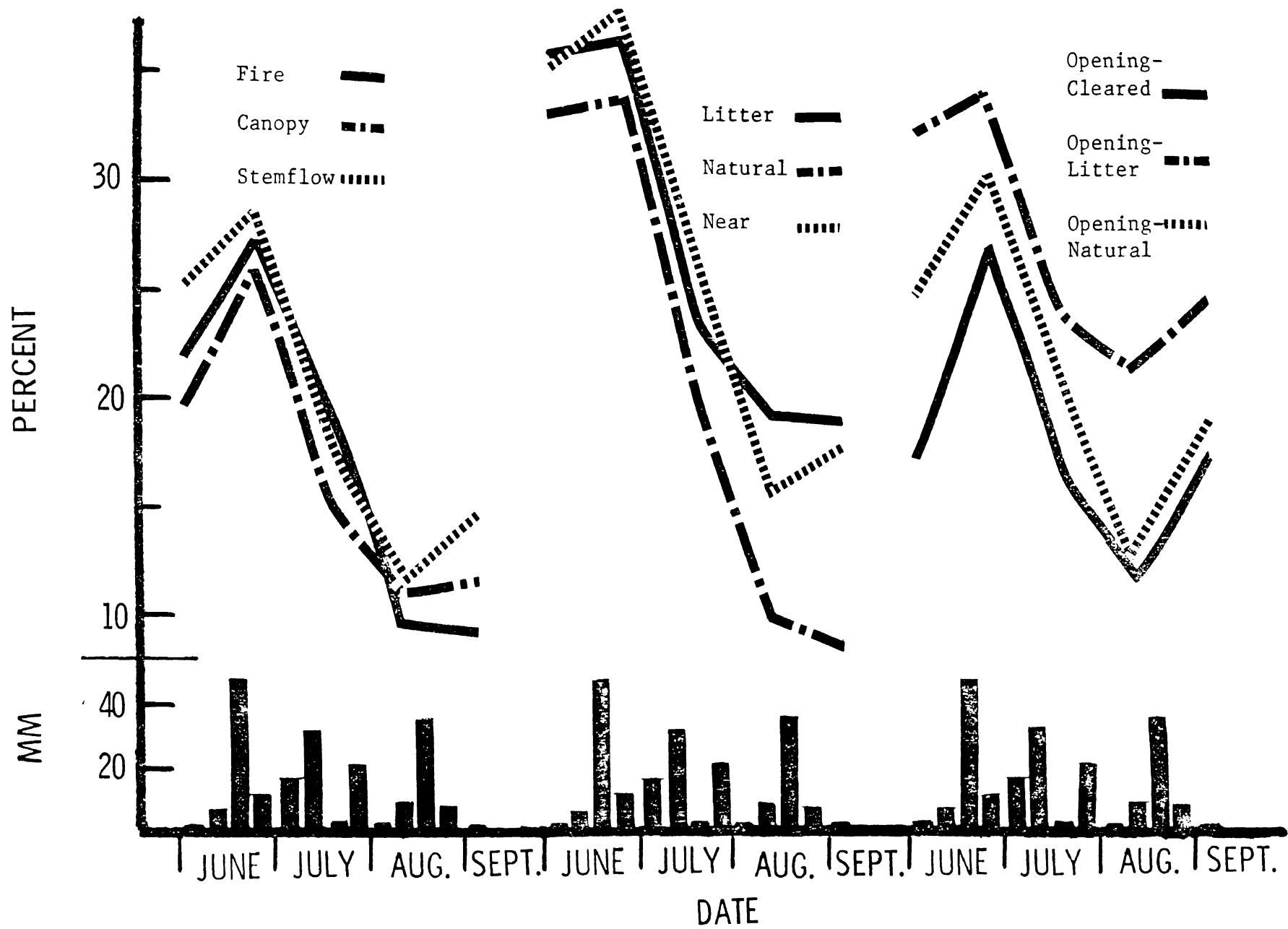


Figure 14. Temporal changes in soil moisture compared to amounts of rainfall.

Snow depths. Closely associated with and influencing soil moisture content, particularly during the spring, is the amount of snow accumulation during the winter months. Snow depth estimates were made for each plot on March 24, 1975, and are shown in Figure 15. As might be expected, the greatest snow depths were found on the opening sites where the pine canopy had no influence. The least snow depths were associated with areas of heavy canopy, although there were exceptions suggesting that the physical arrangement of the canopy and wind drifting could be important. Figure 16 shows canopy snow interception.

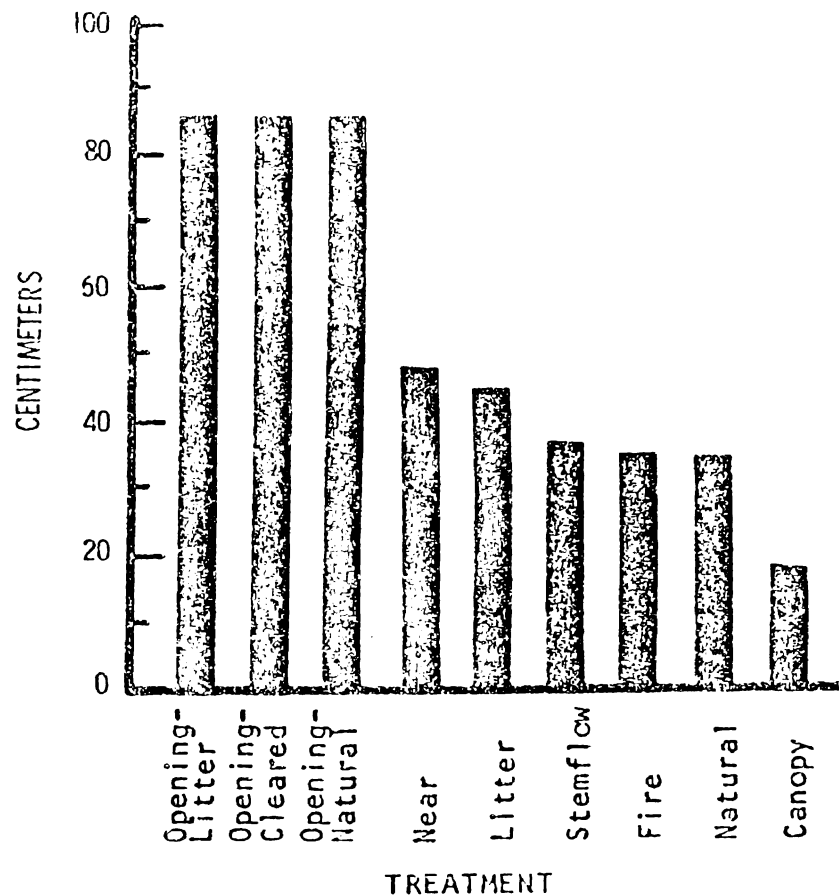


Figure 15. March 24 snow depths on treatment plots.



Figure 16. Example of snow interception by overstory canopy.

Particle size distribution. Soil texture can be a significant factor in soil-plant interactions. High silt and clay contents can retard root growth. Water infiltration and percolation are texturally dependent and particle size distribution also determines the soil's water-holding capacity and water availability. Fine-textured soils have a greater water-holding capacity than course-textured soils, but less of this water is available because of the high tensions exerted on water by the small soil particles. Course-textured soils generally have a low cation exchange capacity and are relatively infertile. Fine-textured soils have a greater ability to hold nutrients from leaching and therefore remain more fertile. Also, better soil aeration and greater temperature fluctuations will occur in course-textured soils.

The results of the mechanical analysis of the upper 15.0 cm of soil from each treatment are presented in Figure 17. The clay contents varied from about 13 to 18 percent with most soils falling in the 14 to 16 percent range. Percent silt varied from about 40 to 55 and the amount of sand ranged from about 31 to 46 percent.

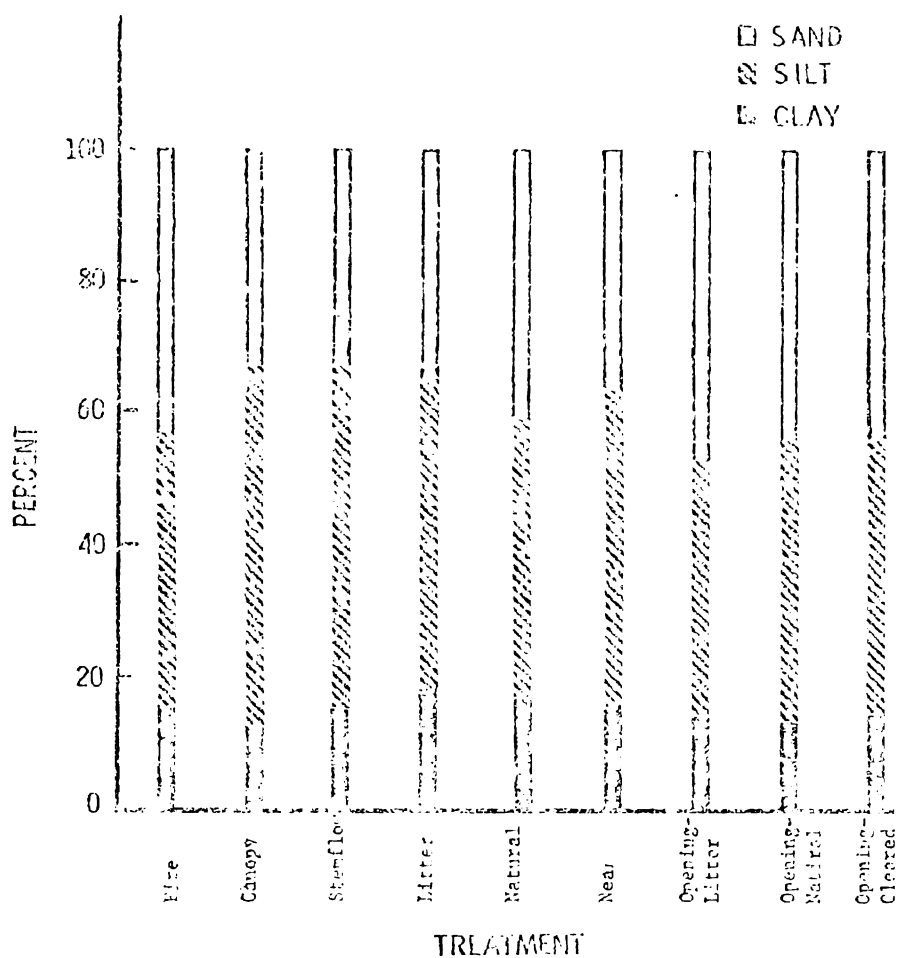


Figure 17. Particle size distribution of surface 15 cm of soil from treatment plots.

The narrow range of clay contents should have created little if any differences in fertility, water-holding capacity, and resistance to root penetration. Treatment differences of silt and sand may have produced differences in soil characteristics and soil capabilities had other

environmental factors, such as amounts of rainfall and depth of organic matter, been equivalent. Because these other factors did vary, due to plot location and treatment effect, the impact of soil texture differences was most likely minimal. In other words, the variation of physical characteristics of the treatments (canopy cover, organic layer depth, amounts of vegetation, etc.) probably had more influence on soil moisture and nutrients than did the slight differences in soil texture. During the 1975 growing season, above average rainfall appeared to permit adequate available moisture on all plots regardless of treatment. Also, soil nutrient analyses showed that, in general, soils within the pine stand were more fertile than those in the openings, regardless of soil texture (Figures 10-13).

Canopy Cover

The amount of canopy cover can have a great influence on the physical and biological factors affecting a particular location within a forest. It can affect the quantity and quality of sunlight, and the amount of precipitation, as well as the volume of organic matter reaching the forest floor.

To measure canopy cover over the respective plots, a densiometer was used. The densiometer was held in the center of the plot and four readings were taken, one facing in each direction (N, S, E, W). The averages of these four readings are shown in Figure 18.

Obviously, the plots located in the openings had the least canopy cover, ranging from 2 to 6 percent. The natural and canopy plots had the

greatest canopy influence, mostly over 80 percent. The canopy coverage on the other plots fell between these two groups, ranging from 35 to 72 percent. It should be noted that the concave mirror of the densiometer can pick up the canopy from large trees that are some distance away. This is why most of the opening plots had a measurable canopy cover although there was no pine canopy directly overhead.

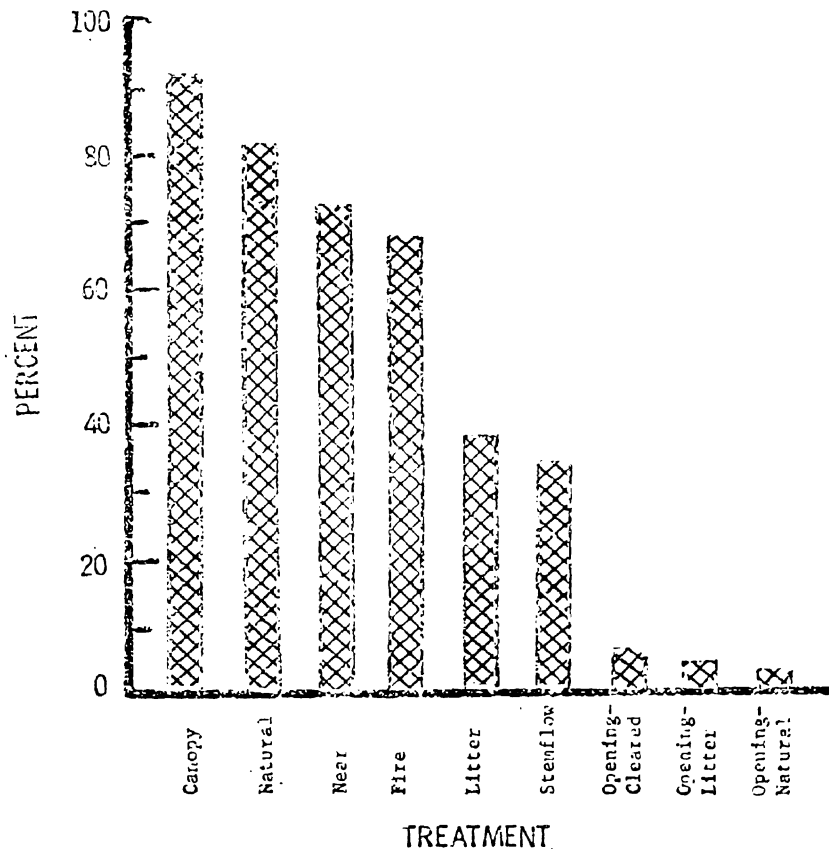


Figure 18. Canopy cover percentage per treatment.

A regression analysis comparing percentage of canopy cover to physical factors indicates the great influence the canopy may have on the forest floor. Table 10 shows the correlation coefficients from linear regressions comparing percentage of overhead canopy on each plot to

average litter depth, total radiation, average maximum soil surface temperature, and soil moisture content shortly after a rainfall.

Table 10. Correlation between percentage of canopy cover and other physical factors

	Percentage canopy cover vs.			
	Litter Depth	Total Radiation (10 am - 3 pm)	Maximum Soil Surface Temp.	Soil Moisture (Sept. 3)
$r(r^2)$ -	+0.85(.72)	-0.91(.82)	-0.78(.61)	-0.84(.70)

As mentioned earlier, the pine canopy produced the bulk of the organic residues. Table 10 shows that increased canopy coverage probably leads to increased organic matter on the forest floor beneath. A larger r^2 value might have been obtained had only pine litter and duff been collected. The shading by the canopy obviously affects the amounts of sunlight reaching the forest floor, as well as soil temperatures. In addition, a negative correlation was found between canopy percentage and soil moisture shortly after a rainfall. Other factors such as vegetation and litter depth will also affect soil moisture, but the interception ability of the pine canopy must be emphasized.

Influential Tree Inventory

The influence a tree has on a particular site is determined by its size and distance from that site. The types of influences can be numerous and varied. For example, an overhead canopy can affect the amounts of litter, radiant energy, and precipitation reaching the forest floor. The degree of shading, and rainfall, can also be affected by a

tree some distance away if it is in the proper position. Root competition some distance beyond a tree's crown can also occur (McDonald, 1976; Ziemer, 1968).

In an effort to determine the degree of overstory tree influence on the individual plots, the number of "influential trees" was measured. An influential tree in this study was defined as one whose distance from the trunk to the closest edge of the plot was less than the height of the tree.

Of course, the plots in the openings had the fewest number of influential trees, and the natural and near plots had the highest numbers (Figure 19). The latter were followed by the fire, the litter, the canopy, and the stemflow plots. The precise amount of influence produced by any one tree is very difficult to determine because, in addition to height and distance from the plot, the canopy size and location (north side, south side, etc.) is also important. Therefore, one plot could have more influential trees around it than another, but the few trees near the latter plot could be larger, closer, or positioned so that they have a greater effect. A case in point concerns the litter plot L1 and the canopy plot C1. L1 had 21 influential trees around it and C1 had only four, yet the influence of the four trees near C1 was equal to or greater than that of the 21 trees near L1 because of their canopy size and physical proximity. This is substantiated by the fact that plot C1 had 91 percent canopy coverage compared to 61 percent above plot L1.

Therefore, a greater number of influential trees does not necessarily mean greater overstory influence. However, this data evaluated simultaneously with the canopy percentage gives an indication of the

overstory situation adjacent to each plot and an implication as to over-story influences.

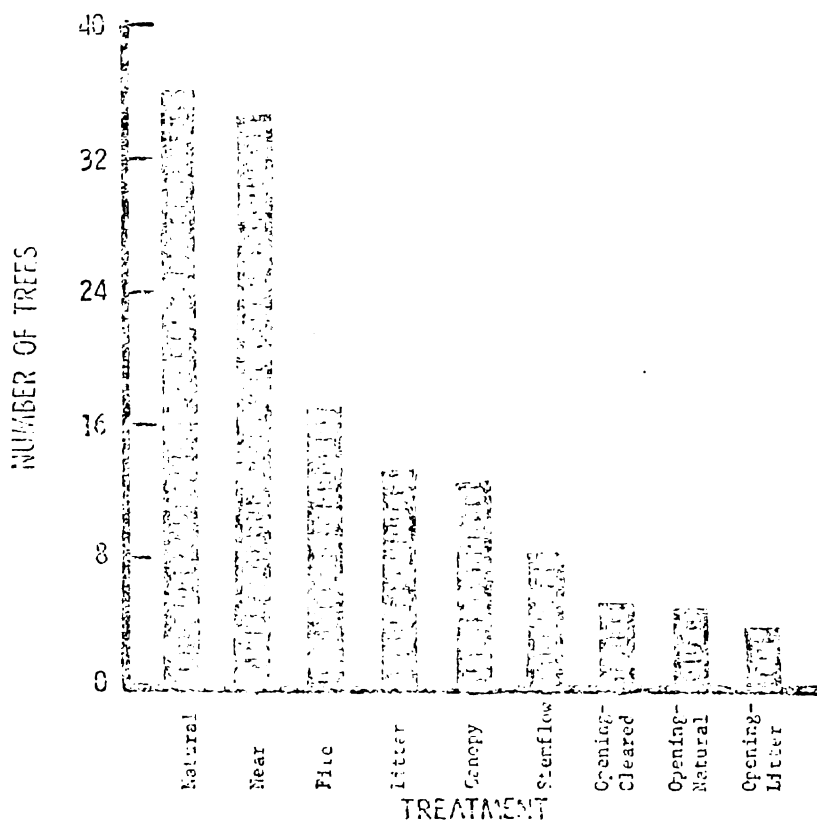


Figure 19. Number of influential trees per treatment.

Solar Radiation

In addition to its effect on temperature, radiant energy is essential for photosynthesis. The success of most species is determined in part by their abilities to perform growth functions under various shade conditions. Many plants thrive under conditions of low energy levels, whereas others cannot survive unless light quantities are near maximum.

Ponderosa pine is considered rather shade intolerant. Too much shading will reduce its competitive ability and often results in its

displacement. This displacement may be the result of subminimal light levels for adequate photosynthesis, subminimal temperatures and humidity for proper growth functions, and reduced growth of shoots and roots thereby permitting only small areas for soil moisture and nutrient absorption.

Because of the selected placement of the field plots (in openings, near large trees, and within groups of trees), obvious differences in shading and resulting amounts of available solar radiation occurred. A 10-junction Eppley pyrliometer was used to measure the total solar radiation. Measurements were made and converted into gram-calories per square centimeter per minute. In order to compare plots under various shading conditions, measurements of solar radiation were taken on cloudless days. Completely cloudless days were infrequent during the summer of 1975 as can be implied by the large number of rainy days (Figure 9). This, plus instrument complications, allowed solar radiation measurement only once, on July 9, 1975. The temperature on this date reached 90°F and the relative humidity dropped to 21 percent. The readings were taken on all plots at 10 a.m., 12 m., and 3 p.m. These three readings allowed comparisons during maximum solar radiation influence and maximum shading potential. In plots with no shade, only one or two measurements were required to obtain a plot average at each of the three time periods. In deeply and partially shaded plots, several readings had to be taken and a plot average determined for each time period. For example, in the stemflow plots the shade produced by the bole of the tree in the center amounted to approximately one-tenth of the plot area. Therefore, the plot average would equal one-tenth of the full shade readings plus nine-tenths of the full sunlight readings, providing the rest of the plot was unshaded.

The periodic changes of radiant energy are shown in Figure 20. Total radiant energy in gram-calories per square centimeter from 10 a.m. to 3 p.m. were calculated assuming the 10 a.m. reading represented the radiant energy received from 10 a.m. to 11 a.m., the 12 m. reading represented the energy from 11 a.m. to 1:30 p.m., and the 3 p.m. reading represented the energy from 1:30 p.m. to 3 p.m. These total values for the five hours are shown in Figure 21.

The plots in the openings received the highest amounts of radiant energy. Some pine-associated plots also received long periods of full sunlight because they were positioned with few or no potential shade trees to the south or overhead. Nearly all variations of shading were encountered. Some plots received full sunlight in the morning with partial to full shade later. Others received full sunlight in the middle of the day with shading in the morning and afternoon. A few plots were completely shaded all day.

Soil Surface Temperatures

The temperature of the soil is an important factor in the establishment of tree seedlings. A minimum temperature must be exceeded for adequate seed germination, and initial radicle and later root growth is to some extent a function of the amount of heat present (Larson, 1967). In addition, early seedling survival can be jeopardized by extreme soil surface temperatures. An internal stem temperature of 55°C (130°F) can be lethal to conifer seedlings (Baker, 1929) and soil surface heating to 57°C (135°F) can create lethal temperatures within the seedlings. Duration of heating is also important. As the heating time increases, the lethal temperature decreases (Baker, 1929).

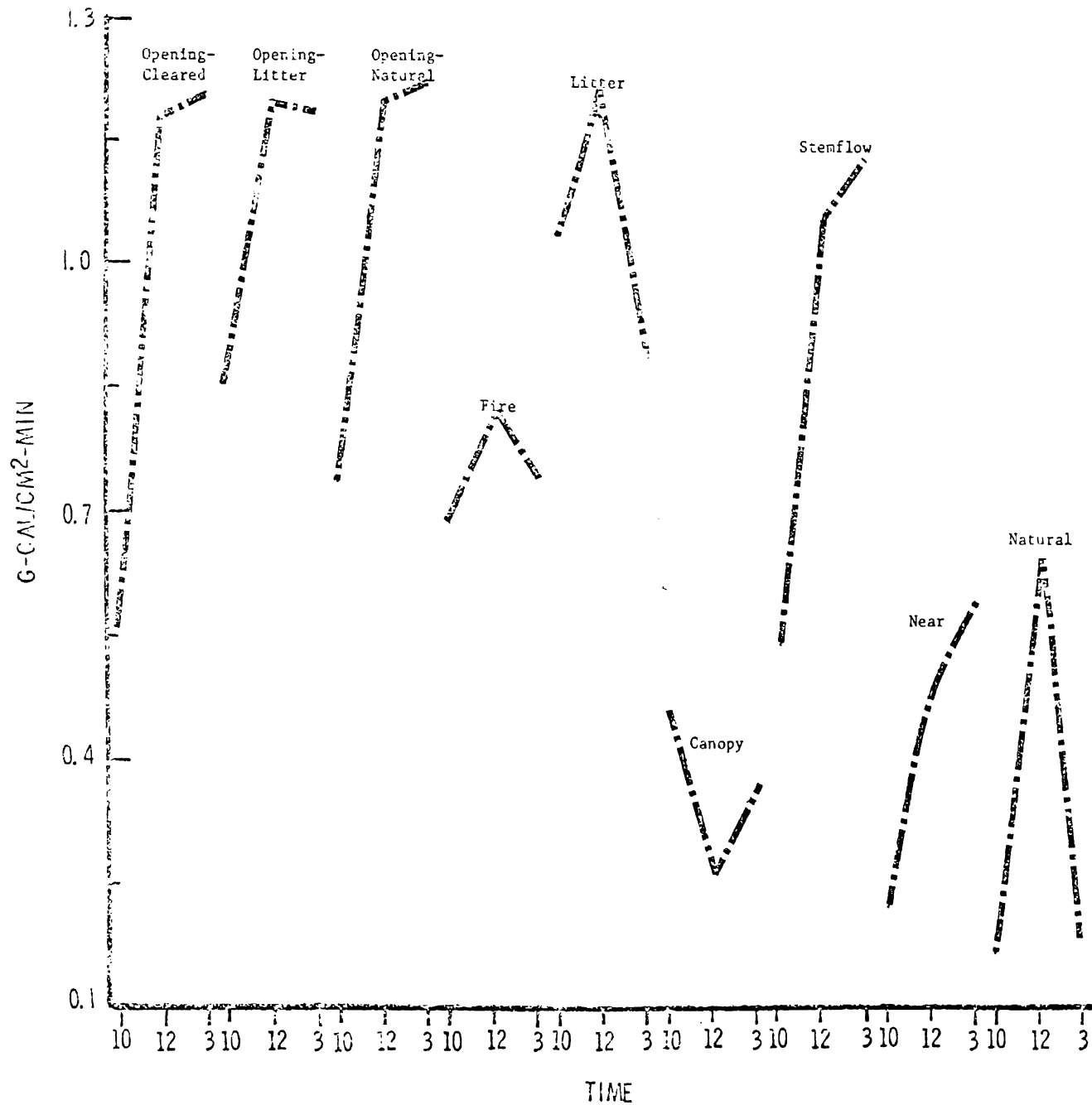


Figure 20. Solar radiation received per treatment at 10 a.m., 12 m., and 3 p.m.

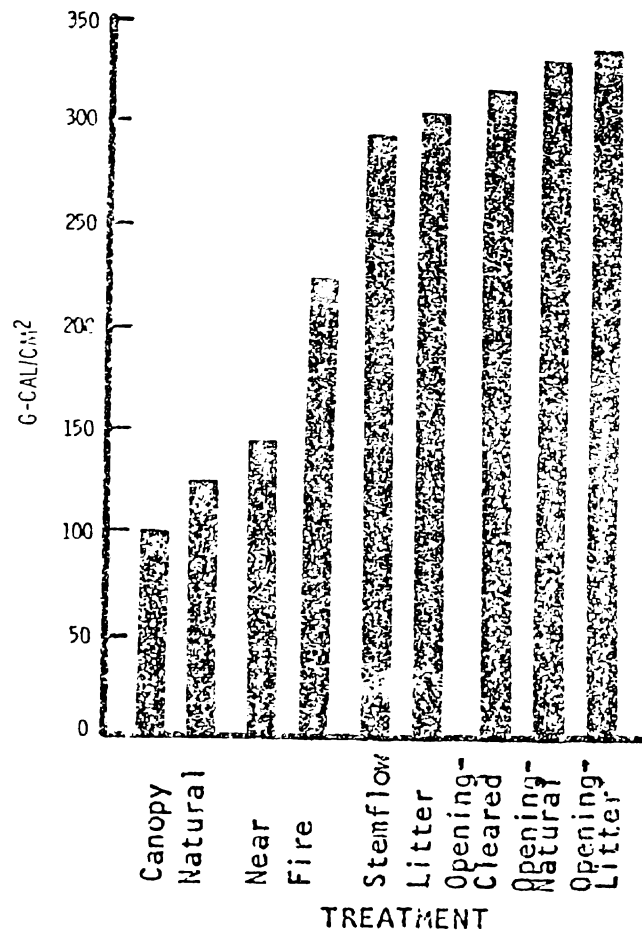


Figure 21. Total solar radiation received per treatment from 10 a.m. to 3 p.m.

An attempt was made to measure maximum soil surface temperatures by placing a series of Tempil Pellets on each plot during the month of July. These pellets were made of heat sensitive material that melted when the corresponding temperature was reached. In each plot, two sets of five pellets were located in representative sites on the soil or litter surface. The temperatures corresponding to the five different pellets were 45°C (113°F), 51°C (125°F), 59°C (138°F), 66°C (150°F), and 73°C (163°F). If a particular pellet melted, but the one corresponding to the next highest temperature did not, then the maximum temperature was considered to be half way between them. Figure 22 represents the average maximum

soil surface temperatures of the two sets of pellets for each treatment.

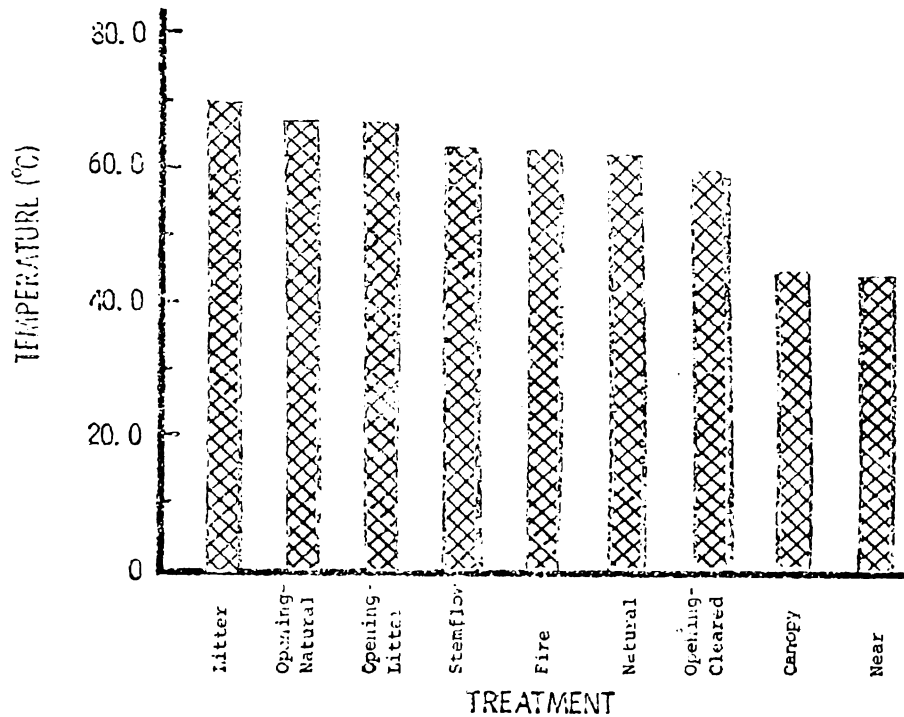


Figure 22. Maximum soil surface temperatures per treatment.

Assuming that 57°C is the minimum soil surface temperature necessary to damage seedlings, then 18 of the 27 plots had temperatures capable of causing seedling injury. Four other plots were within 4°C of this temperature. It should be noted that on most plots, heating of the soil surface to the lethal range could occur on microsites. Therefore, sparse mortality from heat scald would have been possible on most of the plots.

Maximum temperatures were recorded where litter and other organic matter were present; litter, opening-litter, opening-natural, and fire treatments (due to the black surface). The removal of litter and live vegetation in the openings resulted in lower surface temperatures as was

observed on the opening-cleared treatment. Heavy canopy reduced temperatures somewhat, as was evident on two of the three natural plots, but surface temperatures were lowest on those treatments with the combined effects of bare mineral soil and large amounts of canopy cover. This latter situation occurred on the canopy and near treatments. The stem-flow plots had bare mineral soil and some canopy cover, but their soil surface temperatures were still quite high. Although large amounts of organic matter had been removed, the soil surface had a great deal of organic matter in the form of needles and small pieces of bark that continually fell from the trees throughout the season.

CHAPTER V

RESULTS AND DISCUSSION

Seed Germination

The first sign of germination was observed on May 13, 1975, with seed coats splitting open and radicles emerging. On May 14 the first comprehensive seedling count was conducted and continued at weekly intervals through June 23. From July 8 to August 21, germination was recorded once every two weeks. A seed was considered germinated when the radicle had protruded from the seed coat and turned down. A colored toothpick was placed adjacent to each seedling, marking it for future observation; different colored toothpicks corresponded to different weeks of germination. This allowed the age of each seedling to be determined at the end of the growing season. In addition to recording germination, seedling mortality was observed and categorized by suspected cause. Dead seedlings and their toothpicks were removed. In the fall of 1974, a total of 10,800 ponderosa pine seeds were planted on 27 study plots. During the next spring and summer 4,812 or 44.56 percent of these germinated.

Germination percentages were quite varied, ranging from 70 percent to only 16 percent, with the greatest germination occurring in the opening treatments compared to the pine-influenced treatments. Germination in the three opening treatments accounted for about 50 percent of the total germination. Using Scheffe's test, the three opening treatments had an average germination of 65.4 percent which was significantly greater at

the 1 percent level than the pine-influenced treatments, with an average germination of 34.1 percent.

Figure 23 presents germination percentages of the planted seeds for each treatment. In addition, this figure shows a statistical comparison of treatment means. Because of heterogeneous variances, an arcsine of the square root of the percentage transformation was utilized (Snedecor and Cochran, 1971). The transformed data were then compared using Duncan's multiple range test. This test was used in all statistical comparisons on succeeding pages. In all figures, treatment means not underscored with the same line are statistically different at the 5 percent level of significance.

Germination in the opening-litter plots was very similar to that in the opening-cleared plots, indicating that under the environmental conditions of the 1975 growing season, pine litter and duff had no effect on germination in the openings. The opening-natural plots averaged about 12.5 percent less germination than the other two opening treatments, but the differences were not significant (Figure 23). Germination in the opening-natural plots was reduced somewhat because of unsatisfactory seedbeds, such as the middle of, or along side of clumps of bunch grass, or on crusted mosses or lichens. The opening-litter and opening-cleared treatments had significantly greater germination than all pine-influenced treatments, but the opening-natural treatment was statistically similar to the fire, near, litter, and stemflow treatments.

As a group, the fire treatments had the greatest number of germinants of the pine-influenced plots. The fire plots' germination was followed closely by that of the near, the litter, and the stemflow plots.

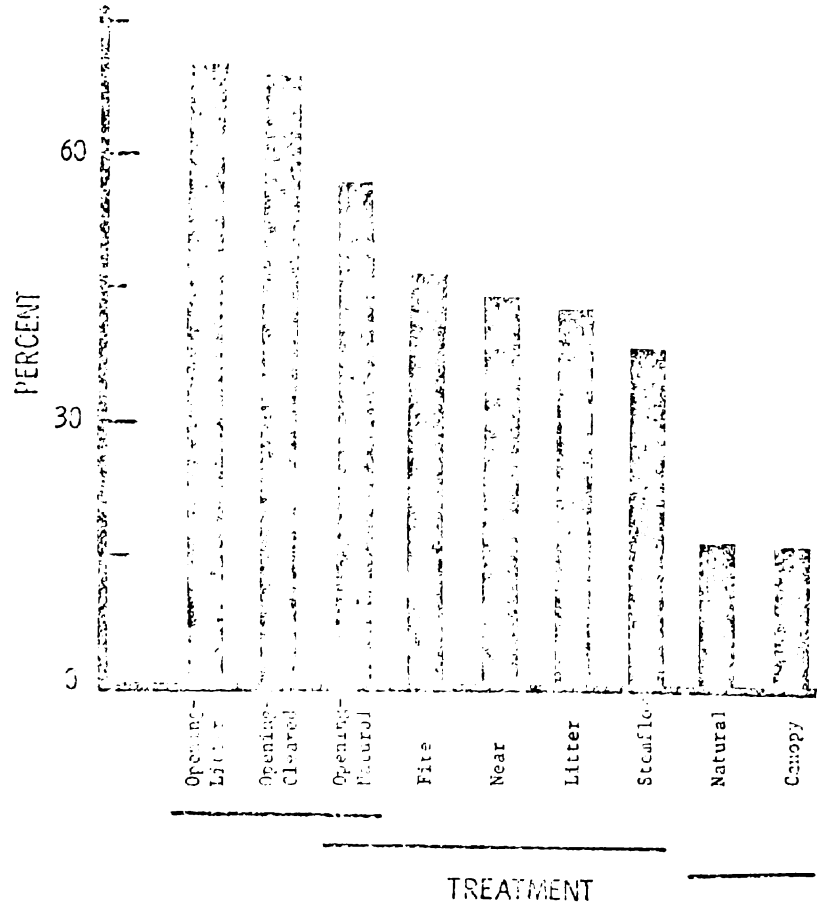


Figure 23. Seed germination percentages with statistical comparisons of treatments.

The natural and canopy plots had by far the lowest germination which was significantly less at the 5 percent level than all other treatments. It is interesting that the fire and near treatments, which had similar germination, also had similar canopy cover (Figure 18) and little or no surface litter. Decreasing the canopy cover and increasing the litter depth, as in the litter plots, decreased germination only slightly compared to the fire and near treatments. However, a combination of heavy canopy and deep litter, as on the natural plots, reduced germination significantly. The stemflow plots should apparently have had better seed germination

because they had little canopy coverage and only small amounts of surface organic matter. Why the stemflow seeds did not germinate better is unclear. Seed predation by birds and small mammals was suspected and most likely contributed slightly to the very poor germination in the canopy treatments. This may have also been true of the stemflow plots. The canopy plots contained an average of 151 naturally fallen seeds/m² in addition to the 400 planted seeds and yet very few germinated. A large number of shelled seed coats were found on the soil surface prior to germination. Undoubtedly, many fell from the cones above the plots as the seeds were eaten, but some were likely eaten on the ground.

The lower germination in the pine-influenced treatments was probably due to a number of environmental factors. Cooler temperatures, due to shading, when moisture conditions were favorable likely reduced germination. The organic matter could create poor soil surface moisture conditions due to high water potentials and the large and irregular shapes which provide inadequate contact between seeds and available moisture (Eyre and LeBarron, 1944). Also, the amounts of far-red light in the shade may have an inhibitory effect on germination (Harrington, 1976). A combination of these factors is likely.

Another explanation could be the overwintering conditions for seeds in the open versus under the canopy. Under the canopy, little snow accumulated and it tended to melt earlier than snow in the openings. This allowed the canopy seeds to be exposed to varying temperatures, warm during the day and cold at night, and dry conditions. The absence of protective snow cover may not have provided proper seed stratification.

The possibility still exists that a chemical germination inhibitor could be involved. Greenhouse experiments revealed that leachates of pine tissues did not affect ponderosa seed germination when directly applied to the seeds (Harrington et al., 1976). However, soils from under pine canopies did reduce germination compared to that in opening soils, even when irrigated with distilled water. Therefore, the accumulation of leachates or decomposition products on the soil surface may have influenced seed germination.

Germination rates, as well as total germination, are important in the establishment of conifer seedlings. If seed germination is spread over a long time interval, the seedlings that germinate late will have less time to become established before the summer dry season or the winter cold arrives. Figure 24 shows the rates of seed germination on the individual treatments.

The germination rates, represented by the slopes of the initial straight portion of the curves, varied as did total germination. This initial slope accounted for at least 85 percent of the total germination. The highest rates were seen in the opening-cleared and opening-litter treatments which averaged 18 seeds per day. These were followed by the opening-natural treatment with 11 seeds per day. Germination rates for four of the pine-influenced treatments were very similar. The fire plots averaged eight germinants per day compared to seven for the near, the litter, and the stemflow plots. The slowest rates occurred again in the canopy treatment with two seeds per day and the natural treatment with just over one seed germinating per day.

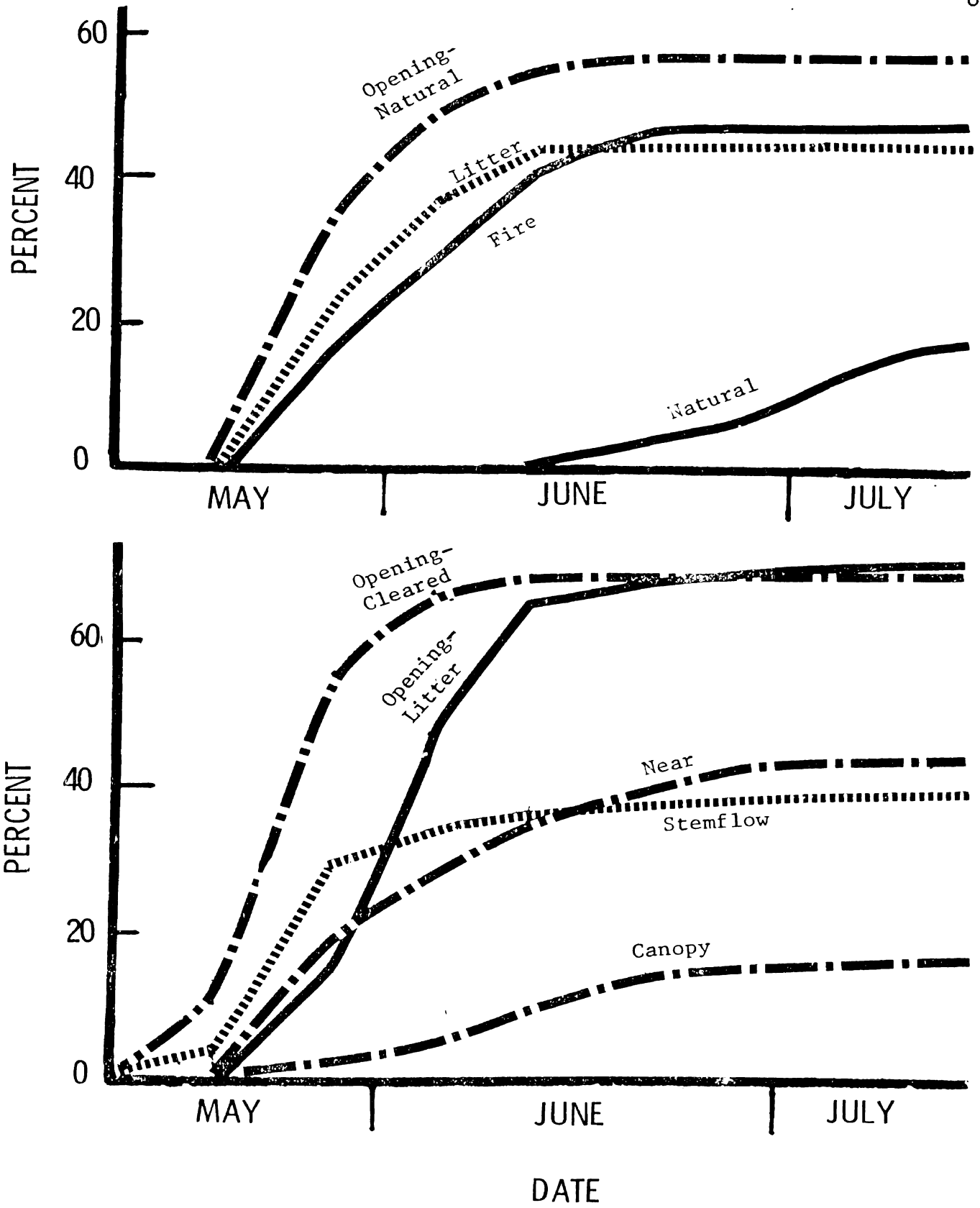


Figure 24. Seed germination rates per treatment.

Other obvious differences reflected by the curves in Figure 24 are the time intervals for germination. Even though the rates may have been similar, germination may have occurred at later dates, thereby not permitting as long a growing period as first season seedlings might need. The opening-cleared and opening-natural seeds germinated earliest with the opening-litter seeds appearing about one week later. Germination in the fire, the near, the litter, and the stemflow treatments took place at times similar to that in the opening-litter. The canopy and natural treatments created situations in which both initiation and termination of germination was three to four weeks behind the other treatments. This caused the average seedling age at the end of the growing season to be only 19.7 weeks for the canopy seedlings and 17.2 weeks for the natural seedlings. The seedling ages of the seven other treatments varied by only 11 days and averaged 22 weeks.

Looking at replications within treatments, it appears that the germination occurred at later dates as the canopy coverage increased. For example, F2 (plots defined in Figure 4), with a canopy cover of 80.7 percent, showed later germination than either F1 or F2 with canopies of 66.7 and 54.7 percent, respectively. The same was true for Z1 compared to Z2 and Z3. Both N2 and N3 had more overhead canopy than N1 and their germination was shifted to later dates. Also, those plots with the greatest canopy (C1, C2, C3, Z1, N2, and N3) all had later initiation and termination dates for germination. Reasons for this are probably the same as for variations in total germination; differences in temperature, moisture, and perhaps light.

Seedling Mortality

On May 22, 1975, during the second week of germination, the first seedling mortalities were observed. From this date on, a record of seedling deaths was maintained, including the seedling age at the time of death and apparent cause. Figure 25 presents the percentage of germinated seedlings that died during the first growing season and a statistical comparison of treatment means at the 5 percent level of significance using Duncan's multiple range test. Treatment means underscored with the same line are not statistically different.

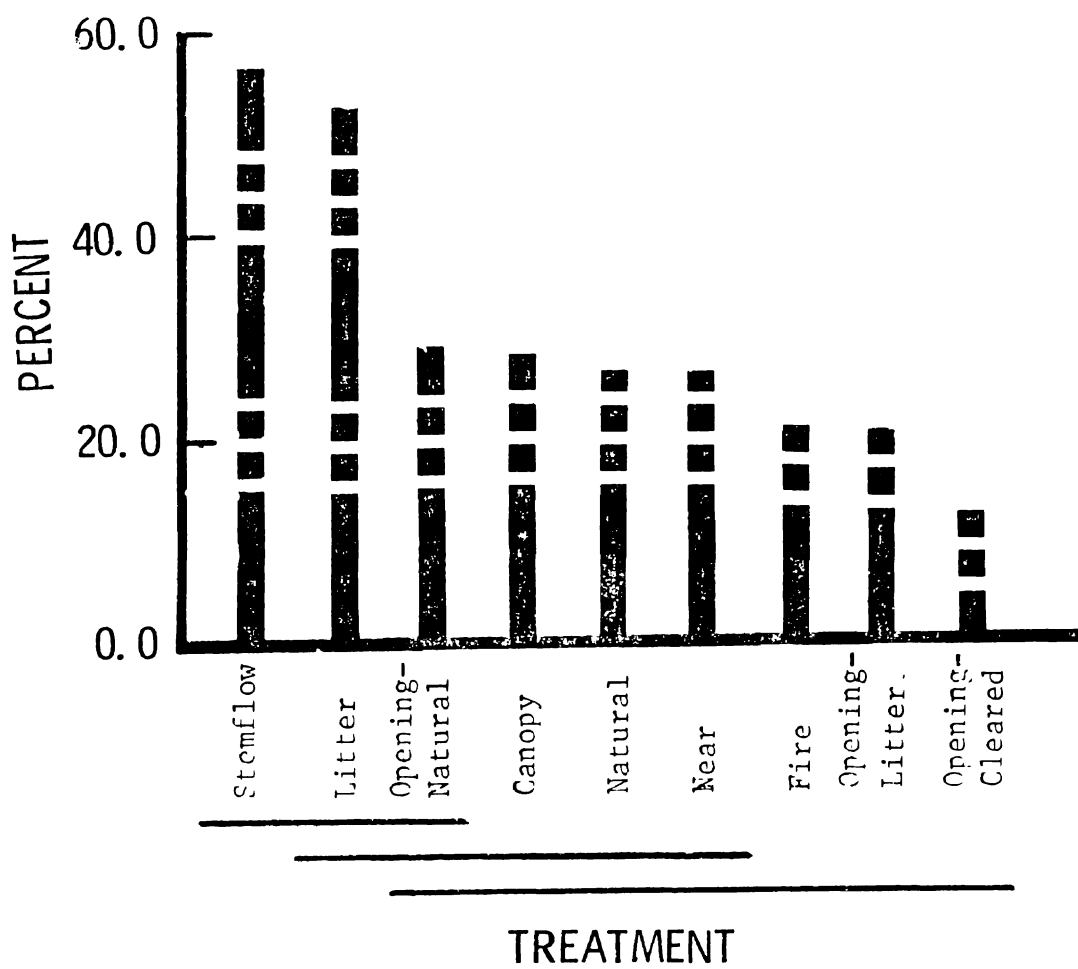


Figure 25. Seedling mortalities as percentages of germinants with statistical comparison of treatments.

The percent mortality ranged from 56.6 to 12.7. The stemflow and litter treatments suffered the greatest damage, losing over half of their seedlings (Figure 25). The next six treatments (opening-natural, canopy, natural, near, fire, and opening-litter) all had very similar losses, 21 to 29 percent, while the opening-cleared treatment averaged only 12.7 percent. The stemflow, litter, and opening-natural treatments had statistically similar seedling deaths, and the first two had significantly greater mortalities than the fire, the opening-litter, and the opening-cleared treatment seedling deaths. The average seedling mortality on the three opening treatments was 21.0 percent which was significantly lower at the 5 percent level using Scheffe's test than the 35.3 percent loss for the pine-influenced treatments.

Of equal importance with total numbers of seedling mortalities were the factors responsible for these deaths. In this study the causes of death were placed into eight categories. (1) Cutworm damage: This was observed as several types of damage; clipping of the stem near ground level leaving the seedling lying on the surface, clipping and eating the stem leaving whole or partially consumed cotyledons, and consumption of the entire above-ground seedling leaving the clipped base of the stem as the only evidence (Figure 26). Similar types of damage by cutworms were reported by Fowells (1940). A number of large, green cutworms were found eating freshly cut seedlings. They were returned to the laboratory where unsuccessful attempts were made at identification.

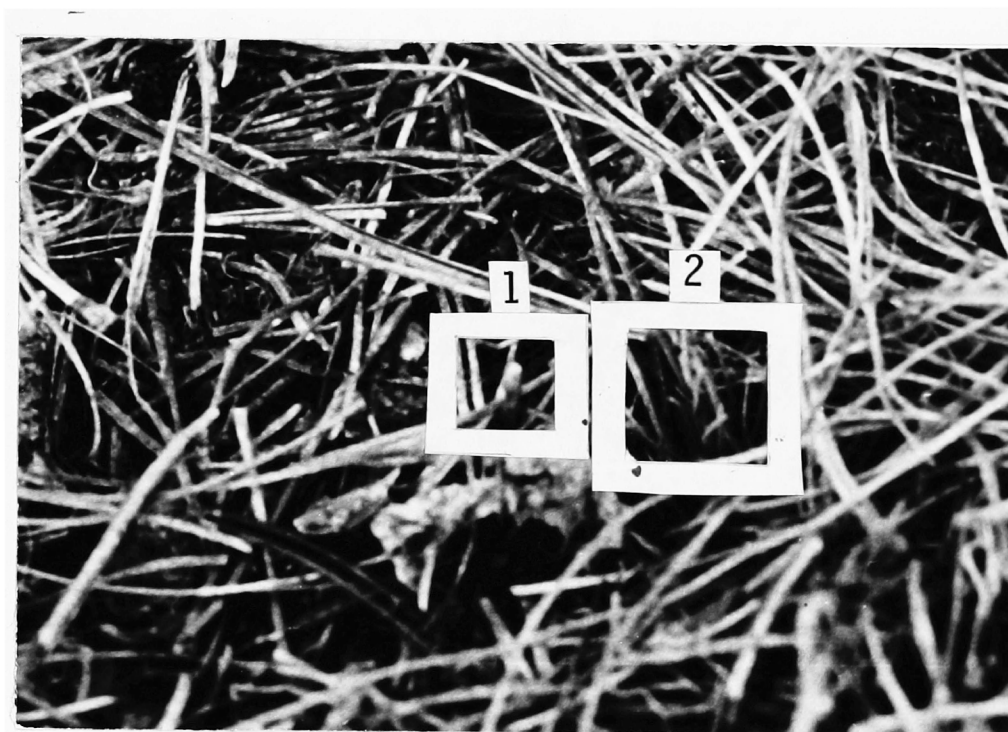


Figure 26. Example of cutworm damage to pine seedling. Box 1 shows severed stem and box 2 shows partially eaten cotyledons pulled into the litter by a cutworm.

(2) Bird or small mammal damage: This occurred predominantly within four weeks after germination while seed coats were still attached to the cotyledons. Both the seed coats and the cotyledons were removed leaving various amounts of the latter, from small stubs to three-fourths of the needle (Figure 27). Small mammals, either voles or deer mice, and birds were the prime suspected causes of this type of seedling damage (Gashwiler, 1971; Lawrence et al., 1961).

(3) Chlorotic and brittle: The seedlings turned red-brown and became hard and brittle while standing upright. They were obviously dehydrated, but water stress was not thought to be the cause of death because in most instances the soil was still moist. The actual cause of mortality was not determined.



Figure 27. Example of bird or small mammal damage to pine seedling. Cotyledons have been severed leaving only small stubs.

(4) Disappearance: When no evidence of a seedling could be found it was placed in this category. It is likely that death was due to cutworms and the entire seedling was consumed. Also if the seedling collapsed into the pine litter it could certainly blend in beyond recognition. (5) Poorly developed or fungal infected roots: Poor root development often occurred when root tips grew against large rocks near the soil surface. Fungal infected roots were rare. (6) Sun scald: This was usually determined by a heat lesion or crack in the stem near ground level. (7) Damping-off: A soft, mushy spot was observed on the seedling at or slightly below ground level. (8) Miscellaneous: This mortality category included cotyledons wrapped in spiders' webs, seedlings crushed by falling pine cones, seedlings buried by erosion, and seedlings stepped on by observers. A

total of 1,324 seedling deaths were recorded during the 1975 growing season. This represented 17.5 percent of seeds that germinated. Table 11 provides a detailed account of seedling mortality by category on each treatment.

Cutworm activity caused the greatest number of mortalities, over 30 percent, and was most prevalent in the litter treatment. Over 61 percent of the seedling deaths in the litter plots were caused by this insect. Other treatments that were substantially affected by cutworms were the opening-litter, the opening-natural, the fire, and the stemflow. The only treatments which did not have significant cutworm activity were the opening-cleared and the natural plots. The absence of cutworms on the opening-cleared plots was most likely due to the lack of protective cover. The natural treatments showed little cutworm damage because the seeds germinated very late in the growing season, after larval activity had declined considerably. Although damage caused by these insects was observed on pine-associated treatments where the ground cover had been removed, the greatest cutworm influence appeared where ground cover was present, such as in the litter, the opening-litter, and the opening-natural treatments.

The second most important cause of death to young pine seedlings was cotyledon clipping. The treatments whose seedlings were most significantly affected by this category were the stemflow, the opening-natural, and the canopy. The opening-litter and the fire treatments had medium clipping damage. The near treatment showed rather high clipping mortalities (Table 11), but 95 percent of these occurred in only one of the three replicate plots, so it was not a general trend. There was an

Table 11. Number and percentage of seedling mortalities by category per treatment

Treatment	<u>Mortality Categories</u>							
	Cutworms/	Birds and Small Mammals/	Unknown (Chlorotic)/	Disappeared/	Poor Root Development/	Sun Scald/	Miscellaneous/	Damping-Off
Opening- Cleared	2- 1.9%	3- 2.9%	30-28.6%	2- 1.9%	49-46.6%	12-11.4%	4-3.8%	3-2.9%
Opening- Litter	76-42.0%	32-17.7%	44-24.3%	18- 9.9%	0	7- 3.9%	3-1.7%	1-0.6%
Opening- Natural	55-26.8%	92-44.9%	30-14.6%	19 9.3%	2- 1.0%	3- 1.5%	4-2.0%	0
Fire	54-45.8%	17-14.4%	23-19.5%	4- 3.4%	3- 2.5%	7- 5.9%	9-7.6%	1-0.9%
Canopy	6-15.8%	13-34.2%	14-36.8%	1- 2.6%	0	0	1-2.6%	3-7.9%
Stemflow	46-18.3%	136-54.2%	49-19.5%	5- 2.0%	5- 2.0%	5- 2.0%	4-1.6%	1-0.4%
Natural	5- 9.6%	2- 3.8%	12-23.1%	26-50.0%	1- 1.9%	0	0	6-11.5%
Litter	169-61.5%	9- 3.3%	43-15.6%	42-15.3%	4- 1.5%	5- 1.8%	2-0.7%	1-0.4%
Near	16-16.3%	42-42.9%	11-11.2%	4- 4.1%	3- 3.1%	13-13.3%	4-4.1%	5-5.1%
<u>Totals</u>	<u>429-32.4%</u>	<u>345-26.1%</u>	<u>256-19.3%</u>	<u>122- 9.2%</u>	<u>67- 5.1%</u>	<u>52- 3.9%</u>	<u>32-2.4%</u>	<u>21-1.6%</u>

interesting relationship between the three opening treatments. The greatest clipping took place in the opening-natural plots, followed by the opening-litter plots, and the lowest damage consistently occurred in the opening-cleared plots. Small mammals would normally shy away from open, unprotected areas where they could be easily spotted by predators. Therefore, it seems logical that their activity be higher in protected areas, such as near large clumps of grass in the opening-natural plots. Even though many of the plots within the pine stand were cleared of all litter and vegetation, the pine trees apparently provided enough cover for the mice to venture into these plots and feed upon succulent young seedlings.

The tunneling ability of the small mammals probably provided their access inside the fences. They could have also climbed over the fences when the snow was deep and lived undetected within the plots. Therefore, the fences were only a partial deterrent to small mammal activity and provided no obstacle for birds. The number of voles and mice was perhaps higher during the summer of 1975 than normal because of the bumper cone and seed crop which occurred the preceding fall and winter. An abundant food supply could decrease the number of winter mortalities among the animals.

Seedling deaths caused by cutworms, small mammals, and birds were similar in that a portion of the seedling was severed. It was believed that these two mortality types could be distinguished by the region of the seedling receiving the injury. Cutworms apparently sever the stem near the ground level, whereas mammals clip a portion of the cotyledons, or the upper stem directly below the cotyledons. Birds likely pluck the

seed coats when they are still attached to the seedling thereby breaking a portion of the cotyledons. These two types of mortal injury (cutworms versus birds and small mammals) occurred at different times, with only a slight overlap (Figure 28). The seedlings most likely provided food for the mammals early in the summer when little else was available, but other more succulent vegetation that appeared later probably became their main food source.

Approximately 20 percent of the seedlings turned brown and became very brittle. This type of casualty was found on nearly all plots but was most frequent in the opening-cleared, the opening-litter, the canopy, and the natural treatments. There was no relationship between open versus canopy, or the presence or absence of litter with this type of mortality. Possible causes were heat stress, physiological drought due to too much soil moisture, or perhaps the expression of a lethal gene.

The disappearance of seedlings accounted for 10 percent of the losses. As mentioned earlier, this could have been the work of cutworms which devoured the entire seedling. The greatest number of disappearances occurred in treatments where there was ground litter or cover—the opening-natural, the opening-litter, the natural, and the litter—which was considered earlier as an important factor for cutworm presence, and where it was more difficult to find the evidence of chewed seedling remains. It was previously stated that seedlings in the natural plots avoided extensive cutworm damage because of late germination. However, if the disappearance of seedlings was the work of these larvae, then cutworms were definitely a factor in seedling mortality in the natural plots.

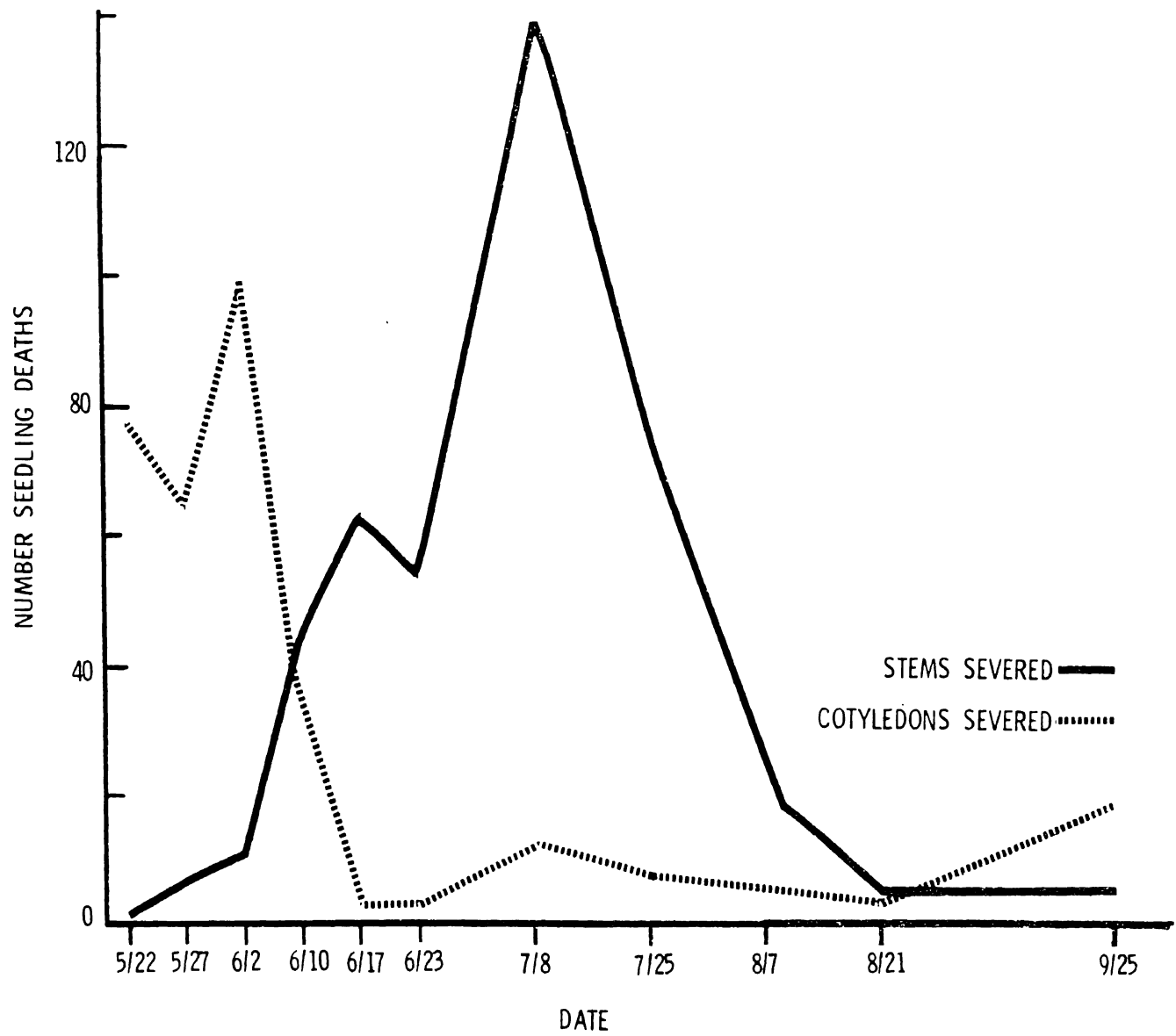


Figure 28. Seasonal variation of seedling deaths due to severed stems and severed cotyledons.

The remaining four casualty classes—poor root development, sun scald, damping-off, and miscellaneous—were responsible for 13 percent of total seedling deaths. Poor root development had its greatest effect in the opening-cleared treatment and very little effect elsewhere. Sun scald was associated with plots receiving the greatest amounts of sunlight. It was particularly noticeable in the opening-cleared, the opening-litter, the fire, and one of the near treatment plots. Conversely, damping-off was more important in plots with heavy shade and deep litter, such as the natural, the canopy, and the near treatments.

Drought has been shown to be the major cause of mortality in early establishment of ponderosa pine seedlings (Foiles and Curtis, 1973; Pearson, 1942; Rietveld and Heidmann, 1976; Wagg and Hermann, 1962). During this study, however, moisture stress was not thought to be significant because of the abnormally high precipitation in June, July, and August (Figure 9). Had the summer of 1975 been "normal" as far as rainfall, it is likely that drought rather than cutworms would have been the leading cause of seedling casualties.

Initial Seedling Establishment

An effort was made to determine in which treatments the greatest number of living seedlings existed at the end of the first growing season. The percentages of initial seedling establishment were calculated by dividing the number of seedlings remaining alive near the end of the growing season (Sept. 25) by the number of seeds planted. These establishment percentages and their statistical comparison are shown in Figure 29. Poor establishment was due either to poor germination or to high germination followed by high mortalities.

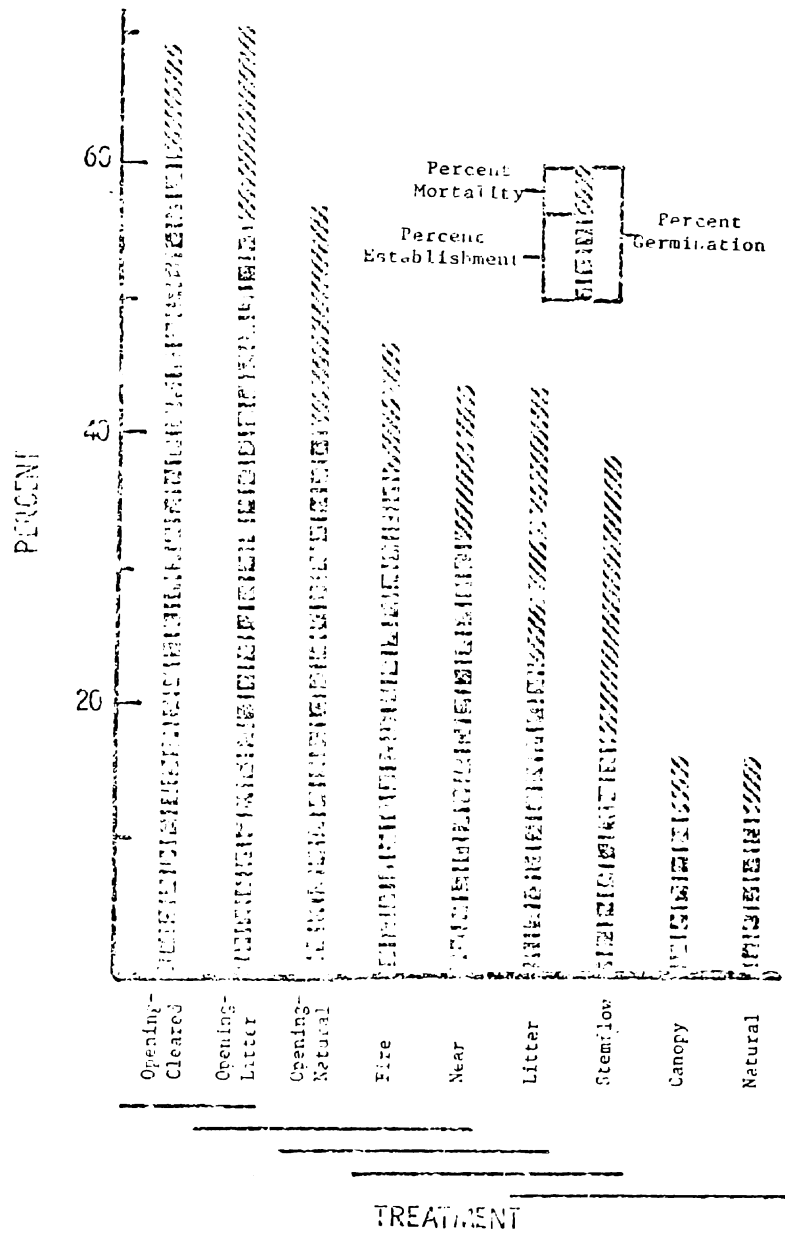


Figure 29. Percentages of live seedlings after one growing season due to germination minus mortality with statistical comparison of treatments.

Treatment averages clearly demonstrate that the opening plots produced the greatest number of surviving seedlings. The opening treatments' 51.8 percent establishment was significantly greater than the 22.5 percent establishment of the pine-influenced plots at the 1 percent level. The opening-cleared treatment produced live seedlings in

significantly higher numbers than the opening-natural and all pine-influenced treatments. The opening-litter and opening-natural plots had greater establishment than the stemflow, the canopy, and the natural plots. The fire and near plots had significantly higher numbers of established seedlings than both the canopy and the natural plots.

The poor seedling establishment on four of the pine-associated treatments--the litter, the stemflow, the natural, and the canopy-- was apparently caused by direct or indirect effects of the organic layer, the overstory canopy, or a combination of these on seed germination and seedling mortalities. Providing the canopy is not too dense, seedling establishment can be enhanced near overstory trees by removing the organic layer and competing vegetation. The method of removal, by fire or mechanical scarification, appears to have little effect on initial establishment numbers if the method is carried out thoroughly. However, the specific type of litter and vegetation removal can have a rather obvious effect on seedling size and vigor, as will be discussed in the next section.

Seedling Productivity

Procedures. To determine the effect of treatment influences on productivity, five randomly chosen pine seedlings including their entire root systems were lifted from each plot during the month of October, 1975. A hole was dug adjacent to an area with an adequate number of seedlings and they were removed by washing the roots free of soil with the aid of a water tanker. The seedlings were tagged for identification, put into plastic bags, and stored on ice until they could be transferred to a cold room at the laboratory. At a later date, total shoot lengths,

crown lengths, taproot lengths, and the lengths of all lateral roots over one centimeter long were measured. In addition, a very generalized estimate of mycorrhizal associations was made. Finally, the combined root biomass of the five seedlings and combined shoot biomass was determined for each treatment by oven drying for 24 hours at 105°C and then weighing.

Shoot lengths. Shoot lengths can be indicators of seedling vigor on a particular site. Specifically, greater crown lengths might imply greater photosynthetic area, and thus greater seedling success.

The average shoot lengths of the opening plot seedlings was 7.1 cm which was not significantly larger at the 5 percent level than the 6.8 cm average for seedlings from the pine-associated plots using Scheffe's test. However, if the seedlings grown in the fire treatment are removed from the comparison, the pine-associated average seedling height falls to 6.2 cm which is significantly smaller at the 1 percent level than the opening seedling heights. Removal of the fire plot seedlings from the comparison was done to better compare similar treatments in the openings with those in the pine stand.

Figure 30 shows treatment shoot lengths described by crown lengths and woody stem or hypocotyl lengths. This figure also presents a statistical comparison of treatment means as a result of Duncan's multiple range test at the 5 percent level of significance. Means not underscored with the same line are significantly different at this level. A log transformation of the data was necessary because of heterogeneous variances (Snedecor and Cochran, 1971).

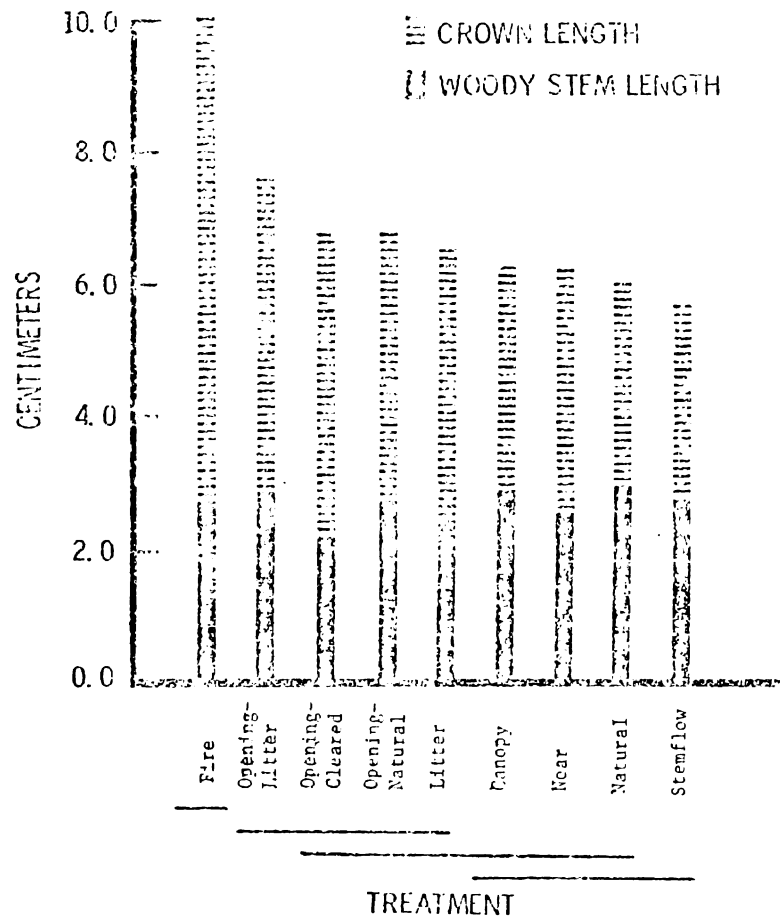


Figure 30. Average seedling shoot lengths with statistical comparison of treatments.

Average shoot lengths ranged from 10.1 cm on the fire plots to 5.7 cm on the stemflow plots. The fire plot seedlings were significantly taller than those on all other treatments. The seedlings from the openings were similar to each other and those grown in the litter plots, and all these were statistically larger than the stemflow seedlings. All other pine-influenced treatment seedlings were statistically the same height.

The crown, or portion of the stem producing needles, accounted for approximately one-half or more of the total shoot lengths, and an increase in total seedling height appeared to be caused by an increase in

crown length rather than hypocotyl length (Figure 30). Again, the average opening treatment seedling crown lengths, 4.4 cm, were similar to the pine-associated seedling crown lengths, 4.1 cm, but were significantly larger (5 percent level) than pine-associated seedling crown lengths excluding the fire plot seedlings, 3.4 cm.

The fire plot seedlings produced the largest crowns by far. The opening plot seedlings were again statistically similar to each other and the litter plot seedlings. The litter and opening-natural treatment seedling crowns were significantly larger than those from the canopy, the stemflow, and the natural treatments. The last three were statistically the same. Again, a log transformation of the data was necessary because the variances were not homogeneous.

Taproot lengths. Investigators believe that survival of ponderosa pine seedlings is dependent on the roots reaching a layer of soil that does not dry out through insolation (Tarrant, 1953). Of all the factors involved in survival on dry sites, depth of root penetration by seedlings is undoubtedly the most important (Pearson, 1924).

Before discussing taproot lengths, it is necessary to note that these measurements are lengths and not depths. For most seedlings lengths could be equated with depths, but on rocky sites where roots grew around large rocks or other roots the two were not exactly equal. Total length, however, implies taproot penetration and therefore, depth of potential water absorption.

The seedlings grown in the opening treatments had taproots which averaged 39.6 cm in length. This was significantly greater at the 5

percent level than the pine-associated treatment average of 34.6 cm, and larger at the 1 percent level than the pine-associated minus fire seedlings, which was 32.4 cm.

Treatment mean taproot lengths varied from a high of 45.9 cm from the litter treatment to a low of 22.0 cm from the natural treatment (Figure 31). A statistical comparison of means showed that the litter, the fire, the opening-cleared, and opening-natural seedling taproots were the longest and similar to each other. The three opening treatments had seedlings whose taproots were similar in length to each other and to those from the near and the canopy treatments. The stemflow and natural seedlings produced taproots which were significantly shorter than those from all other treatments. The litter and fire seedling taproots were significantly longer than taproots on seedlings from the opening-litter and all other pine-associated treatments.

Lateral root numbers. The number of lateral roots can be an important indicator of seedling success and survival potential because it represents the number of moisture and nutrient absorbing tips. The average numbers of lateral roots per seedling ranged from 39.0 for seedlings from the fire plots to 5.6 for seedlings from the natural plots (Figure 32). The fire and opening-cleared treatments had seedlings with the greatest number of laterals. These were statistically greater in numbers than seedlings from all other plots, which, excluding the natural treatments seedlings, were similar. Again, all of the opening and the litter treatments produced seedlings with large numbers of lateral roots. The natural treatment seedlings had significantly fewer laterals than

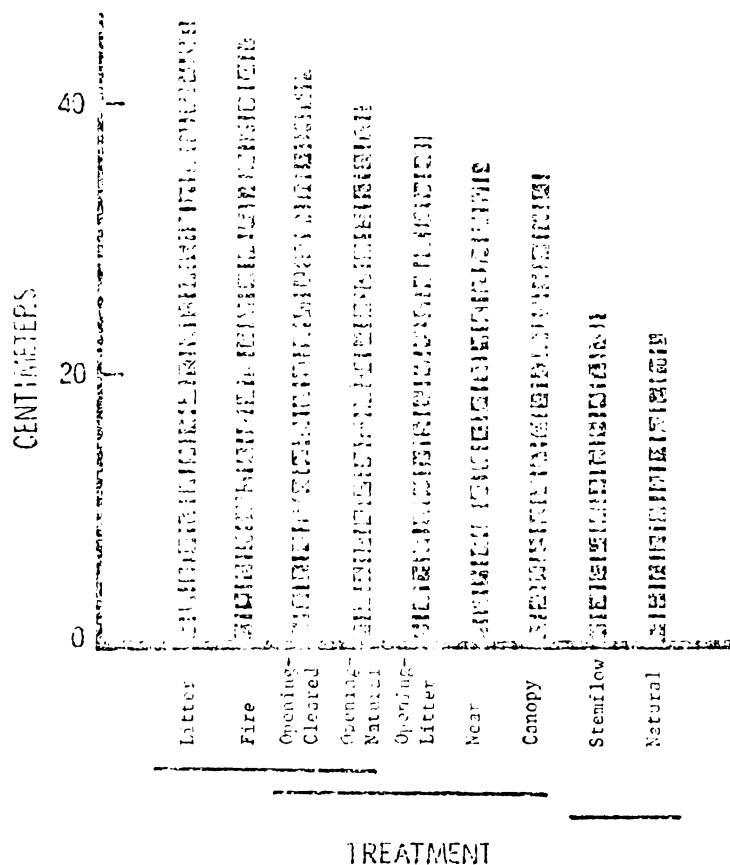


Figure 31. Average seedling taproot lengths with statistical comparison of treatments.

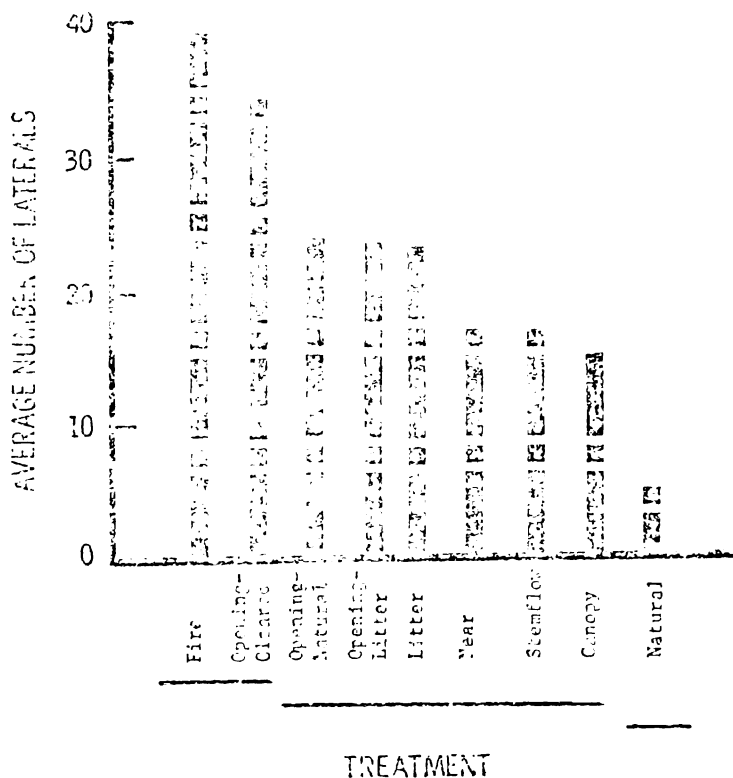


Figure 32. Average number of lateral roots per seedling with statistical comparison of treatments.

those from all other treatments. As a group, the 27.2 lateral roots per opening plot seedling was significantly greater at the 1 percent level than those from the pine-associated plots, 19.7, and excluding the fire seedlings, 15.9.

Lateral root length. Roots obviously reduce soil moisture in their immediate vicinity. Therefore, it is essential for plants living on dry sites to continually push their roots into regions of unexhausted moisture supply. To estimate the relative size of the root systems produced by seedlings in the individual treatments, total root lengths were calculated by summing the lengths of all lateral roots over 1.0 cm (Figure 33). This would indicate the amount of soil being tapped by the seedlings for moisture absorption.

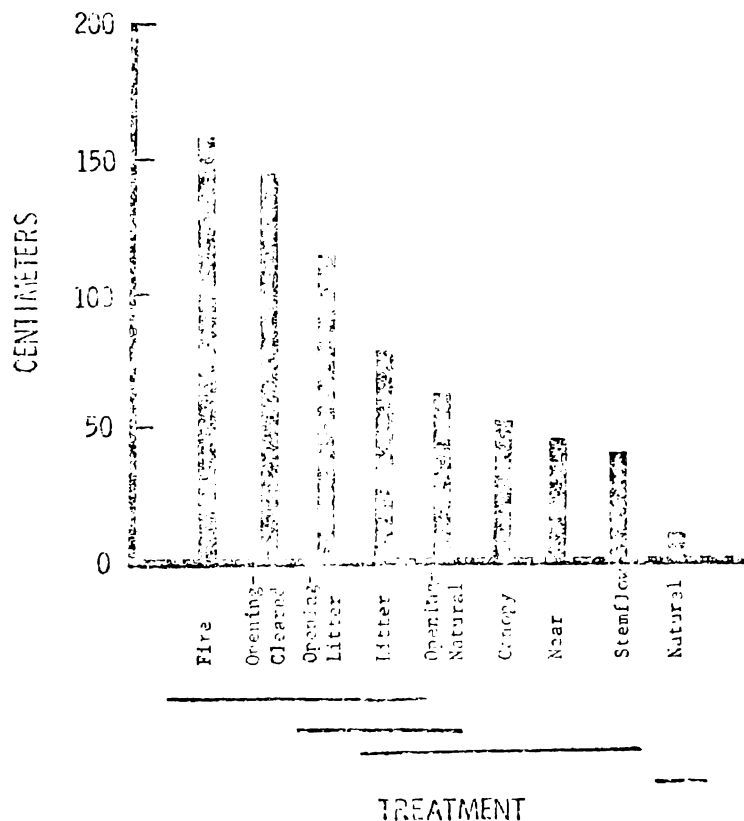


Figure 33. Average length of lateral roots per seedling with statistical comparison of treatments.

As with other measurements, the average lateral root length of 107.9 cm of seedlings grown in the opening treatments was statistically larger at the 1 percent level than the pine-associated seedling root systems, 64.5 cm, and without the fire treatment seedlings, 45.8 cm. As expected, the fire plot seedlings had the largest root systems, and were followed by and statistically equal to the root systems of seedlings from the opening-cleared, the opening-litter, and the litter treatments. The fire and opening-cleared seedling root systems were significantly greater than those from all other plots. The opening-litter seedlings produced lateral roots which were significantly longer than those from the remaining pine-influenced treatments. As before, the natural plot seedlings had root systems which were considerably smaller than other treatment seedling roots. Lateral roots produced on seedlings from the opening-natural treatment were somewhat smaller than those from the other two opening treatments. This was probably due to the presence of active root systems of grasses and herbs in the opening-natural plots. Similar results were reported for ponderosa pine seedlings by Larson and Schubert (1969).

Seedling biomass. As with other measurements, seedling weight is generally a good index of plant prosperity in a particular situation. Shoot and root weights can indicate amounts of photosynthetic and absorption area, respectively. However, care must be taken not to base results entirely on weight measurements, for without shoot heights and root lengths and numbers, weights can be misleading.

As before, the seedlings grown in the opening treatments showed superior growth. The total and shoot weights of these opening seedlings were significantly greater at the 5 percent level than the pine-associated seedling weights and greater at the 1 percent level than the pine-associated minus the fire seedling weights. Besides this, the root weights of the opening seedlings were significantly larger at the 5 percent level than those on the pine treatment seedlings without the fire seedlings included. With the fire treatment seedlings included, roots were heavier, but not significantly so when grown in the openings.

The oven dry weights for shoots and roots of seedlings from the individual treatments are shown in Figure 34. The treatments are ranked according to total seedling weights. Changes in total weights correspond to proportionate changes in shoot weights, $r^2 = .97$, and root weights, $r^2 = .90$. The corresponding changes of shoot and root weights resulted in an $r^2 = .79$. In addition, the figure shows the results of Duncan's range test comparing treatment means. The lines of significance above the x-axis point out shoot weight comparisons, and the lines below show root weight comparisons. Total weight comparisons are similar to those for root weights with one exception. The litter and opening-natural plot seedlings weighed significantly more than those from the natural plots.

The fire plots, again, had the heaviest seedlings, including both shoots and roots. The seedling from the opening-litter and opening-cleared treatments were similar in total seedling weight, with the former having heavier shoots and the latter producing heavier roots. The seedlings from the litter plots were next, having slightly heavier shoots and

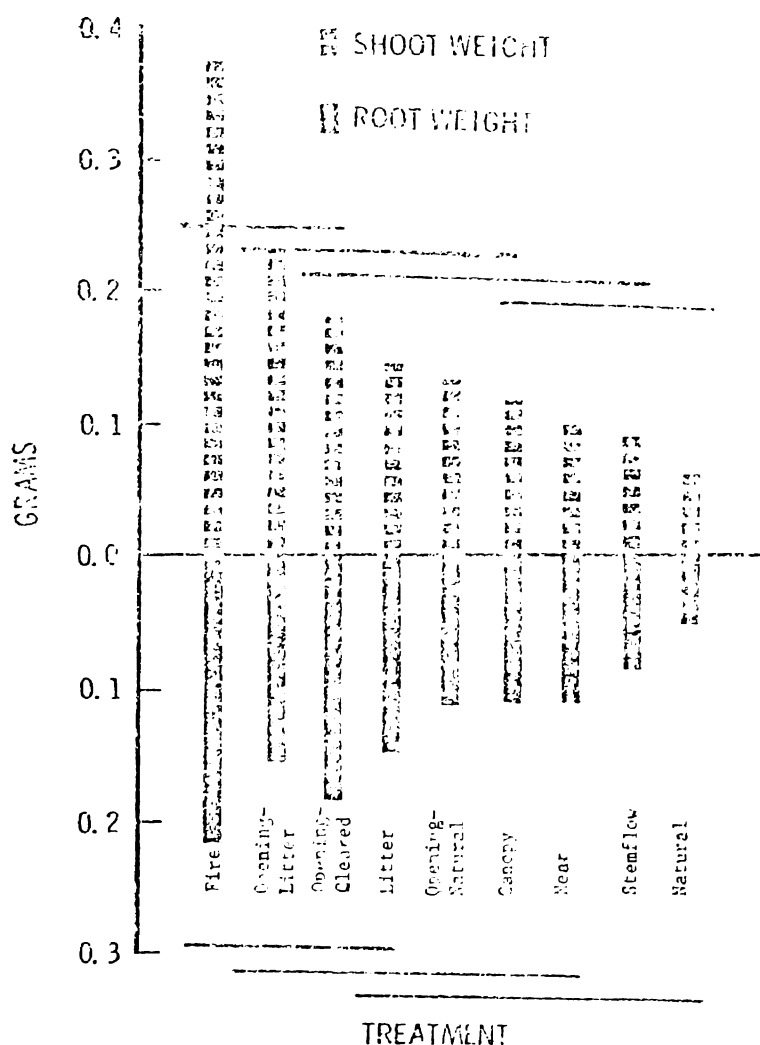


Figure 34. Average seedling shoot and root dry weights with statistical comparison of treatments.

roots than those from the opening-natural plots. Following these were the seedlings grown in the canopy, the near, and the stemflow plots. The natural plots produced seedlings with the least biomass, including the smallest shoots and the smallest root systems (Figure 34).

Statistical analysis of total seedling weights, shoot weights, and root weights (Figure 34) revealed less significant differences between treatments than occurred in shoot and root length analyses. This could be due to the fact that the five seedlings from each replication

of each treatment were weighted together and their weights analyzed together giving an error degrees of freedom of only 18. If all seedlings had been weighed separately, variability would certainly have been greater, but the increase in degrees of freedom to 126 would likely have allowed greater statistically significant differences as it did in previous seedling measurements. Because of heterogeneous variances, a log transformation of total and shoot weight data was necessary.

Mycorrhizae. During root measurements, a generalized estimate was made of the degree of mycorrhizal infection by placing each seedling into one of three categories—light, medium, or heavy—according to the observed number of mycorrhizal tips. The individual tips were not counted and placement was subjectively made on a relative basis. Lightly infected roots were characterized by a few widely spaced mycorrhizae, usually existing as one tip alone (Figure 35). Heavily infected roots had great numbers of fungal tips, often forming clusters and branching. Seedlings whose roots fell between light and heavy were placed in the medium category. Because of the subjective nature of this survey, definite conclusions were avoided.

Figure 36 shows average mycorrhizal infection for the 15 seedlings from each treatment. There were no seedlings that were completely devoid of fungal tips. The fire plots as a group had seedlings with the least infection. This was probably due to increased soil pH, increased soil nutrient status, and the physical action of heat on the fungi (Hacskaylo and Snow, 1959; Wright, 1971). Mycorrhizal associations do not normally occur in great numbers and may be entirely absent when nutrients,

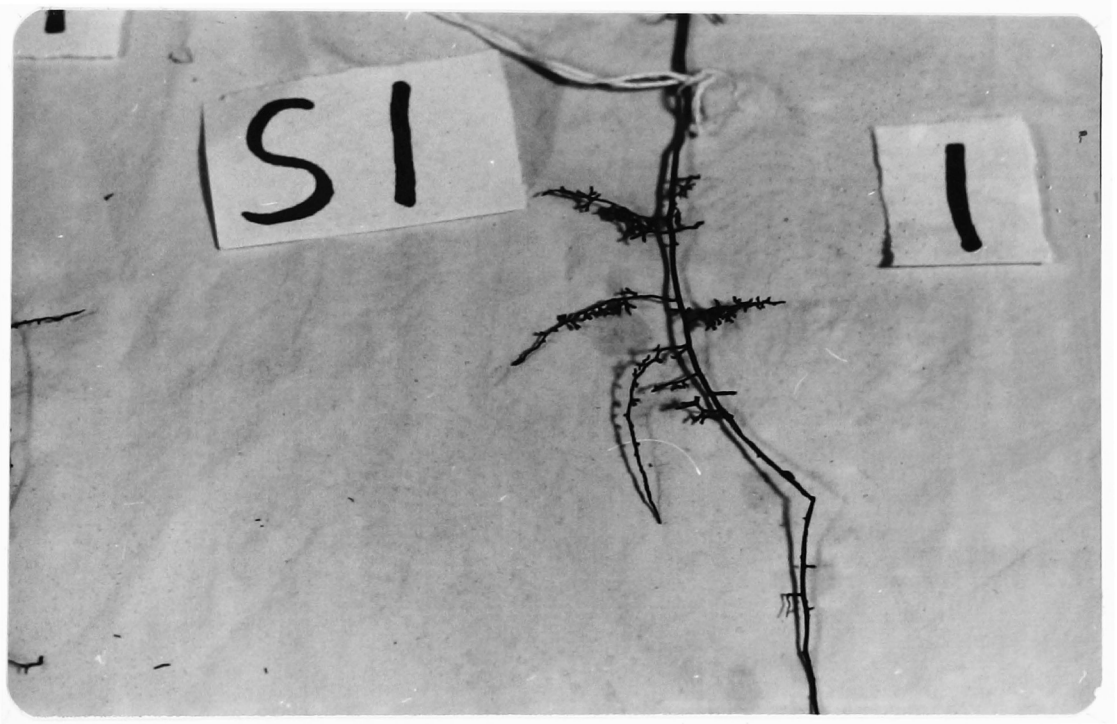
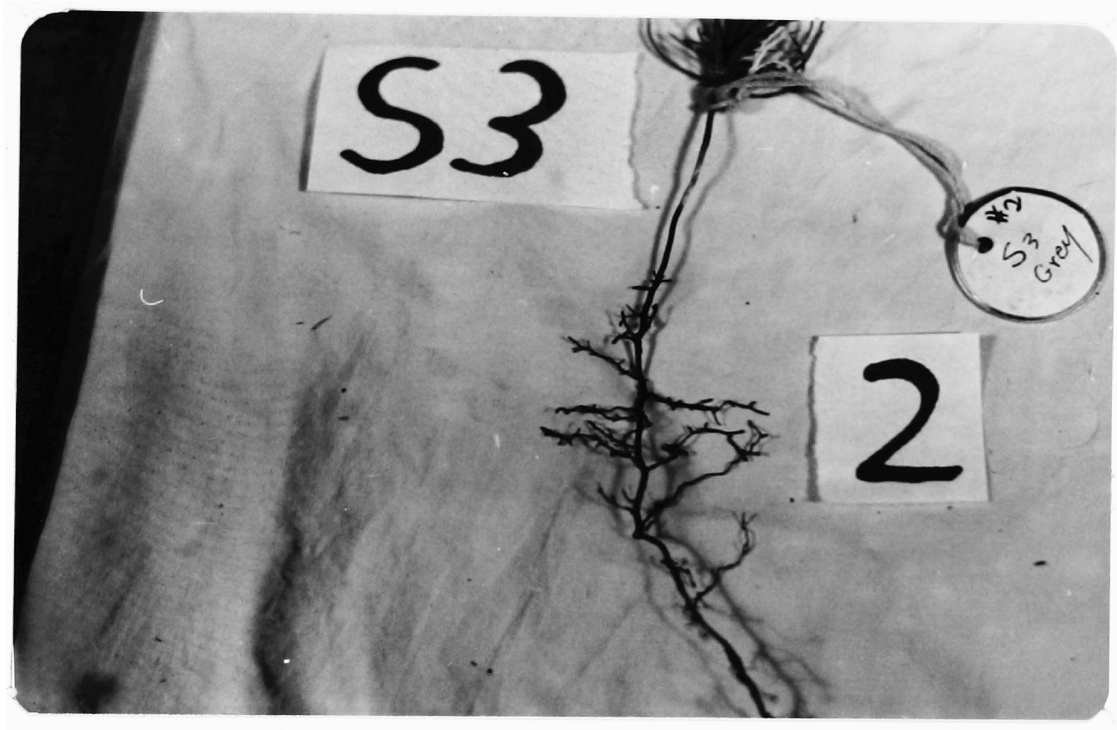


Figure 35. Examples of light (top) and heavy mycorrhizal infections (bottom).

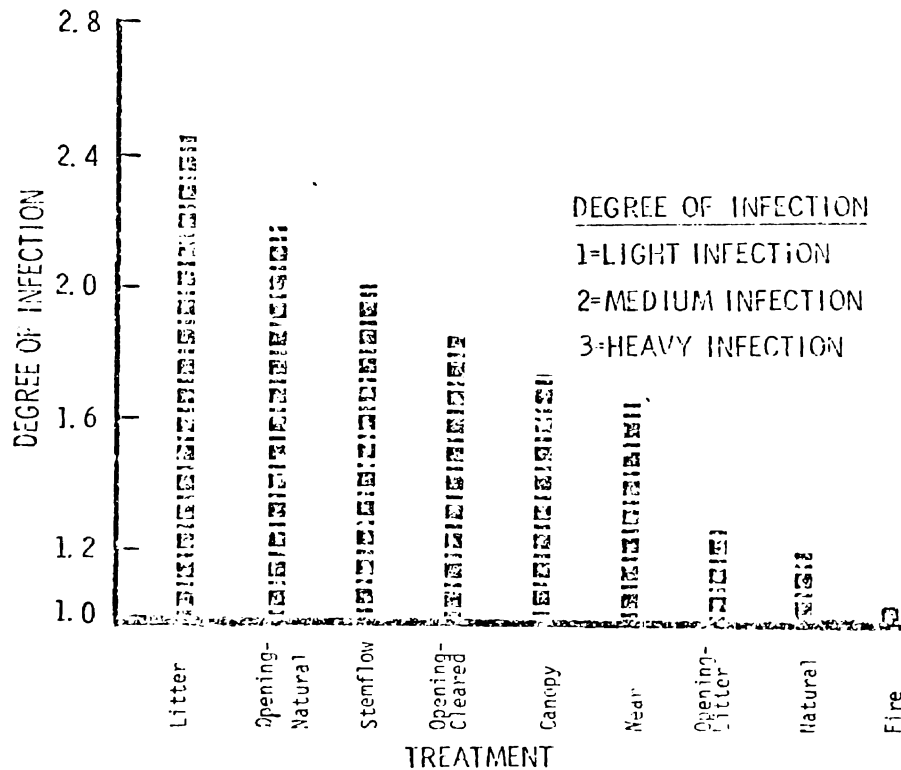


Figure 36. Degree of seedling root mycorrhizal infection per treatment.

especially nitrogen, become less limiting (Fowells and Krauss, 1959). The natural plot seedlings had the next lowest mycorrhizal numbers, slightly below the opening-litter seedlings. Substantial light is apparently a prerequisite for mycorrhizal formation because reserve carbohydrates from high rates of photosynthesis are necessary for fungal associations (Hacskeylo and Snow, 1959). Therefore, the high degree of shading coupled with apparent low soil temperatures caused by the deep litter layer on these natural plots could have been an important factor in causing low numbers of mycorrhizae. The greatest number of tips were observed on the litter treatment seedlings. There were inconsistent results concerning the degree of infection of seedlings from the opening-litter and litter treatments. The litter treatment seedlings had the

greatest infection whereas those from the opening-litter treatment had very few. Both treatments had similar nutrient levels, soil moisture conditions, and sunlight throughout the growing season. Other opening plots near the opening-litter produced seedlings with substantial mycorrhizae, so the potential for infection in the openings was present. The rest of the treatments showed no trends.

The presence of mycorrhizae has been shown to increase ponderosa pine seedling vigor (Wright, 1957). The seedlings may also be able to better withstand stress conditions when these fungal associations are present (Goss, 1960). The size of seedlings from different treatments in this study, however, cannot be correlated with degree of mycorrhizal infection alone.

Discussion. The possible factors influencing the growth of ponderosa pine seedlings, like most other plants, include light (intensity and quality), temperature, soil moisture, nutrients, competition, and phytotoxins. Potential phytotoxins were probably not naturally effective because they did not influence seedling growth in laboratory experiments (Harrington et al., 1976). Therefore, the first five environmental factors were most likely affecting the seedling growth in the various treatments.

Examining Figure 37, it is obvious that the best growth occurred in the fire treatments and decreased on each treatment in about the same order as the total seedling weights (Figure 34). One of the interesting findings was that productivity on the fire treatments was greater than on any of the three opening treatments. Examination of the environmental

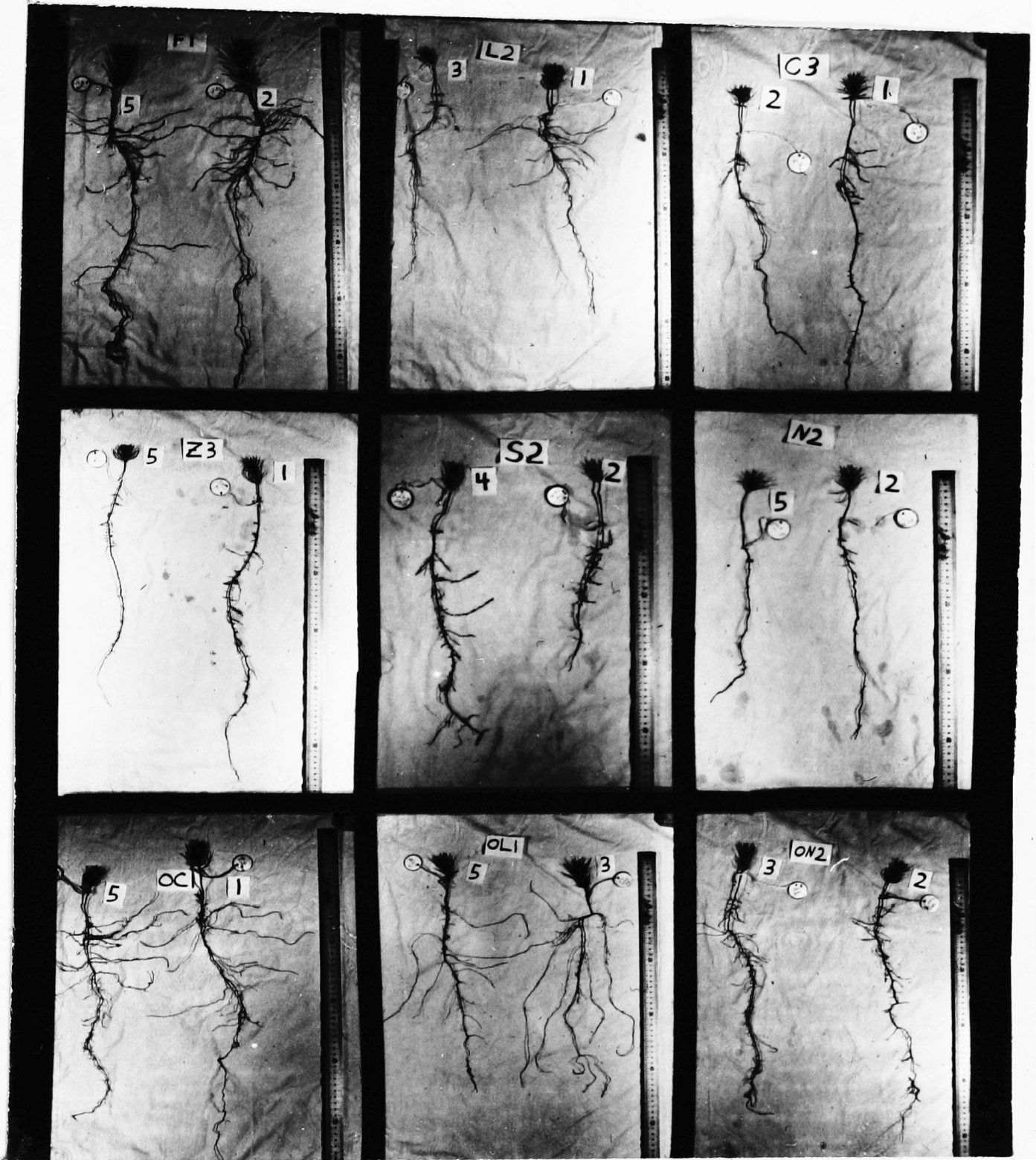


Figure 37. Representative seedlings from each treatment. Starting at top, left to right; fire, litter, canopy, near, stemflow, natural, opening-cleared, opening-litter, opening-natural treatments.

factors on each treatment might help to explain what factors were influencing seedling growth.

The amount of solar radiation reaching the surface of the fire plots was much less than that on the opening treatments due, of course, to shading by the canopy. This most likely caused lower daily air and soil temperatures even though maximum soil surface temperatures for the fire plots were quite high. The duration of heating was certainly not long enough to cause heating of lower soil levels to that of the opening plots. The soil moisture contents were also lower in the fire plots compared to the openings. As stated previously, insufficient moisture was not thought to have been a significant factor, as far as mortalities were concerned, during the summer months of 1975, but may have affected growth. With respect to the three opening treatments, the opening-litter had the most soil moisture throughout the summer, followed by the opening-natural, and finally the opening-cleared. Competition appeared to be the major factor in the opening-natural treatments and of minimal significance in the other two opening groups. Competition did occur to some extent on the fire plots because not all of the grasses and herbs were killed by the fire, and no "weeding" was carried out for the duration of the study. All vegetation on the fire plots was allowed to grow normally.

Examination of the soil nutrient status indicates that the opening treatments were about equal for all cations and anions measured. A comparison of the fire plots with the opening plots clearly demonstrates that the burned areas had greater nutrient concentrations, especially ammonium salts, phosphates, and potassium. The nitrogen (NH_4^+) in

particular is very important in the growth of ponderosa pine seedlings. Potassium, with nitrogen, may play a role in drought resistance of this species.

Comparing the environmental conditions of the fire treatment with those of the opening-cleared and opening-litter treatments, it seems apparent that seedlings from the fire plots had no advantage due to temperature, sunlight, soil moisture, or competition. They were, however, exposed to higher nutrient levels. It is most likely that this greater nutrient regime was responsible for the excess growth of the fire treatment seedlings over those grown in the opening-cleared and opening-litter treatments. The lower light levels probably did not hurt the fire seedlings' growth as much as would be expected. Bates (1925) concluded that if soil conditions (nutrients and moisture) were near optimum then seedlings could tolerate exposure to much less light.

The growth of seedlings in the opening-cleared and opening-litter treatments was nearly equal. It is difficult to say that one was better than the other because the opening-litter seedlings had slightly larger crowns and the opening-cleared had slightly larger root systems. There are two possible explanations for this. The mulching effect of the litter caused soil moistures to be higher in the opening-litter plots, and perhaps high enough to retard root growth because of oxygen deficiencies. Litter also does not conduct heat as readily as mineral soil so soil temperatures were assumed to be lower in the opening-litter plots. Increased soil temperatures up to 25°C have been shown to cause corresponding greater root lengths and weights of ponderosa pine seedlings (Larson, 1967).

It is clear, however, that the seedlings from the two opening plots discussed above grew better than those from the opening-natural plots. The physical characteristics of the opening-natural treatment were comparable to those encountered on the opening-cleared and opening-litter treatments in all respects except competition. These opening-natural plots had all of the native grasses and forbs present throughout the year and their presence can be considered most influential in reducing seedling growth.

The litter plots had environmental conditions which approximated those conditions found on the opening treatments and consequently, the growth was similar, being somewhere between that of the opening-cleared and opening-natural plots.

The reason for the poor growth in the stemflow plots is not apparent when examining the physical characteristics. Temperatures, light, and soil moistures were all comparable to those found in the opening-cleared and opening-litter treatments. The nutrient levels were slightly higher in the stemflow plots than in the openings. Time and rate of germination of the stemflow seeds were similar to those on the opening treatments. The seedlings on the stemflow plots experienced substantial mortalities due to cutworms and birds or small mammals early in the growing season. Many of the seedlings received cotyledon damage and did not die, but suffered growth impairment. Consequently, many of the early germinators were either killed or injured and the late germinators had a shorter growing period, resulting in smaller seedlings.

It was also observed during the excavation of stemflow seedlings that some of their roots grew into the outer corky layer of the large

roots of the center tree. When this happened, there was a considerable reduction in the size of the seedlings' root systems. This root interference was physical and not chemical because seedling roots would not be expected to grow towards high concentrations of growth inhibitors if they were present in the large roots. Therefore, the reduced growth on the stemflow plots was due to the fact that many of the surviving seedlings had been injured early in life. For those that escaped injury, root development was frequently reduced by interference from the center tree.

The remaining three treatments—canopy, near, and natural— had some very similar characteristics and the result was similar seedling growth responses. Surface temperatures were low, except for periodic intervals on the natural plots. However, these temperatures were recorded on the litter surface in the natural plots and the seeds were on the mineral soil surface at the base of 7 to 8 centimeters of litter. There is little doubt that temperatures were much lower at the mineral soil surface. The amount of light received on these three treatments was less than 50 percent of that received on the opening treatments. The reduced light and temperatures made themselves evident by causing later and slower germination rates, particularly in the natural plots. This, of course, reduced the growing period which, coupled with low temperatures and light levels, resulted in small seedlings. Larson (1967) showed that ponderosa pine seedling epicotyl lengths, root penetration, numbers of lateral roots, and dry weights were positively correlated to number of degree-hours. Number of degree-hours would be closely associated with total amounts of solar energy received. Helmers (1963) presented evidence that Jeffery pine seedlings also grow heavier and taller shoots, and

longer and heavier roots as temperatures and degree-hours are increased up to 25°C. So again, the importance of sunlight is emphasized.

Soil moisture on these three last treatments appeared to be adequate and not a limiting factor, although low values were recorded in September for the canopy and near plots. Nutrient levels were equal to or greater than those found in the opening treatments; consequently, it is very unlikely that the nutrient status limited growth. Therefore, temperatures and amounts of sunlight were probably the most influential environmental characteristics affecting seedling growth in the canopy, the near, and the natural treatments. Similar results were found in California where seedling growth under or near seed trees was drastically reduced (McDonald, 1976).

The natural plots differed from the canopy and near plots by the presence of a litter layer and understory vegetation. The effect of the litter layer on seedling growth was probably indirect. It reduced mineral soil surface temperatures and delayed germination to a later date, thereby reducing the growing period. Competition from understory vegetation was not extremely fierce, but under those poor growing conditions any competition would certainly have been an additional detriment.

CHAPTER VI

SUMMARY

In 1974 a group of field plots were established within and near a ponderosa pine stand to test ponderosa seed germination and seedling survival and growth under different treatment conditions. The plots consisted of two major groups, within the pine stand and away from the stand in openings. On each of these major groups, a series of soil surface treatments were performed. The treatments included burning, removing all vegetation and the organic layer, removing the vegetation only, and leaving the plot undisturbed. After treatment, an equal number of seeds were planted in each plot. Germination, survival, and growth were observed during the next growing season.

Approximately 45 percent of all seeds planted during the fall of 1974 germinated in the spring and early summer of 1975. Germination was much higher on the opening treatments than on the pine-associated treatments. The fire plots had the best germination of the pine-associated treatments. The presence of an overhead canopy or a combination of canopy and organic matter reduced germination. In addition to the number of germinants, the dates of germination were canopy dependent. In most instances, the greater the canopy coverage the later the germination. Moisture, temperature, and light quality appeared to be the important factors in the germination of ponderosa pine seeds. Snow did not accumulate as deep under pine canopies and it often melted earlier in the spring than

snow in the openings. This left the pine seeds exposed to fluctuating temperature and moisture conditions under the canopies. Therefore, proper stratification may not have been provided, thus reducing the seeds' ability to germinate. Also, soils with abundant organic matter may have higher moisture tensions and provide poorer seed-soil contact, thereby adding to the unfavorable germination conditions.

The canopy cover and litter layer determine the quantity and quality of light that reaches the forest floor. This affects seedbed temperatures which, in turn, can regulate the dates of seed germinations. In this field study, the germination period was dependent upon the amount of canopy coverage. Laboratory experiments have demonstrated that far-red light, which is prevalent in conifer shade, may inhibit the germination of ponderosa pine seeds (Harrington, 1976).

There is also the possibility that a weak phytotoxin, accumulating from canopy or litter leaching or perhaps decomposition products, is present on the soil surface and is playing a subtle role in germination reduction (Harrington et al., 1976). Therefore, there is a combination of physical and possibly chemical environmental factors that seemingly interact to inhibit the germination of ponderosa pine seeds beneath their own canopies.

Two weeks after the start of germination, seedlings began to die. Eight categories of mortality were recognized and are listed in order of decreasing importance (numbers of seedlings destroyed); cutworm damage, bird or small mammal damage, chlorotic and brittle (unknown), disappearance, poor root development, sun scald, miscellaneous, and damping-off. Drought, normally a significant detriment to seedling establishment, was

not an apparent cause of mortality during this study because of unusually high summer rainfall.

Treatment, as well as location, was a determining factor in the number of seedlings lost. Survival tended to be best on those treatments that were devoid of all surface vegetation. The presence of litter had a variety of effects which likely worked synergistically with other factors such as plot location and amount of overhead canopy. In general, the least mortality was observed on treatments with no ground cover, i.e. bare mineral soil.

Establishment, or actual numbers of living seedlings at the end of the first growing season, was greatest in the opening treatments. When trees were associated with treatments, the removal of ground cover produced the greatest survival. These experimental plots demonstrated that ponderosa pine seed germination and seedling survival were enhanced in the presence of overstory pine trees by the removal of understory vegetation and the organic layer. But better results were obtained by growing the seedlings some distance from the overstory in addition to removing the ground cover.

Although the number of seedlings produced is important in the reforestation of conifers, seedling health and vigor is also significant. The effects of fire stimulated seedling growth above that in all other treatments. Fire reduced litter and competing vegetation. Besides this, it enriched the soil by releasing nutrients from the organic matter, especially ammonium-nitrogen, phosphates, and potassium.

Seedlings grown in the openings were superior in shoot and root lengths and biomasses than seedlings from most other pine-influenced

treatments. Poorest growth in the openings occurred where fierce competition existed between the pine seedlings and grass species. Within the pine stand, reduced seedling size and vigor were attributed to the abundant overstory canopy, which decreased light quantity and soil and air temperatures, to the organic layer, which created poor moisture conditions and a physical barrier to growing seedlings, and to the root systems of larger trees, which were also a physical barrier to seedling root penetration. Moreover, the location of these plots allowed for more seedling injury, as well as mortalities, because of cutworm, small mammal, and bird feeding activities.

Thus, the advantages ponderosa pine seeds and seedlings have in openings away from overstory influences seem obvious. The observations of Weaver (1943, 1951), Cooper (1960), and Biswell (1973) revealed virgin pine stands as having an uneven-aged, park-like structure with various-sized openings in which reproduction flourished. It appears that this structure was maintained by the interaction of the physiological requirements of ponderosa pine, the physical and biological characteristics of the pine's environment, and period fires.

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