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

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# RESEARCH SUMMARY

Study plots were established to determine the effects of various environmental factors on ponderosa pine seed germination and initial seedling establishment and growth. A series of soil surface treatments were performed on plots in two locations: within or under the influence of overstory pine trees and in openings away from the pine influence. Seed germination was significantly greater in the opening plots. The overstory canopy and forest floor restricted the amounts of precipitation, light, and heat reaching the soil and probably decreased germination. Cutworms, birds, and small mammals caused the greatest seedling mortality. The largest seedlings occurred in the fire-treated plots. This was attributed to an increased nutrient supply and reduction of competition. Open-grown seedlings were larger than those growing under the overstory canopy. Amount of sunlight, degree of competition, and susceptibility to injury because of location appeared to be the major factors contributing to the seedling size differences. Because of abnormally high precipitation during the growing season, results may not be typical of average growing seasons.

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# INTRODUCTION

Throughout much of its range, natural regeneration of ponderosa pine (*Pinus ponderosa* Laws.) is usually slow and frequently uncertain. In addition, obtaining artificial regeneration is difficult and often succeeds only after rather drastic measures are applied to the stand or to the site (Wellner 1970). Practices such as clearcutting, burning, and mechanical site preparation that enhance regeneration are questioned by the public (U.S. Congress 1970; USDA Forest Service 1970). Successful forest management requires either prompt regeneration following harvest cutting or the establishment of advanced reproduction. Knowledge of the intricate factors that affect the establishment of ponderosa pine reproduction is vital to obtain a complete understanding of regeneration problems.

Much research has been devoted to ponderosa pine regeneration problems (Hermann 1970). In most cases, these studies have failed to explain where in the pine stand the environmental factors most influential in pine regeneration are working and how various parts of the pine forest (canopies, litter, boles, etc.) affect them. The study reported here was undertaken to provide this information.

# LITERATURE REVIEW

Natural restocking principally requires a good seed crop, a low rodent population, adequate available moisture, and bare mineral soil (Foiles and Curtis 1973). A bare mineral soil seedbed is thought to provide seeds and seedlings with more moisture, nutrients, and sunlight by reducing competing vegetation and by eliminating the dry, dense litter-duff layer. Baker (1951) and Fowells and Schubert (1951) observed that invading pines were more numerous on mineral soil seedbeds than on any other sites.

Removal of the organic layer is thought necessary because the litter and duff, having a lower thermal conductivity and volumetric heat capacity than mineral soil, raise daytime temperatures and lower nighttime temperatures at the litter-air interface (Cochran 1970). Furthermore, pine needles compact poorly and dry rapidly, allowing little moisture for seedling survival (Biswell 1973). Fisher (1935) found that ponderosa seed germination was best on bare or ash-covered soils and was poorest on duff-covered soils. Roe and Squillace (1950) found 8 times as many seedlings and Foiles and Curtis (1965) found 13 times as many pine seedlings on scarified mineral soil seedbeds as on duff-covered, natural soils.

Where mature ponderosa pine stands occur as open forest types, understory vegetation may be well established and vigorously compete with young pine seedlings. In the presence of grass associates, ponderosa pine reproduced at a very low rate compared to nearby areas lacking grasses (Baron 1962; Larson and Schubert 1969; Pearson 1934). Again, many authors advocate scarification of a site to reduce this competition (Fisher 1935; Foiles and Curtis 1965; Van Sickle and Hickmann 1959).

In some instances, intraspecific competition, especially between different age classes of ponderosa pine, can affect a stand. Saplings may 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 stunted and severely weakened (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.

Once a seed has germinated and the seedling begins its struggle for survival, factors other than competition can be destructive. Because pine sites generally have high summer temperatures and low precipitation, the young trees, though drought resistant, can succumb 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). In addition, deep shade can adversely affect or even kill young trees (Pearson 1936).

Weaver (1943, 1951) states that fire played an important role in structuring the pine forests and permitted a continuation of their success on sites that are now stagnating or experiencing a species change due to fire exclusion. Cooper (1960) has also shown the values of periodic burning in ponderosa forests. Fire-treated sites had larger trees, healthier regeneration, and a more open structure thereby providing less intraspecific competition than unburned sites. Biswell (1973) stated, "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."

Because 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 markedly increased pine reproduction. In northwestern Montana, broadcast burning was followed by the establishment of twice as many seedlings as on unburned areas (Shearer and Schmidt 1970). Schultz and Biswell (1959) studied the effects of different seedbed preparations on ponderosa pine seedling emergence. They found that 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 buildup of competition, crusting and smoothing of the soil surface by rain and wind, and the accumulation of fallen needles.

Additional effects of fire upon ponderosa pine regeneration were demonstrated in a number of studies by Vlamis and associates. In the first study they showed that fire increased the amount of nitrogen and phosphates in the soil (Vlamis and others 1955). Later, their experiments revealed that ponderosa pine seedlings responded greatly, by increased growth, to artificially added nitrogen (Vlamis and others 1957), and to burned soils, presumably because of increased nutrients (Vlamis and others 1956).

# STUDY AREA

The study site is 40 miles (64 km) northeast of Missoula and includes about 14 acres (5.6 ha) of level ground on the Blackfoot-Clearwater Game Range. The site is dominated by a ponderosa pine overstory with intermittent openings in the stand where pine regeneration is frequently abundant. Openings are of various shapes, and range in size from a few acres to small spaces between canopies. Pine regeneration is nearly absent in the understory.

The entire stand is 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. The site is very good for ponderosa pine growth, with an index of 95 feet (29 m) in 100 years (Meyer 1938). However, close observation indicates that Douglas-fir is invading the understory and will probably become dominant. This site is therefore a Douglas-fir--pine grass habitat type (*Pseudotsuga menziesii/Calamagrostis rubescens, Agropyron spicatum* phase) (Pfister and others 1977).

*Festuca scabrella* is the dominant vegetative species in the large openings and the intermittent clearings within the stand. This species is also the major component of the understory vegetation beneath the pine as long as the trees do not form a continuous canopy. In heavily canopied areas, *Calamagrostis rubescens* is dominant.

Livestock grazing has not been a significant factor since the early 1950's and the impact of deer and elk has been minimal. Some of the largest pine trees were selectively logged in the early 1950's, but their removal did not influence this study.

# METHODS

The field plots were established in the summer of 1974 and involved two major treatment groups. The first group of plots was situated within a ponderosa pine stand and contained six treatments. The second group was located in large openings near, but not under, the direct influence of the pine stand and had three treatments. Each treatment had three replications giving 27 total plots. Each plot was a square, 13 feet (4 m) on a side. The entire plot received a specific treatment and was fenced with 1/4-inch hardware cloth extending 30 inches (75 cm) above and 6 inches (15 cm) below the ground. A 12-inch (30-cm) strip of heavy-duty aluminum foil was secured along the top of the fence to discourage rodents from climbing into the plots.

A 10- by 10-foot square (3- by 3-m) was centered and permanently marked within each fenced plot. Each square was planted in November 1974 with 400 unstratified ponderosa pine seeds collected on site a month earlier from dominant or codominant trees. After the seeds were thoroughly mixed and their germinative capacity found to be about 84 percent, they were planted in 20 rows and 20 columns spaced 6 inches (15 cm) apart. The seeds were pushed slightly into the ground, but not buried, to prevent rolling or blowing out of place. In plots with organic layers and vegetation left, the seeds were placed next to mineral soil because this is where the majority of naturally fallen seeds were found.

The nine treatments were distinguished by differences in overstory canopy and varying amounts and methods of litter, duff, and vegetation removal (table 1). Treatment designations indicate site features which were emphasized.

A weather station was set up in a small opening near the middle of the study site and a continuous record of air temperature, relative humidity, and precipitation was kept from May 14 until November 11, 1975. Snow depths were determined on all plots on March 24, 1975.

Soil moisture contents were measured gravimetrically from soil samples collected five times during the growing season. Sampling depth varies with collection dates, starting with 0-2.8 inches (7.1 cm) on June 4, 0-4.3 inches (10.9 cm) on June 24, and 0-6 inches (15 cm) on July 21, August 13, and September 3. The depths of the first two collection dates were approximately equal to the lengths of the longest roots of newly germinated seedlings. This was done to compare moisture contents within the seedling root zone.

Table 1.--*Position and treatment of field plots*

| Treatment designation | Pine canopy position relative to plot | Seedbed treatment |
|---|---|---|
| Pine-influenced | | |
| Canopy | Directly overhead | Litter, duff, and vegetation removed to mineral soil |
| Litter | Not directly overhead | Litter and duff undisturbed, vegetation removed |
| Stemflow | Tree in center, small canopy overhead | Litter, duff, and vegetation removed to mineral soil |
| Near | Not directly overhead | Litter, duff, and vegetation removed to mineral soil |
| Natural | Directly overhead | Litter, duff, and vegetation undisturbed |
| Fire | Variable | Litter, duff, and vegetation burned |
| Opening | | |
| Cleared | None | Litter, duff, and vegetation removed to mineral soil |
| Litter | None | Litter, duff, and vegetation removed and replaced with pine litter and duff |
| Natural | None | Litter, duff, and vegetation undisturbed |

During the last week of October 1974, which was an excellent seed year, the number of naturally occurring ponderosa seeds was counted for each plot by a systematic sample using twelve 8- by 20-inch (20- by 50-cm) quadrats.

A spherical densiometer was used to determine amount of canopy covering each plot.

An Eppley pyrheliometer was used to measure solar energy falling on individual treatments. Measurements were made only once, on July 9, 1975, because of infrequent cloudless days and instrument complications. Readings were taken on all plots at approximately 10:00 a.m., 12:00 noon, and 3:00 p.m. (MDT). Total radiant energy from 9:30 a.m. to 3:30 p.m. was calculated by assuming the 10:00 a.m. reading represented energy received from 9:30 to 11:30, the 12:00 noon reading represented energy received from 11:30 to 1:30, and the 3:00 p.m. reading represented that from 1:30 to 3:30.

Maximum soil surface temperatures were measured with a series of heat-sensitive pellets on each plot in July 1975, the month during which the highest air temperatures were recorded.

Soils collected for moisture content were also analyzed for nutrient concentrations. At each of the five dates mentioned earier, ammonium and nitrate ion concentrations were determined by specific ion electrode analyses following KCL and water extraction, respectively. A glass electrode measurement of the water extract was used to determine soil pH. Analyses were also made for manganese, potassium, magnesium, phosphates, calcium, sodium, iron, copper, and zinc on the June 4, July 21, and September 3 samples. Following ammonium acetate extractions, the cations were measured by atomic absorption. Phosphates were determined colorimetrically. The soil sampling depths varied with sample dates, as before, to better compare nutrient concentrations within the seedling root zone.

Seeds began to germinate around May 13, and seedling counts were made weekly from May 14 through June 23, then every 2 weeks until August 21. A record of seedling mortality was kept during seedling counts, including the seedling age and apparent cause of death. In this study the causes of death were placed into eight categories. (1) *Cutworm damage* was observed as clipping of the stem near ground level leaving whole or partially consumed cotyledons separated from the stem. Similar types of damage by cutworms were reported by Fowells (1940). A number of large, green cutworms were found eating freshly cut seedlings. (2) *Bird or small mammal damage* occurred predominantly within 4 weeks after germination while seed coats were still attached to the cotyledons. Both seed coats and cotyledons were removed leaving various amounts of the latter, from small stubs to three-fourths of the needle. Small mammals, probably voles or deer mice, and birds were the prime suspected causes of this type of seedling damage (Gashwiler 1971; Lawrence and others 1961). (3) An *unknown* agent caused seedlings to turn *chlorotic 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. (4) When no evidence of a seedling could be found it was placed in the *disappearance* 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 have blended in beyond recognition. (5) *Poorly developed roots* often occurred when root tips grew against large rocks near the soil surface. Fungal infected roots were rare. (6) *Sun scald* was usually determined by a heat lesion on the stem near ground level. (7) *Damping-off* was observed as a soft, mushy spot on the seedling at or slightly below ground level. (8) *Miscellaneous* mortalities included cotyledons wrapped in spiders' webs, seedlings crushed by falling pine cones, seedlings buried by erosion, and seedlings stepped on by observers.

Initial (first year) seedling establishment was calculated by dividing the number of seedlings remaining alive near the end of the growing season (September 25) by the number of seeds planted (400).

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 October 1975. Total shoot lengths, crown lengths, taproot lengths, and the lengths and number of all lateral roots over 1 cm long were measured. Seedling shoot and root biomasses were determined after overdrying. Before this, a very generalized estimate of mycorrhizal associations was made by placing each seedling into one of three categories according to observed number of mycorrhizal tips. Lightly infected roots were characterized by a few widely spaced mycorrhizae, usually existing as one tip alone, and heavily infected roots had great numbers of fungal tips, often forming clusters. Medium infections fell between these two.

Two tests were used in the statistical analysis of seed germination, seedling mortality, and seedling productivity. A two-sample T test was used to compare the average seedling characteristics of the three opening treatments to those of the six pine-influenced treatments at specified significance levels. To compare the average seedling characteristics of the nine individual teatments with each other simultaneously, Duncan's Multiple Range Test was utilized at the 5 percent significance level. Because of heterogeneous variances transformations of germination percentages, shoot lengths, lateral root lengths, and total and shoot biomasses were required.

# RESULTS AND DISCUSSION

## Fires

The three fire plots were burned in the fall of 1974. Litter and duff moisture contents prior to burning ranged from 6 to 9 percent, and 11 to 19 percent, respectively. During the fires, the average maximum soil surface temperatures for entire plots ranged from 200°F (93°C) to 360°F (182°C) with individual points reaching in excess of 650°F (343°C). Litter and duff reduction by both weight and depth ranged from a low of 65 percent to a high of over 91 percent, indicating that even though the areas involved were small, the fires burned effectively.

## General Weather Conditions

Table 2 presents the average monthly air temperatures and total monthly precipitation occurring on the study site. In addition, this table includes a summary of temperature and precipitation data collected approximately 12 miles (19 km) due east at the Ovando weather station from 1941 to 1970 (U.S. Dep. Comm. 1973). The Ovando data correspond to "normal" weather conditions encountered near the study site, since the same weather systems influenced both areas.

Table 2.--*Average monthly air temperatures and total monthly precipitation at the study site, 1975, and normal monthly approximations*

| Month | Average temperatures | | Total precipitation | | |
|---|---|---|---|---|---|
| | Study site | Normal (Ovando) | Study site | Normal (Ovando) | Difference |
| | *°F* | | *Inches* | | |
| June | 50.4 | 54.3 | 2.69 | 2.47 | +0.22 |
| July | 64.7 | 61.3 | 2.81 | 1.00 | +1.81 |
| August | 57.3 | 59.6 | 2.10 | 0.99 | +1.11 |
| September | 51.3 | 50.7 | 1.15 | 1.22 | -0.07 |
| October | 38.8 | 41.4 | 3.91 | 1.18 | +2.73 |
| Average or total | 52.4<br>(11.3°C) | 53.5<br>(11.9°C) | 12.66<br>(31.7 cm) | 6.86<br>(17.2 cm) | +5.80<br>(+14.5 cm) |

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 1 month receiving above-average amounts of rainfall, resulting in 5.8 inches (14.5 cm) above the normal for the 1975 growing season. The 12.66 inches (31.7 cm) that fell during the 5-month period amounted to over 77 percent of the normal yearly precipitation, and was unequaled during the period from 1931 to 1960.

The greatest snow depths (30-35 inches) (75-88 cm) were found on the opening sites where the pine canopy had no influence. The least snow depths (8-20 inches) (20-50 cm) 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.

## 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 (fig. 1). 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 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 lowest soil moistures for the summer were found in the fire and canopy treatments.

## Natural Seed Occurrence

The plots associated with the pine stand had much greater numbers of natural seeds than plots in the openings. The greatest number of seeds (14.0/ft$^2$) (151/m$^2$) occurred on the canopy plots, and the least (2.7/ft$^2$) (29/m$^2$) were found on the opening-cleared plots. As a group, the opening treatments averaged only 2.9 seed/ft$^2$ (31/m$^2$) compared to 10.4 seeds/ft$^2$ (112/m$^2$) on the pine-associated plots. Thus, the areas immediately adjacent to seed-producing trees have the greatest potential for seedling occurrence due to greater seed numbers.

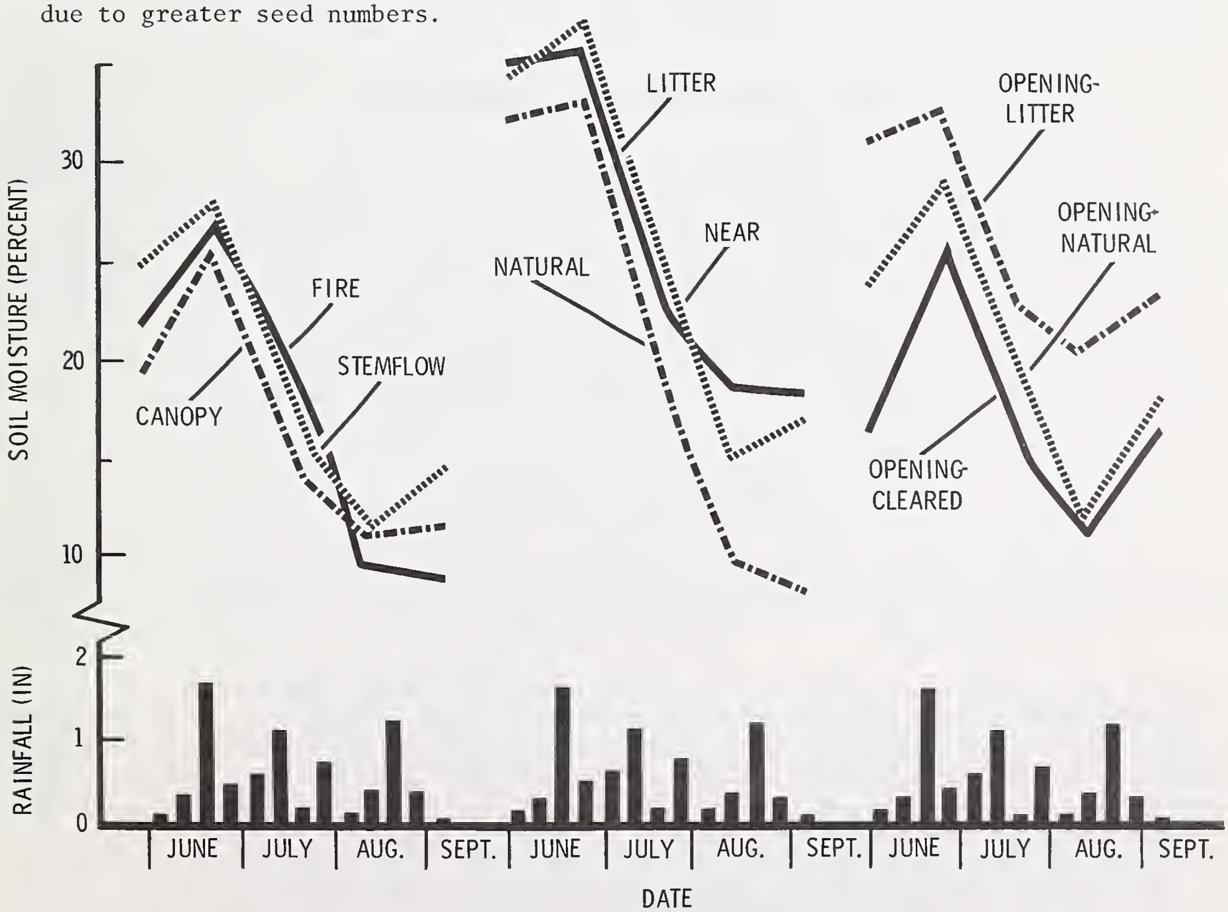



*Figure 1.--Temporal changes in soil moistures compared to amounts of rainfall.*

## Canopy Cover

The plots located in the openings had the least canopy coverage, ranging from 2 to 6 percent. The natural and canopy plots had the greatest canopy influence, with over 80 percent coverage. The canopy coverage on the other plots fell between these two groups, ranging from 35 to 72 percent.

Linear regression analyses comparing percentage of canopy cover to other physical factors give the following correlation coefficients: litter depth, +0.85; total radiation (9:30 a.m. - 3:30 p.m.), -0.91; maximum soil surface temperatures, -0.78; soil moisture 2 days after a rainfall, -0.84. These correlations indicate that increased canopy probably leads to greater amounts of organic matter, and decreased sunlight, soil temperatures, and rainfall occurring on the forest floor. Other factors such as vegetation and litter depth will also affect soil moisture, but the interception ability of the pine canopy must be emphasized.

## Solar Radiation

Total solar radiation amounts for 6 hours received on the opening and pine-associated treatments ranged from 350 to 390 g-cal/cm$^2$ (9 to 10 Btu/in$^2$) and from 130 to 340 g-cal/cm$^2$ (3 to 9 Btu/in$^2$), respectively. The plots in the openings, having little canopy influence, 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.

## Maximum Soil Surface Temperatures

The range of maximum soil surface temperatures for the opening plots was 138° to 151°F (57°-66°C). This was similar to temperatures encountered on the pine-influenced plots, 109° to 158°F (43° to 70°C). Maximum temperatures were recorded where litter and other organic matter were present; the litter, the opening-litter, the opening-natural, and the 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, 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.

## Soil Nutrient Analysis

Three of the eight exchangeable cations--iron, copper, and zinc--showed very little variation between treatments throughout the summer. The iron averaged 2 to 4 μg/g of soil, the copper averaged 2 to 3 μg/g, and the zinc averaged 1 to 2 μg/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 2,300-1,800 μg/g of soil throughout the summer, whereas soil from the pine-influenced plots averaged 2,200-1,600 μg/g over the same period. Sodium from the pine-influenced plots averaged 11 μg/g of soil throughout the growing season. The opening plots contained 2 to 3 μg/g less than these.

The remaining three cations--manganese, potassium, and magnesium--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 opening plots (table 3). The fire-treated soil had appreciably greater amounts of extractable potassium and manganese than all other treatment soils during the entire growing season.

Table 3.--*Treatment effects on soil nutrients from June to September, 1975*

| Treatments | Nutrient concentrations | | | | | |
|---|---|---|---|---|---|---|
| | Mn | K | Mg | $NH_4^+$ | $NO_3^-$ | $PO_4^{-3}$ |
| | - - - - - - - - | - - - - - | - - - *µg/g* | - - - - - | - - - - - | - - - - - - - - |
| Fire treatment | 50-100 | 715-1195 | 150-265 | 26-76 | 2.0-7.5 | 27-35 |
| Pine-associated treatments | 15-80 | 480-880 | 165-200 | 4-7 | 1.5-4.0 | 18-28 |
| Opening treatments | 10-65 | 240-410 | 145-170 | 4-7 | 1.5-5.0 | 8-26 |

Probably because of increased mineralization of organic nitrogen, fire-treated soil had an extremely high ammonium ion content that varied with fire intensity. The fire plots that burned the hottest, causing the greatest litter reduction, had the highest $NH_4^+$ concentrations. There was very little difference in $NH_4^+$ and $NO_3^-$ levels between the rest of the pine-associated plots and the opening plots (table 3). The increased amounts of $NH_4^+$ in the fire treatments did not lead to excessively high $NO_3^-$ concentrations, but the nitrate values were slightly higher than those found in most other treatments.

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

These analyses indicated that the nutrient content of the soils within the pine stand was comparable to or exceeded that in the openings. Rating the treatments in terms of seedling growth potential on the basis of nutrients is very difficult. However, the fire-treated plots do stand out from the other treatments in their high nutrient content, but this was expected (Christenson and Muller 1975; Viro 1974). Of particular interest was the increase in nitrogen ($NH_4$+), because this, along with other nutrients, can have a significant influence on the growth of ponderosa pine seedlings (Cochran 1972; Vlamis and others 1957) and may play a role in the drought-resistant capabilities of ponderosa seedlings (Loewenstein 1970). The particular form of nitrogen may also be important. Ponderosa seedling growth studies indicate that $NH_4^+$ is the preferred source over $NO_3^-$ and urea (Wollum 1968, 1970).

All treatments had similar soil pH values, except for the fire plots which, as expected, had much higher values. 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.

## Seed Germination

Of the 10,800 ponderosa pine seeds that were planted on the 27 study plots the previous fall, 4,812 (44.6 percent) germinated. Germination percentages varied greatly 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. The three opening treatments had an average germination of 65.4 percent, which was significantly greater at the 1 percent level than the six pine-influenced treatments, with an average germination of 34.1 percent.

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 (fig. 2). The opening-natural plots averaged about 12 percent less germination than the other two opening treatments, but the differences were not significant. Germination in the opening-natural plots was reduced somewhat because of unsatisfactory seedbeds, such as the middle of clumps of bunchgrass, or on crusted mosses or lichens. The opening-litter and opening-cleared treatments had significantly greater germination than all pine-influenced treatments. The natural and canopy treatments had by far the lowest germination.

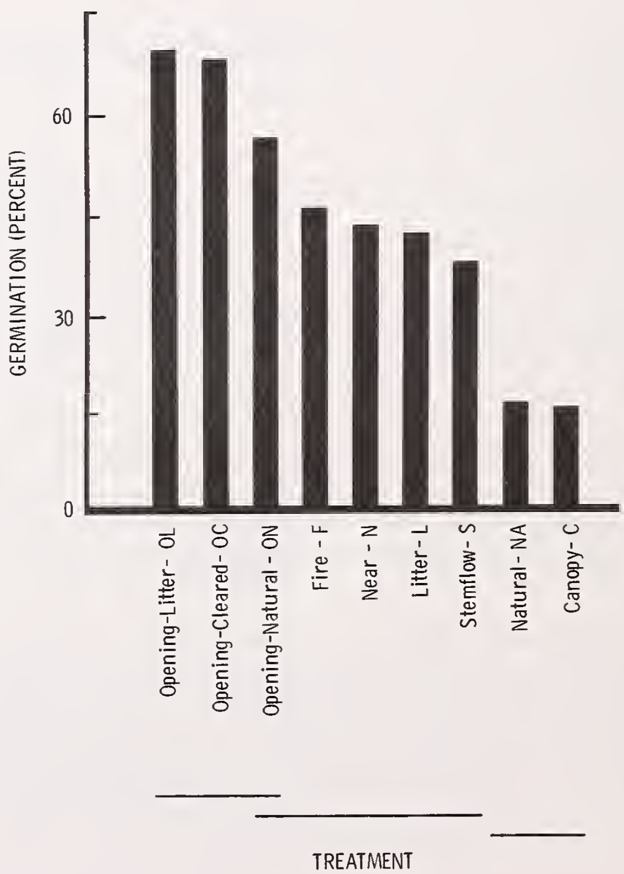



*Figure 2.--Seed germination percentages, with statistical comparisons of treatments. (Treatments not underscored with the same line are significantly different at the 5 percent level.)*

The lower germination in the pine-influenced treatments was probably due to cooler temperatures, as a result of shading, when moisture conditions were favorable. The organic matter could have created poor soil surface moisture conditions due to low water potentials and to the large, irregular shapes which provided inadequate contact between seeds and available moisture (Eyre and LeBarron 1944). Also, the amounts of far-red light in the shade may have had an inhibitory effect on germination (Harrington 1977). In addition to these factors, the absence of a protective snow cover under the overstory canopy may not have provided adequate overwintering conditions for seeds as was found in the openings. The possibility also exists that a chemical germination inhibitor could be subtly involved. Kelsey and Harrington (1979) found that soils from under pine canopies reduced ponderosa seed germination in the greenhouse compared to that in opening soils.

The germination rates, represented by the slopes of the curves, are shown in figure 3. Germination rates in the opening-cleared and opening-litter treatments averaged 18 seeds per day while that in the opening-natural treatment was 11 seeds per day. The fire, the litter, the near, and the stemflow plots had similar rates, averaging 7-8 seeds per day. The slowest rates occurred in the canopy treatment, with two seeds per day and the natural treatment with just over one seed germinating per day.

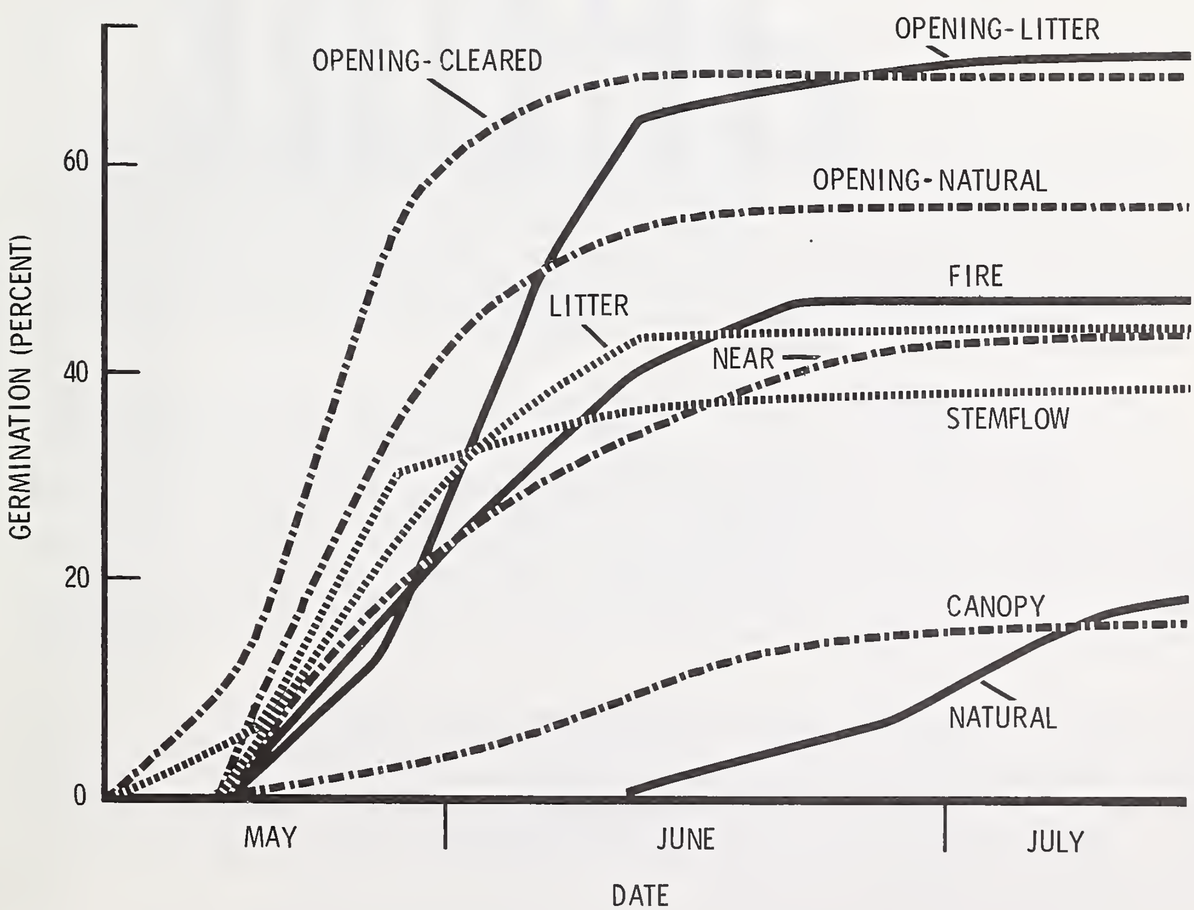



*Figure 3.--Seed germination per treatment*

Other obvious differences reflected by the curves in figure 3 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, the fire, the near, the litter, and the stemflow seeds appearing about 1 week later. The canopy and natural treatments created situations in which germination was 3 to 4 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 compared to an average of 22 weeks for the other seven treatments.

Looking at replications within the natural, the near, and the fire treatments, those plots with the greatest overhead canopy had the slowest and latest seed germination. Reasons for this are probably the same as for the variation in total germination: differences in temperature, moisture, and perhaps light.

## Seedling Mortality

A total of 1,323 seedling deaths were recorded during the 1975 growing season. This represents 27.5 percent of the seeds that germinated. The percent mortality ranged from 56.6 to 12.7 (fig. 4). The stemflow and litter treatments suffered the greatest damage, losing over half of their seedlings. The next six treatments all had very similar losses, 21 to 29 percent, while the opening-cleared treatment averaged only 12.7 percent. The average seedling mortality on the three opening treatments was 21.0 percent which was significantly lower at the 5 percent level than the 35.3 percent loss for the pine-influenced treatments.

Cutworm activity resulted in the greatest number of mortalities, more than 30 percent, and was most prevalent in the litter treatment causing more than 61 percent of the seedling deaths (table 4). 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 plots due to lack of protective ground cover and the natural plots 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, their greatest influence appeared where ground cover was present.

The second most important cause of seedling death was cotyledon clipping due apparently to birds and small mammals. The treatments whose seedlings were most significantly affected by this category were the stemflow, the opening-natural, and the canopy. The near treatment showed rather high clipping mortalities (table 4), but 95 percent of these occurred in only one of the three replicate plots, so it was not a general trend. The fences were apparently only a partial deterrent to small mammal activity and were no obstacle for birds.

Seedling deaths caused by cutworms, and small mammals and birds were similar in that a portion of the seedling was severed. These two mortality types may be distinguishable by the region of the seedling receiving the injury. Cutworms apparently sever the stem near 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 (cutworm versus birds and small mammals) seemed to occur at different times, with only a slight overlap (fig. 5). The seedlings most likely provided food for the mammals in the spring when little else was available, but other more succulent vegetation that appeared later probably became their main food source.

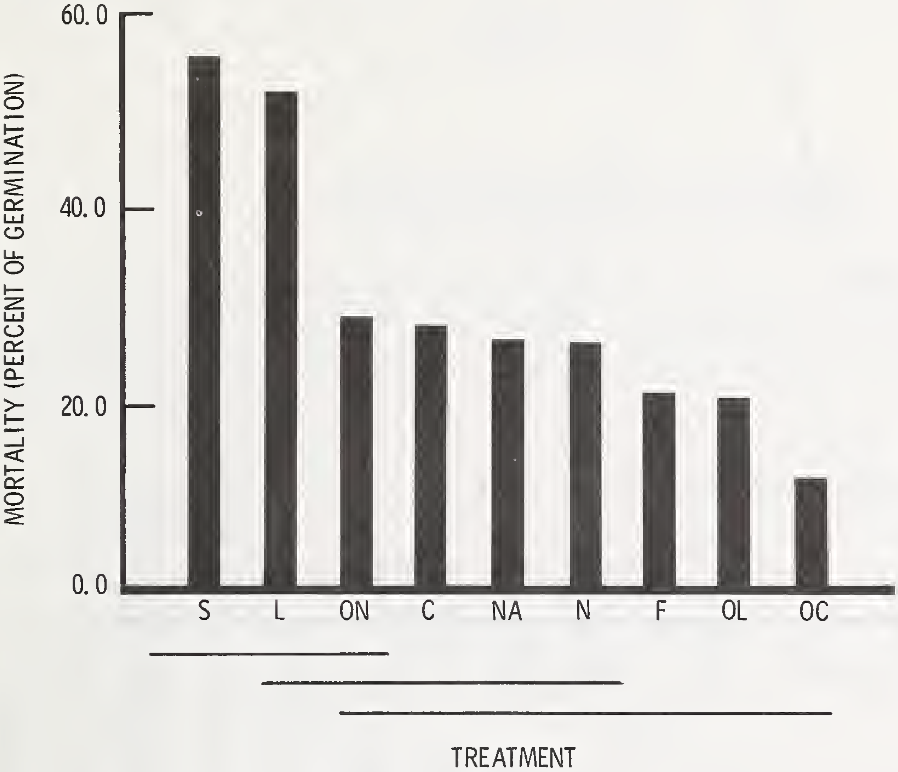



*Figure 4.--Seedling mortalities as percentages of germinants, with statistical comparison of treatments.*

Table 4.--*Numbers and percentages of seedling mortality by category per treatment*

| Treatment | Cutworms | | Birds and rodents | | Unknown (chlorotic) | | Disappeared | | Poor root development | | Sun scald | | Misc. | | Damping-off | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* | *%* | *No.* |
| 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 | 105 |
| Opening-litter | 76 | 42.0 | 32 | 17.7 | 44 | 24.3 | 18 | 9.9 | 0 | -- | 7 | 3.9 | 3 | 1.7 | 1 | 0.6 | 181 |
| Opening-natural | 55 | 26.8 | 92 | 44.9 | 30 | 14.6 | 19 | 9.3 | 2 | 1.0 | 3 | 1.5 | 4 | 2.0 | 0 | -- | 205 |
| 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 | 118 |
| Canopy | 6 | 15.8 | 13 | 34.2 | 14 | 36.8 | 1 | 2.6 | 0 | -- | 0 | -- | 1 | 2.6 | 3 | 7.9 | 38 |
| 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 | 251 |
| Natural | 5 | 9.6 | 2 | 3.8 | 12 | 23.1 | 26 | 50.0 | 1 | 1.9 | 0 | -- | 0 | -- | 6 | 11.5 | 52 |
| 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 | 275 |
| 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 | 98 |
| Totals and percentages | 429 | 32.4 | 345 | 26.1 | 256 | 19.3 | 122 | 9.2 | 67 | 5.1 | 52 | 3.9 | 32 | 2.4 | 21 | 1.6 | 1,323 |

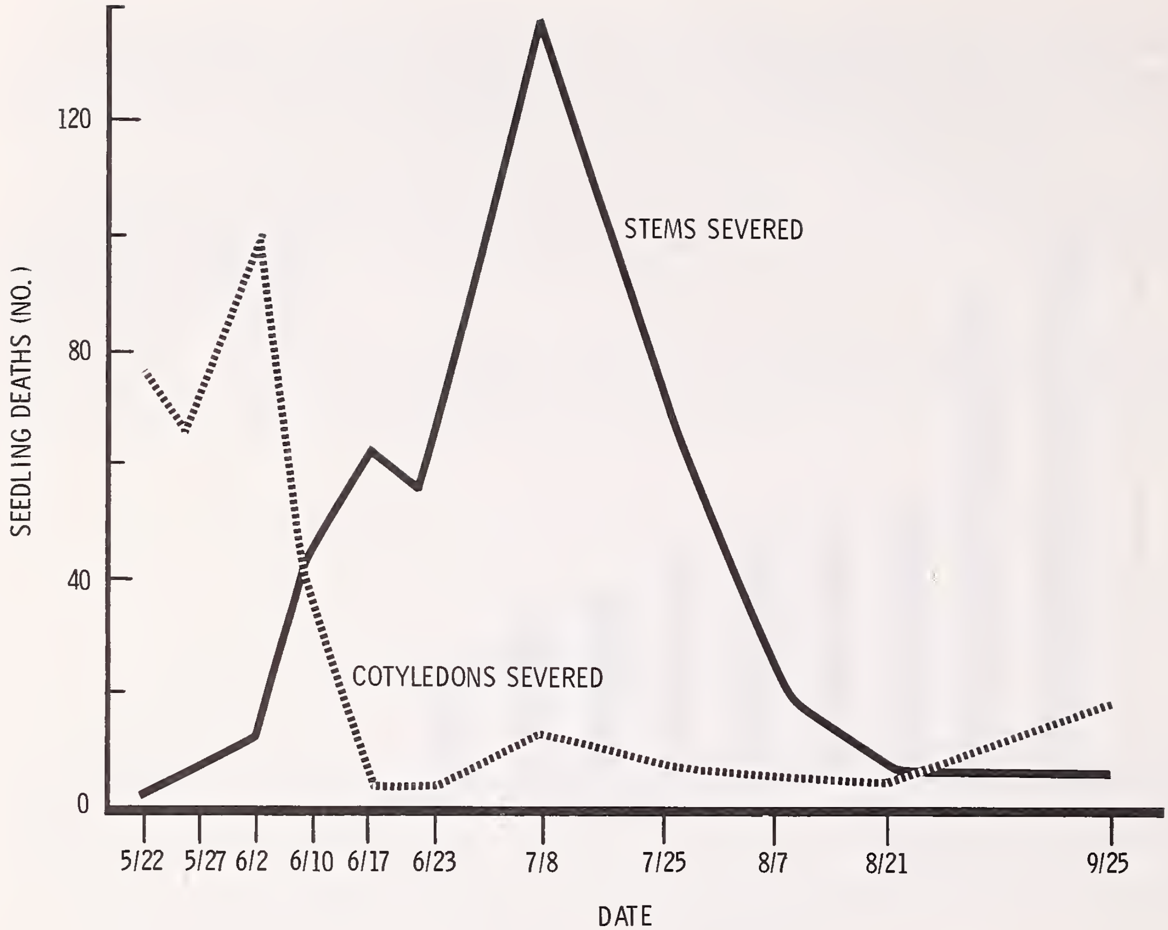



*Figure 5.--Seasonal variation of seedling deaths due to severed stems (cutworms) and severed cotyledons (birds and small mammals).*

Approximately 20 percent of the seedlings turned brown and became very brittle with no obvious cause. This type of casualty was common on nearly all 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, root death due to too much soil moisture or undetected root pathogens, 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 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.

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. Conversely, damping-off was more prevalent in plots with heavy shade and deep litter.

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 (table 2). 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

Poor initial seedling establishment was due either to poor germination or to high mortality. Treatment averages show that the opening plots produced the most surviving seedlings (fig. 6). 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.

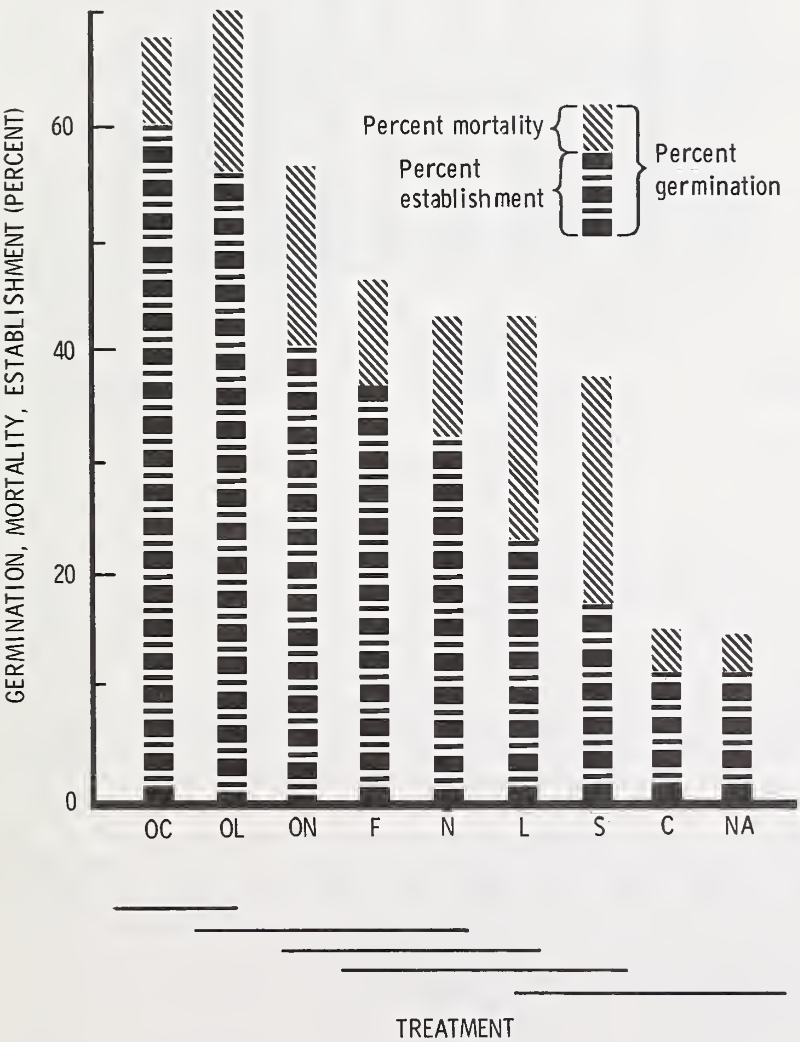



*Figure 6.--Percentages of live seedlings after one growing season due to germination minus mortality, with statistical comparison of treatments.*

The poor seedling establishment on most of the pine-associated treatments 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 was not too dense, seedling establishment was enhanced near overstory trees by removing the organic layer and competing vegetation. The method of removal, by fire or mechanical scarification, appeared to have little effect on initial establishment numbers if the method was carried out thoroughly. However, the specific type of litter and vegetation removal did have a rather obvious effect on seedling size and vigor, as will be discussed in the next section.

# Seedling Productivity

*Opening treatments vs pine-influenced treatments*.--A comparison was made between the average characteristic sizes of seedlings grown in the openings and those grown under an overstory. Another contrast is shown in which the fire seedling dimensions are removed from the analysis for a better comparison of treatments in the openings with those in the pine stand (table 5).

The superiority of seedlings grown in the open is evident. Their average characteristic sizes are greater than pine-influenced seedlings in all cases.

Table 5.--*Characteristics of seedlings occurring in openings compared to those of seedlings occurring under an overstory pine influence*

| Seedling characteristics | Average treatment measurements | | |
|---|---|---|---|
| | Opening | Pine-influenced minus fire | All pine-influenced |
| Shoot length | 7.1 cm | 6.2 cm** | 6.8 cm |
| Crown length | 4.4 cm | 3.4 cm* | 4.1 cm |
| Taproot length | 39.6 cm | 32.4 cm** | 34.6 cm* |
| Lateral root length | 107.6 cm | 45.8 cm** | 64.5 cm** |
| Lateral root number | 27.2 | 15.9 ** | 19.7 ** |
| Total biomass | 334.4 mg | 203.2 mg** | 267.8 mg |
| Shoot biomass | 181.1 mg | 103.3 mg** | 148.3 mg |
| Root biomass | 153.3 mg | 100.0 mg* | 119.5 mg |

* Treatment average significantly smaller than the opening treatment at the 5 percent level.

** Treatment average significantly smaller than the opening treatment at the 1 percent level.

*Shoot lengths*.--Average seedling shoot lengths ranged from 10.1 cm on the fire plots to 5.7 cm on the stemflow plots (fig. 7). The fire plot seedlings were significantly taller than those in all other treatments. These were followed by seedlings from the opening treatments, which were similar in size to those from the litter plots. Seedlings grown in the natural and stemflow treatments were the shortest.

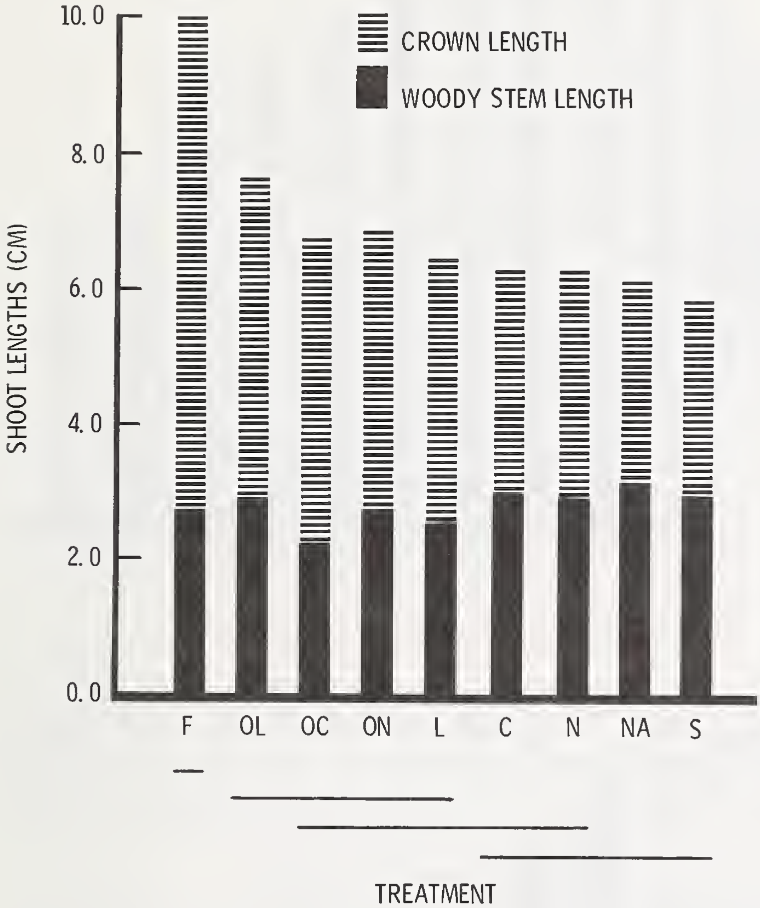


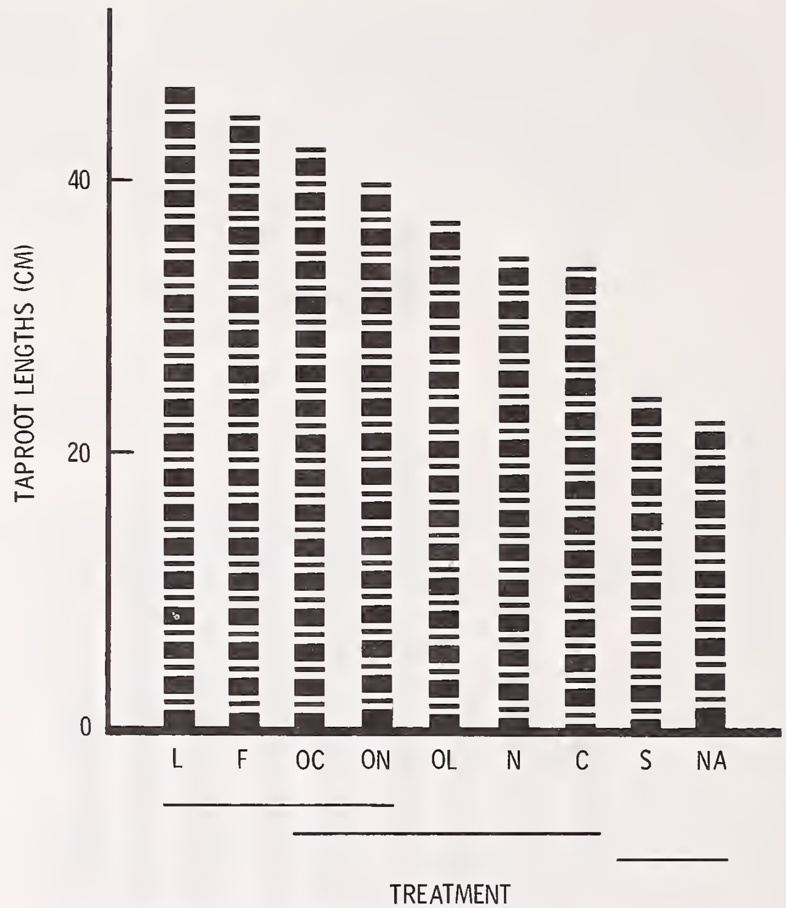

*Figure 7.--Average seedling shoot lengths, with statistical comparisons of treatments.*

The crown 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 lengths. Again the fire plot seedlings produced the largest crowns by far, and were succeeded by seedlings from the opening and litter plots.

*Root lengths and numbers*.--Figures 8, 9, and 10 show root size and number comparisons. The fire plot seedlings produced vast root systems in contrast to other pine-associated plots. The opening plots generally contained seedlings with root systems also superior in size to the majority of seedlings grown within the pine stand.

Treatment mean taproot lengths varied from a high of just under 46 cm in the litter treatment to a low of 22 cm in the natural treatment (fig. 8). Seedling taproot lengths from the fire and opening treatments closely followed those from the litter treatment. The average number of lateral roots per seedling ranged from 39 on fire plot seedlings to just over five on the natural plots seedlings (fig. 9). These numbers also gave the fire treatment seedlings a distinct advantage in lateral root lengths with just under 160 cm of roots (fig. 10). The opening-cleared seedlings grew well with an average of 145 cm of lateral roots but the natural plot seedlings, with few and short roots, averaged only about 11 cm of total lateral root length.

*Figure 8.--Average seedling taproot lengths, with statistical comparisons of treatments.*



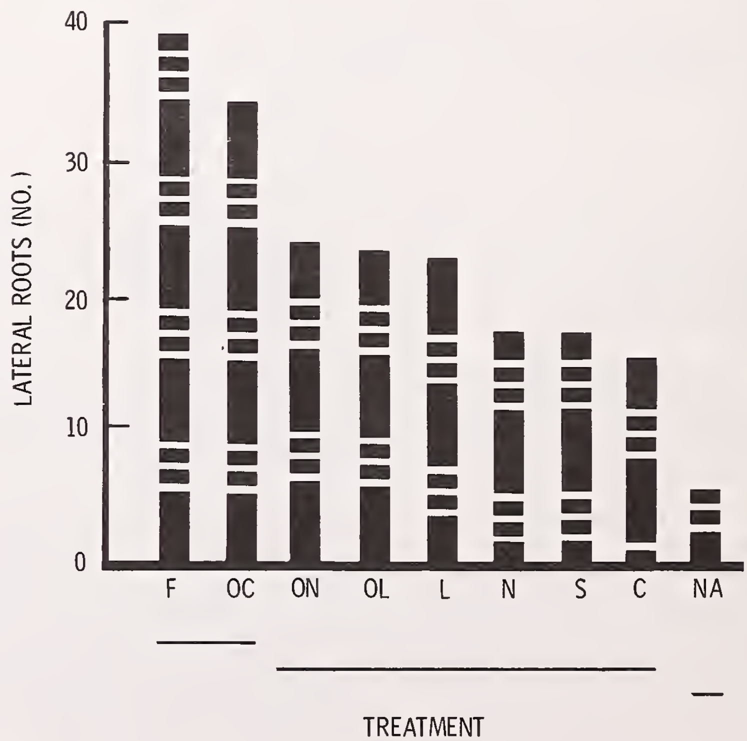




*Figure 9.--Average number of lateral roots per seedling, with statistical comparison of treatments.*

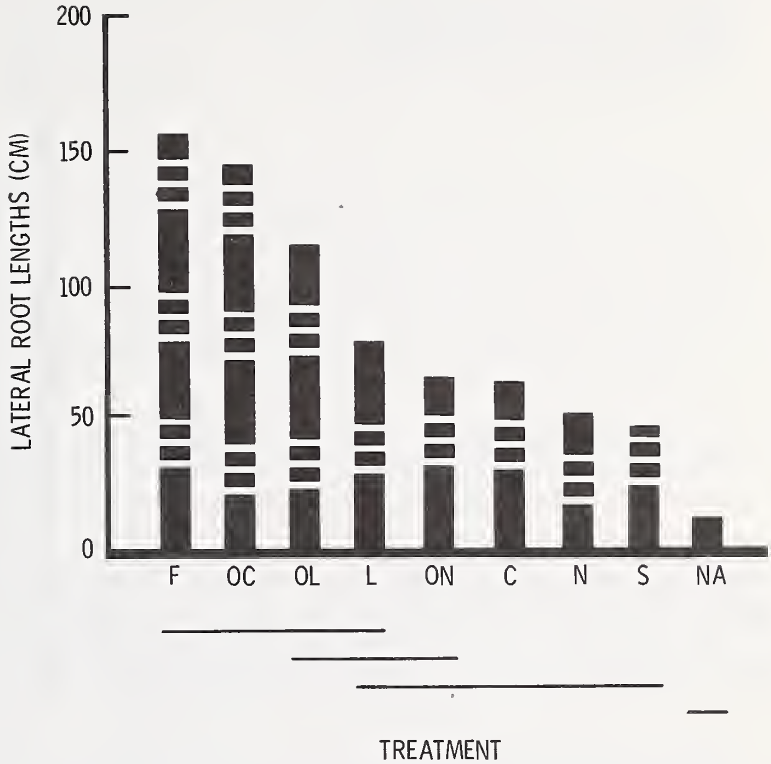


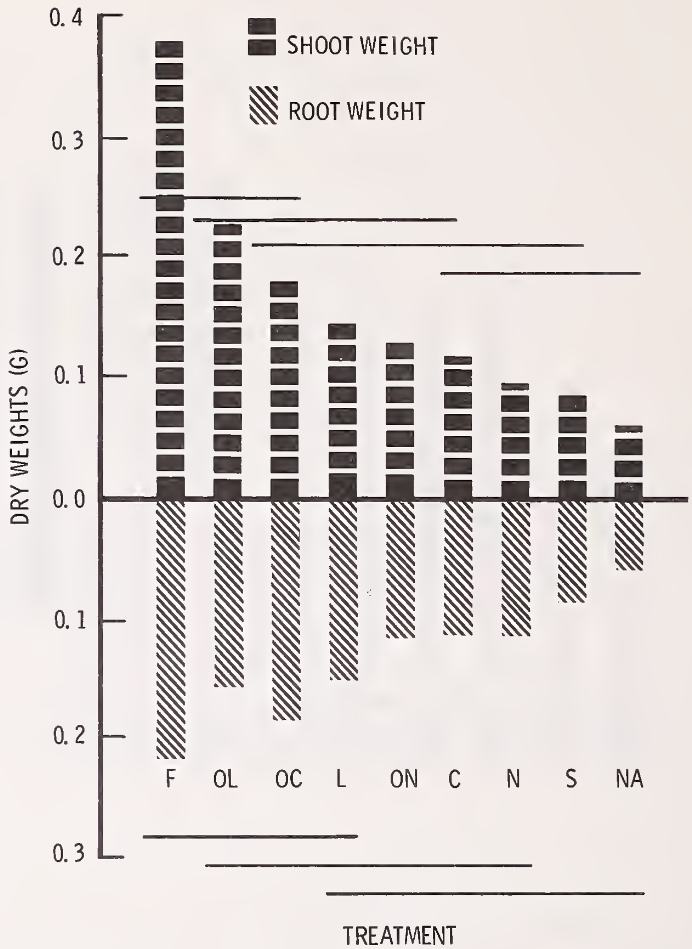

*Figure 10.--Average length of lateral roots per seedling, with statistical comparison of treatments.*

*Seedling biomass.*--The ovendry weights for shoots and roots of seedlings from individual treatments are shown in figure 11. The treatments are ranked according to total seedling weights. The lines of significance above the x-axis point out shoot comparisons, and the lines below show root comparisons. Total weight comparisons are similar to those for root weights.

The fire plots, again, had the heaviest seedlings, including both shoots and roots. The seedlings from the opening-litter and opening-cleared treatments were similar in total 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 roots than those from the opening-natural plots. The natural plots produced seedlings with the least biomass, including the smallest shoots and the smallest root systems.

*Mycorrhizae.*--Figure 12 shows average mycorrhizal infection for the 15 seedlings from each treatment. There were no seedlings that were completely devoid of mycorrhizae. The fire plots as a group had seedlings with the least infection because of increased soil pH, increased soil nutrient status, and the physical action of heat on the fungi (Hacskaylo and Snow 1959; Wright 1957). Mycorrhizal associations do not normally occur in great numbers and may be entirely absent when nutrients, 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 (Hacskaylo 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.

Figure 11.--Average seedling shoot and root dry weights, with statistical comparison of treatments.



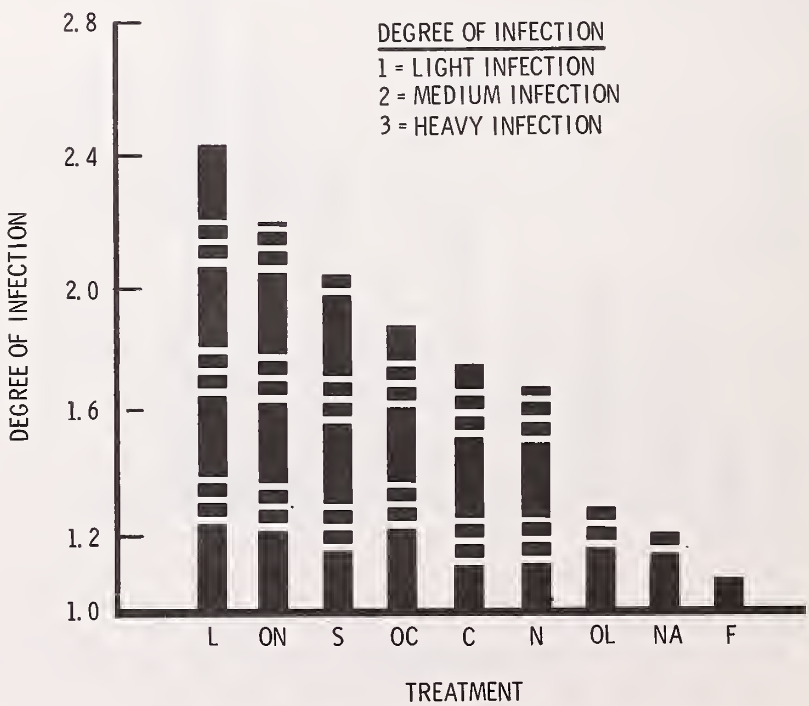




Figure 12.--Degree of seedling root mycorrhizal infection per treatment.

*Discussion.*--The possible factors influencing the growth of ponderosa pine seedlings, like most other plants, include light (quantity and quality), temperature, soil moisture, nutrients, competition, and phytotoxins. Potential phytotoxins were probably not naturally effective because in high concentrations they did not influence seedling growth in laboratory experiments (Kelsey and Harrington 1979).

Seedling productivity on the fire treatments was much greater than that on any other treatment. Comparing the environmental conditions of the fire treatment with those of the opening-cleared and opening-litter treatments, seedlings from the former had no advantage due to optimum temperatures, sunlight, or soil moisture, and experienced greater competition. The fire seedlings were, however, exposed to higher nutrient levels which was most likely responsible for the rapid growth. The lower light levels probably did not hurt the fire seedlings' growth because if soil conditions (nutrients and moisture) are near optimum then seedlings can, perhaps, tolerate exposure to much less light (Bates 1925).

The growth of seedlings in the opening-cleared and opening-litter treatments was nearly equal. Slight differences were likely due to the mulching effect of the litter which permitted higher soil moistures and probably lower soil temperatures.

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 in these plots were all comparable to those found in the openings and the nutrient levels were slightly higher. Time and rate of germination of the stemflow seeds were similar to those on the opening treatments. However, 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. It was also observed during the excavation of stemflow seedlings that some of their roots had grown 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 which certainly affected shoot sizes.

The remaining three treatments--canopy, near, and natural--had some very similar characteristics which resulted in similar seedling growth responses. Soil moisture and nutrients appeared in sufficient amounts so as not to limit growth. However, surface temperatures were low, except for periodic intervals on the natural plots. 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, which reduced the growing period and, coupled with low temperatures and light levels, resulted in small seedlings. Larson (1967) also showed that ponderosa pine seedling epicotyl lengths, root penetration, numbers of lateral roots, and dry weights were positively correlated to number of degree-hours.

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 twofold. It reduced mineral soil surface temperatures and delayed germination to a later date, thereby reducing the growing period. It also appeared to act as a physical barrier to vertical seedling growth. Competition from understory vegetation was low, but under those poor growing conditions any competition would be an additional detriment. McDonald (1976) also observed growth impairments where seedlings grew near large overstory pines.

# SUMMARY AND CONCLUSIONS

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 presence of an overhead canopy or a combination of canopy and organic matter reduced germination percentages and rates.

Moisture, temperature, and light 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, exposing pine seeds to fluctuating temperature and moisture conditions. 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.

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. When mortality and growth data are being considered, careful attention must be given to the unusually high summer precipitation occurring during this study. Drought, normally a significant detriment to seedling establishment, was not an apparent cause of mortality. Even though ponderosa pine is one of the region's most drought-resistant conifers, mortalities would have likely been higher and growth rates lower with normal 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, that is, bare mineral soil.

Initial establishment, or actual numbers of living seedlings at the end of the first growing season, was greatest in the opening treatments. 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. However, better results were obtained when seedlings grew 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 are also significant. The effects of fire stimulated seedling growth above that in all other treatments. Fire reduced litter and competing vegetation, and enriched the soil by releasing nutrients, especially ammonium-nitrogen, phosphates, and potassium, from the organic matter.

Seedlings grown in the openings were superior in shoot and root lengths and biomasses to seedlings from most of the 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 a physical barrier to seedling root penetration. Moreover, the location of these plots allowed for more seedling injury, as well as mortality, because of cutworm, small mammal, and bird feeding activities.

The importance of the removal of litter and competing vegetation in reforestation practices is emphasized here. Small openings within a stand, either man-made or natural, appear to be ideal locations for regeneration, especially pine regeneration in a Douglas-fir habitat type. This study also points out the value of site preparation by fire. Seedlings grown in areas properly treated by fire will likely have distinct survival and growth advantages.

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Plots representing various soil treatments were prepared under mature ponderosa pines and in openings, were planted with ponderosa pine seeds, and then observed during the subsequent growing season. Germination, survival, and growth were superior on plots located in openings and on plots wherein forest litter and competing vegetation had been removed or burned. Cutworms, birds, and rodents caused the highest percentage of seedling mortality.

KEYWORDS: ponderosa pine, seed germination, seedling mortality, seedling productivity.

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Headquarters for the Intermountain Forest and Range Experiment Station are in Ogden, Utah. Field programs and research work units are maintained in:

Billings, Montana
Boise, Idaho
Bozeman, Montana (in cooperation with Montana State University)
Logan, Utah (in cooperation with Utah State University)
Missoula, Montana (in cooperation with University of Montana)
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