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Factors Controlling Initial Establishment of Western White Pine and Associated Species

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YALE UNIVERSITY • SCHOOL OF FORESTRY
BULLETIN NO. 41

FACTORS CONTROLLING INITIAL
ESTABLISHMENT OF WESTERN
WHITE PINE AND ASSOCIATED
SPECIES

BY

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NEW HAVEN

Yale University

1936

A Note to Readers

2012

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FOREWORD

THIS investigation was made possible largely as a result of cooperation between the Yale University School of Forestry and the Northern Rocky Mountain Forest and Range Experiment Station, Forest Service, United States Department of Agriculture. The field studies were made at the Priest River Experimental Forest of the Northern Rocky Mountain Station; additional studies and laboratory work were undertaken at Yale University, where the writer held the Charles Boughton Wood Fellowship during the scholastic year 1932-33.

The original manuscript covering this investigation was submitted as a dissertation in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Yale University.

ACKNOWLEDGMENTS

THE writer wishes to acknowledge with gratitude his numerous obligations to all who have assisted in these studies. He is particularly indebted to Ralph C. Hawley, Morris K. Jesup Professor of Silviculture, Yale University, and to Lyle F. Watts, Director, and R. H. Weidman, Senior Silviculturist, of the Northern Rocky Mountain Forest and Range Experiment Station, for advice and criticism throughout in the arrangement and conduct of the studies and in the preparation of the report. He is also under special obligation to many others, chiefly to M. F. Morgan of the Connecticut Agricultural Experiment Station for suggesting the method and furnishing considerable of the equipment used in the soil nutrition studies, to K. D. Swan of the United States Forest Service for taking numerous photographs at the suggestion of the writer, to C. A. Wellner for comprehensive aid in compilation and analysis, and to Helen R. Haig for valuable assistance in both field and office. The writer would also like to acknowledge his indebtedness to various members of the staff of the Northern Rocky Mountain Experiment Station, especially to G. M. Jemison for aid in the statistical analysis, to John B. Thompson for substantial help in making the original field installations, and to various field assistants who aided him at the Priest River branch, particularly K. P. Davis, Lincoln Ellison, Carl Ostrom, and M. A. Huberman.

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FACTORS CONTROLLING INITIAL ESTABLISHMENT OF WESTERN WHITE PINE AND ASSOCIATED SPECIES

INTRODUCTION

PRACTICAL knowledge of the conditions favoring regeneration is, of course, essential to the practice of silviculture in any given forest type. Much of the information of this sort that exists, even in regions of intensive forestry, is based largely upon observation, or upon trial and error, rather than upon careful analytical studies. Foresters have been keenly aware of the desirability of supplementing such knowledge with quantitative data upon which to judge the relative importance of various site factors and the specific rôle which each factor plays in stand regeneration. It seems obvious that only in this way can silvicultural practices be placed upon a sound scientific basis.

The primary object of this study in the mixed western white pine type was to extend the information gained by previous investigators as to the rôles played in seedling establishment by physical factors of site. In the mixed western white pine type one of the chief silvicultural problems has been to obtain as large a proportion as possible of the more valuable species in the seedling stand. Under such circumstances it is especially important to know the effect of individual site factors and how they may be altered by stand treatment, in order that adequate reproduction of the more desirable species may be encouraged wherever possible by proper cutting practices. Because of the great complexity of any general study of site factors, the present investigation was limited for the most part to a study of initial or first-year survival in one set of general site conditions. As density of the residual stand is usually the most important single factor controlled by the silviculturist during the regeneration period, seedling establishment was studied principally as influenced by that factor.

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FORESTERS, necessarily students of applied ecology, have long been aware of the influence of various biotic and climatic factors upon forest regeneration. Even the ancients possessed considerable silvicultural

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knowledge of this sort, Pliny (89) discussing in some detail the light requirements and tolerance of various trees and shrubs. Though attempts to correlate vegetation and habitat were at first necessarily empirical and speculative, the desirability of placing silviculture upon a sound scientific basis was early appreciated. As a result Du Hamel du Monceau in France and Enderlin and Beckmann in Germany were pointing out by the middle eighteenth century the necessity of lifting silviculture from the realm of empiricism; and gradually, under the leadership of such men as Cotta, Hartig, Hundeshagen, Pfeil, and Carl Heyer, the study of silvics began to break away from its empirical basis and seek a foundation in the underlying sciences (32, 103). However, it was not until 1852 that Gustav Heyer published the first comprehensive study of a site factor, a detailed investigation of light relationships in the forest. During the following decade Mathieu in France and Ebermayer in Germany established the first forest meteorological stations, and this action was followed a few years later by the founding of experiment stations along modern lines (103).

As the point of view toward silvical research gradually changed, the collecting of information by observation, although still extensively and usefully employed, was supplemented by more exact methods. The rise of plant ecology as a distinct branch of botanical science has proved particularly stimulating in this respect. Especially helpful has been the emphasis laid by such men as Clements (25) upon the necessity of organizing ecological research upon a quantitative basis, with the employment of instruments of precision clearly indispensable and a study of habitat factors incomplete without an accompanying investigation of plant response.

Owing to this long-continued interest in site factors and their measurement and effect, the published literature in this field is extremely abundant. The present review will be confined to papers dealing with initial survival or bearing on this subject. Because most of these studies deal largely with individual site factors rather than with the entire environmental complex, most of the investigations will be discussed under the main topic involved.

LIGHT AND SOIL MOISTURE AS FACTORS IN SURVIVAL

The first comprehensive study of light! as a factor in the forest was made by Gustav Heyer (155), who in developing the theory of light and

1. The term "light" is used commonly throughout this dissertation in the sense of total solar radiation.

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shade species laid a foundation for silvicultural practice which remained unchallenged for over half a century. Heyer's work, however, was based wholly on observation, and Theodor Hartig (154) was probably the first to make instrumental measurements of light conditions in the forest. In this task he was followed shortly by Wiesner (186), Cieslar (144), and other investigators scattered throughout central and northern Europe. Most of these early investigators employed some photochemical method of measuring light and were chiefly interested in determining the reduction in light intensity by forest canopies and the effect of such reduction upon forest floor vegetation.

Attempts were made, also, to investigate the effect of light quality. Wiesner (186), for example, using Rhodamin-B paper, studied the composition of light in forest habitats and concluded that the spectral quality of light under crown canopies is practically the same as in the open as long as the light intensity is not less than one-eightieth of full daylight. Zederbaur (187), working with a crude spectroscope, showed some important differences in light composition in the forest and concluded that these are silviculturally important. Knuchel (160), in one of the most comprehensive studies of light quality, found that although the light under hardwood stands differs considerably in composition from full daylight, being particularly rich in yellow and green, the light under coniferous stands is practically the same in composition as the diffuse daylight above the crowns. Shirley (179) points out that these relations do not hold if the light under forest stands is compared with direct sunlight. Klugh (158) found light under forest canopies much richer in blue than direct sunlight. Gast (151) mentions that the percentage penetration of the entire solar spectrum is considerably different from the percentage penetration of the blue-ultraviolet portion. In general, the present consensus seems to be that although light quality does affect growth and development (137, 160, 168, 169, 178) the differences encountered in the forest are too small to be of much practical importance.

Light intensity, therefore, deserves paramount consideration from the standpoint of seedling survival, and in the last twenty-five years a number of excellent papers dealing with this phase have appeared. Many of these studies were directed primarily at measuring the minimum light intensities necessary for seedling survival. Wiesner (186) concluded in his comprehensive studies of light requirements that the minimum intensities for survival varied from about 1 per cent of full sunlight for shade species to 5 per cent for sun species. Shantz (176),

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working with crop plants such as corn, found light intensities of about 6 per cent necessary for survival. Burns (141), growing tree seedlings under artificial light, found a light intensity of about 2 per cent the minimum capable of producing a favorable respiration-photosynthesis ratio in sugar maple, and 17 per cent of full sunlight necessary for ponderosa pine. Coupin (145), testing seedlings of seventeen types of plants in a dark chamber, reported that coniferous seedlings are particularly resistant to lack of light, the hardiest living several times as long as the longest-lived crop plant under similar treatment. Bates and Roeser (135, 136) placed the minimum requirement of coniferous seedlings at 0.6 to 6.3 per cent of full summer daylight. Gia (152) found that at Grafrath fifteen native tree species were able to survive under one-eightieth of full daylight, but for satisfactory regeneration required from one-fourth to one-seventy-second of full daylight, respectively. Grasovsky (153) found 3 per cent of full sunlight sufficient for seedling survival under pine woods at Keene, N. H., several species living over a period of ten months in light never exceeding 300 candle power. Shirley (178), in a well-planned and comprehensive study, concluded that 1 per cent of full sunlight was enough for initial or first-year survival of most species tested, but that ultimate survival of tree seedlings under such low light intensities was extremely dubious. In general, these investigators are in reasonably good agreement that tree seedlings can survive at least a single growing season in very weak light but may finally succumb, directly or indirectly, to the deleterious effects of such a condition. Indeed, though very low light intensities may be adequate for initial survival and even permit survival over considerable periods, it seems evident that the effects of light upon root and top development may be of very great importance in ultimate survival and proper development (5, 103, 138, 172).

Most of these studies necessarily dealt with light as an individual factor entirely separate from the remainder of the environmental complex. In order to segregate light effects in many of the experiments, all other factors were maintained at favorable levels. This fact must be remembered, of course, in any application of the results thus obtained to specific natural habitats; for, as Fricke (149) proved in his frequently cited trenching experiments, it is impossible to ignore the fact that forests cause not only a diminution in light intensity but **also**, through root competition, a material reduction in available soil moisture. Other investigators (134, 147, 165) have called attention to the impossibility

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of ignoring additional climatic factors, particularly temperature. In interpreting light relationships in forest environments.

Although Fricke (149) was the first to emphasize the particular importance of the effect of full crown canopies on soil moisture, foresters had long realized that moisture was an influential and often a decisive element among the factors governing stand regeneration. Soil moisture conditions vary so widely from place to place and season to season that the great majority of studies dealing with this factor do not lend themselves well to generalization or are applicable only to a specific locality or forest type. There are, however, a number of investigations dealing with the peculiarities of soil moisture conditions in the forest and some dealing with the fundamentals of soil moisture availability which are of particular importance when considered in relation to the rôle played by this factor in seedling survival.

One group of these experiments deals primarily with light and moisture relationships, particularly as affected by root competition. These studies were largely the result of Fricke's attack in 1904 upon the then widely accepted theory of light tolerance. In brief, Fricke (149) trenched some seedlings growing under a seventy- to one hundred-year-old white fir stand in such a manner as to cut off all root competition from the overwood trees. The seedlings immediately responded with better needle and height growth, and the trenched area was quickly invaded by species of *Campanula*, *Fragaria*, *Hieracium*, *Rumex*, and *Epilobium* almost entirely absent in the same stand under heavy shade. As soil moisture was found to be materially higher within the trenched area, and as the light conditions were unchanged, Fricke concluded that lack of vegetation or poor development of vegetation under closed forest canopies was due primarily to lack of moisture resulting from root competition rather than to lack of light as was commonly supposed. Fiirst (*I So*) failed to shake Fricke's main contentions, and subsequent investigations, as Tourney (184) pointed out, have on the whole tended to confirm them. Craib (221) and Tourney and Kienholz (18S), for example, obtained results with trenching experiments at Keene fully as striking as those reported by Fricke.

Pearson (166) and Fabricius (148), however, have demonstrated the dangers of overemphasizing the limiting character of soil moisture and have shown the necessity of considering all phases of the environmental complex. Pearson (166) pointed out that air and leaf temperatures have a material effect upon photosynthetic activity and showed that where

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temperature conditions were critical an increase in available soil moisture failed to bring about an increase in growth in seedlings of ponderosa pine. Under such circumstances an increase in light intensity, resulting in higher temperatures, was much more effective. The need of considering the entire environment has been very clearly demonstrated by Fabricius (148) in one of the most comprehensive trenching experiments, using duplicate installations under two very different climatic environments at Schwaback and Grafrath, respectively. Clear-cut, part-cut, and uncut areas were utilized in this study at each location. Using total seedling weight as the best measure of plant response, Fabricius found this item to vary with both light and moisture conditions. Oak at Schwaback, for example, not only did materially better on the trenched quadrats, other factors being equal, but showed an increase in total weight with increase in light intensity. Pine also showed the effects of increased light intensities in tests in which moisture was kept optimum throughout. But the response to given light and moisture conditions varied both with species and with climate. For example, oak made better growth in total weight at Schwaback in full shade and on untrenched quadrats than at Grafrath on the clear-cut area with optimum light and moisture conditions, a phenomenon that could be explained only by the dominant influence of the more generally favorable soil and climatic conditions at Schwaback. Pine failed to respond materially to increased soil moisture in full shade at Grafrath, but its response in the warmer, sunnier climate at Schwaback was very marked. Larch failed to respond to increased light in the warmer climate of Schwaback, if soil moisture was unfavorable, as on the untrenched quadrats, but did make material response under similar conditions at Grafrath.

In addition to the literature cited above, it is highly desirable in connection with a study of seedling survival to review a number of papers dealing with the fundamentals of soil moisture availability. Forest vegetation, of course, obtains the water essential to its existence almost exclusively from the soil. It has been realized since the time of Sachs that not all soil water is available to the plant; Briggs and Shantz (208), in a study of great importance, showed that the proportion available was primarily a function of soil texture. All plants growing in a given soil were found to wilt permanently at about the same soil moisture content, which was called the wilting coefficient. Veihmeyer and Hendrickson's recent work (292) has in general substantiated this conclusion. Early investigators reasoned that when wilting occurred the water-

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absorbing forces of the plant must be evenly balanced by the water-retaining forces of the soil, which are closely associated with soil texture. But this hypothesis did not completely satisfy the facts. For example, it was proved (278) that plants were able to extract water from the soil even after permanent wilting had occurred; and Caldwell (210), in a very careful and exact set of experiments, demonstrated that under certain circumstances permanent wilting was associated with rate of transpiration as well as with soil texture. Blackman (201), in summing up these early studies, stated that although the quantity of moisture left in the soil at the time of wilting-the so-called wilting coefficient-seems related to soil texture, Caldwell's work proved that beyond a certain limit this constant is determined by transpiration rate. Later investigations (236, 244, 245, 279, 291, 292) have shown that water becomes nonavailable at a certain soil moisture content, largely determined by soil texture, not because the plant becomes unable to absorb water against the retentive pull of soil forces (279), but because the capillary forces moving soil moisture to the points of absorption become ineffective; in other words, that permanent wilting results from inability of the soil at low moisture contents to supply water fast enough for plant needs. As the rapidity of movement of soil moisture is closely associated with soil texture, the wilting-coefficient theory is generally applicable, though occurrence of wilting may vary to some extent with environmental conditions. Livingston and co-workers have emphasized the dynamic relationships of soil moisture conditions in a number of important papers (248, 249, 251, 301).

These findings not only tend to clear up discrepancies between the views of earlier workers upon the character and importance of the wilting coefficient (273) but tend to alter the entire **concept** of soil moisture availability (5, 274). This is particularly clear when one takes into consideration the facts recently brought out by Keen (245), Veihmeyer and Hendrickson (236, 291, 292), and other workers on the true **rôle** of capillary flow in the transfer of water in soils. Until recently, for example, it was supposed that if moist and dry layers of soil were in contact, water would gradually be transferred from the one soil to the other until the moisture contents of the two were approximately alike and the water distributed evenly through the entire soil mass. The work cited above shows that except under very special circumstances this even distribution does not result; that the **rôle** of capillary **flow** has been greatly exaggerated. Because of the predominant importance of water supply

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these new conceptions are of very great interest from the standpoint of seedling survival.

As is pointed out by Livingston (248, 249) and by Conrad and Veihe-meyer (216), because roots tend to reduce the soil moisture in their immediate vicinity and because capillary action cannot be depended upon to replace this water with sufficient rapidity under drought conditions, it is essential that root growth continually push new absorbing surface into regions of unexhausted moisture supply. Considerable physiological evidence is available to indicate that close contact between fresh growing tips and moist soil, particularly, is essential. Coupin (218, 219, 220) has shown, for example, by suspending seedlings with only 2 to 3 mm. of the root tips in water, that seedling plants are able to absorb sufficient water and nutrients with this contact alone, and he even goes so far as to state that under normal conditions the seedling plant absorbs most of its water in this way. Though the validity of his findings has been challenged by Priestly and others (267, 228), and it is certainly clear that absorption is not confined to this point (222), there is little reason to doubt that the chief region of absorption is near the growing tip. Accordingly, initial root activity resulting in pushing the growing tips into regions of unexhausted soil moisture must be **considered** essential to survival with many plants in any region or habitat where soil moisture content is critically low at some period during the growing season.

Weaver and Kramer (300), pointing out that the amount of water and nutrients made available to the seedling depends in large measure upon the initial root habit, have asserted that this habit in most cases is not at once modified by external conditions. Tourney (288) also emphasized the inherent nature of root habit. But the work of Cannon (211), Haasis (234), Holch (240), Howell (241), Adams (303), Anderson and Cheyney (195), and others (295, 299) indicates that, while root type is often closely associated with species, the depth of initial penetration is markedly affected by soil texture, nutrients, aeration, temperature, and similar habitat factors. Accordingly, as Tourney and Neethling (333) have stated in discussing soil moisture as a factor in survival, the true rôle of this factor in a given instance can be properly defined only through determination of both depth of root penetration and moisture conditions in the soil layers thus reached.

It is true, of course, that almost all plants and certainly most seedling conifers (265) are capable in certain stages of their development of adapting themselves to drought conditions by automatic reduction of

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their transpiration needs. For example, Pearson (75) found this phenomenon very important in the economy of ponderosa pine in the Southwest. But during certain periods of the year, and particularly during initial establishment, favorable water relations are essential to existence.

TEMPERATURE AS A FACTOR IN SURVIVAL

Temperature of both air and soil has long been acknowledged as an important factor in plant distribution, not only through its general effect upon vegetative hardiness and seeding capacity, but also through its direct effect on initial survival and early development (44, 60, 68, 92, 113, 322, 336). Frost, for example, is a commonly recognized agent affecting forest regeneration, though for various reasons heavy losses from frost are infrequent in many forest habitats (319, 47, 308). High surface soil temperature has recently been identified as a common cause of mortality in seedling stands on regeneration areas. Because of the great importance of high surface soil temperatures in initial survival, the major part of this section is devoted to reviewing literature in this field.

Although Sachs (329) as early as 1864 showed that the green tissue of land plants was severely injured or killed by temperatures of about 122°F. or more, it was not until 1913 that Munch (325) first awakened foresters to the fact that such temperatures were frequently reached in surface soil layers exposed to direct sunlight. It is true, as Von Tubeuf (335) points out, that other investigators had called attention to this girdling injury, Hartig (312) attributing it tentatively to frost, and Von Tubeuf and others (334) to fungous attack. But Munch was the first to present substantial evidence of the important rôle played by this factor.

Since Munch's initial report numerous investigators have emphasized the rôle of insolation as a factor in seedling mortality. Hartley (313,314), in a series of interesting papers, calls attention to heat lesions on young seedling conifers. MacMillan and Byars (324) and other investigators (315) report insolation as a factor with field crops. Tourney and Neethling (333), in one of the most comprehensive field studies of this factor, show its importance upon clear-cut forest areas in New England. Isaac (46), Li (320), Phillips (80, 81, 82, 83, 85, 88), Schuster (330), and others (6, 1a, 11,43,46,54,77,306,318,321,328) report heat girdling as an important cause of mortality in various and diverse forest habitats. Roeser (328) points out that excessive heating of the surface soil, through its effect on tree seedlings, may well be an important factor in

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limiting the natural occurrence of some forest trees. Baldwin (306) reports that border cuttings in northern Europe have as their chief purpose the protection of seedlings from dangerously high temperatures. Although the rôle of surface temperature has been given increasing recognition in recent years, it is highly probable that in the past many seedling deaths due to this cause have been erroneously attributed to drought or to damping-off fungi (5, 321).

Some species are remarkably resistant to high temperatures (II, 75, 82); and, as Shreve and others (331, 11) point out, its importance in natural habitats varies with aspect, shade, and numerous other conditions.

Bates and Roeser (307) and later Baker (305), working under laboratory conditions, have shown that the critical temperature for young conifer seedlings lies at about 120° – 122° F., as reported by Sachs (329) for plants in general, varying somewhat with the seedlings' age and species. Baker, using a laboratory technic that gave particularly exact results, found that damage may result from temperatures of 117° F. and up; that injury becomes common above 130° F.; and that above 150° F. few young seedlings survive. The shading effect of many or large cotyledons and the value of various other seedling characteristics in this connection were studied by Baker in detail and found to influence materially the relative resistance of various tree seedlings.

Although heat-girdling injuries are primarily confined to the initial season, Korstian and Fetherolf (318) and other investigators report losses in older plants.

Temperature also has an important indirect effect on seedling survival through its influence on root activity. Cannon (309) has pointed out that the successful establishment of a species may depend very largely upon its ability to make satisfactory root growth under prevailing soil temperature conditions; and Adams (303), in a very interesting experiment, has demonstrated the important effect of soil temperature on initial root growth and its consequent effect in maintaining contact of the seedling with moist soil. This factor is of great importance in forest habitats where soil temperature is materially affected by the density of the over-wood stand (2, 47, 53, 319, 331).

BIOTIC AGENTS AS A FACTOR IN MORTALITY

Certain diseases, generally grouped under the head of damping-off, are recognized as widespread causes of seedling mortality. Although such

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diseases have been chiefly of concern in nursery practice (118, **121**, **122**, **123**, **127**, **128**, 131, 133), existence of the causal agents in forest habitats is well known (124). Indeed, so many common soil fungi are capable of attacking coniferous stems (**125**) that total absence of such attacks would be rather surprising. It is probable that the losses actually incurred are larger than realized, for Rathbun-Gravatt has shown (**126**) that some fungi can kill the seedling before it appears above ground and others can attack unruptured seed.

Although fungous activities have frequently been studied and described, relatively little published material is available bearing on the rôle played in forest habitats by other important biotic agents such as birds, insects, and rodents. Dearborn (117), Garman (37), Wahlenberg (107), and Ellison (119) have noted the significant part played by one or more of these agents in northwestern forest habitats. Wahlenberg (107) describes extensive seed destruction by the western chipmunk (*Tamias quadriuitatus*) and a similar animal, Say's spermophile (*Spermophilus lateralis*), on burned areas in the northern Rocky Mountain region. Ellison (119) notes seedling injury by the junco (*Junco hyemalis connectens*) on the Priest River Forest in connection with the present study. As both rodents and birds prefer larger seed, and are therefore more destructive to some tree species than to others, their activities affect the composition as well as the density of seedling stands.

MISCELLANEOUS STUDIES

In addition to the investigations previously cited, there are some other papers bearing on initial survival or early seedling development of special interest in connection with the present study. Burns (**21**), for example, has published an instructive paper describing the initial development of white pine (*Pinus strobus*) seedlings in nursery beds in full, half, and no shade. Sturdier plants with greater green and dry weights and markedly better root development were typical on the no-shade area, a phenomenon immediately reflected in much better survival. Moore (70, 71, **262**) investigated some of the factors affecting the regeneration of northeastern conifers and found germination and survival materially affected by surface conditions, duff being a particularly unsatisfactory medium. Gail (36), reporting a study of Douglas fir regeneration on aspect, attributed the first-season mortality under such conditions to a combination of critical soil moisture conditions and high transpiration rates. Boerker (17), studying seedling germination and

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development in three grades of light, found the germination of many Rocky Mountain species as good in shade as in full light, or better. But growth was much superior in full light, and all seedlings in heavy shade showed etiolation. Korstian (52) made a careful and thorough investigation of the factors controlling germination and early survival in oaks, listing deer, rodents, drought, and character of the soil and litter as important factors in the early regeneration period. Barr (198), investigating spruce regeneration in British Columbia, found soil moisture the most important element. A number of instrumental studies by Pearson (74, 77), Bates (10, 12), and Baker and Korstian (6), though devoted particularly to delimiting the ranges of vegetative types, yielded considerable information bearing on early survival and development in natural habitats. Moreover, a number of investigations bearing on the rôle of various habitat factors in relation to seedling reproduction are now under way at forest and range experiment stations of the Forest Service, United States Department of Agriculture. Isaac, who has published some preliminary results from one of these studies (45, 46), emphasized the important part played by high surface soil temperatures in seedling mortality of Douglas fir.²

In addition, there have been a number of investigations in the northern Rocky Mountain region which bear directly upon regeneration problems. One of the most interesting of these from the standpoint of the present paper is an ecological study³ started by D. R. Brewster at the Priest River Experiment Station⁴ in 1913. This study was in many ways the prototype of the one reported upon in this paper. Seedling germination and survival were followed upon a series of quadrats installed at each of three meteorological stations: one located on a northeast aspect typical of the western white pine type, one on a southwest aspect representative of ponderosa pine conditions, and a third on a dry bench characteristic of larch-fir areas. At each station the seed of six species common in the region-western white pine (*Pinus monticola*),"

2. The writer is indebted to Mr. Isaac for access to his working plan for this study prior to the initiation of the study herein described.

3. Brewster, D. R. Factors governing natural reproduction on various sites. Manuscript (Working Plan). 13 p. 1913.

4. Now a branch station of the Northern Rocky Mountain Forest and Range Experiment Station.

5. The tree nomenclature throughout this dissertation follows that of Sudworth, G. B. Check list of the forest trees of the United States, their names and ranges. U. S. Dept. Agr. Misc. Circ. 92. 295 p. 1927.

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ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga taxijolia*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) were sown on paired quadrats with burnt mineral soil and natural duff surfaces in the open and on paired trenched and untrenched quadrats with undisturbed surfaces located in the shade of timber or heavy brush. Lowland white fir (*Abies grandis*) could not be included for lack of seed. Seed was sown heavily enough—at the rate of about 125 seed per square foot—to furnish a stand of seedlings sufficient for observation on survival and to give some idea of the difference in germination between various sites. The trenched quadrats were denuded of all vegetation in order to eliminate root competition and thus permit evaluation of this factor under conditions of relatively heavy shade.

At each station measurements were made of maximum and minimum air temperatures, wind velocity, air humidity, precipitation, and soil temperatures at 12- and 24-inch depths. In addition, maximum and minimum temperatures were taken at the surface on each of the exposed quadrats, the bulbs being buried at about the same depth as the seed. Soil moisture was measured at weekly intervals. Each pair of quadrats was inclosed in a 4- by 12-foot nursery screen with a cover of $\frac{1}{2}$ -inch hardware mesh as a protection against rodents. Cultures were made from dying seedlings to determine whether or not damping-off fungi were present. Seedling counts were made at weekly intervals.

This experiment furnished information upon germination and survival by surface and habitat condition of immediate value in the solution of silvicultural problems. Some interesting data were also obtained upon the activity of various killing agents. Damping-off proved a particularly virulent agent on the moister sites, in shady habitats, and upon natural surfaces. Drought was an active agent on the drier areas. Where soil moisture conditions were critical, it was shown that the competition of subordinate vegetation was an important factor, mortality being much higher on the undisturbed surfaces than on denuded areas. Some seedlings were killed also by cutworms, rodents, and frost. In general, survival was somewhat better on the burnt or denuded mineral surfaces.⁶ All of these facts are in reasonably good agreement with results from the present study. However, the rather small number of seedlings germinating in the 1913 work and the lack of systematic replication of similar

6. Brewster, D. R., and J. A. Larsen. Study of factors affecting natural reproduction. Progress Report. 8 p. 1916.

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quadrats prevented any critical evaluation of comparative losses between various mortality agents, species, and habitats. It also seems probable that losses from insolation, though probably held in check by the protective overhead and side screens and the relatively moist character of the 1913 and succeeding growing seasons, may have occurred on the drier sites and been classified as due to fungi and drought. Indeed, it was not until 1916 that attention was first called to this type of injury in any American journal (313). Larsen (54), summarizing these survival data some years later, presented gross figures by surface, site, and species without reference to comparative losses by cause. Though no experimental data were available showing actual losses due to insolation, Larsen called attention to the dangerous surface temperatures recorded on some habitats and shrewdly surmised that "the extremely high surface soil temperatures which occur on cleared and exposed flats and south slopes are injurious to establishment of seedlings of western white pine, cedar, and hemlock, and this explains the general scarcity of these species on sites exposed to the sun and wind and the difficulty of restocking these after clear-cutting on a large scale."

In this publication (54) Larsen also presented some very interesting data on the effect of soil surface conditions upon germination and initial survival on a clear-cut, exposed flat. Better germination was obtained on bare soil, partly burnt duff and charcoal, and ashes than on unburnt deep duff for western white pine, western larch, and Engelmann spruce alike. Western larch and Engelmann spruce also showed better survival on ashes and bare soil than on duff, but some of the results with western white pine were erratic. Larsen called attention in this publication to the fact that the great fluctuations in moisture content taking place in duff would be a disadvantage to seed germination and that newly germinated seedlings on duff surfaces would often be overtaken by drought before the roots could become properly established in the underlying soil.

A reforestation study by Wahlenberg (107), although not primarily concerned with problems of natural reproduction, also yielded valuable information on the character and importance of various agents affecting initial survival. Wahlenberg was making a study of the possibilities of reforestation by sowing. In prepared seed spots in the northern Rocky Mountain region he followed germination and survival on thirty tests each of three hundred prepared spots during the six-year period 1916-21. Each seed spot was visited at seven- to ten-day intervals during the first two growing seasons, and germination and mortality were recorded by

EXPERIMENTAL CONDITIONS AND PROCEDURE

cause, each seedling being marked with a toothpick at the time of germination in order to insure complete and accurate counts. In general the survival was very poor, the best record being about 20 per cent for Douglas fir, with other species, including western white pine, western yellow pine, Engelmann spruce, western larch, and western red cedar, not above 15 per cent in any case. Because of rodents most of the large seed sown never germinated. Among the seedlings which did start, Wahlenberg records that by far the heaviest losses were caused by drought, with cutworms next in destructiveness. Losses from frost heaving and fungi were also noted. Although Wahlenberg mentions that stones lying on the surface may attain temperatures injurious to growing tissue and possibly cause the death of near-by seedlings, high surface soil temperatures, probably rare in any event upon the steep north and northwest slopes studied, were not listed among the common agents of mortality. However, because of the extensive nature of the tests, no instrumental measurements were made of soil moisture or of surface soil temperatures. In another study Wahlenberg (110) recorded maximum surface soil temperatures up to 145°F. in the open on an east slope. Such temperatures would quickly result in injury and death to succulent young seedlings.

EXPERIMENTAL CONDITIONS AND PROCEDURE

IN THE present investigation the three individual study areas used were located on a large exposed river flat of uniform topography and elevation within the Priest River Experimental Forest, on the Kaniksu National Forest, Idaho. They differed only in character of overhead shade. These stations were within 1,400 feet of one another and were essentially similar as to the texture and chemical composition of the soil and obviously alike as to general environment. Station 1 was entirely devoid of overhead shade, the original stand having been clear-cut; Station 2 had been cut over in a logging operation that removed 77 per cent of the trees more than 9.5 inches in diameter at breast high but left a heavy understory of small hemlock; Station 3 was located in a mature virgin stand of great density. The very different appearance of the areas is clearly illustrated in Plates 2 to 4, inclusive. Larsen (53) and Jemison (47) have both presented ample evidence as to the material habitat differences resulting from this variation in shade.

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INSTRUMENTAL BATTERY

Each station had a fairly complete battery of meteorological instruments: rain gauge, hygrothermograph, maximum and minimum air thermometers, soil thermometers, an air and duff psychrograph, anemometer, and duff hygrometer.⁷ Water content equipment was available (Plate *SA*). In addition, equipment was available for measuring light intensities, including a stop-watch photometer with soliopaper, Shirley thermopile, and Livingston black and white porous atmometer spheres (Plate *SB*). Seedling phytometers, both sealed and free, also were employed. Soil temperatures were taken at the surface and at 1- and 2-foot levels. In all cases surface soil temperatures were taken with mercuric maximum recording thermometers, of which the $\frac{1}{4}$ -inch bulb was half buried in the surface soil and protected from direct insolation by only a very thin layer of the surface medium. Wind velocities were measured at the standard 8-foot level. Soil-moisture determinations were made at weekly to ten-day intervals.

A cooperative Weather Bureau station, located at the Priest River branch headquarters of the Northern Rocky Mountain Forest and Range Experiment Station within one-half mile of the study areas (Plate I), provided a twenty-year record of meteorological conditions with which the records of conditions existing during the period of this study might be compared.⁸ This control station had equipment similar to that listed for each habitat area plus Bates evaporimeters (black-pan type), snow stake, trip-bucket rain gauge, barograph, and mercurial barometer. A special unit comprising anemometer, wind-direction indicator, and sunshine recorder (United States Weather Bureau type) was exposed at a 150-foot level near the cooperative station.

SOIL CONDITIONS

Not only topographic conditions but soil conditions were essentially similar. All three stations were located on the same soil type, Mission silt loam.⁹ This soil, of obscure and probably mixed origin, consists of a

7. Most of this equipment had been installed several years earlier by H. T. Gisborne in a study of the relation of weather and stand conditions to fire danger.

8. Jemison, G. M. Climatological summary of the Priest River Forest Experiment Station, 1912- 1931, inclusive. Mimeographed. 27 p. 1932.

9. Lapham, M. H., and F. O. Youngs. Soil survey of the Priest River Experiment Station. Manuscript. 9 p. 1925. The names used in this report are tentative and used merely to identify temporarily the soil types described.

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layer of friable, light yellow-brown soil¹⁰ 12 to 18 inches deep overlying a compact layer of gray clay. The surface layer was undoubtedly laid by water. It contains a considerable amount of water-worn and heavily weathered rock fragments, usually in the form of fine to medium gravel. It is derived from the schist and quartzite strata overlying the granite core of the surrounding mountains. In common with the majority of the soils of this general locality the surface soil contains a great deal of fine, floury, windborne material probably carried in from the semi-arid regions to the west and southwest. It appears in excellent tilth for all three stations, and the only marked external difference is a more distinct yellow coloration in the soil of the full-shade station, a color difference readily detectable only when the soil is moist. The underlying layer of gray clay is undoubtedly somewhat poorly drained, as shown by ferru-

TABLE I. TEXTURAL COMPOSITION* OF SOIL† (PER CENT) OF RIVER FLAT STATIONS

<i>Station</i>	<i>Fine gravel</i>	<i>Coarse sand</i>	<i>Me- dium sand</i>	<i>Very fine sand</i>	<i>Silt</i>	<i>Clay</i>
1 (full-sun).....	3	4	4	23	53	13
2 (part-shade).....	4	4	3	24	52	13
3 (full-shade).....	1	4	2	25	53	15
Average.....	3	4	3	24	53	13

* As determined by Bouyoucos hydrometer method (203, 204).

† Mission silt loam.

ginous, yellow-brown mottling, but is by no means impermeable, as indicated by the fact that in the spring of 1932, following a winter of extremely heavy snowfall, no standing water could be detected in this layer ten days after the disappearance of the snow cover.

The soil on all three stations is essentially identical in textural qualities (Table 1). It contains over 50 per cent silt (0.005 to 0.05 mm.), some 13 per cent clay (less than 0.005 mm.), and about 34 per cent sand, most of which is in fine and very fine fractions (223). The so-called "total colloidal content" averages 28 per cent (204). The soil is relatively free from coarse material, containing less than 10 per cent gravel and very few stones.

10. The dry soils when matched against standard colors prove to be light brown with a slight yellowish cast.

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The relatively fine texture is reflected, of course, in a high moisture-holding capacity (Table 2). Moisture-holding indices are essentially similar for all three stations. Moisture equivalent, a very useful single measure of the relative water-retaining capacity of the soil (216, 235, 255, 292), has been used in computing the wilting coefficient. The field capacity, computed also from the moisture equivalent, is approximately 70 per cent, a figure checking closely with the moisture content of this soil in the springs of 1932 and 1933 after excess moisture from melting snow had largely drained off. The hygroscopic coefficient was derived directly by oven-drying.

TABLE 2. MOISTURE-HOLDING INDICES OF SOIL* OF RIVER FLAT STATIONS

<i>Station</i>	<i>Moisture factors in terms of oven-dry weight of soil</i>		
	<i>Moisture equivalent, per cent</i>	<i>Hygroscopic coefficient, per cent</i>	<i>Wilting coefficient, per cent</i>
1 (full-sun).....	27.6	5.1	15.0
2 (part-shade).....	31.9	4.5	17.3
3 (full-shade).....	28.5	4.5	15.5
Average.....	29.3	4.7	15.9

* Mission silt loam.

In general, Mission silt loam is considered moderately fertile. Some differences with regard to available soil nutrients were readily detectable between stations. The soil of the area on which the timber was clear-cut and the slash burned broadcast some fourteen years previously was found superior in many respects to soils partially protected during the same period by a residual stand (Tables 3 and 4). As a comparison in general terms was all that the nature of the study required, the chemical composition of the soil (aside from pH and total carbon) was determined through microchemical soil tests devised by M. F. Morgan of the Connecticut Agricultural Experiment Station, New Haven, Conn. (264). Morgan's more accurate revised methods were followed with measured amounts of soil and leaching solution. The soil samples used were composites taken from six to nine points. Each test was repeated at least three times. The results of the tests are given in Tables 3 and 4.

In general, the soil was only mildly acid; according to potentiometer

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measurements using the quinhydrone electrode, the hydrogen-ion concentration of the surface layer ranged from 6.14 on the full-shade area to 6.48 on the full-sun area. Carbon content, determined by loss on ignition, did not vary materially among the study stations. Although a podsol layer was present on the part- and full-shade stations, it rarely ex-

TABLE 3. COMPARATIVE FERTILITY OF SOIL OF RIVER FLAT STATIONS IN DIFFERENT LAYERS
(In terms of mineral nutrients and other important soil characteristics.)

<i>Soil layer</i>	Hydrogen-ion concentration, pH	Total organic carbon, per cent	<i>Parts per million</i>							
			<i>Nitrate nitrogen</i>	<i>Ammonium nitrogen</i>	<i>Available phosphorus</i>	<i>Replaceable potassium</i>	<i>Replaceable calcium</i>	<i>Available magnesium</i>	<i>Active manganese</i>	<i>Active aluminum</i>
Surface layer, 0-9 inches, full-sun station.....	6.48	10.2	5	T*	15	200	600	70	0	1
Surface layer, 0-9 inches, part-shade station.....	6.25	8.6	T	1	15	100	150	30	T	1
Surface layer, 0-9 inches, full-shade station.....	6.14	9.5	0	2	20	100	150	50	1	1
F layer, † part-shade station.....	5.98	..	0	0	10	20	0	5	1	0
F layer, † full-shade station.....	5.98	..	0	0	15	10	0	20	5	0
Podsol layer, part-shade station.....	5.95	..	0	1	15	T	0	0	1	1
Podsol layer, full-shade station.....	5.95	..	0	2	15	10	50	40	5	1

* T = trace.

† Chiefly needle litter.

ceeded one-half inch in thickness, was only mildly acid (pH 5.95), and was relatively high in nutrients. Both replaceable potassium and calcium were materially higher on the full-sun station. The tabular figures indicate that nitrate nitrogen and available magnesium, also, ran somewhat higher on the clear-cut area, though these and the remaining differences derived by microchemical tests are probably within the range of experimental error. The F layer also was mildly acid and relatively high in available nutrients (see Table 3). The small amount of active aluminum is a favorable indication. Though the A layer was rather low according to standards for crop soil, it was probably quite satisfactory for tree growth, particularly as conifers seem relatively unexacting in their soil requirements.

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TABLE 4. COMPARATIVE FERTILITY OF TOPSOIL* OF FULL-SUN AND PART-SHADE STATIONS
(The important mineral nutrients are expressed in parts per million.)

<i>Station</i>	<i>Nitrate nitrogen</i>	<i>Ammonium nitrogen</i>	<i>Available phosphorus</i>	<i>Replaceable potassium</i>	<i>Replaceable calcium</i>	<i>Available magnesium</i>	<i>Active manganese</i>	<i>Active aluminum</i>
Full-sun.....	5	1	30	200	1,500	50	0	1
Part-shade.....	1	1	20	70	350	40	2	1

* The 0- to 3-inch layer.

Such differences as do exist in nutrient content were accentuated in the upper few inches of soil (Table 4). Nitrate nitrogen, available phosphorus and magnesium, and replaceable potassium and calcium all ran somewhat higher in the top 3 inches of soil on the exposed full-sun station than in the same layer under part shade (Table 4). In view of the character of the principal killing agents, it is extremely doubtful that the small differences detected materially influenced the survival figures.

PROCEDURE

On each station quadrats were sown to western white pine and its five principal associates, western larch, Douglas fir, western hemlock, western red cedar, and lowland white fir. Sowings were made in 1932 and again in 1933. Lowland white fir was unavoidably omitted in 1932, owing to the lack of local seed.

Three principal types of surface material were used: duff, mineral soil, and burnt mineral soil. The duff surfaces were all taken from the same spot under an eighty-year-old western white pine stand and installed with a minimum of disturbance. Where burnt mineral soil quadrats were desired, a duff layer was laid in place, covered with twigs and small limb wood, and then burnt off to produce surface conditions comparable to those after slash burning or fire. As this process resulted in a change in hydrogen-ion concentration and in addition of mineral nutrients to the soil, as well as in blackening of the soil surface, it was decided to segregate these items by blackening the surface of some quadrats without subjecting them to a slash fire. Accordingly, in 1932, two mineral soil quadrats on each area were blackened with charcoal. In addition, as an aid in segregating the influence of various killing factors, one quadrat

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was trenched and two were watered on each study area. Soil pans were also employed, as these permitted partial control of soil moisture conditions. Each type of surface material was used on two or more quadrats.

The general quadrat arrangement in 1933 for the clear-cut area, Station 1, is shown roughly to scale in Figure 1. On each of the quadrats, listed in these diagrams by type of surface, plats 16 to 20 inches square were sown with seed of each species sufficient to furnish 200 to 500 seedlings on each plat. (See Plates 6A and 6B.)

Each quadrat was examined at two- to ten-day intervals, depending upon the extent and character of current mortality losses, and every dead and dying seedling was classified as to cause of death after an individual examination. The accuracy of this diagnosis was increased by use of the instrumental setup, which currently furnished an excellent picture of the physical conditions under which death had occurred. In addition, ten seedlings were taken up carefully at weekly to ten-day intervals from special beds for determination of root penetration, the data thus obtained being used in conjunction with soil moisture measurements in deciding upon the current effect of drought. In spite of these precautions some 6.4 per cent of the losses in 1932 and about 2.6 per cent of those in 1933 could not be classified as to cause. For computational purposes these deaths were assumed to have been due to the same causes, in exactly the same ratio, as those actually classified as to cause.

In 1933 most of the special installations were discontinued in order to concentrate on the principal surfaces. The watered quadrats were replaced, however, with screened quadrats on which the surface soil temperature was never allowed to become dangerously high. This proved a much more satisfactory arrangement. Watering, in addition to being laborious, practically eliminated dangerous surface soil temperature as well as drought. Screening, on the contrary, eliminated dangerous soil temperatures but had little effect on critical soil moisture conditions, and hence helped to segregate the action of heat and drought as killing agents.

HABITAT CONDITIONS, 1932

GENERAL CHARACTER OF GROWING SEASON

IN GENERAL the 1932 season, as compared with the average of twenty preceding seasons, was one of slightly higher soil and air temperatures, somewhat lower humidities, and slightly higher wind

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velocities (Table 5). The main departure from average conditions was precipitation, which averaged 19.1 per cent below normal. A more detailed picture of seasonal conditions is shown in Table 6. Although May was wet, precipitation averaging 49.8 per cent above normal, June, July, and August were extremely dry, ranging from 44.2 to 66.1 per cent below normal. Such wide departures of precipitation from normal are not uncommon; in seven years out of the preceding twenty, growing-season precipitation was less than in 1932 (Table 7). In only three years of the preceding twenty, however, was rainfall during the summer

TABLE 5. WEATHER CONDITIONS IN THE 1932 GROWING SEASON (MAY THROUGH AUGUST)
COMPARED WITH 20-YEAR NORMALS*

<i>Weather factor</i>	<i>20-year normal</i>	<i>1932</i>	<i>Departure of 1932 record from normal</i>
Total precipitation, in inches.....	5.86	4.74	-1.12 (-19.1%)
Average relative humidity at 5 P.M., per cent.....	44.6	41.2	-3.4 (-7.6%)
Mean air temperature, degrees Fahrenheit..	58.6	59.2	+0.6 (+1.0%)
Average daily maximum air temperature, degrees Fahrenheit.....	76.4	76.0	-0.4 (-0.5%)
Average daily minimum air temperature, degrees Fahrenheit.....	40.9	42.3	+1.4 (+3.4%)
Average hourly wind velocity at 8-foot level, miles per hour.....	1.96	1.99	+0.03 (+1.5%)
Average soil temperature at 1-foot level, degrees Fahrenheit.....	56.8	57.9	+1.1 (+1.9%)

* Records taken at the coöperative Weather Bureau station at the Priest River Experimental Forest headquarters.

months (June, July, and August) less than in 1932. September, also, was unusually dry in 1932.

The fact that measurable rains occurred less frequently in the growing season of 1932 than in the average growing season was at least partially compensated for by the fact that clear days, also, occurred less frequently (see Table 8).

Temperatures were about normal in May, above average in June and August, and somewhat below average in July. Three killing frosts were recorded in May, and one in early June. Such late frosts are not at all unusual in the Priest River section; the twenty-year normal shows no frost-free month. The frost-free season in 1932 was 88 days, compared with a normal of only 62 days.

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Primarily because of subnormal precipitation but also because of slightly higher temperatures and lower humidities, the 1932 season is regarded as moderately severe to severe with regard to weather conditions affecting initial seedling survival.

LIGHT INTENSITIES

It has been noted (47, 53) that the microclimate varied significantly among the study stations owing to differences in canopy conditions. In

TABLE 6. MONTHLY WEATHER CONDITIONS AT THE PRIEST RIVE

<i>Weather factor</i>	<i>May</i>			<i>June</i>		
	<i>20- year nor- mal</i>	<i>1932</i>	<i>Departure of 1932 record from normal</i>	<i>20- year nor- mal</i>	<i>1932</i>	<i>Departure of record from 1</i>
Total precipitation, in inches.	2.01	3.01	+1.00 (+49.8%)	1.78	0.84	-0.94 (-5)
Average relative humidity at 5 P.M., per cent.	50.6	54.2	+3.6 (+7.1%)	49.0	41.5	-7.5 (-1)
Mean air temperature, degrees Fahrenheit.	50.7	51.1	+0.4 (+0.8%)	57.6	59.3	+1.7 (+)
Average daily maximum air temperature, degrees Fah- renheit.	66.1	65.1	-1.0 (-1.5%)	74.0	75.5	+1.5 (+)
Average daily minimum air temperature, degrees Fah- renheit.	35.3	37.1	+1.8 (+5.1%)	41.3	43.1	+1.8 (+)
Average hourly wind velocity at 8-foot level, miles per hour.	2.12	2.22	+0.10 (+4.7%)	2.07	1.92	-0.15 (-)
Soil temperature at 1-foot level, degrees Fahrenheit.	49.3	50.2	+0.9 (+1.8%)	56.3	57.6	+1.3 (+)

general, removal of part or all of the overwood stand had resulted in higher air and soil temperatures, lower humidities, and greatly increased wind velocities and evaporation rates. These differences, all treated statistically and found significant by Jemison (47), are shown in Table 9. Similar trends were recorded by Larsen in an earlier publication (53).

The most striking difference, however, is found in radiation intensity, which, as shown in Table 10, averaged only 3 to 5 per cent in full shade, and 23 to 26 per cent in part shade, of the intensity recorded in full sun. Records were taken with paired black and white Livingston atmometer

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spheres¹¹ (162, 140) and checked against readings taken with a Shirley nonrecording thermopile (180) and with a Clements stop-watch photometer (25). The atmometer readings are based upon the average values of two pairs of black and white bulbs displayed upon each area during July and August in 1932 and 1933. The instruments were placed so as to display the bulbs about 6 inches above the ground surface, the water reservoirs being encased in wood and sunk below ground. (See Plate 5A.) The values obtained with the Shirley thermopile and with the Clements

ROUGH SEPTEMBER, 1932, COMPARED WITH 20-YEAR NORMALS

<i>July</i>		<i>August</i>				<i>September</i>		
<i>Departure of 1932 record from normal</i>	<i>20- year nor- mal</i>	<i>1932</i>	<i>Departure of 1932 record from normal</i>	<i>20- year nor- mal</i>	<i>1932</i>	<i>Departure of 1932 record from normal</i>		
8 -0.38 (-44.2%)	1.21	0.41	-0.80 (-66.1%)	1.84	0.50	-1.34 (-72.8%)		
-4.1 (-11.1%)	41.9	36.2	-5.7 (-13.6%)	65.9	51.5	-14.4 (-21.9%)		
-1.4 (-2.2%)	62.4	63.8	+1.4 (+2.2%)	53.1	54.4	+1.3 (+2.4%)		
-2.9 (-3.5%)	82.1	83.0	+0.9 (+1.1%)	69.7	74.1	+4.4 (+6.3%)		
0.0 0.0	42.7	44.6	+1.9 (+4.4%)	36.6	34.7	-1.9 (-5.2%)		
0 +0.18 (+9.4%)	1.71	1.72	+0.01 (+0.6%)	1.50	1.34	-0.16 (-10.7%)		
+0.9 (+1.5%)	60.9	62.2	+1.3 (+2.1%)	55.2	56.6	+1.4 (+2.5%)		

photometer are based upon a series of comparative readings taken as rapidly as possible under shade and in the open upon several clear days

11. The sets on the part-shade and full-sun stations were shifted several times a season to equalize the possible effect of position with regard to light or shade "spots." Owing to the fact that the atmometers furnished continuous records based on total radiation over at least a two months' period in two successive years, they are regarded as giving the best measure of radiation conditions. The differences in evaporation losses between the black and white spheres upon the part-shade and full-shade areas, respectively, in per cent of similar differences upon the full-sun station, were used in computing relative light intensities.

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during the growing season of 1932. Some twenty to forty-eight readings with the thermopile were used in each series to assure a good sample. The operator paced back and forth over each area when using the Clements photometer to assure the same end result.

TABLE 7. GROWING-SEASON PRECIPITATION AT THE PRIEST RIVER STATION,
1912 THROUGH 1933

<i>Year</i>	<i>Average precipitation, in inches</i>				
	<i>May</i>	<i>June</i>	<i>July</i>	<i>August</i>	<i>Total</i>
1912	2.68	2.14	2.58	2.68	10.08
1913	2.24	3.31	1.22	0.69	7.46
1914	2.36	2.94	1.83	0.17	7.30
1915	3.69	1.52	3.13	0.33	8.67
1916	2.54	3.16	1.75	1.23	8.68
1917	3.00	1.76	0.04	0.06	4.86
1918	1.24	0.84	0.60	4.22	6.90
1919	2.23	0.20	0.24	1.52	3.99
1920	2.99	2.07	1.07	0.82	6.95
1921	0.91	0.87	0.14	0.48	2.40
1922	1.07	0.14	0.20	0.68	2.09
1923	2.26	2.06	0.68	1.12	6.12
1924	0.82	1.50	0.33	1.41	4.06
1925	2.59	1.22	0.07	0.40	4.28
1926	2.06	0.85	0.16	4.24	7.31
1927	2.71	3.23	0.76	1.52	8.22
1928	0.81	1.79	1.93	0.60	5.13
1929	0.74	2.76	0.03	0.31	3.84
1930	2.18	1.63	0.06	1.78	5.65
1931	1.10	1.55	0.49	T	3.14
1932	3.01	0.84	0.48	0.41	4.74
1933	1.49	1.97	0.08	0.29	3.83
20-year normal*	2.01	1.78	0.86	1.21	5.86

* Based on data for 1912 through 1931.

All three instruments, in good agreement, reveal marked differences between the study habitats with regard to light intensity. Radiation intensities varied materially on the part-shade area, averaging 17 per cent

HABITAT CONDITIONS, 1932

of full sunlight on the sheltered portion and 37 per cent on the exposed portion.

TABLE 8. FREQUENCY OF RAINY DAYS AND OF CLEAR DAYS AT THE PRIEST RIVER STATION, MAY THROUGH AUGUST, 1932, COMPARED WITH 20-YEAR NORMALS

<i>Month</i>	<i>Number of days having 0.01 inch or more rain</i>		<i>Number of clear days</i>	
	<i>20-year normal</i>	<i>1932</i>	<i>20-year normal</i>	<i>1932</i>
May.....	11.2	11	12.0	8
June.....	10.2	6	12.7	12
July.....	5.0	5	20.8	16
August.....	6.3	4	19.4	16
Total.....	32.7	26*	64.9	52†

* Departure from normal, -6.7 days.

† Departure from normal, -12.9 days.

TABLE 9. WEATHER CONDITIONS ON RIVER FLAT STATIONS IN JULY AND AUGUST, 1931 THROUGH 1933*

<i>Weather factor</i>	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>
Maximum air temperature, degrees Fahrenheit.....	84.1	81.7	79.3
Average soil temperature at 1-foot depth, degrees Fahrenheit.....	59.6	53.9	51.4
Relative humidity at 4.30 P.M., per cent.....	27.3	29.0	35.8
Absolute humidity at 4.30 P.M., grams per cubic foot.....	2.82	2.89	3.34
Daily wind movement, miles.....	32.6	18.8	3.8
Evaporation, † grams.....	163.0	77.0	40.0

* Data taken and analyzed by G. M. Jemison.

† Average evaporation by ten-day periods for 1931 and 1932 only, determined by use of Bates "sun" evaporimeter, type 4.

SURFACE SOIL TEMPERATURE

This difference in exposure was reflected directly in two edaphic factors of great consequence in seedling survival, namely, surface soil tem-

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perature and soil moisture. The resulting inequality in surface soil temperatures and the dangerous character of this factor upon the full-sun station are depicted for mineral quadrats in Tables 11 and 12. As is shown in these tables, maximum daily surface temperatures upon mineral soil quadrats reached or exceeded **120°F.** as early as June 27 upon the full-sun station, and remained dangerous upon this area until late September except during rare periods of rain or of cloudy weather. Temperatures of **120°F.** or more occurred on this area on every clear day when surface materials were dry, proving that this clear-cut site in a region characterized by clear, cloudless days and light, infrequent summer rains is very severe.¹² As is shown in Table 12, giving records for the period May 5 through September 19, surface soil temperatures on this area reached or exceeded **120°F.** on 4 days in June, **22** each in July and

TABLE 10. RADIATION INTENSITIES ON RIVER FLAT STATIONS

<i>Instrument used</i>	<i>Light intensity (per cent), in terms of full sunlight</i>		
	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>
Paired black and white atmometer spheres ...	100	26	5
Shirley nonrecording thermopile.	100	23	3
Clements stop-watch photometer.	100	24	4

August, and 10 in September, or a total of 58 days during the 138-day period. Some 16 days in the period produced surface soil temperatures of 135°F. or more, temperatures exceedingly dangerous to seedling existence.

As is shown in Table 11, conditions were markedly different upon the other study areas. No killing temperatures whatever were recorded upon the full-shade station, the maximum temperature there being 89°F., recorded on August 17 and September 10. Days on which maximum temperatures for mineral soil quadrats on the part-shade area averaged **120°F.** or more were relatively few. But as would be expected, the uneven

12. As noted in the literature review, Munch and many later investigators (314, 307, 333, 305) have called attention to heat-girdling deaths in young conifers accompanying surface soil temperatures in excess of 120°F., and Baker (305) has pointed out that temperatures in excess of 135°F. are almost instantly fatal to young green tissues.

TABLE II. AVERAGE DAILY* MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT)
ON MINERAL SOIL QUADRATS IN 1932, BY MONTH

Date of month	May	June	July			August			September		
	Station 1 (full-sun)	Station 1 (full-sun)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)
1	(119)†	125	115	67	99	68	61
2	(120)†	(106)†	..	134	114	74	112	93	63
3	134	127	80	114	95	69
4	137	124	84	122	102	72
5	84	..	110	101	69	138	119	79	131	111	77
6	88	90	120	93	67	137	117	82	131	107	73
7	80	96	129	100	68	136	117	88	124	108	83
8	84	92	122	113	66	133	122	86	124	92	70
9	88	94	126	104	69	120	111	74	120	102	81
10	86	92	112	86	66	108	82	62	124	102	89
11	84	96	114	95	65	105	93	75
12	92	97	126	106	70	102	73	67	115	90	79
13	84	77	124	98	68	113	84	76
14	88	98	114	95	64	130	108	71	120	98	86
15	92	76	132	127	70	144	122	79	120	98	80
16	92	82	138	110	74	142	126	87	120	102	84
17	104	97	114	83	65	140	126	89	100	83	64
18	80	84	127	101	66	127	118	85	92	61	53
19	98	96	124	104	66	129	116	82	54	49	44
20	86	98	131	110	72	128	104	73
21	..	104	136	117	75	130	107	79
22	..	96	144	131	82	98	86	65
23	82	108	136	116	80	118	90	67
24	74	113	136	116	78	136	114	79
25	77	115	129	110	80	132	120	78
26	90	112	140	128	80	134	120	77
27	..	121	140	124	81	136	120	83
28	..	127	133	119	82	118	98	73
29	85	125	130	113	75	101	92	65
30	88	128	124	98	68	83	67	55
31	128	115	68	96	70	57
Average...	87	101	128	108	72	125	107	75	113	91	73

* Data as to temperatures on Stations 2 and 3 are missing for the whole months of May and June. Other days for which no records are given were days of cloudy or rainy weather on which temperatures did not approach dangerous heights.

† Figures in parentheses were not used in calculating monthly averages.

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density of the overwood shade upon this area was reflected in surface soil temperature conditions, the more exposed quadrats being subjected to high temperatures comparable with those recorded upon the clear-cut station (Table 13).

TABLE 12. EFFECT OF OVERHEAD SHADE ON SURFACE SOIL TEMPERATURES ON MINERAL QUADRATS IN 1932

<i>Month</i>	<i>Station</i>	<i>Number of days on which designated temperatures occurred</i>		<i>Daily maximum temperature, degrees Fahrenheit</i>	
		<i>120° F. or more</i>	<i>135° F. or more</i>	<i>Average</i>	<i>Highest</i>
May	{ 1 (full-sun)	0	0	87	104
	{ 2 (part-shade)
	{ 3 (full-shade)
June	{ 1 (full-sun)	4	0	101	128
	{ 2 (part-shade)
	{ 3 (full-shade)
July	{ 1 (full-sun)	22	7	128	144
	{ 2 (part-shade)	4	0	108	131
	{ 3 (full-shade)	0	0	72	82
August	{ 1 (full-sun)	22	9	125	144
	{ 2 (part-shade)	9	0	107	127
	{ 3 (full-shade)	0	0	75	89
September	{ 1 (full-sun)	10	0	113	131
	{ 2 (part-shade)	0	0	91	111
	{ 3 (full-shade)	0	0	73	89
Total or seasonal	{ 1 (full-sun)	58	16	112	144
	{ 2 (part-shade)	13	0	104	131
	{ 3 (full-shade)	0	0	73	89

The surface soil medium greatly influenced surface temperatures under otherwise similar habitat conditions. The great differences explainable in this way are shown in Tables 14 and 15. For example, temperatures of 120°F. or more were reached on duff some six weeks before similar temperatures occurred on mineral and burnt mineral surfaces, primarily

HABITAT CONDITIONS, 1932

TABLE 13. AVERAGE DAILY MAXIMUM SURFACE SOIL TEMPERATURES ON SHADED AND LIGHTLY SHADED MINERAL SOIL QUADRATS OF STATION 2 IN 1932
(Degrees Fahrenheit.)

<i>Date of month</i>	<i>July</i>		<i>August</i>	
	<i>Shaded portion</i>	<i>Sunny portion</i>	<i>Shaded portion</i>	<i>Sunny portion</i>
1	..	124	98	132
2	84	128	96	132
3	114	140
4	114	134
5	106	96	108	130
6	79	107	112	122
7	86	114	106	128
8	103	123	116	128
9	88	119	108	114
10	72	100	82	83
11	74	116
12	77	136	69	77
12	89	106
14	78	112	90	125
15	119	135	109	135
16	85	134	119	133
17	71	95	121	131
18	80	122	131	122
19	77	132	110	123
20	86	134	96	111
21	92	142	101	113
22	104	158	84	87
23	110	122	79	101
24	95	138	107	120
25	95	125	114	125
26	115	140	116	123
27	105	142	119	122
28	102	136	96	100
29	102	124	91	94
30	86	110	65	69
31	104	126	67	74

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TABLE 14. AVERAGE DAILY MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT)
ON FULL-SUN STATION IN 1932, BY SURFACE MATERIAL

<i>Date of month</i>	<i>May</i>			<i>June</i>			<i>July</i>			<i>August</i>			<i>September</i>		
	<i>Duff</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Duff</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Duff</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Duff</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Duff</i>	<i>Mineral</i>	<i>Burnt mineral</i>
1	143	119	118	140	125	138	108	99	107
2	146	120	128	144	134	140	130	112	126
3	145	134	142	126	114	118
4	153	137	147	131	122	127
5	116	84	80	140	110	104	156	138	149	135	131	136
6	126	88	88	126	90	90	150	120	118	155	137	148	129	131	134
7	107	80	80	119	96	94	142	129	127	154	136	147	130	124	126
8	111	84	81	114	92	88	152	122	126	148	133	142	124	124	124
9	118	88	84	107	94	90	160	126	128	126	120	132	123	120	125
10	119	86	80	118	92	88	130	112	114	109	108	109	127	124	126
11	128	84	93	130	96	94	128	114	110	103	105	109
12	134	92	82	142	97	95	142	126	132	113	102	91	123	115	121
13	115	84	78	142	77	94	124	124	126	115	113	115
14	128	88	81	144	98	93	128	114	112	135	130	133	125	120	126
15	131	92	81	98	76	74	136	132	126	151	144	147	124	120	125
16	124	92	82	120	82	82	140	138	132	153	142	151	123	120	125
17	134	104	86	128	97	87	128	114	117	148	140	146	104	100	102
18	88	80	76	116	84	82	148	127	130	145	127	145	96	92	87
19	129	98	91	102	96	84	147	124	128	143	129	136	57	54	53
20	84	86	85	124	98	89	142	131	131	139	128	139
21	123	104	96	151	136	137	143	130	138
22	106	96	92	154	144	141	113	98	107
23	83	82	78	137	108	97	151	136	144	131	118	122
24	77	74	75	146	113	98	150	136	134	152	136	143
25	76	77	74	140	115	100	152	129	139	141	132	140
26	105	90	86	148	112	114	152	140	144	153	134	146
27	154	121	118	160	140	151	149	136	140
28	155	127	120	150	133	138	133	118	123
29	105	85	82	136	125	133	145	130	140	119	101	111
30	102	88	86	140	128	136	142	124	132	99	83	84
31	143	128	139	117	96	97
Average...	111	87	82	129	101	97	145	127	129	138	125	132	118	113	116

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because the light, porous character of duff results in early surface drying and more rapid absorption of heat. Out of the 138-day period, May 5 through September 19, average maximum duff temperatures upon the full-sun station reached or exceeded 120°F. on 90 days as against 58 and 60 days for natural and burnt mineral soil surfaces, respectively. The effect of

TABLE 15. EFFECT OF SURFACE SOIL MATERIAL ON SURFACE SOIL TEMPERATURES ON FULL-SUN STATION IN 1932

<i>Month</i>	<i>Surface soil material</i>	<i>Number of days on which designated temperatures occurred</i>		<i>Daily maximum temperature, degrees Fahrenheit</i>	
		<i>120° F. or more</i>	<i>135° F. or more</i>	<i>Average</i>	<i>Highest</i>
May	{ Duff	8	0	111	134
	{ Mineral	0	0	87	104
	{ Burnt mineral	0	0	82	93
June	{ Duff	17	11	129	155
	{ Mineral	4	0	101	128
	{ Burnt mineral	3	1	97	136
July	{ Duff	28	24	145	160
	{ Mineral	22	7	127	144
	{ Burnt mineral	21	9	129	151
August	{ Duff	24	20	138	156
	{ Mineral	22	9	125	144
	{ Burnt mineral	24	19	132	151
September	{ Duff	13	1	118	135
	{ Mineral	10	0	113	131
	{ Burnt mineral	12	1	116	136
Total or seasonal	{ Duff	90	56	130	160
	{ Mineral	58	16	112	144
	{ Burnt mineral	60	30	113	151

surface material on the incidence of temperatures of 135° or over was even more marked. Between May 5 and September 19, inclusive, on the full-sun station daily maximum temperatures of that range occurred 56 times on duff as compared with 16 times on natural mineral and 30 times on burnt mineral soil. Although the average daily maximum

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temperature on burnt mineral soil was only 1° higher, than on natural mineral, owing apparently to the slower drying of this surface and hence a lag in temperatures in the spring months, the better absorption on the blackened surfaces resulted in higher maximum temperatures once this surface was air-dry. The highest daily maxima recorded during 1932 were 160°F. on duff and 144°F. and 151°F. on mineral and burnt mineral surfaces, respectively. Surface soil materials must be air-dry before their temperatures can become dangerous to green tissue.¹³ In the period covered no temperature approaching 120°F. was recorded in moist duff or moist soil.

Surface temperature influences on seedling mortality obviously depend upon duration as well as magnitude of temperatures. As Jemison has shown (47) in a tabulation reproduced in part as Table 16, high tempera-

TABLE 16. DURATION OF HIGH TEMPERATURES ON DUFF SURFACE ON FULL-SUN STATION.

<i>Temperature</i>	<i>Duration</i>
120°F. or more	4.2 hours
130°F. or more	2.9 hours
140°F. or more	2.0 hours

* Data taken and compiled by G. M. Jemison (47).

tures were of considerable duration on the full-sun station. Although the maximum temperatures reached on the part-shade station are of similar magnitude, their duration was undoubtedly less.

SOIL MOISTURE

The great difference in microclimates characteristic of the three study stations was reflected in an additional important edaphic factor, namely, soil moisture. Owing to the quantity and distribution of the annual precipitation in the Priest River section, 86 per cent coming in the fall, winter, and spring months, a large share of it as snow, the soil is characteristically wet from the surface to considerable depths at the opening of the growing season in late April and early May. The excess ground water quickly drains off, and water losses thereafter are primarily due to surface evaporation and to vegetation needs. As the moisture thus lost

13. Wood, O. M. Litter cover and soil surface temperatures, oak-pine type. Allegheny Forest Experiment Station, Tech. Note NO.3.

HABITAT CONDITIONS, 1932

TABLE 17. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1932

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight				Remarks
		Station 1 (full-sun)	Station 2 (part-shade)		Station 3 (full-shade)	
			Sunny portion	Shady portion		
May 9	0-2	66	74	77	82	
18	0- $\frac{1}{2}$	<u>10*</u>	Before rain.
	0-3	45	49	..	64	
	3-6	50	63	
20	0- $\frac{1}{2}$	55	
	0-3	48	
	3-6	55	
30	0-3	65	80	
June 10	0-3	63	74	77	75	
	3-6	64	
20	0-3	46	..	70	..	
	3-6	45	..	58	..	
	6-9	60	..	53	..	
July 1	0- $\frac{1}{2}$		<u>15</u>			
	0-1 $\frac{1}{2}$	<u>8</u>	..			
	0-3	29	44	59	50	
	3-6	35	64	55	49	
	6-9	40	50	53	29	
2	0-1	40	67	After rain of 0.21 inch.
11	0-1	<u>16</u>	<u>12</u>	71	..	
	0-3	20	36	68	47	
	3-6	34	50	44	44	
	6-9	40	52	53	35	
21	0-1	<u>5</u>	<u>5</u>	..†	..	
	0-3	<u>16</u>	22	55	36	
	3-6	26	44	46	38	
	6-9	33	38	45	32	

* Underscored values at or less than average wilting coefficient.

† Only the extreme surface layer was air-dry.

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TABLE 17. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1932 (continued)

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight				Remarks
		Station 1 (full-sun)	Station 2 (part-shade)		Station 3 (full-shade)	
			Sunny portion	Shady portion		
July 31	0-1 ‡	..	<u>16</u>	Rain of 0.19 inch on Aug. 11.
	0-3	<u>13</u>	28	53	31	
	3-6	26	27	45	35	
	6-9	28	39	47	..	
Aug. 11	0-1	28	..	64	41	
	2-3	<u>7</u>	<u>14</u>	
	0-3	<u>16</u>	42	58	26	
	3-6	20	48	43	28	
	6-9	23	37	42	..	
21	0-1½	<u>14</u>	
	0-3	<u>5</u>	17	46	20	
	3-6	18	27	44	28	
	6-9	17	28	44	..	
31	0-3	<u>13</u>	24	45	28	
	3-6	<u>16</u>	31	42	27	
	6-9	19	30	38	..	
Sept. 11	0-1½	<u>13</u>	
	0-3	<u>4</u>	<u>14</u>	32	20	
	3-6	<u>13</u>	29	42	25	
	6-9	20	26	36	..	
21	0-3	24	46	50	44	
	3-6	<u>16</u>	32	41	26	
	6-9	19	26	41	21	

‡ Top 2 inches were air-dry.

will not readily be restored by capillary forces (291, 236), unless it is replaced by precipitation, a deficit develops. Data on moisture content in the upper 9 inches of soil at intervals during the 1932 season are given in detail in Table 17.

HABITAT CONDITIONS, 1933

As is shown in this table, the upper 2 inches of soil contained 66 to 82 per cent of moisture on May 9, 1932, when the first samples were taken. A casual examination at that time indicated that the soil was wet to at least a 36-inch depth. Rapid surface drying during the next ten days reduced the soil moisture content in the top $\frac{1}{2}$ -inch layer on the clear-cut area to 10 per cent, a ratio precarious for survival of newly germinated and short-rooted seedlings. Though this situation was relieved by rain in late May and soil moisture conditions remained favorable throughout most of June, surface drying during early July again made drought a possible mortality agent. By July 11 the top inch contained only 12 to 16 per cent of moisture in the more exposed situations. Drought conditions became steadily more serious, and in early August the moisture content had been reduced on the full-sun station to or below the wilting coefficient in the upper 6 inches of soil and to a dangerously low level in the 6- to 9-inch layer. By this time the top 3 inches of the exposed portion of the part-shade area and the uppermost layers on the more sheltered portion, also, were dangerously dry. Drought conditions remained unrelieved until rains in late September or early October removed all further danger from this factor.

Upon the habitats studied evaporation played a very important part in reducing soil moisture content, drying progressing visibly from the surface downward. The effect of vegetational use is apparent, however, in the lower water content under full shade as compared with part shade and in the frequently lower content at the 6- to 9-inch depth where root competition is probably more of a factor.

HABITAT CONDITIONS, 1933

GENERAL CHARACTER OF GROWING SEASON

IN GENERAL, the growing season of 1933 was similar in character to that of 1932, being considerably drier than average, with somewhat lower humidities and slightly higher soil and air temperatures (Table 18). As in 1932, the main departure from normal was in growing-season precipitation, which averaged 34.6 per cent below normal. Only three years in the preceding twenty-one on record, 1912-32, show growing-season precipitation totals lower than that of 1933. July and August were especially dry (Table 19), the combined precipitation for these months being less than in any other years on record except 1917 and

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1929 (Table 7). As shown in the monthly summaries, June was the only growing-season month of better than normal precipitation, May, July, and August averaging 25.9, 90.7, and 76.0 per cent, respectively, under normal. But September was moist; relieving rains occurred during the first week, with particularly heavy rains upon the fourteenth and twenty-fourth. Although measurable rains came less frequently than in the average year, as shown in Table 20, the number of clear days (conducive to killing surface soil temperatures) also was somewhat smaller. Only six more clear days occurred during the growing season of 1933 than in that of the preceding year. During 1933 frosts were recorded in

TABLE 18. WEATHER CONDITIONS IN THE 1933 GROWING SEASON (MAY THROUGH AUGUST)
COMPARED WITH 20-YEAR NORMALS*

<i>Weather factor</i>	<i>20-year normal</i>	<i>1933</i>	<i>Departure of 1933 record from normal</i>
Total precipitation, in inches.	5.86	3.83	-2.03 (-34.6%)
Average relative humidity at 5 P.M., per cent.	44.6	37.7	-6.9 (-15.5%)
Mean air temperature, degrees Fahrenheit.	58.6	59.1	+0.5 (+0.9%)
Average daily maximum air temperature, degrees Fahrenheit.	76.4	76.8	+0.4 (+0.5%)
Average daily minimum air temperature, degrees Fahrenheit.	40.9	41.5	+0.6 (+1.5%)
Average hourly wind velocity at 8-foot level, miles per hour.	1.96	1.96	0 0
Soil temperature at 1-foot level, degrees Fahrenheit.	56.8	58.0	+1.2 (+2.1%)

* Records taken at the cooperative Weather Bureau station at the Priest River Experimental Forest headquarters.

all the growing-season months, the longest frost-free period being June 11 through July 29, a period of only forty-nine days. In general, primarily upon the basis of subnormal precipitation but also because of higher temperatures and lower humidities, the 1933 season is regarded as severe to very severe from the standpoint of initial seedling survival.

SURFACE SOIL TEMPERATURE

As in 1932, conditions varied significantly among the study stations. On mineral quadrats surface temperatures on the full-sun station reached dangerous maxima in the latter part of June, and such temperatures

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continued to occur throughout July and August except for short periods of rainy or cloudy weather (Table 21). Dangerous temperatures on similar surfaces on the part-shade area were not reached until mid-July and continued only intermittently until mid-August. The figures tabulated on the part-shade area are somewhat deceptive; the highest daily maxima reached on sunny portions were comparable in magnitude with those reached on similar surfaces under full sun, though they were probably of shorter duration. As during 1932, injurious temperatures were never reached on any quadrats on the full-shade station.

Maximum values again varied markedly with surface (Table 22). Duff temperatures ran particularly high during the very dry, hot 1933 growing season, reaching injurious levels as early as May 11 on the full-sun station with over 64 daily maximum temperatures in excess of 13SoF. during June, July, and August. A number of maxima exceeded 150°F. and a seasonal maximum of 161°F. was reached in surface duff upon August 14. As during the 1932 season, the burnt mineral surfaces dried somewhat more slowly and tended to remain cooler during May and June than corresponding mineral surfaces but averaged 4° to 6°F. higher during the remaining summer months.

Owing to lessened precipitation, lower humidities, and a larger number of clear, cloudless days, surface temperatures during 1933, summarized in Table 23, were much more severe than in the preceding summer. The number of days with maximum temperatures of 13SoF. or more was greater by 12 for duff and by 4 to 8 for mineral soil surfaces than during the 1932 season.

SOIL MOISTURE

Soil moisture contents were less during the 1933 season, as was to be expected in view of the lower precipitation and humidities and higher temperatures. Moisture conditions first became dangerous about June 25, when surface drying reduced moisture content in the upper inch of soil to 11 per cent, or well below the wilting coefficient (Table 24). A light rain on June 28 temporarily restored satisfactory moisture conditions, but measurements taken on July 11 and July 14 indicated a critical situation in the top 3 inches of soil on the full-sun area and in the top inch of soil on unshaded portions of the part-shade station. By the end of July the surface layers were dangerously dry on all the habitat stations, and a serious drought condition prevailed from this time until the fall rains in mid-September.

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TABLE 19. MONTHLY WEATHER CONDITIONS AT THE PRIEST RIVER

<i>Weather factor</i>	<i>May</i>			<i>June</i>		
	<i>20-year normal</i>	<i>1933</i>	<i>Departure of 1933 record from normal</i>	<i>20-year normal</i>	<i>1933</i>	<i>Departure record from normal</i>
Total precipitation, in inches...	2.01	1.49	-0.52 (-25.9%)	1.78	1.97	+0.19 (-)
Average relative humidity at 5 P.M., per cent.....	50.6	46.3	-4.3 (-8.5%)	49.0	40.1	-8.9 (-)
Mean air temperature, degrees Fahrenheit.....	50.7	48.5	-2.2 (-4.3%)	57.6	58.8	+1.2 (+)
Average daily maximum air temperature, degrees Fahrenheit.....	66.1	61.7	-4.4 (-6.7%)	74.0	75.8	+1.8 (+)
Average daily minimum air temperature, degrees Fahrenheit.	35.3	35.3	0.0 (0.0%)	41.3	41.8	+0.5 (+)
Average hourly wind velocity at 8-foot level, miles per hour.	2.12	2.42	+0.30 (+14.2%)	2.07	1.90	-0.17 (-)
Soil temperature at 1-foot level, degrees Fahrenheit.....	49.3	48.6	-0.7 (-1.4%)	56.3	57.4	+1.1 (+)

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THROUGH SEPTEMBER, 1933, COMPARED WITH 20-YEAR NORMALS

<i>July</i>		<i>August</i>				<i>September</i>		
<i>1933</i>	<i>Departure of 1933 record from normal</i>	<i>20- year nor- mal</i>	<i>1933</i>	<i>Departure of 1933 record from normal</i>	<i>20- year nor- mal</i>	<i>1933</i>	<i>Departure of 1933 record from normal</i>	
.08	-0.78 (-90.7%)	1.21	0.29	-0.92 (-76.0%)	1.84	2.28	+0.44 (+23.9%)	
.1	-7.0 (-18.9%)	41.9	34.4	-7.5 (-17.9%)	65.9	63.1	-2.8 (-4.2%)	
.4	+0.6 (+0.9%)	62.4	64.8	+2.4 (+3.8%)	53.1	51.5	-1.6 (-3.0%)	
.3	+0.9 (+1.1%)	82.1	85.2	+3.1 (+3.8%)	69.7	65.5	-4.2 (-6.0%)	
.5	+0.2 (+0.5%)	42.7	44.5	+1.8 (+4.2%)	36.6	37.5	+0.9 (+2.5%)	
.91	-0.01 (-0.5%)	1.71	1.59	-0.12 (-7.0%)	1.50	1.51	+0.01 (+0.7%)	
.0	+2.2 (+3.6%)	60.9	62.9	+2.0 (+3.3%)	55.2	55.2	0.00 0.0	

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TABLE 20. FREQUENCY OF RAINY DAYS AND OF CLEAR DAYS, MAY THROUGH AUGUST, 1933,
COMPARED WITH 20-YEAR NORMALS

<i>Month</i>	<i>Number of days having 0.01 inch or more rain</i>		<i>Number of clear days</i>	
	<i>20-year normal</i>	<i>1933</i>	<i>20-year normal</i>	<i>1933</i>
May.....	11.2	13	12.0	6
June.....	10.2	8	12.7	13
July.....	5.0	2	20.8	21
August.....	6.3	3	19.4	18
Total.....	32.7	26*	64.9	58†

* Departure from normal, -6.7 days.

† Departure from normal, -6.9 days.

TABLE 21. AVERAGE DAILY* MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT) ON MINERAL SOIL QUADRATS IN 1933, BY MONTH

Date of month	May		June			July			August		
	Station 1 (full-sun)	Station 2 (part-shade)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)	Station 1 (full-sun)	Station 2 (part-shade)	Station 3 (full-shade)
1	(98)†	(88)†	..	102	82	60	140	121	78
2	(105)	(92)	..	110	86	64	150	125	80
3	(65)†	..	(110)	(94)	..	122	99	70	118	90	66
4	(75)	..	(100)	(79)	..	122	110	69	124	100	72
5	(65)	..	106	84	63	128	114	70	102	78	56
6	(79)	..	70	58	50	130	116	72	128	105	68
7	(77)	..	85	70	54	121	112	72	134	113	72
8	(59)	..	60	59	52	112	90	66	139	114	80
9	(71)	..	94	76	56	130	115	71	138	120	85
10	(75)	..	88	87	60	104	84	60	136	118	82
11	(83)	..	94	90	64	132	110	69	140	119	85
12	(87)	..	100	96	71	132	116	72	140	121	86
13	78	73	98	87	68	134	122	74	142	121	88
14	83	78	108	99	76	144	125	76	142	115	86
15	69	56	106	96	76	144	124	76	142	117	79
16	76	58	106	92	70	137	118	73	140	119	82
17	76	59	100	90	64	132	115	71	140	119	87
18	62	44	105	84	60	133	120	72	128	105	78
19	88	82	113	92	66	130	110	70	118	92	70
20	90	83	112	97	68	130	118	73	92	78	58
21	80	69	121	101	70	134	123	71	128	101	72
22	78	70	114	96	65	135	119	79	132	110	79
23	82	75	106	85	62	142	124	81	131	110	82
24	82	63	113	89	65	146	130	87	124	90	64
25	90	89	94	77	68	142	128	86	124	101	78
26	82	68	112	90	65	141	130	88	128	107	76
27	78	66	126	106	70	128	120	79	132	114	78
28	94	86	72	62	56	130	119	76	124	110	79
29	89	82	104	87	65	117	96	66	109	90	69
30	84	74	97	72	60	132	116	74	75	64	57
31	91	87	134	121	71	72	62	55
Average...	82	72	100	85	64	129	113	73	126	105	75

* Figures in parentheses were not used in calculating monthly averages.

† Data for May 1-12 are lacking for Station 2, and data for the whole of May are lacking for Station 3. Other days for which no records are given were days of cloudy or rainy weather on which temperatures did not approach dangerous heights.

TABLE 22. AVERAGE DAILY MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT)
ON FULL-SUN STATION IN 1933, BY SURFACE MATERIAL

Date of month	May			June			July			August		
	Duff	Mineral	Burnt mineral	Duff	Mineral	Burnt mineral	Duff	Mineral	Burnt mineral	Duff	Mineral	Burnt mineral
1	134	98	90	130	102	105	158	140	145
2	141	105	96	126	110	106	148	150	152
3	96	65	76	151	110	104	146	122	124	110	118	118
4	85	75	74	130	100	92	150	122	130	122	124	130
5	75	65	66	142	106	103	154	128	134	117	102	105
6	108	79	78	78	70	70	152	130	136	155	128	136
7	114	77	78	100	85	84	140	121	134	154	134	139
8	65	59	59	63	60	57	121	112	116	151	139	139
9	76	71	72	90	94	84	146	130	138	153	138	141
10	99	75	78	134	88	89	112	104	108	152	136	144
11	121	83	85	142	94	93	147	132	145	152	140	144
12	132	87	90	151	100	98	142	132	135	154	140	144
13	106	78	80	146	98	94	148	134	142	154	142	146
14	129	83	85	146	108	102	152	144	146	161	142	142
15	78	69	71	146	106	101	156	144	147	142	142	144
16	96	76	76	138	106	95	149	137	140	146	140	144
17	102	76	75	137	100	97	151	132	136	148	140	145
18	67	62	60	148	105	98	151	133	136	131	128	128
19	113	88	88	132	113	101	134	130	136	124	118	123
20	128	90	90	144	112	108	141	130	139	97	92	98
21	112	80	81	150	121	116	145	134	141	140	128	132
22	112	78	80	138	114	112	154	135	138	145	132	136
23	122	82	81	133	106	108	146	142	142	147	131	137
24	118	82	85	138	113	116	154	146	148	136	124	120
25	144	90	91	116	94	98	154	142	148	140	124	127
26	102	82	81	142	112	118	156	141	146	144	128	131
27	118	78	79	152	126	124	144	128	137	146	132	135
28	136	94	90	76	72	72	142	130	134	138	124	130
29	141	89	90	118	104	104	126	117	124	117	109	114
30	114	84	83	120	97	100	148	132	140	80	75	78
31	138	91	91	158	134	141	72	72	73
Average...	109	79	80	129	101	97	144	129	135	137	126	130

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TABLE 23. EFFECT OF SURFACE SOIL MATERIAL ON SURFACE SOIL TEMPERATURES ON THE FULL-SUN STATION IN 1933

Month	Surface soil material	Number of days on which designated temperatures occurred		Daily maximum temperature, degrees Fahrenheit	
		120° F. or more	135° F. or more	Average	Highest
May	{ Duff	9	4	109	144
	{ Mineral	0	0	79	94
	{ Burnt mineral	0	0	80	91
June	{ Duff	23	17	129	152
	{ Mineral	2	0	101	126
	{ Burnt mineral	1	0	97	124
July	{ Duff	30	25	144	158
	{ Mineral	26	8	129	146
	{ Burnt mineral	27	21	135	148
August	{ Duff	25	22	137	161
	{ Mineral	24	12	126	150
	{ Burnt mineral	25	17	130	152
Total	{ Duff	87	68	130	161
	{ Mineral	52	20	109	150
	{ Burnt mineral	53	38	110	152

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TABLE 24. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1933

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight				Remarks
		Station 1 (full-sun)	Station 2 (part-shade)		Station 3 (full-shade)	
			Sunny portion	Shady portion		
May 13	0-0.5	51	..	76	..	
	0.5-3	54	..	73	..	
24	0-0.5	59	..	75	..	Trace of rain.
June 4	0-3	36	57	64	70	Rain of .02 inch.
	3-6	37	59	65	64	
13	0-3	44	65	78	72	
	3-6	46	78	70	70	
	6-9	45	63	61	57	
25	0-1	<u>11</u> *	
	0-2	23	
30	0-3	32	52	..	61	Rain of .02 inch on June 28.
	3-6	35	63	57	57	
	6-9	38	48	53	57	
July 11	0-1	<u>12</u>	28	Rain of .04 inch on July 10.
	0-2	<u>16</u>	29	
	0-3	20	37	
14	0-1	..	<u>14</u>	
	0-3	<u>13</u>	25	45	51	
	3-6	27	49	45	42	
	6-9	32	41	48	44	
29	0-1	<u>14</u>	Trace of rain.
	0-3	<u>13</u>	<u>14</u>	40	25	
	3-6	19	36	36	36	
	6-9	26	34	42	38	
Aug. 5	0-1	<u>15</u>	Rain of .02 inch.
	0-3	<u>8</u>	<u>12</u>	..	17	

* Underscored values at or less than average wilting coefficient.

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TABLE 24. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1933 (continued)

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight				Remarks	
		Station 1 (full-sun)	Station 2 (part-shade)		Station 3 (full-shade)		
			Sunny portion	Shady portion			
Aug. 11	0-1	<u>10</u>		
	0-3	<u>7</u>	<u>9</u>	29	19		
	3-6	20	24	44	33		
	6-9	22	24	43	28		
18	0-2	12		
	0-3	..	<u>5</u>	20	17		
	3-6	18	23	30	..		
	6-9	23		
30	0-3	<u>5</u>	<u>8</u>	24	<u>14</u>		Trace of rain.
	3-6	<u>15</u>	17	38	26		
	6-9	19	25	43	29		
Sept. 18	0-3	25	41	55	42		Rain of 0.17 inch.
	3-6	24	33	45	42		
	6-9	23	30	48	..		

SEEDLING MORTALITY RECORDS, 1932

THE very great inequalities among the microclimates of the study habitats were reflected in material differences in seedling mortality. This situation is briefly summarized for the 1932 season in Table 25. Part-shade conditions proved much more favorable to initial survival than either full-sun or full-shade conditions; only 45 per cent of the seedlings died on the part-shade habitat during the first growing season, in contrast with 87 and 63 per cent, respectively, on the full-sun and full-shade areas. Although activity of biotic agents was disproportionately great on the full-sun area, these differences were due primarily to the varying action of two physical factors, insolation and drought. Insolation resulting in high surface temperatures was by far the most active agent of mortality on the full-sun station, killing some 40 per cent of total germination on the so-called mineral surfaces, namely, natural mineral,

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burnt mineral, and charcoal. Drought, though it accounted for only 12 per cent mortality on the full-sun station, proved to be the most important killing agent in full shade. Insolation was the most active single agent in part shade, killing 26 per cent of total germination on this habitat. Most of these deaths were directly attributable to heat girdling caused at the ground line by high surface soil temperatures. On the part-shade station, of course, such losses were lower than on the full-sun station, as the residual overwood lessened the occurrence and duration of dangerous surface temperatures and surface drying was counterbalanced by moderately deep root penetration.

TABLE 25. SEEDLING MORTALITY OF ALL SPECIES IN 1932, BY STATION AND CAUSE

<i>Cause</i>	<i>Mortality percentage, by station, in terms of total germination</i>			<i>Average</i>
	<i>Station 1 (full-sun)</i>	<i>Station 2 (part- shade)</i>	<i>Station 3 (full- shade)</i>	
Fungi.....	29	11	15	18
Insects and birds.....	6	4	3	4
Insolation.....	40	26	0	22
Drought.....	12	4	45	21
Total.....	87	45	63	65

SEASONAL COURSE OF MORTALITY

The chronology of seedling germination and mortality in 1932 is summarized in Table 26. Germination began shortly after the disappearance of the snow cover, in ground thoroughly soaked to considerable depths by melting snow. On the full-shade habitat the beginning of germination was somewhat delayed by the presence of snow, but the course of seedling mortality was not abnormally prolonged by this circumstance. Mortality began with the appearance of the first seedlings and was closely linked with edaphic conditions. Early losses, with few exceptions, were caused by biotic agents, namely, insects, birds, rodents, and fungi. Losses caused by these agents occurred almost exclusively during the period when the seedlings were succulent and tender, and ceased with complete drying out of the surface soil, which began about July 5 on the full-sun station and some three weeks to a month later in

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full shade. Insolation and drought injuries, on the contrary, never occurred until the surface soil began to dry.

A few deaths from causes other than biotic occurred during May on the duff surfaces of the full-sun area. Some of these losses were caused by heat girdling, dangerous temperatures having followed the drying out of the surface duff on May 6. After some fourteen seedlings in all had

TABLE 26. CHRONOLOGY OF CERTAIN WEATHER AND EDAPHIC CONDITIONS AND OF SEEDLING GERMINATION AND MORTALITY IN 1932

<i>Item</i>	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>
Snow disappears; ground practically bare.....	April 10	April 15	May 5
Germination of fall-sown species begins.....	April 28	May 1	May 20
Germination of fall-sown species completed.....	May 15	June 1	July 1
Germination of spring-sown species begins.....	May 11	May 19	June 10
Germination of spring-sown species completed.....	June 5	June 30	July 15
Last stragglers appear.....	July 5	July 27	July 28
First deaths from fungi occur.....	May 4	May 7	May 27
Deaths from fungi become rare.....	July 5	July 27	Aug. 3
First drying of surface soil	Duff.....	Date unknown	Date unknown
	Mineral....	May 11	May 19
First surface temperature of 120°F. or more	Duff.....	May 6	May 12
	Mineral....	June 25	June 27
First deaths from insolation occur.....	Duff.....	May 13	May 13
	Mineral....	June 25	June 28
First deaths from drought occur	Duff.....	None	June 28
	Mineral....	June 24	June 30

been killed in this manner the small number remaining on duff, seventy-three western white pines and one cedar, were killed by frost on the night of May 14. These individuals collapsed overnight, without noticeable constriction or discoloration of their stems. All pine and cedar seedlings on near-by mineral plots escaped frost injury. Subsequent measurements showed that the minimum temperatures reached in duff surfaces ran 6° to 8°F. lower than air temperatures recorded in the near-by

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standard weather shelter and several degrees lower than the minima in near-by surface soil. Isaac¹⁴ has previously recorded this phenomenon. Temperatures high enough to kill seedlings were recorded on duff on four of the remaining days of May. On mineral surfaces, although drying in isolated patches was observed as early as May 11, the cool, moist weather which followed quickly eliminated any chance of dangerous soil temperatures.

By late June material drying of topsoil was followed by high surface temperatures, and insolation became the most active agent of mortality on cutover areas. The clear cloudless weather typical of summer in this region now resulted day after day in extremely high surface soil temperatures readily capable of destructive injury to unprotected plant tissue. These temperatures are summarized in Tables 14 and 15. July records show some 22 days with maximum surface temperatures on mineral quadrats in excess of 120°F. and over 7 days with maximum surface temperatures of 135°F. or up. August was even more severe. (Peak maxima of 144°F. were recorded in both of these summer months.) As a result seedlings on the full-sun station succumbed rapidly to heat girdling at the ground line. Cedar disappeared entirely by the end of July and hemlock by the end of August, and the number of live seedlings of more resistant species was seriously depleted. Heat deaths continued on the full-sun station well into September.

On the part-shade area, also, high surface soil temperatures resulted in a large number of deaths. Conditions varied markedly with character and density of overwood shade (Table 27). Although the total radiation received on the sunny portion of the part-shade area was only 37 per cent of that recorded under full sun, temperatures on the more exposed quadrats were comparable in magnitude with those recorded on similar surfaces with full sunlight. (See Tables 13 and 14.) Dangerous surface temperatures were recorded in part shade as early as May 12, with deaths recorded the following day coincident with similar mortality on the full-sun station. Even on mineral surfaces the first losses from insolation on the part-shade habitat occurred only a few days after similar losses in full sunlight, and the insolation losses on three exposed mineral quadrats actually averaged higher than similar losses on the full-sun station. Deaths from insolation totaled 54 per cent of total germination

14. Isaac, L. A. Seedling establishment in relation to environmental factors on logged-off land in the Douglas fir region. 120 p. Manuscript. 1934.

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on the exposed as against 5 per cent on shaded mineral quadrats on Station 2, averaging 26 per cent for the whole area as against 40 per cent for similar quadrats in full sunlight. Losses from fungi, insects, and drought were slightly higher on the sunny portion. Insolation never became a factor in full shade, the highest temperatures recorded during 1932 being 89° and 115°F. on mineral and duff surfaces, respectively.

Drought, of course, was most active from midsummer on. The effect of drought on initial survival depends upon the ever-changing balance between root penetration, tending to keep the seedling in contact with moist soil, and progressive soil drying from the surface downward. The very rapid drying which took place upon the full-sun station during clear weather resulted in some early-season mortality among short-

TABLE 27. SEEDLING MORTALITY OF ALL SPECIES ON MINERAL SURFACES OF STATION 2 IN 1932, AS AFFECTED BY SHADE CONDITIONS

<i>Cause</i>	<i>Mortality percentages, in terms of total germination</i>		
	<i>Sunny portion</i>	<i>Shady portion</i>	<i>Weighted average</i>
Fungi.....	13	10	11
Insects and birds.....	4	3	4
Insolation.....	54	5	26
Drought.....	5	3	4
Total.....	76	21	45

rooted or freshly germinated seedlings. A small number of cedars were killed in this way on May 18, 1932. But for the most part the rapid and relatively deep drying characteristic under full sun was largely counter-balanced by equally characteristic deep root penetration. In 1932, although soil moisture had decreased dangerously to a depth of 6 to 9 inches by mid-August, the deeper-rooted species surviving were still for the most part in contact with soil containing water sufficient for their needs. The importance of a favorable root penetration-soil moisture balance was strikingly illustrated on the relatively moist full-shade area. Here, although the low evaporation rate had produced only shallow surface drying, and this, except for one short spell about July 1, relatively late in the season, surface drying killed large numbers of the exceptionally shallow-rooted species characteristic of this habitat.

TABLE 28. SOIL DRYING AND ROOT PENETRATION ON FULL-SUN STATION IN 1932

Date	Depth, in inches, to which topsoil was dry*	Depth, in inches, of penetration of seedling roots, by species										Remarks
		Western white pine		Douglas fir		Western larch		Western hemlock		Western red cedar		
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	
May 10	0	1.0	1.7	0.5	1.0	A few cedar killed. Frequent rains, May 20-June 8, inclusive.
18	1.0	1.2	2.4	1.0	2.3	0.3	1.1	0.3	1.1	0.5	1.3	
20	0	1.2	2.6	1.0	2.4	0.4	1.2	0.4	1.2	0.5	1.3	
June 1	0	1.5	3.5	1.3	3.0	0.6	1.7	0.5	1.7	0.6	1.9	
10	0	1.7	4.4	1.6	3.8	0.9	2.4	0.6	2.0	0.7	2.5	
20	1.0	2.1	5.3	2.2	5.2	1.5	3.8	0.8	2.5	0.9	3.4	
July 1	2.0	2.6	6.2	3.0	7.9	2.7	6.0	1.0	3.1	1.2	4.3	Considerable number of hemlock and cedar killed. A few pine, Douglas fir, and larch killed. Rain on July 3 and 4. A few drought deaths, from July 11 on, of all species, but mostly of hemlock and cedar.
3	0	2.7	6.4	3.2	8.2	3.0	6.3	1.1	3.2	1.3	4.4	
11	2.0	3.1	7.1	4.1	9.2	3.9	7.3	1.3	3.7	1.7	5.0	
20	3.0	3.8	7.8	5.0	10.1	4.3	8.1	1.5	4.2	2.0	5.5	
Aug. 1	4.0	4.6	8.7	6.0	11.0	5.5	9.0	
11	5.0	5.3	9.5	6.8	11.6	
21	6.0	6.0	10.2	7.4	12.1	
Sept. 1	7.0	6.8	10.9	8.0	12.7	Rain of 0.21 inch on Aug. 29 penetrated 1.5 inches.
11	7.0	7.5	11.5	8.5	13.1	Rain on Sept. 19 wet surface only.
21	8.0	8.2	12.0	8.9	13.6†	8.2†	13.1†	2.9†	4.8†	3.2†	7.1†	
Oct. 13	0	Rain on Oct. 13.

* Moisture content at or near wilting coefficient to this depth.

† These measurements were taken Sept. 27 on watered quadrats.

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TABLE 29. SOIL DRYING AND ROOT PENETRATION ON PART-SHADE STATION IN 1932

Date	Depth, in inches, to which topsoil was dry*	Depth, in inches, of penetration of seedling roots, by species										Remarks	
		West-ern white pine		Douglas fir		West-ern larch		West-ern hemlock		West-ern red cedar			
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.		
May	10	0	0.6	1.6	0.2	0.7	0.2	0.6	A few cedar killed on one dry quadrat. Frequent rains, May 20-June 8, inclusive.
	18	0.5	0.9	2.1	0.4	1.9	0.4	1.0	0.3	0.8	
	20	0	0.9	2.3	0.5	2.0	0.4	1.1	0.3	0.9	
June	1	0	1.3	3.1	0.7	2.9	0.7	1.5	0.5	1.4	
	10	0	1.6	3.8	1.0	3.6	1.0	1.8	0.6	1.9	
	20	0.5	1.9	4.6	1.4	4.5	0.5	1.3	1.2	2.1	0.8	2.5	
July	1	1.0	2.3	5.4	1.9	5.5	0.8	2.2	1.6	2.5	1.1	3.1	A few deaths of all species, constituting total drought deaths on this area. Rain on July 3 and 4.
	3	0	2.3	5.6	2.0	5.8	0.9	2.4	1.6	2.6	1.2	3.2	
	11	1.5	2.7	6.1	2.5	6.7	1.1	3.1	1.8	2.9	1.5	3.5	
	21	2.0	3.1	6.7	3.3	7.7	1.5	4.0	2.1	3.3	1.8	3.9	
Aug.	1	2.5	3.7	7.2	4.1	8.8	1.9	4.7	2.4	3.6	2.2	4.3	
	11	3.0	4.3	7.7	4.8	9.8	2.4	5.3	2.6	3.9	2.6	4.7	
	21	3.0	4.9	8.1	5.5	10.6	2.8	4.2	2.9	5.0	
Sept.	1	0	5.5	8.4	5.6	11.4	3.1	4.5	3.1	5.4	Rain on Aug. 29 penetrated 1.5 to 2 inches. Rain on Sept. 19.
	11	2.0	6.0	8.8	6.5	12.1	3.3	4.8	3.3	5.7	
	20	0	6.4	9.0	3.4	5.1	3.5	6.0	

* Moisture content at or near wilting coefficient to this depth.

The changing balance between root penetration and surface soil drying is depicted for the three study stations in Tables 28-30, inclusive.

Soil moisture contents of 16 per cent or less were considered dangerous; this wilting coefficient was regarded only as an indicator, however, and

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all seedlings dying were subjected to individual inspection and diagnosis before their deaths were classified by cause.

As indicated in the tables, root penetration varied greatly with both species and habitat. During 1932 in full sun Douglas fir, western larch,

TABLE 30. SOIL DRYING AND ROOT PENETRATION ON FULL-SHADE STATION IN 1932

Date	Depth, in inches, to which topsoil was dry*	Depth, in inches, of penetration of seedling roots, by species										Remarks
		West- ern white pine		Dou- glas fir		West- ern larch		West- ern hemlock		West- ern red cedar		
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	
May 10	0	Surface soil still wet.
20	0	0.4	1.8	
June 1	0	0.6	2.0	1.1	2.0	0.3	0.8	0.4	0.8	Frequent rains up to June 8.
10	0	0.7	2.2	1.1	2.1	0.3	0.9	0.4	0.8	
20	0	0.9	2.3	1.1	2.2	0.4	1.1	0.3	0.9	0.4	0.8	
July 1	0.5	1.1	2.5	1.2	2.4	0.5	1.1	0.4	1.0	0.4	0.9	A few pine and cedar killed. Rain on July 3 and 4.
10	0	1.2	2.7	1.3	2.6	0.5	1.2	0.4	1.0	0.4	0.9	
21	0.5	1.4	2.9	1.4	2.8	0.5	1.2	0.4	1.1	0.5	0.9	
Aug. 1	1.0	1.6	3.1	1.6	3.2	0.6	1.2	0.5	1.1	0.5	1.0	Rain penetrated 0.5 inch.
11	1.5	1.8	3.3	1.8	3.7	0.6	1.3	0.5	1.2	0.5	1.1	
21	2.0	2.0	3.4	2.0	4.2	0.6	1.3	0.6	1.3	0.5	1.2	
Sept. 1	2.0	2.3	5.0	0.7	1.3	0.7	1.3	0.6	1.4	Rain on Aug. 29 penetrated 0.5 inch.
11	3.0	2.5	5.6	0.7	1.3	0.7	1.3	0.6	1.6	
20	0	2.8	6.3	0.7	1.3	0.7	1.4	0.7	1.7	Rain on Sept. 19.

* Moisture content at or near wilting coefficient to this depth.

and western white pine seedlings, which were larger and sturdier than those of other species, showed the best root penetration, in about the order named, and consequently suffered least from drought. Cedar and hemlock were very much shorter-rooted than their associates and suffered heavily from drought. The losses in these species would probably

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have been much higher if insolation had not wiped out large numbers of them before drought had a chance to act. Cedar has a slight but consistent advantage over hemlock in root penetration and as a result suffered appreciably less from drought. Larch, though one of the deeper-rooted species on the full-sun station, had the shortest roots in full shade of any species tested and consequently suffered heavily from drought there. The balance between root penetration and soil moisture was most favorable on the part-shade station, with the result that drought deaths here were very much less than on either the full-sun or the full-shade habitat. Indeed, during 1932 drought conditions existed on the part-shade area only for a short period around July 1, when shallow surface soil drying killed a few short-rooted individuals of every species present. Although the surface soil was dangerously dry to much greater depths later in the season, favorable root penetration at that time eliminated the possibility of further drought deaths.

LOSSES DUE TO BIOTIC FACTORS

Although the field arrangements were designed primarily to study the rôles played by physical factors, it proved feasible to gather some information on deaths caused by biotic factors as well. It is clear, of course, that losses due to biotic factors cannot be compared directly with losses from insolation and drought, owing to direct interference with the natural play of biotic agents. For example, rodents were successfully excluded from all except the full-shade station by screening, and on this area rodent damage was reduced to a minimum by trapping and poisoning the few individuals that found their way into the screened enclosure. The activity of fungi, insects, and birds, on the contrary, may have been stimulated by the abundant food supply resulting from an unnatural concentration of seedlings upon the study plots. Nevertheless, all quadrats were equally exposed to such attack, and losses by it do not affect the comparison of the relative susceptibility of the various tree species.

Losses due to biotic agents are summarized by species, station, and principal surfaces in Table 31. These losses were fairly heavy, ranging from 15 per cent in half shade to 35 per cent on the full-sun area. The great majority were due to damping-off organisms common to practically all forest habitats. Brewster¹⁶ had previously reported the presence of at least *Rhizoctonia* in this vicinity. In general, losses from fungi did not

15. *Open c;t*, p. 12.

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vary significantly among the so-called mineral surfaces; all the differences shown by average values, with the possible exception of values for charcoal surfaces on the full-sun station, proved not significant upon statistical analysis.¹⁶ Table 32 lists the average losses on some quadrats together with the standard error derived by a statistical examination of the variation existing among the mortality averages for the individual quadrats.

TABLE 31. SEEDLING MORTALITY CAUSED BY BIOTIC AGENTS* IN 1932

<i>Agent and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of total germination</i>												<i>Grand average</i>
	<i>Station 1 (full-sun)</i>				<i>Station 2 (part-shade)</i>				<i>Station 3 (full-shade)</i>				
	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Charcoal</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Charcoal</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Charcoal</i>	<i>Duff</i>	<i>Weighted average</i>	
Fungi													
Western white pine.....	24	20	44	28	11	6	12	9	10	21	15	15	17
Douglas fir.....	14	8	23	15	11	9	10	10	16	17	12	15	13
Western larch.....	10	17	16	13	17	15	6	14	8	13	19	13	13
Western hemlock.....	24	36	68	40	18	8	6	11	7	5	12	8	20
Western red cedar.....	45	38	60	47	11	14	14	13	12	18	44	26	29
Average.....	23	24	42	29	14	10	10	11	11	15	20	15	18
Insects and birds													
Western white pine.....	2	10	2	4	6	4	3	5	6	7	10	8	5
Douglas fir.....	1	6	6	4	6	4	2	5	10	3	2	5	5
Western larch.....	3	2	4	3	5	2	2	3	0	1	2	1	2
Western hemlock.....	1	6	4	3	3	2	2	2	0	0	0	0	2
Western red cedar.....	18	18	13	16	6	3	1	3	1	0	0	1	7
Average.....	5	8	6	6	5	3	2	4	3	2	3	3	4
Total.....	28	32	48	35	19	13	12	15	14	17	23	18	22

* Some deaths not tabulated were caused by rodents and miscellaneous biotic agents.

No differences in excess of three times the standard error (approximately twice the standard error of the difference) are indicated in this table,

16. Differences between average values were tested wherever possible by the methods developed for the study of variance by R. A. Fisher and co-workers (33, 34). For a discussion of the more important variance tables, see the Appendix.

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though that for charcoal approaches this limit. Usually only differences larger than this are regarded as real, i.e., not due to accidents of sampling. Even on mineral surfaces watered daily the death rate failed to show a difference greater than this, though on such surfaces deaths from fungi occur at any time throughout the season. Deaths from fungi on burnt mineral surfaces, averaging about 17 per cent on Stations 1 and 2 combined, also failed to differ significantly from those on the other classes of mineral surfaces. The four duff plots on the part-shade and full-sun stations showed a much higher kill from fungi, averaging about 34 per cent of total germination as against 18 per cent for corresponding mineral surfaces. This 1932 finding, based upon a sample too meagre to permit analysis, is confirmed by the 1933 records. In full shade the losses on duff and mineral surface quadrats were not significantly different.

TABLE 32. EFFECT OF SURFACE MATERIAL OR TREATMENT ON SEEDLING MORTALITY CAUSED BY FUNGI IN 1932

	<i>Surface material or treatment</i>				<i>Mean</i>	<i>Standard error</i>
	<i>Mineral</i>	<i>Charcoal</i>	<i>Watered</i>	<i>Trenched</i>		
Average mortality percentage, in terms of total germination.....	16.1	22.2	15.7	19.2	18.3	±2.3

Similar examination of variation in mortality by stations indicates an indisputably heavier kill by fungi on the full-sun station. But the erratic character of such differences is shown by the reversal of this situation in 1933, when a slightly heavier kill occurred in full shade. The 1932 records show some significant differences between species, notably somewhat heavier loss in western red cedar. Owing to many eccentricities these items are reserved for later discussion in conjunction with the 1933 records.

Losses from insects and birds were largest on the full-sun station but were small on all stations, ranging from 3 per cent in full shade to 6 per cent in full sun. Insects, chiefly *Noctuidae* larvae¹⁷ caused larger losses than birds, though juncos (*Junco hyemalis* var.) caused an appreciable mortality. They were observed several times during May

17. Identified for the writer by R. B. Friend, Yale University.

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industriously nipping off the succulent cotyledons of newly germinated seedlings, apparently having been attracted by the seed coats retained by some of the seedlings. Some breakage was caused by birds in hunting for ungerminated seed lying on the surface or partially buried in duff. Whereas insects, with the exception later noted, worked rather indiscriminately on all species, birds inflicted greatest injury on western white pine (119). Douglas fir and western larch suffered to some extent from birds. A small type of *Noctuidiae* larva, working almost exclusively on western red cedar, caused significantly larger losses in this species on the full-sun area than elsewhere. Losses in western red cedar in 1932 averaged four to five times more in this species than in others and account for practically all of the significant differences in biotic losses among stations and species. No significant differences in losses from biotic agents could be detected among surfaces, the observed variations falling well within the limits of sampling error.

The limited losses from rodents during 1932 were almost entirely confined to western white pine. Rodents searched out the plots of this species on eight scattered quadrats, entirely ignoring (except for one or two Douglas fir beds) the immediately adjacent sowings of other species. Some 36 per cent of the western white pine seedlings germinating in full shade were destroyed in this way. It is probable that wood rats (*Neotoma* sp.) were responsible for most of this damage, though the Douglas or pine squirrel (*Sciurus douglasii*) and a species of flying squirrel are other seed eaters known to frequent the full-shade habitat. Most of the destruction caused by rodents consisted in breakage incident to digging up sown seed buried in the surface duff or soil. Some direct loss was caused by rodents biting off the succulent tops of freshly germinated seedlings.

LOSSES DUE TO PHYSICAL FACTORS

Tables 31 and 32 show the proportion of seedling losses attributed to biotic factors, the data for each quadrat being given equal weight in computing averages. A much clearer idea of the potential danger from insolation and drought is obtained, however, if the number of seedlings that died in early spring because of biotic agents is subtracted from the total number that germinated and if the number killed by physical factors is expressed in terms of the residual value. This sort of presentation is necessary if species differences are to be compared fairly, as the heavy mortality caused by biotic factors early in the season varied considerably among species. Obviously, for example, if 90 per cent of one

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species is killed by biotic agents early in the season, only 10 per cent, at most, can be killed by physical factors no matter how destructive these may be when they once begin to act; and unless the percentages killed in this way are the same for each species and each surface, a direct comparison of losses due to physical agents is inaccurate and misleading. Accordingly, as the principal object of this study was to determine the rôles of various physical factors of site and the manner in which their action can be influenced by the density of overwood shade, the losses due to physical agents are summarized (in Table 33) in terms of the number of seedlings left after biotic agents had taken their toll. Only data for quadrats having 50 or more residual seedlings were used in deriving the values tabulated. The seedling sample per quadrat was very much larger in most cases, averaging some 280 seedlings.

Table 33 shows that the total loss from physical factors varied widely with station, species, and cause. High surface soil temperatures and drought accounted for about 99 per cent of these losses. The former, by far the most important agent on the full-sun and part-shade areas, killed 59 and 31 per cent, respectively, of the residual seedlings on these habitats. Drought was a fairly important agent on the full-sun station, where it killed 21 per cent of the residual seedlings. In part shade it proved very much less effective, causing only 4 per cent mortality. Under full shade drought was the only important physical agent, killing some 59 per cent of the residual seedlings.

Although surface soil temperatures averaged somewhat higher during July and August on burnt mineral than on natural mineral surfaces (Table 14), the average mortality from insolation was not significantly different on the two materials on the full-sun station. On the part-shade area losses from insolation averaged only 27 per cent on natural mineral as against 40 per cent on burnt mineral surfaces. It is known that this difference was due at least in part to factors other than character of surface, the burnt mineral quadrats being less sheltered than the natural mineral quadrats with which they were compared. Accordingly, blackening the surface did not greatly increase mortality losses.

Insolation losses on duff were greater in general than those on mineral surfaces. Fairly satisfactory data on the part-shade habitat show insolation losses of 62 per cent on duff as against 31 per cent on comparable mineral surfaces. Satisfactory records for the full-sun station are not available because of poor germination. No insolation deaths occurred in full shade.

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Species were found to vary materially in susceptibility to insolation. In general, western red cedar and western hemlock proved least resistant to insolation, and western larch, Douglas fir, and western white pine most resistant. This fact is somewhat obscured on the full-sun station,

TABLE 33. SEEDLING MORTALITY CAUSED BY PHYSICAL FACTORS IN 1932

<i>Agent and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of residual seedlings</i>								
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>		
	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Duff</i>	<i>Weighted average</i>
Insolation									
Western white pine.....	43	47	44	6	9	7	0	0	0
Douglas fir.....	72	72	72	13	27	20	0	0	0
Western larch.....	62	58	60	27	45	30	0	0	0
Western hemlock.....	55	54	55	40	66	48	0	0	0
Western red cedar.....	61	71	64	51	55	51	0	0	0
Average.....	59	60	59	27	40	31	0	0	0
Drought									
Western white pine.....	13	9	12	0	1	T	29	30	30
Douglas fir.....	11	12	11	1	0	T	17	18	17
Western larch.....	6	7	6	2	7	5	96	93	95
Western hemlock.....	42	44	43	16	8	12	98	94	97
Western red cedar.....	38	29	34	0	2	1	62	54	58
Average.....	22	20	21	4	4	4	60	58	59
Total (including miscellaneous)									
Western white pine.....	56	56	56	6	10	8	29	30	30
Douglas fir.....	83	84	83	14	28	21	17	18	17
Western larch.....	68	66	67	29	52	38	96	93	95
Western hemlock.....	100	100	100	56	76	62	99	94	97
Western red cedar.....	100	100	100	51	58	53	62	54	58
Average.....	81	81	81	31	45	36	61	58	59

where drought killed a disproportionate number of cedar and hemlock and thus limited the percentage of seedlings of these species subject to fatal injury from insolation. Relative susceptibility to insolation is shown more accurately on the part-shade station, for on this habitat

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drought mortality was slight and total mortality even of the more susceptible species did not approach 100 per cent. In 1932 insolation losses ranged from 7 per cent in western white pine to 51 per cent in western red cedar. Almost all of the insolation losses on Station 2 occurred on the sunny portion.

As shown in Table 33, drought deaths did not vary appreciably by surface. Drought mortality did vary appreciably by station, totaling only 4 per cent of residual seedlings on the part-shade area as against 21 per cent in full sun and 59 per cent in full shade.

Average mortality for individual species from all physical factors on cut over areas is shown in Table 34. Mortality from physical causes in western hemlock and western red cedar was significantly greater, and that in western white pine was significantly lower than the average, the variation being more than three times the standard error. The values shown

TABLE 34. RELATIVE SUSCEPTIBILITY OF VARIOUS SPECIES TO PHYSICAL FACTORS ON CUTOVER AREAS (STATION 1 AND 2) IN 1932

<i>Item</i>	<i>West- ern white pine</i>	<i>Doug- las fir</i>	<i>West- ern larch</i>	<i>West- ern hem- lock</i>	<i>West- ern red cedar</i>	<i>Mean</i>	<i>Stand- ard error</i>
Average mortality percentage, in terms of residual seedlings	38.3	54.4	53.0	77.7	73.8	59.4	±4.1

for Douglas fir and western larch may be somewhat high, however, owing to the late germination of these spring-sown species and their consequent inability to harden as early as white pine.

In full shade the short-rooted character of western larch placed it in the same class with western hemlock as to susceptibility to physical factors, drought killing 95 per cent of the larch and 97 per cent of the hemlock. The consistently better root penetration shown by western red cedar on this habitat resulted in materially better survival, only 58 per cent of this species being killed. Strange to say, the best initial survival was shown by Douglas fir, only 17 per cent of this species succumbing to drought in full shade. Western white pine was second in this respect with a mortality of only 30 per cent. These differences are entirely due to the better root penetration shown by Douglas fir and white pine under a full timber canopy. Drought losses did not vary appreciably between duff and mineral surfaces in full shade in 1932. Drought was the only impor-

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tant direct agent of mortality in full shade, exclusive of biotic agents. Although sunlight intensities averaged only 3 to 5 per cent of full sunlight, initial survival was very high on quadrats that were watered.

During 1932 an attempt was made to isolate the effect of root competition by daily watering of so-called control quadrats. The average values for these surfaces compared with average values for other mineral surfaces are shown in Table 35. Practically all losses from non-biotic causes were eliminated by surface watering. Watering entirely eliminated high surface soil temperatures, and, although the penetration effected even with heavy watering was not deep, it was sufficient in this case to alleviate drought conditions largely due to surface soil drying. The effect of

TABLE 35. SEEDLING MORTALITY ON WATERED, TRENCHED, AND UNTREATED MINERAL SURFACES IN 1932

<i>Cause</i>	<i>Mortality percentages, by surface material or treatment, in terms of total germination</i>								
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>		
	<i>Watered</i>	<i>Trenched</i>	<i>Mineral</i>	<i>Watered</i>	<i>Trenched</i>	<i>Mineral</i>	<i>Watered</i>	<i>Trenched</i>	<i>Mineral</i>
Fungi.....	26	36	29	6	7	11	13	15	15
Insects and birds.....	6	14	6	4	4	4	4	3	3
Insolation.....	2	22	40	0	14	26	0	0	0
Drought.....	0	16	12	0	1	4	0	15	45
Total.....	34	88	87	10	26	45	17	33	63

trenching, unfortunately, is not so clear; one quadrat only on each area was trenched, and previous tabulations show that considerable variation results from undefined sampling errors alone. The appreciably lower drought mortality on the trenched quadrats of Stations 2 and 3, where root competition was more severe owing to the presence of an overwood stand, and the total lack of such difference on the clear-cut station, indicate that root competition played a part in causing drought conditions fatal to one-year-old seedlings. But as the drying most effective in causing initial mortality occurred (Figure 2) in a rather even layer from the surface downward, evaporation was probably of greater importance as far as initial mortality is concerned.

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One other **interesting** feature was the occurrence of a small number of insolation deaths on full-sun quadrats constantly watered. These deaths were due to vertical lesions one-tenth to one-quarter inch long in the cortical layer of the seedling stem, apparently caused by the heat due to direct sunlight. Such lesions occurred on all sides of the stem, regardless of cardinal direction. This type of injury occurred only in late June and early July and was common only on western white pine, causing some 20 per cent of the total insolation loss in this species. It is possible that insolation produces such lesions only during periods of rapid stem expansion accompanied by considerable hardening of the stem cortex.¹⁸ In most cases the appearance of sizable lesions was accompanied by gradual drying out and yellowing of the leaves directly above this injury. Severe attacks resulted in death. Lesions were found at any point on the seedling stem between the ground line and the base of the cotyledons.

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DURING 1933 the early deaths with few exceptions were caused by biotic agents, chiefly damping-off fungi. Heavy mortality due to insolation followed on the full-sun station, with some moderate losses from drought, while on the full-shade station heavy losses were brought about by drought alone. Moderate losses from both insolation and drought characterized mortality on the more favorable part-shade station, with insolation playing the more important rôle.

Table 36 shows mortality by cause in terms of total germination for the three major habitat stations. As summarized in this table some 72 per cent of the total germination was killed by the principal biotic and edaphic factors, less than 1 per cent being killed by miscellaneous causes not here included. Losses averaged 95 per cent of the total germination on the severe full-sun habitat from which all overwood shade had been removed, 76 per cent under the unfavorable conditions existing in full shade, and 46 per cent on the relatively favorable part-shade habitat.

SEASONAL COURSE OF MORTALITY

As shown in Table 37, the course and character of mortality were closely linked with edaphic conditions. Although the preceding winter

18. E. E. Hubert, then of the School of Forestry, University of Idaho, suggested this possibility.

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was comparatively mild and snowfall light, germination began during May (Plate 6) in soil soaked to considerable depths by melting snow and

TABLE 36. SEEDLING MORTALITY OF ALL SPECIES IN 1933, BY STATION AND CAUSE

<i>Cause</i>	<i>Mortality percentages, by station, in terms of total germination</i>			<i>Average</i>
	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>	
Fungi.....	28	27	34	30
Insects and birds.....	12	3	4	6
Insolation.....	51	13	0	21
Drought.....	4	3	38	15
Total.....	95	46	76	72

TABLE 37. CHRONOLOGY OF CERTAIN WEATHER AND EDAPHIC CONDITIONS AND OF SEEDLING GERMINATION AND MORTALITY IN 1933

<i>Item</i>	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>
Snow disappears; ground practically bare....	April 15	May 1	May 5
Germination begins.....	May 1	May 10*	May 24*
Germination completed.....	May 30	June 30	July 15
Last stragglers appear.....	June 23	July 10	Aug. 1
First deaths from fungi occur.....	May 2	May 10	May 24
Deaths from fungi become rare.....	June 30	Aug. 15†	Aug. 15
First drying of surface soil	Duff..... May 10	May 20	June 23
	Mineral.... June 4	June 23	July 14
First surface temperature of 120°F. or more	Duff..... May 11	May 25	None
	Mineral.... June 21	July 4	None
First deaths from insolation occur	Duff..... ..	June 11	None
	Mineral.... June 27	July 6	None
First deaths from drought occur	Duff..... May 29	June 11	June 27
	Mineral.... June 23	June 28	July 20

* A few seedlings, however, appeared as early as May 1.

† On sheltered quadrats, but about July 15-20 on exposed quadrats.

spring rains. Deaths from biotic agents began to appear almost coincident with seedling germination and ended with the first complete drying

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out of the surface soil. Losses from physical causes appeared somewhat later than in 1932, for, although precipitation during May was sub-normal, the occurrence of light, frequent rains throughout May and heavy rains in early June retarded surface soil drying to such an extent that appreciable mortality from insolation and drought did not begin until early July. But about July 5 on the clear-cut area, and a week or so later in part shade, losses from insolation and drought became common. Heavy mortality continued until the fall rains about September 18 broke an almost uninterrupted series of hot, dry days that had produced dangerous soil temperatures and moisture conditions on both duff and mineral quadrats.

TABLE 38. SEEDLING MORTALITY OF ALL SPECIES ON MINERAL SURFACES OF STATION 2 IN 1933, AS AFFECTED BY SHADE CONDITIONS

<i>Cause</i>	<i>Mortality percentages, in terms of total germination</i>		
	<i>Sunny portion</i>	<i>Shady portion</i>	<i>Weighted average</i>
Fungi.....	23	28	27
Insects and birds.....	2	4	3
Insolation.....	37	1	13
Drought.....	3	4	3
Total.....	65	37	46

Insolation conditions were particularly critical during 1933, records on the full-sun habitat (Table 23) showing temperatures above 120°F. on some 26 days during July and on 24 days during August and exceedingly dangerous temperatures of 135°F. or over on 20 days on mineral and 68 days on duff surfaces during the growing season.

Insolation losses were directly influenced by overhead shade, as effectively demonstrated by the part-shade area records summarized in Table 38. Insolation killed some 37 per cent of total germination on the sunny portion as against 1 per cent on quadrats in heavier shade. Losses from other factors did not vary materially between the exposed and sheltered portions. Insolation never became a factor in full shade.

Drought conditions were very critical in 1933. A few early deaths were recorded during May, particularly on duff. About June 19 surface drying

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became appreciable, and dry soil to a depth of about 1.5 inches between June 23 and June 27 resulted in the death of a few of the short-rooted hemlocks and cedars upon the full-sun area. This critical situation was temporarily relieved by light rains on June 28 and 29, but drying weather again followed, and beginning July 5 many cedars and hemlocks whose root penetration averaged only slightly more than 2 inches were killed in surface soil dangerously dry to approximately a 3-inch depth. A few

TABLE 39. SOIL DRYING AND ROOT PENETRATION ON FULL-SUN STATION IN 1933

Date	Depth, in inches, to which topsoil was dry*	Depth, in inches, of penetration of seedling roots, by species											
		Western white pine		Douglas fir		Western larch		Lowland white fir		Western red cedar		Western hemlock	
		Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
May 10	0	0.3	0.8	0.5	1.3	0.1	1.1	1.2	2.2	0.2	0.4	0.3	0.5
June 10	0	2.0	4.1	1.7	4.3	1.7	4.6	1.9	5.3	0.7	1.4	0.6	1.6
25	1.0	2.9	5.8	2.6	6.4	2.6	6.4	3.1	7.3	1.0	2.0	1.0	2.3
July 1	0.5	3.2	6.5	2.9	7.3	2.9	7.0	3.7	8.1	1.2	2.4	1.2	2.6
5	1.5	3.4	7.0	3.1	7.8	3.1	7.5	4.1	8.5	1.3	2.6	1.3	2.8
11	2.0	3.6	7.7	3.5	8.5	3.5	8.2	4.7	9.2	1.5	3.1	1.5	3.1
14	3.0	3.8	8.0	3.7	8.8	3.6	8.5	5.0	9.5	1.5	3.3	1.7	3.3
29	5.0	4.4	9.7	4.5	10.1	4.5	10.2	6.5	11.0	1.7	4.3	2.3	4.0
Aug. 11	5.5	4.8	11.0	5.3	10.8	5.2	11.7	7.7	12.0				
18	6.0	5.0	11.5	5.6	11.1	5.6	12.5	8.3	12.5				
30	7.0	5.2	12.0	6.2	11.5	6.1	13.4	9.3	13.2				
Sept. 5	7.0	5.3	12.2	6.5	11.6	6.2	13.7	9.8	13.4				
18	0	5.3	12.2	7.1	11.8	6.2	13.9						

* Moisture content at or near wilting coefficient to this depth.

deaths scattered throughout the season were also recorded among other species.

These deaths were directly governed by the soil moisture-root penetration relationships tabulated in Tables 39 to 41 for the three habitats, respectively. Figure 2 illustrates graphically the amount and character of surface soil drying and root penetration upon each habitat. The number of rains and the amount of precipitation received on each habitat has also

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been listed in this figure. Western white pine, one of the deeper-rooted species, and western hemlock, the shallowest-rooted species, have been used, maximum and minimum root depths being shown for each species at various times. The unshaded soil is dry to or below the wilting coefficient, approximately 16 per cent by oven-dry weight. As pictured in this diagram, soil drying in the upper layers, of great importance in initial survival, takes place almost entirely from the surface downward.

TABLE 40. SOIL DRYING AND ROOT PENETRATION ON PART-SHADE STATION IN 1933

Date	Depth, in inches, to which topsoil was dry*	<i>Depth, in inches, of penetration of seedling roots, by species</i>											
		<i>Western white pine</i>		<i>Douglas fir</i>		<i>Western larch</i>		<i>Lowland white fir</i>		<i>Western red cedar</i>		<i>Western hemlock</i>	
		<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>
June	1	0.8	1.9	1.5	2.9	0.8	1.5	1.3	2.8	0.3	1.1	0.3	0.7
	13	1.2	2.4	2.4	4.3	1.1	3.5	2.5	3.9	0.5	1.5	0.6	1.4
	25	1.6	3.2	3.2	5.5	1.5	4.8	3.5	5.3	0.7	2.0	0.9	2.2
July	1	1.9	3.7	3.6	6.1	1.8	5.4	4.0	6.3	0.9	2.4	1.0	2.6
	5	2.1	4.3	3.9	6.5	2.0	5.7	4.3	6.8	1.0	2.7	1.2	2.9
	14	2.5	5.4	4.4	7.4	2.4	6.4	5.0	8.0	1.3	3.7	1.6	3.5
	29	3.3	6.6	5.3	8.7	3.2	7.3	5.9	9.3	1.9	5.1	2.3	4.3
Aug.	11	3.9	7.4	6.0	9.8	3.8	8.1	6.6	10.2	2.5	6.0	2.6	4.9
	18	4.3	7.8	6.3	10.3	4.2	8.4	7.0	10.6	2.8	6.4	2.7	5.2
	30	4.7	8.3	6.8	11.0	4.7	9.0	7.5	11.1	3.3	6.8	2.8	5.5
Sept.	5	5.0	8.5	7.0	11.4	5.0	9.2	7.8	11.3	3.5	7.0	2.9	5.6
	18	5.5	8.8	7.4	11.9	5.6	9.7	8.2	11.7	4.0	7.1	2.9	5.8

* Moisture content at or near wilting coefficient to this depth.

Although soil drying on the full-sun habitat was rapid and relatively deep, this was compensated for in part by deeper root penetration, particularly in the more resistant species, i.e., western white pine, Douglas fir, western larch, and lowland white fir. (See Plate 7.) Although the soil had dried to a depth of 7 inches by late August, deeper-rooted individuals of these species had roots penetrating 11 inches or more (Table 39), and relatively few deaths resulted. The shorter-rooted species were unable to maintain a favorable root penetration-soil moisture balance and conse-

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quently suffered heavily from drought. Drought losses began as soon as soil moisture content dropped below the wilting coefficient in the layer in which seedlings were rooted. This situation, depicted for short-rooted species on the full-sun habitat about June 25, 1933, immediately resulted in drought deaths in hemlock and cedar.

On the part-shade station as shown in Figure 2 and Table 40 the root penetration-soil moisture balance was favorable during 1933 to practically all species except cedar and hemlock. Surface drying, beginning

TABLE 41. SOIL DRYING AND ROOT PENETRATION ON FULL-SHADE STATION IN 1933

Date	Depth, in inches, to which topsoil was dry*	<i>Depth, in inches, of penetration of seedling roots, by species</i>											
		<i>Western white pine</i>		<i>Douglas fir</i>		<i>Western larch</i>		<i>Lowland white fir</i>		<i>Western red cedar</i>		<i>Western hemlock</i>	
		<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>	<i>Min.</i>	<i>Max.</i>
June 10	0					0.5	1.1	1.5	2.8	0.2	0.6		
20	0	0.8	1.9	0.8	2.3	0.5	1.1	1.6	2.9	0.2	0.7	0.4	0.9
July 1	0	1.1	2.2	1.3	2.7	0.5	1.2	1.6	3.1	0.3	0.9	0.5	1.0
15	0.5	1.4	2.4	1.8	3.0	0.5	1.4	1.7	3.3	0.4	1.1	0.5	1.1
26	1.0	1.6	2.5	1.9	3.1	0.5	1.5	1.7	3.4	0.4	1.2	0.5	1.1
30	1.5	1.7	2.5	2.0	3.1	0.5	1.5	1.8	3.5	0.5	1.2	0.6	1.1
Aug. 11	2.0	1.9	2.5			0.5	1.6	1.8	3.6	0.5	1.4	0.6	1.2
30	3.0	2.1	2.6			0.5	1.8	1.9	3.9	0.7	1.6	0.7	1.3
Sept. 5	3.0												
18	0												

* Moisture content at or near wilting coefficient to this depth.

about June 25, caught a few short-rooted hemlock on mineral surfaces, a condition almost immediately relieved by rains on June 28 and 29. But about July 6 surface drying again began to kill some cedar and many hemlock on exposed quadrats, and this condition lasted (Figure 2) until the fall rains. Only a few short-rooted individuals of other species were killed by drought in 1933.

In full shade surface drying began much later and reduced soil moisture to the wilting coefficient or below to a maximum depth of only 3 inches. Nevertheless, drought deaths were heavy, a paradoxical situa-

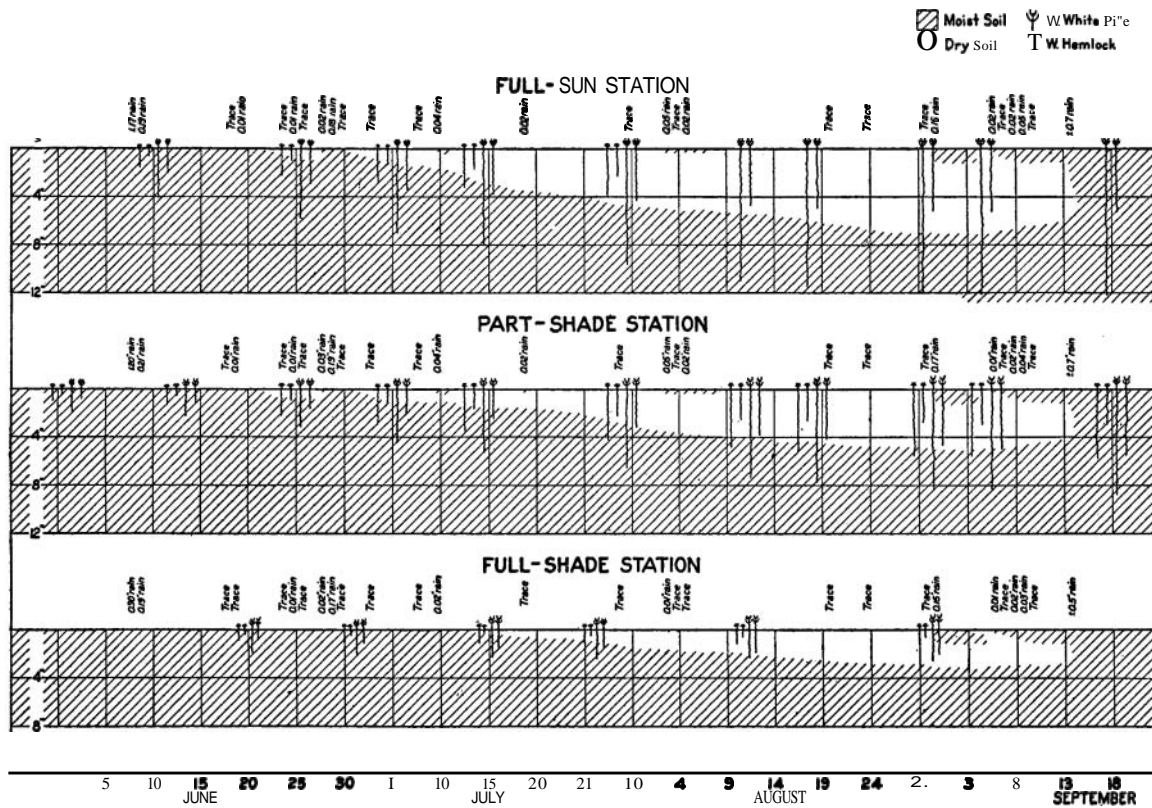


Figure 2
Root penetration and progressive soil drying in 1933

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tion explained by Figure 2 and Table 41, which show the manner in which shallow root penetration accompanied by shallow drying endangered all species on the full-shade habitat. Drought losses began about July 20 and continued until early September. On the full-shade habitat even relatively small differences between species in root penetration resulted in material differences in the number of deaths from drought.

Drought losses upon the full-sun station were somewhat obscured and would undoubtedly have been higher if insolation had not killed appreciable numbers of cedar and hemlock early in the season. Such heavier drought losses are shown in Table 42, which compares mortality on

TABLE 42. SEEDLING MORTALITY ON UNSHADED AND SHADED MINERAL SURFACES ON FULL-SUN STATION IN 1933

<i>Cause</i>	<i>Mortality percentages, by species, in terms of total germination</i>													
	<i>Unshaded mineral quadrats</i>							<i>Shaded mineral quadrats</i>						
	<i>WWP</i>	<i>DF</i>	<i>WL</i>	<i>LWF</i>	<i>WH</i>	<i>WRC</i>	<i>Average</i>	<i>WWP</i>	<i>DF</i>	<i>WL</i>	<i>LWF</i>	<i>WH</i>	<i>WRC</i>	<i>Average</i>
Fungi.....	32	40	17	29	40	24	30	33	41	20	29	36	16	29
Insects and birds.....	14	12	6	10	22	36	17	1	1	4	2	15	16	7
Insolation.....	40	40	68	53	28	32	44	0	0	0	0	0	0	0
Drought.....	1	0	1	1	10	7	3	0	0	1	1	32	17	8
Total.....	87	92	92	93	100	99	94	34	42	25	32	83	49	44

shaded and exposed mineral quadrats. On the shaded quadrats protective screening kept surface temperatures well below 120°F. and consequently eliminated surface soil temperature as a killing agent. Soil moisture conditions on both sets were substantially the same in spite of the screening except for a slight time lag (Table 43), the screens being placed in such a fashion as to permit free circulation of air over the sheltered quadrats. Under these circumstances drought losses did not vary in the deeper-rooted species but were substantially increased in the shorter-rooted species—from 10 to 32 per cent with hemlock and 7 to 17 per cent with cedar. The number of seedlings remaining alive under screens, where insolation was not a factor (Plate 8), shows graphically the excellent survival on the full-sun habitat when this mortality agent

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is eliminated. Even an unfavorable root penetration-soil moisture balance beginning as early as July 5 failed to result in complete killing of the species involved where insolation was eliminated. Although the surprisingly high survival recorded is probably due in part to the somewhat slower soil drying under shade (Table 43), and possibly in part to a lower transpiration rate, a large proportion of this survival is undoubtedly attributable to the drought-resistant qualities of the conifers concerned. Early setting of terminal buds, beginning July 20 with some species on the full-sun area, indicates lessened activity and probably reduced transpiration rates during the driest portion of the season. But the larger drought losses on shaded surfaces, shown in Table 42, indicate the possibility that drought may play a much more important rôle on

TABLE 43. SOIL MOISTURE CONDITIONS ON UNSHADED AND SHADED MINERAL QUADRATS IN 1933

<i>Date</i>	<i>Depth, in inches, of dangerous* soil drying</i>	
	<i>Unshaded mineral quadrats</i>	<i>Shaded mineral quadrats</i>
June 1	0	0
July 1	0.5	0.2
15	3.0	2.0
30	5.0	4.0
Aug. 15	6.0	6.0
30	7.0	7.0

* Moisture content at or near wilting coefficient to this depth.

habitats where insolation is eliminated by aspect, overhead shade, or similar factors if the root penetration-soil moisture balance remains unfavorable.

LOSSES DUE TO BIOTIC FACTORS

Losses caused by biotic factors were largely due to the activity of damping-off organisms supplemented to some extent by defoliating insects and seed-eating birds and rodents. These losses, exclusive of those caused by rodents, are summarized in Table 44. Biotic agents killed 36 per cent of the total number of seedlings germinating. Losses due to fungi varied erratically among species, surfaces, and stations. These losses were heaviest under full shade, though the total maximum range

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between stations is only 7 per cent. No significant differences could be detected in losses from fungi between plain and burnt mineral surfaces.

Losses due to insects were slightly heavier in 1933, averaging 3 and 4 per cent of total germination on the part-shade and full-shade areas, respectively, and 12 per cent under full sun. Western red cedar suffered

TABLE 44. SEEDLING MORTALITY CAUSED BY BIOTIC AGENTS* IN 1933

<i>Agent and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of total germination</i>										
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>			<i>Grand average</i>	
	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Duff</i>	<i>Weighted average</i>		
	Fungi										
Western white pine.....	32	32	32	22	18	20	44	18	33		28
Douglas fir.....	40	27	33	37	42	38	66	19	43	38	
Western larch.....	17	12	14	7	6	7	61	30	46	22	
White fir.....	29	17	23	34	46	39	55	26	40	34	
Western hemlock.....	40	41	41	25	24	25	18	6	12	26	
Western red cedar.....	24	19	22	31	32	31	37	18	27	27	
Average.....	30	25	28	26	28	27	47	20	34	30	
Insects and birds											
Western white pine.....	14	5	10	4	1	3	0	5	2	5	
Douglas fir.....	12	3	7	1	6	4	6	4	4	5	
Western larch.....	6	5	5	4	6	5	9	24	16	9	
White fir.....	10	5	8	1	2	1	2	0	1	3	
Western hemlock.....	22	8	15	1	4	2	1	1	1	6	
Western red cedar.....	36	17	26	3	6	4	0	1	1	10	
Average.....	17	7	12	2	4	3	3	6	4	6	
Total.....	47	32	40	28	32	30	50	26	38	36	

* Some deaths not tabulated were caused by rodents and miscellaneous biotic agents.

very heavily on the full-sun area, 26 per cent of this species being killed by insects compared with 5 to 15 per cent in associated species.

LOSSES DUE TO PHYSICAL FACTORS

Losses from insolation and drought for 1933 are summed up for the principal surfaces in Table 45 in terms of total number of seedlings germi-

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nated less biotic losses. As heretofore explained, this permits a more intelligent presentation of the relative susceptibility of various species.

TABLE 45. SEEDLING MORTALITY CAUSED BY PHYSICAL FACTORS IN 1933

<i>Agent and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of residual seedlings</i>								
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>		
	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Duff</i>	<i>Weighted average</i>
Insolation									
Western white pine.....	76	82	78	10	32	20	0	0	0
Douglas fir.....	84	87	86	13	18	14	0	0	0
Western larch.....	87	98	93	18	35	26	0	0	0
Lowland white fir.....	91	86	88	6	24	15	0	0	0
Western hemlock.....	74	67	71	46	45	46	0	0	0
Western red cedar.....	83	90	87	52	43	48	0	0	0
Average.....	82	85	84	24	33	28	0	0	0
Drought									
Western white pine.....	T*	1	1	0	1	T*	63	37	50
Douglas fir.....	T	0	T	0	0	0	20	17	18
Western larch.....	1	T	1	0	0	0	84	93	89
Lowland white fir.....	1	2	1	0	0	0	13	24	19
Western hemlock.....	26	33	29	19	22	20	98	98	98
Western red cedar.....	17	10	13	3	11	7	57	81	69
Average.....	8	8	8	4	6	5	56	58	57
Total (including miscellaneous)									
Western white pine.....	77	83	79	10	33	20	63	37	50
Douglas fir.....	84	87	86	13	18	14	20	17	18
Western larch.....	88	98	94	18	35	26	86	93	89
Lowland white fir.....	92	88	90	6	24	15	13	24	19
Western hemlock.....	100	100	100	65	67	66	98	98	98
Western red cedar.....	100	100	100	55	54	55	58	81	69
Average.....	90	93	92	28	39	33	56	58	57

*T = Trace.

The undoubtedly greater susceptibility of the slender-stemmed western hemlock and red cedar to heat girdling, indicated by the rapidity with which the seedlings die in the field, is obscured by the greater susceptibility of these species to drought. As drought and insolation are active

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during the same period, it is obvious that any substantial increase in the percentage attributed to one cause will automatically reduce the percentage attributed to the other. For example, when 29 per cent of the hemlock loss is classified as due to drought, as in 1933 on the full-sun station, only 71 per cent can possibly be allotted to insolation, regardless of the relative severity of this factor on hemlock as compared with other species. It is impossible to prevent this interaction from influencing the size of the component figures. The relative susceptibility of the various species to insolation is better shown, therefore, on the part-shade area where the combined losses are not as high. On the part-shade area hemlock and cedar show 46 and 48 per cent mortality from insolation, respectively, as against losses of 14 to 26 per cent in associated species. Mortality values from the sunny and shaded portions of Station 2 have been given equal weight in arriving at these averages. No insolation losses were recorded under full shade.

Drought losses were relatively light on the cutover areas. Hemlock, showing the weakest initial root penetration, suffered most heavily from drought, losing about 24 per cent of residual germination on the cutover areas. Cedar, the next most susceptible species, lost an average of 10 per cent on similar sites. The relatively deep-rooted western white pine, western larch, Douglas fir, and lowland white fir lost only 1 per cent or less on these habitats. Drought was an important killing agent with all species on the full-shade area. All of the shorter-rooted species, including larch on this habitat, suffered very severely. In full shade Douglas fir and lowland white fir were by far the hardiest, as far as initial mortality is concerned, and western hemlock and larch the most susceptible. Western white pine and western red cedar occupied intermediate positions.

The relative resistance of the associated species to physical factors is also depicted in the section showing total kill in terms of all physical factors combined. This comparison indicates clearly the far greater susceptibility of hemlock and cedar. These species were wiped out completely on the clear-cut area. Substantial losses of 79 to 94 per cent were recorded for the other species. Losses on the part-shade area totaled 66 per cent and 55 per cent in hemlock and cedar, respectively, as against 14 to 26 per cent in other species. In addition to losses caused by insolation and drought, a few seedlings died in 1933 from frost and from minor miscellaneous causes, some short-rooted individuals, for example, being washed out by rain.

DISCUSSION AND COMPARISON

DISCUSSION AND COMPARISON

IT IS clear from the preceding sections that the general course of mortality during 1932 and 1933 was very similar as far as the nature and activity of the important agents are concerned. In both seasons the causes of early-season deaths were largely biotic, principally insects and damping-off organisms. The completion of germination, the hardening of seedling tissues, and the gradual drying out of the surface soil slowly brought about a cessation of biotic activities, and beginning in late June or early July losses were due primarily to insolation and drought.

RÔLE OF BIOTIC FACTORS

In general, with the possible exception of rodents, which were successfully excluded from two habitats and greatly hampered in their activity on the third, damping-off organisms proved to be the most important biotic agents, killing from four to five times as many seedlings as insects and birds combined. Fungi attacked vigorously all of the species commonly associated in the western white pine type. Species losses from fungous attack were in some instances so different as to suggest unequal distribution of conditions favorable to fungous development or of more virulent fungous strains. The differences were not sufficiently consistent between stations or seasons to imply susceptibility differences among the species studied.

In neither season could any significant difference in losses from fungi be detected between plain and burnt mineral quadrats. But on cutover areas fungi proved to be much more active in duff surfaces. The available data on this point are summarized in Table 46, together with comparable data for the full-shade station, where losses on duff were not significantly different from losses on mineral surfaces. The activity of fungi on the full-sun station during both years, and the substantially heavier losses on duff, seem to indicate that the better temperature conditions prevailing in duff surfaces on the part-shade area and on all surfaces on the full-sun area more than compensate for a somewhat shorter season of plant activity and poorer moisture conditions due to earlier drying. In full shade, where surface temperatures did not vary so markedly between duff and mineral surfaces, losses were somewhat higher on mineral, averaging 29 per cent on such surfaces for the two seasons combined as against 20 per cent on duff. Considerable variation between seasons indicates the impossibility of clarifying this complex situation without records extending over a fairly long period.

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Losses from insects were slightly heavier in 1933 than in 1932, averaging 3 and 4 per cent of total germination on the part-shade and full-shade areas, respectively, and 12 per cent under full sun. During both 1932 and 1933 losses were materially higher on the full-sun station than on either of the others, largely owing to the very heavy mortality in western red cedar on that area. But the insect losses in species other than

TABLE 46. SEEDLING MORTALITY CAUSED BY FUNGI ON DUFF AND MINERAL SURFACES IN 1932 AND 1933

<i>Station, year, and surface material</i>	<i>Mortality percentages, by species, in terms of total germination</i>						<i>Average</i>
	<i>West- ern white pine</i>	<i>Doug- las fir</i>	<i>West- ern larch</i>	<i>Low- land white fir</i>	<i>West- ern hem- lock</i>	<i>West- ern red cedar</i>	
Station 1 (full-sun)							
1932	{ Duff.....	46	46
	{ Mineral soil.....	24	24
1933	{ Duff.....	72	97	96	100	..	91
	{ Mineral soil.....	32	33	14	23	..	26
Station 2 (part-shade)							
1932	{ Duff.....	18	22	32
	{ Mineral soil.....	10	17	11
1933	{ Duff.....	25	37	70	38	51	51
	{ Mineral soil.....	20	38	7	39	25	31
Station 3 (full-shade)							
1932	{ Duff.....	15	12	19	..	12	44
	{ Mineral soil.....	10	16	8	..	7	12
1933	{ Duff.....	18	19	30	26	6	18
	{ Mineral soil.....	44	66	61	55	18	37

cedar did not vary consistently between species and habitat during the years covered.

In some contrast with insects and fungi, birds, which frequent the cutover areas, and climbing rodents, such as mice, wood rats, and squirrels, were highly selective, their damage being largely confined to western white pine. It is possible that under critical regeneration conditions

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rodent and bird action might adversely affect the composition of the new stand by reducing the amount of white pine during the period of germination and early development. Biotic agents exclusive of rodents caused mortality averaging some **28** per cent of total germination for **1932** and 1933 combined. Total biotic losses for the two years averaged 38 per cent on the full-sun station, **22** per cent in part shade, and **28** per cent in full shade, respectively. It is impossible to judge how fairly these figures represent the mortality that would be caused by biotic agents in seedling stands less dense than those on the study plots. Undoubtedly, however, biotic agents are a potent if somewhat erratic and uncontrollable factor in initial mortality of seedlings in the western white pine type.

INSOLATION AS A FACTOR IN MORTALITY

Insolation was the most important single agent of mortality on the river flat stations. Direct exposure to sunlight resulted in the development of injurious temperatures as soon as a thin top layer of soil or duff was dry, and these temperatures were directly responsible for the great majority of losses on the full-sun (clear-cut) and part-shade (part-cut) habitats. The large number of sunny days and the low summer precipitation characterizing the regional climate were both conducive to frequent occurrence of dangerous surface temperatures. The effects of insolation and drought and of miscellaneous physical factors, including frost, are summed up in terms of residual seedlings in Table 47. The lowland white fir mortality values presented in the table are based on the more severe 1933 season only. As shown here, insolation was by far the most important agent on the cutover habitats. Although the 1933 season was drier and warmer than the preceding, losses from insolation (Table 36) when expressed in terms of total germination were about the same, averaging **21** per cent in 1933 as against **22** per cent in the preceding year (Table **25**). The real effect of the warmer weather was somewhat obscured, however, by the fact that a heavier kill by biotic agents reduced automatically the mortality per cent that can be attributed to physical factors, particularly where the total kill from all agencies combined reached or approached 100 per cent, as in this instance. The comparative severity of insolation conditions between the **1932** and 1933 seasons is more accurately depicted, therefore, when physical-factor mortality is expressed in terms of residual germination.

In general, insolation accounted for from five to six times as many seedling deaths as drought on the cutover areas, killing 73 per cent of

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TABLE 47. SEEDLING MORTALITY* CAUSED BY PHYSICAL FACTORS IN 1932 AND 1933

<i>Factor and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of residual seedlings</i>								
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>		
	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral</i>	<i>Burnt mineral</i>	<i>Weighted average</i>	<i>Mineral†</i>	<i>Duff</i>	<i>Weighted average</i>
Insolation									
Western white pine.....	55	66	60	6	22	14	0	0	0
Douglas fir.....	78	84	81	9	19	14	0	0	0
Western larch.....	74	79	75	16	32	24	0	0	0
Lowland white fir‡.....	91	86	88	6	12	8	0	0	0
Western hemlock.....	62	56	58	33	41	37	0	0	0
Western red cedar.....	71	80	75	38	35	37	0	0	0
Average.....	72	75	73	18	27	22	0	0	0
Drought									
Western white pine.....	8	6	7	T	I	T	47	34	41
Douglas fir.....	6	4	5	I	I	I	16	20	17
Western larch.....	4	4	4	I	3	2	90	94	93
Lowland white fir‡.....	1	2	1	0	0	0	8	24	16
Western hemlock.....	37	43	39	16	19	18	93	97	95
Western red cedar.....	28	20	24	2	10	6	51	68	60
Average.....	14	13	13	3	6	5	51	56	54
Total (including miscellaneous)									
Western white pine.....	63	72	67	6	23	14	47	34	41
Douglas fir.....	84	88	86	10	21	15	16	20	17
Western larch.....	78	83	80	17	35	26	91	95	93
Lowland white fir‡.....	92	88	89	6	12	8	8	24	16
Western hemlock.....	100	100	100	49	60	55	93	97	95
Western red cedar.....	100	100	100	40	45	43	52	68	60
Average.....	86	88	87	21	33	27	51	56	54

* Figures presented are averages of 1932 and 1933 figures.

† Including charcoal quadrat values.

‡ 1933 values only.

the residual seedlings on the full-sun habitat and 22 per cent under part shade. If the effect of insolation is studied on the part-shade station, where it is less obscured by concurrent effect of drought, it is clear that lowland white fir, Douglas fir, and western white pine form a relatively

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resistant group, and that western hemlock and western red cedar are distinctly more susceptible than the average. Western larch falls between these extremes. This comparison is shown in Table 48. Lowland white fir, not shown in this tabulation because of lack of data for the 1932 season, showed a lower loss than any other species in 1933, namely 7.9 per cent. Its mortality percentage in 1933 did not, however, differ significantly from those of western white pine and Douglas fir.

To some extent, of course, mortality due to insolation depends upon cortical development, as the hardening of exterior stem tissue undoubtedly increases resistance to temperature. That cortical development varies with the severity of temperature conditions is shown by the coarse, woody appearance in midseason of seedling stems on the full-sun station as compared with stems of similar species under part or full shade. This is illustrated in Plate 9. Undoubtedly the relatively thick cortex

TABLE 48. RELATIVE SUSCEPTIBILITY OF VARIOUS SPECIES TO INSOLATION IN PART SHADE
IN 1932 AND 1933

<i>Item</i>	<i>West- ern white pine</i>	<i>Doug- lasfir</i>	<i>West- ern larch</i>	<i>West- ern hem- lock</i>	<i>West- ern red cedar</i>	<i>Mean</i>	<i>Stand- ard error</i>
<i>Average mortality percentage, in terms Of residual seedlings.</i>	14.0	14.2	23.6	37.3	37.1	25.2	±4.2

developed on more severe sites explains why seedlings of the larger and sturdier species are able to survive on these sites in the face of the extremely high temperatures recurring day after day.

As previously recorded, losses were higher on duff surfaces than on mineral or burnt mineral surfaces, owing primarily to the fact that dangerous surface temperatures were higher and more frequent on duff.

On the cutover areas, i.e., the full-sun and part-shade stations, quicker surface drying, earlier and extremely high surface temperatures, and a greater daily range in temperature, with increased danger from frost, all tended to make duff surfaces extremely dangerous from the standpoint of initial mortality. Not a single seedling managed to survive on exposed duff quadrats on the full-sun area, and very few survived on the less sheltered portions of the part-shade area (Table 49). This was due to temperature conditions; once root penetration has placed seedlings

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on duff surfaces in contact with mineral soil, the moisture conditions there are at least as favorable as on mineral quadrats (Table 50).

In both seasons insolation losses averaged slightly higher on blackened surfaces. The differences were very small, particularly on the full-sun station, where conditions were so severe and losses so heavy that temperatures averaging a few degrees higher raised the average mortality

TABLE 49. SEEDLING MORTALITY CAUSED BY INSOLATION AND DROUGHT ON DUFF AND MINERAL SURFACES ON PART-SHADE HABITAT IN 1932 AND 1933

<i>Agent and tree species</i>	<i>Mortality percentages, by surface soil material, in terms of residual seedlings</i>			
	1932		1933	
	<i>Duff</i>	<i>Mineral</i>	<i>Duff</i>	<i>Mineral</i>
Insolation				
Western white pine.....	22	7	62	20
Douglas fir.....	21*	0*	44	14
Western larch.....	52	26
Lowland white fir.....	30	15
Western hemlock.....	62*	11*
Western red cedar.....	71*	12*
Average.....	22	4	54	16
Drought				
Western white pine.....	2	T	T	0
Douglas fir.....	1	T	1	0
Western larch.....	T	0
Lowland white fir.....	1	0
Western hemlock.....	10*	26*
Western red cedar.....	7*	5*
Average.....	2	T	3	5

* Values from shaded portion only.

only 1 or 2 per cent. The effect of blackening was somewhat more marked on the part-shade station, where conditions were less severe and small differences in temperature had a greater effect on average mortality. If 1932 and 1933 mortality values for individual species on natural mineral quadrats and burned mineral quadrats, respectively, are averaged with corresponding values for the sunny portion of the part-shade area, mortality averaged 61.9 per cent for mineral as against 67.4 per cent for

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burnt mineral quadrats. The difference, 5.5 ± 2.8 , is probably significant.

DROUGHT AS A FACTOR IN MORTALITY

Drought losses were affected directly by the rapidity and depth of initial root penetration. Important differences in this respect are shown in Plate 7. Drought was far less important on the dry, hot, full-sun station than on the relatively cool, moist, full-shade station, paradoxical as this may seem, because on the full-sun station rapid and deep surface soil drying was largely counter-balanced by equally rapid and deep initial root penetration, while in full shade shallow surface soil drying was accompanied by shallow root penetration. On the habitats studied sur-

TABLE 50. MOISTURE CONDITIONS ON DUFF* AND MINERAL SURFACES IN 1932 AND 1933

Date	<i>Depth, in inches, to which dangerous dryness extended, by surface material</i>											
	<i>Station 1 (full-sun)</i>				<i>Station 2 (part-shade)</i>				<i>Station 3 (full-shade)</i>			
	<i>Duff</i>		<i>Mineral</i>		<i>Duff</i>		<i>Mineral</i>		<i>Duff</i>		<i>Mineral</i>	
	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933	1932	1933
May 1	0	0	0	0	0	0	0	0	0	0	0	0
28	0	2	0	0	0	2	0	0	0	0	0	0
June 28	2	2	2	1	2	2	1	1	1	0.5	0.5	0
Aug. 1	5	3	4	5	3	2	2.5	3	2	2	1	1.5
28	8	6	7	7	3.5	3	3	5	2	3	2	3

* Forming a layer 2 inches thick over mineral soil.

face evaporation was a very important agent in creating critical drought conditions. The soil was often drier at somewhat greater depths than at the surface, owing in all probability to vegetational usage; but usually, as is shown in Figure 2, drying affected a well-defined layer from the surface downward, under full timber as well as in full sunlight.

Table 51 shows drought losses by species. On the cutover areas the four larger and hardier species, western white pine, Douglas fir, western larch, and lowland white fir did not differ significantly from one another in resistance to drought during the initial season following germination. Western red cedar and western hemlock again formed a more susceptible group. In this case cedar was distinctly less susceptible than hemlock, a fact probably due at least in part to its slightly but consistently deeper

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root penetration. In full shade the species were more sharply differentiated with regard to drought resistance. The extremely weak penetra-

TABLE 51. RELATIVE SUSCEPTIBILITY OF VARIOUS SPECIES TO DROUGHT IN 1932 AND 1933

<i>Species</i>	<i>Mortality percentages, in terms of residual seedlings</i>		
	<i>Station 1 (full-sun)</i>	<i>Station 2 (part-shade)</i>	<i>Station 3 (full-shade)</i>
Western white pine.....	7	0 ¹ ?	41
Douglas fir.....	5	1	17
Western larch.....	4	2	93
Lowland white fir.....	1*	0*	16*
Western red cedar.....	24	6	60
Western hemlock.....	39	18	95
Average†.....	16	5	61
Standard error.....	± 2.2	± 2.1	± 4.8

* 1933 records only.

† For all species but lowland white fir.

TABLE 52. PROGRESS OF SURFACE SOIL DRYING IN 1932 AND 1933

<i>Date</i>	<i>Depth, in inches, of soil drying*</i>					
	<i>Station 1 (full-sun)</i>		<i>Station 2 (part-shade)</i>		<i>Station 3 (full-shade)</i>	
	<i>1932</i>	<i>1933</i>	<i>1932</i>	<i>1933</i>	<i>1932</i>	<i>1933</i>
June 1	0	0	0	0	0	0
20	1.0	0.5	0.5	0	0	0
July 1	2.0	0.5	1.0	0.5	0.5	0
11	2.0	2.0	1.5	1.5	0	0
20	3.0	4.0	2.0	2.5	0.5	0.5
Aug. 1	4.0	5.0	2.5	3.0	1.0	1.5
11	5.0	5.5	3.0	4.0	1.5	2.0
21	6.0	6.5	3.0	4.5	2.0	2.5
Sept. 1	7.0	7.0	0	5.0	2.0	3.0
11	7.0	7.0	2.0	0	3.0	0
20	8.0	0	0	0	0	0

* Moisture content at or near wilting coefficient to this depth.

tion of western larch made this species one of the most susceptible to drought injury in heavy shade. Hemlock and larch were distinctly more

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susceptible and Douglas fir and probably lowland white fir distinctly less susceptible to drought injury in full shade, white pine and cedar forming an intermediate group (Table 51). On the basis of available records white pine is significantly less susceptible than cedar, an observation **supported** by its relatively deeper root penetration. As shown by the root penetration data, drought susceptibility ratings of the species exactly parallel their ratings as to initial root penetration.

In spite of the drier character of the season in 1933 drought deaths were actually less. Though part of this may be due directly to the increased insolation percentages, and the consequent automatic reduction in the percentages that can be attributed to drought, it seems probable that a portion of the decrease can be directly allotted to certain favorable aspects of the 1933 season. Although growing-season precipitation was materially less in 1933, it came in such a fashion that surface drying was considerably delayed. As a result, during the early part of the season when the race between root penetration and surface drying is particularly keen, seedlings had a better chance to push their absorbing roots deeper into moist soil before drying started, and the substantial **early-season** drought losses characterizing the **1932** season were practically lacking. In addition, critical drought conditions lasted somewhat longer in **1932** than in 1933, because of the absence of substantial early September rains. This situation, depicted in Table **52**, undoubtedly resulted in additional drought deaths, particularly on the full-sun station, where the soil in the late summer of **1932** dried appreciably deeper than it did at any time in the following year. Drought losses were not materially different between the two seasons on either the part-shade or **the** full-shade habitat, though the depth of soil drying on these stations was somewhat greater in the 1933 season.

Drought losses in full shade did not vary materially between duff and mineral. Losses on duff averaged **2** per cent lower in **1932** as against 6 per cent higher in 1933 when compared with losses on mineral surfaces.

LIGHT AS A FACTOR IN SURVIVAL

Light proved to have no important direct influence on initial survival. Even on the full-shade area, where the total radiation received averaged only **5** per cent of the total measured on the full-sun station, seedlings otherwise protected from adverse factors managed to survive the first season. This was clearly demonstrated on the quadrats on which drought was eliminated by watering (Table 35); only **1** per cent of all seedlings

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(other than those killed by biotic agents) died on these quadrats, and even this loss is directly attributed to miscellaneous causes other than lack of sufficient light. Though the indirect effects of light intensity may be very important (Plates 7, 9, and 10), lack of light was not in itself a

TABLE 53. SEEDLING MORTALITY ON MINERAL SURFACES OF STATION 2, AS AFFECTED BY SHADE CONDITIONS

<i>Agent and tree species</i>	<i>Mortality percentages, in terms of residual seedlings</i>					
	<i>Sunny portion</i>			<i>Shady portion</i>		
	<i>1932</i>	<i>1933</i>	<i>Average</i>	<i>1932</i>	<i>1933</i>	<i>Average</i>
Insolation						
Western white pine.....	14	34	24	0	0	0
Douglas fir.....	38	29	34	2	0	1
Western larch.....	46	46	46	15	0	8
Lowland white fir.....	..	24	24	..	0	0
Western hemlock.....	78	82	80	18	7	12
Western red cedar.....	97	93	95	6	4	5
Drought						
Western white pine.....	1	0	1	0	1	1
Douglas fir.....	1	0	1	0	0	0
Western larch.....	13	0	6	2	0	1
Lowland white fir.....	..	0	0	..	0	0
Western hemlock.....	18	16	17	6	27	17
Western red cedar.....	3	7	5	0	5	3
Total (including miscellaneous)						
Western white pine.....	15	34	25	0	1	1
Douglas fir.....	40	29	35	2	0	1
Western larch.....	59	46	52	17	0	9
Lowland white fir.....	..	24	24	..	0	0
Western hemlock.....	98	99	98	25	34	30
Western red cedar.....	100	100	100	6	9	8

direct agent of mortality on the habitats studied even in the full shade of a dense, overmature virgin timber stand.

Although deficiency of light was not a direct factor, the greatest differences in mortality brought about by physical factors were associated with differences in overhead shade, as has been shown in preceding sections, and very great variations in the cause and extent of mortality

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losses can be effected by reducing or increasing the density of the residual stand. Table 53, comparing losses on sunny and shady portions of the part-shade area in 1932 and 1933, illustrates this very effectively.

In general, the most favorable conditions for initial survival on the river flat stations used in this study are created by a relatively even residual stand permitting only about one-fifth of total radiation to reach the ground surface. As the overwood shade is reduced, insolation and drought losses increase, always somewhat more rapidly in some species than in others, until full exposure results in unsatisfactory survival in all species alike.

TABLE 54. RELATIVE SUSCEPTIBILITY OF VARIOUS SPECIES TO PHYSICAL AGENTS OF MORTALITY ON CUTOVER AREAS (STATIONS 1 AND 2) IN 1932 AND 1933

<i>Species</i>	<i>Mortality* from physical factors</i>	<i>Remarks</i>
Western white pine.....	38%	Least susceptible group; pine and white fir not significantly different.
Lowland white fir.....	41%†	
Douglas fir.....	47%	Moderately susceptible group; Douglas fir and larch not significantly different.
Western larch.....	50%	
Western red cedar.....	68%	Most susceptible group; hemlock probably significantly more susceptible.
Western hemlock.....	75%	

* Standard error ± 2.9 per cent.

† Based on records for 1933 only.

Cedar and hemlock are less resistant to effects of exposure than western white pine, Douglas fir, lowland white fir, and western larch. Cedar and hemlock were both wiped out entirely on the full-sun station in the 1932 and 1933 seasons. Their survival was appreciably lower also in the part-shade environment, losses being practically as severe with these species on the sunny portion of the part-shade habitat as on the full-sun habitat.

Mortality of various species from physical factors on the cutover habitats is summarized in Table 54. Among the more resistant species western white pine shows significantly lower mortality losses than its associates, with the exception of lowland white fir. This difference is very marked on the full-sun area, emphasizing the fact that, other things

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being equal, western white pine is favored over most of its associates by clear-cutting. As shown in Tables 73 and 74, these relationships are maintained through the second growing season. Douglas fir and western larch are also splendidly equipped through sturdy stems and relatively deep root penetration to survive the hardships of the initial season even on severe habitats, and losses of these species did not vary by more than 12 per cent from the losses of their hardier associates. Western hemlock is least well equipped of all species in the western white pine type to resist mortality factors in the initial season. In the face of its known abundance in seedling stands it is self-evident that high initial losses are often more than compensated for by other silvical factors, such as early and abundant seeding.

SEEDLING MORTALITY AND DEVELOPMENT, 1934

ALTHOUGH the present study was devised primarily to follow seedling survival under one set of severe site conditions, some data on initial survival of western white pine and western hemlock were gathered during 1934 on a new set of habitat stations located on a lower north slope in the Benton Creek drainage of the Priest River Experimental Forest. This relatively cool, moist site was more representative of sites commonly occupied by the western white pine type than the more severe site of the older stations on the Priest River valley flat. Accordingly the data gathered in 1934 are well worth discussion in spite of their preliminary character.

HABITAT CONDITIONS

As before, the stations varied only in the character of overhead shade, which ranged from full sun to heavy shade. Owing to the favorable aspect and to a fringe of uncut trees, the clear-cut station received less direct solar radiation than the term "full sun" implies. However, only a few isolated trees remained on this area in contrast with the moderate and heavy residual stands retained on the other stations. Solar radiation received at the ground surface on the full-shade and part-shade stations averaged only 7 and 52 per cent, respectively, of that received on the full-sun area. The stations were located within a few hundred feet of one another on a steep lower slope. The areas were not fenced. The instrumental setup was comparatively simple, consisting only of surface soil thermometers, paired black and white atmometer spheres, and soil

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moisture equipment. It was felt in the light of preceding work that these instruments would suffice to measure the principal physical factors concerned.

All the new habitat stations were located on the same soil type, Huckleberry silt loam. The type is by far the most important soil on the Priest River unit, overlying more than three quarters of the Benton Creek drainage.¹⁹ It consists of 12 to 18 inches of light, yellowish-brown soil containing a variable percentage of angular stones and gravel over a subsoil of similar fine, friable material with a slightly lighter or more grayish color and a large percentage of gravel and rocks. The weathered material is distinctly micaceous, having formed in place from the schists and quartzites which occur in alternating layers over the granite backbone of the main range. Although the soil is usually 4 to 5 feet deep,

TABLE 55. TEXTURE* OF SOIL† OF NORTH-SLOPE STATIONS

<i>Item</i>	<i>Per cent</i>
Fine gravel.....	10.4
Coarse sand.....	5.0
Medium sand.....	1.6
Fine sand.....	3.3
Very fine sand.....	8.6
Silt.....	52.6
Clay.....	14.3

* As determined by the Bureau of Chemistry and Soils.

† Huckleberry silt loam.

rock outcrops are of frequent occurrence. Huckleberry silt loam shows a medium to strong acid reaction. In common with most other soils in the same region it contains an appreciable amount of loess brought in from the semi-arid regions to the west and southwest. The soil horizons are poorly defined.

This soil is very similar in textural though not in profile characteristics to the Mission silt loam underlying the river flat stations. As shown in Table 55, it contains an appreciably larger amount of angular stones and coarse and fine gravel and a smaller amount of very fine sand. The

19. This type is mapped over most of this area in two coarser textural classes, fine sandy and very fine sandy loam. The type name was tentatively assigned for descriptive purposes only. Lapham, N. H., and F. O. Youngs. *Op. cit.*

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relatively fine texture²⁰ is reflected in a high moisture-holding capacity, the moisture equivalent being 30.5 per cent and the wilting coefficient 16.6 per cent.

In general the soil is in good tilth and, as shown in Table 56, about equal in fertility to the Mission silt loam of the older study habitats. As indicated by this table, based on microchemical tests (264), Huckleberry silt loam is somewhat richer in available phosphorus and calcium and somewhat poorer in replaceable potassium.

TABLE 56. COMPARATIVE FERTILITY OF SOIL* OF NORTH-SLOPE STATIONS IN TERMS OF IMPORTANT MINERAL NUTRIENTS
(The mineral nutrients are expressed in parts per million.)

<i>Station</i>	<i>Nitrogen</i>		<i>Available phosphorus</i>	<i>Replaceable potassium</i>	<i>Replaceable calcium</i>	<i>Available magnesium</i>	<i>Active manganese</i>	<i>Active aluminum</i>
	<i>Nitrate</i>	<i>Ammonium</i>						
Full-sun.....	1	1	40	50	1,600	60	T†	1
Part-shade.....	1	1	50	50	200	40	T	1
Full-shade.....	1	1	40	70	500	70	T	1

* Huckleberry silt loam.

† T = trace

CHARACTER OF GROWING SEASON

The growing season of 1934 (May through August), was unusually severe. In the vicinity of the Priest River unit it was not only drier but also warmer and windier than most of its predecessors during the last twenty years. (See Table 57.) Precipitation was 60.1 per cent below normal, with 1922 the only other year on record having a lower seasonal total. Average relative humidity was the lowest on record with the exception of 1931. Mean air temperature, average maximum air temperature, and average hourly wind velocities were the highest ever recorded. Soil temperatures at the 1-foot level were also very high, being equaled only by the 1914 record. As shown in Table 58, these severe conditions were sustained, for almost all items, throughout the length of the growing season. In addition, the fall rains were again greatly delayed and Sep-

20. Determinations of texture and moisture equivalent made for the writer by the Bureau of Chemistry and Soils, United States Department of Agriculture.

SEEDLING MORTALITY AND DEVELOPMENT, 1934

tember was extremely dry, though somewhat colder than average. The number of summer rains of 0.01 inch or over was exceptionally small, only two years on record showing as low a number as this period (Table 59), though the number of clear days was close to average. All of these factors tended to induce severely critical soil temperature and soil moisture conditions relatively early in the season.

TABLE 57. WEATHER CONDITIONS IN THE 1934 GROWING SEASON (MAY THROUGH AUGUST)
COMPARED WITH 20-YEAR NORMALS*

<i>Weather factor</i>	<i>20-year normal</i>	<i>1934</i>	<i>Departure of 1934 record from normal</i>	<i>Remarks</i>
Total precipitation, in inches. . .	5.86	2.34	-3.52 (-60.1%)	Only 1922 lower.
Average relative humidity at 5 P.M., per cent.	44.6	34.7	-9.9 (-22.2%)	Only 1931 lower.
Mean air temperature, degrees Fahrenheit.	58.6	60.7	+2.1 (+3.6%)	Highest on record.
Average daily maximum air temperature, degrees Fahrenheit.	76.4	79.2	+2.8 (+3.7%)	Highest on record.
Average daily minimum air temperature, degrees Fahrenheit.	40.9	42.2	+1.3 (+3.2%)	
Average hourly wind velocity at 8-foot level, miles per hour.	1.96	2.17	+0.21 (+10.7%)	Highest on record.
Soil temperature at 1-foot level, degrees Fahrenheit.	56.8	60.3	+3.5 (+6.2%)	Only 1914 as high.

* Records taken at the cooperative Weather Bureau station one mile west of area at the Priest River Experimental Forest headquarters.

SURFACE SOIL TEMPERATURE

Under these circumstances it is interesting to note the very marked effect which a northerly aspect has upon the occurrence and magnitude of killing temperatures. As shown in Table 60, dangerous temperatures were reached only 8 times on mineral quadrats during the severe growing season of 1934 on the north-slope, full-sun habitat, as compared with 63 times on the full-sun habitat on the Priest River flats (Table 61). The relative severity of the 1934 season is shown by the fact that on the clear-cut flat only 48 and 52 daily maxima of over 120°F. had occurred in the

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1932 and 1933 seasons, respectively. Moreover, many of these additional days of dangerous temperatures occurred early in the season when seedling stem tissues were still succulent and relatively susceptible to heat girdling. In general, temperature conditions on the full-sun, north-aspect station were very much like those under part shade on the river flat areas, the average daily maximum being exactly the same and the highest maximum and the number of days of dangerous temperatures being

TABLE 58. MONTHLY WEATHER CONDITIONS AT THE PRIEST RIVE

<i>Weather factor</i>	<i>May</i>			<i>June</i>		
	<i>20- year nor- mal</i>	<i>1934</i>	<i>Departure of 1934 record from normal</i>	<i>20- year nor- mal</i>	<i>1934</i>	<i>Departure of 19 record from norm.</i>
Precipitation, in inches. . . .	2.01	1.47	-.54 (-26.9%)	1.78	.75	-1.03 (-57.9)
Average relative humidity at 5:00 P.M., per cent. . . .	50.6	45.2	-5.4 (-10.7%)	49.0	40.9	-8.1 (-16.5)
Mean air temperature, de- grees Fahrenheit.	50.7	55.5	+4.8 (+9.5%)	57.6	59.2	+1.6 (+2.8)
Average daily maximum air temperature, degrees Fah- renheit.	66.1	71.4	+5.3 (+8.0%)	74.0	75.8	+1.8 (+2.4)
Average daily minimum air temperature, degrees Fah- renheit.	35.3	39.6	+4.3 (+12.2%)	41.3	42.6	+1.3 (+3.1)
Average hourly wind veloc- ity at 8-foot level, miles per hour.	2.12	1.95	-.17 (-8.0%)	2.07	1.93	-.14 (-6.8)
Soil temperature at 1-foot level, degrees Fahrenheit.	49.3	54.8	+5.5 (+11.2%)	56.3	59.5	+3.2 (+5.7)

only slightly different. Tables 60 and 61 show 8 dangerous daily maximum temperatures on mineral quadrats on the full-sun, north-slope station in 1934 as compared with 6 on the part-shade river flat area.

A full summary of daily maximum surface temperatures for all north-slope stations is given in Table 62. Under the conditions existing on the north slope dangerous soil temperatures occurred only rarely on mineral quadrats, but much more frequently on duff quadrats. A total of 76 dangerous daily maximum temperatures of 135°F. or more were recorded on duff surfaces in 1934, including 43 on Station 4. Table 63 shows the

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great contrast in temperature conditions between comparable duff and mineral surfaces on the full-sun station. It is probable that the duration of dangerous temperatures is very much less on the north-slope habitats than on other aspects. Indeed, so far as mineral surfaces are concerned, a **limited** number of thermograph records indicate that killing temperatures last only about half as long on the north-slope areas as under similar conditions on the river flats.

THROUGH SEPTEMBER, 1934, COMPARED WITH 20-YEAR NORMALS

<i>July</i>	<i>August</i>				<i>September</i>				
<i>Departure of 1934 record from normal</i>	<i>20-year normal</i>	<i>1934</i>	<i>Departure of 1934 record from normal</i>	<i>20-year normal</i>	<i>1934</i>	<i>Departure of 1934 record from normal</i>	<i>20-year normal</i>	<i>1934</i>	<i>Departure of 1934 record from normal</i>
-.82 (-95.3%)	1.21	.08	-1.13 (-93.4%)	1.84	.81	-1.03 (-56.0%)	1.84	.81	-1.03 (-56.0%)
-10.4 (-28.0%)	41.9	26.1	-15.8 (-37.7%)	65.9	46.3	-19.6 (-29.7%)	65.9	46.3	-19.6 (-29.7%)
+0.6 (<+0.9%)	62.4	63.8	+1.4 (+2.2%)	53.1	51.9	-1.2 (-2.3%)	53.1	51.9	-1.2 (-2.3%)
+0.6 (+0.7%)	82.1	85.5	+3.4 (+4.1%)	69.7	67.8	-1.9 (-2.7%)	69.7	67.8	-1.9 (-2.7%)
+0.4 (+0.9%)	42.7	42.0	-0.7 (-1.6%)	36.6	36.0	-0.6 (-1.6%)	36.6	36.0	-0.6 (-1.6%)
+.25 (+13.0%)	1.71	2.63	+.92 (+53.8%)	1.50	1.39	-.11 (-7.3%)	1.50	1.39	-.11 (-7.3%)
+2.9 (+4.8%)	60.9	63.2	+2.3 (+3.8%)	55.2	56.8	+1.6 (+2.9%)	55.2	56.8	+1.6 (+2.9%)

SOIL MOISTURE

The ameliorating effect of the northerly aspect upon temperatures is not accompanied by a similar ameliorating effect on soil moisture conditions. Table 64 depicts the depth and rapidity of soil drying on cutover sites during 1934 in comparison with preceding seasons. In 1934 the soil became effectively dry to greater depths on the more sheltered north-slope areas, except under full shade. If the entire series of soil moisture measurements (Table 65) are carefully examined, it is seen that this critical condition was due at least in part to vegetative use. For example,

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as early as June 22 the soil moisture content at the 3- to 6-inch level on the unshaded quadrats of the full-sun north-slope station was already as low as that in the 0- to 3-inch level. A week or two later it was even

TABLE 59. FREQUENCY OF RAINY DAYS AND OF CLEAR DAYS AT PRIEST RIVER STATION, MAY THROUGH AUGUST, 1934, COMPARED WITH 20-YEAR NORMALS

Month	Number of days having 0.01 inch or more rain		Number of clear days	
	20-year normal	1934	20-year normal	1934
May.....	11.2	11	12.0	12
June.....	10.2	6	12.7	11
July.....	5.0	2	20.8	15
August.....	6.3	1	19.4	25
Total.....	32.7	20*	64.9	63†

* Departure from normal, -12.8 days.

† Departure from normal, -1.9 days.

TABLE 60. EFFECT OF SURFACE SOIL MATERIAL ON SURFACE SOIL TEMPERATURES ON FULL-SUN NORTH-SLOPE STATION IN 1934

Month	Number of days on which designated temperature occurred, by surface material				Daily maximum temperature, degrees Fahrenheit			
	120° F. or more		135° F. or more		Average		Highest	
	Duff	Min-eral	Duff	Min-eral	Duff	Min-eral	Duff	Min-eral
May.....	10	0	4	0	106	86	152	111
June.....	20	0	14	0	122	97	151	114
July.....	25	6	18	0	133	111	156	134
August.....	21	2	7	0	123	106	146	122
Total or seasonal.....	76	8	43	0	121	100	156	134

lower, indicating that vegetative use was reducing soil moisture content in the 3- to 6-inch depths faster than evaporation could reduce it in the surface layer. This phenomenon was noted on the other stations, but

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usually at lower levels where it did not affect initial survival to so great an extent. Apparently the moderately dense vegetation which had encroached upon the cutover habitats in the ten-year period since logging was drawing its soil moisture from the same levels occupied by roots of one-year-old seedlings. This caused unusually dangerous drought conditions. It seems probable that on freshly cutover north-slope areas where this vegetation is lacking, soil moisture conditions would more nearly approximate those on the part-shade station on the river flats. This is indicated by the fact that drying from the surface proceeds at about the same rate on Stations 4 and 5 as on the part-shade river flat areas, as

TABLE 61. EFFECT OF HABITAT CONDITIONS ON SURFACE SOIL TEMPERATURES ON MINERAL QUADRATS OF RIVER FLAT STATIONS IN 1934

<i>Month</i>	<i>Number of days on which designated temperatures occurred, by stations</i>				<i>Daily maximum temperatures, degrees Fahrenheit</i>			
	<i>120° F. or more</i>		<i>135° F. or more</i>		<i>Average</i>		<i>Highest</i>	
	<i>Station 1</i>	<i>Station 2</i>	<i>Station 1</i>	<i>Station 2</i>	<i>Station 1</i>	<i>Station 2</i>	<i>Station 1</i>	<i>Station 2</i>
May.	0	0	0	0	91	87	110	118
June.	17	0	1	0	113	95	136	114
July.	27	4	10	0	130	111	146	132
August.	19	2	13	0	120	106	140	121
Total or seasonal.	63	6	24	0	114	100	146	132

long as it is not influenced by drying from below due to vegetative use (see Tables 64 and 65). The less severe evaporation conditions on the north-slope area are indicated also by the fact that on Station 6, where vegetative encroachment has been slight, progressive drying from the surface downward was appreciably shallower than on the full-shade river flat station. But under the actual conditions prevailing in 1934 drought was unusually severe on the cutover north-slope habitats.

SEEDLING MORTALITY, 1934

In general, the chronology of seedling germination and mortality in 1934 was very similar to that in the two preceding seasons. It is sum-

TABLE 62. AVERAGE DAILY MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT) ON MINERAL QUADRATS ON NORTH-SLOPE HABITATS IN 1934, BY MONTH

Date of month	April			May			June			July			August			September		
	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)	Station 4 (full-sun)	Station 5 (part-shade)	Station 6 (full-shade)
1				80	74	50	72	62	52	109	98	70	121	112	76	90	85	59
2				70	62	52	77	67	56	118	105	69	116	114	81	95	88	61
3				77	75	50	77	67	57	115	97	67	72	64	62	95	91	71
4				71	62	50	77	72	54	117	105	72	97	83	62	103	94	69
5				79	68	52	89	85	59	117	105	76	108	99	66	97	95	67
6				82	73	54	88	75	60	106	106	78	105	96	68	95	91	59
7				79	73	54	76	71	59	104	90	68	111	107	56	85	83	56
8				79	61	52	94	84	62	100	97	70	113	106	66	86	83	57
9				80	69	50	100	90	68	110	110	72	122	114	66	85	72	55
10				80	76	55	102	99	68	113	103	72	119	111	63	75	70	52
11				78	64	54	106	103	72	110	111	76	109	106	60	71	64	53
12				78	70	56	111	99	70	105	96	73	119	112	67	72	66	50
13				85	78	59	103	96	68	103	99	78	114	111	66	68	59	43
14				91	90	62	112	99	70	119	114	78	112	113	62	67	59	47
15				91	72	64	109	93	71	112	111	76	119	117	66	72	63	51

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16				76	69	68	110	92	67	88	93	72	111	118	72	72	66	46
17				73	64	51	109	93	72	104	105	71	113	112	62	73	69	53
18				81	74	54	105	91	66	118	114	72	108	101	53	71	66	48
19				81	72	54	103	86	66	113	109	77	113	107	62	64	60	36
20				81	68	50	103	99	69	90	85	64	112	105	60	53	49	44
21				87	82	54	114	92	66	97	86	65	102	92	59			
22				89	85	60	102	93	64	105	93	65	101	95	65			
23				96	86	64	97	87	62	117	112	74	100	99	60			
24	85	72	58	99	97	68	113	94	64	111	117	80	93	86	60			
25	75	67	57	99	96	70	110	110	73	100	100	72	98	100	61			
26	81	79	60	109	98	68	75	72	68	123	120	83	107	94	68			
27	83	83	60	111	102	70	88	84	62	122	121	90	95	95	69			
28	75	67	52	111	99	72	88	85	62	130	124	90	103	101	60			
29	74	72	49	96	92	61	103	93	64	134	120	84	83	82	63			
30	71	63	48	81	70	54	110	96	68	124	107	78	94	93	60			
31				82	69	53				121	106	72	82	80	64			
Average...	78	72	55	86	77	58	97	88	65	111	105	74	106	101	64	79	74	54

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TABLE 63. AVERAGE DAILY MAXIMUM SURFACE SOIL TEMPERATURES (DEGREES FAHRENHEIT)
ON FULL-SUN NORTH-SLOPE STATION IN 1934, BY SURFACE MATERIAL

Date of month	April		May		June		July		August		September	
	Duff	Mineral	Duff	Mineral	Duff	Mineral	Duff	Mineral	Duff	Mineral	Duff	Mineral
1			89	80	89	72	130	109	144	121	102	90
2			84	70	79	77	138	118	146	116	113	95
3			87	77	78	77	126	115	76	72	113	95
4			78	71	92	77	148	117	98	97	121	103
5			87	79	121	89	138	117	117	108	110	97
6			89	82	113	88	139	106	128	105	115	95
7			90	79	86	76	115	104	126	111	100	85
8			84	79	116	94	122	100	135	113	103	86
9			87	80	120	100	136	110	133	122	93	85
10			98	80	141	102	134	113	136	119	86	75
11			75	78	151	106	135	110	130	109	72	71
12			90	78	147	111	123	105	139	119	85	72
13			109	85	136	103	140	103	134	114	72	68
14			113	91	145	112	156	119	136	112	74	67
15			123	91	138	109	145	112	139	119	80	72
16			94	76	141	110	106	88	134	111	79	72
17			83	73	139	109	139	104	126	113	93	73
18			101	81	137	105	147	118	125	108	91	71
19			102	81	124	103	130	113	128	113	71	64
20			110	81	138	103	101	90	133	112	66	53
21			133	87	139	114	113	97	109	102		
22			126	89	133	102	116	105	123	101		
23			130	96	138	97	142	117	122	100		
24	103	85	131	99	143	113	127	111	104	93		
25	93	75	136	99	143	110	117	100	120	98		
26	96	81	137	109	81	75	140	123	118	107		
27	102	83	151	111	96	88	149	122	115	95		
28	82	75	152	111	106	88	148	130	126	103		
29	78	74	120	96	121	103	152	134	99	83		
30	79	71	96	81	130	110	140	124	111	94		
31			114	82			144	121	97	82		
Average...	90	78	106	86	122	97	133	111	123	106	92	79

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marized in Table 66. Although the winter of 1933-34 was very mild and snow had disappeared at the control station by March 10, about a month earlier than in 1932 and 1933, germination did not begin until late April. Germination of fall-sown seed was prompt, and was practically complete by June 11. Rodent depredations, however, necessitated resowing most of the white pine plats, and germination from this sowing was not finished until about mid-July. As before, losses from fungi, insects, and rodents began shortly after germination started and continued until thorough drying out of the topsoil and general loss in succulence

TABLE 64. PROGRESS OF SOIL DRYING ON RIVER FLAT AND NORTH-SLOPE AREAS IN 1932-1934, INCLUSIVE

Date	Depth, in inches, to which soil was dry,* by year, area, and station				
	1932	1933	1934		
	River flat	River flat	River flat		North-slope
	Station 1 (full-sun)	Station 1 (full-sun)	Station 1 (full-sun)	Station 2 (part-shade)	Station 4 (full-sun)
May 10	0	0	0	0	0
June 10	0	0	1.0	0.5	0.5
July 10	2.0	2.0	5.0	2.0	2.0
Aug. 10	5.0	5.5	7.0	4.0	7.0
Sept. 10	7.0	7.0	8.5†	5.0	10+
Oct. 10	0	0	0	0	0

* Moisture content at or near wilting coefficient to this depth.

† A thin layer of soil between depths of about 8 and 9 inches had a moisture content slightly above the wilting coefficient. Both above and below this level the soil was much drier.

had taken place. Owing to the severe character of May and June, topsoil drying was prompt. Drought and insolation deaths began about two weeks to one month earlier, despite the sheltered north-slope conditions, than on the river flat stations in the two preceding seasons.

The general nature and extent of mortality in 1934 on the north-slope stations is summarized for mineral surfaces in Table 67. On mineral quadrats fungi accounted for 20 per cent and insects, birds, and rodents, combined, for about 19 per cent mortality in terms of total germination. Biotic agents were particularly active in full shade, killing 91 per cent of the white pine and 33 per cent of the hemlock. As the areas were un-

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TABLE 65. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1934

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight									
		Station 1 (full-sun)		Station 2 (part-shade)		Station 3 (full-shade)	Station 4 (full-sun)		Station 5 (part-shade)		Station 6 (full-shade)
		Unshaded quadrats	Shaded* quadrats	Sunny portion	Shady portion	Full shade	Unshaded quadrats	Shaded* quadrats	Unshaded quadrats	Shaded* quadrats	Full shade
May 10	0-1					68					
	0-3	51	54	57	79	63					
	3-6	53	52	74	79						
	6-9	49	60	63	68						
12	0-1										
	0-3						59	57	44	40	
	3-6						38	35	42	38	
24	0- $\frac{3}{4}$						10†				
	0-1					47				90	
June 8	1-2					44				85	
	2-3					46				81	
	0-3	29	30	36	63	48	45	43	41	46	
	3-6	32	38	44	63		34	43	37	38	
	6-9	36	40	41	51						
	0-1					31				42	
	1-2					36				73	
	2-3					38				56	
15	0-3	16	26	17	54	43	27	40	34	29	
	3-5					38				70	
	3-6	21	30	39	55		27	39	25	45	
	6-9	26	34	41	45						
	9-12	17									
	0-1					20				18	
	1-2					27				34	
	2-3					32				51	
22	0-1 $\frac{1}{2}$						22	20			
	0-2								24	32	
	0-3	23	21	18	46	28	31	26	21	45	
	3-5					30					
	3-6	23	27	29	50		31	41	20	37	
	6-9	27	34	31	49						
	9-12	24									

* By screening.

† One sample from a large dry spot on quadrat 4.

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TABLE 65. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1934 (continued)

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight									
		Station 1 (full-sun)		Station 2 (part-shade)		Station 3 (full-shade)	Station 4 (full-sun)		Station 5 (part-shade)		Station 6 (full-shade)
		Unshaded quadrats	Shaded* quadrats	Sunny portion	Shady portion	Full shade	Unshaded quadrats	Shaded* quadrats	Unshaded quadrats	Shaded* quadrats	Full shade
June 29	0-1					33					55
	1-2					27					64
	2-3					33					61
	0-2						38	28	28	40	
	0-3	19	27	32	50	32	33	29	27	42	81
	3-6	33	30	33	50		20	32	21	28	
	6-9	22	34	36	44						
	9-12	15									
	3-5					33					
July 6	0-1					13					33
	1-2					26					82
	2-3					32					82
	0-2						19	20	23	35	
	0-3	15	23	20	39	27	30	23	26	27	42
	3-6	22	29	36	50		18	29	31	22	
	6-9	25	36	30	42						
	9-12	21									
	3-5					34					
13	0-1					10					10
	1-2					14					21
	2-3					21					43
	0-2						9	8	10	11	
	0-3	5	8	21	26	17	12	15	13	13	31
	3-6	16	21	26	33		18	19	17	19	
	6-9	17	29	24	32						
	9-12	11									
	3-5					20					
20	0-1					7					11
	1-2					13					20
	2-3					19					33
	0-2						11	8	9	10	
	0-3	9	12	9	21	8	12	10	15	13	31
	3-6	12	21	22	35		15	19	17	22	
	6-9	18	27	25	44						
	9-12	13									
	3-5					29					

*By screening.

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TABLE 65. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1934 (continued)

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight									
		Station 1 (full-sun)		Station 2 (part-shade)		Station 3 (full-shade)	Station 4 (full-sun)		Station 5 (part-shade)		Station 6 (full-shade)
		Unshaded quadrats	Shaded* quadrats	Sunny portion	Shady portion	Full shade	Unshaded quadrats	Shaded* quadrats	Unshaded quadrats	Shaded* quadrats	Full shade
Aug. 1	0-1					7					10
	1-2					11					16
	2-3					15					27
	0-2						7	6	5	11	
	0-3	6	7	7	22	12	13	6	12	11	19
	3-6	13	18	16	31		13	15	16	17	
	6-9	18	21	19	33						
	9-12	17									
	3-5					24					
	0-1					8					12
10	1-2					10					16
	2-3					14					34
	0-2						5	6	6	8	
	0-3	8	10	8	17	11	6	7	9	9	23
	3-6	14	22	19	31		12	15	11	14	
	6-9	19	27	23	34						
	9-12	14									
	3-5					21					
	0-1					8					10
	1-2					10					21
20	2-3					12					24
	0-3	8	9	9	17	10	6	8	7	7	16
	3-6	15	15	15	36		12	13	10	11	
	6-9	18	22	21	30	16	13	18	12	14	
	9-12	12		19	39	20					
	12-18	13		15	24	9					
	3-5					17					30
	0-1					9					8
	1-2					10					13
	2-3					10					16
30	0-3	8	8	9	14	9	5	9	6	6	15
	3-6	11	17	17	25		9	17	10	10	
	6-9	20	23	19	31		10	19	13	9	
	9-12	12									
	3-5					13					27

*By screening.

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TABLE 65. SOIL MOISTURE CONDITIONS ON MINERAL SOIL QUADRATS IN 1934 (concluded)

Date	Depth of sample, inches	Moisture content of soil (per cent), in terms of dry weight										
		Station 1 (full-sun)		Station 2 (part-shade)		Station 3 (full-shade)	Station 4 (full-sun)		Station 5 (part-shade)		Station 6 (full-shade)	
		Unshaded quadrats	Shaded* quadrats	Sunny portion	Shady portion	Full shade	Unshaded quadrats	Shaded* quadrats	Unshaded quadrats	Shaded* quadrats	Full shade	
Sept. 10	0-1					11					16	
	1-2					10					19	
	2-3					11					22	
	0-3	8	10	11	15	11	9	9	8	9	24	
	3-6	13	14	20	23		8	16	8	9		
	6-9	21	16	24	27		7	17	10	10		
	9-12	15										
	3-5					14					50	
	20	0-1					11					31
		1-2					13					24
		2-3					12					22
		0-3	8	9	16	21	13	17	9	9	11	26
3-6		14	11	20	24		11	13	9	11		
6-9		20	19	20	32		10	17	9	11		
9-12		15										
3-5						15					24	
Oct. 1	0-1					30					54	
	1-2					29					48	
	2-3					23					40	
	0-3	17	20	33	37	29	26	13	15	19	51	
	3-6	17	17	26	37		23	13	12	20		
	6-9	22	25	24	28		16	14	15	17		
	9-12	19										
	3-5					18					39	

*By screening.

fenced, rodent damage was extensive in spite of active trapping and poisoning. Mice (*Peromyscus maniculatus* var.)²¹ were particularly abundant. Mortality due to rodents was confined almost entirely to pine. Numerous seedlings were bitten off, but even greater numbers

21. Identified for the writer by S. C. Ball, Yale University.

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were broken by rodents engaged in digging up ungerminated seed. These losses left only a small sample of seedlings, some 200 all told, upon which to follow white pine mortality from other causes. Western hemlock did not suffer from rodents, and the seedling sample of this species totaled about 3,000 on all quadrats combined.

One of the outstanding features of mortality on the north-slope habitats was the reversal of rôles between insolation and drought. The northern exposure effectively eliminated insolation as an important agent of

TABLE 66. CHRONOLOGY OF CERTAIN EDAPHIC CONDITIONS AND SEEDLING GERMINATION AND MORTALITY ON NORTH-SLOPE STATIONS IN 1934

<i>Item</i>	<i>Station 4 (full-sun)</i>	<i>Station 5 (part-shade)</i>	<i>Station 6 (full-shade)</i>
Germination of fall-sown species begins*	April 25	April 21	April 25
Germination of fall-sown species completed..	June 5	June 5	June 11
Germination of spring-sown western white pine begins.	June 10	June 10	None sown
Germination of spring-sown western white pine completed.	July 15	July 3	None sown
Last stragglers appear.	July 30	July 3	June 27
First deaths from fungous attack.	April 29	April 27	May 6
Deaths from fungous attack become rare.	June 11	June 15	June 20
First drying of surface soil	{ Duff. April 23	{ April 23	{ April 23
	{ Mineral. May 22	{ June 11	{ June 15
First surface temperature of 120°F. or more	{ Duff. May 15	{ May 24	{ None
	{ Mineral. May 28	{ June 26	{ None
First deaths from insolation occur	{ Duff. May 25	{ May 24	{ None
	{ Mineral. May 28	{ June 27	{ None
First deaths from drought occur	{ Duff. May 25	{ May 24	{ June 14
	{ Mineral. June 11	{ June 14	{ June 18

* Snow disappeared at the control station on March 10.

mortality even on the full-sun station; only 3 per cent of pine and 9 per cent of hemlock were killed by insolation on mineral surfaces on the full-sun station. Critical soil moisture conditions, on the contrary, were not greatly affected by aspect, and drought became the more important factor in mortality. On the cutover areas, for example, an average of 52 per cent of hemlock and 22 per cent of pine died of drought, as compared with insolation losses of 6 per cent in hemlock and 2 per cent in pine. As before, drought was the only physical agent of importance in full shade. The comparison between stations, also, is reversed on the

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north slope. At least, in 1934 the smallest losses were on the full-sun area, only 66 per cent of total germination dying on this habitat as compared with 73 and 97 per cent, respectively, in part and full shade.

TABLE 67. SEEDLING MORTALITY OF ALL SPECIES ON NORTH-SLOPE AREA IN 1934, BY STATION AND CAUSE

Cause	Mortality percentages, by station and species, in terms of total germination						Average
	Station 4 (full-sun)		Station 5 (part-shade)		Station 6 (full-shade)		
	West-ern white pine	West-ern hem-lock	West-ern white pine	West-ern hem-lock	West-ern white pine	West-ern hem-lock	
Fungi.....	11	23	7	20	47	12	20
Insects, birds, and rodents.....	11	7	20	13	44	21	19
Insolation.....	3	9	1	4	0	0	3
Drought.....	19	48	25	56	9	61	36
Total.....	44	87	53	93	100	94	78
Average.....	66		73		97		

TABLE 68. SEEDLING MORTALITY ON DUFF AND MINERAL SURFACES ON CUTOVER NORTH-SLOPE STATIONS IN 1934

Cause	Mortality percentages, by species and surface, in terms of total germination			
	Western white pine		Western hemlock	
	Duff	Mineral	Duff	Mineral
Fungi.....	10	9	28	22
Insects, birds, and rodents.....	36	16	8	10
Insolation.....	7	2	21	6
Drought.....	12	22	38	52
Total.....	65	49	95	90

Duff again proved to be a more severe surface on full-sun and part-shade habitats. As shown in Table 68, insolation losses were materially higher on duff; some 21 per cent of hemlock was killed on duff as against

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6 per cent on mineral, and comparable losses in pine averaged 7 per cent on duff as against 2 per cent on mineral. Losses from fungi and insects, also, were somewhat higher on duff. Drought losses, on the contrary,

TABLE 69. SOIL DRYING AND ROOT PENETRATION ON FULL-SUN STATION IN 1934

Date	Depth, in inches, to which soil was dry*	Depth, in inches, of penetration of seedling roots, by species				Remarks
		Western white pine		Western hemlock		
		Min.	Max.	Min.	Max.	
May 10	0	1.3	2.0	0.4	0.6	
25	¼	1.4	2.4	0.5	1.1	Many hemlocks dead on one very dry quadrat.
June 5	0	1.7	3.0	0.5	1.4	May 29-June 4, frequent rains totaling 0.66 inch.
15	½	1.9	3.9	0.6	1.8	Hemlock deaths begin.
25	1	2.3	4.8	0.8	2.1	Many hemlocks succumbing.
30	0	2.6	5.2	0.9	2.3	June 26-27, rains totaling 0.32 inch. Deaths decline.
July 10	2	3.2	6.1	1.2	2.6	Hemlock deaths resume in large numbers.
20	4½	3.8	6.9	1.4	2.9	
Aug. 1	5½	4.4	7.7	1.6	3.2	Aug. 3, rain of 0.08 inch, penetrating ¼-½ inch on Jurgens Flat.
10	7	4.8	8.2	1.7	3.5	
20	9	5.2	8.8	1.8	3.7	Several white pine deaths. Large, steady loss of hemlock.
30	10	No data		2.0	4.0	
Sept. 10	10+	"	"	2.1	4.3	Rain of 0.06 inch penetrating ½ inch on Jurgens Flat.
20	10+	"	"	2.2	4.5	Sept. 10-16 and 22-28, light rains.
Oct. 1	6-9	"	"	No data		Surface soil moist with dry layer beneath.
10	0	"	"	" "		

* Moisture content at or near wilting coefficient to this depth.

were consistently lower on duff quadrats, though drought remained the more important physical factor on both types of surface.

The critical soil moisture conditions existing in 1934 are depicted in

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Tables 69 to 71, inclusive, which show how soil drying progressed in relation to depth of root penetration. As shown in these tables, threatening drought conditions existed on the full-sun and part-shade areas from

TABLE 70. SOIL DRYING AND ROOT PENETRATION ON PART-SHADE STATION IN 1934

Date	Depth, in inches, to which soil was dry*	Depth, in inches, of penetration of seedling roots, by species				Remarks
		Western white pine		Western hemlock		
		Min.	Max.	Min.	Max.	
May 10	0	1.4	2.2	0.3	0.9	
25	0	1.6	2.5	0.4	1.4	May 29-June 4, frequent rains totaling 0.66 inch.
June 15	½	2.2	3.4	0.7	2.0	A few hemlock dead on dry quadrats.
25	¾	2.8	4.1	0.8	2.3	More hemlock deaths.
30	0	3.0	4.6	0.9	2.5	June 26-27, rains totaling 0.32 inch. Deaths decline.
July 10	2	3.7	5.6	1.2	2.9	Hemlock deaths resume in large numbers.
20	3½	4.3	6.6	1.4	3.1	
Aug. 1	5	5.1	7.8	1.6	3.5	Aug. 3, rain of 0.08 inch penetrating ¼-½ inch on Jurgens Flat.
10	7½	5.7	8.7	No data		Large, steady drought loss in hemlock.
20	10	6.3	9.7	“	“	
30	10+	No data		“	“	
Sept. 10	10+	“	“	“	“	Rain of 0.06 inch penetrated ½ inch on Jurgens Flat. White pine deaths reach maximum.
20	10+	“	“	“	“	Sept. 10-16 and 22-28, light rains.
Oct. 1	3-9	“	“	“	“	Surface soil moist with slightly dry layer beneath.
10	0	“	“	“	“	

* Moisture content at or near wilting coefficient to this depth.

about June 15 on for hemlock and from July 20 on for pine. These critical conditions existed unbroken until early October. Drought deaths occurred as early as June 18 in full shade. There is little doubt, however, that the rôle of drought is somewhat if not greatly exaggerated in the

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summaries presented for 1934 mortality on north-slope habitats. Not only was the 1934 season unusually severe, but, as explained in the discussion of soil moisture conditions, drought was particularly acute because of the material amount of subsurface drying on the part-cut and

TABLE 71. SOIL DRYING AND ROOT PENETRATION ON FULL-SHADE STATION IN 1934

Date	Depth, in inches, to which soil was dry*	Depth, in inches, of penetration of seedling roots, by species				Remarks
		Western white pine†		Western hemlock		
		Min.	Max.	Min.	Max.	
May 10	0	1.2	1.7	0.4	0.8	May 29-June 4, frequent rains totaling 0.66 inch.
25	0	1.3	1.8	0.5	0.9	
June 5	0	1.5	2.0	0.5	0.9	Starting June 18, large numbers of western hemlock killed. June 26-27, rains totaling 0.32 inch.
15	¼	1.6	2.1	0.5	1.0	
25	¾	1.8	2.2	0.6	1.1	
30	0	1.8	2.3	0.6	1.2	
July 10	½	1.9	2.4	0.7	1.4	Western hemlock again dying in large numbers.
20	1	No data		0.7	1.5	
Aug. 1	2	“	“	0.8	1.8	Several western white pine succumb to drought. Western hemlock virtually all killed.
10	2	“	“	No data		
20	1½	“	“	“	“	
30	3	“	“	“	“	
Sept. 10	1	“	“	“	“	Sept. 10-16, light rains.
20	0	“	“	“	“	

* Moisture content at or near wilting coefficient to this depth.

† Lack of data for July 20 and later dates is due chiefly to insufficient germination.

full-sun habitats caused by the water demands of brush and seedling vegetation. Vegetation of this density would not exist upon most freshly cut areas in the western white pine type, and seedlings starting in the first few years after logging would consequently be freed of such competition for moisture. If brush conditions were more normal, it seems prob-

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able that soil moisture conditions on full-sun and part-shade north-slope habitats would more closely approximate conditions on the part-shade area of the river flat stations. Certainly rapidity and depth of root penetration are fairly comparable between these habitats (Table 72).

Under these circumstances, and because the small sample of white pine seedlings precludes statistical analysis of the data, it is obvious that considerable additional work is needed, preferably upon newly logged habi-

TABLE 72. RELATIVE DEPTH AND PROGRESS OF ROOT PENETRATION ON RIVER FLAT AND NORTH-SLOPE AREAS

<i>Date</i>	<i>Species</i>	<i>Average maximum depth, in inches, of penetration of root tip, by area, year, and station</i>					
		<i>River flat</i>				<i>North slope</i>	
		<i>1932</i>		<i>1933</i>		<i>1934</i>	
		<i>Station 1 (full- sun)</i>	<i>Station 2 (part- shade)</i>	<i>Station 1 (full- sun)</i>	<i>Station 2 (part- shade)</i>	<i>Station 4 (full- sun)</i>	<i>Station 5 (part- shade)</i>
May 10	{ Western white pine	1.7	1.6	0.8	..	2.0	2.2
	{ Western hemlock	1.1	0.7	0.5	..	0.8	0.9
June 10	{ Western white pine	4.4	3.8	4.1	2.3	3.4	3.3
	{ Western hemlock	2.0	1.8	1.6	1.3	1.6	1.9
July 10	{ Western white pine	7.1	6.1	7.7	4.8	6.1	5.6
	{ Western hemlock	3.7	2.9	3.1	3.2	2.6	2.9
Aug. 10	{ Western white pine	9.5	7.7	11.0	7.4	8.2	8.7
	{ Western hemlock	..	3.9	..	4.9	3.5	3.6
Sept. 10	{ Western white pine	11.5	8.8	12.1	8.6
	{ Western hemlock	..	4.8	..	5.7	4.3	..

tats, before the exact rôle of physical factors can be defined. However, it seems probable that insolation will never be much of a factor on more sheltered habitats, and that upon such areas drought will play the more important rôle. As drought is much more effective with western hemlock and western red cedar and under certain circumstances with western larch than with their common associates, it is apparent that, although conditions are generally favorable for all species upon northerly aspects,

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they are relatively more favorable for western white pine, lowland white fir, and Douglas fir. In addition, because dangerous surface soil temperatures are largely eliminated on northern aspects, it seems probable that

TABLE 73. FIRST-WINTER AND SECOND-GROWING-SEASON SEEDLING MORTALITY ON MINERAL SURFACES

<i>Station and tree species</i>	<i>Seedling mortality percentages, in terms of total germination</i>	
	<i>Winter, 1933-1934</i>	<i>Summer, 1934</i>
Station 1 (full-sun)		
Western white pine.....	4	3
Douglas fir.....	3	12
Western larch.....	7	26
Lowland white fir.....	4	18
Western hemlock.....	6	0
Western red cedar.....	37	1
Average.....	10*	10*
Station 2 (part-shade)		
Western white pine.....	1	7
Douglas fir.....	3	3
Western larch.....	16	2
Lowland white fir.....	2	2
Western hemlock.....	7	3
Western red cedar.....	11	2
Average.....	7	3
Station 3 (full-shade)		
Western white pine.....	20	1
Douglas fir.....	14	0
Western larch.....	4	0
Lowland white fir.....	20	17
Western hemlock.....	1	1
Western red cedar.....	24	11
Average.....	14	5

* Based on one quadrat only. This quadrat was shaded during the initial season.

on such aspects, clear-cutting can be employed with reasonable safety and with considerable promise that it will result in an appreciably greater proportion of western white pine.

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SECOND-SEASON MORTALITY

During 1934 a record was kept of winter and second-growing-season mortality on a number of quadrats on the river flat stations. The records for mineral and duff quadrats, respectively, are summarized in Tables 73 and 74. Though the basis is small, it is apparent that winter losses and second-year losses, even in a season as severe as 1934, were much lower than losses in the initial growing season. Second-season losses were

TABLE 74. FIRST-WINTER AND SECOND-GROWING-SEASON SEEDLING MORTALITY ON DUFF SURFACES

<i>Station* and tree species</i>	<i>Seedling mortality percentages, in terms of total germination</i>	
	<i>Winter, 1933-1934</i>	<i>Summer, 1934</i>
Station 2 (part-shade)		
Western white pine.....	1	1
Douglas fir.....	1	2
Western larch.....	1	1
Lowland white fir.....	2	1
Western hemlock.....	0	0
Western red cedar.....	0	0
Average.....	1	1
Station 3 (full-shade)		
Western white pine.....	38	5
Douglas fir.....	17	35
Western larch.....	2	1
Lowland white fir.....	6	21
Western hemlock.....	0	1
Western red cedar.....	2	13
Average.....	11	13

* No data were obtained for the full-sun station.

often serious, however, particularly with more susceptible species. On mineral quadrats on the full-sun station winter and second-season losses ranged from 7 per cent in western white pine to 100 per cent of all remaining seedlings in hemlock and cedar. Short-rooted species suffered most heavily in the winter, largely because of frost heaving. Winter losses were very heavy in full shade, and at the end of the second growing season only 2 per cent of lowland white fir and 1 per cent of Douglas fir

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were left alive on this habitat. The losses in part shade were the smallest, averaging only 7 per cent during the first winter and 3 per cent in the second summer in terms of total germination of all species combined, another indication of the favorable condition of this habitat from the standpoint of early survival. On both cutover habitats western white pine continued to show the lowest mortality at the end of the second season (including both initial and second-season losses), with lowland white fir, western larch, and Douglas fir following closely in the order named. During the second growing season insolation was again the most important physical agent of mortality on the full-sun station; on an exposed quadrat where high surface soil temperatures and drought were both active about 15 per cent of all seedlings died as against 1.5 per cent on a near-by quadrat where dangerous temperatures were eliminated by protective screening.

No seedlings remained alive on duff surfaces on the full-sun area. On the other areas winter and second-year losses were less severe on duff than on mineral surfaces. On duff in part shade 2 per cent only of the total germination died during the winter and second growing season, although only 13 per cent of the total germination had survived the first season. Under full shade 31 per cent of lowland white fir, 12 per cent of Douglas fir, and 1 per cent each of pine and cedar were still alive on duff surfaces at the end of the 1934 season.

SEEDLING DEVELOPMENT

During the 1932-34 growing seasons some interesting data on seedling development were gathered on the river flat stations. Information was obtained not only upon the growth of freshly germinated seedlings but also on that of transplanted standard planting stock of western white pine and western red cedar. Some western white pine transplants were placed in sealed pots to permit the measuring of water requirements. The discussion here will be largely restricted to the 1934 records, which are relatively complete. These are in reasonably good agreement with the available 1932 and 1933 figures.

These data show that three species, out of the four upon which comparable figures are available, find the part-shade area the most favorable for initial development, at least as far as top growth is concerned.²²

²². K. D. Doak, Bureau of Plant Industry, who examined two-year-old seedlings from the river flat stations, reported that mycorrhizae were found on western white pine only. Pseudomycorrhizae were the predominating types throughout, with this one exception.

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These figures are summarized in Table 75. As shown in that table, the green weights attained at the end of the second growing season by Douglas fir, western larch, and lowland white fir are much higher for the part-shade area than for any of the other habitat stations. Unfortunately, comparable measurements are not available on western hemlock and western red cedar, these species having been completely wiped out on full-sun quadrats. White pine alone shows the best gain in top weight on the full-sun station, another indication of the tendency of this remarkable species to develop well under full-sun conditions. White pine tops averaged 0.61 gram on full-sun mineral quadrats as against 0.35 gram on similar surfaces in part shade. All species showed better growth

TABLE 75. GREEN WEIGHT OF TOPS OF TWO-YEAR-OLD SEEDLINGS,* BY STATION AND SURFACE

Species	Average weight, in grams, by station and surface					
	Station 1 (full-sun)		Station 2 (part-shade)			Station 3 (full-shade)
	Un- shaded min- eral	Shaded min- eral	Duff	Min- eral	Burnt min- eral	Duff and mineral
Western white pine.....	0.61	0.86	0.44	0.35	0.85	..
Douglas fir.....	0.38	0.97	0.36	0.53	0.86	0.07
Western larch.....	0.28	0.84	0.79	0.60	1.64	..
Lowland white fir.....	0.45	1.53	0.78	0.71	1.41	0.14
Western hemlock.....	0.11	0.24	..
Western red cedar.....	..	0.18	..	0.16	0.45	..

* Basis: 40 to 100 seedlings for each value shown.

on the full-sun habitat if given some shelter such as was artificially introduced by screening some quadrats during the 1933 and 1934 seasons. It seems probable, in view of the smaller top-root ratio on the full-sun station, that if weights of roots and tops were combined it would be found that the gains were greater on the full-sun habitat. This is indicated in Table 76, the gains in combined green weights of roots and tops of transplants being greater on the full-sun station.

Top growth, as shown in Tables 76 and 77, was considerably better under part shade. On the part-shade station as compared with the full-sun station the height growth of Douglas fir, western larch, and lowland white fir was practically twice as great and the height growth of pine showed a marked advantage (Table 77). Potted and sealed western white

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pine phytometer records show, however, that if soil moisture is favorable the largest average gain in weight for tops and roots combined is made on the full-sun station. Plate 10 shows the much better root growth made

TABLE 76. DEVELOPMENT OF WESTERN WHITE PINE TRANSPLANTS ON CUTOVER AREAS DURING APRIL-OCTOBER, 1934

<i>Item</i>	<i>Tree species</i>	<i>Station 1 (full-sun)</i>		<i>Station 2 (part-shade)</i>	
		<i>Un- shaded</i>	<i>Shaded</i>	<i>Sunny</i>	<i>Shaded</i>
Gain in green weight, per cent. .	{ Western white pine	24	21	19	5
	{ Western red cedar	..	49	32	5
Average leader length, in inches*.	Western white pine	0.77	0.74	0.85	0.97
Mortality percentage, in terms of total planted.....	{ Western white pine	17	6	0	2
	{ Western red cedar	100†	12†	15	21

* No data were obtained for western red cedar.

† Based on 50 planted seedlings. All other figures based on 100 planted seedlings.

TABLE 77. TOTAL HEIGHT OF TWO-YEAR-OLD SEEDLINGS,* BY SURFACE AND STATION

<i>Tree species</i>	<i>Average total height, in inches, by station and surface</i>					
	<i>Station 1 (full-sun)</i>		<i>Station 2 (part-shade)</i>			<i>Station 3 (full-shade)</i>
	<i>Un- shaded min- eral</i>	<i>Shaded min- eral</i>	<i>Duff</i>	<i>Min- eral</i>	<i>Burnt min- eral</i>	<i>Duff and mineral</i>
Western white pine.....	1.5	2.0	2.3	2.0	2.7	..
Douglas fir.....	1.7	2.9	2.9	3.4	4.2	1.9
Western larch.....	1.6	3.7	4.4	3.8	8.1	..
Lowland white fir.....	1.3	2.3	3.6	3.7	5.1	2.0
Western hemlock.....	1.8	3.0	..
Western red cedar.....	..	1.4	..	2.1	3.2	..

* Each value shown based on 45 to 50 seedlings.

in full sunlight. Gains for root and tops combined averaged 137 per cent on this habitat as against 95 per cent under part shade in forty-eight sealed white pine phytometers grown under optimum moisture condi-

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tions. The water requirement during 1934 was less on the full-sun area, some 569 grams of water being used here for each gram of dry matter produced, as compared with 644 grams under part shade. The much larger gains in weight made by watered phytometers as compared with free phytometers indicate the limiting action of water upon seedling

TABLE 78. COMPARATIVE FERTILITY OF SOIL ON PLAIN AND BURNT MINERAL QUADRATS IN TERMS OF MINERAL NUTRIENTS AND OTHER IMPORTANT SOIL CHARACTERISTICS

	Station 1 (full-sun)				Station 2 (part-shade)			
	0-3 inches		0-9 inches		0-3 inches		0-9 inches	
	Plain mineral	Burnt mineral	Plain mineral	Burnt mineral	Plain mineral	Burnt mineral	Plain mineral	Burnt mineral
Hydrogen-ion concentration, pH.....	6.48	7.26	6.25	..
Total carbon, per cent.....	10.2	8.0	8.6	..
Nitrate nitrogen, parts per million.....	5	30	5	30	1	15	T*	10
Ammonium nitrogen, parts per million.....	1	1	T*	1	1	1	1	1
Available phosphorus, parts per million.....	30	60	15	30	20	60	15	25
Replaceable potassium, parts per million.....	200	200	200	200	70	100	100	80
Replaceable calcium, parts per million.....	1,500	2,000	600	2,000	350	2,000	150	750
Available magnesium, parts per million.....	50	40	70	100	40	50	30	50
Active manganese, parts per million.....	0	T*	0	T*	2	3	T*	1
Active aluminum, parts per million.....	1	1	1	1	1	1	1	1

* Trace.

growth under the dry summer conditions typical of northern Idaho. It is true that 1934 was unusually dry.

One interesting feature brought out in Tables 75 and 77 is the marked effect of burnt mineral soil upon seedling development. During the 1932 season it was noticed that seedlings on burnt mineral quadrats, particularly under part shade, were somewhat larger and appeared more

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vigorous than their associates on near-by natural mineral soil. An end-of-season check on western larch confirmed this observation, the dry material in larch tops averaging about half again as great on the burnt mineral quadrats. Microchemical tests proved that following destruction of a duff layer by fire, the method used in creating burnt mineral surfaces, the supply of several important mineral nutrients, was materially raised. This effect was still appreciable one to two years after the burning. As shown in Table 78, the fire had resulted in a slight to very marked increase in the amount of active manganese, available magnesium, nitrate nitrogen, available phosphorus, and replaceable calcium. It had reduced total carbon content only slightly. Available phosphorus was about doubled on the burnt mineral quadrats, and the change in replaceable calcium and nitrate nitrogen were even larger. These differences were considerably greater in the top 3 inches than at lower levels. The seedling response to more favorable soil conditions was immediate and marked and continued to at least the end of the second growing season (Tables 75 and 77). The tops of western larch, a species particularly sensitive to habitat changes, showed an average green weight of 1.64 grams at the end of the second growing season on burnt mineral as compared with one of 0.60 gram on plain mineral quadrats. In general the material produced in tops, by all species combined, was about twice as much on burnt mineral quadrats as on natural mineral quadrats. The effect of burning on leader growth was even more marked; all species made their best leader growth on burnt mineral quadrats.

Mortality figures for 1934 on transplant stock are summarized in Table 76. Even at this fairly advanced age it was evident that insolation was still an active factor of mortality in full sun, 17 per cent of the white pine and 100 per cent of the cedar dying on exposed parts of the full-sun area, compared with 6 and 12 per cent, respectively, under artificial screens. On the shady portion of the part-shade study station the losses ran higher, but it is impossible to say without further experimentation whether these differences are real or accidental.

No transplant stock was used during the 1934 season on the full-shade river flat habitat, experience during the two preceding seasons having shown that western white pine fails to establish itself on this area. In full shade the gain in weight even by cedar transplants is so small as to make accurate comparisons difficult. The relative success of cedar and the complete failure of white pine under full shade are apparently caused by the ability of cedar to produce new root growth in full-shade condi-

SUMMARY AND CONCLUSIONS

tions and thus develop normally, if very slowly, and the inability of pine to produce enough new root shoots to maintain the necessary absorbing surface. Though pine transplants produced new leader growth and leaves on the full-shade habitats in the two years studied, at the end of the growing season their green weights were actually less than at the beginning and the plants gave evidence through the relative brittleness of their stems and leaves of slow death by drought. New root growth on pines was for the most part rare, and the root systems were badly decayed by the end of the growing season (Plate 10 C). Cedar root systems, though not vigorous, displayed a reasonable number of new shoots. Fundamental silvical differences of this sort may have an important bearing on successional trends in the western white pine type and may partially explain the abundance of cedar and the scarcity of pine in climax stands.

SUMMARY AND CONCLUSIONS

DURING the seasons of 1932 and 1933 on three habitat stations at the Priest River Experimental Forest a study was made of seedling mortality of western white pine (*Pinus monticola*) and the following associated tree species: western larch (*Larix occidentalis*), Douglas fir (*Pseudotsuga taxifolia*), lowland white fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). These stations were all located on a large river flat that represented severe to moderately severe conditions for western white pine, though up to the time of logging it had been covered with a magnificent stand of western white pine and associated species. The stations were within several hundred feet of one another, on the same soil type, and varied materially only in density of overwood. One station had been clear-cut; one had been part-cut, a fairly heavy stand mostly of hemlock and cedar (including a number of understory trees) being reserved; the third station was located in an uncut, dense, overmature stand consisting largely of western red cedar and western hemlock.

The variation in density of the overwood stand was directly reflected in important differences in microclimate. In general, temperatures, wind velocity, evaporation, and radiation intensities increased materially with decrease in overwood shade. These differences influenced in turn the character and extent of seedling mortality in the first season following germination, the most critical part of the regeneration period. Losses

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were studied by means of small sown plats, scattered over the habitat areas, the surface layers of which were of natural mineral soil, burnt mineral soil, and duff. Some quadrats were specially treated, i.e., watered, trenched, or screened. Each plat was sown heavily enough to insure a large sample of seedlings. The number present on the mineral soil surfaces averaged 348 per plat in 1932 and 185 per plat in 1933. In spite of **extra-heavy** sowing, germination on duff quadrats was practically a failure on the full-sun station, partially a failure on the part-shade station, and really satisfactory in full shade only.

The principal object of the study was to determine the rôles played by important physical factors of site, chiefly as these vary with overhead shade and hence are within the control of the silviculturist at the time of logging. No special effort was made to study the effect of biotic agents under natural conditions. Indeed, in order to insure as large a sample of seedlings as possible on which to follow losses caused by physical factors, biotic agents were discouraged wherever feasible. But as records of all mortality losses were kept by cause, some information was collected on the activity of biotic factors. Seedlings were classified as to cause of death only after a careful diagnosis and with knowledge of the important agents operating at the time death occurred. Certain check quadrats were used effectively in segregating causes; but the most satisfactory control came in instrumental measurement of important site factors, including surface soil temperature and soil moisture. As a necessary adjunct in following the occurrence of critical soil moisture conditions, current measurements were made of root penetration.

In addition to the 1932 and 1933 studies, some preliminary data were gathered in 1934 upon the rôle of various agents in mortality of first-year seedlings on a sheltered north slope and in mortality and development of second-year seedlings on the river flat stations. In general, the following conclusions were drawn directly only from the relatively severe river flat areas:

(1) The important direct agents of mortality, in addition to rodents, are soil fungi, soil insects (cutworms), surface soil temperature, and soil moisture.

† (2) Among the biotic agents, with the possible exception of rodents, damping-off organisms are the most effective, killing four to five times as many seedlings as insects and birds combined. Mortality due to fungi and insects varies erratically by habitat, year, and-species. Losses from fungi average materially heavier on duff than on mineral surfaces, except

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under full shade, and are 'equal to or heavier on full-sun than on the part- and full-shade habitats.⁷

(3) Insolation and drought are the most important physical factors affecting initial seedling mortality. Insolation is by far the most important factor on relatively severe cutover areas, and drought the most important under full timber. But on more favorable cutover areas, such as northerly slopes, insolation may be the minor and drought the major killing agent.

(4) Light is not a direct factor in initial mortality. Seedlings are able to survive the first season under intensities as low as 5 per cent of full sunlight if not killed by biotic agents or drought. Light may, however, be an important indirect factor in survival through its effect on growth, particularly on initial root penetration.

(5) Losses due to insolation are, of course, materially higher on exposed quadrats, i.e., on the full-sun station or on sunny portions of the part-shade area.

(6) Losses from insolation on cutover areas are materially higher on duff surfaces than on mineral surfaces.

(7) Losses due to drought are primarily caused by surface drying. The amount of such loss is directly linked with the root penetration-soil moisture balance. It is greatest in full shade, where shallow surface drying effectively overtakes shallow root penetration; very much less in full sun, where rapid and relatively deep drying is largely compensated for by rapid and relatively deep root penetration; and least in part shade, where moderate conditions of both drying and root penetration create the most favorable soil moisture-root penetration balance. Where brush cover is moderately heavy, vegetative competition for moisture may play an important part in creating drought conditions.

(8) In general, the species studied fall into two classes with regard to their relative resistance to adverse physical factors. Western white pine, lowland white fir, Douglas fir, and western larch are relatively resistant on cutover areas, while western red cedar and western hemlock are relatively susceptible. Western white pine and lowland white fir are apparently somewhat more resistant to killing agents than their relatively hardy associates; but, as overwood shade increases, this distinction decreases, Douglas fir and larch being as hardy as pine under part shade. Of the two susceptible species, western red cedar is somewhat hardier than hemlock.

(9) On the severe river flats the best survival during the critical initial

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season occurred under a relatively heavy overwood stand. Any decrease in shade caused direct **increase** in deaths from insolation, while an increase in shade increased mortality due to drought. The parallel course of microclimatic factor and seedling mortality over the 1932 and 1933 seasons indicates that the rôles played therein by the principal habitat factors will be repeated from year to year during moderate to severe seasons. Reduction in surface soil temperatures, however, brought about either by overhead shade or by change in aspect, will immediately lower the proportion of insolation deaths with an appreciable relative increase in drought deaths. This has already been observed on a lower north-slope site typical of western white pine conditions. On such northerly slopes regeneration of white pine is probably favored by clear-cutting or by retention of not more than a very light residual stand.

APPLICATION IN SILVICULTURAL PRACTICE

IT IS apparent from the foregoing discussion that in the western white pine type the silviculturist can materially modify the quantity and to some extent the composition of the regeneration by adroit manipulation of the character and density of the residual stand. In general, upon the severe to moderately severe river flat sites forming the main study habitats in this investigation, the most abundant regeneration is brought about by retaining a fairly heavy residual stand, which moderates the effects of insolation while maintaining a favorable root penetration-soil moisture balance. Under these conditions insolation and drought, the main physical agents of initial mortality, are largely eliminated, biotic losses are relatively low, and initial survival of all species is correspondingly high. The conditions created by part shade proved to be favorable not only to initial survival but also to survival and growth during the second season. On the clear-cut flats insolation, drought, and various biotic causes united to eliminate 87 to 95 per cent of the entire seedling crop, with insolation the most dangerous factor. Preliminary **work** indicates, as would logically be expected, that on less severe sites, such as northerly aspects, insolation is largely eliminated as a killing factor; consequently, on such aspects clear-cutting can be practiced without unduly endangering the entire seedling crop.

Adequate regeneration, however, in point of number of seedlings per acre, is only one phase of the problem with which the silviculturist must

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deal in the complex western white pine type. Attention must also be given to the often more difficult problem of obtaining the most desirable composition in the seedling stand. It is obvious that composition is governed by a number of factors in addition to those affecting initial seedling survival. It cannot be too strongly emphasized that this report deals solely with initial survival and that in applying its conclusions additional factors, such as seed supply and later development of the seedling stand, must be considered. Nevertheless, within these limits, it is apparent that material changes can be introduced in stand composition by proper control of overwood shade. Clear-cutting on severe habitats will tend to reduce materially the percentages of western red cedar and western hemlock, as these species are far more susceptible to the resulting severity of insolation and drought conditions than their common associates. **Western** white pine and lowland white fir, on the contrary, as nearly as can be judged from the 1932 and 1933 records, tend to reach maximum stand percentages under full-sun conditions, as they are hardier on exposed areas. Upon the more severe habitats, however, clear-cutting is followed by mortality losses so heavy as to endanger the prospect of obtaining a seedling stand adequate in numbers. In addition, manipulation of the composition of the initial seedling stand by density of overhead shade is limited by the fact that it is apparently impossible, except within narrow limits, to encourage the commercially valuable western red cedar without also encouraging western hemlock, a species of low commercial value, or to encourage the highly valuable western white pine **without** also encouraging the commercially inferior lowland white fir. This distinct limitation to the practical influence of silvicultural methods affecting density of residual stand is by no means the least important finding of this study. It indicates the probable necessity of employing cultural methods, such as weedings, if composition of the final crop is to be effectively controlled.

In general, survival records, summarized in Table 79, indicate that on moderately severe to severe areas it is advisable to leave a moderate amount of shade in order to ameliorate the influence of insolation and assure a satisfactory quantity of regeneration. On the severe river flat-habitats from 44 to 92 per cent of residual seedlings of all species survived under part shade, compared with only 13 per cent under full sun. This simply confirms and furnishes a more exact understanding of the best present practice on such areas. Under full-sun conditions, however,

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western white pine and its hardier associates are favored over cedar and hemlock. The retention of too heavy part shade, on the contrary, results in an appreciable increase of the more susceptible species, other factors being equal. Except for its undesirable effect on composition, the records indicate that part shade will furnish satisfactory conditions on severe, warm sites for both early survival and development, even where only 15 to 20 per cent of total solar radiation reaches the ground level.

Data on north-slope conditions (Table 79), although very meagre, indicate that clear-cutting offers the best promise of producing the seedling stand most desirable in both quantity and composition. On

TABLE 79. INITIAL SURVIVAL ON MINERAL SURFACES, BY SPECIES AND HABITAT

<i>Species</i>	<i>Survival percentages, in terms of residual seedlings</i>					
	<i>River flat, 1932-1933</i>				<i>North slope, 1934</i>	
	<i>Full-sun area</i>	<i>Part-shade area</i>			<i>Full-sun area</i>	<i>Part-shade area</i>
		<i>Sunny</i>	<i>Shady</i>	<i>Average</i>		
Western white pine.....	33	76	100	86	73	60
Douglas fir.....	14	66	99	85
Western larch.....	20	47	91	74
Lowland white fir*.....	11	76	100	92
Western hemlock.....	0	1	71	45	7	4
Western red cedar.....	0	0	93	57
Average.....	13	44	92	73	40	32

* 1933 record only.

such slopes insolation is largely eliminated as a killing factor by aspect alone, and western white pine is otherwise favored by full-sun conditions. Drought, even on such areas, materially reduces the crop of cedar and hemlock, but may spare an appreciable percentage of even these species. These facts, again, simply confirm the best present practice. They indicate, however, that leaving much heavier residual stands—as is done in selective logging or under the present policy of the United States Forest Service Region One which leaves a large volume of sound mixed species on the sale areas of national forests—although it tends to insure a full and adequate seedling stand and create conditions for satisfactory initial development, will tend also, entirely aside from its effect on seed

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source, to reduce materially the proportion of western white pine and other relatively hardy associates and increase the proportion of western red cedar and western hemlock.

This study brings out also the fact that duff surfaces are relatively unsatisfactory from the standpoint of both germination and initial survival, first-year seedling losses being materially higher on duff than on mineral soil. If in the future it should prove desirable to leave the forest floor undisturbed wherever possible, in an effort to discourage the germination of *Ribes* seed and thus aid in blister rust control, it must be remembered that undisturbed natural duff layers present a particularly hazardous condition from the standpoint of initial survival, particularly on severe sites.

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METHODS OF STATISTICAL ANALYSIS USED

THE statistical analysis made in connection with this study²³ consisted in a detailed examination for significant variation in mortality losses between the various tree species common in the western white pine type on the surfaces and habitat stations tested. In general, the analysis followed the methods outlined by Fisher and Wishart in *The Arrangement of Field Experiments and the Statistical Reduction of the Results*, Imperial Bureau of Soil Science, Tech. Com. 10, 1930. However, in testing mean squares for significance it was found more convenient to use the tabular values of F listed by Snedecor (97), Table XXXV. For explanation of the principles and computational technique involved, the reader is referred to these and other publications on variance and covariance. This section summarizes the major features of the statistical analysis underlying comparisons made in this bulletin.

This analysis was somewhat complicated by certain features of the field arrangement, particularly the lack of replication of quadrats in equal numbers for each type of surface for all stations and years. For example, charcoal, watered, and trenched quadrats were used only during the 1932 season, and burnt mineral quadrats were never installed under full shade. There were also a number of unavoidable gaps of other kinds; data on lowland white fir are totally lacking for 1932, because local seed was unobtainable; and values for duff quadrats are frequently lacking, because of unsatisfactory germination on that medium. In addition, owing to the fact that small changes in the environmental complex between seasons may have different effects on different species and thereby change the magnitude or trends of mortality losses between species,

23. The writer wishes to acknowledge his debt to F. X. Schumacher, United States Forest Service, for valuable suggestions in connection with this section.

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TABLE 80. SEEDLING MORTALITY CAUSED BY FUNGI IN 1932, BY SPECIES, STATION, AND SURFACE MATERIAL OR QUADRAT TREATMENT

<i>Species</i>	<i>Mortality percentages, by station and material or quadrat treatment, in terms of total germination</i>												<i>Total</i>
	<i>Station 1 (full-sun)</i>				<i>Station 2 (part-shade)</i>				<i>Station 3 (full-shade)</i>				
	<i>Mineral</i>	<i>Charcoal</i>	<i>Watered</i>	<i>Trenched</i>	<i>Mineral</i>	<i>Charcoal</i>	<i>Watered</i>	<i>Trenched</i>	<i>Mineral</i>	<i>Charcoal</i>	<i>Watered</i>	<i>Trenched</i>	
Western white pine.....	24	44	18	36	10	12	22	4	10	21	21	13	235
Douglas fir.....	14	23	18	39	11	10	6	4	16	17	2	8	168
Western larch.....	10	16	11	33	17	6	1	4	8	13	10	18	147
Western hemlock.....	24	68	32	24	18	6	3	17	6	5	21	23	247
Western red cedar.....	45	60	37	47	17	14	12	7	12	18	21	11	301
Total.....	117	211	116	179	73	48	44	36	52	74	75	73	1,098

TABLE 81. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY FUNGI ON MINERAL SURFACES IN 1932*

<i>Source of variance</i>	<i>Degrees of freedom</i>	<i>Sum of squares</i>	<i>Mean square</i>	<i>Ratio</i>	<i>Values for</i>		<i>Significance</i>
					<i>0.05</i>	<i>0.01</i>	
Species.....	4	1,295.6	323.9	3.98	2.78	4.22	Medium
Surface.....	3	414.7	138.2	1.70	3.01	4.72	None
Station.....	2	5,086.9	2,543.4	31.2	3.40	5.61	High
Interaction:							
Species x surface.....	12	414.3	34.5	0.42	2.50	3.78	None
Species x station.....	8	1,042.6	130.3	1.60	2.36	3.36	None
Surface x station.....	6	1,146.2	191.0	2.35	2.51	3.67	None
Error.....	24	1,954.3	81.4				
Total.....	59	11,354.6					

* Mortality values are given in Table 80.

surfaces, and stations, it is necessary to consider all combinations involving year with considerable caution.

Most of these limitations are illustrated in the analysis of mortality losses caused by soil-inhabiting fungi. The first step in this analysis was an examina-

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tion for significant differences among the losses recorded in 1932 for five species on four types of mineral surface and three habitat stations. The data are given in Table 80. Because mortality values were available for only one trenched quadrat on each station, the replicated values for each of the kinds of nontrenched quadrats were averaged to get a single comparable figure. The undesirable features of this procedure, including the consequent reduction in supporting data and the possibility that significant trends may be somewhat obscured, are recognized. In other parts of the analysis values for individual quadrats have been employed so far as possible. The possibility of grave errors is very remote, however, for the composite values are never based on an average

TABLE 82. SEEDLING MORTALITY DUE TO FUNGI ON MINERAL SURFACES IN 1932

<i>Item</i>	<i>Western white pine</i>	<i>Douglas fir</i>	<i>Western larch</i>	<i>Western hemlock</i>	<i>Red cedar</i>	<i>Mean</i>	<i>Stand- ard error</i>
Average mortality percent- age, in terms of total germa- ination.....	19.6	14.0	12.2	20.6	25.1	18.3	±2.6

TABLE 83. SEEDLING MORTALITY* DUE TO FUNGI IN 1932, AS AFFECTED BY SURFACE MATERIAL OR TREATMENT

<i>Item</i>	<i>Mineral</i>	<i>Charcoal</i>	<i>Watered</i>	<i>Trenched</i>	<i>Mean</i>	<i>Standard error</i>
Average mortality percentage, in terms of total germina- tion.....	16.1	22.2	15.7	19.2	18.3	±2.3

* All species combined.

of more than four quadrats. In Table 80 all the values other than those for the trenched quadrat are averages of values for two or three quadrats.

The resulting variance table (Table 81) shows that the mortality values listed vary significantly by species and station, the mean squares of these items being materially higher than would be expected on the basis of chance, while average mortality losses on the various surfaces tested do not vary significantly one from the other. Interaction values also are not significant. Under these circumstances Fisher and Wishart (see pages 14-15) suggest that standard error be computed from the mean square of error and the average values compared in tables such as Tables 82 to 84 inclusive. (Except to illustrate the method, mortality losses by surfaces would not be tabulated, as they have been shown in Table 81 not to vary significantly.) The standard errors shown apply to any one

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of the mean values given in the same summary. The product of standard error multiplied by 3, used here as the measure of the limits of significant differences, approximates that obtained by multiplying the standard error of the difference by 2. Any individual differences larger than the values so derived, with items shown to vary significantly on the whole, are usually regarded as significant.

TABLE 84. SEEDLING MORTALITY* DUE TO FUNGI IN 1932, AS AFFECTED BY STATION

<i>Item</i>	<i>Station 1 (full- sun)</i>	<i>Station 2 (part- shade)</i>	<i>Station 3 (full- shade)</i>	<i>Mean</i>	<i>Standard error</i>
Average mortality percentage, in terms of total germination.	31.2	10.0	13.7	18.3	±2.0

* On mineral surfaces, all species combined.

TABLE 85. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY FUNGI ON MINERAL SURFACES* IN 1932 AND 1933 COMBINED

<i>Source of variance</i>	<i>Degrees of freedom</i>	<i>Sum of squares</i>	<i>Mean square</i>	<i>Ratio</i>	<i>Values for</i>		<i>Signifi- cance</i>
					<i>0.05</i>	<i>0.01</i>	
Species.	4	1,022.82	255.70	3.03	2.52	3.65	Medium
Station.	2	2,134.42	1,067.21	12.66	3.15	4.98	High
Year.	1	5,872.54	5,872.54	69.66	4.00	7.08	High
Interaction:							
Species × station.	8	3,872.25	484.03	5.74	2.10	2.82	High
Species × year.	4	1,464.49	366.12	4.34	2.52	3.65	High
Station × year.	2	3,295.78	1,647.89	19.55	3.15	4.98	High
Remainder (2d order interaction).	8	2,982.02	372.75	4.42	2.10	2.82	High
Error.	60	5,058.00	84.30				
Total.	89	25,702.32	288.79				

* Basic data consist of mortality losses in percentage of total germination for five species on three habitat stations, respectively. All values were from individual species plats on three mineral or burnt mineral quadrats on each area.

With these preliminary results as a working base, the logical next step involved a study of records from both the 1932 and the 1933 season to see whether the relations found were constant from season to season. The main variance table used in this analysis is Table 85. The general indications from this analysis, which have been confirmed in a number of similar computations involving data

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drawn from different combinations of station, surface, and year, are that losses from fungi may be significantly different among various species or stations in a given season but that this relation varies from season to season. On Station 2, for example, western larch showed the heaviest loss from fungi in 1932 but showed a significantly lower loss than any other species in 1933. In the same manner losses from fungi were significantly higher on Station 1 in 1932 but were somewhat higher on Station 3 in the following year. This situation is indicated in Table 85 in the significantly high interaction values between species \times year and station \times year, respectively. Both species and station means tend to vary

TABLE 86. SEEDLING MORTALITY* CAUSED BY ALL PHYSICAL FACTORS COMBINED IN 1933

<i>Species</i>	<i>Mortality percentages, by station, shade condition, and quadrat, in terms of residual seedlings</i>												<i>Total</i>	
	<i>Station 1 (full-sun)</i>			<i>Station 2 (part-shade)</i>						<i>Station 3 (full-shade)</i>				
				<i>Shady portion</i>			<i>Sunny portion</i>							
	<i>Quadrat No.</i>													
	<i>1</i>	<i>2</i>	<i>3</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>1</i>	<i>2</i>	<i>3</i>		
Western white pine.....	50	56	99	0	0	0	11	15	22	46	67	75	441	
Douglas fir.....	78	86	89	0	1	0	28	18	33	45	16	0	394	
Western larch.....	89	91	85	1	0	0	54	14	56	72	100	100	662	
Western fir.....	80	95	100	0	0	0	12	7	17	0	32	8	351	
Western hemlock.....	100	100	100	31	1	56	100	100	100	94	100	100	982	
Western red cedar.....	100	100	100	4	1	22	100	100	100	17	81	76	801	
Total.....	497	528	573	36	3	78	305	254	328	274	396	359	3,631	

* Basis data on losses of each species on three quadrats under each set of habitat conditions, respectively.

differently in magnitude and trend in the two seasons. It is obviously impossible to average out such eccentricities and reveal average trends on the basis of two years' records. Accordingly, the available data on mortality from fungi can only be interpreted as showing that although significant differences may exist between species and station losses, respectively, high interaction values indicate that such relationships will vary materially from season to season. All combinations involving year must, therefore, be regarded with considerable caution where interaction is significant, and differences in losses between species and stations in individual years must be regarded as indicative of only temporary relations. Mortality from fungi does not vary significantly between

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TABLE 87. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS IN 1933*

Source of variance	Degrees of freedom	Sum of squares	Mean square	Ratio	Values for		Significance
					0.05	0.01	
Species.....	5	26,644.0	5,328.8	25.63	2.41	3.43	High
Station.....	3	62,048.0	20,682.7	99.48	2.80	4.22	High
Interaction:							
Species x station.....	15	20,507.0	1,367.1	6.58	1.91	2.48	High
Error.....	48	9,980.7	207.9				
Total.....	71	119,179.7	1,678.6				

* Mortality values are given in Table 86.

TABLE 88. SEEDLING MORTALITY CAUSED BY ALL PHYSICAL FACTORS ON CUTOVER AREAS (STATIONS 1 AND 2) IN 1932

Station	Quadrat	Mortality percentages, by species, in terms of residual germination					Total
		Western white pine	Douglas fir	Western larch	Western hemlock	Western red cedar	
1	2	28	88	67	100	100	383
1	7	81	83	69	100	100	433
1	12	59	75	67	100	100	401
1	3	35	87	74	100	100	396
1	11	78	82	58	100	100	418
1	8	51	92	65	100	100	408
1	13	83	99	78	100	100	460
2	3	0	0	5	16	0	21
2	6	0	0	1	3	2	6
2	2	0	6	46	57	17	126
2	4	1	0	5	17	14	37
2	14	11	28	54	100	100	293
2	16	19	51	59	95	100	324
2	15	91	70	94	100	100	455
Total.....		537	761	742	1,088	1,033	4,161

the so-called mineral surfaces subjected to varying treatment. Mineral versus burnt mineral surfaces, also, show a similar lack of significant difference.

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Eccentric variation between seasons appears also when losses due to insects and birds are examined in the same way. In this case, however, differences between surfaces are not significant.

TABLE 89. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON CUTOVER AREAS (STATIONS 1 AND 2) IN 1932*

Source of variance	Degrees of freedom	Sum of squares	Mean square	Ratio	Value for		Significance
					0.05	0.01	
Species.....	4	14,721.7	3,680.4	15.46	2.55	3.71	High
Quadrats.....	13	76,689.3	5,899.2	24.79	1.93	2.52	High
Error.....	52	12,378.3	238.0				
Total.....	69	103,789.3					

	Western white pine	Douglas fir	Western larch	Western hemlock	Western red cedar	Mean	Standard error
Average mortality percentage, in terms of residual germination.....	38.3	54.4	53.0	77.7	73.8	59.4	±4.1

* Mortality values are given in Table 88.

TABLE 90. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON CUTOVER AREAS (STATIONS 1 AND 2) IN 1933

Source of variance	Degrees of freedom	Sum of squares	Mean square	Ratio	Value for		Significance
					0.05	0.01	
Species.....	5	16,173.7	3,234.7	12.91	2.35	3.29	High
Quadrats.....	14	129,636.5	9,259.8	36.95	1.85	2.39	High
Error.....	70	17,545.0	250.6				
Total.....	89	163,355.2					

The analyses of mortality due to physical factors were undertaken in the same fashion. As before, a series of variance tables were prepared for different balanced combinations of data, showing the manner in which such losses varied by species, station, surface, and year. Table 86 presents one of the most instructive

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of such combinations, used to test variation between species and station in losses recorded on mineral surfaces (mineral and burnt mineral quadrats) during the 1933 season. As shown in the accompanying variance table (Table 87), losses differ significantly between species and between stations. Other combinations indicate that losses caused by all physical factors combined did not vary materially between treated and untreated mineral quadrats, except that losses were very low, of course, on the watered quadrats. Further tests showed that mortality from physical causes did not vary significantly by year, all stations considered, being somewhat higher in 1933 on the full-sun station and slightly lower on both of the other habitats. Even more important is the high interaction

TABLE 91. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON CUTOVER AREAS (STATIONS 1 AND 2) IN 1932 AND 1933

Source of variance	Degrees of freedom	Sum of squares	Mean square	Ratio	Value for		Significance
					0.05	0.01	
Species.....	4	28,521.6	7,130.4	28.90	2.45	3.49	High
Quadrats.....	28	184,672.0	6,595.4	26.73	1.54	1.83	High
Error.....	112	27,628.0	246.7				
Total.....	144	240,821.6					

	<i>West- ern white pine</i>	<i>Doug- las fir</i>	<i>West- ern larch</i>	<i>White fir</i>	<i>West- ern hem- lock</i>	<i>West- ern red cedar</i>	Mean	Stand- ard error
Average mortality percent- age, in terms of residual germination.....	37.7	47.0	49.8	(40.7)	75.3	68.4	55.6	±2.9

of species \times station shown in Table 87, indicating, as does inspection, that species means tend to vary differently on different stations in their relations to one another. For example larch, fairly resistant to physical factors of mortality on the full-sun habitat, is one of the least resistant to them under full shade. For this reason and other reasons it is obvious that a study of species variations in a sample drawn from all stations would not reveal the true relationships.

Combination of data for Stations 1 and 2 only is somewhat less objectionable from this point of view and has the compensating value of furnishing averages for the cutover areas as a unit. Accordingly, by use of data from both these stations, comparison tables have been prepared for 1932 and 1933 separately and for the 1932 and 1933 records combined (Tables 88, 89, 90, and 91).

APPENDIX

The setup used in these tables, designed solely to study variation between species, is based upon the principle of collecting all quadrat data on species variation under one head. This arrangement seems to be entirely satisfactory in the present study, as station values must be treated separately for the most part and variation by surface and year is not significant. The data in Table 88 are for quadrats on two stations, differing as to surface and treatment. The table contrasts mortality losses among five species on each of these quadrats. It is reasoned that it is permissible to present such data so as to contrast species alone, all other variation recognized being included under "quadrats." This method furnishes a much better basis than would be possible in the present

TABLE 92. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON FULL-SUN STATION IN 1932 AND 1933

<i>Source of variance</i>	<i>Degrees of freedom</i>	<i>Sum of squares</i>	<i>Mean square</i>	<i>Ratio</i>	<i>Value for</i>		<i>Significance</i>
					<i>0.05</i>	<i>0.01</i>	
Species.....	4	12,037.3	3,009.3	23.29	2.55	3.71	High
Quadrats.....	13	2,803.2	215.63	1.67	1.93	2.52	None
Error.....	52	6,719.5	129.2				
Total.....	69	21,560.0					

	<i>Western white pine</i>	<i>Douglas fir</i>	<i>Western larch</i>	<i>Western hemlock</i>	<i>Western red cedar</i>	<i>Mean</i>	<i>Standard error</i>
Average mortality percentage, in terms of residual germination.....	65.7	85.8	78.5	100	100	86.0	±3.0

study with a balanced combination involving the same number of quadrats of each type of surface on each station.

The principle involved is exactly the same, for example, as in comparing the yields of different varieties of grain tested on fields significantly different in soil fertility. The yields per field may vary materially because of the difference in fertility, just as in this study mortality losses have varied materially among quadrats; but unless the interaction of variety \times field is significant, the comparison of variety yields can best be made on the complete basis available, a combination of data from all the areas studied.

The combination upon which the comparison between species losses given in Table 91 is based, data drawn not only from different mineral surfaces and sta-

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TABLE 93. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON PART-SHADE STATION IN 1932 AND 1933

Source of variance	Degrees of freedom	Sum of squares	Mean square	Ratio	Value for		Significance
					0.05	0.01	
Species.....	4	27,065.1	6,766.3	20.10	2.48	3.55	High
Quadrats.....	21	110,441.2	5,259.1	15.62	1.70	2.12	High
Error.....	84	28,278.1	336.6				
Total.....	109	165,784.4					

	<i>Western white pine</i>	<i>Douglas fir</i>	<i>Western larch</i>	<i>Western hemlock</i>	<i>Western red cedar</i>	Mean	Standard error
Average mortality percentage, in terms of residual germination.....	26.4	22.1	29.9	61.3	53.3	38.6	±3.9

TABLE 94. SOURCES AND COMPONENTS OF VARIANCE IN MORTALITY CAUSED BY PHYSICAL FACTORS ON FULL-SHADE STATION IN 1932 AND 1933

Source of variance	Degrees of freedom	Sum of square	Mean square	Ratio	Values for		Significance
					0.05	0.01	
Species.....	4	43,749.7	10,937.4	30.60	2.55	3.71	High
Quadrats.....	13	42,804.9	3,292.7	9.21	1.94	2.52	High
Error.....	52	18,582.7	357.4				
Total.....	69	105,137.3					

	<i>Western white pine</i>	<i>Douglas fir</i>	<i>Western larch</i>	<i>Western hemlock</i>	<i>Western red cedar</i>	Mean	Standard error
Average mortality percentage, in terms of residual germination.....	32.1	13.4	77.4	76.7	47.6	49.4	±5.1

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tions but also from both years, gives the very satisfactory basis of 144 degrees of freedom, of which 112 can be attributed to error. These data, of course, include the values for 1932 shown in Table 88.

It has been emphasized that when interaction between species and any of the items grouped under quadrats is significant the combination of such items in one table will tend to obscure the true relations present. Significant interaction is apparent in this instance between species and station. Not only are losses among stations significantly different, as indicated in Table 87, but the species means tend to vary differently between stations in their relationship to one another. Although this is largely due to the very markedly different conditions existing on Station 3, where drought alone was a factor, some such difference exists between Stations 1 and 2. Accordingly, though it is desirable to present a composite picture of mortality from drought and insolation combined upon the cutover areas (Stations 1 and 2), it is necessary also to study separately the mortality losses on each of these stations in order. Tables 92, 93, and 94 present variance data for Stations 1, 2, and 3, respectively. As interaction between species and years is not material, it is permissible to base each table upon a combination of records for the two seasons.

It is apparent from these tables that combining the values for Stations 1 and 2 actually obscured a trend having an important bearing on silviculture of the white pine type; namely, that western white pine, although it is significantly harder than all other species on the full-sun station (with the possible exception of lowland white fir), it is not significantly harder than Douglas fir and western larch under part-shade conditions.

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PLATES

PLATE 1

COOPERATIVE WEATHER BUREAU STATION
PRIEST RIVER EXPERIMENTAL FOREST HEADQUARTERS



PLATE 2
FULL-SUN HABITAT
STATION 1



PLATE 3
PART-SHADE HABITAT
STATION 2

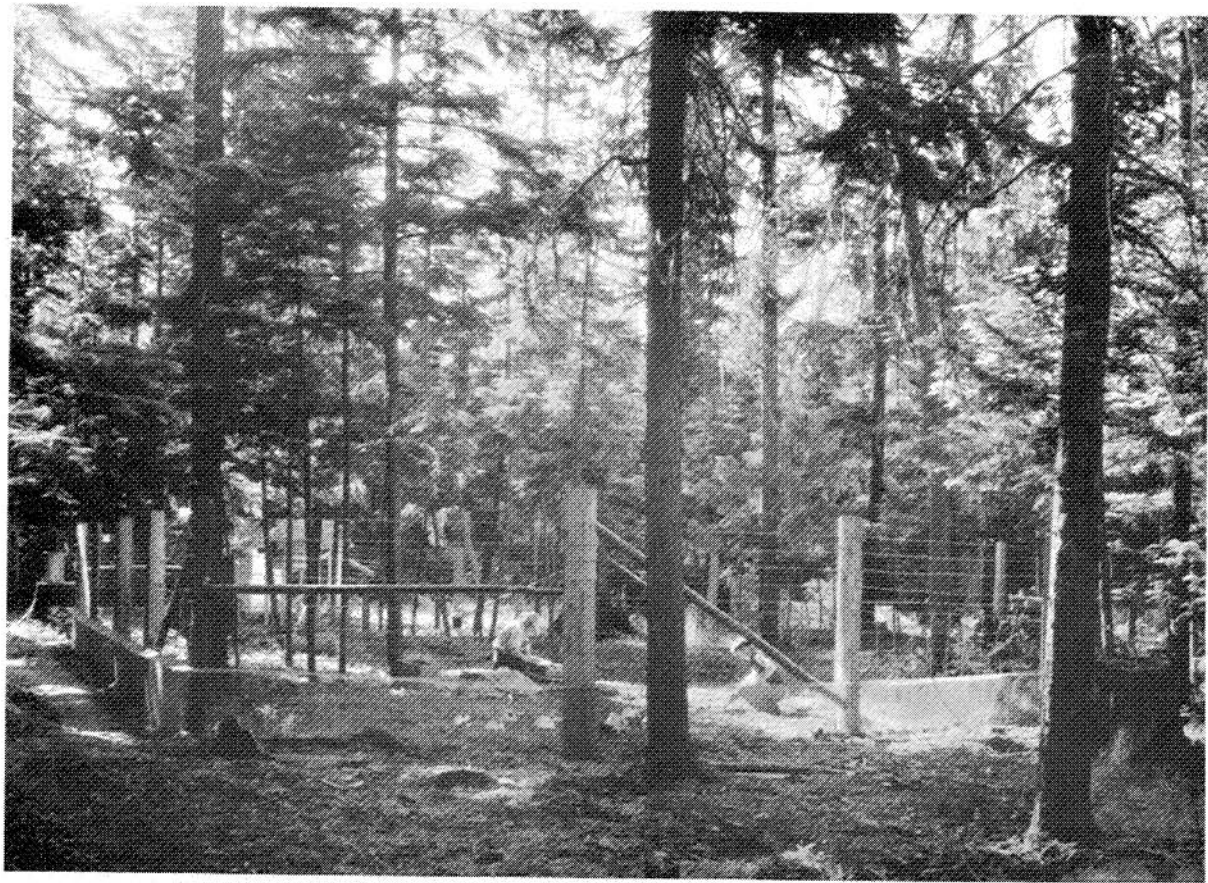


PLATE 4
FULL-SHADE HABITAT
STATION 3

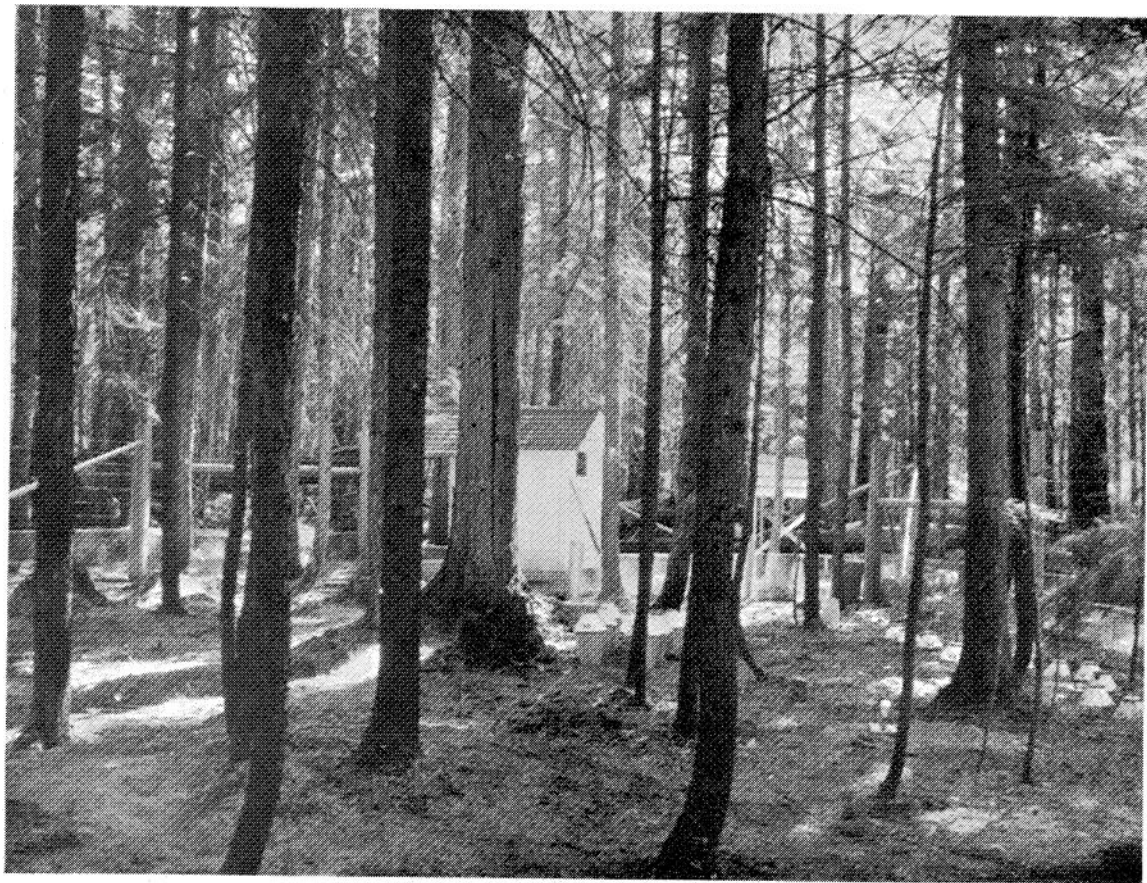


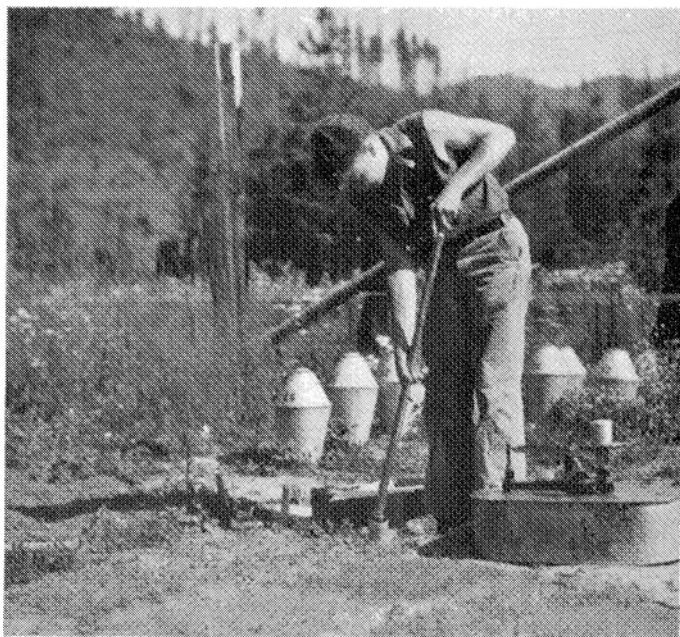
PLATE 5

A

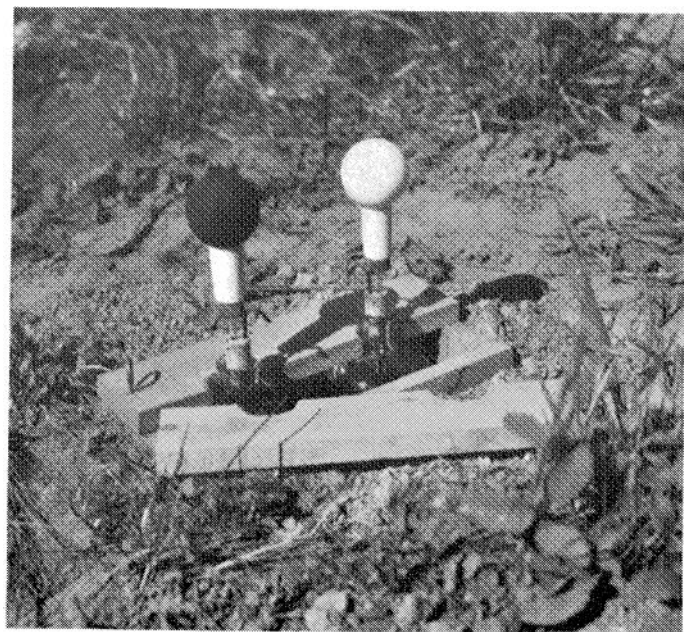
GEOTOME, SOIL CANS, AND SCALES FOR SOIL MOISTURE
DETERMINATIONS

B

PAIRED BLACK AND WHITE ATMOMETER SPHERES
USED IN MEASURING EVAPORATION
AND RADIATION INTENSITY



A



B

PLATE 6

A

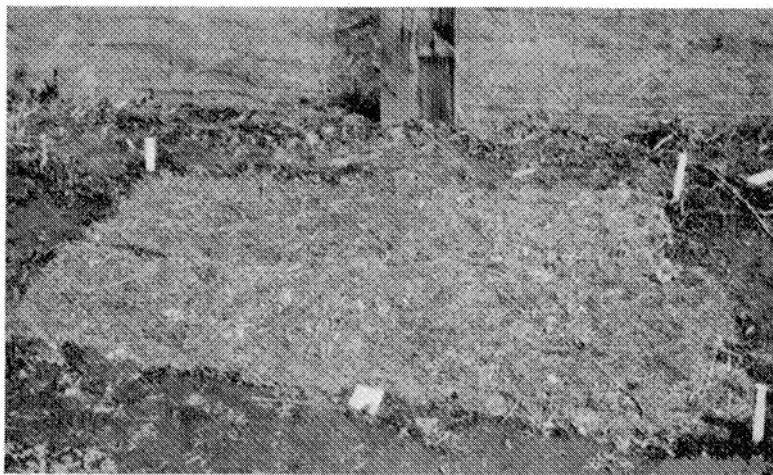
GERMINATION ON DUFF QUADRAT, FULL-SUN
HABITAT, MAY 6, 1933

Each tooth-pick marks a seedling

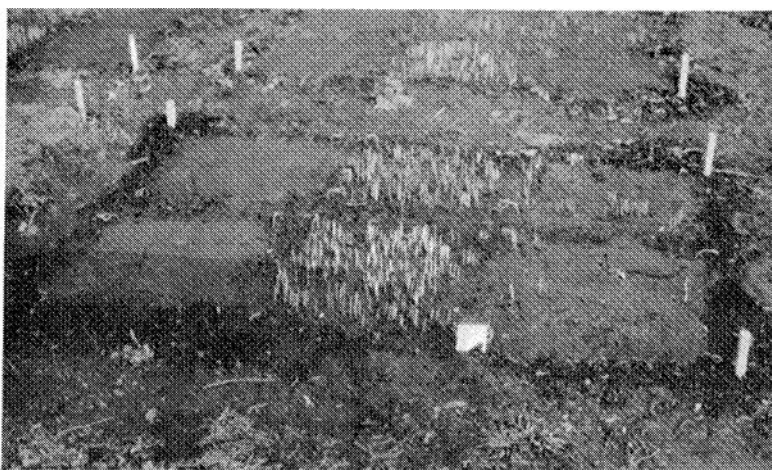
B

GERMINATION ON BURNT MINERAL QUADRAT,
FULL-SUN HABITAT, MAY 6, 1933

Each tooth-pick marks a seedling



A



B

PLATE 7

ROOT PENETRATION, 1933

Groups, left to right, taken from full-sun, part-shade, and full-shade habitat, respectively. Seedlings, left to right, are lowland white fir, Douglas fir, western larch, western white pine, western red cedar, and western hemlock, respectively. Scale in inches.

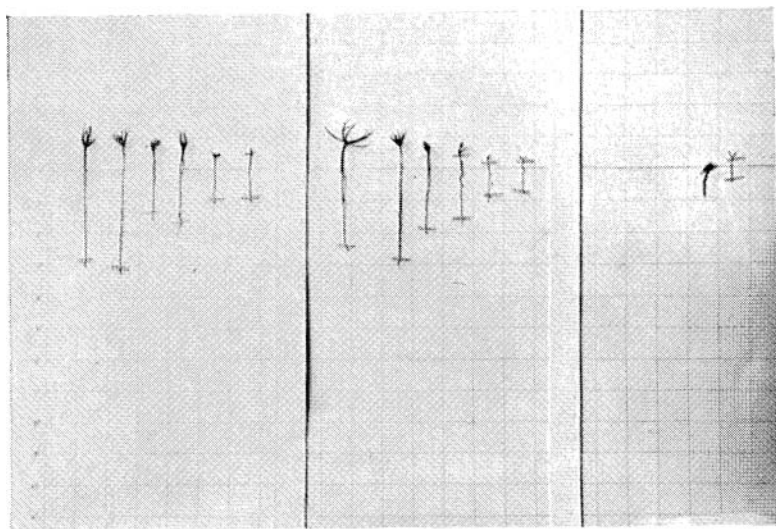
A

ROOT PENETRATION, MAY 30, 1933

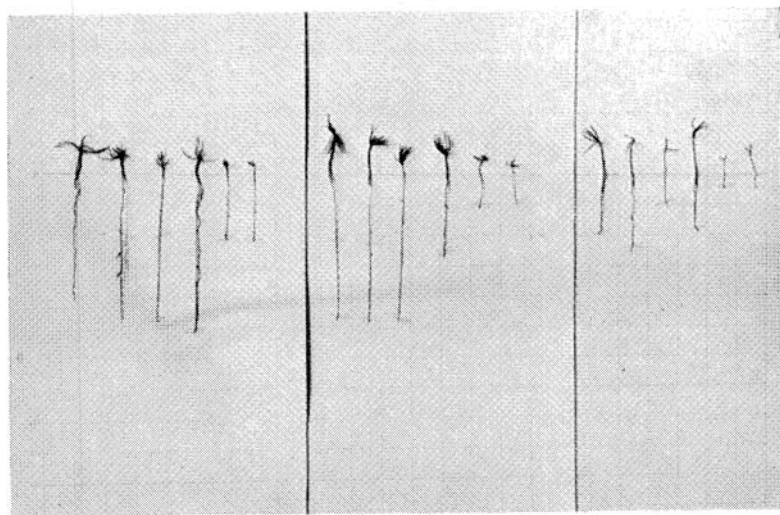
Only western white pine and western red cedar have germinated under full shade

B

ROOT PENETRATION, JUNE 30, 1933



A



B

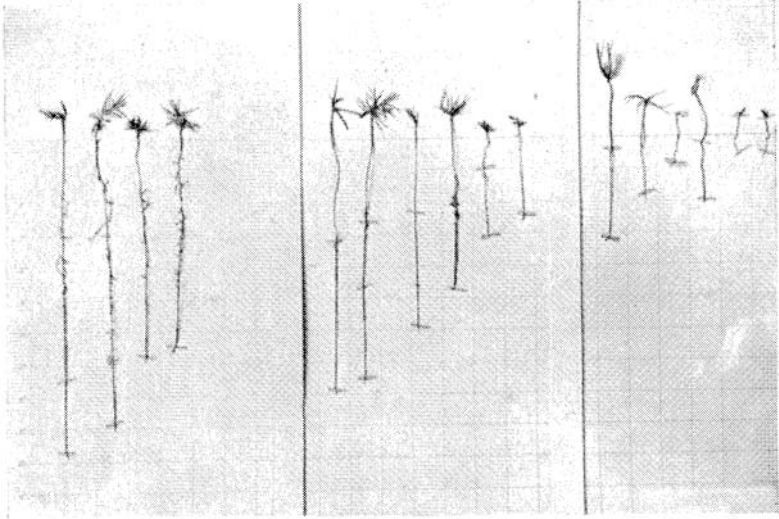
PLATE 7

C

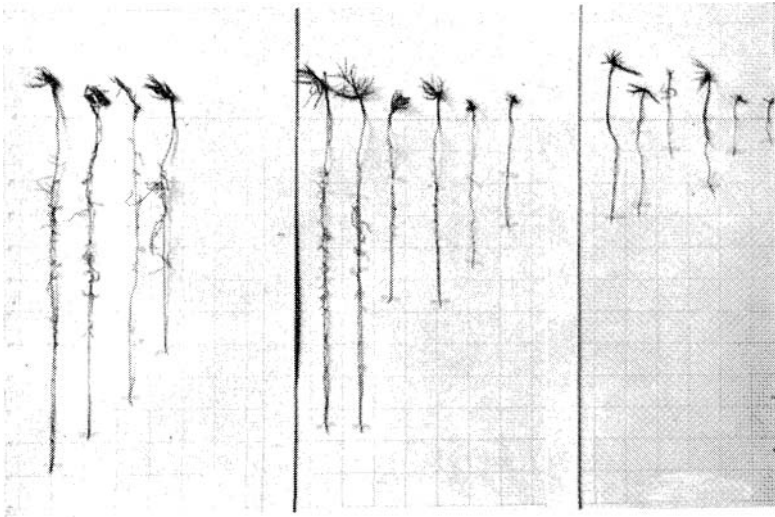
ROOT PENETRATION, JULY 30, 1933

D

ROOT PENETRATION, AUGUST 30, 1933



C



D

PLATE 8

A

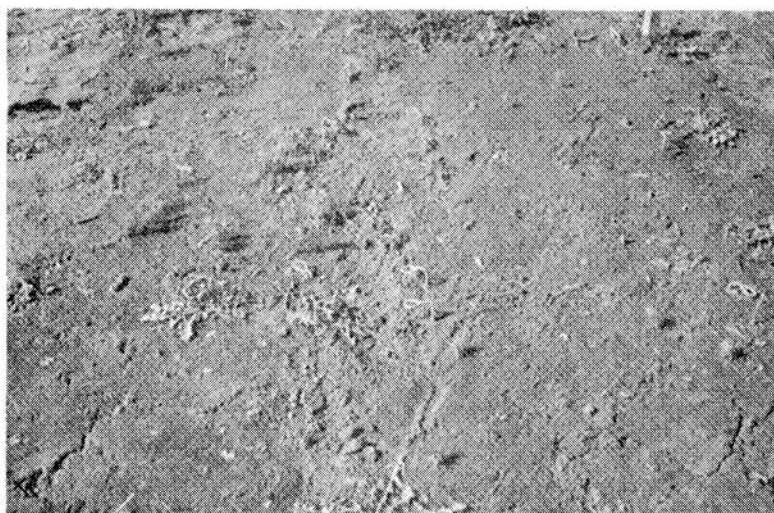
SEEDLING SURVIVAL WHERE INSOLATION WAS
NOT A FACTOR

B

SEEDLING SURVIVAL WHERE INSOLATION WAS
A FACTOR



A



B

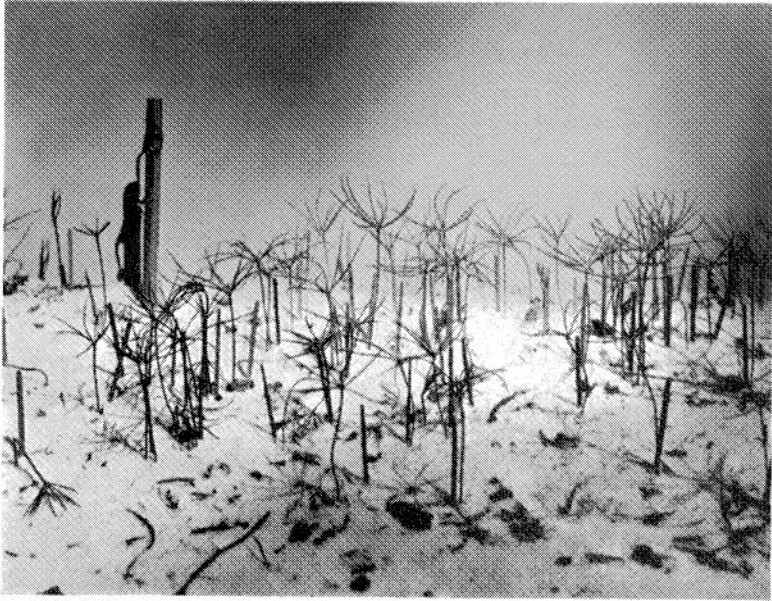
PLATE 9

A

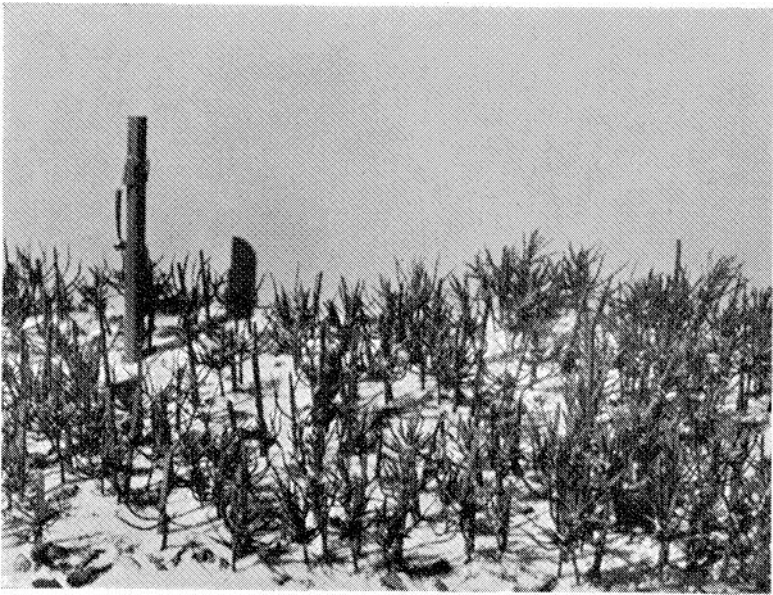
ETIOLATED SEEDLINGS IN FULL SHADE, 1932

B

STOCKY SEEDLINGS IN FULL SUN, 1932



A



B

PLATE 10

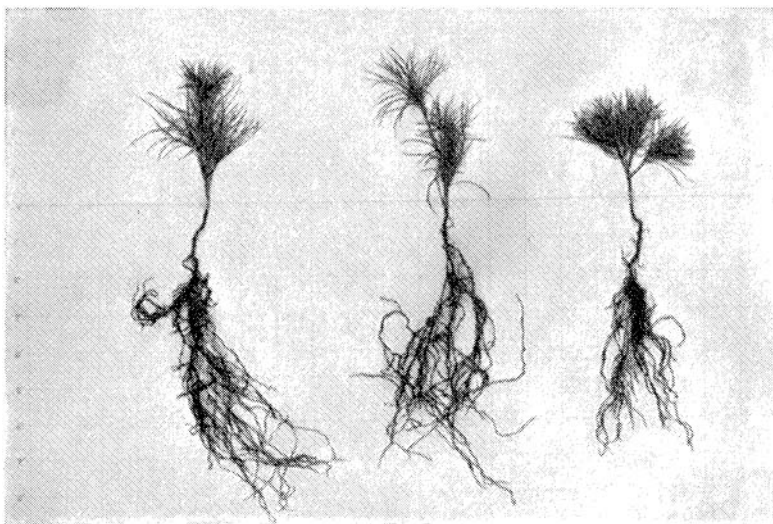
ROOT AND TOP DEVELOPMENT OF WESTERN WHITE
PINE TRANSPLANTS IN 1933

A

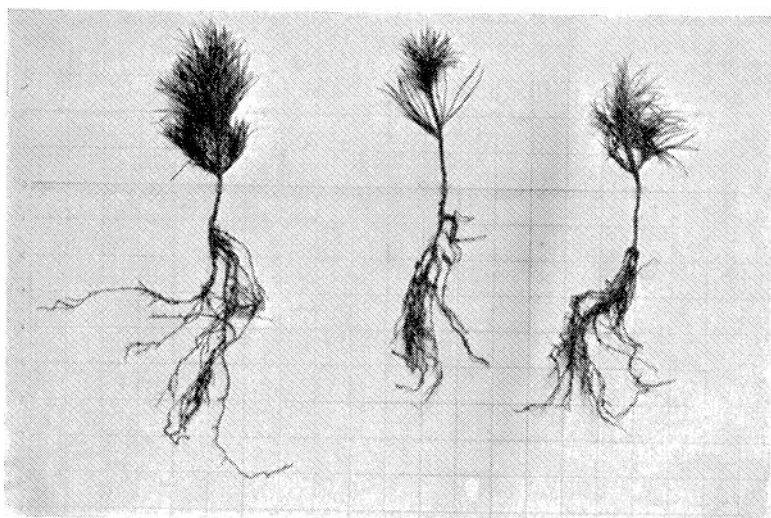
FULL-SUN STATION

B

PART-SHADE STATION

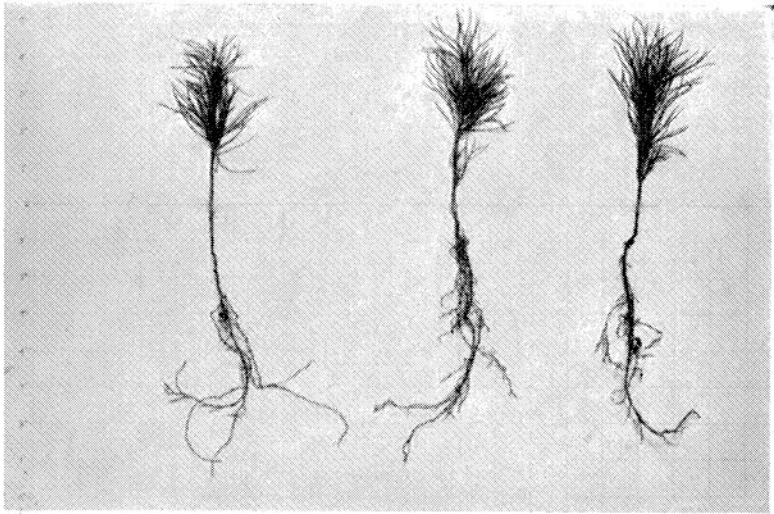


A



B

PLATE 10
C
FULL-SHADE STATION



C

THINNING AND MANAGEMENT OF
EASTERN WHITE PINE

This publication is financed by the
Charles Lathrop Pack Foundation
at Yale University.

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