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The Influence of Seedbed Conditions On the Regeneration of Eastern White Pine

by David M. Smith

THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION, NEW HAVEN

Cover picture shows first-year white pine seedling growing with its stem in the shade of a chip of logging debris lying in the middle of a strongly insolated expanse of pine litter.

TABLE OF CONTENTS

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The Influence of Seedbed Conditions on the Regeneration of Eastern White Pine

David M. Smith[1]

One of the most critical stages in the life-cycle of eastern white pine[2] comes between the time of seed dispersal and the middle of the first growing season. The quality and composition of the future stand are largely determined by the factors which control the number of seedlings present at the end of this period. The main objective of this investigation was to ascertain the nature and extent of the influence of seedbed characteristics during this stage of the process of regenerating white pine.

REVIEW OF PREVIOUS STUDIES

The silvical axiom that light-seeded species, including eastern white pine, regenerate most vigorously on moist, bare mineral soil has stood the test of time. All too often consideration of seedbed conditions has stopped there. One of the first to pursue this matter further in the case of eastern white pine was Spring (57) who studied the natural establishment of pine on abandoned farmlands in New England. He found that polytrichum moss was an especially favorable seedbed, whereas thick, dense grass was detrimental. Light or moderate shade provided by a sparse cover of herbaceous plants, shrubs or pioneer tree species, such as gray birch, aspen or pitch pine, enhanced regeneration, particularly on dry sites. Open areas protected from the direct rays of the sun by adjacent stands often supported numerous seedlings. Spring concluded that soil moisture was the most important controlling factor. Sterrett (59) arrived at similar conclusions in the southern Appalachians and also noted that thin hardwood litter was more favorable than coniferous litter.

Knechtel (33), in Ontario and the Adirondacks, observed that white pine seedlings were not abundant except on rotten logs or where mineral soil had been exposed by fire or other agencies. Fisher and Terry (18) also found that pine regeneration in New England was hampered by the presence of thick litter, dense ground vegetation and slash. They indicated that favorable seedbeds were almost as necessary as a good seed supply.

Toumey and Neethling (61) demonstrated that heat injury caused high mortality among white pine seedlings growing on surfaces of dry mineral soil even though soil moisture was not deficient in the root zone.

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[1] Formerly assistant in Forestry, The Connecticut Agricultural Experiment Station. This publication is condensed from a dissertation submitted to the Graduate School of Yale University for the degree of Doctor of Philosophy. More complete information on statistical analysis and experimental data is contained in manuscripts on file at the School of Forestry and the Sterling Memorial Library, Yale University.

[2] The scientific names of plants referred to by common names in the text are indicated in the Appendix.

FIGURE 1
Dense clump of white pine seedlings established on a large mat of polytrichum moss.

Cline and Steed (13) found that the best pine regeneration, following group-selection cuttings on very dry sites, occurred on seedbeds of polytrichum and hypnum moss. Areas exposed to strong sunlight were invaded by low-bush blueberry, checkerberry and dewberry which formed a dense cover detrimental to seedling development. Seedbeds composed of lichens were favorable only where shaded by gray birches.

Hopkins and Little (31) observed that germination and survival of white pine seedlings was far better on polytrichum and hypnum moss than on any other type of seedbed commonly found in old-field stands of white pine. Partially shaded seedbeds of pure pine litter, sedges, low-bush blueberry and various lichens were conducive to either poor germination or high mortality.

L. F. Smith (54) compared seedbeds of pine litter and mineral soil on clear-cuttings as well as beneath unthinned and heavily thinned stands of eastern white pine. His experiments showed that germination was largely dependent on moisture conditions, being better in shade than in the open and better on mineral soil than on litter. Few seedlings germinated on exposed pine litter, even when it was irrigated daily, and those which did germinate were all killed by heat injury. About half the seedlings which germinated on mineral soil in the open were killed by heat injury. It was found that lethal temperatures occurred far more frequently on insolated litter than on mineral soil; this difference was ascribed to the more stable moisture supply of the bare soil. Drought and damping-off eliminated many of the slow-growing seedlings beneath the unthinned stand. The success of regeneration in the heavily thinned stand depended largely on whether the seedlings were protected from direct sunlight; results were generally better there than in either the open area or the unthinned stand. Smith found that the roots of thrifty seedlings in open or partially shaded areas elongated rapidly enough to remain in contact with moist strata as the superficial layer of dry soil became progressively deeper. Haig (28) obtained very nearly the same results with western white pine in a similar experiment in northern Idaho.

Lutz and Foster (39) sampled the distribution of established white pine seedlings in an old-field stand near Norfolk, Connecticut, and found them occurring at the rate of 13,560 per acre on polytrichum moss, 8,600 per acre on hypnum moss and 584 per acre on pine litter. Figure 1 shows a dense clump of young white pines on a mat of polytrichum moss similar to those encountered by Lutz and Foster.

Shirley (52), in Minnesota, found that, on dry sites supporting jack pine, partial shade was beneficial to germination and survival of white pine in spite of accompanying reduction in growth. On moist sites the drying and heating effects of direct sunlight were not serious and the partial shade of aspen growing there provided no benefits.

CONDITIONS AND PROCEDURE OF INVESTIGATION

Experimental Area

The investigations described in this bulletin were performed during 1947 and 1948 near Litchfield, Connecticut, on the lands of the White Memorial Foundation. All plots were located within a circle one mile in diameter on a sandy plain of deltaic origin lying northeast of Bantam Lake; the area was 900 to 915 feet above sea level. The soils were loamy sands, texturally uniform but varying in moisture content, depending on the position of the water table. Most of the soils were well-drained members of the Merrimac series but some found in the low, dissected portions of the plain were poorly-drained and of the Sudbury series.

Practically all of the experiments were carried out in pure, old-field stands of white pine between 40 to 55 years of age. One small group of plots was in a poorly stocked 20-year old stand of pine, aspen and red maple. Investigations of lichen seedbeds were made in an irregular stand of pine, hemlock and mixed oak on a dry site too elevated to be influenced by the water table.

On areas with a high water table there was a hardwood understory of moderate density which was sparse or absent elsewhere. Red maple was the most prominent species of the understory, although shadbush, black cherry, choke cherry, various oaks, chestnut sprouts and winterberry were often present. There were also scattered clumps of young white pine and hemlock. The herbaceous ground flora was most luxuriant on the moister sites, particularly in openings. The most important species were false lily-of-the-valley, wild sarsparilla, polytrichum moss, dewberry, partridgeberry, lycopodium club-moss, sedges and hypnum moss.

The small differences in height of the surface above the water table produced a wide variation in site quality even though the range of elevation was scarcely 15 feet. Each of the three recognized site qualities (20) could be found in the area, with the slowest growth occurring on the highest ground.

Climatic Conditions

The results obtained in the experiments were strongly influenced by differences in rainfall between 1947 and 1948. In Table 1 measurements of monthly precipitation at the experimental area during the two growing seasons are compared with the monthly averages for Torrington, which is seven miles distant. The precipitation during late spring was normal in 1947 and abnormally heavy in 1948. This difference was of considerable importance, because the germination in 1948 was far better than that in 1947. The vigor of germination in 1947 was about the same as that observed by Toumey and Neethling (61) and Smith (54), who conducted somewhat similar experiments in periods of average or abnormally low rainfall near Keene, New Hampshire. Both 1947 and 1948 were marked by protracted droughts in late summer and early fall and the intervening winter was characterized by very heavy snowfall; the latter abnormalities had little effect on the experiments.

TABLE 1. PRECIPITATION DURING THE GROWING SEASON

	Inches of Rainfall		
	Experimental Area		Torrington
Month	1947	1948	Averages[1]
May	4.15	6.58	3.60
June	4.59	8.04	4.48
July	4.97	3.59	4.29
Aug.	1.31	1.84	4.34
Sept.	2.48	1.10	4.42
Oct.	0.85	0.74	4.99

[1] For period 1919-1940 (63:993).

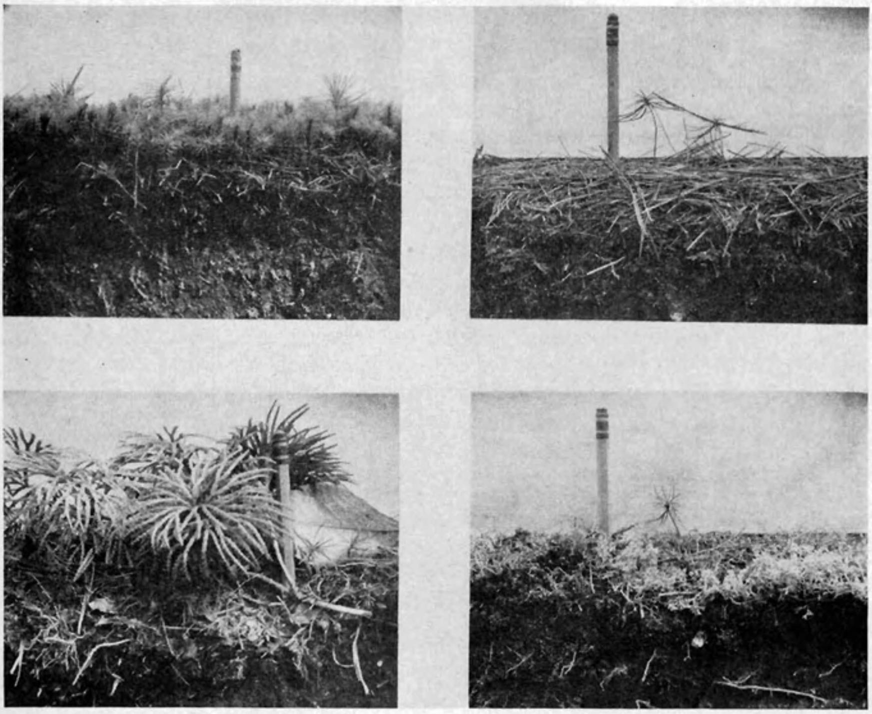

FIGURE 2

Vertical sections through typical examples of various seedbeds supporting white pine seedlings. Upper left, polytrichum moss; upper right, white pine litter; lower left, lycopodium club-moss (seedlings at right of pencil); and lower right, lichens.

Experimental Procedure

The investigation included two major experiments and a number that were of subsidiary character. Both major experiments consisted essentially of observations of the germination, survival and growth of seedlings arising from fixed numbers of seeds sown on screened sub-plots six inches in diameter. The seeds used were stratified in moist sand slightly above freezing temperature for three months before sowing. No seeds which would pass a 2-millimeter sieve were used. All were sown so that they reached positions similar to those attained in nature. The protective screens were removed as soon as the seed-coats were shed and the seed-spots were kept free of extraneous vegetation and debris throughout the experiments.

The first experiment was started in April 1947 and continued through two growing seasons, although it has, for convenience, been designated as the 1947 experiment. It was largely exploratory and included a wide variety of types of seedbeds and treatments. A randomized split-plot design in six replicated blocks was employed, with statistical analysis carried out accordingly. The arrangement proved so unwieldy, however, that it is expedient to consider only certain segments of this experiment.

The common seedbed types included were: polytrichum moss, white pine litter, white pine slash, lycopodium club-moss and hardwood brush, which was made up of various understory species. Another type, composed of various lichens, was found chiefly on very dry sites and was considered in a separate, parallel experiment. Several of these types of seedbeds are illustrated in Figure 2.

The arrangement of this experiment is indicated in Table 2. Some seed-spots were screened against rodents while others were unprotected; unfortunately, the screens were only two inches high and not completely effective in excluding rodents or preventing them from biting seeds from the cotyledons of germinating seedlings. Certain seed-spots were also treated by removing the type of seedbed material in question; the kinds of surfaces exposed by this treatment are indicated in Table 2. Except for the data in Table 16 (page 51), no use was made of observations from the unscreened seed-spots.

TABLE 2. ARRANGEMENT OF THE 1947 EXPERIMENT, SHOWING DISTRIBUTION OF NUMBERS OF SUB-PLOTS[1]

Type of Seedbed	Cover Undisturbed		Cover Removed[2]	
	Screened	Unscreened	Screened	Unscreened
Polytrichum Moss	24	12	Mineral Soil 12	12
White Pine Litter	24	12	Mineral Soil 12	12
White Pine Slash	24	12	White Pine Litter[3] 12	12
Hardwood Brush	24	12	Litter or Moss 12	12
Lycopodium Club-moss	24	12	Litter or Moss 12	12
Lichens[4]	24	12	Mineral Soil 12	12

[1] Equally distributed among six replicated blocks.
[2] Type of seedbed exposed in treatment also designated.
[3] In this bulletin data from these sub-plots included with undisturbed white pine litter.
[4] Not included in main experiment.

The seeds used in 1947 had been gathered commercially in Ontario the previous fall and 75 were sown on each seed-spot in April. The plots were located in openings created by the removal of single trees in improvement cuttings during the six preceding years, except on the lichen area where natural gaps characteristic of such dry sites were used. An effort was made to locate sub-plots in places open to the sky, but partially or completely shaded from the side, in order to reduce the influence of excessive solar heating. This restriction was not imposed rigorously, with the result that some of the seed-spots were strongly influenced by brief exposure to direct sunlight. Fortunately, this shortcoming in the arrangement revealed the critical importance of seedbed conditions on insolated surfaces.

The second experiment, designated as the 1948 experiment, was designed to test some of the conclusions derived from the 1947 experiment. Instead of superimposing the experimental design on purely natural conditions, the plots were concentrated in three specially created openings and the seedbed materials were moved about to fit the split-plot design. The openings were located close to one another in a 55-year old pine stand on a good site. They were made by removing adjacent pairs of wolf-trees so that the long axes of the openings ran north and south. Each was about 130 feet long and from 20 to 70 feet wide. Four straight lines of seed-spots were laid out east and west in each opening or experimental block. Certain details of the arrangement are summarized in Table 3.

TABLE 3. ARRANGEMENT OF 1948 EXPERIMENT, SHOWING DISTRIBUTION OF NUMBERS OF SUB-PLOTS[1]

			Type of Seedbed		
Line No.	Exposure to Sunlight	Average Distance from South End of Opening	Polytrichum Moss	Mineral Soil	White Pine Litter
1	0 days	7.6 ft.	6	6	6
2	± 44 days	15.8 ft.	6	6	6
3	± 160 days	33.2 ft.[2]	6	6	6
4	> 300 days	50.6 ft.	6	6	6

[1] Equally distributed among three replicated blocks with two sub-plots of each type randomly placed on each line.

[2] Arbitrarily placed half-way between lines 2 and 4.

The lines of sub-plots were located with respect to the crowns of the trees at the south ends of the openings so that the sun could shine on the ground during a specified period at each location. The first line in each block was at the southern end of the opening, where direct sunlight was entirely excluded by side-shade, although there was no cover directly overhead. The second line was laid out a short distance to the north where the sun could shine part of each day from June 1 to July 14. The fourth lines were located at the northern ends of the openings where the sun could shine practically every day of the year. The third lines were placed half-way between the second and fourth lines mainly to fill in the wide gap; actually conditions on the third lines were somewhat more rigorous than those on the fourth lines, because the openings were wider in the centers than at the ends.

Only three types of seedbeds, polytrichum moss, pine litter and mineral soil, were studied in the 1948 experiment. Two sub-plots of each, 2½ feet square, were randomly distributed on each line of plots. The polytrichum moss was transported in large turfs from a dense and uniform patch of moss in an adjacent stand. On April 26, 1948, 24 stratified white pine seeds, which had been collected from the experimental area the previous fall, were sown at the center of each sub-plot. All were protected with wire screens, 6 inches square and 4½ inches tall, which completely excluded rodents.

In each experiment an inventory was made of every seed-spot at intervals of two weeks or one month. These inventories continued through the first two growing seasons of the 1947 experiment and during the first growing season of the 1948 experiment. At each inspection the fate of every dead seedling and the development of the larger survivors were noted. Evaluation of causes of mortality was based on the criteria recommended by Davis et al. (15).

The results of the two main experiments and the subsidiary investigations are presented according to the sequence of events occurring in natural regeneration, starting with the time of seed-fall. Seedbed conditions first influence the results by affecting the penetration of seeds into the forest floor. This process was considered in one of the subsidiary experiments.

PENETRATION OF SEED INTO SEEDBED

The ability of a seedling to germinate and survive is often determined by the depth of penetration of the seed into the seedbed. A seed falling on bare mineral soil is, of course, immediately in contact with the most favorable substratum available. If the mineral soil is not highly aggregated, the seeds may be buried when the soil is splattered about by large raindrops. Seeds landing on organic materials are blocked from immediate contact with mineral soil.

Detachment of Wings

The wings attached to white pine seeds often prevent them from falling through small crevices in the forest floor. Observations indicate, however, that the wing is almost invariably broken from the seed before germination. The wing is so firmly attached to one side of the seed that it cannot be entirely removed even when moist; detachment is accomplished by some force which breaks off the free portion of the wing along the edge of the seed. Dengler (16:242) has suggested that, in Scotch pine, separation may result from shrinking and swelling caused by freezing and thawing or wetting and drying. However, in this investigation it was found that the force of large drops of water falling on white pine seeds was far more effective.

One 50-seed sample was subjected to daily cycles of soaking and oven-drying for 20 days; five wings were accidentally broken off during handling but the remainder were firmly attached at the end of the trial. A similar sample, continously moist, was subjected to at least three cycles of freezing and thawing without breakage of any wings. On the other hand, wings of moist seeds broke away rapidly when drops of water were allowed to fall on them from a height of three feet for periods of about four minutes. In one trial, 28 out of 50 seeds lost their wings, and in another, 39 out of 50. These seeds had been placed on moist paper towelling, a medium which did not offer the restraint to sideways motion which must exist on the forest floor.

Observations of Seed Penetration

On September 23, 1947, a series of screened seed-spots was established on several different types of seedbeds under varying amounts of overhead cover. Six seed-spots with 25 winged seeds each were allotted to each condition; the seeds were dropped from a height of two feet and were whirling when they landed. Periodically throughout the autumn the number of seeds which had passed from view on each spot was recorded. A number of plots were ruined by mice. After one very light rain and a killing frost the litter which had accumulated atop the screens was sprinkled on the seed-spots and the plots were left until early July. The seedlings then present were pulled so that the total depth of penetration of the seeds could be determined. This was done by measuring the distance from the tallest adjacent obstacle to the membranous sheath of the old embryo, a structure which was regarded as marking the position of the germinating seed. The data obtained are shown in abbreviated form in Table 4.

TABLE 4. PENETRATION OF WINGED SEEDS INTO VARIOUS TYPES OF SEEDBEDS[1]

	No. Seeds in F-layer[2] on:		Seedlings Alive July, 1948	
Type of Seedbed	Sept. 27	Oct. 9	No.	Av. Depth of Seed
Polytrichum in Opening	50	98	59	2.21″
Polytrichum under High Cover	70	114	87	2.22″
Pine Litter in Opening	11	26	10	0.45″
Pine Litter under High Cover	19	36	86	0.56″
Lichens in Opening	9	19	51	0.86″

[1] 150 winged seeds sown on each type of seedbed, September 23, 1947.

[2] Layer of partially decomposed needles beneath the undecomposed L-layer.

Seeds falling on pine litter infiltrated only to a very small extent. Many would have remained entirely exposed but for the autumnal accretion of litter which amounted to about one-half inch and fell after most of the seeds had been shed. The needles of white pine litter are relatively fine and horizontally oriented so that they offer an almost impenetrable barrier to pine seeds even after the wings are lost. A similar effect has been noted by Osborne and Harper (46) with the two long-leaved southern pines which have much coarser litter. They observed poorer penetration and lower germination with the large-seeded long-leaf pine than in slash pine, which has smaller seeds.

The vertically arranged strands of polytrichum moss were relatively ineffective in blocking the passage of seeds. Many slipped through the fresh, green moss as soon as they landed; subsequently the alternate opening and closing of the leaves of the moss under the influence of desiccation agitated the seeds enough to cause further penetration. Gemmer et al. (24) likewise found that horizontally arranged litter resisted penetration of longleaf pine seeds more than grass, which is vertically arranged.

Additional observations indicated that the agitation of hardwood leaves in the wind and the shrinking and swelling of lichens also enhanced seed penetration. Loosely arranged surface vegetation such as lycopodium and dewberry did not bar seeds from the underlying litter. The presence of crowns of pine trees overhead had little influence on seed penetration beyond determining the amount of litter falling on the seeds.

GERMINATION

The most important influence of seedbed conditions on natural regeneration of white pine is their effect on germination, which is governed largely by moisture conditions. Observations of germination constituted a major

TABLE 5. GERMINATION OBSERVED ON VARIOUS TYPES OF SCREENED SEEDBEDS, 1947 EXPERIMENT[1]

Type of Seedbed	No. of Seed-spots	Percentage of Spots on Which the Number of Germinating Seeds Was:					Av. No. of Germinating Seeds per Spot
		0	1-7	8-27	28-47	48-67	
Mineral Soil in Polytrichum[2]	11	..	..	9	27	64	51.5
Mineral Soil in Litter[2]	12	..	..	17	17	66	49.8
Pine Slash	24	..	..	25	42	33	38.1
Polytrichum Moss	23	..	4	18	65	13	36.0
Hardwood Brush	20	..	5	30	40	25	34.6
Lycopodium Club-moss	24	..	8	42	42	8	28.8
Openings in Brush[3]	12	..	33	42	8	17	19.6
Openings in Lycopodium[3]	12	8	17	50	25	..	17.4
White Pine Litter	36	14	17	44	22	3	17.3
Mineral Soil in Lichens[2]	12	17	42	33	..	8	11.6
Lichens	24	29	29	29	13	..	10.7

[1] An average of 67 sound seeds was sown on each sub-plot; data for plots invaded by mice are omitted.

[2] Patches of mineral soil six inches square surrounded by material designated.

[3] Openings up to three feet wide and of varying length; actual seedbeds composed of pine and hardwood litter or moss.

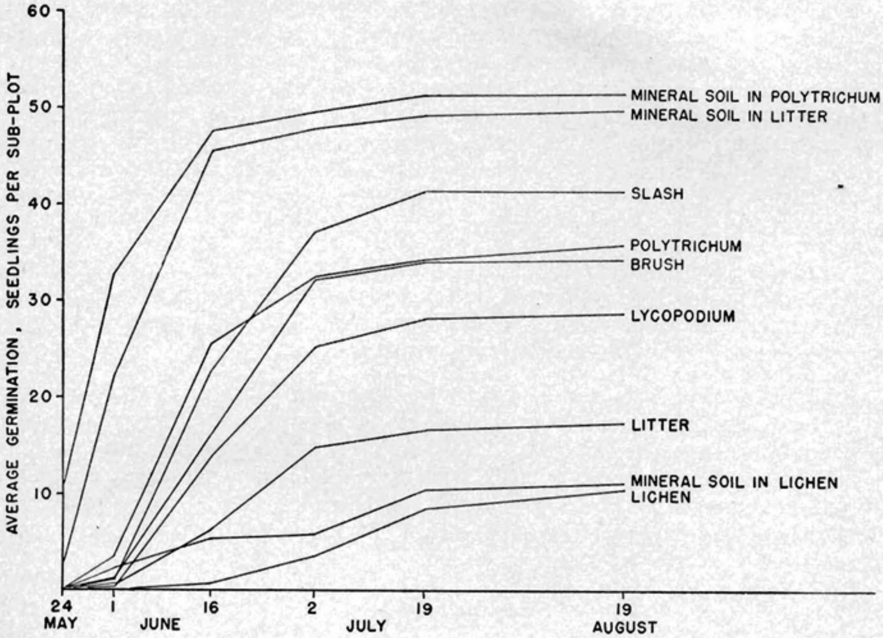

FIGURE 3

Average cumulative germination with respect to date, 1947 experiment. Each screened sub-plot was sown with an average of 67 sound seeds.

part of the two main experiments described previously. Several subsidiary experiments were also performed in an attempt to explain the variations in germination which were observed.

1947 Experiment

The data obtained in the 1947 experiment are presented in Table 5; they indicate the average vigor of germination during a period of normal precipitation on a variety of seedbeds subjected to a wide range of exposure to direct sunlight. In uniformly moist media virtually all sound seeds germinated; on surfaces which were frequently dry, seeds lay for months without germinating, even though they retained capacity to do so. Excessive dryness was practically always confined to surfaces subject to strong heating when exposed to direct sunlight.

On relatively moist sites, germination on mineral soil exposed by removing polytrichum moss and pine litter was significantly[1] better than that on any other kind of surface. At the other extreme, germination on dry

[1] In this publication, use of the term "significant", or derivatives thereof, denotes statistical significance at the level of 5 per cent or better. All statistical techniques employed conform with those described by Snedecor (55).

mineral soil exposed by removing lichens or on patches of undisturbed lichens was significantly lower than on other surfaces. Significantly fewer seedlings appeared on white pine litter than on any other seedbeds except those associated with lichens; litter in narrow openings exposed by removing brush or lycopodium was fully as detrimental as that which covered wider surfaces. Germination on seedbeds protected by pine slash, polytrichum moss, hardwood brush or lycopodium was good but not excellent. The high germination obtained when seeds are in close contact with continuously moist mineral soil has been commented on frequently (4, 6, 24).

Seedbeds which were continuously moist or composed of materials which shaded the forest floor supported uniformly good germination. Germination on the poorer seedbeds, such as dry mineral soil, lichen and pine litter, was greatly improved by protection from direct sunlight.

In general, seedbeds which supported high germination were also conducive to rapid and early germination, as demonstrated by the cumulative germination curves in Figure 3. Although excessively high temperatures tend to prevent germination, it is also true that low ones delay it (1). This phenomenon appears to account for the fact that germination was earliest on bare mineral soil and somewhat earlier in polytrichum moss than beneath hardwood brush or slash.

1948 Experiment

The 1948 experiment was arranged to allow more direct evaluation of the effects of direct sunlight on germination of white pine seeds sown on polytrichum moss, white pine litter and bare mineral soil. Abnormally heavy rains during the germination period kept all surfaces moist for such long periods that the effects of desiccation were masked. The data in Figure 4 and Table 9 (page 26) do show a slight tendency for germination in pine litter to have been reduced by long-continued insolation. Statistical analysis revealed significant differences between the extreme values. Nevertheless, these results were important chiefly because they revealed that abundant moisture could sustain good germination even on white pine litter. It has already been shown that, in 1947, germination was poor on strongly insolated litter when the rainfall during the germination period was normal. Similarly, L. F. Smith (54) observed very poor germination on exposed litter during two years when precipitation in the same period was below normal.

The graphs of germination with respect to time shown in Figure 4 again indicate that seeds germinate more quickly on moist mineral soil than on organic surfaces. Particularly prompt germination occurred on shaded mineral soil.

Irrigation of Insolated Litter

Further evidence of the favorable effect of a uniform supply of moisture on germination, as well as survival, was provided by a small experiment conducted in 1948. Eight screened seed-spots were established at the north end of one of the large openings created for the main 1948 experiment; these plots were in pairs and one member of each pair was continuously

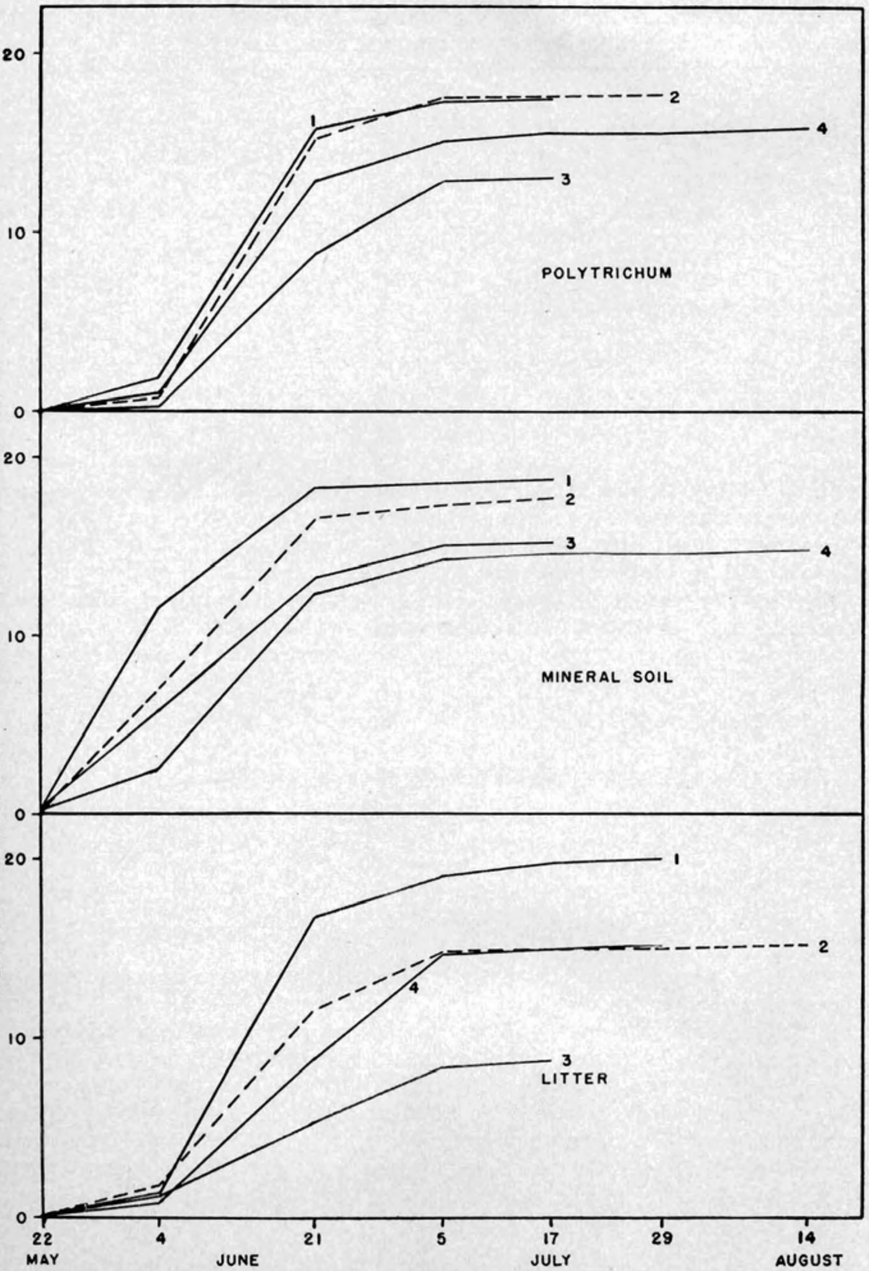

FIGURE 4

Average cumulative germination with respect to date, 1948 experiment. Each sub-plot was sown with an average of 22 sound seeds; each line on the graph represents 6 sub-plots. Numbers indicate periods of exposure to full sunlight: (1) 0 days, (2) ± 44 days, (3) ± 160 days, and (4) > 300 days.

TABLE 6. EFFECT OF IRRIGATION ON GERMINATION AND SURVIVAL OF WHITE PINE SEEDLINGS ON INSOLATED LITTER

	Plot			
	A	B	C	D
	Numbers of Seedlings			
Irrigated				
Germination	18	18	11	18
Survival	14	16	9	3
Not Irrigated				
Germination	8	8	0	2
Survival	3	0	0	0

irrigated. Twenty-four seeds, of which an average of 22 were sound, were applied to each seed-spot. The irrigation devices consisted of siphons made of rubber tubing fitted with loose clamps which permitted water to drip slowly onto the plots through the screens. L. F. Smith (54) had found daily irrigation insufficient because of the tremendous evaporation. The results obtained from continuous irrigation, which are shown in Table 6, are consistent with the contention that germination is seriously reduced by desiccation. They also show that irrigation causes subtantial reduction in loss from heat injury, a matter which will be considered later.

Effect of Moisture on Germination

A number of attempts were made to relate germination on the various types of seedbeds to measurements of ecological factors connected with desiccation.

Correlation of Germination with Insolation and Temperature

One of the more successful of these attempts was the correlation of germination on white pine litter with measurements of solar radiation during the middle of the day. The average percentage of full sunlight at each seed-spot was determined for the period between 11 A. M. and 3 P. M., local sun time, by periodic readings of a Weston Model 603 illuminometer. Measurements were made only on cloudless days and were related to curved, simultaneous values of full sunlight. These data showed a highly significant correlation with germination; the regression of germination over percentages of full light could be fitted adequately by a straight line, as shown in Figure 5.

Additional evidence was provided by a highly significant correlation between average germination and average weekly maximum temperature of the seedbed during the germination period (May 17 to June 30). These temperatures were obtained from mercurial maximum thermometers placed at the levels occupied by the seeds on half of the plots of the 1947 experiment.

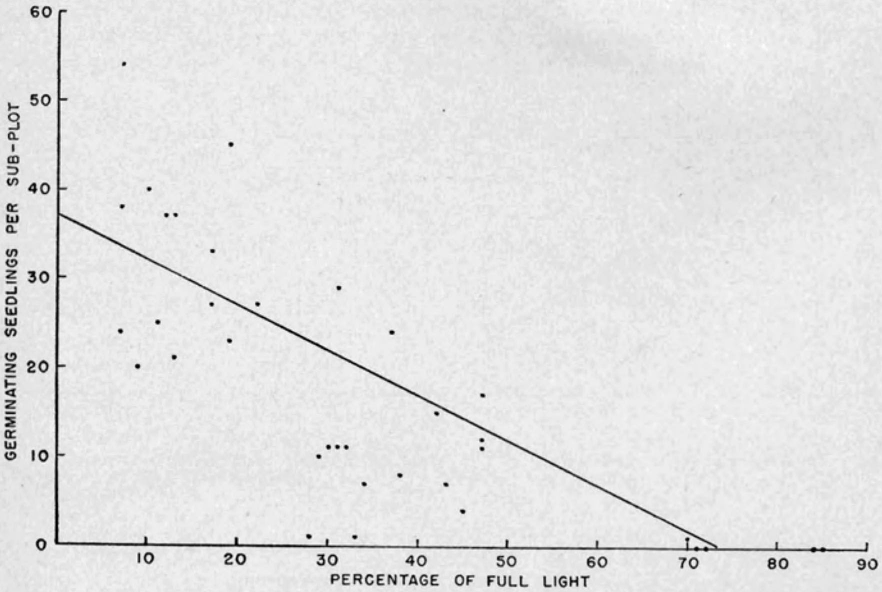

FIGURE 5

Regression of germination on white pine litter over the percentage of full light for the period 11 A. M. to 3 P. M. Each point represents one screened sub-plot with 67 sound seeds. The slope of the straight line is significant and the correlation coefficient is — 0.435 (significant at 1 per cent level).

The average values of germination were drawn from the three appropriate screened sub-plots adjacent to each thermometer. Data from all six types of seedbeds were considered together, although they are distinguished in Figure 6, which illustrates the relationship graphically. These data, as well as those in Figure 5, demonstrate that germination is significantly inhibited by some factor associated with strong insolation and high temperature.

Investigation of Effects of Heat and Moisture in the Laboratory

One partially successful attempt was made to segregate the effects of heat and moisture under controlled conditions in the absence of direct sunlight. Stratified seeds were placed in Jacobsen germinator cups and subjected to four different treatments. Three hundred seeds, of which 270 were sound, were used in each treatment, distributed equally among six cups.

The first treatment was a control in which the seeds remained constantly moist at room temperature. The second group of seeds was taken from the cups daily and dried on paper towelling at room temperature; unfortunately, the seeds did not dry to any great extent under this brief treatment. The third group was treated similarly except that the seeds were dried daily in a ventilated oven at 110°F., successfully simulating conditions in strongly insolated pine litter. The fourth treatment consisted of heating the seeds in the moist condition to 110° F. daily. The three latter treatments were

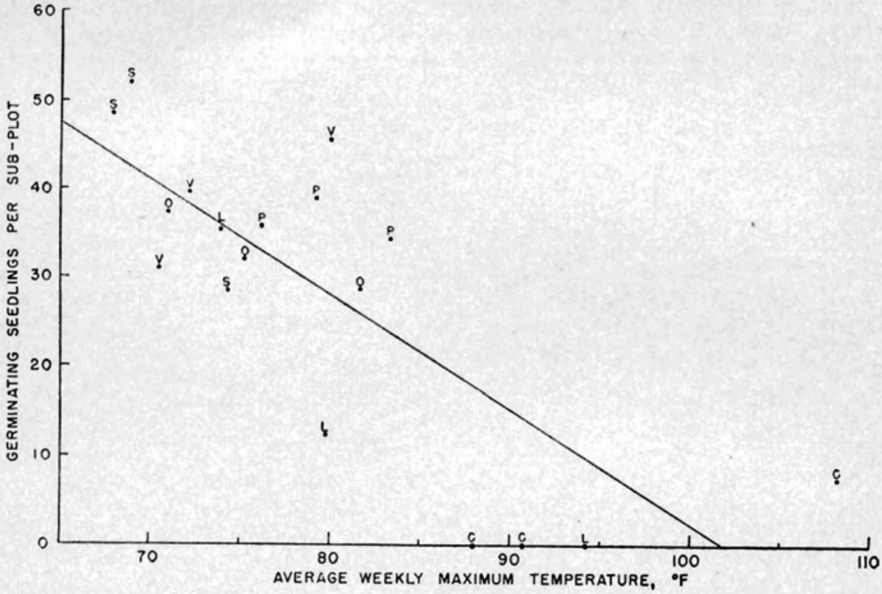

FIGURE 6

Regression of germination over average weekly maximum temperature at the level occupied by the seed for the period May 17 to June 30, 1947. Each point represents one screened sub-plot with 67 sound seeds. Letters indicate type of seedbed: P—polytrichum moss, L—white pine litter, S—dense pine slash, V—hardwood brush, O—lycopodium club-moss, and C—lichens. The slope of the straight line is highly significant and the correlation coefficient is — 0.776 (significant at 0.1 per cent level).

carried out for periods of 3 to 9 hours daily for 12 days; thereafter, the seeds remained moist at room temperature continuously. The filled seeds from all treatments which did not germinate after 42 days failed to do so after subsequent stratification; therefore, it was unlikely that any had lapsed into secondary dormancy.

The results of this experiment are shown in Table 7. The most important conclusion drawn was that stratified seeds exposed to alternations between cool, moist conditions and hot, dry ones do not lapse into secondary dormancy and suffer only slight reduction in germinative vigor. This observation suggests that the natural phenomenon of delayed germination in white pine may be due to excessively hot and dry conditions in the seedbed. Previous observations (62), however, indicate that white pine seeds do not remain viable in the litter beyond the second spring after dissemination.

The seeds which were partially dried at room temperature germinated more rapidly, but no more completely, than those in the controls, indicating that conditions in the ordinary germinator cups may have been too moist. Seeds heated to 110° F., without being allowed to dry, were killed. This observation is in accord with previous experience (5, 30, 67) which has shown that seeds will survive high temperatures only when dry.

TABLE 7. EFFECT OF VARIOUS PERIODIC TREATMENTS INVOLVING HEATING AND DRYING ON THE GERMINATION OF STRATIFIED WHITE PINE SEEDS

	Cumulative Germination, in Number of Seeds[1]						
Elapsed time in days:	6	12	18	24	30	36	42
Untreated control, constantly moist at room temperature	79	176	207	213	216[2]		
Partially dried at room temperature daily	202	215[3]	216	217[2]			
Dried at 110° F. daily	0	0[3]	15	154	185	192	196
Heated to 110°F. daily, constantly moist	0	0[3]	0	0	0	0	0

[1] 300 seeds in each treatment.

[2] Germination complete.

[3] Treatments continued for 3 to 9 hours daily for the first 12 days; seeds constantly moist at room temperature thereafter.

This experiment did demonstrate that diurnal heating and drying, in combination, were sufficient to cause complete, but reversible, inhibition of germination even in the absence of direct sunlight. Nevertheless, it was no more successful than the field experiments in differentiating the separate effects of heat and moisture. The matter is one of little practical importance, however, because high temperatures almost invariably produce desiccation and low temperatures are usually associated with high moisture content. The important point is that forces which induce desiccation of seedbeds can cause very significant reductions in germination.

MORTALITY AND SURVIVAL

Observations of mortality clearly indicated that the conditions most favorable for germination of white pine seeds were generally most conducive to survival of seedlings during the first two years of life.

1947 Experiment

Inventories were made bi-weekly or monthly during the growing seasons of 1947 and 1948 in order to determine the factors responsible for mortality among the seedlings which germinated in 1947. The results, adjusted to show the fate of 1,000 sound seeds sown on each type of seedbed, are presented in Table 8; data from unscreened sub-plots are not included.

Some of the sub-plots supported such vigorous germination that it was necessary to reduce the numbers to 16 seedlings per sub-plot during the first summer. This thinning was performed, according to an arbitrary spacing, in two operations starting in the middle of July, which was after the period of heaviest mortality. Sparsely stocked sub-plots were not thinned lest information on growth be lost as a result of subsequent mortality. Some germinating seedlings were also lost when rodents bit the seeds from

TABLE 8. GERMINATION, MORTALITY AND SURVIVAL FOR TWO GROWING SEASONS, 1947-8, IN NUMBERS OF SEEDLINGS PER 1,000 FILLED SEEDS, 1947 EXPERIMENT

	Polytrichum Moss	Mineral Soil in Polytrichum	Mineral Soil in Litter	Lycopodium Club-moss	Hard-wood Brush	Openings in Hardwood Brush	Openings in Lycopodium	Pine Litter	Mineral Soil in Lichens	Lichens	Dense Pine Slash
Not Germinating	465	234	259	571	484	733	741	739	828	842	433
Germinating	**535**	**766**	**741**	**429**	**516**	**267**	**259**	**261**	**172**	**158**	**567**
Natural Losses, Summer of 1947	59	80	164	120	185	47	105	96	49	48	498
Damping-off	*11*	*11*	*26*	*6*	*141*	*16*	*5*	*14*	*12*	*4*	*474*
Drought	...	...	*5*	*3*	*6*	*1*	*5*	*8*	...	*1*	...
Heat Injury	*22*	*42*	*105*	*31*	...	*17*	*53*	*52*	*20*	*26*	...
Caterpillars	*12*	*2*	*1*	*27*	*29*	*3*	*10*	*2*	*2*	*6*	*24*
Pine Locusts	*3*	*20*	*21*	*47*	*7*	*3*	*27*	*11*	...	*2*	...
Unknown	*11*	*5*	*6*	*6*	*2*	*7*	*5*	*9*	*15*	*9*	...
Abnormal Losses, 1947[1]	244	480	386	165	160	98	65	72	56	36	58
Total Alive, November 1947	**232**	**206**	**191**	**144**	**171**	**122**	**89**	**93**	**67**	**74**	**11**
Winter Losses, 1947-8	11	3	13	6	39	10	2	6	...	5	9
Fungi	*4*	...	...	*4*	*30*	*5*	...	*3*	...	*2*	*5*
Breakage	*2*	*3*	*8*	*1*	*7*	*3*	*2*	*3*	...	*2*	...
Rodents	...	...	*5*	...	...	...	...	...	...	...	...
Unknown	*5*	...	...	*1*	*2*	*2*	...	...	...	*1*	*4*
Total Alive, Spring 1948	**221**	**203**	**178**	**138**	**132**	**112**	**87**	**87**	**67**	**69**	**2**
Summer Losses, 1948	16	...	...	4	10	7	5	6	3	12	...
Fungi	*1*	...	...	...	*6*	*1*	...	*2*	...	...	...
Drought	...	...	...	*1*	*1*	*2*	*2*	*4*	*3*	*12*	...
Heat Injury	*2*	...	...	...	...	...	...	...	...	...	...
Caterpillars	*2*	...	...	...	*1*	*2*	...	...	...	...	...
Pales Weevils	*2*	...	...	...	...	...	...	...	...	...	...
Suppressed	*5*	...	...	...	...	...	...	...	...	...	...
Unknown	*4*	...	...	*3*	*2*	*2*	*3*	...	...	...	...
Total Alive, November 1948	**205**	**203**	**178**	**134**	**122**	**105**	**82**	**81**	**64**	**57**	**2**
Basis: Sub-plots[2]	(23)	(11)	(12)	(24)	(20)	(18)	(12)	(36)	(12)	(24)	(24)

[1] Due to thinning and rodent depredations.

[2] Average of 67 filled seeds on each sub-plot.

cotyledons projecting up through the low screens. These losses were combined with those resulting from thinning and listed as "abnormal losses". Where dead seedlings could not be found, the cause of death was listed as "unknown". Screened sub-plots actually invaded by rodents have been omitted in Table 8 although the data lost were replaced by missing-plot techniques for analysis of variance. Differences in final stocking of the order of 30 seedlings were statistically significant.

The data in Table 8 show that differences in the ultimate stocking of seedlings on various types of seedbeds were very largely determined by the influence of the seedbeds on germination. The only place where losses following germination exceeded losses due to germination failures was in seedbeds formed by dense white pine slash beneath which virtually all of the seedlings were killed by damping-off. In all types the greatest mortality occurred during the early part of the first summer; most seedlings which survived the first summer without damage lived through the second summer. No single cause of mortality was pre-eminent. Losses to biotic agencies were most prominent on shaded types of seedbeds. Heat injury was most important in unshaded places on types of seedbeds susceptible to high temperatures.

The best results were observed on seedbeds of polytrichum moss and on those seedbeds of mineral soil created by removing litter and polytrichum moss itself. On the moss, germination was exceptionally uniform rather than extremely high; mortality was very low. The two kinds of bare mineral soil mentioned supported very high germination in moist or shaded situations and comparatively low germination on dry, unprotected spots. The most important source of mortality on mineral soil was heat injury occurring on the drier spots.

Both germination and survival were comparatively good beneath hardwood brush and lycopodium, although growth was frequently poor and it is unlikely that many of these seedlings will survive very long. No great advantage was secured by removing small patches of brush or lycopodium, because the resultant exposure of the litter to sunlight caused significant reductions in germination and survival. The commonest type of seedbed, white pine litter, was generally unfavorable to germination and survival; heat injury caused considerable mortality. However, germination and survival were excellent on sub-plots composed of litter shielded from the sun. A similar situation prevailed on the lichen plots; the results were very poor except in rare shaded situations, where germination and survival were high. Removal of the lichens to expose the dry mineral soil beneath did not alter the outcome.

The results of the 1947 experiment are indicative of those which might occur when precipitation during the first growing season was normal. It should be noted that they were based on data from seed-spots which were located under a wide variety of exposures to sunlight, although the ambiguous term, "partial shade", could be applied to the whole range of conditions.

1948 Experiment

The second major experiment embraced fewer types of seedbeds but was arranged so that the effects of variation in exposure to direct sunlight could be adequately distinguished. It has already been shown that heavy precipitation during May and June eliminated practically all variation in germination such as that observed in 1947. The precipitation in

TABLE 9. GERMINATION, MORTALITY AND SURVIVAL FOR THE FIRST GROWING SEASON OF THE 1948 EXPERIMENT, IN NUMBERS OF SEEDLINGS PER 1,000 FILLED SEEDS[1]

	Direct Sunlight Possible on:			
	0 days	± 44 days	± 160 days	> 300 days
POLYTRICHUM MOSS				
Not Germinating	177	185	400	269
Germinating	**823**	**815**	**600**	**731**
Mortality	38	61	54	93
Damping-off	*8*	*8*	*15*	*15*
Heat Injury	..	..	*39*	*54*
Insects	*23*	*38*	..	*8*
Rodents	*7*	*8*	..	*8*
Unknown	..	*7*	..	*8*
Surviving	**785****	**754***	**546***	**638***
BARE MINERAL SOIL				
Not Germinating	138	185	300	323
Germinating	**862**	**815**	**700**	**677**
Mortality	123	84	246	177
Damping-off	*15*	..	*31*	*31*
Erosion	*93*	*54*	*146*	*69*
Heat Injury	..	*15*	*54*	*54*
Drought	..	*15*	*8*	*15*
Insects	..	..	*7*	..
Rodents	*15*	..	..	*8*
Surviving	**739***	**731***	**454†**	**500†**
WHITE PINE LITTER				
Not Germinating	77	292	600	300
Germinating	**923**	**708**	**400**	**700**
Mortality	54	246	362	631
Damping-off	*46*	*46*	..	..
Insects	*8*	*46*	..	..
Heat Injury	..	*108*	*362*	*631*
Drought	..	*38*	..	..
Unknown	..	*8*	..	..
Surviving	**869****	**462†**	**38††**	**69††**

1 Each treatment involved an average of 130 filled seeds distributed over 6 seed-spots.

** Significantly above average.

* Above average, but not significantly so.

† Below average, but not significantly so.

†† Very significantly below average.

July was normal; consequently, it was possible to determine the influence of seedbed conditions on mortality, exclusive of the effect of large variations in germination.

Bi-weekly inventories were made of each sub-plot during the first growing season just as in the 1947 experiment. No thinning was necessary and all plots were screened well enough to prevent losses from rodents, except for a few seedlings lost because they germinated after the screens were removed.

The results, adjusted to show the fate of 1,000 sound seeds sown on each type of plot, are presented in Table 9. Statistical analysis revealed that differences of the order of 250 seedlings in the results shown in this table were significant. Over-all variations between types of seedbeds, between different degrees of exposure to sunlight, and the interaction between these two effects were all highly significant.

The most significant variations occurred on plots of white pine litter. Both germination and survival were higher on litter completely protected from sunlight than on any other group of sub-plots in the experiment. Sub-plots on litter exposed to the sun on the 44 longest days of the year had significantly more seedlings than those exposed for the whole summer. Heat injury killed practically all of the seedlings which appeared on litter where the sun could shine every day of the summer.

There was some tendency for frequent exposure to direct sunlight to be detrimental to the germination and survival of seedlings on polytrichum moss and mineral soil. The differences, although statistically significant in some instances, were not great enough to be of high practical importance. The most outstanding source of mortality on the mineral soil was erosion, which undermined some germinating seedlings during very heavy showers in June. The remaining sources of mortality on these two favorable types of seedbeds were of sporadic occurrence.

Causes of Mortality

Heat Injury and Surface Temperature

The results of the two main experiments left little doubt that variations in surface temperature on the various insolated seedbeds were responsible for many of the most important differences in germination and survival. Maximum surface temperatures for each week showed that temperatures were characteristically higher on the litter than any other seedbed, except possibly for lichens and dry mineral soil. Temperatures on ordinary mineral soil and polytrichum moss were invariably lower than on litter, even though the amount of direct sunlight was the same. These data did not provide any information concerning the causes of the variations in temperature nor did they indicate the duration of extremely high temperatures. A large amount of data was obtained and discarded before a satisfactory procedure of measuring surface temperature under direct solar radiation was developed.

The thermocouples finally used in making the observations were made of 14-gauge iron and constantan wires twisted together, coated with silver-solder and polished. The sensitive elements were approximately three millimeters in diameter; when used for measuring surface temperatures, they were not covered with any of the material constituting the surface. Vaartaja (64) has demonstrated that thermocouples as large as this give readings which are several degrees lower than actual surface temperatures. However, the results indicated at least approximate temperatures of solid substances in the stratum where girdling from heat injury is observed, which is actually several millimeters above the surface (23:176). The fundamental criterion, in this case, is the temperature of solid substances rather than of the air itself. A Foxboro potentiometer (Model 8105) was used for measuring the temperature of the thermocouples, to which it was connected by a 20-way switchbox. It was found that the switch-box had to be cooler than any of the thermocouples to give correct readings.

Three samples from several series of readings on adjacent plots representing seedbeds of pine litter, mineral soil and polytrichum moss have been selected as satisfactory examples and are shown in Figure 7. These observations were obtained from a small group of stations clustered in the center of the widest opening used in the 1948 experiment.

Since the opening was only 70 feet wide, the sun shone on the sampling location for only two hours each day. The beginning of the periods of exposure to full sunlight was controlled by a cheese-cloth screen which was removed from all three plots simultaneously. Measurements were continued until the shade of the tree-crowns had been re-established over all three plots. Readings were made at intervals of 3 to 15 minutes depending on the rate of change of temperature. An effort was made to select cloudless days for the observations. Such days are rare and only one series of observations was not complicated by variable cloudiness.

The observations made on August 8, 1948, were cut short by rapid cloud formation but proved valuable in spite of their brevity. This was one of the coolest clear days of the month with a strong northwesterly flow of polar continental air of Canadian origin. All surfaces were nearly saturated with dew when first exposed. In spite of the wind and low air temperature, surface temperatures rose fully as rapidly as on much warmer days; they fell with equal suddenness when the sun was covered by thick cumulus clouds. The surface of the pine litter attained 55°C. (131°F.), the temperature which marks the threshold of heat injury (36), less than 10 minutes after complete exposure. The mineral soil became slightly warmer than the warmest stratum in the moss, but neither reached 55°C.

Conditions for the observations of August 15, 1948, were ideal due to the absence of clouds. This day was also cool and dry, with a northwesterly flow of polar continental air, but had been preceded by three days of rain. All surfaces were thoroughly soaked when first exposed to the sun, but signs of drying were obvious after 20 minutes and each surface appeared dry and desiccated after 70 minutes. The high initial moisture content retarded the rate at which temperatures rose. However,

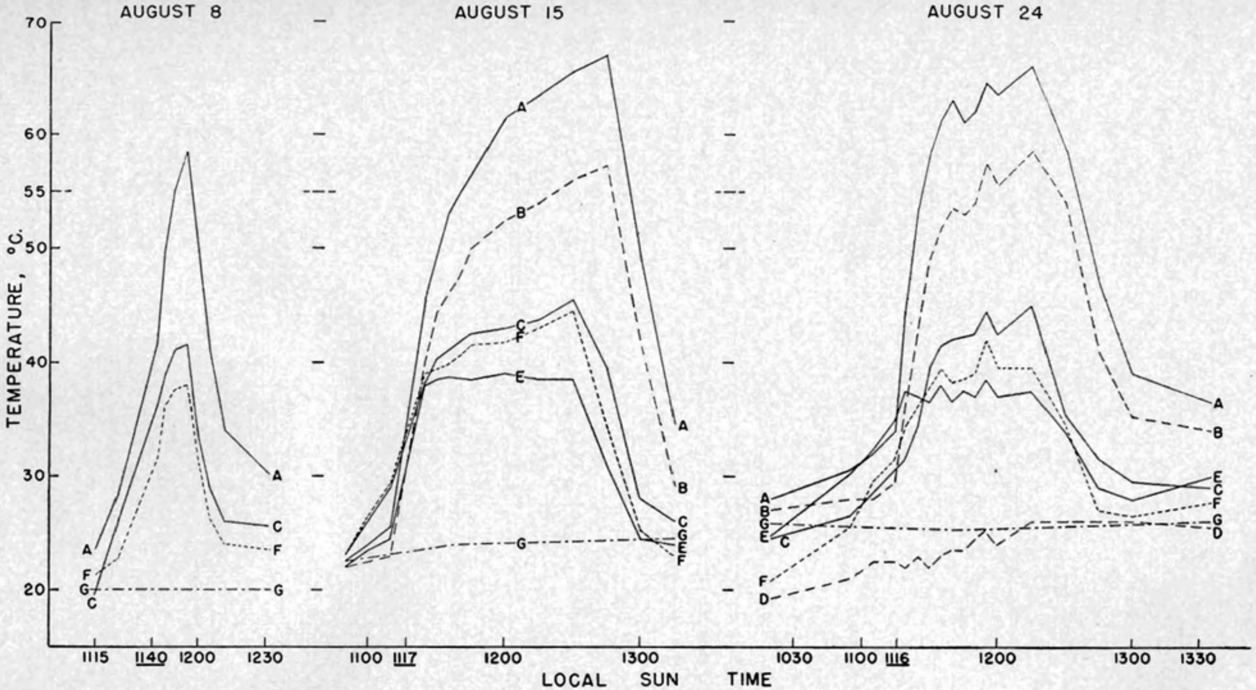

FIGURE 7

Graphs showing the course of temperature at various levels in different types of seedbeds exposed to direct sunlight. In each case, complete exposure began at the time which is underlined. AA—surface of white pine litter; BB—level ½ inch below surface of white pine litter; CC—surface of bare mineral soil; DD—1 inch below surface of bare mineral soil; EE—topmost surface of polytrichum moss; FF—surface of litter beneath polytrichum moss; and GG—air temperature 4½ feet above ground. The tissues of white pine seedlings may be injured by heat at temperatures above 55°C.

this retardation was of little practical importance because the temperature of the litter attained the lethal level in slightly less than 25 minutes rather than the usual 10 minutes. Temperatures of the other surfaces levelled off well below the lethal range. In polytrichum moss the level of highest temperature was not at the top of the moss but at the surface of the litter which had filtered down through the moss. This litter was exposed to sunlight when the drying leaves of the moss folded upward against the stems.

The final observations were made on August 24, 1948, during a period when the sun was partially but infrequently obscured by small cumulus clouds. There was a light southwesterly wind at the time with warm, tropical maritime air from the Gulf of Mexico. Although there had been no rain of any consequence for 10 days, none of the surfaces were completely desiccated because dew had formed during the preceding night. A complete series of readings was obtained, including observations of temperature below the surface of the mineral soil. The temperature below this surface increased gradually as heat was conducted downward through the mineral soil.

These observations demonstrated that surface temperatures responded rapidly to variations in incident solar radiation. They also showed clearly that surface temperature was in no way dependent on air temperature at conventional levels of measurement. In fact, there was some tendency for surface temperatures to be higher on cool days than on warm days. This was due to the fact that cool, polar continental air over New England is normally more transparent than warm, tropical maritime air which frequently contains much water vapor, smoke and haze. High initial moisture content of surfaces retarded the rise of temperature only temporarily. White pine litter attained consistently higher temperatures than either of the other surfaces: neither polytrichum moss nor bare mineral soil attained lethal temperatures during more than one hour of exposure to full sunlight, while white pine litter did so in 10 to 25 minutes.

During the same period, measurements of mid-day temperature one inch below the surface of the mineral soil were made at a similar location. Fifteen measurements beneath each of the three types of surfaces gave the following average values of temperature (in degrees C.): mineral soil, 21.0; polytrichum moss, 19.0, and pine litter, 19.0.

In the absence of more precise observations, explanation of these differences in surface temperature must rest on intuitive grounds, supported by the evidence of others, notably Geiger (23). The highest temperatures are generally attained at the solid surfaces which the sunlight first strikes. The temperature of any substance depends on the amount of heat absorbed, the rate at which heat is lost and the specific heat of the substance itself. If unshaded seedbeds attain different temperatures under equal insolation, it must be assumed that some lose heat to the soil and atmosphere more rapidly than others or that their specific heats differ.

The processes responsible for dispersion of heat from insolated surfaces are as follows:

1. Reflection, particularly of infra-red wave-lengths.
2. Downward conduction through the soil.
3. Intermolecular conduction upward into the atmosphere.
4. Long-wave radiation to space or the atmosphere.
5. Convection or turbulent mixing.
6. Evaporation of water.

Data summarized by Geiger (23) showed that green vegetation is the only substance found in the forest which has outstandingly high reflective ability. This extraordinary ability applies only to the infra-red wave-lengths, which contribute more heat than the visible wave-lengths. Green vegetation reflects infra-red radiation to the extent of about 44 per cent; most bare soils reflect only 2 to 11 per cent, although they reflect more when dry than when moist. Clark (11) concluded that the unusual ability of green leaves to reflect infra-red radiation is caused by the presence of chlorophyll and is greatly diminished when the chlorophyll is destroyed. Therefore, it appears probable that the difference in temperature between the polytrichum moss and the pine litter can be accounted for in some measure by this ability of the green moss to reflect infra-red radiation. The reflection of these wave-lengths by pine litter and bare soil is probably low and not sufficiently variable to account for much difference in temperature.

Mineral soils conduct heat downward much more rapidly than do organic materials. Bouyoucos (7) found that sandy soils were two to five times as efficient as peat in conducting heat. Albrecht (2) determined that downward conduction accounted for the dissipation of more than half of the solar energy received by mineral soil surfaces. The relatively high temperatures observed beneath bare mineral soil demonstrate this effect clearly. Mats of polytrichum moss and white pine litter form such good insulators that they conduct far less heat downward than bare mineral soil. The measurements of temperature one inch below the surface of mineral soil covered by moss or litter indicate that both are almost equally inefficient in conduction.

Geiger (23) has concluded that intermolecular conduction and long-wave radiation are generally less important than convection in dispersing heat from insolated surfaces into the atmosphere. Actually each process operates in a manner which would reduce rather than increase the observed differences in temperature. The rate of conduction depends on the temperature gradient; the loss of heat through radiation is proportional to the fourth power of the absolute temperature of the radiating body. In the absence of these two processes, surface temperatures of pine litter would be even higher than the observed values. It should be noted that conduction and radiation are regarded as responsible for much of the transfer of heat from solid surfaces to the thin boundary layer above them where the damage to seedlings occurs. They do not, however, operate in a manner which would account for the observed differences in temperature.

In turbulent mixing or convection, masses of heated molecules are removed from the hot boundary layer and carried aloft, being replaced by cooler masses from above. The rate of heat transfer by turbulent mixing depends largely on the speed of horizontal air movement which, together with the gradient of temperature, initiates the process. Byram and Jemison (10) and Vaartaja (64) have shown that reduction of air movement causes increases in temperature at the surface of the forest floor.

It is difficult to speculate on the effect of such a minute process without precise observations on air movement. However, convection is probably most active above surfaces which are interrupted by large pores. It would not proceed as rapidly over a smooth, rigid surface, like that of bare mineral soil, as over a more porous surface, like that of pine litter. Compared with polytrichum moss, white pine litter has a relatively tight, flat and rigid surface. The moss has a surface which becomes very porous under the influence of direct sunlight. As the vertical strands of moss dry out, the leaves fold upward against the stems, causing the continuous mats of moss to become open stands of small, widely spaced stems. The exposed area is greatly increased and acquires substantial distribution in depth. Such a surface would offer less resistance to the removal of groups of heated air molecules than the comparatively compact pine litter. This high rate of convection may account for part of the superior cooling of insolated polytrichum moss.

The removal of water vapor from surface materials — the process of evaporation — is accomplished largely by convection. The conversion of liquid water to vapor requires a substantial amount of heat, which is carried aloft with the water vapor. Much heat is dispersed from the surface of moss and litter in this manner, particularly if these hygroscopic substances are saturated with dew or rain when first exposed to sunlight. However, a number of comparisons between polytrichum moss and pine litter showed no consistent differences in water-holding capacity. Therefore, variations in loss of heat through evaporation could not account for the consistent differences in temperature. Evaporation is of lesser importance in cooling bare mineral soil because of the low saturation moisture content of soil.

A given amount of heat does not cause different substances to assume the same temperatures. Bouyoucos (7) and Mitscherlich (42:31) demonstrated that dry peat and humus had a specific heat about half that of an equal volume of sand. The difference was ascribed almost entirely to the high air content of the organic materials and did not prevail at higher moisture contents. From this it may be deduced that the surface temperature of pine litter, when dried by the sun, will be raised almost twice as much by a given amount of heat as will a bare sandy surface. However, the specific heat of polytrichum moss is probably little different from that of pine litter.

Another factor of some importance in controlling temperature is the spatial distribution of the absorbing surface. Pine litter and bare mineral soil must absorb the incident radiation on a surface which is nearly flat. Dry polytrichum moss presents a porous and irregular surface distributed in a horizontal zone as much as an inch and a half thick. Stems of seedlings growing in this zone are frequently shaded and the heat transferred from the seedbed is spread through a much deeper layer of air than with the other substances.

It is reasonable to assume that the high specific heat and conductivity of moist, bare mineral soil are sufficient to account for the relatively low temperatures observed. Mortality from heat injury on dry mineral soil at other locations was presumably caused by the lower specific heat and conductivity of the coarser and dryer soil. The effect of decreasing moisture content in reducing specific heat and conductivity of sand has been demonstrated by Bouyoucos (7).

The efficient dispersal of solar energy by polytrichum moss is probably a result of outstanding ability to reflect infra-red radiation and the irregularities of surface which may favor convection and cause the heat in the boundary layer to be less concentrated.

The comparatively high surface temperatures of insolated pine litter were apparently due to relatively inefficient export of heat by conduction and convection, low reflection of infra-red radiation and low specific heat.

The dense foliage of eastern white pine absorbs much of the solar radiation incident upon it; therefore, the canopy rather than the shaded forest floor is the surface of maximum heat transfer. Consequently, the temperature of the shaded forest floor remains quite uniform and well below the lethal range regardless of its composition.

The devastating effect of heat injury to white pine regeneration is often overlooked because it is serious only when the seedlings are very young. The dead seedlings soon fall and turn brown, becoming invisible to casual observation. It is also noteworthy that a few hours of bright sunshine can cause fatal injury.

Mortality from heat injury is rare after the middle of July when most of the seedlings harden. The stems then become straw-colored rather than red or green. This change has been attributed to the desiccation and collapse of the cortex, hitherto succulent (3). The resulting air spaces within the cortex then greatly impede the conduction of heat to the living tissues inside the stem.

Drought

Young white pine seedlings are quite resistant to drought. Both 1947 and 1948 had unusually long droughts occurring late in each growing season, but comparatively few seedlings died as a result, even on dry sites under dense shade. Few of the seedlings remaining at the end of the experiments succumbed to drought during the summer of 1949, which was also very dry.

Most of the plots of the 1947 experiment and all of those of the 1948 experiment were situated on ground within a few feet of the water table. A large number of measurements of soil moisture were made periodically at depths of one inch in the mineral soil with Bouyoucos gypsum blocks

(8). Moisture content of soil on areas with a high water table rarely fell far below field capacity, except in a few small patches. On plots above the influence of the water table, however, soil moisture remained in the wilting range for weeks at a time, yet mortality from drought was not outstanding.

During the late summer drought of 1948, similar measurements were made beneath surfaces of polytrichum moss, litter and bare mineral soil on a high and dry site. There were indications that bare mineral soil was subject to fairly rapid fluctuations in soil moisture, depending on the periodicity and intensity of rainfall. The moisture content of mineral soil beneath both polytrichum moss and pine litter was more stable; these materials tended to delay desiccation to the wilting range and also intercepted up to one-half an inch of each fall of rain. Periods of moisture deficiency beneath all three types of surfaces were generally several days shorter in areas open to the sky but shielded from the sun than in places completely shielded or fully exposed. None of these variations appeared to be of much importance as far as survival of pine seedlings was concerned. Natural seedlings less than one year old survived periods of moisture deficiency up to 38 days in length on the area where the measurements were made.

It has been argued that many white pine seedlings on litter die of drought because their roots do not penetrate to mineral soil. Work done by Moore (43, 44) has been cited as proof of this contention, although Moore showed that such was the case only in red spruce and balsam fir. He indicated that the long primary root of a white pine seedling was often capable of penetrating to mineral soil.

On June 10, 1948, the writer dissected the root systems of 120 natural white pine seedlings which had germinated between May 22 and June 4. These seedlings were equally distributed among three different degrees of shade and, where possible, two classes of thickness of litter. In areas exposed to direct sunlight, litter thicker than 1½ inches could not be found. There, 95 per cent of the seedlings had established contact with the mineral soil. Of the seedlings protected by side-shade, 90 per cent had done so, regardless of whether the litter was 1½ or 2 inches thick. Under full shade, however, only 45 per cent of the seedlings had roots which were in contact with mineral soil in each category of thickness of litter. The slow-growing seedlings in this situation were sampled again on June 22. By then 90 per cent of the roots had reached mineral soil where the litter was 1½ inches thick and 55 per cent where it was 2 inches thick. All of the seedlings observed had formed single, nearly vertical, primary roots.

It would appear that few white pine seedlings die of drought because of failure to penetrate to the mineral soil. It is, however, possible that difficulties might arise when a very dry period occurred immediately after germination or occasionally in rare situations under full shade where the litter was thicker than two inches.

Biotic Agencies

Rodents and Birds. Mice and squirrels constitute the most serious biotic menace to regeneration of white pine because they eat large quantities of seed before germination. The damage which they cause afterwards by nipping the seeds from germinating seedlings is less important but by no means negligible. The latter type of damage is not always fatal for it was found that seedlings could survive and grow slowly with damaged cotyledons no more than $\frac{1}{16}$ inch long. There was no direct evidence of damage by birds, although it is probable that they eat limited quantities of seeds.

During this investigation efforts were made to exclude seed-eating animals from all but a few of the plots. There was evidence in the 1947 experiment that depredations by rodents were subject to extreme local variation. The most outstanding example was noted in one situation where mice consumed all of the seeds on an entire block of plots, regardless of whether they were screened or not; this particular block had to be re-established elsewhere. Fifty yards from this block was another where seeds sown the same day remained undisturbed on the surface of unscreened mineral soil for several weeks. In general, seedbed conditions could not be associated with any consistent variations in rodent depredations.

Insects. Damage by insects was sporadic in occurrence, being serious only in exceedingly localized spots where groups of seedlings, rather than isolated individuals, were destroyed. Possibly the high concentration of seedlings on the seed-spots caused injury by insects and other biotic agencies to be unnaturally high.

Feeding by the most serious pest of white pine regeneration, the pales weevil (*Hylobius pales* Boh.) was an important factor only in the 1948 experiment. Here the openings used for the plots were made by cutting trees several weeks before the seeds were sown. The adult weevils attracted to the freshly cut stumps caused considerable damage to previously existing natural regeneration during the summer of 1948. Damage to seedlings established by sowing in 1948 did not appear until the summer of 1949. Seedlings growing in polytrichum moss were far more seriously affected than those in pine litter or mineral soil; however, none of the stocked seed-spots was completely destroyed. This observation substantiates those of Peirson (48) and Friend and Chamberlin (19) who found that damage was most severe in moist seedbed materials, particularly polytrichum moss.

The pine locust or pine grasshopper (*Melanoplus punctulatus* Scudder).[1] an insect which has been described by Morse (45), caused fully as much damage as the pales weevil. These insects ordinarily feed on the needles in the tops of large white pine trees, frequently thinning out the foliage substantially, although rarely causing serious damage. During the late fall the females come down to the ground to lay their eggs in bark crevices or other openings in living trees, stumps or large pieces of slash. On cold days they are very feeble and congregate on surfaces exposed to sunlight. At such times they feed on the foliage and stems of pine seedlings of all ages growing in full sunlight. In several cases it was found that they had consumed all of the above-ground parts of first-year seedlings. The

[1] **Identified by C. T. Parsons, The Connecticut Agricultural Experiment Station.**

preference of the locusts for warm feeding grounds was so great that on several densely stocked seed-spots they started feeding at the south edges and worked gradually northward.

Damage by caterpillars was most common in shaded locations, although it was rarely severe enough to be of much practical importance. Most of them were species which feed on practically any succulent vegetation. Dr. H. W. Capps, of the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, identified immature larvae of the families Phalaenidae, Geometridae and Tortricidae among the specimens submitted. The cut-worms, members of the first family named, were the most injurious.

Fungi. The only fungi which caused primary damage during the experiment were the weak parasites, which cause damping-off and snow mold. Virtually all of the etiolated seedlings which appeared in large numbers under the dense slash piles established in the 1947 experiment were swiftly killed by damping-off. Losses from damping-off were relatively unimportant under more favorable growing conditions; in general, they were more common in the shade than in the open and may have been unnaturally high because of the close spacing of the seedlings.

Following the heavy snows of the winter of 1947-1948, large patches of whitish snow mold were found on the forest floor throughout the experimental area. A few of the less vigorous seedlings were apparently killed outright by this fungus. More often, seedlings killed by this agency had previously been broken over by the snow or by falling objects. In these cases breakage was regarded as the primary cause of death.

During the spring of 1948 a few seedlings on excessively moist areas were killed by unidentified root-rots. Several seedlings in luxuriant moss on these spots failed to grow in height as rapidly as the moss. These suppressed seedlings eventually died from fungus infections.

SEEDLING DEVELOPMENT

The growth of white pine seedlings during their first two years is always relatively slow and of little immediate consequence compared with the question of survival. Gast (21, 22), Mitchell (41) and Shirley (52) have shown that growth is controlled almost exclusively by light at intensities below 20 to 30 per cent of full sunlight. At higher light intensities, they demonstrated that growth increased with additional increments of light up to full sunlight only if sufficient inorganic nutrients were available. In other words, nutrient deficiencies can prevent the growth of pine seedlings from responding to increases in light.

The current investigation, conducted in the forest with less adequate control over the environment, indicated that light intensities found beneath full shade were hardly sufficient to support life indefinitely. The partial shade which is often necessary to insure germination and survival is not, in the long run, conducive to proper development of the seedlings. On the other hand, there was also evidence that the growth of seedlings on different insolated seedbeds varied significantly due to factors other than light or nutrition.

Approximately the same procedure of observing growth was followed in both of the main experiments. The largest three or five seedlings on each seed-spot were selected for measurements. This policy was followed because the continual suppression of the smallest by the largest is one of the most fundamental characteristics of an aggregation of trees.

When the seedlings were removed from the seed-spots, all possible criteria of development were measured. Many of these criteria, however, cannot be measured without killing the seedling. Therefore, epicotyl length was employed as an index of development when the seedlings could not be pulled up. This structure is the part of the stem above the cotyledons, while the part below is known as the hypocotyl. The length of the epicotyl appears to be very satisfactory for this purpose and, in very young seedlings, may even be a more useful measurement than dry weight, which is the standard criterion of development. The growth of the epicotyl takes place after the seed is shed and is probably not greatly influenced by variations in seed weight, which Spurr (58) has shown to be important.

The length of the whole stem is not a good measure of growth, because the hypocotyl makes up most of the height of young seedlings. The length of the hypocotyl was found to bear an inverse relation to the amount of light (see Tables 10 and 11). Seedlings growing under slash, for example, were taller than those in the open. This curious response to light has considerable survival value because it often results in the elevation of the cotyledons above low cover like that of polytrichum moss. The growth in length of the hypocotyl is probably dependent on materials derived from the endosperm.

Whenever seedlings were removed the extent of mycorrhizal development

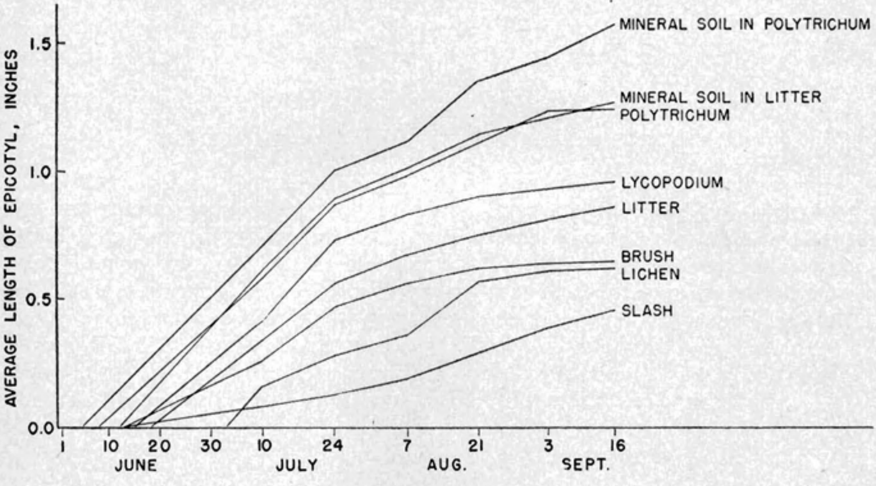

FIGURE 8

Average cumulative growth of epicotyls of first-year seedlings from various types of seedbeds, 1947 experiment.

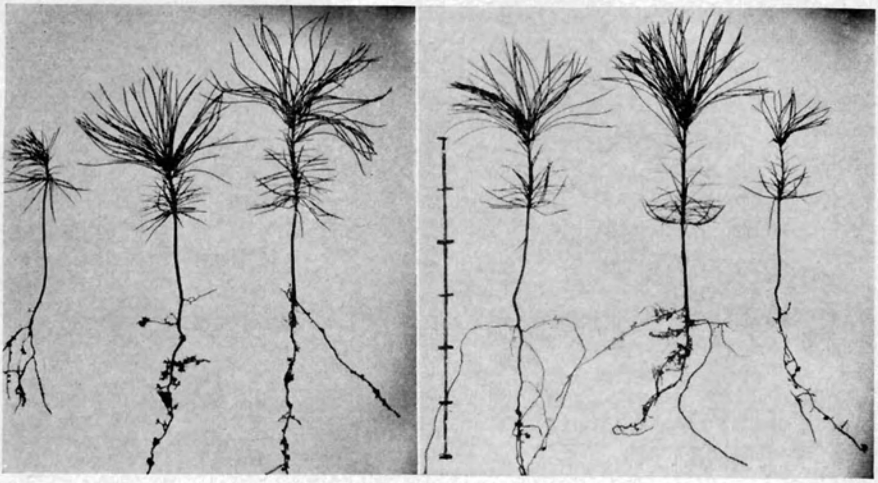

FIGURE 9

Typical second-year seedlings, 1947 experiment. Seedbed types represented are, from left to right: hardwood brush, white pine litter, mineral soil in pine litter, polytrichum moss, mineral soil in polytrichum moss and lycopodium club-moss. Each division on the scale in the center equals one inch.

was noted. It was found that mycorrhize formed on virtually all seedlings within a few weeks after germination, regardless of seedbed conditions.

1947 Experiment

During the first summer of the 1947 experiment, periodic measurements of the length of the epicotyl, inclusive of the topmost primary needles, were used to evaluate growth. The average cumulative growth of groups of 18 seedlings, representative of each important type of seedbed, is shown in Figure 8. There was a strong tendency for growth to be best where germination was the earliest, at least on the more open seedbeds. In other words, delayed germination inhibited development merely by shortening the growth period.

During August of the second year of the 1947 experiment the five largest seedlings were removed from one seed-spot representing each of the important seedbeds on each of the six blocks of the experiment. Some types of seedbeds could not be sampled because of poor survival. The average measurements of these seedlings are given in Table 10, while representative seedlings from each type appear in Figure 9. Analyses of variance for these data revealed highly significant differences between types. Individual averages for given types of seedbeds were generally significantly different from similar averages for types which did not rank next greatest or next smallest.

The poor growth beneath brush and lycopodium was doubtless caused by low light intensity. The excellent growth of roots beneath bare mineral soil probably accounts in some measure for the rapid growth of seedlings

TABLE 10. AVERAGE MEASUREMENTS OF 2-YEAR OLD SEEDLINGS FROM 1947 EXPERIMENT[1]

	Top Length, Inches			Weight, Mg.			Ratio
Type of Seedbed	Epicotyl[2]	Hypocotyl	Total	Total	Top	Root	Top Wt. / Root Wt.
Mineral Soil, Polytrichum	.215	.164	.379	423	304	119	2.64
Mineral Soil, Litter	.148	.169	.317	332	203	129	1.93
Polytrichum	.154	.194	.348	283	202	81	2.73
Pine Litter	.098	.174	.272	189	122	67	2.25
Lycopodium	.100	.200	.300	107	74	33	3.01
Brush	.050	.200	.250	57	43	14	3.59
Least Significant Difference[3]	.016	.021	.049	155	113	57	1.10

[1] Each value represents an average frcm 30 seedlings.
[2] Stem, exclusive of primary needles.
[3] At 2 per cent level.

there. However, so many of the variations were inexplicable that the 1948 experiment was arranged to elucidate some of them.

1948 Experiment

Measurements of seedlings grown under three different light intensities in the 1948 experiment were made in November, after one growing season. Seedlings were removed from seed-spots selected at random and measured in the same manner as those removed from the 1947 plots. The third lines of plots were not sampled because of excessive mortality among seedlings grown on litter; however, conditions there were little different from those on the fourth lines. Only three types of seedbeds were represented: polytrichum moss, bare mineral soil and white pine litter. Average measurements are summarized in Table 11, while representative seedlings are shown in Figure 10. The differences in growth were actually quite small.

The size of seedlings on continuously shaded sub-plots was fairly uniform regardless of the type of seedbed. On the other plots, the characteristic which showed greatest and most consistent variation was the length of the epicotyl. Epicotyls of seedlings growing on polytrichum moss increased with each increase in exposure to direct sunlight according to a statistically adequate straight-line relationship. On the other hand, epicotyls of seedlings growing on mineral soil showed no significant response to increases in light; those on pine litter were slightly (but not significantly) retarded by exposure to sunlight.

No proven explanation can be advanced for the failure of seedlings grown on the three different types of seedbeds to respond similarly to increased light. It would appear that seedlings grown on mineral soil and

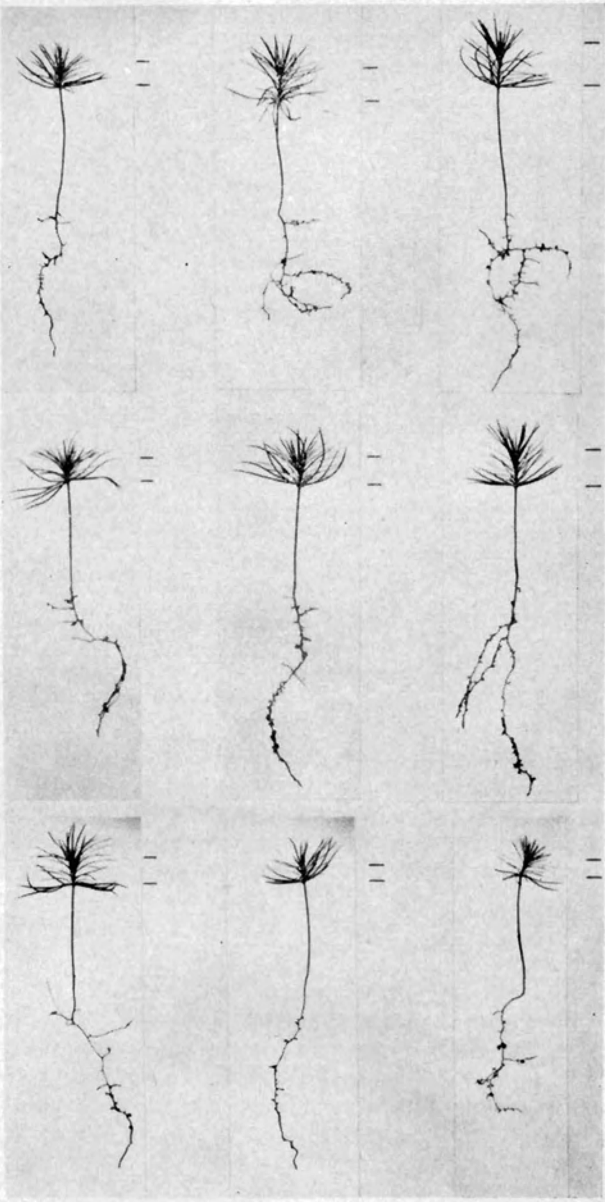

FIGURE 10

First-year seedlings representative of each type of seedbed and degree of exposure to direct sunlight, 1948 experiment. Horizontal rows, from top to bottom: (1) polytrichum moss, (2) bare mineral soil and (3) white pine litter. Vertical rows, from left to right: never exposed to direct sunlight, exposed ± 44 days, and exposed > 300 days. Pictures slightly less than one-third natural size. Marks at right of each photograph show the lengths of the epicotyls.

TABLE 11. AVERAGE MEASUREMENTS OF FIRST-YEAR SEEDLINGS FROM 1948 EXPERIMENT[1]

Days of Possible Sunlight	Epicotyl Length, Inches[2] P	M	L	Hypocotyl Length, Inches P	M	L	Total Length of Roots, Inches[3] P	M	L
0	.353	.277	.340	2.21	1.68	1.84	6.47	4.31	5.16
±44	.400	.343	.203	1.93	1.71	1.79	6.84	4.64	3.04
>300	.563	.357	.243	1.96	1.69	1.74	7.30	5.37	4.05
L. S. D.[4]		.177			0.34			3.03	

	Total Wt., Mg. P	M	L	Top Wt., Mg. P	M	L	Root Wt., Mg. P	M	L
0	86	77	79	46	42	45	40	35	34
±44	71	103	55	40	46	32	31	57	23
>300	89	98	60	54	48	34	35	50	26
L. S. D.		36			17			22	

	Top/Root Ratio[5] P	M	L
0	1.54	1.29	1.43
±44	1.32	0.86	1.69
>300	1.60	1.08	1.62
L. S. D.		0.58	

P — Polytrichum Moss
M — Bare Mineral Soil
L — White Pine Litter

[1] Each value represents 15 seedlings.
[2] Stem, exclusive of primary needles.
[3] Exclusive of branch-roots less than 0.25 inch long.
[4] Least significant difference at 2 per cent level.
[5] Weight basis.

pine litter were affected by unfavorable conditions not found on polytrichum moss. Differences in the length of the growing period could have caused little of the variation because germination occurred at about the same time on all plots. Periodic measurements of soil moisture showed that the mineral soil beneath virtually all plots was close to field capacity throughout the growing season; consequently, the differences could not have been caused by variations in moisture supply.

All of the seedlings which had been measured were ashed and their content of certain inorganic elements analysed spectrographically to determine whether nutrient deficiencies might have caused the variations in growth. The results, together with corresponding optimum values determined by Mitchell (41), are shown in Table 12. The material available was not sufficient for nitrogen determinations or replication for statistical analysis. The most important fact revealed was the very low content of all the elements concerned. Mitchell found that growth of seedlings with an even higher content of these elements was far below optimum. It seems certain that the deficiencies of nutrients on the experimental area were large enough to prevent light from operating as the sole factor limiting growth.

On the other hand, the analyses showed, with one exception, that the seedlings had relatively uniform content of all five elements regardless of the type of seedbed. Seedlings grown on moss and litter had essentially

TABLE 12. AVERAGE CONTENT OF CERTAIN NUTRIENT ELEMENTS IN SEEDLINGS FROM THE 1948 EXPERIMENT[1]

Type	Days of Possible Sunlight	Percentage of Element, Oven-dry Basis				
		K	Ca	P	Mg	Mn
Polytrichum Moss	0	.60	.21	.33	.14	.024
	±44	.64	.25	.41	.16	.038
	>300	.68	.22	.35	.15	.048
	Mean	.64	.23	.36	.15	.037
Bare Mineral Soil	0	.54	.22	.33	.16	.016
	±44	.48	.20	.28	.14	.020
	>300	.46	.19	.28	.12	.019
	Mean	.49	.20	.30	.14	.018
White Pine Litter	0	.57	.23	.33	.18	.060
	±44	.50	.19	.34	.19	.035
	>300	.53	.21	.31	.18	.050
	Mean	.53	.21	.33	.18	.048
Optimum[2]		1.72	.33	.69	[3]	[3]

[1] Each value represents one sample composed of 15 seedlings.
[2] Determined by Mitchell (41).
[3] Not investigated by Mitchell.

the same nutrient content; those grown on mineral soil were also the same, except for distinctly low values of manganese. The supply of this element was probably lowered by removal of the litter; Gutschick (27) has demonstrated that the manganese of forest soils is mostly bound up in the humus layers. It is possible, but by no means certain, that deficiencies of manganese or some other element may have caused the seedlings on mineral soil to respond to increases in light less vigorously than those on the moss. LeBarron (34) also found symptons of nutrient deficiency in stunted jack pine seedlings growing on mineral soil.

It appears unlikely that the difference in growth between seedlings on moss and on litter could be due to variation in nutrition. It is possible that further investigation might reveal that the microclimate of insolated pine litter is fully as unfavorable for growth as for germination and survival. In this connection, it is interesting to note that McArdle (40) found that greenhouse temperatures above 86°F. reduced the growth of white pine seedlings.

If seedbed conditions have any important influence on the growth of unshaded seedlings, it is probably of short duration. Within a few years they would grow up out of the thin stratum where unfavorable microclimatic conditions might exist. Local nutrient deficiencies which might possibly be caused by removal of litter would persist only if the patches affected were very large and were not covered again by subsequent deposition of litter.

It is of some practical significance to note that the side-shade which promotes good germination and survival of seedlings on pine litter provides better conditions for early growth than those in direct sunlight or beneath overhead shade.

PROPERTIES OF THE SOIL

At the beginning of the investigation it appeared logical to believe that some of the variations in vigor of regeneration on different seedbeds might be the result of differences in the soils beneath. Some of the relatively stable chemical and physical properties of soils under polytrichum moss and white pine litter were examined to determine whether any important differences were associated with these two seedbeds. Comparisons were confined to the A-layer of soils on a high, dry section of the experimental area.

Organic matter was determined by the wet combustion method (47), and total nitrogen content, by the Kjeldahl method. Total pore volume was measured by the method of Lutz (38). Field capacity was found on two occasions by oven-drying samples collected 48 hours after heavy rains. The difference between field capacity and total pore volume was accepted as air capacity. Measurements were also made of the time required for one liter of water, with an initial head of 10 centimeters, to infiltrate the mineral soil. The results are summarized in Table 13. Statistical analyses revealed that the differences involved lacked significance.

TABLE 13. AVERAGE VALUES OF CHEMICAL AND PHYSICAL PROPERTIES OF THE A-HORIZONS OF SOILS BENEATH POLYTRICHUM MOSS AND PINE LITTER

	Polytrichum Moss	White Pine Litter	Number of Samples
Total organic matter, percentage by weight	2.86	3.59	6
Total nitrogen, percentage by weight	0.132	0.147	6
Total pore volume, per cent	58.1	59.9	9
Field capacity, per cent	18.9	16.6	6
Air capacity, per cent	39.1	43.2	..
Infiltration time, seconds per liter	345	339	7

Spectrographic analyses of the ash of samples of moss and litter were also carried out immediately after the period of maximum needle-shedding in the fall. Samples from polytrichum moss included the litter which had been deposited on the moss. The values obtained, on the basis of percentage by weight and weight per unit area, are shown in Table 14. Interpretation of these results is difficult, although there are indications that the nutrient cycle is accelerated by more rapid decomposition of litter in the moss.

TABLE 14. AVERAGE CONTENT OF VARIOUS NUTRIENT ELEMENTS IN POLYTRICHUM MOSS AND WHITE PINE LITTER[1]

Type of Seedbed	K	Ca	Mg	P	Mn	Zn
	Percentage by Weight					
Polytrichum Moss	.31	.23	.12	.24	.08	.03
White Pine Litter	.23	.34	.12	.22	.16	.03
	Grams per Square Foot of Surface					
Polytrichum Moss	.43	.30	.16	.34	.10	.04
White Pine Litter	.42	.60	.23	.42	.28	.03

[1] Each value represents 3 samples.

Determinations of pH were performed on material from various strata within the two kinds of seedbeds and in the mineral soil beneath them. The values ranged from 4.10 to 4.82, being lowest in the F-layers; there were no consistent differences between either of the seedbeds.

The observations failed to reveal any differences in these soil properties of sufficient magnitude to account for the superiority of seedbeds of polytrichum moss over those of pine litter. It is believed that all of the observed differences in regeneration on different seedbeds can be accounted for independently of soil properties other than those which actually influence the moisture content of the soil.

OBSERVATIONS OF NATURAL REGENERATION

The good seed crop of 1947 offered an excellent opportunity to determine whether the phenomena observed on artificial seed-spots occurred in natural conditions. Intensive observations were confined to a single section of one of the highest and driest parts of the experimental area. The plot selected was roughly 70 x 100 feet in size and contained one large opening running north and south as well as a circular one resulting from the removal of a large tree. The openings had been created during improvement cuttings early in 1947, when the stand was about 40 years old. The slash was piled and burned following the cutting; pure white pine litter covered most of the forest floor.

Quarter mil-acre plots were laid out on a 10 x 10 foot spacing. Total germination on each of these plots was determined by counting all new seedlings, living and dead, late in June, 1948. First-year survival was determined by counting living seedlings on September 26, 1948. These data were superimposed on a crown map of the area (Figure 11). The few plots not covered with pine litter are specially designated on the map.

Both germination and survival were fairly closely correlated with the degree of protection from direct sunlight. Results were far better under full shade and along the southern and western margins of the openings than along northern and eastern margins. The adverse influence of the

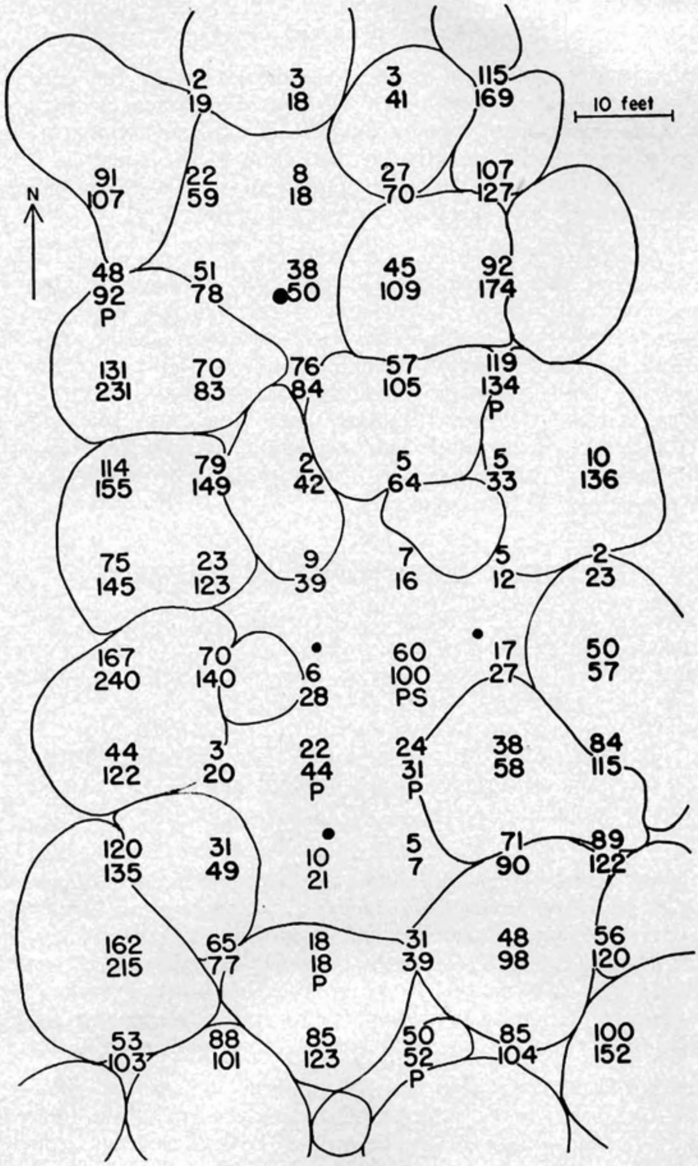

FIGURE 11

Crown map of a 40-year old white pine stand showing germination and survival of seedlings. Upper values indicate survival and lower ones, germination, in numbers of seedlings on quarter mil-acre plots centered at 10-foot intervals. Dark circles show position of stumps of trees. All seedbeds are composed of pure pine litter except for those designated "P" which include varying amounts of polytrichum moss and one designated "PS" which is composed of polytrichum moss, fine slash and litter.

slanting rays of the afternoon sun was evident in the low survival on plots under trees at the northeast corners of the openings.

The abnormally good results on several plots near the center of the larger opening could be accounted for by the presence of polytrichum moss or small sticks from logging debris. The initial supply of seeds was doubtless better directly beneath the trees than in the openings. Inspection of the map will, however, reveal a number of discrepancies which cannot be explained entirely by variations in seed supply.

It is unlikely that the numerous seedlings in dense shade will survive for many years. None of those which must have appeared after previous seed crops in shaded parts of this area were alive in 1947. Nevertheless, tremendous numbers of seedlings growing in dense shade were still alive in late 1949, in spite of severe droughts in 1948 and 1949. The evidence indicates that young white pine seedlings are highly resistant to moisture deficiencies. Craib (14) and Rhodes[1] have suggested that slow-growing pine seedlings in dense shade are eliminated largely because they are gradually buried by falling needles; observations made in this investigation appear to substantiate this view.

ARTIFICIAL TREATMENTS OF SEEDBEDS

The excellent 1947 seed crop also provided a convenient situation for testing certain treatments which seemed promising as means of ameliorating unfavorable seedbed conditions. The quarter mil-acre test plots were treated in August and September before the seeds were released. Each treated plot was laid out adjacent to an untreated one of similar size; all were on high and dry sites in openings surrounded by white pine. Distinction was made between plots exposed to direct sunlight and those protected by side-shade. Newly germinated seedlings were counted on July 2, 1948, and those surviving the first year, on October 1, 1948.

Treatments applied to plots exposed to direct sunlight consisted of: (1) complete exposure of mineral soil and (2) covering of litter with thin, loose layers of fresh pine slash varying from one-half to two feet in thickness. On shaded plots there were three treatments: (1) exposure of mineral soil, (2) destruction of the L-layer by burning and (3) mixing and overturning of humus layers by raking without exposing mineral soil. Germination and survival on each sub-plot are indicated in Table 15.

On the insolated plots, exposure of mineral soil caused consistent and important increases in survival. The thin layers of slash induced some improvement in germination but the tops of many seedlings shrivelled and died when they came in contact with the needles of the slash. It could not be determined whether heat injury or damping-off caused this mortality. Heavy rainfall during the germination period caused good germination on untreated pine litter, but most of the seedlings later succumbed to heat injury. The few seedlings which survived on untreated litter were mostly in minute patches of shade behind the parental cones.

[1] A. D. Rhodes, University of Massachusetts, personal communication, 1947.

TABLE 15. RESULTS OF TRIALS OF CULTURAL TREATMENTS OF SEEDBEDS OF WHITE PINE LITTER MADE PRIOR TO RELEASE OF 1947 SEED CROP

	PLOTS EXPOSED TO DIRECT SUNLIGHT		
Plot[1]	Mineral Soil Exposed	Thin Slash Cover	Untreated Control
A	14 - 3[2]	16 - 4	12 - 1
B	25 - 13	21 - 3	7 - 1
C	33 - 19	51 - 4	17 - 1
D	21 - 7	4 - 2	15 - 3

	PLOTS PROTECTED FROM DIRECT SUNLIGHT			
Plot	Mineral Soil Exposed	L-Layer Burned	Litter Raked and Mixed	Untreated Control
E	51 - 43	94 - 76		64 - 34
F	88 - 69	59 - 32		71 - 24
G	16 - 15	30 - 9		18 - 10
H			74 - 36	12 - 1
I			54 - 43	44 - 28
J			57 - 14	21 - 5
K[3]	15 - 8	4 - 2	2 - 0	3 - 1

[1] Each plot one-quarter mil-acre in size.
[2] First figure represents germination; second, first-year survival.
[3] Inadvertantly located in an area exposed to the sun during early summer.

The treatments applied in shade generally caused improvement in stocking. Enough seedlings survived on untreated litter, however, to give an average stocking of 68,000 per acre. Consequently, treatment of continuously shaded litter would hardly seem necessary. It was noteworthy that exposure of mineral soil proved more effective than raking or burning on one plot inadvertantly located in an unprotected spot. The burning, incidentally, destroyed only the superficial L-layer, leaving the charred surface of the F-layer exposed. Such a seedbed would be unfavorable if exposed to sunlight. Presumably a hotter fire or a series of fires which consumed all of the forest floor might prove more conducive to regeneration, although the writer was too cautious to attempt such treatments.

CHARACTERISTICS OF INDIVIDUAL TYPES OF SEEDBEDS

Mineral Soil

Seedbeds of mineral soil may be created naturally by fires, animals or the uprooting of trees; they are ordinarily created, however, by artificial scarification, intentional or otherwise. They are very favorable to white pine regeneration, unless subject to extreme desiccation. There are no barriers to penetration of seed and the radicles of germinating seedlings quickly establish contact with the substratum, except in occasional instances when they are eroded from sandy soils by heavy rains. Bare, insolated mineral soil conducts heat downward so efficiently and has such a high specific heat that lethal surface temperatures occur only when the soil is very dry. Mortality from other causes is negligible. Growth of seedlings on mineral soil is generally good, although there is evidence that the removal of litter may induce detrimental nutrient deficiencies. Such deficiencies are not likely to be long-enduring if the litter is renewed by subsequent leaf-fall or if the exposed patches are no more than a few inches in size.

Pope (49) and Eklund and Huss (17) have demonstrated that the best form of scarification is that which creates long, narrow strips with the greatest possible marginal area. Westveld (66) obtained evidence in Maine that drastic exposure of mineral soil by severe fires was detrimental. It does not appear that any practical advantage is to be gained by exposing mineral soil on continuously shaded areas. The properties of insolated seedbeds on abnormally dry soils are not likely to be improved by scarification.

Polytrichum Moss

Polytrichum commune, a common moss of white pine forests, proved to be the most uniformly favorable seedbed. White pine regeneration on this moss was not as good as that on moist mineral soil, but always better than that on dry mineral soil. Falling seeds readily filter through the loosely arranged, vertical strands of polytrichum moss. Germination is fairly good and the roots of the seedlings soon come in contact with mineral soil. The seedlings grow as well as light intensity (and possibly inorganic nutrition) will permit. This moss dries out quickly in direct sunlight and the resulting diffuse, irregular surface loses heat so rapidly that lethal temperatures rarely occur; it is probable that the green leaves also reflect substantial amounts of infra-red radiation.

According to Bowen (9), polytrichum moss receives most of its moisture directly from the atmosphere in the form of rain or dew. Its sturdy roots apparently have no function other than that of support; consequently this moss is incapable of active competition for water and nutrients in the soil. The stems are provided with external canals which conduct water up and down between the stems and leaf-bases. Nutrients are absorbed from dust and rain-splash.

Polytrichum moss thus provides a fine medium for germination and protects the seedlings from all microclimatic extremes, but rarely competes with them. The height growth of the moss on poorly-drained spots is sometimes more rapid than that of two-year old seedlings which are occasionally suppressed as a result. However, this phenomenon is probably rare in the relatively warm and dry summer climate of southern New England. In the cool, moist, maritime climate of northwestern Europe polytrichum moss grows so vigorously that it often makes a very poor seedbed (16:177, 29). The only distinctly bad feature of polytrichum moss as a seedbed is that it may harbor a high population of pales weevils. On the other hand, the moss generally supports more seedlings than can be disposed of by this insect.

Hypnum moss is probably favorable to regeneration for somewhat the same reasons as polytrichum moss, although it is generally confined to shaded situations where seedbed conditions are of low importance. The effects of other, less common, mosses are unknown. Seedbeds of mineral soil created by removing polytrichum moss are usually moist enough to be superior to those of moss itself. However, results on undisturbed moss are good enough to make scarification of little practical value.

Attempts to encourage or establish polytrichum moss proved fruitless. It was, however, observed spreading rather rapidly over areas of exposed mineral soil. Similar observations have been made in Europe by Romell and Malmström (50) and Germeten (25). Invasion of scarified surfaces by moss might occasionally conserve the beneficial effect of such treatment.

White Pine Litter

The most common seedbed found in white pine forests is that created by deposition of litter from the pines themselves. Seedbeds of pure pine litter are very unfavorable to pine regeneration if exposed to direct sunlight. The litter is so resistant to the penetration of seeds that many of them would remain entirely exposed if most of the annual increment of dead needles did not fall from the trees shortly after the seeds. However, this half-inch covering is not adequate to protect the seeds from the wide fluctuations of moisture and temperature which may occur at the surface. This condition is particularly detrimental on insolated areas, where germination is good only if there is very heavy and frequent rain during the germination period. Even if they germinate, seedlings on insolated litter are generally killed by heat injury. It was found that the surface of white pine litter could attain lethal temperatures after 10 to 25 minutes of exposure to direct sunlight. There were indications that these severe microclimatic conditions also hampered the growth of surviving seedlings.

The roots of white pine seedlings can penetrate as much as two inches of litter in two weeks or less, except under a full canopy where up to one month is necessary. Since white pine litter is rarely thicker than this, it appears unlikely that many seedlings die because their roots fail to penetrate to mineral soil.

White pine litter that is protected from direct sunlight makes fully as good a seedbed as any other material and need not be treated to encourage regeneration. Optimum conditions for regeneration on litter are found where the side-shade of trees to the south cuts off direct sunlight but presents no barrier to diffuse radiation from above. Favorable conditions also prevail on minute patches of litter shaded by small herbaceous plants or scattered pieces of debris. Unfavorable microclimatic conditions may be ameliorated by exposing the mineral soil or scattering slash thinly over the insolated litter. The latter treatment would be superior to scarification on very dry sites because of the unfavorable nature of the surface of dry mineral soil.

Very little information is available on the influence of hardwood litter on white pine regeneration. Brief investigations did indicate that the rustling of oak leaves in the wind promoted rapid penetration of seeds into the litter. Most of these seeds penetrated so deeply that the germinating seedlings died before the cotyledons were elevated to the surface. Scarification of hardwood litter enhanced germination and survival. This type of seedbed is probably not favorable to pine regeneration, although it is unlikely that hardwood litter has the same influence as pine litter.

White Pine Slash

Dense piles of fresh pine slash are thoroughly detrimental to pine regeneration. Germination beneath them is good, but virtually all of the slender, etiolated seedlings die of damping-off soon after they appear. On the other hand, a thin scattering of woody debris over the surface of insolated litter provides the beneficial type of "dead shade" described by Isaac (32). The photograph on the cover is a fine illustration of this favorable influence. A thin covering of fresh pine slash is somewhat detrimental because the tops of the seedlings shrivel and die when they touch the needles on the slash. Spaulding (56) found that two years were usually required for the shedding of needles from white pine slash; therefore, dead branches rather than live ones should be used for shading purposes. Actual contact between seedlings and large pieces of slash is probably undesirable because Gottlieb (26) has observed that such surfaces can attain lethal temperatures in spite of their elevation above the ground.

Ground Flora

The effect of small plants of the forest floor on pine regeneration varies considerably depending on the growth habit of the species involved. *Lycopodium complanatum,* a trailing evergreen club-moss, was the only one of these plants investigated thoroughly. This is generally detrimental because it provides a cover too high for first-year seedlings to surmount, although they will occasionally develop properly in gaps. Lycopodium also grows faster in height than second-year seedlings. The effect of removing it depends on the type of seedbed remaining. Other evergreen vines, especially dewberry, are believed to have the same influence.

False lily-of-the-valley appears from general observations to be favorable to pine regeneration. The small leaves of this herbaceous perennial appear before the germination period of white pine and shade minute patches of litter throughout the period when microclimatic conditions are critical. The leaves rarely form a closed canopy and do not rise far above the seedlings. It is possible that wild sarsparilla is similarly favorable, although it develops later in the season, grows taller and casts denser shade.

Hardwood Brush

The shade cast by hardwood brush is conducive to good germination and early survival of white pine but is far too dense for subsequent development. The influence of removing such overtopping vegetation depends on the seedbed conditions prevailing after removal.

Lichens

Lichens occur mainly on very dry sites in natural openings. According to evidence presented by Romell and Malmström (50), it is possible that such openings may be so fully occupied by the roots of adjacent trees that attempts at establishing regeneration there are futile. As seedbeds, lichens are closely similar to pine litter, being favorable only where they are shaded. On insolated areas, no advantage is gained by removing the lichens to expose mineral soil because of the inherent dryness of the sites. It would be better to shade such areas by scattering slash thinly over them.

SILVICULTURAL APPLICATIONS

Direct Seeding

Artificial regeneration by direct seeding has always intrigued foresters, although it has generally proven unsuccessful because of rodents and unfavorable microclimatic factors. Most of the experiments which have been described involved artificial application of seed, even though every attempt was made to simulate natural processes. The results make it obvious that the environment of the young seedling is determined largely by the seedbed and the amount of direct sunlight reaching it. The nature of the seedbed, on the other hand, bore little relationship to depredations by rodents.

The unscreened seed-spots established in the 1947 experiment provided some indication of the results which might be obtained by direct seeding on a practical basis. The high concentration of seeds, 75 per spot, may have made them unduly attractive to rodents. Comparative second-year survival

TABLE 16. COMPARISON OF SURVIVAL OF SEEDLINGS ON SEED-SPOTS WHICH WERE SCREENED AND UNSCREENED DURING GERMINATION PERIOD[1]

Type of Seedbed and Treatment		Number of Seed-spots[2]	Percentage of Seed-spots Where Surviving Seedlings Numbered:		
			>5	1-5	0
Mineral Soil in	(S)	12	92	8	0
Polytrichum	(U)	6	50	50	0
Polytrichum Moss	(S)	24	88	12	0
	(U)	12	50	8	42
Mineral Soil in	(S)	12	83	17	0
Litter	(U)	6	33	34	33
Hardwood Brush	(S)	24	58	29	13
	(U)	12	8	25	67
Lycopodium	(S)	24	54	29	17
Club-moss	(U)	12	33	25	42
White Pine Litter	(S)	36	36	28	36
	(U)	18	11	6	83
Lichens	(S)	24	29	29	42
	(U)	12	0	17	83
Mineral Soil in	(S)	12	25	50	25
Lichens	(U)	6	0	0	100

[1] Based on inventory made in August 1948 when the seedlings were in the second growing season.

[2] (S) - screened; (U) - unscreened. Data from screened plots invaded by mice are included in this case.

obtained on screened and unscreened seed-spots on the more important types of seedbeds is indicated in Table 16. These results show that the presence of favorable types of seedbeds greatly increases the chance of success. Direct seeding would have been moderately successful in this case, if confined to polytrichum moss and moist mineral soil; similar results have been obtained in the Lake States (60). The stands would have lacked uniform stocking, because the losses to rodents were often concentrated in certain areas.

Direct application of stratified seeds on favorable spots during the germination period would appear to be a technique worthy of further trial. Indiscriminate broadcasting of relatively small amounts of seed is unlikely to prove worthwhile, particularly if the seeds are not stratified.

Natural Regeneration

The intensities of solar radiation required for satisfactory growth of established white pine seedlings are frequently detrimental to adequate germination and early survival. The shelterwood method of regeneration is the only one by which this difficulty can be overcome. Only this method can insure an adequate source of seed and the partial shade necessary for the establishment of regeneration, coupled with provision for eventual exposure of the seedlings to full sunlight. The clear-cutting or seed-tree methods of cutting provide neither the seed nor the protection essential for adequate stocking. The various selection systems of cutting are effective only when sufficiently modified to incorporate principles of shelterwood cutting.

For all practical purposes, natural regeneration of white pine occurs only after occasional good seed years. Therefore, heavy regeneration cuttings should be made only when a good seed crop is in prospect in the stand to be cut. Planning for these cuttings is aided by the fact that the immature cones appear about one year before the seeds are shed. Heavy shelterwood cuttings made too far in advance of the establishment of a good crop of pine seedlings usually give hardwood brush too much of a start over the pine. In no case should the protection and seed source provided by the residual stand be removed until the new crop is firmly established. When no seed crop is in prospect, operations in white pine stands near maturity should be confined to lighter intermediate cuttings for stand improvement or thinning. Recent experience of foresters in the Northeast has demonstrated that such a policy is economically feasible.

The objective in marking for shelterwood cuttings should be to allow a maximum of diffuse radiation and a minimum of direct solar radiation to reach the forest floor. Unfortunately, the mid-day sun over southern New England is approximately 70 degrees above the horizon during the critical period when germination occurs and heat injury is most likely. This elevation is so close to the vertical that the zone of protection provided by the overstory is very narrow. Areas north of the stumps of dominant trees are rarely protected. The sketches in Figure 12 illustrate the manner in which the crown canopy would shade the ground under various conditions. It is virtually impossible to make any kind of harvest cutting without ex-

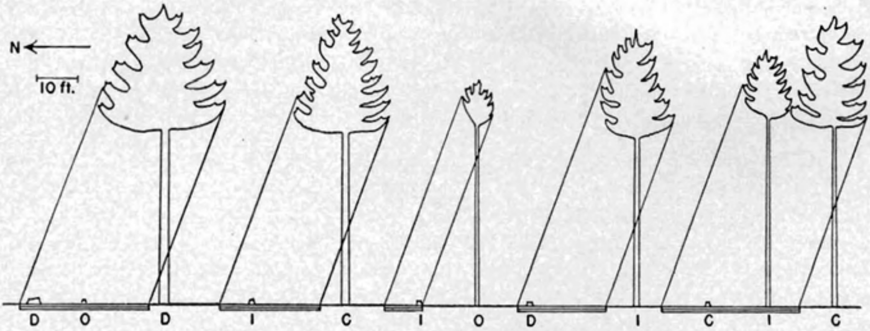

FIGURE 12

Sketch showing the amount of shade cast by isolated trees of various crown classes remaining after a hypothetical cutting in a fully stocked stand. The slanting lines represent the angle of the sun's rays as being 20° from the vertical at mid-day on one of the longest days of the year. D—dominant, C—co-dominant, I—intermediate, and O—overtopped. This sketch is not intended to represent any particular method of cutting, recommended or otherwise.

posing about half of the resulting open area to direct sunlight. It would be ideal if regeneration could have been established in earlier cuttings, but it is almost inevitable that cuttings will result in exposing areas without regeneration to the direct rays of the sun.

It has been shown that seedbed conditions are of practical importance mainly on such insolated areas. Treatments to ameliorate seedbed conditions should be confined to those types known to be unfavorable. Sunlit areas covered with moss or patches of litter protected by a very light covering of slash or low herbaceous growth should become stocked without further treatment. Unprotected expanses of litter should be scarified to expose long strips of mineral soil no more than six inches wide or they should be partially shaded by scattering small amounts of slash. The best type of slash to scatter is that composed of large, dead branches. Treatment with slash is preferable to scarification on very dry sites, particularly those occupied by lichens.

Heavy concentrations of unfavorable vines may be temporarily held in check by scarification. Pre-existing clumps of hardwood brush probably constitute the most difficult areas to regenerate, even though germination and early survival are good beneath them. Where possible, clumps of brush should be broken up during logging operations. Subsequent cleanings will, however, be necessary to release white pine seedlings from this type of competition. The problem of dealing with hardwood brush that comes in simultaneously with white pine regeneration is only slightly less difficult. In this connection it is interesting to note that Li (35) found that seedlings of certain Chinese hardwoods were far more resistant to heat injury than those of Masson's pine. Cline and Lockard (12) and Shirley (51) have observed that white pine seedlings are more nearly capable of competing on equal terms with hardwoods in partial shade than in the open. It appears, therefore, that hardwood competition would be more easily dealt with in partial shade than where drastic openings had been made.

Some scarification and slash distribution may be accomplished deliberately during logging operations. Unavoidably heavy accumulations of slash will cause least economic loss if deposited on unfavorable seedbeds. Slash left beneath the trees of the residual stand may eventually provide favorable dead shade if it becomes well rotted before the areas are exposed.

Shelterwood cuttings frequently can be arranged so as to avoid exposing too much ground to direct sunlight. Schemes of making openings along east-west or northwest-southeast axes would be highly advantageous, while the creation of long openings oriented north and south is very undesirable. Procedures which tend to concentrate cutting in long, narrow strips have several advantages. The trees are easier to fell because there is less risk of lodging them in other trees. The products are closely concentrated so that less ground need be covered in extracting them than if they were evenly distributed throughout the stand. Furthermore, strip cutting offers a solution to the problem of insuring sustained yield from small ownerships. Long openings would allow more air movement than is possible in small openings; the resulting increases in turbulent mixing would reduce surface temperatures.

The logical end-point of this line of reasoning is consideration of the methods of cutting in progressive strips which have been employed to advantage in Europe (65). These methods consist essentially of removing the old stand in narrow, consecutive strips which start at the north and advance to the south. Ordinary seed cuttings may also be carried out in narrow strips just ahead of the final cuttings. Sufficient diffuse light would come in under the northern edges of the canopy to allow the establishment of white pine regeneration. In this way, the problem of obtaining regeneration on insolated areas would rarely occur once the cutting series was in satisfactory operation. Another prospective advantage of this method would be the eventual production of stands streamlined against southerly winds. The writer (53) has shown that the entire portion of southern New England east of the western margin of the Connecticut Valley is seriously endangered by southerly winds in tropical hurricanes like those of 1788, 1815 and 1938. Any method of cutting which might reduce the risk of losses similar to those which occurred in 1938 should be worth considering, regardless of its merits with respect to regeneration.

CONCLUSIONS

1. The variable influence of seedbed conditions on germination and early survival of white pine seedlings is confined almost entirely to areas exposed to direct sunlight. These variations are due chiefly to differences in the efficiency with which seedbed materials dissipate heat received from the sun. Seedbeds which lose heat slowly attain high surface temperatures. Extreme desiccation associated with these temperatures causes significant reductions in germination. Heat injury also kills many seedlings on such seedbeds.

2. Insolated polytrichum moss and moist mineral soil are far less subject to lethal surface temperatures and make better seedbeds than white pine litter, lichen and dry mineral soil.

3. Very heavy shade cast by dense piles of white pine slash is conducive to excellent germination but the seedlings soon die of damping-off. Overhead shade cast by white pine trees, hardwood brush and lycopodium clubmoss favors germination and early survival but is incompatible with proper growth. Forms of partial shade which shield very young seedlings from direct sunlight but do not substantially reduce diffuse radiation offer nearly optimum conditions. This type of protection may be provided by the side-shade of trees, low herbaceous plants or pieces of debris lying to the south of the seedlings. A thin covering of pine slash is favorable only if it bears no needles, because the tops of young seedlings often die from either heat injury or damping-off when in contact with dead needles.

4. Falling seeds penetrate loose materials composed of vertically oriented elements more readily than those of horizontally arranged strands. Seeds readily filter through polytrichum moss but white pine litter is an effective barrier to seed penetration. The wings of white pine seeds are apparently detached chiefly by the battering action of raindrops; therefore, it is likely that the wings hinder seed penetration only temporarily.

5. Young white pine seedlings rarely die from drought even during extended periods when the moisture content of the soil is below the wilting coefficient. The roots of germinating seedlings can penetrate as much as two inches of pine litter within two weeks; consequently, few seedlings die as a result of inability to establish contact with the mineral soil.

6. Risk of stem-girdling from high surface temperature was substantially reduced during late July of the first growing season when the hardening stems of the seedlings became straw-colored rather than red or green. Most of the seedlings which survived the first growing season without damage lived through the second.

7. Limited observations of the activities of rodents showed them to be erratically distributed in a manner unrelated to seedbed conditions. Other losses caused by biotic agencies were of less importance than those due to physical agencies. Damage from damping-off fungi and insect larvae was somewhat more common in shade than in full sunlight. Pine locusts congregated on sunlit portions of the forest floor during the late fall and killed moderate numbers of seedlings growing there. In one instance, pales weevils caused considerable damage to second-year seedlings growing in polytrichum moss.

8. Growth of seedlings in full and partial shade was apparently proportional to light intensity. However, seedlings growing on insolated surfaces of both pine litter and bare mineral soil failed to respond to increases in solar radiation. Seedlings in polytrichum moss grew in direct proportion to light intensity in both sunlight and shade. It is postulated that unfavorable microclimatic conditions hamper the growth of seedlings on insolated litter. Reductions in growth of seedlings on mineral soil may be due to losses of nutrients through removal of litter. This was the only evidence that seedbed conditions were associated with any variations in the relatively stable physical and chemical properties of the soil.

9. White pine regeneration is best obtained by cuttings which allow a minimum of direct sunlight and a maximum of diffuse light to reach the forest floor. Once established, however, the seedlings will grow satisfactorily only if direct sunlight is increased to a maximum. The shelterwood method of cutting, applied on either a uniform or strip-wise basis, is best adapted to supply this sequence of conditions. Even this method of cutting is bound to expose unstocked patches of pine litter or other unfavorable seedbeds to direct sunlight. Conditions on such surfaces may be ameliorated by scarification or the scattering of large, dead branches. Only the latter treatment is satisfactory for abnormally dry sites, where the mineral soil exposed by scarification makes an unfavorable seedbed.

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APPENDIX

Scientific Names of Plants

Common Name	Scientific Name
Aspen, large-toothed	*Populus grandidentata* Michx.
Aspen, quaking	*Populus tremuloides* Michx.
Birch, black	*Betula lenta* L.
Birch, gray	*Betula populifolia* Marsh.
Blueberry, low-bush	*Vaccinium angustifolium* Ait., var. *laevifolium* House
Checkerberry	*Gaultheria procumbens* L.
Cherry, choke	*Prunus virginiana* L.
Cherry, black	*Prunus serotina* Ehrh.
Chestnut, American	*Castanea dentata* (Marsh.) Borkh.
Chokeberry, black	*Pyrus melanocarpa* (Michx.) Willd.
Dewberry	*Rubus hispidus* L.
False lily-of-the-valley	*Maianthemum canadense* Desf.
Fir, balsam	*Abies balsamea* (L.) Mill.
Hemlock, eastern	*Tsuga canadensis* (L.) Carr.
Hypnum moss	*Hypnum schreberi* Willd.
Lichens (in mixture)	*Cladonia rangiferina* (L.) Web. *Cladonia subtenuis* (des Abbayes) Evans *Cladonia uncialis* (L.) Web.
Lycopodium club-moss	*Lycopodium complanatum* L.
Maple, red	*Acer rubrum* L.
Oak, black	*Quercus velutina* Lam.
Oak, red	*Quercus rubra* L.
Oak, scarlet	*Quercus coccinea* Muench.
Oak, white	*Quercus alba* L.
Partridgeberry	*Mitchella repens* L.
Pine, eastern white	*Pinus strobus* L.
Pine, jack	*Pinus banksiana* Lamb.
Pine, longleaf	*Pinus australis* Michx. f.
Pine, Masson's	*Pinus massoniana* Lamb.
Pine, pitch	*Pinus rigida* Mill.
Pine, Scotch	*Pinus sylvestris* L.
Pine, slash	*Pinus caribaea* Morolet
Pine, western white	*Pinus monticola* Dougl.
Polytrichum moss	*Polytrichum commune* Hedw.
Sarsparilla, wild	*Aralia nudicaulis* L.
Sedges	*Carex* spp.
Shadbush	*Amelanchier arborea* (Michx. f.) Fern.
Spruce, red	*Picea rubens* Sarg.
Winterberry, common	*Ilex verticillata* (L.) Gray