Effect of Seedbeds on Germination and Survival of Douglas-Fir

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FOREST RESEARCH LABORATORY

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The current report stems from studies of forest management.

PURPOSE . . .

Develop the full potential of Oregon's timber resource by:

- increasing productiveness of forest lands with improved practices.
- improving timber quality through intensified management and selection of superior trees.
- reducing losses from fire, insects, and diseases--thus saving timber for products and jobs.

Keep development of the forest resource in harmony with development of other Oregon resources.

PROGRAM . . .

REGENERATION through studies of producing, collecting, extracting, cleaning, storing, and germinating seed, and growing, establishing, and protecting seedlings for new forests.

YOUNG-GROWTH MANAGEMENT through studies of growth and development of trees, quality of growth, relationship of soils to growth, methods of thinning, and ways of harvesting to grow improved trees.

FOREST PROTECTION through studies of weather and forest fire behavior to prevent fires, of diseases and insects to save trees, and of animals to control damage to regrowth.

TREE IMPROVEMENT through studies of variation, selection, inheritance, and breeding.

Contents

SUMMARY

Germination and survival of Douglas-fir on seedbeds of unburned, lightly burned, and severely burned soil, charcoal, litter, and sawdust, exposed to 100, 75, and 25 percent of full light, were studied on a south-facing clearcutting in the Coast range of Oregon.

Irrespective of exposure to light, germination was best on charcoal and on severely burned soil, which was attributed to prolonged preservation of moisture at the surfaces of these materials. Differences in germination among these two and other seedbeds were statistically significant. The initial advantage of high germination on charcoal and severely burned soil was still apparent after six growing seasons. Stocking of trees remained highest on these seedbeds in spite of considerable mortality in the first growing season.

Loss of seedlings was severe during, and shortly after, the period of germination. Then mortality decreased and became insignificant in following years. Rodents, heat, and damping-off, in this order, were the major causes of mortality. Heat was the predominant cause of mortality in the open, but rodents and damping-off fungi took the heaviest toll in shade. A preference of rodents for particular seedbeds was not apparent. To what extent mortality by heat and by damping off reflected influence of seedbeds could not be determined because of the confounding effect of rodents.

Almost daily, temperatures of 140° F (60° C) were maintained for 2-5 hours at the surface of seedbeds in the second half of the first growing season. Perhaps because of hardening of seedlings, mortality by heat decreased steadily in spite of increase in temperatures in the latter half of the season.

Pronounced differences were not found in rate of depletion of moisture in the soil underneath various seedbeds. The supply of moisture became critically low only for a short period at the end of summer, apparently a consequence of absence of herbaceous vegetation.

Growth in height of seedlings and development of their roots in the first year seemed to be unrelated to characteristics of seedbeds.

Results of the present study are considered to be representative of initial development of Douglas-fir seedlings on south-facing clearcut areas in the Coast range of Oregon, provided germination occurs early and competing vegetation is absent.

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INTRODUCTION

The present study was designed to distinguish microenvironmental characteristics of seedbeds commonly found on clearcut and burned-over southern slopes in the Coast range. The problem was to ascertain to what extent conditions of temperature and moisture vary among different seedbeds in the absence of herbaceous vegetation and to determine the effect on germination and survival of Douglas-fir seedlings.

Establishing new stands of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) on south-facing slopes denuded by clearcutting or forest fires is a troublesome problem in many parts of the Pacific Northwest. Loss of the forest cover drastically changes the climate of such slopes, creating an environment adverse to regeneration of Douglas-fir. Being warmer than other exposures, bare southern slopes seem to become preferred habitats of animals that feed on seeds and seedlings of Douglas-fir. Excessively high temperatures on the ground and rapid desiccation of the upper layers of soil threaten germination of seeds and survival of the seedlings that were not destroyed by animals.

Conditions of site, however, are not uniformly severe on exposed southern slopes. Changes in microrelief and ground cover result in a mosaic of microsites with differing regimes of temperature and moisture; moreover, countless microsites exist within the same seedbed. But microsites within seedbeds of like kind possess environmental characteristics that closely resemble each other.

Importance of microenvironmental differences among kinds of seedbeds for initial development of tree seedlings has been demonstrated by investigations in several of the forested regions of North America (Haig 1936, Linteau 1947, Smith 1951, Place 1955). Studies of regeneration of Douglas-fir in the Pacific Northwest have yielded conflicting results in regard to influence of seedbeds on establishment of this species. Condition of seedbeds was found to be without consequence for germination and survival of seedlings in the eastern foothills of the Coast range (Tiedemann 1934) and in the Tillamook Burn (Lavender 1958). Contrary to these findings, Isaac's (1943) studies in Oregon and Washington showed that the nature of seedbeds was important for both germination and survival of seedlings. Investigations in British Columbia (Garmann 1955) indicated that seedbeds were a factor in survival of seedlings, but effects on germination were not apparent.

Several circumstances likely account for discrepancy in results of work in the Douglas-fir region. Climate and soil differed considerably among locations where investigations were conducted. Furthermore, seedbed materials and degree of vegetative cover varied from one area of study to another. Much confusion has arisen from failure to realize these differences, and particularly changes in microclimatic conditions on seedbeds as soon as a successional flora appears.

Figure 1. Plots studied, and the immediate area.

METHODS

A gentle, south-facing slope at an elevation of 1,700 feet (500 meters) in the Coast range 15 miles (24 kilometers) southwest of Corvallis, Oregon, was chosen for study (Figure 1). The slope had been covered by a stand of mature Douglas-fir until it was clearcut and burned in 1955. The soil on this slope, a well-drained brown latosol, was classified tentatively as a Hembre silt loam. The parent material is residuum from basaltic rock. Depth of the soil varies from 45 to 50 inches (112-125 cm).

One-half of one acre was cleared of logging debris and vegetation, and 90 plots, 3.2 by 3.2 feet (1 by 1m) in size, were laid out. Distance between plots was 3.2 feet (1 m).

Unburned mineral soil, hard-burned soil, light-burned soil, charcoal, litter, and sawdust were selected as seedbeds. To obtain as good a replication as possible, seedbeds were prepared by spreading the seedbed materials on unburned mineral soil in a layer one inch deep. The sawdust came from newly cut logs of Douglas-fir. The other seedbed materials were collected from a nearby area recently cut and burned, to keep variations within materials at a minimum. The following criteria were used in the collection:

1) Hard-burned soil-- mineral soil transformed by fire to bright red cinders.

2) Light-burned soil-- mineral soil that had attained a grayish-black color through burning and was mixed with ashes, but whose particles were not baked together.

3) Charcoal -- thoroughly charred chips from logs and branches; largest chips were about 1/4 of an inch (0.6 cm) in diameter.

4) Litter -- a mixture of unburned small twigs, needles, leaves, and dried mosses.

During the growing season in 1958, plots were subjected to one of three conditions of light: full exposure, light shade, and heavy shade. On lightly shaded plots, the intensity of light was reduced to 75 percent of full sunlight, and on heavily shaded plots to 25 percent of full sunlight. Degree of shade was controlled by cheesecloth-covered frames. Light intensities were determined with a Weston light meter, model 614. Each combination of seedbed material and exposure to light was replicated 5 times. Treatments were assigned randomly.

Each plot was sown with 500 unstratified seeds of Douglas-fir in January 1958. Seeds were broadcast, with no attempt to press them into the soil or to cover them with the seedbed materials. Seeds were provided by the Manning Seed Company and had been coated with endrin, a repellent against rodents. According to the attached bonding certificate, seeds were collected from a 20-year-old stand on a southeastern slope at an elevation of 900 feet in Washington County, Oregon.

Emerged seedlings were recorded and marked every week from the beginning of germination until July. Biweekly counts of mortality were made from April 1958. Cause of death was recorded where it could be determined. Plots were weeded continually through the growing season of 1958 to eliminate competition by herbaceous vegetation.

Temperature of the air 4.5 feet (1.4 m) above ground was measured by a Taylor recording thermometer installed in a standard weather shelter. Four Tempscribe temperature recorders, placed along a diagonal line from the northwestern to the southeastern corner of the study area, recorded air temperature 1 inch (2.5 cm) above ground. These instruments were in white cardboard containers that had slits to allow sufficient circulation of air.

Mercury-in-glass maximum thermometers were placed on the surface of all plots and read once a week. Daily course of temperature on and beneath the surface of seedbeds was recorded several times during the growing season with a portable Brown potentiometer, model 126 W2P. The thermocouples used as sensors were made of 22-gauge copper and constantan wires.

Precipitation in the study area was measured with a standard rain gauge of the U. S. Weather Bureau. The gauge was checked daily from the beginning of May to the end of September and twice a week in other months.

Seasonal course of soil moisture at 2 and 8 inches (5 and 20 cm) depth was followed on all plots by means of Bouyoucos-type plaster of paris blocks. Resistance measurements were taken every two weeks with a Coleman soil moisture meter, model 300, and converted to moisture percentages. Moisture percentages at tensions of 0.5, 1, and 15 atmospheres were determined by pressure-membrane equipment.

RESULTS

The growing season of 1958 was one of the warmest and driest on record in western Oregon. From January to September, weather stations registered temperatures that were much above the long-time average for this period (U. S. Department of Commerce, 1958). High temperatures were accompanied by a dry period that lasted from the end of June to the close of August.

Seedlings in the study area experienced far more adverse conditions of temperature in their first than in their second growing season. Mean monthly maxima and minima of air temperature from May to October were consistently higher than in the following year (Figure 2).

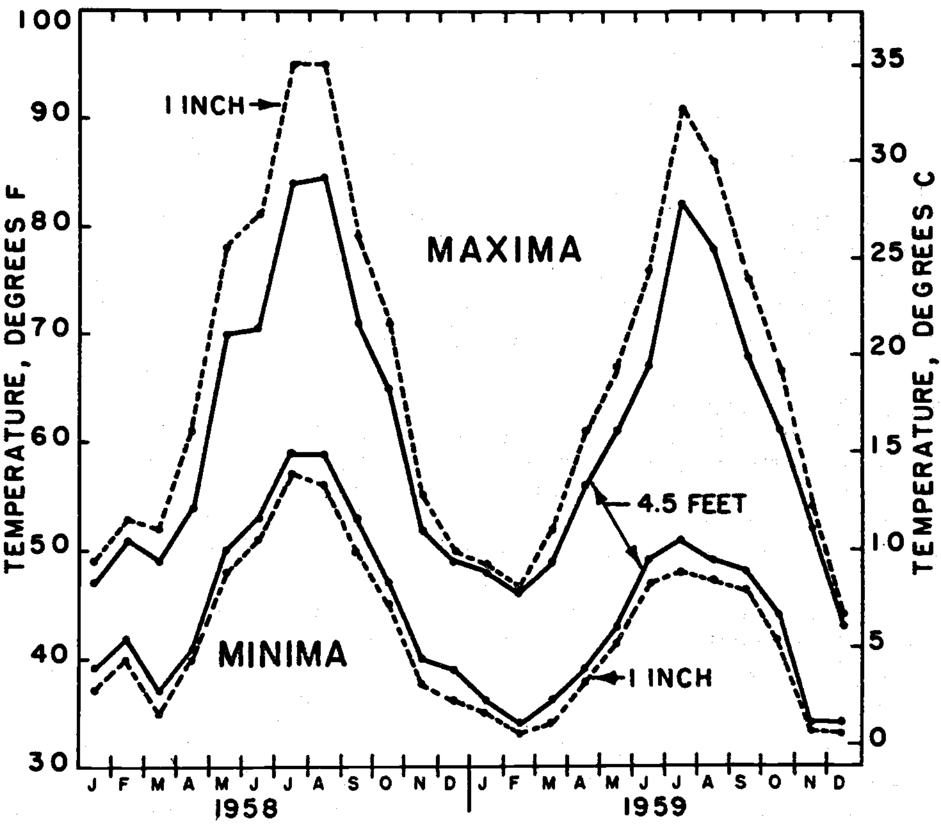

Figure 2. Mean monthly maxima and minima in temperature 1 inch (2.5 cm) and 4.5 feet (1.4 m) above ground in the study area.

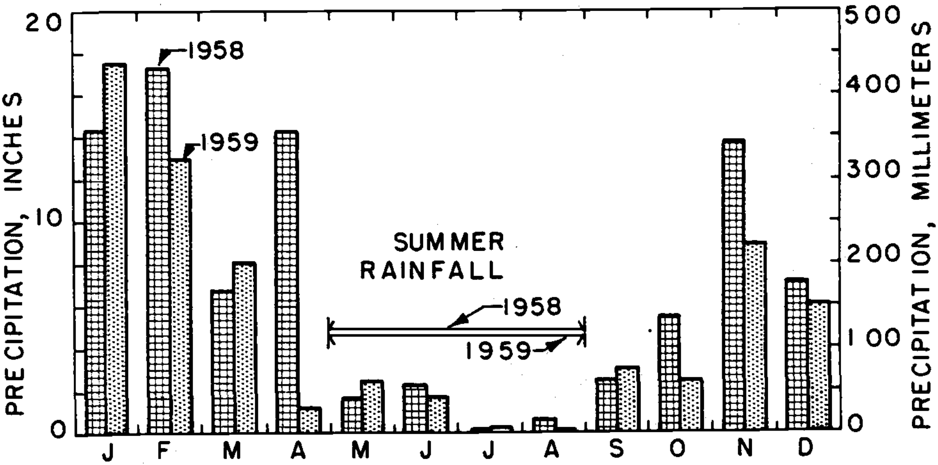

Figure 3. Precipitation in the study area in 1958 and 1959.

Seasonal distribution of precipitation in the study area (Figure 3) followed a pattern prevalent in many parts of the Pacific Northwest--high precipitation in winter and low rainfall in summer. In 1958, the study area remained without precipitation from June 28 to August 31, except for a trace of rain on July 10. The only anomaly was high rainfall in April 1958. Almost all precipitation occurred as rain in the winter of 1958-59. Snow fell once, in February, and melted after three days.

Temperature of seedbeds

Temperatures on surfaces of unshaded seedbeds remained until the end of April 1958 below levels that are considered injurious to seedlings. From then on, maximal temperatures on seedbeds rose to 125° F (52° C) and above until September, except for short periods of cooling in May and June caused by rain (Figure 4). The most severe conditions prevailed during the second half of the growing season. Weekly maxima of temperature exceeded 140° F (60° C) on all seedbeds for 10 consecutive weeks. Lightly burned and unburned mineral soil reached temperatures almost as high as on charcoal and litter, but sawdust and severely burned soil remained appreciably cooler (Figure 4).

Light shade reduced maximal temperatures on the surface of seedbeds around 17° F (9° C). Since the decrease in temperature was about the same for each kind of seedbed, seasonal course of maxima on lightly shaded seedbeds was largely a replica of that on open seedbeds. Heavy shade eliminated any distinctive differences of maximal temperatures among seedbeds. Maximal temperatures on heavily shaded seed-

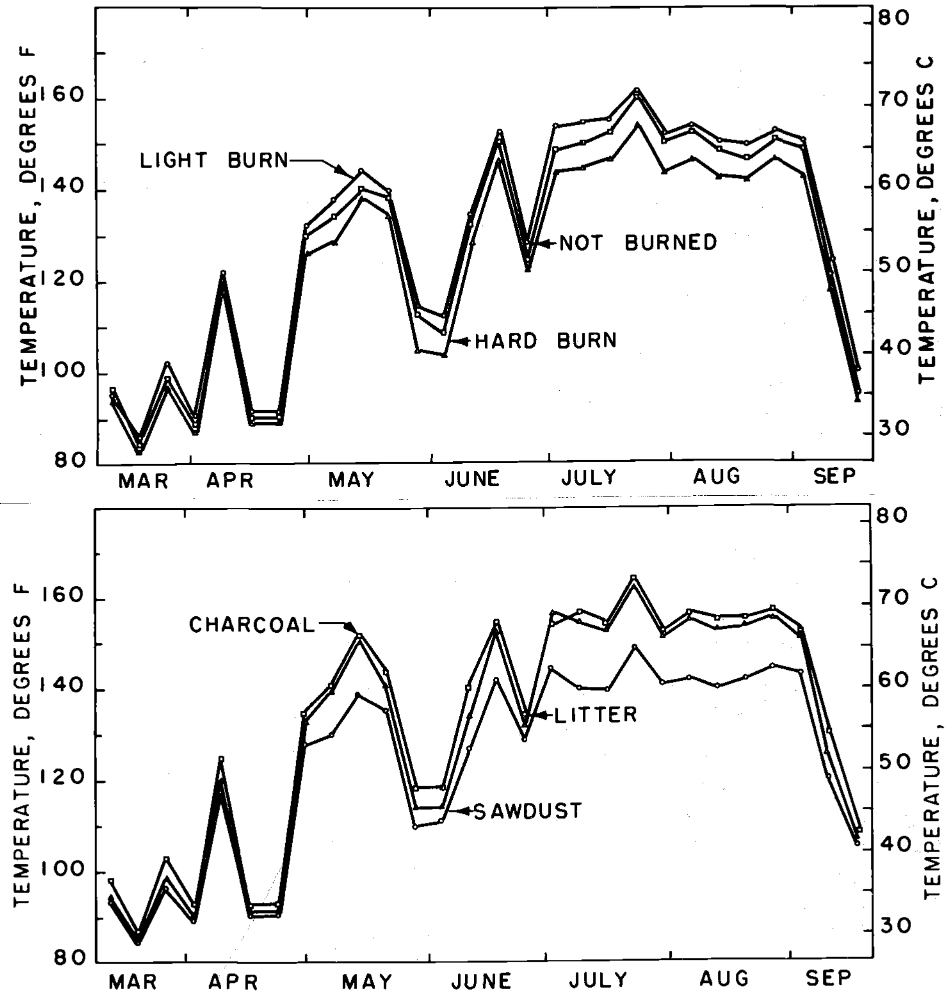

Figure 4. Mean weekly maxima in temperature on unshaded seedbeds in the growing season of 1958. Each point represents the mean of five readings.

beds did not exceed 110° F (43° C) in the first half of the growing season and ranged between 110° F and 120° F (43° C - 49° C) during the hot spell in July and August.

Turning again to unshaded seedbeds, high temperatures on their surfaces often lasted for several hours on a single day. Measurements taken with thermocouples on 15 days in June, July, and August indicated that temperatures above 140° F (60° C) on seedbeds prevailed from 1 1/2 to 6 hours (Table 1). Data in Table 1 may be considered representative for the three months. Incidence of cloud cover was extremely low so that temperatures could rise on seedbeds almost every day.

Effect of seedbeds was not limited to the thermal regime at the surface, but extended to about 7 inches (18 cm) into the ground. Organic materials proved to be highly efficient insulators. While charcoal and litter created a more severe microclimate at the surface than did mineral seedbeds, the converse was true below ground. This situation is well illustrated by observations taken on July 26 (Figure 5). The quick rise of temperatures on seedbeds in the forenoon and rapid fall in the afternoon were most pronounced on charcoal and litter. At 2-inch (5-cm) depth, however, soil below organic seedbeds underwent more gradual changes of temperature and remained far cooler in daytime than soil beneath mineral seedbeds.

Table 1. Duration in Minutes of Temperatures above 140° F (60° C) on Seedbeds. Data are Based on Observations Made on Fifteen Days Throughout June, July, and August of 1958.

Seedbed	Period		
	Shortest	Longest	Average
Charcoal	270	370	320
Litter	260	350	300
Light burn	190	300	240
No burn	135	255	210
Hard burn	110	225	165
Sawdust	90	160	130

Soil moisture

In 1958, soil moisture remained at low tensions, that is below one atmosphere, until the end of June. From then on, supply of moisture declined rapidly until it was replenished by precipitation in September (Figure 6).

In the open, desiccation proceeded more rapidly beneath unburned and severely burned soil than beneath lightly burned soil and organic materials. But tensions of 15 atmospheres were not reached at all at 8-inch (20-cm) depth, nor exceeded for several weeks at 2-inch (5-cm) depth beneath any of the seedbeds, with the exception of unburned soil.

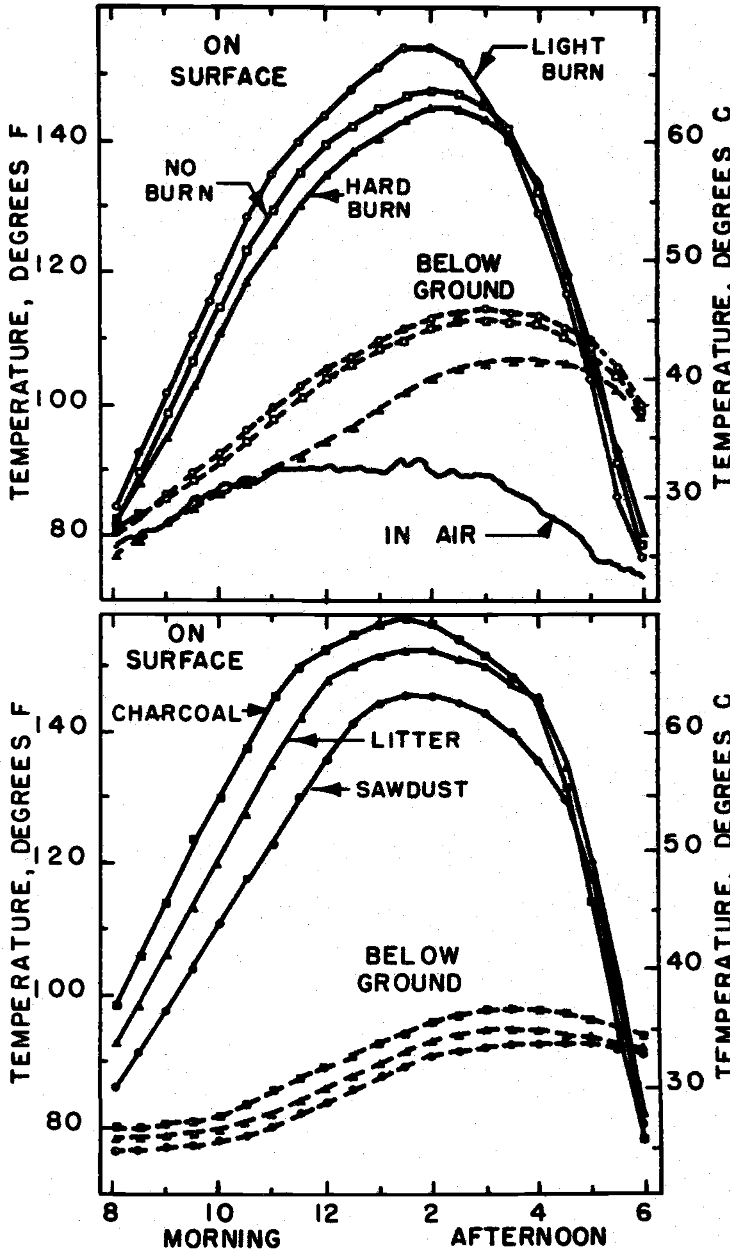

Figure 5. Course of temperature in air, on surfaces of the seedbeds, and 2 inches (5 cm) beneath surfaces on July 26, 1958, as measured with thermocouples.

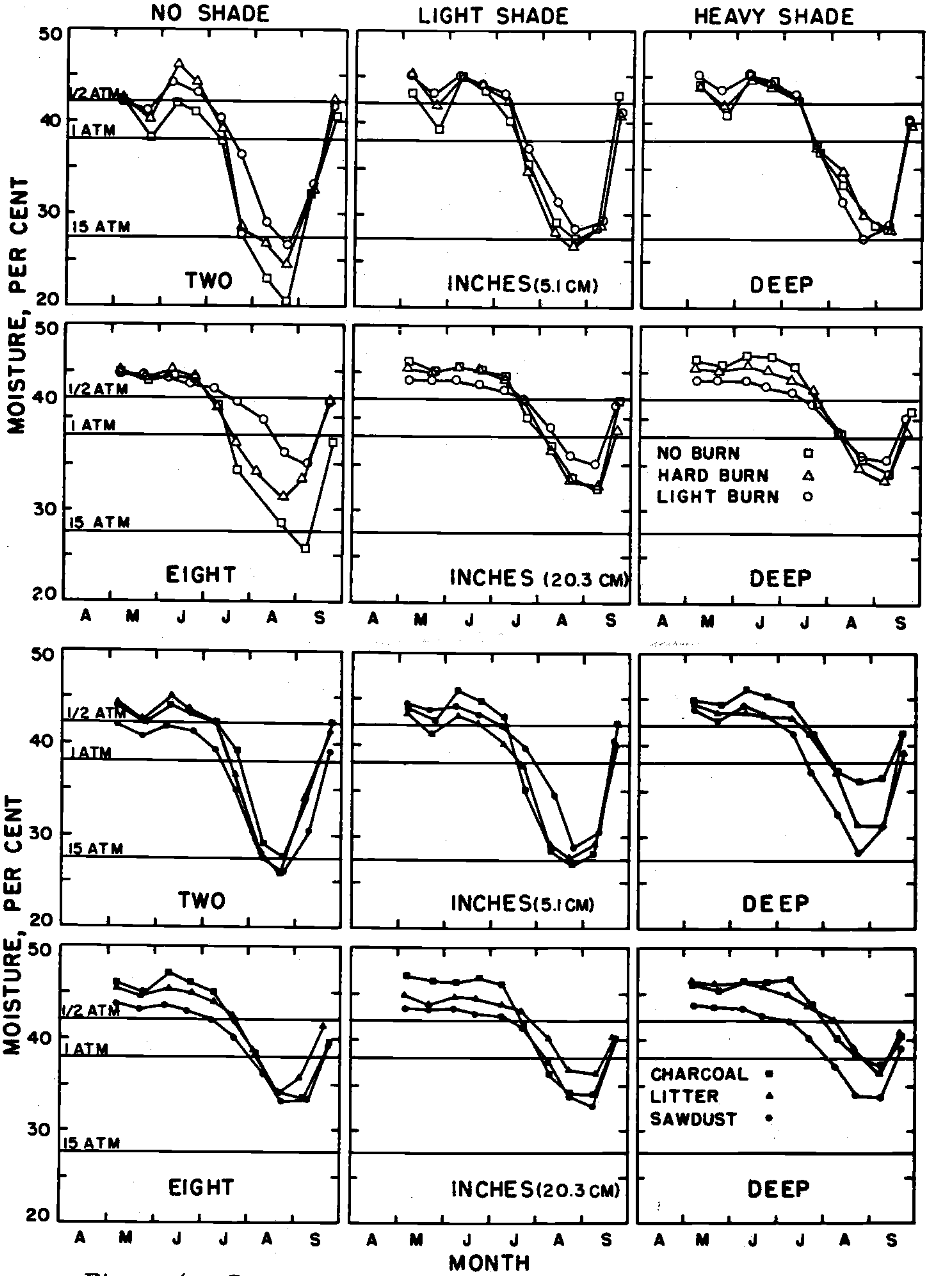

Figure 6. Course of soil moisture beneath seedbeds in the growing season of 1958. Each point represents the mean of five readings.

In shade, depletion of moisture varied little beneath different seedbeds, with one exception. Retention of moisture was considerably higher at 2 inches (5 cm) under charcoal in heavy shade than at the same depth beneath other seedbeds.

Germination

Seeds started to germinate on both open and shaded seedbeds early in March, but germination remained low until the second week of April. Then, a sharp rise in numbers of germinating seeds occurred simultaneously on all seedbeds. The rise continued to mid-May on charcoal and severely burned soil, but germination on the other seedbeds began to decrease again at the end of April (Figure 7). Germination ceased first at the end of May in the open, but the last in heavy shade was almost two months later.

When germination was completed in July, it ranged from 10 percent on lightly shaded sawdust to 93 percent on unshaded charcoal (Figure 7). Less than 1 percent of seeds was eaten by either rodents or birds, so this large range undoubtedly reflected microenvironmental differences among seedbeds. Analysis of variance (Table 2) showed that both seedbeds and exposure to light were significant variables, although independent of each other. Seedbeds accounted for the major share of variation, however, as indicated by their large value of mean square.

Under all conditions of exposure to light, germination was best on charcoal and severely burned soil. A multiple-range F-test (Table 3) showed that numbers of germinated seeds were significantly higher on charcoal than on severely burned soil, and that both of these materials were significantly better media for germination than were the other seedbeds. Differences among the latter were not significant.

Significance of the effect of intensity of light on germination was determined by the method of individual degrees of freedom (Table 4). Germination in the open was significantly higher than in shade, but did not differ under the two conditions of shade at the 5 percent level of significance.

Mortality

Mortality was high in the first growing season. Nearly 10,200 seedlings, that is 62 percent of those that emerged, were killed from March to November 1958. Destruction by animals and injury by heat were the principal causes of mortality during this period (Figure 8). Losses through the following winter totalled 899 seedlings. Some died of delayed effects of previously received heat injuries, but most were killed by deer and rabbits.

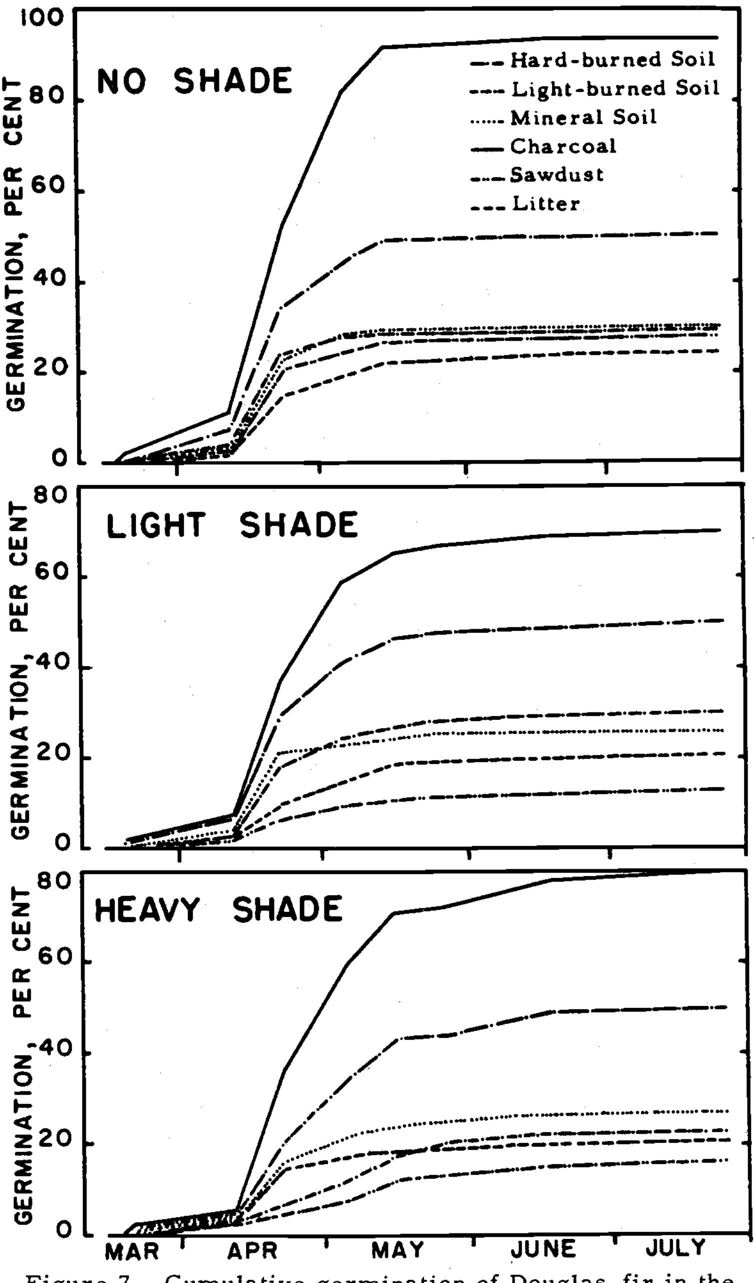

Figure 7. Cumulative germination of Douglas-fir in the spring of 1958. Each curve represents the mean of five replications.

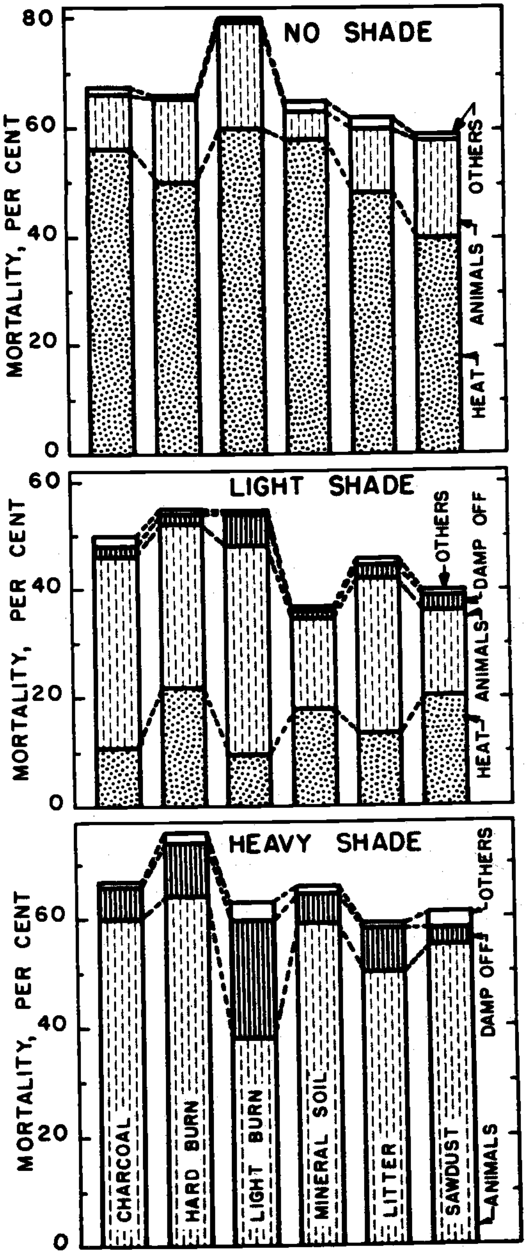

Figure 8. Mortality of Douglas-fir seedlings and causes in the first growing season (in 1958). Percentages are based on emerged seedlings.

Then, mortality decreased sharply. Only 41 seedlings died in the second growing season. A count at the close of the sixth growing season indicated loss of 203 seedlings from fall of 1959 to fall of 1963. Plots were not thinned, and most of the seedlings that died probably failed in the competition for moisture and light. Few of the dead trees showed any identifiable signs of external injury.

Considering again events in the first growing season, white-footed deer mice clipping cotyledons and stems of newly emerged seedlings were responsible for the largest share of mortality caused by animals. Since mice seemed to prefer heavily shaded plots for their activities, losses caused by animals increased from 13 percent on seedbeds in the open to 31 percent in light shade, and to 57 percent in heavy shade (based on seedlings emerged).

Likewise, damping-off occurred more frequently the more heavily plots were shaded. Percentages of seedlings that were attacked by Fusarium and Rhizoctonia species were 0.1, 3, and 9 on open, lightly shaded, and heavily shaded seedbeds, respectively.

In regard to mortality caused by heat, the situation was reversed. Heat killed 53 percent of seedlings in the open, but only 15 percent in light shade and none in heavy shade. However, differences in magnitude of losses among kinds of seedbeds did not follow the same pattern in the open and in shade (Figure 8). Lack of a consistent pattern indicated that influence of seedbeds on lethal injury of seedlings by heat probably was confounded by mortality because of animals.

Mortality in the first growing season was at a peak when seedlings emerged (Table 5). Clipping of seedlings by mice began to cease gradually as the period of germination drew to a close, and mortality attributable to animals declined. Similarly, seedlings were injured lethally by heat mainly in the first month following emergence. Although insolation increased with advance of the growing season, injury by heat became less and less frequent. Damping-off occurred only early in the season before seedbeds started to dry appreciably. The renewed rise of mortality in fall reflected beginning of browsing by deer and rabbits.

Survival and growth

Survival, expressed as percentage of seeds sown, was best on charcoal and severely burned soil (Figure 9). Using numbers of seeds sown as a basis for comparison of survival, rather than numbers of seedlings emerged, demonstrated that higher mortality did not offset the initial advantage of abundant germination on charcoal and severely burned soil. The same was not true, however, in regard to the effect of degree of exposure to light. Germination in the open was not sufficiently higher than under shade to compensate for greater losses of

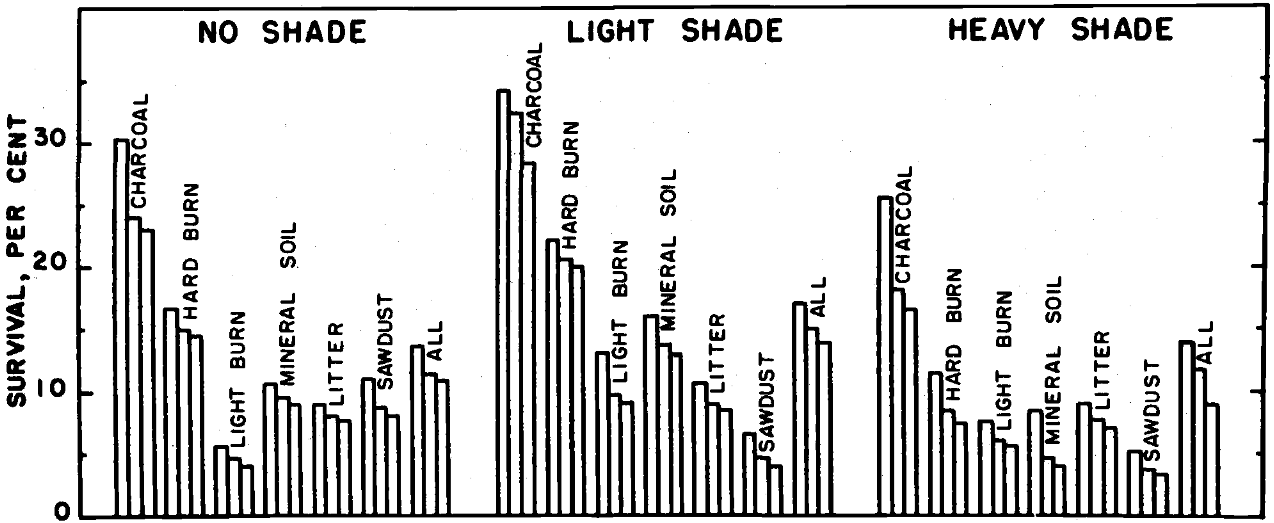

Figure 9. Live seedlings after the first, second, and sixth, growing seasons, based on seeds sown. Shade was applied only during the first season.

seedlings on fully exposed seedbeds. Statistical treatment of data on first-year survival, taking amounts of seeds sown as point of reference, indicated that seedbed materials were the only significant source of variation (Table 6). A multiple-range F-test (Table 7) showed significantly higher stocking on charcoal than on unburned soil, lightly burned soil, sawdust, and litter. Numbers of live seedlings on severely burned soil were neither significantly lower than on charcoal, nor significantly higher than on the other seedbeds. Some mortality occurred over the next 5 years, but differences in stocking among seedbeds at the end of the first growing season remained essentially the same during subsequent years.

Early in the first growing season, surviving seedlings grew vigorously, and an attempt was made to determine whether their development was influenced by seedbed conditions. Length of the crown, from the cotyledon to the tip of the shoot, of all living seedlings was measured in mid-July 1958 and again in mid-September. Seedlings were growing actively when the first measurements were made, but most had gone into dormancy at the time of the second measurements. Bud-set began in the middle of August and extended to the end of September. Seedlings in heavy shade were the first and seedlings in the open the last to complete bud-set.

Crowns of seedlings ranged in length from 0.8 inch to 4 inches (2-10 cm) in July. Mean height of seedlings on each kind of seedbed increased with decrease in exposure to light, except for lightly burned soil where mean height was greater in light shade than in heavy shade. In general, variations in heights of individual seedlings were greater in shade than in the open, which is indicated by the higher standard deviations of mean heights under low intensities of light (Figure 10). Growth in height, however, was not consistently better on any of the seedbeds under all three conditions of light (Figure 10).

When measurements were taken again in September, about 30 percent of the seedlings could not be included because they had lost their leaders through browsing. Since seedlings so injured usually had been the tallest on each plot, their exclusion resulted in lower values than would otherwise have been obtained. Crowns of measured seedlings ranged from 1.2 to 8.4 inches (3 to 21 cm) indicating that some had grown as much as 4.4 inches (11 cm) during 8 weeks. Measurements in September failed to show any consistent trend in regard to the influence of either seedbed materials or exposure to light on growth in height (Figure 10).

In October 180 seedlings, 10 from each combination of seedbed and exposure to light, were dug. Roots varied in length from 6 to 9 inches (15 to 23 cm), but neither length nor other characteristics of

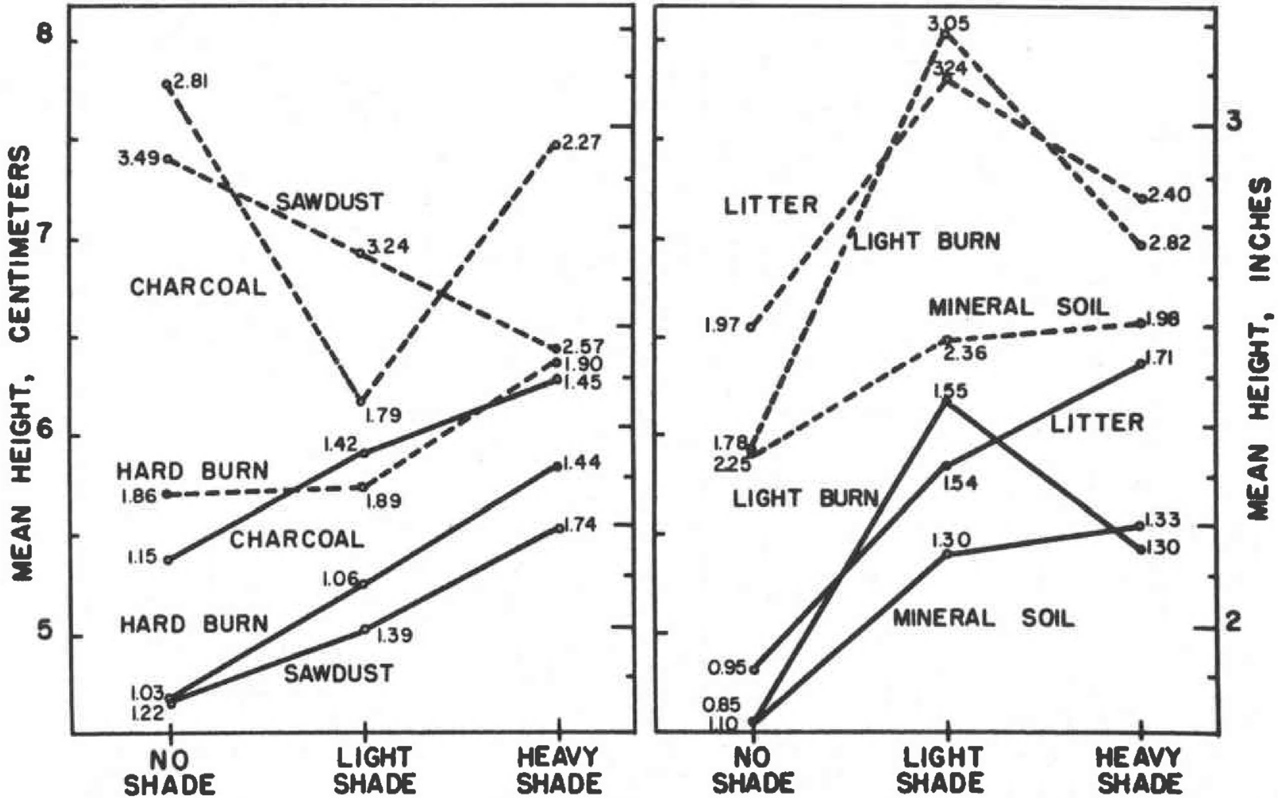

Figure 10. Mean heights of seedlings on the several seedbeds at the middle and at the end of the first growing season. Variation in height of seedlings for each combination of seedbed and exposure to light is indicated by the standard deviation of mean height, computed on metric measurements.

root systems showed any recognizable effect from seedbed conditions.

Most live seedlings were browsed heavily during the winter of 1958-59 and became short and bushy. These seedlings recovered remarkably in the second growing season, and many developed leaders that were from 8 to 12 inches (20 to 30 cm) long. Height of trees varied from 4 to 7 feet (1.2 to 2.1 meters) at the end of the sixth growing season, averaging about 5 feet (1.5 meters) (Figure 11).

Figure 11. Plots at the end of the sixth growing season, in 1963.

Table 2. Analysis of Variance of Number of Douglas-Fir Seed That Germinated on Six Kinds of Seedbeds Exposed to Three Different Degrees of Intensity of Light.

Source of variation	Degrees of freedom	Mean square
Replication	4	8,478
Seedbed (S)	5	214,642**
Intensity of light (L)	2	15,158*
S x L	10	3,456
Error	68	4,313

*Significant at 5 percent level.
**Significant at 1 percent level.

Table 3. Mean Numbers of Seeds That Germinated on Six Kinds of Seedbed*.

Sawdust	Litter	Light burn	No burn	Hard burn	Charcoal
84	108	130	133	243	401

*Any means not underscored by the line are significantly different at the 5 percent level, as judged by multiple-range F-test. Any 2 means underscored are not significantly different.

Table 4. Comparison of Influence of Degree of Light Intensity on Germination of Douglas-Fir Seeds by the Method of Individual Degrees of Freedom.

Percentage of full sunlight	Total number of seeds germinated	F-value
100	6,274	6.98*
75	5,054	0.05
25	5,166	--

*Significant at 5 percent level.

Table 5. Monthly Tally of Mortality in the First Growing Season. Numbers Represent Totals for All Combinations of Seedbed and Degree of Exposure to Light.

Month	Numbers of seedlings killed by: Animals	Heat	Damping-off	Other
March	252	00	00	47
April	2,397	123	64	22
May	1,091	2,863	491	40
June	686	492	33	7
July	49	410	00	6
August	00	41	00	10
September	98	00	00	7
October	784	00	00	3
All	5,345	4,093	588	144

Table 6. Analysis of Variance of Numbers of Live Seedlings at the End of the First Growing Season.

Source of variation	Degrees of freedom	Mean square
Replication	4	7,171
Seedbed (S)	5	27,137*
Intensity of light (L)	2	6,482
S x L	10	878
Error	68	3,255

*Significant at 1 percent level.

Table 7. Mean Numbers of Seedlings on Six Different Seedbeds at the End of the First Growing Season.

Sawdust	Light burn	Litter	No burn	Hard burn	Charcoal
37.3	43.7	47.7	58.2	83.5	150.4

*Any 2 means not underscored by the same line are significantly different at the 5 percent level as judged by multiple-range F-test. Any means underscored by the same line are not significantly different.

DISCUSSION

The unusually warm growing season in 1958 provided ideal conditions for the present study. Weeks of continuously hot and dry weather accentuated the harshness of climate near the ground, and confronted seedlings with an extremely adverse environment in initial stages of growth. If seedbeds possessed characteristics that were beneficial or detrimental to establishment of seedlings, they could be expected to become apparent under these circumstances. And, indeed, seedbeds exerted a strong influence, manifested mainly by their effect on germination.

Excellent germination on charcoal and severely burned soil in the open and in shade seems to have been mainly a consequence of relatively long maintenance of favorable conditions of moisture. Germination continued to be high on these two seedbeds, while it declined on others with the onset of dry weather in late April. Both charcoal and severely burned soil were coarse textured and still retained moisture at the bottom of particles and in crevices after surfaces of the other, finer textured seedbeds had dried. Desiccation of seedbeds could not be determined quantitatively, but some measure of it was given by *Funaria hygrometrica*, a moss present on most plots. In the open, the moss remained succulent on charcoal and severely burned soil until mid-May, and in heavy shade until the end of June. On other seedbeds, *Funaria* began to shrivel and turn brown from 3 to 5 weeks earlier.

Differences of temperature among seedbeds apparently influenced germination considerably less than did moisture. Although temperature varied more from the open to heavy shade on each seedbed than among seedbeds in either the open or shade, seedbeds had far greater effect on germination than did degree of exposure to insolation.

Whether abundant germination on charcoal was aided by some component of this material is uncertain, but cannot be discounted entirely. A promoting effect of charcoal on germination has been mentioned in the literature (Baldwin 1942, Mes 1954, Went 1953). Went attributed the effect of charcoal to inactivation or absorption of germination inhibitors.

In spite of slow loss of moisture and a longer period of germination, fewer seeds germinated on shaded than on exposed seedbeds. The explanation may be that temperatures in shade were not optimal for germination until moisture became limiting. There is also the possibility that changes in the spectral composition of light brought about by covers had a depressing effect on germination. Covers may have filtered out red light while allowing infra-red radiation to pass through. An inhibitory effect of far-red radiation on germination has been reported for seeds of many plants (Amen 1963) and was found recently in seeds of Douglas-fir (Johnson, Leroy and H. Irgens-Møller, in press).

Coincidence of most of the first-year mortality with the period of germination showed clearly the vulnerability of seedlings in the earliest stages of growth. This applied to seedlings on exposed and shaded seedbeds alike. Although shade reduced or eliminated injury by heat, more favorable conditions were provided for damping-off fungi and the protection afforded rodents resulted in high mortality through clipping of seedlings. Unfortunately, the losses caused by rodents prevented accurate judgment as to what extent incidence of injury by heat and by damping-off reflected the influence of seedbeds.

Damping-off ceased when seedbeds became dry, as was to be expected, but decline in losses of seedlings because of heat when temperatures continued to rise on seedbeds with advance in the growing season raised again the often-debated question as to whether seedlings increase their tolerance to heat as they grow older. Several explanations have been proposed:

One of these explanations attributed early occurrence of the largest share of mortality by heat to elevation of temperatures on seedbeds beyond lethal levels early in the growing season. Shaded microsites (Isaac 1938) and protection by favorable heat-transfer properties of their seedbeds (Silen 1960) were considered responsible for the survival of remaining seedlings. Results of the present study, however, could not be explained satisfactorily in this manner. Bases of some seedlings' stems may have been shaded by other seedlings or by coarse particles on the ground, but during noon hours when seedbeds were hottest, protective shades were not cast, because of the southern exposure. Some of the seedbeds, such as charcoal and litter, had highly adverse heat-transfer properties, and temperatures and their duration on exposed seedbeds (Table 1) through most of the summer were in a range where killing of seedlings could be anticipated.

Another attempt to reconcile apparently conflicting evidence regarding range of lethal temperatures is Silen's (1960) hypothesis that amount of energy transferred into a seedling's stem may vary greatly at a given temperature. His hypothesis is based on the assumption that dissipation of total radiation as reflection, downward conduction, and the amount that enters the seedling, depends largely on the physical properties of the seedbed. But this interpretation did not help to clarify why, for instance, heat killed few seedlings in the second half of the growing season in 1958 on charcoal, a material that was a poor conductor and had a low albedo. Convectional losses of heat hardly could have been of such magnitude as to consider it an important factor in lowering mortality by heat.

Several investigators (Baker 1929, Roeser 1932, D. Smith 1951) suggested that maturation of tissues in older seedlings could explain an increase in resistance to heat. However, F. Smith and Silen (1963) in a recent study of the anatomy of heat-damaged Douglas-fir seedlings came to the conclusion that this theory was not tenable.

The observations made in practically all field studies, including the present, that older seedlings appeared to become more resistant to heat, may indicate some physiological change or "preconditioning effect" in seedlings. Investigations of coniferous seedlings regarding this aspect of tolerance to heat have not been reported. However, possibility of a physiological basis in the development of greater tolerance to heat has been suggested by indication of physiologically controlled changes of resistance to heat in several dicotyledonous plants (Laude 1939, Schwemmle and Lang 1959, Yarwood 1961).

Injury by heat was easily identifiable. A lesion developed on the south side of the stem, usually close to (from 2 to 5 mm) the surface of the ground. In some instances, when the seed cap was still in the ground, the lesion formed on the back of the curved hypocotyl. In seedlings less than a month old, the lesion spread rapidly and formed a constriction that led to toppling of the plant. Older seedlings developed deep constrictions, but usually remained upright.

Seedlings that turned brown without any external signs of injury were considered as having been killed by drought. Few seedlings fell into this category.

Lack of mortality by drought in the first growing season was explained, at least in part, by the seasonal course of soil moisture in 1958 (Figure 6). By the time soil moisture was held at high tensions 2 inches (5 cm) in the ground, roots already had extended into deeper layers of soil. At 8-inch (20-cm) depth, supply of moisture was critically low for only a short time toward the end of the season. In this period, condensation of atmospheric moisture in the early morning may have eased moisture stress to which seedlings were subjected. Whether direct uptake of water by surface organs of plants occurs has not been entirely clarified (Arvidsson 1951). But results of experiments by Stone and his collaborators (Stone and Fowells 1955, Stone et al. 1956, Stone 1957) with application of artificial dew to coniferous seedlings kept under conditions of soil drought supported the view that dew leads to resaturation of tissues in needles and prolongs endurance of drought. That seedlings in the study area began to go into dormancy when supply of moisture became low may have been another aid to alleviate the period of drought.

Although in spring, texture of seedbeds influenced rate of drying at the surface, it was of little consequence to seasonal course of moisture in the soil underneath. Extremely high precipitation in April may have contributed to slow decrease of soil moisture in the growing season of 1958. But absence of competing vegetation was probably the principal reason for moisture not becoming a limiting factor.

In conclusion, consider briefly the question of to what extent findings of this study are representative of initial development of Douglas-fir on south-facing clearcuttings in the Coast range. If germination is early--this is ordinarily the situation in the Coast range--and if competing vegetation is absent, results are likely to be similar to those reported here. Initial advantage of emergence of many seedlings on seedbeds conducive to abundant germination probably will outweigh losses of seedlings later in the season.

Influence of seedbeds on mortality might be more pronounced and assume much greater importance under circumstances that would cause delayed germination, such as an unusually cool spring, high elevation, late sowing, seeds from provenances slow to germinate, or any combination of these. The further germination is shifted toward beginning of summer, the greater is the possibility that it will become sparse and that mortality by heat will be so high as to eliminate any advantage of more abundant germination. This possibility would be particularly likely on seedbeds with highly adverse heat-transfer properties.

Presence of competing vegetation may be expected to largely eliminate effect of seedbeds on establishment of seedlings. Several studies indicate that severe or total loss of seedlings by drought has to be anticipated in the Coast range when Douglas-fir has to compete with successional vegetation (Owen 1953, Youngberg 1955, Youngberg and Lowry 1955) or with a nurse crop (Finnis 1957, McKell and Finnis 1957).

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