A Symposium

on the Factors Affecting Natural Establishment of Seedlings in the Forest

by

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INTRODUCTION

**Purpose**

In the past there has been much writing and research relating to the many factors affecting the reproduction of commercial forest tree species. Investigators have delved deeply into the many ecological and physiological factors that influence the germination and final establishment of tree seedlings, but there has been very little work done to integrate these findings into one publication which gives the complete picture of the present status of our total knowledge of the subject in the light of past findings. It is the principal objective of this paper to commence such an integration; to combine past findings in such a way as to point out more intelligently the paths of practice and research in the contemporary fields of forestry.

**Choice of Subject**

Since the methods used in this paper are not strictly conventional for thesis writing, the reasons for their use had best be explained here. The choice of the thesis subject was preceded by an inquiry conducted among various state, private, and national users of forestry practices in an endeavor to determine to what line of research the thesis efforts might best be applied. The answers received varied considerably, but generally speaking, the suggested topics included important questions but were of very narrow scope. A combining of
several of these answers gave rise to the choice of this subject.

As the forester must of necessity seek the broadest training possible, it was decided to write on a somewhat broader scope than had been suggested for any one topic. In order to gain the greatest possible knowledge in return for the time spent, it was decided that an individual research problem would not fulfill the specifications. In the course of conducting an original experiment and recording the results, the senior may possibly gain a somewhat better understanding of his particular narrow subject and of the techniques of experimentation involved. Once his work has been completed, however, its end has been served. Rarely will the writer or anyone else have occasion to refer to the usual unauthoritarian research problem of the bachelor's thesis. It will remain under the sanctity of a heavy coating of dust in the school library representing only the tangible evidence of the fulfilment of a graduation requirement.

The problem of seedling establishment was finally chosen because of the breadth and importance of the principles involved. As will be noted there is much material herein contained which can be classified under the subjects of ecology, soils, physiology, silviculture, etc. Although the application is specific, the principles are general and can be applied to many other phases of plant and tree growth.

It is felt that a thorough understanding of the growth processes of the tree in its various environments is prerequisite to the intelligent study of forest management and silviculture. It has often been said that soil is the basic resource; therefore, the study of the effect of the soil upon the plant cover -- especially forest tree seedlings in this case -- and the cover in turn upon the soil, are the
basic considerations. With this fundamental knowledge, more intelligent study of the managerial and silvicultural aspects of forestry will be possible.

Need for the Study

The demand for the best knowledge of soils and growth thereon is steadily increasing and is exceeded only by its need and importance to the national welfare. There has been a growing realization of the necessity for land use planning so as to place land in the kind of productivity where it can permanently be of greatest use to society. Much land is required for forests and a great portion of our population is dependent upon that forest land for its existence. With huge areas of cut-over and otherwise denuded forest land reverting to governmental agencies for non-payment of back taxes every year; with the many ghost lumber towns scattered throughout these barren areas standing as mute reminders of the people who can no longer depend upon the woods for their living, of the governmental subdivisions that are staggering under an increasing tax load with a decreasing tax base, and finally of the necessity of regeneration of forests on the land and rehabilitation of the communities dependent thereon, with these conditions existent the importance of reforestation is self-evident. Under the present critical national conditions these pictures are apt to become increasingly common. If they do, it will be decidedly dangerous to the national welfare both from the standpoint of supplying the wood products essential to defense and from the standpoint of the welfare of our forest dependent population. It is the primary objective of this thesis to facilitate this necessary planning by establish-
ing a firm basis for further work along this line; to point to better forestry practice by integrating the knowledge of present methods of utilization as they affect the establishment of a new forest crop to replace the harvested trees.

Methods Used

The accumulation of knowledge takes considerable time and effort. These requirements are extended even further when the attempt is made to integrate the total separate conclusions from previous investigations in the many phases of a broad subject so as to combine the various sources of our present knowledge under one cover. The investigator will first emerge with a doubtful and disorganized array of reports, facts, and conclusions. Conjectural statements and contradictory results will be represented. Such a nebulous mass of wordiness and repetition of similar experiments encourages cursory treatment of these voluminous reports, and the average forester, without time for extensive research, continues to practice without the benefit of the best that is known. The integration and analysis of these conclusions has been initiated herein, and though not complete, it is indicative of the present level of our collective knowledge on the subject, and as such, serves to point the way to the most important research problems of reforestation today.

In order to eliminate the risk of misinterpretation, of presenting only part of the picture, and of losing track of the importance of the thought content stressed by the source or authority used, the policy in this writing has been to preserve for the most part the original wording of the investigators referred to. The original
thoughts are presented classified by subject as they permit, but the conclusions and interpretation for the most part have been left to the discretion of the reader. It is hoped that the many scientific periodicals, government bulletins, and text books quoted will be themselves referred to where there is any vagueness or discontinuity of thought, or when there is a particular interest aroused in any phase of this subject. It must be borne in mind that this work is not original, but merely a compiling of the thoughts of others in a semi-usable form. Neither is it meant to be a substitute for the authorities quoted each of whom give more intensive consideration to their particular subjects than can be permitted here. This thesis has been written to clarify the general picture of seedling establishment by selecting the best that is known on each of the many factors involved and combining these authoritative quotations into a useable reference form which can readily serve as a basis for original research work.
Importance of Reforestation

The principles of silviculture and forest management are being more widely practiced in this country as the original supply of virgin forest diminishes. The demand for wood and wood products will exist for a long time to come, but man must play an increasingly important part in insuring that there continues to be a source of wood sufficient to supply the demand. In order to do this the forester must provide for the perpetuation of the forests by means of such practices as will bring forth a new crop of trees in the place of those harvested. He may do this either by the transplanting of nursery stock, or he may depend upon natural reforestation. The latter may require supplemental treatment by the former, but in the final analysis he will depend upon natural regeneration of the forest whenever possible due to the excessive cost of the artificial methods. Without regeneration, silviculture and management cannot exist; the various factors influencing regeneration of the forest must be well understood if the best interests of silviculture, management, and, primarily, society are to be served.

Various authors have expressed the need for this type of study. Isaac (26) states: "Throughout the Douglas fir region of western Washington and western Oregon one of the most productive forest regions
in the United States, wide variation is observed in the rate and adequacy of natural restocking of forest land following deforestation by logging or fire or both. On some deforested areas a dense stand of reproduction soon appears, but others lie treeless for many years. The causes for this variation in restocking are not well understood."

"Lands in the Douglas fir region that have been deforested since white settlement by logging or fire or both total approximately 11 million acres. It is estimated that at least 20 percent of this enormous area, although logged or burned prior to 1920, has failed to reforest at all, and that an additional 50 percent has failed to restock sufficiently well to insure a full forest crop."

Kirkland and Brandstrom (31) give a similar picture: "The failure of existing methods to maintain productivity is amply shown by examination of cut-over lands. Strip surveys made recently in connection with the forest survey on private lands logged from 1920 to 1923, inclusive, aggregating 201 miles in 15 counties of western Washington and western Oregon, show the following degrees of restocking:*

Well stocked 12 percent
Medium stocked 17 percent
Poorly stocked 29 percent
Nonstocked 42 percent

"The forest survey also disclosed that on the average 3.9 percent of the acreage logged since 1920 has burned annually. The conversion

* date of data is 1936
of forests into waste lands or into poorly stocked stands of open- 
grown, low-quality trees is certain to be followed by declines in 
industry, wealth, population, and tax revenues."

Speaking from the national standpoint, Coile (12) makes some 
similar observations: "The millions of acres of denuded land that 
require forest cover present a major undertaking in reforestation. 
The problem is being augmented by continued abandonment of acreage 
from agricultural use. Furthermore, harvesting of forest crops and 
devastating forest practices will continue to add to the amount of 
land that must be ultimately planted."

"In the development of a forestation program for any region, the 
requisite judicious selection of species for planting may be made 
from a study of the distribution of native vegetation and succession 
of plant associations from denuded lands to the acceptable forest 
stands, evaluation of relationships between soils and plant behavior, 
deductions made from behavior of previous plantings, and application 
of practices acceptable in nearby sections where environmental 
conditions approximate those of the area in question." Although 
these factors are spoken of in relation to artificial reforestation, 
they are no less important to natural regeneration and will be 
considered in the pages to follow.

Necessity for the Best Scientific Techniques

It is not a new idea, that there is a necessity for the actual 
application of the facts research workers are able to point out. 
Bates and Roeser emphasize this notion in their report of experiments 
carried out to determine the effects of heat on tree seedlings (14).
In a later publication, Bates (5) presents the question as follows:

"Is it not evident, therefore, that if we would be able to anticipate what results are to follow the cultural operation of forestry, we must be able to put our finger on what may be called the 'sensitive point' of the species we are dealing with, and likewise be able to see how the site condition, or factor, which bears on this point, is going to be affected by the operation? In all cutting practice there is need for a much higher grade of intelligence than is usually exercised, bearing first upon a knowledge of the relative requirements of the species to be dealt with, and secondly upon a knowledge of the physics of forest conditions, natural and artificial."

To obtain this knowledge, Bates suggests: "The fundamentals of the ecology of forest trees -- and particularly tree seedlings -- are to be arrived at by studying the physiological reactions to specific and more or less controlled conditions, by observing the adaptations of form and structure to the conditions whose significance is in doubt; likewise by observing the adaptation and as far as possible the physiology of the indicator plants of the site and of those competitors of the trees which appear to establish themselves most readily."

Pearson (49), who has done extensive work along the lines above suggested by Bates, in the southwest yellow pines, collaborates in these sentiments: "It is reasonable to expect that silviculture can be improved by making use of exact quantitative data on temperature, moisture, and soil with reference to the requirements of species and the characteristics of forest zones and sites. This class of data would supplement and refine rather than supplant existing methods."
The quest for this data has been in progress for some time, but the significance of the many factors involved is disputed even by the authorities. Touney (60) stated: "The theory that light intensity on the forest floor controls reproduction has been much over-stressed. It is only beginning to be appreciated that factors other than light are often of equal or even greater importance in determining the origin, growth, and development of vegetation forming the subordinate layers beneath the canopy." To an extent, this is characteristic of much of the best that is known of the effects of forestry practices on the site factors and in turn on the seedlings themselves, even today. There is consequently much room for additional research and it is hoped that this review can give some hint as to where this research effort may best be applied.

**Complexity of Classification**

It is very difficult to attempt building up the complete picture of this problem from the bottom step by step; there is such a galaxy of factors and their combinations that an orderly analysis and synthesis can only in part be attained. Of this characteristic of plants, Meyer and Anderson (36) comment as follows: "The environment of living organisms is so complex as to defy any completely logical analysis. However, the important physical factors of the environment which ordinarily exert a more or less direct effect upon the growth and development of terrestrial plants can be recognized and are enumerated in the following list: 1 Temperature (soil and air), 2 Radiant energy, 3 Humidity, 4 Soil water, 5 Soil aeration, 6 Concentration of solutes in the soil solution, 7 Concentration of gasses in the atmosphere,
Gravity, Atmospheric pressure." In further describing the complexity of analysis of these factors, they write: "Environmental factors influence plant development only because of their effects upon internal physiological conditions which are also conditioned . . . by the genetic makeup of the organism. Different combinations of factors often have a similar effect upon the internal physiological conditions in a plant. It is therefore entirely possible for approximately the same end result in terms of plant development to be induced by dissimilar combinations of environmental factors. The precept that the same internal physiological conditions, and the same developmental reactions can be brought about by different combinations of environmental factors is sometimes called the principle of multiple causation."

This principle will be brought out clearly in the conclusions reached by the many investigators herein referred to or quoted. Because of this complexity of factors it has been next to impossible to segregate the principles involved into completely separate divisions. It has been attempted to insure a continuity of thought, however, and to cover more or less completely the many important factors involved in that portion of the life of a tree between pollination of the seed and establishment of the seedling on the forest floor.

The Problems Stimulating this Inquiry

In order to more clearly set forth the problems of present forestry practice upon which this symposium may throw some light, a few of these are set forth in the following questions. It may be well to keep these in mind while perusing the following pages.
1. To what extent does the seed source influence the establishment of seedlings?

2. What physiological processes are involved in germination and in subsequent growth?

3. How do various soil and weather factors influence germination and final establishment?

4. What role does competition in the plant community play in establishment?

5. What effects do various methods of slash burning have upon the site factors affecting germination and establishment? Repeated burnings?

6. What effects does the degree of cut have upon the factors of site influencing the germination and establishment?

7. How do various cultural forestry practices change the pertinent soil and weather factors, i.e. the microclimate?

8. How are certain conditions of the site factors indicated and measured?

9. What are the suggested lines of research indicated by the vacancies in the present knowledge of these factors and their application?
Chapter ii
THE FACTORS INVOLVED IN SEEDLING ESTABLISHMENT:
SEED SOURCE AND SEED DISPERAL

* * *

The first essential of seedling establishment is a source of seed. There has been considerable written on the bearing of seed by trees, on its dispersal from the trees, on seed storage in the duff, and on the eventual fate of seed falling on the forest floor. These points must be taken into consideration if the complete picture is to be presented.

Seed Trees

Not all trees of the same species on the same site have a similar potential for seed production. In the choosing of individual trees to be left for the purpose of furnishing a seed source to aid in the reforestation of a cut-over area, it is very necessary to know which are the best trees to leave for this particular purpose. Of course the characteristics of the best seed trees will differ somewhat by regions and species; however, several authors have written enlightening discussions on seed trees.

Show (54) writes as follows about the type of tree to be left for seed in the California pine: "The first essential is to leave trees of a size that can be counted on to produce seed immediately after cutting, for then seedlings establish themselves more readily than after brush has invaded the ground .... It was found that the percentages of trees in each diameter class bearing no cones, which
at 10 inches is 100, drops rapidly reaching 8 percent at 18 inches and zero at 20 inches. The percentage of trees producing a light crop rises rapidly, reaching the peak with the 16-inch class, and then drops more gradually, reaching the zero point at 32 inches. Trees producing a medium crop first appear at 18 inches, increase to a peak with the 28-inch class, and then drop. Trees producing a heavy crop do not show up till a diameter of 28 inches is reached, after which the curve appears to be essentially the same as for the other categories. The study indicates that yellow pine trees 18 and 20 inches in diameter have considerable cone production, whereas smaller trees bear at best only a light and uncertain crop. In the Southwest, Pearson has found that yellow pines smaller than 20 inches in diameter are ineffective seed producers." He further states in the same publication that it is not sufficient to know the size of trees to be left, but the forester must also know what number will produce enough seed to give satisfactory reproduction. He mentions a study made by Pearson in Arizona in 1912 in which it was determined that "the germination percentage of seed from blackjack trees was uniformly higher than that from the older yellow pines, and that for trees of the same size the blackjack produced more seed than the yellow pine. Therefore, for seed production, as well as for rapid growth, thrifty young trees should be reserved wherever available."

There has been considerable discussion of the probability of hereditary characteristics and their transmission from the seed tree to the progeny. Along this line, Munger (42) makes this statement: "The wisdom of leaving conky trees for seed has been questioned.
This need not be gone into here more than to say that the prevalent fungus which causes conk rot (*Fremetes pini*) is a disease of the heartwood, and therefore does not affect the vitality of the tree; that the disease is not transmitted through the seed; that it is a disease of old trees and therefore not to be greatly feared in the new crop which will be harvested probably before it comes to the age of bad infection in the new crop and that the cutting of these few conky trees merely to rid the area of infection would be a trifling measure, so universal is the disease."

Many of the characteristics of a good seed tree from the seed production standpoint found for Ponderosa pine in the southwest are also characteristic of Douglas fir (*Pseudotsuga menziesii*). "Douglas firs produce both male and female flowers on the same tree and fertile seed may be borne from the time they are 25 years or so old until they are several hundred years old. The frequency and abundance of seed bearing of any individual tree varies greatly. An open-grown tree with a big crown may bear seed very frequently, and a tree in a dense stand may not bear any for decades. The above is also true of the principal associates of Douglas fir, West Coast hemlock, Western red cedar, Sitka spruce, and the balsam firs -- except that they do not begin to bear seed so early."

In the leaving of seed trees, other factors than ability to produce seed must be considered. In the Douglas fir region the tree "should also be of a type to withstand wind and slash burnings. Douglas fir is preferred, because of its thick fire resistant bark and relative wind firmness, but other species are acceptable provided they have a good chance to survive."
"Experience has proved that the mortality of mature Douglas fir left as seed trees is high. In an 8-year period it amounted to 64 percent of the trees left in a series of tests. Windthrow caused 45 percent of the loss, fire 25 percent, and other causes 30 percent. Conky trees are particularly susceptible to catching fire and burning off at the rotten knots. Fire-killed seed trees are of course a menace as potential fire-spreading snags."

When the above figures are considered, it may be readily understandable why the same bulletin recommends as follows: "The single seed tree method of providing for reforestation is not recommended except where defective trees are so numerous that a sufficient seed source will be left to assure restocking; where there is a fair chance that the trees will survive fire and wind; where logging will not be too seriously inconvenienced by these standing trees; and where other methods that would break up the area into compartments are not practicable."

Seed Years

The wise choice of seed trees for hardiness and fruitfulness does not insure the establishment of a fine stand of reproduction immediately or even a good crop of seed. There are many variables involved in the production of a good seed crop as is described by Wakeley for the southern pines (64): "Southern pine seeds, like those of most other pines, take two growing seasons to mature. Rain or frost during pollination in the spring may ruin the crop that would normally mature in the fall of the succeeding year, and adverse weather or insect attack at any time during either of the two summers
or the winter intervening can destroy the cones or seed.... Pine pollen is wind-blown... The time during which cone flowers are receptive to pollen is very short, and differs somewhat among individual trees of the same species. Moreover, the male and female flowers of an individual tree do not always mature simultaneously; in some instances at least, the male flowers mature first and shed most or all of their pollen before the scales of the cone flowers on the same tree open to receive it. This difference in date of maturity, together with the location of most of the female flowers in the crown, above most of the male flowers, may account for the failure of some trees to produce seed abundantly, and may also permit some cross-pollination that would not otherwise take place. Cross-pollination makes it difficult to obtain seed of known male parentage and even leads to hybridization, as of longleaf with loblolly..... Records for longleaf pine on specific areas show 2 and 3 good seed crops in consecutive years, and 5 fair to heavy crops within 10 years."

To a great extent the same factors enter into the production of seed crops in the Douglas fir region causing the occurrence of good or bad seed years. Munger (43) reports that heavy crops of Douglas fir seed occur at irregular intervals, the period between good seed years usually being 2 to 5 years.

Seed Dispersal

In order to best know how great a distance may be left between seed trees or between other sources of the seed such as staggered settings and long corners, the distances to which sufficient seed
will be dispersed from these sources must be known. McArdle gives a very complete account of the methods used and results obtained in the determination of the effective seeding radius of individual Douglas fir trees (35). This account is as follows:

"A series of seed traps were located on logged off land at various distances from growing timber seed source. Some seed was found to carry a half mile but sufficient quantity for satisfactory stocking was found not farther than 1000 feet from the timber."

"Another series of tests was made over level ground, the seed being released from a kite in different wind velocities at an altitude of 200 ft. With a wind velocity of seven miles per hour, the heaviest fall of seed was 1000 feet from the point of release, and the maximum distance of flight was 1800 feet. Seed similarly released in a 23-miles-per-hour wind fell in greatest density 1,600 feet from the point of release and the maximum distance of seed flight was 3,500 feet......Local topography greatly influences the vertical and horizontal air currents which carry seed. Douglas fir seed falls at the rate of less than two miles per hour and it is easy to understand how rising air over a warm slope may carry seed astonishingly long distances.

"The presence of a nearby block of uncut timber is the surest source of an adequate supply of seed. Single seed trees scattered over the logged area at the rate of about two seed trees per acre have been tried on timber sale areas in the national forests but this has not been especially successful. In some instances trees of considerable value must be left, many of them are injured in logging and soon die, others are killed by the slash fire or are blown down, and
within five years after logging less than half the seed trees are left. The average seed tree produces about 40,000 seeds in a good year; at least ten times this amount of seed is needed to restock a single acre.

"Douglas fir seed is particular attractive to birds and rodents, and unless there is more than enough seed produced to satisfy the food demands of the animal population, there is relatively little left for the perpetuation of the forest. Unless there are ten to a dozen seed trees to each acre or a block of uncut timber within a quarter of a mile it is fairly safe to assume that adequate natural restocking of most cut-over or burned-over areas will be extremely slow and unsatisfactory."

Seed Storage in the Duff

Once the seed has been produced and reached the ground its subsequent existence has many possibilities. For some time it was thought that seed from Douglas fir could remain viable in the forest duff for a number of years. In propounding this theory Hoffman (29) lists many illustrations which seem to be valid. In the case where all seed sources were removed by fire, but where soil conditions were such that the duff was not destroyed, Douglas fir reproduction was found to be plentiful. He also found that if Douglas fir slash is burned in the spring so that the duff is not completely destroyed, reproduction is plentiful without any standing seed source. It is probable that Hoffman did not give sufficient credit to the ability of Douglas fir seeds to be widely scattered by the wind. Hoffman's bulletin was published in 1924 and it was not until 1930 that the
account of Isaac's previously described experiments with the wind dispersal of Douglas fir seeds was published. In 1931 Isaac (27) reported that he found direct evidence that seed stored in the soil or duff will germinate profusely the first season after it falls either under old-growth timber or in the open. Seedlings did not survive under the old-growth timber, however. Again in 1933 Isaac (25) stated: "Douglas fir seed not eaten by birds, insects, and rodents either germinates or decays within a year after it falls, both under virgin timber and on open logged-off land." The "stored in the duff" theory has not been accepted since this time as far as Douglas fir is concerned.

Although seed storage in the duff has been found not to be a factor in the regeneration of denuded Douglas fir lands, according to Weaver and Clements (67) seed storage in other species of plants is not uncommon. Their statement is as follows:

"Where seeds have been buried at a depth of 3 feet in open bottles in moist sand for a period of 40 years, 10 out of 22 species remained viable. Seeds of many land plants have been shown to lie dormant in mud covered with water for a period of several years. Where abundant organic matter is decaying in the soil, so much carbon dioxide may be evolved as to delay germination. This may occur in garden or forest soils or where the oxygen supply is low, as in the mud of ponds. It is a notable fact that when a forest is cut over or burned, many seeds which have found conditions unfavorable for germination, rapidly produce seedlings. (this is probably doubtful for some species in view of later studies)"* Temperature, water-

* parenthetical statement mine
content, and oxygen supply may all be involved."

The Eventual Fate of Seed on the Forest Floor

It has been found (44) that "Most of the seed that is scattered over logged-off land by adjoining forest or isolated trees is promptly eaten by mice, birds or insects. Much of the rest falls on rocks, logs or in thickets of weeds where it has no chance to germinate and survive. The remainder of the seeds, provided they have moisture, warmth and a chance at the soil, will germinate ordinarily in May." McAr Cole (35) reported on the causes of seedling death as follows: "Intensive studies of seedling survival on cut-over areas near the Wind River Branch of the Pacific North-west Forest Experiment Station show that from 66 to 95 percent of the annual seedling crop dies from one cause or another. The principal causes of seedling mortality, in the approximate order of their importance are: heat injury to the stem (sun scald), drought, rodents, competition of other vegetation, and frost."

It has often been observed that rodents of various species are very destructive to Douglas Fir seeds and seedlings. In a recent bulletin Moore (40) summarizes rodent work as follows: "Seed-eating mammals, active at all times of the year, find in forest-tree seeds a favorite food. White-footed mice are the most important consumers, as they occur over the entire region. The shrew and related forms, although classed as insect eaters, also take heavy toll of seeds, owing to their great abundance in the coastal strip. Squirrels, chipmunks, and other mammals are of minor importance in total seed consumption."
"Reproduction from such seeds as escape and germinate furnishes food for browsing animals. The brush and snowshoe rabbits, common in the region, do the greatest amount of cropping. The mountain beaver plays a minor role, as apparently do big-game animals also. Artificial reforestation appears to suffer more from animal attack than does natural regeneration. Population counts of animals give unstable readings as to measurements of damage, because of the ever-present factor of variables."
The process of germination is a complicated one controlled by the many factors that go to make up the physical environment in which the seed lies and by the individual characteristics of the seed itself. There is such a variety of seed types, each with widely different requirements for germination, that only the general, rather than the specific, physiology of the process can be touched on here.

The Role of Water

The processes involved, even in the initial absorption of water by the seed coat, are of such complexity that for the most part the descriptions are taken verbatim from Meyer and Anderson, Plant Physiology (36).

"The initial step in germination is the imbibition of water by the various tissues within the seed. This generally results in an increase in its volume. The increase in the hydration of the seed coats usually causes a pronounced increase in their permeability to oxygen and carbon dioxide, which is very low in the dry seed coats. The swelling of the seed often reverts the seed coat, but in some species this does not occur until the emergence of the primary root.

"With an increase in the hydration of the cells, enzymes become activated and zymogens are converted into enzymes.... Stored foods, whether they occur in the endosperm or cotyledons, are digested and the soluble products of the digestion process are translocated towards
the growing points of the embryo....A large proportion of the fats present are usually converted, after digestion, into soluble carbohydrates. The soluble carbohydrates are not present during the later stages of germination in amounts quantitatively equivalent to the starch or other storage carbohydrates digested during the process, indicating that a large proportion of these compounds is consumed in respiration or assimilated in the construction of the carbohydrate constituents of cell walls.....Digested proteins are usually represented in the seeds by quantitatively equivalent amounts of amino acids, asparagine, etc. This indicates that proteins are not consumed in respiration but are utilized in the synthesis of the organic nitrogen compounds of the growing embryo."

"A low water content is one of the prominent characteristics of resting seeds and since physiological processes occur largely in an aqueous medium, germination cannot occur unless the seed can absorb water from its environment. In general, however, complete germination of seeds will not occur in a soil with a water content below the wilting percentage.

"Water-vapor as well as liquid water can be imbibed by seeds. Most seeds will therefore pass through the earlier stages of germination in an atmosphere which is saturated, or nearly so, but if the vapor pressure of the atmosphere is appreciably below the saturation value, germination will be checked or inhibited." (36)

The importance of water to the germinating seed in the forest has been brought out in experiments conducted by Tourney (60). He observed that the appearance of pine seedlings and other vegetation under a heavy canopy of white pine was governed mainly by the moisture
of the surface soil. This he obtained over a period of years, paying particular attention to the more critical seasons on both trenched and untrenched plots and on ground from which the litter had been removed and from which it had not. Where the competition from outside trees and other vegetation was cut off, and where the seeds were permitted an unobstructed contact with the "sublitter" soil, by far the greater amount of reproduction appeared.

Other factors influencing the availability of moisture in the soil will be discussed in the chapter on the Physical Factors Influencing Seedling Development.

**Importance of Oxygen**

When the seed coat swells from imbibed water, we found that it becomes more permeable to the passage of oxygen. The importance of this element in germination is brought out by Meyer and Anderson (36).

"The respiration of germinating seeds proceeds at a rapid rate especially during the early stages of germination. The partial pressure of oxygen in the atmosphere can be considered reduced, however, without greatly interfering with the rate of respiration.... Seeds of many terrestrial plants can germinate under water where the concentration of oxygen often corresponds to a partial pressure of oxygen very much less than that of the atmosphere (Morinaga, 1926). It is probable that seeds buried deeply in compact soils are often prevented from germination by the very low partial pressure of oxygen in such an environment. During the early stages of germination of seeds of pea and some other species respiration is largely or
almost entirely of the anaerobic type because of the relative impermeability of even the hydrated seed coats of such species to oxygen. As soon as the seed coats are ruptured however, aerobic respiration replaces anaerobic oxidative processes even in seeds of this type."

Chemical Composition of Seed Bed

The presence of nutrient salts in solution evidently has little or no effect upon the germinating seed. This is substantiated by Meyer and Anderson and by experiments conducted by Hoffman (24). The latter found that the early development of Douglas fir seedlings was dependent upon the food stored in the endosperm of the seed. This he demonstrated by germinating and growing Ponderosa pine, Western hemlock, Western red cedar, and Douglas fir seeds in contact with soil, sand, nutrient solution, and distilled water. There was no difference noted between the seedlings in the different media until after the endosperm food was exhausted. The importance of this factor to germination is very often overemphasized, due to its pronounced effects upon subsequent growth.

Influence of Light

There are various opinions regarding the role of light in the process of germination. Miller (37) states that it is certain that some seeds are very sensitive to light in the germinative period, either positively or negatively. This sensitivity is especially well illustrated by lettuce seeds which were found to be stimulated into germination by red, orange, and yellow rays of light, while green,
blue, and violet rays inhibited germination. No positive results are known to have been obtained from work with the seeds of forest tree species. It is evident that radiative energy in the form of heat plays an important part in germination, however, as is indicated by the following discussion.

Temperature and Germination

For a very good account of the part played by the temperature factor in the activation of the life processes in seeds, we again turn to Meyer and Anderson (36). "In the absence of other limiting factors, the seeds of any species will germinate within a certain range of temperatures, but at temperatures above or below this range no germination will occur. As a rule, the seeds of species indigenous to temperate regions germinate in a lower range of temperatures than seeds of species whose native habitat is in tropical or subtropical regions.... The optimum temperature is usually about midway between the two extremes of temperature at which germination will occur. It is not possible to designate any exact temperature as the optimum for germination as this varies with the other prevailing environmental conditions and also with the exact criterion selected as an index of germination. The most favorable temperature for the elongation of the primary root, for example, does not always correspond to the most suitable temperature for the development of the plumule." More on the influence of heat on growth will be heard in a later chapter.
Dormancy in Seeds

Meyer and Anderson (36) relate the following in this regard: "Many kinds of seeds, apparently ripe, fail to germinate even if placed under such conditions that all environmental factors are favorable. In such seeds resumption of growth by the embryo is arrested by conditions within the seeds themselves.

"Failure of seeds to sprout does not necessarily mean that they are dormant. Environmental conditions may be unfavorable for germination. The water supply may be inadequate, or the temperature may be unfavorable. Deeply buried seeds are often prevented from germinating by an inadequate oxygen supply, or certain kinds of light-sensitive seeds may fail to germinate because of unfavorable light conditions. The term dormancy as applied to seeds is generally restricted to those which fail to germinate as a result of internal causes."

Dormancy of seeds is due to one or a combination of several different factors. "It may be due to the impermeability of the seed coats to water or to oxygen. Some seed coats are so strong that expansion of the embryo cannot rupture them. In other seeds the embryos are not completely developed at the time the seeds are shed. A period of 'after-ripening' is required by other seeds."

Some Results of Experimentation: Physical Condition of Seed Bed

In his experimentation with the establishment of seedlings of northeast conifers, Moore (41) concluded: "The experiments show that germination and survival are very poor on both coniferous and broadleaf humus. The reason appears to be insufficient moisture,
and inability of the seed to penetrate beneath the surface. The
layer of needles which falls every autumn appears to correct this
difficulty to a certain extent under natural conditions. Germination
on mineral soil was good....Germination was slightly better in the
openings, except for the spruce type and humus flats...Growth of the
survivors in the open was many times that of the seedlings in the
shade, in spite of (added) minimum ample moisture in the shade."

Gemmer, Maki, and Chapman (15) working with the regeneration of
longleaf pine in Mississippi, state: "Greenhouse tests showed that
longleaf seed germinated and became established best on mineral soils
and on light, well-watered humus. Heavy deposits of ash from
recently burned litter were very detrimental to the establishment
of longleaf seedlings. The physical condition of the surface soil
was also important; while the hardness or compaction of the soil
did not lower materially the germination of pine seed, it affected
noticeably the penetration of the soil by the radicles. Mechanical
loosening of dense soils favored decidedly the establishment of the
seedlings. The rate of germination of longleaf seed varied with the
quantity of water applied and the frequency of application." In a
field trial the authors found that better germination was secured
by the natural fall of seed on unchanged ground than it was on
burned-over or cultivated ground. Note the discrepancy between
these results and the conclusions of other investigators.

Once the seed has germinated, an entirely different group of
processes come into prominence. These we shall consider next.
Importance of Light

Nearly all growth processes of plants depend upon light either directly or indirectly. Its most common association with plant growth is in the processes of photosynthesis which is carried on by all green plants. In short, this process involves the synthesis of carbon dioxide from the air with water from the growing medium to form plant sugars which are essential to the growth of all green plants. The process is a function of the chlorophyll and is carried on only in the presence of light. The quantities and qualities of light involved in this process for different species of plants are of course variable. It is in this variability of the light requirement that the study of the influence of light on the growth of seedlings in the forest is of prime importance.

Physiological Processes Involving Light

Again we will turn to Meyer and Anderson (36) for the general picture. "The energy stored by green plants in the molecules of simple sugar during photosynthesis can be supplied only by light, and in the absence of illumination photosynthesis fails to occur. Any source of radiant energy which furnishes wave lengths within the range of the visible spectrum will induce photosynthesis provided its intensity is sufficiently great. Although a few of the longer wave
lengths of ultraviolet apparently are effective in photosynthesis, in general this process can occur only in radiation of the visible part of the spectrum.

"A number of studies have been made of the minimum light intensities at which various species of plants are just barely able to survive. Unless reserve foods have previously accumulated, the minimum light intensity at which a plant will remain alive for indefinite periods during its normally active seasons must permit sufficient photosynthesis to compensate for both day and night respiration, and in all probability must also allow for some assimilation.

"Bates and Roeser (1928) studied the effects of low light intensities upon the growth of a number of species of evergreens native to the western United States. The seedlings were exposed to a 200 watt, blue tungsten lamp for 10 hours a day. Differences in light intensity were obtained by growing the seedlings at different distances from the source of illumination. Their results show that redwood seedlings were able to maintain their initial dry weight in a light intensity less than 1 percent of full sunlight, while pinon pine required about 5 percent, and the other three species were intermediate in their requirements.

Light Quality

Light which has been filtered through the crown of a tree is usually proportionately richer in green rays than direct sunlight because of the greater proportionate absorption in the red and blue portions of the spectrum. This effect upon light quality is most
marked in hardwood forests in which the tree crowns form an almost continuous canopy. The herbs, shrubs, and smaller trees growing in such forests are subjected to light which is not only of much lower intensity than full sunlight, but is also different in quality from the light impinging upon the forest canopy.

**Light Intensity**

"Relatively high light intensities result in most species in shorter internodes, plants of lower stature, and smaller leaves, but the dry weight, number and size of the branches, size of the root system, and production of flowers and fruits is greater than in weaker light intensities. Many species show increased growth in terms of dry weight increment with increased light intensity up to 100 percent of summer sunlight, if no other factor is limiting. All phases of the growth of typical shade species are usually retarded, however, by high light intensities." Weaver and Clements (67) add: "The optimum amount (of light) for many species is less than full sunshine; some plants make their best development in light of low intensity. Thus, the seedlings of Douglas fir thrive best at about 50 percent full sunshine."

Grasovsky at Yale (17) found that there was a minimum light intensity at which seedlings could continue to live. A moderate increase over this minimum intensity was necessary to maintain growth. An intensity of approximately 170 foot candles was necessary to balance, through photosynthesis, the amount of CO₂ given off in respiration and that used by photosynthesis. An additional 170 foot candle was found to be sufficient to maintain growth. His
final conclusion was: "...the intensity and quality of the light reaching the forest floor are not the determining factors in accounting for the presence or absence of reproduction in the fully stocked forest where the investigation was made."

Mitchell (39) found that young coniferous seedlings grown in low light intensities are actually taller, and have more numerous and longer needles than those exposed to higher intensities, but they are light, spindly, succulent and have poorly developed roots. High light intensities, like root pruning and low seed bed density, tend to produce heavier, stockier, hardier plants with well developed roots and a more favorable balance between root and shoot weight.

In the same publication, Mitchell further stated: "Available data indicate that the chemical and physical properties of the soil govern, to a large extent, the effect that increased solar radiation will have upon the absorption of mineral nutrients by white pine seedlings....But in soils and inorganic culture solutions where the majority of nutritive elements are free in solution, it appears that the root size, which increases with light intensity, has little or no influence upon nutrient absorption."

In his experimentation with the ecological influences of light, Shirley (53) came to the following conclusions: "When light intensity is too low for the growth (increase in dry weight) of species intolerant of shade, it is also too low for appreciable growth of the most tolerant. The real difference between the tolerant and intolerant species, in so far as light requirements are concerned, is the length of time they can survive in light intensities too low for growth. When light intensities are high enough for appreciable
growth of either species, the one having the most rapid rate of growth, which is usually the least tolerant, will outgrow the others."

"Therefore, it may be safely concluded that the changes in spectral energy distribution of light in the forest have only a secondary influence on the growth of plants on the forest floor, and are of less importance than the changes of intensity."

"The actual light intensity required for the survival of plants, is low --one to five percent -- and is close to the value at which photosynthesis balances respiration."

"Light intensity also influences, to some extent, the mineral nutrition of plants, particularly their nitrogen metabolism. Unless plants receive enough light for rapid photosynthesis, they accumulate but cannot utilize nitrogen effectively and, conversely, if they do not receive sufficient nitrogen they accumulate but cannot utilize carbohydrates effectively."

Bates and Roeser (6) measured the light intensity requirements of various coniferous seedlings and came to the following conclusions: "With a minimum requirement of three-fourths of one percent, and increasing its original size almost ten times in light of ten percent intensity, redwood stands out as by far the most efficient mechanism for photosynthesis.....Englemann spruce and the two forms of Douglas fir fall not far behind redwood though perhaps requiring twice as much light for appreciable growth...The pines, in general, fall in a group requiring three to four times as much light as redwood, while pinon stands quite apart from the others, requiring an intensity of 5 percent or more."

G. A. Pearson, who has done much work on the role played by
light in the establishment of reproduction in the Ponderosa pine stands of the southwest, arrived at the following conclusions: (47) "In the forests of the Southwest, heat appears to be scarcely less important than moisture. The upper altitudinal range of all species is determined by low temperatures and the lower altitudinal range by deficient soil moisture. Each species, in a considerable portion of its range, encounters temperatures which are too low for vigorous growth. When the air temperature is too low, the heat deficit may be in a measure made up by the heat of direct sunlight. This, rather than energy for photosynthesis, is thought to account for the relatively high light requirements of such species as western yellow pine. In very low light intensities, but with adequate moisture, all species in the Southwest tend to assume a slender and weak form." In the respect that heat rather than light may be the limiting factor of seedling establishment under certain conditions, Pearson has come to the same conclusion as several authors whose results have also been quoted.

Concerning the importance of light in the establishment of Western white pine seedlings, Haig (19) found the following: "Insolation and drought are the most important physical factors affecting initial seedling mortality. Insolation is by far the most important factor on heavily cut-over areas, and drought the most important under full timber. Light is not a direct factor in initial mortality. Seedlings are able to survive the first season under intensities as low as 5 percent 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."
Temperature

"The rate of every physiological process occurring in plants is markedly influenced by the all-pervading factor of temperature. Similarly the rate of growth, as measured in terms of any of the usual quantitative indices, is profoundly influenced by this factor. Temperature, however, exerts qualitative as well as quantitative effects upon the development of plants. In other words the structural development and physiological reactions of a plant may vary greatly, depending upon the temperature pattern of that plant's environment. Finally, whether or not a plant can survive in a given habitat often depends upon the temperature extremes which occur in that habitat."

Temperature in its extremes is highly important in the survival of seedlings due to the inability of tender seedlings to withstand the highest and lowest temperatures under certain circumstances. Boyce (7) gives a very detailed account of the various types of non-infectious diseases of seedlings due to both heat injuries and freezing injuries. (Boyce, pp. 77-81) Suffice it to say here that the maximum lethal temperature for seedlings is between 120 and 130 degrees F. Injuries due to freezing include freezing back of succulent growth by late and early frosts, frost heaving, mechanical root
injury, and winter drying. For the most part, these diseases have been studied extensively only under nursery conditions.

Bates (4) in investigating the relative resistance of tree seedlings to heat, stated, "The meager data on surface soil temperature that are so far available indicate that the difference between sites which encourage species are far greater than might be thought possible -- at least three or four times as great as the differences between temperatures at a depth of one foot."

After extensive experimentation with Douglas fir seedlings under various conditions, McArdle (35) set forth the following findings: "Colour has a pronounced effect on the temperature attained at the soil surface. Dark soils, especially those containing a large admixture of charcoal from a slash fire, experience much higher temperatures than light soils. With air temperatures of 90°F. (sheltered), the average temperature at the surface of a yellow soil was 132°F., whereas the same soil covered with a thin layer of burned duff and charcoal had a surface temperature of 150°F. (both in full sunlight). The highest temperature recorded in these experiments was 166°F. at the surface of a charcoal blackened soil when the air temperature was 102°F. In as much as seedlings begin to die when soil surface temperatures reach 123°F., it is easy to understand that blackening the soil surface by burning may of itself cause the destruction of a seedling crop." Bates (3) working in the central Rocky Mt. region reported the following conclusion: "A review of the facts that have been presented leaves little doubt that the several tree species of the central Rocky Mountains are controlled in their distribution almost wholly by the degree of insolation of the site,
the resultant temperature, and the closely related surface moisture conditions." Thus we see that temperature data cannot be taken alone when summing up results.

**Moisture**

Water is often spoken of as the great solvent. In plants it is the solvent, and its pronounced importance in this role is reflected in the vast amount of data relative to the availability of water in various types of soils, and to the functions of water in the plant. Here there is only space enough to touch on the basic influences of water as related by the best that has been brought out by the wide experimentations of many research experts. As has been the case when other single factors were emphasized, here again we find that it is impossible to completely isolate the functions performed by water from the effects of the many other factors influencing plant growth. In keeping with their excellent account of the subject, we again turn to Meyer and Anderson (36) for our basic information before turning to the specific research data.

**Soil Conditions Influencing the Availability of Water**

"Although transpiration can continue for short periods at rates considerably in excess of the rate of absorption of water, in general, if soil conditions are such that absorption of water is appreciably retarded, the rate of transpiration will soon show a corresponding retardation. The availability of soil water to the plant is therefore an important and, in fact, often the limiting factor in transpiration. The principal soil factors which affect the rate of absorption of water
by plants are: 1 available soil water, 2 soil temperature, 3 aeration of the soil, and 4 concentration of solutes in the soil solution.

"In many soils the water table lies so far below the soil that it has little or no effect on the soil moisture conditions in the soil layers which are penetrated by the roots of most plants. Generally speaking even in loam or clay loam soils, a capillary rise of water from a zone of complete saturation is probably ineffective in providing the roots of most species of plants with any considerable part of the water which they absorb unless the water table is within about 15 feet of the surface. Some of the more deeply rooted species may obtain some water from a water table located at depths as great as about 30 feet, but the presence of a water table at greater depths than this is a negligible factor in supplying the roots of any species of plants with water.

"There are two principal conditions under which capillary translocation of water can occur in soils at appreciable rates: 1 in any zone of soil which is not more than a few feet above the water table, and 2 in the upper layers of any soil after a heavy rain or irrigation, but before the water content of the soil has become attenuated to its field capacity. As the water in the films surrounding the soil particles with which the root tips are in contact becomes depleted, more water moves towards those particles by capillarity. The actual rate of such capillary movement of water through the soil may become a factor influencing the rate of absorption. Root systems, however, are not static, but are more or less continually growing through the soil. This continued growth of root tips through the soil brings them into contact with other portions of the soil water, so even if capillary
movement to certain points ceased, capillary movement of water to the
carroes may be re-established by the extension of the root tips themselves
into zones of the soil which have not yet been depleted of available
water.

"Many plants, much of the time, grow in soils at water contents
between the wilting percentage and the field capacity. In this range
of soil water contents capillary movement of water is negligible. Once
most of the film water present on the soil particles with which the root
tips are in contact has been absorbed it cannot be replaced in any
significant quantity by capillary movement from adjacent regions of
the soil if the soil water content is below the field capacity.
Neither does water move in vapor form through soils towards the absorbing regions of roots at appreciable rates. Under such conditions the absorbing region of every rootlet often becomes surrounded with a narrow cylindrical zone of soil which has been depleted to a water content much below that of the surrounding soil....Considerable water may be absorbed by the plants merely by continued growth of the roots...
As a general rule, however, the water content of any soil must exceed a certain value if roots are to continue to grow through it...
Experimentation has shown this value to correspond to the wilting percentage....Water enters the roots through the walls of the root hairs and epidermal cells of the root tip."

Weir (69) states: "Capillary rise of soil water is negligible
over 3 feet. The ground zone from which plants may obtain their water
is about 6 feet deep....Absorption of nutrients by plants takes place independently of absorption of water....For each texture type of soil there is a definite percentage of moisture that is absolutely necessary
for the production of crop plants and below which water cannot be absorbed by the plants in sufficient quantity for continued growth. This percentage of water has been designated as the wilting coefficient. Within certain limits plants growing on soils that are well supplied with available plant nutrients require less water than when growing on infertile soils...Crummy soil has higher water retaining power."

Factors Influencing the Rate of Water Absorption

1. **Available Soil Water**  Within limits a more rapid rate of absorption of water is possible when the available soil water content is higher than when it is low.

2. **Soil Temperature**  The influence of soil temperature upon the rate of absorption of water varies greatly with the species....The mechanism whereby low soil temperatures cause a retardation in the rate of absorption is undoubtedly a complex one. Among the factors involved are probably: 1 increase in the viscosity of water, 2 decrease in the permeability of the cytoplasmic membranes of the root cells to water, and 3 a diminution in the physiological activity of the root cells.

3. **Aeration of the Soil**  In general absorption of water by the root systems of most species of plants proceeds more rapidly in well aerated soils than in those which are not.

4. **Concentration of the Soil Solution**  The concentration of the soil solution of most soils is so slight as to have little or no influence on the diffusion pressure deficit of the soil water, which in most soils, as long as they are fairly moist, does not
exceed 1 atmosphere."

The Role of Water in Photosynthesis

"Less than 1 percent of the water absorbed by a plant is used in photosynthesis. It therefore seems probable that the indirect effects of the water factor upon photosynthesis are more pronounced than its direct effects. In other words deficiency of water as a raw material is not commonly a limiting factor in photosynthesis. Nevertheless, a reduction in the water content of leaves generally results in a decrease in the rate of photosynthesis. There are probably two principal ways in which this effect can be exerted: 1 reduction in the diffusive capacity of the stomates resulting from the decreased leaf water content, and 2 reduction in the hydration of the chloroplasts and other parts of the protoplasm." (36)

Miller (37) states that roots in the soil are positive in their reaction to the presence of water, turning toward the higher water content, "but as the stimulus from the hydrotropic reaction occurs in the root tip, roots will not respond unless already in close association with the moister soil"...In the case of some plants if a portion of the root system is in contact with sufficient moisture other portions of the system are able to continue development through dry soil and be in readiness for moisture when it is contacted.

The Wilting Coefficient

The wilting coefficient is a term widely used to measure the amount of water in the soil available for plant use. It is that moisture content of the soil at which plants growing therein will permanently
wilt. This value is not a constant but varies considerably by soil type, e.g. the wilting coefficient for wheat varies from .88 percent in coarse sand to 14.5 percent in clay loam. There is no great difference between the abilities of various types of plants, such as mesophytic and xerophytic, to obtain water from the soil; consequently, for any one type of soil, the wilting coefficient will not vary greatly between the most succulent growth and the most drought enduring. For the most part, the wilting coefficient depends on the factors governing evaporation. (37)

In his work with Douglas fir seedlings, Hoffman (24) found that the wilting coefficient of a 2 year old seedling was 1.25 percent for a certain soil north of Mt. Adams. On a south slope the moisture of the surface soil reached 0.18 percent in July and did not go above 0.85 percent in August. At a depth of 6 inches, however, the soil was found to have a moisture content of 6.55 percent in July and 5.50 percent in August. His conclusion was that it would be impossible for D. fir seedlings to become established on this site unless they could penetrate to the 6 inch depth before July of their first season. This type of information can give the forester a very good indication of the probable success of naturally and artificially established seedlings under various soil and cover conditions.

The Conclusions of Various Investigators

Touney (60) "...the forest soil with its normal layer of litter has the greatest amount of moisture after mid summer in the upper 4-inch layer even during the dryest periods, and the amount of water in each successive layer progressively decreases with soil depth down to
at least 3 feet. This apparently explains why very tolerant species like eastern hemlock and flowering dogwood, that germinate and persist under dense canopies, have shallow initial root systems."

McArdle (35) "On the fully exposed cut-over area, the soil always had less moisture at a depth of three inches than a soil under mature Douglas fir timber or under brush cover. At a depth of six inches the soil moisture content on the three areas was about equal. At a depth of 12 inches, however, there was more moisture in the soil of the fully exposed area. Occasionally the moisture content of the soil at the three inch depth dropped below the wilting point for Douglas fir seedlings on the fully exposed area, but this did not occur under brush or forest cover. Contrary to the findings in many other forest regions, practically all soil moisture during the summer months was found to be capillary water; the top six inches of soil invariably was drier than lower strata." (It would be interesting to have a comparison between regions correlated with respective rainfall records.)

Working with white pine, Haig (19) found that "Losses due to drought are primarily due to surface drying. The amount of such loss is directly linked with root penetration; very much less in full sun, where rapid and relatively deep drying is 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."
Craib (13) brought emphasis on the idea of measuring the moisture content of the soil during driest periods of the year in order to get the most significant results, rather than during the entire year. Some of his conclusions were as follows:

1. Both in the open and in the forest there was considerably more moisture present during the growing season in the upper soil layers than in the lower. The amount of soil moisture consistently decreased with increase in depth, at least to 100 cm.

2. Both in the open and in the forest there was rapid falling off in the amount of water present in the soil layers down to a depth of about 40 cm. below which there was much less change.

6. In the open there was more moisture in the second 10 cm. of soil than in the first. This was due to the drying effect of the exposure of the litter layer to sun and wind.

7. The soil became progressively drier in the forest with increase in depth, despite the fact that the tree roots were largely concentrated in the surface soil layers. Little moisture was lost by direct evaporation, due to the thick covering of needle litter.

8. The open soils contained considerably more moisture during dry periods than the forest soils. The difference was greatest in the upper soil layers and became progressively less with increase in depth.

9. Soil, both in the open and in the forest, consistently increased in density with increase in depth. This was due to the greater biological activity in the upper soil layers.

10. Open soils were considerably denser than forest soils. From 0 to 10 cm. below the surface, the soil in the denuded areas was 26
per cent denser than that of the forest area.

11. The moisture-holding capacity of the forest soil, when based upon volume, was only slightly greater than that of the soil from the denuded area. When based upon weight, the forest soil had a very much higher moisture-holding capacity than the open soil, at least to a depth of 40 cm. This was due to the mathematical distortion of the capacity values for the forest because of its relatively low soil density.

15. During the driest periods of the year there was more than twice the actual volume of moisture in the first 90 cm. of soil available to plants in the open than in the forest. This difference between open and forest soils is reduced if moisture is expressed as a percentage of weight of dry soil.

16. During these dry periods the actual volume of available moisture present in the open was 27 per cent of the actual volume of available moisture which the soil could hold. In the forest there was present only 13 per cent of this amount during the driest periods.

18. The maximum volume of available moisture which a soil can hold and the actual volume of available moisture which it does hold during the driest periods of the growing season, are good indices to its productivity.

21. Other things being equal, the moisture content of a soil sample varies as the organic content, the soil composition, and the space arrangement of the soil particles vary. For this reason no two soil samples were absolutely comparable. Results in good agreement were obtained, however, by securing the average values for a large number of samples."
(NOTE: The following are results of the second part of Craib's study carried on under the canopies of stands of white pine which differed in age, density, and degree of stocking. A trench 1 foot wide and 3 feet deep isolated the quadrats from outside root competition.)

"22. The amount of available soil moisture is greatly increased by the elimination of root competition. During periods of extreme dryness there was from 2 to 9 times as much moisture in the first six inches of soil available to plants in the trenched quadrats as there was in the untrenched (adjacent) check plots.

23. There was usually more moisture available in the surface soil layer than at increased depths. This was true of both the trenched and untrenched quadrats, and helped to explain the prevalence of the roots in the uppermost foot of soil.

24. During the three driest months of the year, namely, July, August, and September, the amount of available soil moisture sometimes fell below the minimum amount necessary to sustain the life of the lesser vegetation. This fact was of great significance in accounting for the survival of reproduction beneath forest canopies. These results apply to the particular conditions of soil and climate under which the investigations were made."

The findings of Barr(2), who worked with the establishment of spruce reproduction in British Columbia, were as follows:

"9. In the forest, artificial watering produced considerable germination on the humus but no particular change in germination on the mineral soil. In the greenhouse, germination took place freely on the humus soil when it was watered daily; under the same conditions good germination occurred on the cldy soil, and in addition delayed germination
took place when the intervals between watering were increased. Germination was good on sand with no delayed results. It is concluded, therefore, that spruce seed will germinate freely on humus, sand, or clay soil if the proper amount of moisture is available during the period of germination of the seeds.

10. The germination period is shorter on humus than on clay.

16. Shading did not produce any significant difference in soil moisture.

20. The failure of seeds to germinate on humus soil in the forest was due to their inability to absorb moisture from the particles of organic matter with which they were in contact. When the season was sufficiently advanced for temperature conditions to be suitable, the humus did not remain moist long enough for germination to take place. In the mineral soil sufficient water remained available for absorption by the seeds to enable germination to occur.

21. Natural regeneration of spruce may be secured in mature spruce-balsam stands by artificially breaking up the layer of raw humus on the forest floor and exposing the mineral soil. The operation should be carried out at a sufficient interval before logging to enable the seedlings to become securely established." (The species used in the above referred to experiments were Picea engelmanni, P. canadensis, and Abies lasiocarpa).
chapter vi

EDAPHIC FACTORS INFLUENCING SEEDLING DEVELOPMENT:

CHEMICAL

* * *

The absorption of nutrients by plants is a very important process. Once the supply of these necessary elements has been exhausted in the seed itself, the young plant must draw its supply from the soil. "The total ash content of plant tissue and organs varies from a fraction of 1 per cent to 15 per cent or even more of the dry weight of the plant material. Fleshy fruits and woody tissues are usually low in ash content, often yielding less than 1 per cent, while the ash content of leaves is usually relatively high, often exceeding 10 per cent." (36)

It is probable that all of the elements are found to be present in plant tissues. Forty have been isolated from the tissues, but only about 15 of these are generally considered to be essential to the growth of the plant. (36) Their presence in the soil in an available form for use by plants depends upon many things. The first dependent is the character of the parent material which decomposed to form the soil. The chemical characteristics of the soil govern the type of plant cover it will support, and the cover in its turn will have a great effect on the continued formation of the soil and the availability of the essential elements. These two factors depend upon meteorological conditions for their differences between localities as well as on their interaction with and its result on the formation of the soil.

Many processes are involved in the absorption of nutrients by the plants, and it is probably best that we become acquainted with these processes before we turn to the results of experimentation in the field.
of soils and seedling growth. In this way we can have a much better chance to discover the true significance of the great amount of research to be summarized. The first process to be considered is inseparably connected with the absorption of the basic elements from the growing media by the roots. This is the phenomena of base exchange. As this is of great importance in the complete understanding of the processes of plant growth, especially of seedlings, it is considered here in some detail as set forth by Meyer and Anderson (36).

Base Exchange

"The fundamental physico-chemical properties of most soils are due mostly to the clay fraction, except in soils relatively rich in organic compounds in which they also play an important part in determining soil properties. The clay fraction of the soil consists entirely of particles of colloidal dimensions. The clay particles of the soil are apparently composed largely of alumino-silicates and although of colloidal dimensions possess a definite crystalline structure.

"Although it is known that certain uni- and bivalent cations, especially $K^+$ and $Mg^{++}$, may occur within the crystalline lattice of the micelles of colloidal clay, from the standpoint of plants a much more important role in the ionic relations of soils is played by cations located at the surface of the clay particles. The micelles of colloidal clay are almost invariably negatively charged, and the cations associated with them may be regarded as occupying a position analogous to the ions in the outer layer of an electrical double layer. The cations most commonly associated with the clay particles of natural soils in this manner are $Ca^{++}$, $Mg^{++}$, $K^+$, $Na^+$, and $H^+$. Cations are also similarly
associated with the soil colloidal particles of organic origin.

"Under certain conditions some of the cations of one kind can be displaced from the micelles by another kind of cation. For example, if a neutral soil is treated with a potassium chloride solution, some of the added K⁺ ions replace Ca²⁺ ions associated with the clay micelles, an equivalent quantity of Ca²⁺ ions being displaced into the solution, pairing off with the residual chloride ions.....

"The phenomenon which has just been described is called base exchange or cation exchange. Such interchanges of cations take place very rapidly and are reversible. In neutral and slightly alkaline soils Ca²⁺ is the principal replaceable cation, although appreciable quantities of Mg²⁺ may sometimes also be present. The H⁺ ion is the principal replaceable cation in acid soils, and the Na⁺ ion occupies a similar position in alkali soils. All of the exchangeable cations are not retained by the micelles with equal effectiveness. The order of the retentive capacity of the micelles for cations is H⁺, Ca²⁺, Mg²⁺, K⁺, NH₄⁺, Na⁺. In other words, of the ions in the above series, the H⁺ ions are most tenaciously bound to the colloidal particles and are the most difficult to displace, while the converse is true of the Na⁺ ions.

"Of the five principal anions found in the soils -- Cl⁻, SO₄²⁻, NO₃⁻, HCO₃⁻, and PO₄³⁻ -- only the last is retained by the soil particles as such in any appreciable quantities. The other four anions usually leach out of soils rather rapidly.....

"The region of the root in which intake of water occurs is also, in general, the zone in which absorption of ions takes place, and the pathway which solutes follow in passing from the soil to the stele is
the same as that followed by water. The root tips are, under favorable conditions, not only rapidly growing organs, but centers of high metabolic activity. Carbon dioxide resulting from respiration is continuously being released into the soil in which it reacts with water forming carbonic acid. Around each root tip there will usually be, therefore, a localized zone of high carbonic acid content. In this zone H⁺ ions from the carbonic acid may displace adsorbed cations on the clay micelles. This is especially likely to happen to the micelles in intimate contact with the root tips. The cations released as a result of this ionic exchange can then be absorbed by the plant. That plants can release adsorbed Ca⁺⁺ ions from soil colloids in this manner has been demonstrated experimentally (Jenny and Cowan, 1933) and other kinds of ions undoubtedly can be displaced from the clay micelles in the same way. Since roots are more or less continuously growing through the soil they are constantly coming into contact with additional micelles from which cations can be displaced and absorbed. In many soils, in fact, it is only by continuous growth of the roots through the soil that a continued absorption of mineral salts can take place. The rate of root growth is therefore often an important factor both in the absorption of water and the absorption of mineral salts. As a result of ionic exchanges of this type neutral soils tend to become more acid with continuous cropping unless calcium is supplied from time to time." Wilde and Patzer (75) stated: "General observations indicate that the absorbing and base exchange effects of soil organic matter are at least two and one-half times as great as those of fine soil material, i.e., material less than 0.05 mm in diameter...This implies that a considerably lower content of mineral colloids is adequate for successful
planting on soils high in organic matter."

Miller (37) goes into even greater detail in describing the intake of solutes by the plant. "It has generally been observed that the protoplastic membrane of the cells bordering upon the soil or the medium in which the plants are growing is permeable to practically all the inorganic solutes present in the soil solution.

"Some of the various forces that may be concerned in the accumulation of solutes in the cell sap are: 1 the attraction of colloids for ions, 2 the amphoteric nature of protoplasm, 3 Donnan equilibrium, 4 ionic exchange, and 5 metabolic activity.

"1 The demand for the various elements originates in the tissues of the plants and is carried to the absorbing surface of the root by means of unsaturated colloidal compounds bearing a plus or minus electric charge.

"2 The outer surface of the protoplasm of a plant cell may be in contact with a medium that is either neutral or alkaline to it, while at the vacuole it may be in contact with a medium that is on the acid side of its isoelectric point. As the protoplasm rotates or circulates in the cell, every part of it is alternately in contact with the exterior medium; when it is on the alkaline side of its isoelectric point it combines with cations and releases anions. As circulation continues it comes in contact with the acid cell sap, releases its cations, and combines with anions. This theory accounts in part for the "heaping up" or accumulation of cations in the cell sap. (Lapique)

"Davidson assumed that there is a wide range in the isoelectric points of the plant ampholytes allowing the occurrence of both electro-
positive and electronegative ampholytes within certain limits of hydrogen-ion concentration. This makes possible the simultaneous accumulation of cations and anions. A change in the reaction of the medium may modify to some extent the reaction within the plant cells and thus shift some of the electropositive ampholytes to the negative side, and vice versa. This might cause an increased absorption of cations and anions.

"...It was considered by Casale that the ectoplasm yields hydrogen ions to the soil solution and thereby establishes a difference of potential between the plant cell and the soil particles. In the process of equalization of those charges, the more distant particles yield cations to the nearer ones, and these in turn yield them to the ectoplasm. Thus fertilizers act, in part, by changing the difference of potential between cells of the plant root and the soil particles."

Buffer Action

Another phenomenon characteristic of organisms in general as well as of soils is buffer action. Van Slyke (63) defines it as follows: "By buffer action we mean the ability of a solution to resist change in pH through the addition or loss of alkali or acid....Buffers are substances which by their presence in solution increase the amount of acid or alkali that must be added to cause unit change in pH...The buffer effect of weak acids or bases is due to the relatively slight extent to which they undergo electrolytic dissociation."

Tottingham (59): "Buffer systems of the organism prevent sudden changes of reaction in the sap which might injure the protoplasm. These are of three principal types, namely: organic acids and their
salts, mixtures of phosphates of different basicities, and peptides or amino acid."

Gortner (16): "A weak acid or base is characterized by the fact that a large portion of the material in solution is present in the form of undisassociated molecules....All reactions of living protoplasm take place in buffered media....Most biological reactions take place in an essentially neutral or slightly acid medium, and as a rule, biological organisms have a greater capacity for the buffering of acid solutions than for bases."

Remington (50): "The mechanism whereby buffer solutions function may be conveniently illustrated by using an acetic acid and sodium acetate buffer system as the example. In a solution containing these substances, the sodium acetate, being a strong electrolyte, is practically completely ionized. The acetic acid, being a weak electrolyte, is but slightly ionized, indeed, its slight ionization into hydrogen and acetate ions is further reduced by the mass action or repressing effect of the high concentration of acetate ions. The solution, therefore, contains relatively large amounts of acetic acid molecules and sodium and acetate ions and a small number of hydrogen ions, the reaction of the solution being slightly acid. Furthermore, the hydrogen and acetate ions and the molecules of acetic acid are in equilibrium in accordance with the law of mass action as formulated for weak acids. Now if more hydrogen ions are added to the solution, the equilibrium between hydrogen and acetate ions and molecules of acetic acid is disturbed and in order to restore equilibrium again a part of the comparatively large reserve of acetate ions will combine with the added hydrogen ions to form un-ionized acetic acid molecules. In so doing
the original pH of the solution will be restored, or at most only slightly changed."

It may appear that the subject of base exchange as well as that of buffer action have little relation to the main subject at hand -- the factors relating to the establishment of seedlings. It might be possible to simply enumerate the findings of each investigator in this field and to derive there-from a fair idea of the present status of knowledge, or rather its factual indicators; but to get an understanding of these facts, and to be able to interpret, analyze, and apply these findings wisely, demands that all the processes involved be considered. Unfortunately, there is not sufficient time nor space to really adequately cover the entire subject in all its important ramifications. As a consequence, the greater emphasis has been placed on the facts while the amount of enlightenment derived from their subsequent combination and correlation must for the present be left to the reader.
## Proximate Composition of Some Natural Organic Material

<table>
<thead>
<tr>
<th></th>
<th>Pine Needles</th>
<th>(mature yellow) Oak</th>
<th>Green Oak</th>
<th>Rye Straw</th>
<th>Hardwood Humus</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Cold to hot H₂O soluble organic material</td>
<td>13.02</td>
<td>15.32</td>
<td>22.02</td>
<td>9.90</td>
<td>7.00</td>
</tr>
<tr>
<td>2. Hemicellulose</td>
<td>14.68</td>
<td>15.60</td>
<td>12.90</td>
<td>22.90</td>
<td>18.52</td>
</tr>
<tr>
<td>3. Cellulose</td>
<td>18.26</td>
<td>17.18</td>
<td>15.92</td>
<td>36.29</td>
<td>11.44</td>
</tr>
<tr>
<td>4. Lignin</td>
<td>27.63</td>
<td>29.66</td>
<td>20.67</td>
<td>19.80</td>
<td>47.64</td>
</tr>
<tr>
<td>5. Crude Proteins</td>
<td>8.53</td>
<td>3.47</td>
<td>9.18</td>
<td>1.06</td>
<td>10.06</td>
</tr>
<tr>
<td>6. Ether soluble</td>
<td>7.65</td>
<td>4.01</td>
<td>7.75</td>
<td>1.26</td>
<td>5.34</td>
</tr>
<tr>
<td>7. Ash</td>
<td>3.08</td>
<td>4.68</td>
<td>6.40</td>
<td>3.90</td>
<td>5.60</td>
</tr>
</tbody>
</table>

## Proximate Composition of Natural Forest Humus

<table>
<thead>
<tr>
<th>Soil type</th>
<th>AII</th>
<th>AIII</th>
<th>BII</th>
<th>BIII</th>
<th>CI</th>
<th>CII</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reaction pH</td>
<td>5.6</td>
<td>4.9</td>
<td>5.1</td>
<td>4.4</td>
<td>4.4</td>
<td>4.3</td>
</tr>
<tr>
<td>Cold to Hot H₂O Sol.</td>
<td>5.80</td>
<td>2.73</td>
<td>5.03</td>
<td>4.66</td>
<td>5.14</td>
<td>3.63</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>15.28</td>
<td>12.39</td>
<td>15.43</td>
<td>17.87</td>
<td>17.50</td>
<td>17.30</td>
</tr>
<tr>
<td>Cellulose</td>
<td>9.14</td>
<td>2.56</td>
<td>7.28</td>
<td>3.84</td>
<td>9.62</td>
<td>5.64</td>
</tr>
<tr>
<td>Lignin</td>
<td>29.30</td>
<td>50.39</td>
<td>38.38</td>
<td>37.29</td>
<td>42.26</td>
<td>44.88</td>
</tr>
<tr>
<td>Crude Prot.</td>
<td>8.29</td>
<td>7.51</td>
<td>8.02</td>
<td>7.04</td>
<td>6.84</td>
<td>5.15</td>
</tr>
<tr>
<td>Ether Soluble</td>
<td>4.14</td>
<td>2.99</td>
<td>5.21</td>
<td>3.96</td>
<td>3.58</td>
<td>3.94</td>
</tr>
<tr>
<td>Ash</td>
<td>9.20</td>
<td>11.61</td>
<td>7.94</td>
<td>13.67</td>
<td>6.05</td>
<td>10.57</td>
</tr>
</tbody>
</table>
Use of Nutrients by the Seedling

Although it is thought that there is a possibility of all known elements being found within plant cells, the utilization of these elements by the plant is a completely different consideration. Not all of the elements absorbed will be utilized by the plant; many will remain inert. Those mineral elements that are utilized by the many processes of the plant, are known as mineral nutrients. Their general roles have been classified as follows: \(^{(36)}\)

1. Building material from which parts of protoplasm and cell walls are constructed.
2. Influence on the osmotic pressure of plant cells.
3. Influence on acidity and buffer action.
4. Influence on the hydration of cell colloids.
5. Toxic effects of mineral elements.
6. Influence on the permeability of membranes.
7. Antagonistic effects.
8. Catalytic effects.

The Individual Elements

The following information has been gathered from Meyer and Anderson \(^{(36)}\) and Miller \(^{(37)}\):

Carbon, Hydrogen, and Oxygen enter into the composition of practically all the compounds of the plant and make up approximately 95% of its dry weight. Water is the great solvent without which plant processes would be non existent.
Phosphorus is present in relatively great amounts in seeds. To a certain extent, an increase in soil phosphorus shows an increase in plant growth and substance. Within the plant the regions of fast growth show a greater concentration of phosphorus. It is characteristically easily distributed from one part of the plant to where it is needed. In this sense, young growing tissues may gain in phosphorus content at the expense of older tissues. It is present in certain nucleic acids. When added to the soil, it often favors stimulated root development.

The actual physiological role is many phased. The reduction of nitrates is slowed without sufficient P. Phosphates have been found to have a direct relation to the respiration of CO₂ due to action on sugars. In its absence, the transformation of starch to water soluble carbohydrates is slowed. It is important in ripening processes of grains. It is utilized in considerable quantities in the formation of nucleo-proteins in meristematic tissues.

Sulfur as a rule is well distributed throughout the plant. Its presence in the soil greatly increases root development. Deficiency may be marked by yellowness of the leaves. An abundance of this element favors the development of root nodules on legumes. Sulfur is a constituent of the amino acid, cystine, from which plant proteins are in part synthesized. Much of the sulfur in plants remains in the inorganic form as sulfates. It may be redistributed to other organs.

Calcium. The largest portion of calcium in plants is located in the leaves. Though a considerable portion remains in a soluble form,
that which has been utilized by the plant is not available for redistribution.

The part played by calcium in the plant physiological processes is varied. It is a structural component of plant cell walls in the form of the calcium pectate of the middle lamella. Calcium ions have pronounced effects upon the permeability of the cytoplasmic membranes and upon the hydration of colloids. Deficiency of calcium results in a stunting of root development of many species. Calcium is of frequent occurrence in plant cells in the form of insoluble crystals of calcium oxalate, and also forms salts by reactions with other organic acids. Some investigators consider that calcium performs an important function in combining with the organic acids which are by-products of protein synthesis, thus preventing the accumulation of organic acids within the cells. Lack of calcium encourages an abnormal accumulation of starch in many plants. The presence of Ca\(^{++}\) ions in solution along with other metallic ions increases the diffusion of the latter into root cells.

There is a definite action between calcium and magnesium, each one tending to neutralize the toxic effect of the other.

**Magnesium** is the only mineral constituent of the chlorophyll molecule. Seeds are rich in Mg. Redistribution of Mg from older to younger organs occurs readily. Deficiency of magnesium results in the development of a characteristic chlorosis. It is believed that Mg is intimately related to oil formation and to the synthesis of nucleo-proteins in plant cells. Here it may act as a carrier of phosphates. Plants or seeds containing more than average oil have been found to have greater amounts of Mg.
Potassium in plants is largely absorbed in its earlier life stages. It is not definitely known to be built into organic compounds of fundamental physiological significance. It occurs almost solely as soluble inorganic salts. It is an indispensable element and cannot be completely replaced even by such similar elements as sodium or lithium. Meristematic and young tissues are always rich in K. Only a low portion is found in seeds. Redistribution throughout the plant occurs readily and continuously. It is present in the regions of photosynthesis, translocation, storage, and other special activities.

The role of potassium is probably largely catalytic. While the evidence for none of these effects can be regarded as incontrovertible, potassium appears to be necessary for the normal maintenance of the following processes: 1 the synthesis of simple sugars and starch, 2 translocation of carbohydrates, 3 reduction of nitrates, 4 synthesis of proteins, particularly in meristems, and 5 normal cell division. The K⁺ ion is usually the most abundant univalent cation in plant cells and undoubtedly has important effects upon permeability of the cytoplasmic membrane, hydration of the protoplasm, etc.

Iron is rarely found to be deficient in soils though it may be present in an insoluble form, esp. in the more basic soils. Fe is indispensable for the synthesis of chlorophyll in green plants -- its deficiency results in chlorosis. It is also supposed to act as a catalyst or oxygen-carrier in oxidation-reduction processes occurring in living cells. It is one of the most immobile elements within plants.
Boron is essential for many species of plants although it is required in minute quantities. Annual plants have least boron whereas the greatest deposits are in the wood and bark. Cotton seems to have the highest boron requirement and the cereals, the lowest.

Manganese is, as a rule, most abundant in the physiologically active portions of the plant. It is supposed to play a part in oxidation and reduction phenomena. It is related in some way to chlorophyll synthesis. It is most concentrated in the leaves. The absence of Mn has resulted in disturbed carbohydrate metabolism, chlorosis, retarded growth, a decrease in ash content, and failure to reproduce.

Copper. Very little is known of the actual function of this element. Tests on crops grown in raw peat soils of Florida showed great increases in yield with addition of CuSO₄.

Zinc, although its actual function is not known, is essential in some plants.

Sodium always occurs in the ash of plants, but does not seem to be one of the essential elements. It may partially replace potassium in some plants.

Silicon is relatively abundant in the bark of trees. It appears to exert an important influence upon the phosphate metabolism of plants.

Chlorine is found universally in plants, but is present in the form of inorganic chlorides. Its necessity and function are not definitely known to exist.
Aluminum is one of the most abundant elements in the soil, but it is chiefly in insoluble form. It may be present in soluble form in highly acid soils. It is universally present in plants, exerts pronounced effects upon them (usually detrimental), but is not credited as essential.

Nitrogen Nitrogenous compounds absorbed from the soil serve as the sole source of nitrogen for all terrestrial green plants. Such plants can utilize four kinds of nitrogen compounds: 1 nitrates, 2 nitrites, 3 ammonium salts, and 4 organic nitrogen compounds. Nitrates apparently can be absorbed by many kinds of plant cells against a concentration gradient and are absorbed in essentially the same manner as other ions. The first step in the utilization of nitrates (in which form nitrogen usually enters the plant) is their reduction to nitrites which are subsequently reduced to the NH$_2$ and NH$_3$ groups found in organic compounds. N is present in the amino acids which are synthesized to form proteins which are essentially found in the living portions of the cells, e.g., the nucleus. The entire subject of nitrogen metabolism is equally important as, and inseparable from carbohydrate metabolism, but it will not be treated further here. Suffice it to say that both are indispensable processes in living green plants.

Experimental Data

Various experimental data also point to the importance of nitrogen to the forest. Mitchell (39) found that for both Scots and white pine seedlings, the optimum concentration of nitrogen was 300 p.p.m. He found that relatively accurate estimates of the Nitrogen present in nutrient material could be made by differences in the needle color of
white pine seedlings; the brightest yellow corresponding to the least concentration and the dark color to the greater concentration.

In investigating the influence of available nitrogen in the establishment of Sitka spruce and western hemlock seedlings in Alaska, Taylor (58) found: "Nitrogen in available form is an important factor in the occurrence of Sitka spruce and western hemlock seedlings. Small quantities of nitrate nitrogen are correlated with low percentages of spruce seedlings. With increasing quantities of nitrate nitrogen comes a marked increase in the percentage of spruce" to .5 p.p.m.

Root Development Solutes

Miller (37) mentions the following: "The relation of direction of root growth to nutrient concentration is not conclusive, but there appears to be no tendency for roots to seek out the nutrients they need. (A recent article in the Science News Letter claims to disprove this theory, stating that roots actively seek out needed nutrients to a certain extent.)

"The presence of nitrogen compounds has been found to have a strikingly stimulating effect upon the production of secondary roots in seedlings of corn, peas, and other leguminus plants....The presence of layers of soil bearing nitrogen compounds was found to stimulate root growth and branching in that layer, but it also appeared to retard further penetration. Potassium and phosphorus were found to stimulate root growth...It has been noticed that in some experiments plants commencing growth in soil already supporting other plants, will be retarded in growth. The two explanations offered are 1 a poisoning effect on the soil directly by the first plants, and 2 utilization of
the mineral nutrients by the first plants. Increased concentration of nutrients have been found to decrease transpiration as might be expected due to the increased pressure gradient."

Nitrification and Other Experimental Data

Although a discussion of the processes of nitrification might well be classed with that portion of this paper pertaining to the soil microorganisms, it is so closely related to the utilization of the product that it is included here. Concerning nitrification in the soil, Waksman, Tenney, and Stevens (65) say that: "Nitrogen fixing bacteria in forest soils can withstand a higher acidity than in agricultural soils; soils of mixed forests contain more bacteria than soils of deciduous forests, and these more than soils of coniferous forests although, from the relation of bacteria to pH, one would expect that forests of mixed conifers and deciduous species, since they are generally more acid than deciduous forests, would have less various anaerobic bacteria, especially the butyric acid bacteria are found abundantly in forest soils, while the number of nitrifying bacteria is very low....Both aerobic nitrogen fixing and the nitrifying bacteria were found only in soils having a neutral reaction.

"The higher the pH value of the organic matter the higher its nitrogen content. In the decomposition processes taking place in "raw-humus" soil, the nitrogen is liberated as ammonia, while in the so-called 'mull' soils, the ammonia is rapidly changed to nitrate. The optimum pH for ammonia formation was found to be 4.5 to 5.0, for nitrate formation, in case the soil is inoculated, pH 5.5 to 6.0, and nitrate formation in uninoculated soil pH above 6.0... The so-called
'mull' type of forest soils contain considerable quantities of nitrate while the 'raw humus' soils contain only traces of assimilable nitrogen but considerable quantities of combined nitrogen.

"In soil layers exposed to light, nitrification takes place actively; in shady forests ammonia formation takes place under their cover, but little nitrogen is liberated under the thick cover of 'raw humus'. One may, therefore, justify the general conclusion that the nature of forest vegetation and tree growth depends upon the transformation of nitrogen in the soil, and in turn largely affects the nitrogen conditions....Aaltonen (1926) and Hesselman (1926, 1927) agreed that forest soils can be classified into nitrifying (grass-herb forests) and non nitrifying (moss forests)."

Soil Acidity (36)

"The effects of acids upon chemical reactions and upon physicochemical conditions generally in both inorganic systems and in living organisms are due principally to the hydrogen ions which they produce when in solution. Some of the most fundamental of physiological phenomena are markedly influenced by the concentration of hydrogen ions in the medium in which they occur. For many purposes therefore it is more important to have some sort of measuring stick of the concentration of hydrogen ions present in a solution than the total acidity of the solution... pH may be defined as the logarithm of the number of liters of solution that contains one gram atomic weight of hydrogen ions)... It is the negative of the logarithm of the hydrogen ion concentration in terms of normality."
The influence of the acidity of the soil upon plant growth, upon availability and presence of nutrient salts, and upon the actual species of plants present, make it a very important concept in the study of factors influencing the establishment of tree seedlings. Considering its importance, it is probable that this factor deserves more attention than it has received in the past. The data below, however, will show where this concept fits in to the general picture.

On the subject of soil acidity, Truog (62) gives us the following:

"The indirect influence of reaction on plants is through the effects of reaction on physical condition of the soil, availability of essential elements, activity of soil microorganisms, solubility and potency of toxic agents, prevalence of plant diseases, and competitive powers of different species of plants. The direct influences of reaction on plants are in extreme acidity or alkalinity, a toxic or destructive effect on plant tissues of excess of hydrogen (acid) or hydroxyl (alkaline) ions; an unfavorable balance between the acidic and basic constituents available for absorption by plants."

**Indirect Influence of Reaction on Plants**

"The physical condition of clay soils is known to be affected unfavorably by an acid condition, because of an insufficient supply of calcium bicarbonate in the soil solution to keep the base exchange material well saturated with calcium and the clay particles coagulated (flocculated) -- a condition that is necessary for the highly desirable granular or crumb structure. In sandy soils the presence of lime carbonate probably improves the physical condition by acting as a binding agent. In improving the physical condition of soils in these ways, the
presence of lime carbonate thus indirectly helps in the proper regulation of the air and moisture supply of soils, which in turn is the fundamental basis for developing their proper biological and chemical activity. Both a highly acid or a highly alkaline condition may, by inducing separation of the colloidal particles (deflocculation), cause a movement of valuable colloidal material from the surface soil into the subsoil where it may be precipitated in the form of a detrimental hardpan.

"The availability of all the essential elements obtained by plants from the soil is affected in one way or another by the reaction of the soil. Phosphorus in particular becomes less available as the pH value drops below 6.5 to points of greater acidity.

"The influence of reaction on the availability of potassium is not very clearly understood as yet and needs further study. With increasing acidity, calcium and magnesium become less available to plants because of a decreasing supply and a greater competition for them by the hydrogen-saturated exchange acids. Iron, manganese, copper, zinc, and possibly boron appear to become less available when the pH value rises above the neutral point, and this may limit plant growth in certain cases, especially when the soil is sandy and low in organic matter. This lowering in availability of certain elements may explain the unfavorable results occasionally reported from liming. This needs further study. The activity of many soil micro-organisms is greatly retarded by an acid reaction, and this in turn affects the availability of the nitrogen, sulphur, and other elements whose liberation is dependent on the decomposition of organic matter brought about by the micro-organisms. Many species of the nitrogen-fixing bacteria are especially sensitive to acidity and can exist for only a comparatively
short period in distinctly acid soils. The root nodule bacteria of alfalfa and sweet clover do not persist well in a soil when its pH value is below 6.5. High acidity may bring about toxic concentrations of iron and aluminum salts, and in very special cases copper and zinc salts.

"The balance between basic and acidic constituents available for absorption by plants varies directly with the reaction of soils and is probably the most important factor involved in the relation of soil reaction to plant growth. In neutral soils the active basic constituents are just equal to the active acidic constituents, in an acid soil the acid constituents are in excess, and in an alkaline soil the basic constituents are in excess."

Wilde (72) in his article on forests and soil reaction, makes the following observations: Soil reaction affects the growth of trees by influencing the availability of nutrients, potency of toxic agents, activity of useful and parasitic soil organisms, and physical conditions of the soil. Neither mineral nor organic soils more acid than pH 3.7 support normally developed forest stands.

Wilde (72) lists the growth characteristics of soils in general by divisions of pH as follows:

- pH 3.7: heaths, low shrubs, lichens, Scotch pine (sporadically)
- pH 3.7-4.5: Black spruce, tamarack, hemlock, etc. and some light demanding deciduous trees (aspen, paper birch). To the majority of other forest trees these, very strongly acid soils are unfavorable, due to toxicity of ferrous iron, manganese, and especially aluminum, which are liberated to a considerable extent as soon as the reaction of a soil is less than pH 4.5.
pH 4.5-5.5  Well adapted to the majority of conifers and many of the deciduous trees with the exception of some of the better hardwoods (white ash, basswood, etc.). The low availability of nutrients, viz. nitrate nitrogen, calcium, and phosphates, is the reason for the absence or inferior growth of these latter species on acid soils.

pH 5.5-6.9  High activity of micro-organisms, energetic humification, high availability of mineral plant nutrients, friable structure and good aeration. These soils produce high yields of timber especially the better hardwood species. However, when the reaction of soil approaches neutrality, certain conifers (Norway spruce) often become subject to fungous diseases.

pH 7.1-8.0  Support largely the stands of southern hardwoods (oaks, hickories, walnuts, etc.); the majority of other valuable trees, especially conifers, do not grow on alkaline soils, or grow unsatisfactorily. The unfavorable influence of alkaline soils upon the forest trees is due either to toxicity of OH-ions which are considerably more injurious than H-ions, or to the excess of calcium or magnesium carbonates, causing a lack of available iron (chlorosis), a general disturbance in the assimilation of other nutrients, and often fungous diseases.

pH 8.1-8.5  Contain an excess of OH-ions as well as those of sodium, chloride, and sulphate, which make the soils of this reaction toxic to all forest trees.

pH 8.5  Occupied only by lower plants of halophytic nature.

Dr. Eugene Frank (14) made the following observations of forest soil acidity in Germany.

2. Acidity of the upper layer (0 to 8 inches) depends mainly upon the composition of forest stand and the density. With the greater depth the acidity of soil decreases (with the exception of podsolic soils with hardpan layer.)

3. The soils with raw humus have the highest acidity....

4. The higher elevation (over 2,500 feet above sea level) have an average higher acidity than the lower elevations. The ridges, tops of hills, and higher plains are more acid than adjoining lower localities.
The northern exposures are the most acid.

5. ...Opening of the stand results in a decrease in acidity; for this reason before underplanting older stands on the acid soil, the soil acidity should be reduced by partial cuttings.

7. Local climate has an influence on soil reaction. The acidity changes with the season of the year. Running waters moderate acidity; stagnant waters produce acidity.

8. High acidity as well as alkalinity of soil are unfavorable for the germination of seeds and for the growth of trees."

Dr. Albert (1), also working in Germany, found that the pH value of Douglas fir soil litter is 3.93 and 4.56 for the two inch layer of leached soil directly beneath the litter.

Humus

Some indication has already been made of the importance of humus to the forest soil, the growth thereon, and in this instance, particularly to seedlings. Waksman (66) tells us just what humus is. "Those tree residues which consist largely of needles and other products of a coniferous forest are attacked largely by fungi which reduce slowly the cellulose and hemicellulose, leaving the lignins to accumulate; an organic mat results which is low in bases, is acid in reaction, is low in nitrogen, decomposes only slowly, and undergoes leaching easily. On the other hand the plant residues which consist largely of broad leaves and other products typical of deciduous forests, are attacked by numerous fungi, bacteria, and invertibrates, which decompose the cellulose, hemicellulose and lignins; a type of protein results which is high in bases, less acid in reaction, is higher in protein, and the humus is bound by
the base in a form not readily leached."

"Forest humus contains a large part of its nitrogen in organic, undecomposable compounds...Humus has a favorable effect on forest trees, brought about through the continuous supply of available nitrogen; pine, spruce, and oak trees provided with raw humus grew far better than when supplied with artificial nitrogenous fertilizers."

There are two types of humus, the mull and the mor. Romell (51) of Cornell University tells us about these types. "Mull is an ecologically richer type than mor. Mor is predominant in the belt of coniferous forests on podsol soils extending through the colder parts of the temperate zone, with oases of mull in localities favored by lime in rock and in soil or by drainage conditions (slopes with high and yet not stagnating ground-water, even in regions very poor in lime) Mull is characteristic of the forest of mostly broad-leaved trees extending in a zone with a somewhat milder temperate climate, much independently of geology but with islands of mor on too dry, too wet, and geologically very poor sites.

"Such different measures as thinnings, covering with green slash, clear cutting, light burning, ripping of the more cover, or any other form of soil working, and liming have shown a surprisingly similar effect in activating a mor, starting nitrification and frequently changing the humus layer also morphologically to approach or even to become a mull. The same effect can be seen as a result of the girdling practices recently in favor in this country. It may also set in under an undisturbed tree cover as a result of trenching, burning, and other disturbances. On the other hand, lack of protection of the ground has long been known to easily start a degeneration of a good mull condition."
"The difference between mull and mor lies rather in the way in which a mixture of humus with the mineral soil is formed... Mull has practically always been found to be nitrifying... In a pronounced mor the soil life is completely dominated by fungi. The mull harbors a relatively scarce fungus vegetation, and instead a more efficient animal life."... The animal population of a mull are very important in maintaining its equilibrium which is rather weak. A mor appears to represent an equilibrium incomparably stronger, self-stabilizing to such a degree that a mor type would tend to become more and more pronounced once it had started to form."

Wilde and Patzer (75) studied the role of soil organic matter in reforestation. "The results obtained in the study of jack and red pine plantations, as well as some incidental observations of white pine and white spruce plantations, suggest that the following minimum contents of soil organic matter are required by these species: Jack pine, 0.6%; red pine, 1.8%; white pine, 2.5%; white spruce, 3%. These figures approximate the absolute minimum requirements which should be respected in planting, regardless of other conditions."

Working with Buron and Galloway, Wilde found that there was a distinct relation between the parent material from which the soil was formed and the type of duff deposited by the same cover. "The white pine duff formed on a well-drained, morainic sandy loam of granitic origin has a fairly high content of nutrients. On the other hand, the same duff formed on sandstone outcrops has only a negligible fertilizing value." They further stated that "the chemical composition of organic remains is an important factor in the beneficial effect which they exert on the growth of forest seedlings." Also "in an analysis of various types of
duff layers to determine their respective properties as fertilizers it was found that the nutritive properties, base exchange capacity, and reaction of the duff varied with the character of the underlying soil.

Podsolization (8)

Podsolization is dominant in areas of high humidity and forest vegetation and is one of the most important processes in the formation and modification of the Pedalfer soils. The process comprises two phases. One of these is the accumulation of a peaty mat of organic matter on the surface and removal of clays and iron compounds from an upper to a lower layer, with consequent whitening of the soil layer immediately beneath the surface organic matter. The translocated materials are partly assorted (fractionated), and different ingredients are deposited in different horizons of the profile. Suspended organic matter is deposited just below the bleached layer, together with a considerable quantity of iron and aluminum compounds. Iron compounds are deposited next, often to serve as cementing agents, while clays are carried still deeper by the filtering waters. There is considerable overlap between these horizons. This process results in the formation of members of the great group of soils called Podzols. Typical profiles are usually found on coarse-textured parent material.

The A2 and B2 horizons are usually very distinct, but their thickness varies extremely within short distances. In some places there is a thin transition layer between them. The soils have a low natural fertility but some of them respond well to fertilization.

The organic layer overlying Podzol soils is usually so strongly acid and of such low base content that bacteria act upon it only very slowly.
Fungi usually dominate the microflora. It is possible also that in some cases toxic organic constituents, such as tannic acid, may restrain decomposition. As the acid organic matter slowly decomposes and a part of it dissolves in the presence of iron-bearing minerals, the solution of iron in the ferrous state is promoted. Water carrying such compounds in solution or in a state of dispersion may also carry other organic material or dispersed inorganic soil colloids. As this water percolates through the profile it often soil layers less acid than the surface, and oxidation more readily takes place, rendering the iron less soluble. Such material as may be precipitated under the slightly changed conditions serves as a filter mat to remove still more material from the percolating waters. This may account for the high sesquioxide and organic matter content of the upper portion of the B horizons of many Podzols. The total clay content of this horizon is not usually high, but it is usually composed of a high percentage of aluminum and iron hydroxides and a very low content of silica. Surprisingly large quantities of highly dispersed organic matter are frequently found in the C horizons of such soils.

"It is possible for the removal of fine material to take place without much fractionation, and this results in the development of a grayish-brown, whitish, or gray layer in the upper part of the mineral soil without the formation of a very dark brown B₂ horizon. Such a process is also called podzolization, but it does not produce profiles in all respects characteristic of the Podzols...In consequence we have podozolization, as a process, operating to produce modifications in soils of several broad groups wherever sufficient rainfall occurs to produce percolation of water through soil covered with acid organic matter. Podzolization is effective under both coniferous and hardwood
forests and in temperate and tropical climates.

Weir (69) defines Podsolization as follows: "Podsolization is principally a dissolving process which involves both true solutions and sols and hence is a deterioration process which takes place in acid mediums in all humus regions of the world. It is typical in cool regions under cover of coniferous forests and heaths. It does not take place in neutral and alkaline soils. It begins when sufficient basic elements have been leached out to effect acidity. When acidity develops, removal of the basic elements continues, sometimes thoroughly leaching the top soils... Under acid conditions humus and clays become less stable and disperse. Aqueus solutions that percolate from the soil coverings of acid organic material and that contain humic acid, react with iron and aluminum compounds and carry them downward to be deposited mostly in the subsoils... Podsolization results in the relative increase in silica in the surface layers and relative decrease in the subsoils." A complete and somewhat more technical account is given of the various aspects of the podsolization processes by Joffe (30).

Stickel (57) gives an account of the silvicultural importance of the podsol soil. His conclusion follows: A tendency toward podsolization can be combated by opening up the stand and by encouraging the admixture of hardwoods such as ash, birch, maple, and beech. Such silvicultural measures hasten the activities of micro-organisms and decomposition, produce alkaline buffer substances which react against the unfavorable humic acids, and produce a more lively nitrogen transformation.
chapter vii

EDAPHIC FACTORS INFLUENCING SEEDLING DEVELOPMENT:

PHYSICAL AND BIOTIC

* * *

Physical Factors

Physical Factors have to some extent already been discussed under the many other headings already explored and will be further expanded in certain details in later portions. However, there is certain experimental data that should be mentioned here. Concerning the significance of soil texture in forestry, Wilde (73) stated, "The ability of the soil to retain water depends upon the amount of the fine soil material present. The higher the amount, the greater is the soil moisture content, other conditions being the same. Since the soil pores are filled with either water or air, an increase in the fine soil material, and consequently in soil moisture, leads to a decrease in soil aeration. Finally the particles are the chief source of easily soluble substances, which serve the tree as nutrients...Because various tree species have different requirements for these three factors, their distribution and rate of growth are often closely correlated with the soil texture.

"In artificial reforestation, the soil of a cut-over or burned-over area has no protection from wind and sun rays. Such soils lack, as a rule, the protective layer of much, as well as humus. Their readily available nutrients are leached away by rains which fall on the exposed barren surface. Under these conditions the fine soil material becomes the decisive factor in the successful establishment of planted seedlings."
Pearson (45) has found several physical factors of the soil which influence the growth of reproduction. "Where the soil is sandy or gravelly, reproduction is seldom a matter of serious concern. Clay soils on the other hand are unfavorable to reproduction. Clay is rendered more favorable by the admixture of large proportions of gravel or stones." As you may recollect from previous discussion, this probably is due to the greater amount of hygroscopic water in clay soils which is not available to the plants. Soils with larger particles mixed in will not have such a large percentage of the unavailable water and will also have a lower wilting percent.

The cover of the ground also exerts certain physical influences which in the region covered by Pearson (the southwest pine) are very important to seedling establishment. He describes them in this way: "Herbaceous vegetation favors germination and protects young seedlings against excessive insolation, winter-killing, and frost-heaving; but after the first year these benefits are counterbalanced by the unfavorable effects of root competition and shade. This condition manifests itself in slow growth as well as in high rate of mortality."

**Biological Factors**

The fauna of the soil may have considerable effect upon the seedling establishment due to the functions of aeration, fertilization, cultivation, etc. by worms, insects, mice, etc. These, however, have not been included in the present discussion though we will go into the subject of mycorrhizae. The investigators of the functions of mycorrhizae are not in agreement so that the significance of the facts here presented cannot be vouched for.
Meyer and Anderson (36) state the general situation. "Undoubtedly the mycorrhizal fungi associated with chlorophyllous plants obtain most or all of their carbon-containing compounds from the species on which they grow. Hence some authorities consider them to be no more than root parasites. At least some mycorrhizas, however, are apparently beneficial to their associates. This seems to be especially true to the mycorrhizas of conifers, particularly when they are growing in distinctly acid soils which are low in nitrates. There is evidence that on such soils mycorrhizas aid in making available to their host plants some of the nitrogen of the complex organic compounds found in the humus (Rayner, 1926, 1927)."

Weaver and Clements: "In such soils, where the nitrogen supplies exist in the form of organic compounds of relatively complex type, coniferous mycorrhizas abound. Experiments show that on such soils tree growth with mycorrhiza is much greater than without, the fungi making the nitrogen readily available for the forest trees."

Hatch (20): "The mycorrhizal fungi are lacking in the American prairies in common with those of other unforested regions (except where trees have been introduced as transplants). In the absence of mycorrhizal fungi the absorption of nutrient elements by trees is apt to be inadequate to support normal growth, Mycorrhizal fungi constitute the specific biological factor which is necessary for the survival of trees in prairie regions."

McArdle (34): "No mycorrhizae were found in that part of the spruce stand where raw humus is absent and the soil brakes hard and dry." This may be an explanation of the lack of seedlings on certain denuded south
slopes and burned areas. Although it was found that where nurseries of exogenous tree species were established in Australia, seedlings failed to grow until the soil was inoculated with some soil from their native habitat; the evidence presented is non conclusive as to the precise function and relation of mycorrhizae forming fungi to the establishment of seedlings, however.

The subject of nitrogen fixation in the soil as carried on by the various nitrogen fixing bacteria should also be included here. However, it is a topic demanding very wide coverage and for that reason must be omitted.

Haig (19) on biotic agents: "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 birds and insects 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 under full shade, and are equal to or heavier on full-sun than on the part-and full-shade habitats."
There is a great deal written about the establishment of plant types in a habitat, the gradual change toward a climax type for the habitat, and the many ecological factors that combine to produce such tendencies. When applied to this subject as it should be, plant ecology tends to give the immediate glimpse of forest conditions a place in the long time picture. For every habitat there is a definite long time ecological trend which, when understood, can enable the forester to better analyze the reasons and remedies for a given growth condition.

Weaver and Clements (67) have gone into this subject extensively. Only short quotations are here selected to give the general idea of what is involved in seedling establishment from the standpoint of the ecologist.

"Ecesis is the adjustment of the plant to a new home. It consists of three essential processes, germination, growth and reproduction. It follows migration and sooner or later results in competition. Ecesis comprises all the processes exhibited by an invading germule from the time it enters a new area until it is thoroughly established.

"Invasion is the movement of one or more plants from one area into another and their establishment in the latter. It is thus the complete and complex process of which migration, ecesis, and competition are the essential parts. It is going on at all times and in all directions. Invasions may occur in bare areas or in areas already occupied by plants."
"Invasion into a new area or plant community begins with migration and is followed by aggregation and competition, with increasing reaction. In an area already occupied by plants, ecesis is immediately followed by competition and reactions, e.g. decrease of light and water is quickly produced."

"The phenomena of plant succession, whether ecesis, competition, reaction, or stabilization, are controlled so largely by edaphic conditions and particularly by water content that they can be properly interpreted and their true significance understood only by a thorough knowledge of root relations. It is an aid to the forester in selecting sites for reforestation and afforestation. Yellow pine, for example, because of its prompt germination and immediate deep rooting, can grow on dry, warm slopes. Likewise, Douglas fir germinates quickly and produces roots 6 to 8 inches deep during the early part of the season. It thus becomes established where the slower growing and more shallow-rooting spruce, hemlock, and cedar fail."

Clements, Weaver, & Hanson (11): "Ecesis or establishment is the direct outcome of response to the physical factors of the habitat only in such open pioneer groupings that competition has not begun. In all communities proper it is determined as much or more by competition and reaction than by the initial factors themselves. Ecesis represents the outcome in terms of survival, of which dominance, suppression, and subordination are the several phases, while extinction is the complimentary result.

"With the definite constitution of the climax as the mature stage in harmony with the climate, major functional activity ceases, but competition continues in a secondary degree. If the climate were com-
pletely uniform or static, the species of each climax community would be in equilibrium and competition would practically cease. On the contrary, the climate is constantly changing in cycles of varying duration and intensity; the factors of the habitat change in correspondence and the process of competition is set in motion or kept in motion."

Pearson (45) describes the ecological effects on seedling establishment in the southwest: "Excessive shade is limited to a zone which lies well within the crown projection on the south side of a tree or group, but extends to the north a distance about equal to one-third the height of the trees. Root competition, in a degree which, though rarely killing seedlings, noticeably retards their growth, occurs on a patch extending from 50 to 75 feet in all directions from the base of tree or outer edge of group concerned." Pearson suggests that the optimum number of seed trees per acre is 4 over 20 inches d.b.h. or perhaps 3 where conditions are especially favorable. If more are left, they may limit the establishment of reproduction through competition with the seedlings for water or heat or both.
chapter ix

EFFECT OF CERTAIN PRACTICES ON SEEDLING ESTABLISHMENT

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In various regions different practices have been found to have certain effects upon the establishment of seedlings. In many cases investigators have found that it was not the reproduction that became established after the timber crop had been removed that was important, but rather that the advance reproduction already on the ground and perhaps several years old that perpetuated the stand. The burning of slash has considerable effect upon advance reproduction as well as upon the subsequent seedlings that may become started on the area. Partial cutting has many aspects that contribute to the survival or failure of advance reproduction. The authorities on these problems are quoted below.

Advance Reproduction

Weidman (68): The natural process by which a forest reproduces itself is one of the most important considerations in timber growing. Second growth in the ponderosa pine forest does not spring up as a crop of new seedlings immediately after logging, as is ordinarily the case in the neighboring Douglas fir and western white pine regions. In the open ponderosa pine stands, seed germinates under the mature trees soon after it falls to the ground. This results in what is called advance reproduction....A cover of advance reproduction is not the result of one seed crop, but the combined result of a number of years of
seedling, germination, and establishment of seedlings. There are several reasons for this long period of regeneration in ponderosa pine. One is that although this species bears a little seed from year to year, good seed years come only at intervals as great as 5 or more years. Another is that the seed furnishes an attractive food for squirrels and other rodents, which in the years of meager seed production consume almost the entire crop. Cone-boring insects are also a cause of reducing the seed supply. But even though successful germination, following a good seed year may give rise to an adequately stocked cover of seedlings, the severe summer droughts and frosts of this region may in the first 2 or 3 years cause so heavy a mortality among the tender seedlings that only a small proportion will survive. Under these difficult conditions of establishment it requires a number of years—sometimes as much as 20 or 25 years— for the few seedlings which may survive from year to year to make a cover of established young growth that can be counted upon to start a second crop of timber after logging. Such advance reproduction is, however, fairly abundant over most of the region, and the forest, if allowed to do so, reproduces itself almost entirely by this slow method."

Show (54): "In all of the older cut-over areas examined, age counts made on seedlings showed that, except in rare cases, what appeared to be young seedlings that had come up after logging were in actuality advance reproduction."

**Size of Opening**

The influence of surrounding trees on the establishment of seedlings varies considerably by regions and species. In some cases, where temper-
ature is the limiting factor as in the southwest pine, seedlings cannot become established under a canopy or even partial shade due to lack of sufficient heat. Just the opposite condition exists in the Douglas fir where protection against excessive heat is essential to survival. The limiting factor may be water in which case there might not be sufficient water in the soil to sustain tender seedling growth within a wide radius of growing trees. On the other hand where rainfall is more plentiful but where evaporation is rapid, the forest may exert a retarding influence on evaporation to the advantage of the seedling which cannot absorb sufficient water from the desiccated exposed soils. The problem is a complicated to the extent that the factors true in one habitat might be just the reverse for another.

Lord (32) found that openings in a second growth Douglas fir forest that were less than one tenth acre, were below minimum size for successful Douglas fir regeneration. He found that under the conditions of his experiment, one fifth acre could be considered sufficiently large for the satisfactory establishment of seedlings.

Pearson (48): "As a specific example in forest management let us consider again western yellow pine, commercially the most important species in the south-west. Natural reproduction is the foremost silvicultural problem in cutting. If the site is near the lower altitudinal range of the species, moisture is probably more critical than temperature. One way to increase the supply of soil moisture available to seedlings is by heavy cutting. But heavy cutting may be followed by luxurient herbaceous growth, and it is well to consider whether this will create more root competition than would have resulted if the trees had been left. Exposure to sun and wind also dries out the surface soil more than does
the root action of old trees, and thus creates conditions unfavorable to germination. Shade and litter favor germination and if, as has been assumed for the site in question, temperature is relatively high, moderate shade will not interfere with the early development of the seedlings. Under such conditions it will generally be advisable to leave a plentiful supply of trees for seed and shelter, or preferably obtain reproduction in advance of cutting. After a stand of seedlings is established, the major portion of the old stand should be removed in order to give the seedlings the benefit if as much root space as possible." If the site is near the upper altitudinal range of the species, moisture is less critical than temperature. Shade will favor germination, but it will distinctly retard the development of western yellow pine seedlings and will favor Douglas fir and white fir. If, therefore, it is desired to perpetuate a pure stand of western yellow pine, cutting should be as heavy as is consistent with the requirements for a good seed supply of this species."

**Effect of Slash and Other Burning**

The effect of slash burning upon the productive capacity of the land and more specifically upon the germination and establishment of seedlings has been subject to much experiment. The situation in the Douglas fir region as stated by Munger (42) shows vividly the importance of this topic.

"Fresh seed that becomes mixed with mineral soil or lies in a protected spot may escape destruction by the slash fire, but tender seedlings can not. This is something to remember. If logged-off land carries a supply of seed -- either that shed by the forest before cutting..."
and stored in the duff (since disproved) or that blown in from near-by standing timber after logging -- it is better to burn the slash before that seed has germinated than to delay the burning until after the seed sprouts. If the slash burning lags a year, or even a summer season, after logging, the majority of the seed supply then on the ground will have germinated and the tender sprouts are almost sure to be wiped out by the fire. In such an event the only chances for the area to reforest naturally come from such seed trees as may be left, from an occasional ungerminated seed that still lies dormant in the duff, or from seed blown in from a neighboring bank of green timber. Be it remembered, more-over, that in the normal progress of a logging job the standing timber retreats farther and farther from the older cut-over land; it is the first season after logging that land has the best chance of being reseeded from the virgin stand. If the full benefit of seed from the neighboring uncut timber is to be obtained the slash burning ought to be done before this seed is dispersed....

"The season of the year at which slash burning should be done is of considerable moment, not only because of the effect upon reproduction but because of the relative difficulty of handling fire in the spring and in the fall.

"Spring slash fires consume less of the deeper layer of duff and humus than do fall fires. Consequently more of the seed of the last and earlier seed crops might be expected to survive spring fires than fall fires." He states that there are also some disadvantages to spring burning, however, in that there is generally not a complete burn and re-burn conditions are very favorable, and also that there is a chance of some fire holding over until the dangerous fire season."
A very complete picture of the effects of slash burning upon the soil in the Douglas fir region is presented by Isaac and Hopkins (28). They found that the thickness of the duff layer averages about 1.5 inches. An analysis of the duff on an average acre was estimated to total 32 tons and contained approximately 28 tons of organic matter 594 lbs. of nitrogen, 76 lbs. of phosphorus, 555 lbs. of calcium, and 121 lbs. of potassium. They found that "the usual heavy slash fire results in almost complete destruction of the duff layer. Involved in and associated with this destruction, on the particular area studied, were the following: 1 a loss per acre of 25 tons (89%) of the organic matter contained in the duff; 2 a change in duff reaction from a highly acid condition (pH 4.95) to an alkaline condition (pH 7.6); 3 the escape of approximately 435 lbs. of nitrogen per acre; 4 an increase in the supply of plant nutrients available in the surface soil. This resulted from deposition at the surface, in highly soluble form, of a part of the nutrients present in the duff, which in the absence of fire would probably have become available gradually over a long period of years. Serious subsequent losses by leaching appeared probable; and 5 an indicated loss of a considerable part of the mineral nutrients contained in the duff, presumably carried off by the smoke.

"The action of slash fire upon the surface zone of mineral soil causes some dehydration of secondary minerals, colloidal break down, change from a favorable to an unfavorable structure, and reduction of moisture holding capacity to a point at which seedling survival is seriously affected.

"Blackening of surface soil greatly increases its heat absorption capacity, and can cause its temperature to rise high enough to kill
tree seedlings at times when the surface temperature of adjacent, unburned, natural-colored soil remains so low as to cause no injury to seedlings.

"The greater than normal quantity of plant food available in the surface soil for a year or more after a slash fire may have an undesirable effect on Douglas fir regeneration. It tends to cause first year seedlings to develop luxurient crowns and small, shallow root systems, which unfit them for withstanding the usual summer drought. Drought conditions are made more severe by the reduction of the organic content effected by the fire, and this reduction cannot be expected to be remedied within the period (ten years) required for reseeding of Douglas fir cut-over areas."

Because of the above quoted findings "this study has lead to the conclusion that the harmful effects of the ordinary slash fire more than outweigh any beneficial effects it may have on the productivity of Douglas fir forest soil. The study indicates further that the harm done is roughly proportional to the completeness with which the fire consumes the duff and the organic matter in the surface soil."

Heyward (21) found that in the longleaf pine, burned and unburned forest soils were similar beneath the A1 horizon. This is, however, the most important soil layer. The burned soils were characterized by a vigorous ground cover which, upon the cessation of burning, died out very rapidly, the characteristic A1 horizon returning to its original state in 10 to 15 years of protection.

Fowells and Stephenson (65) made the following observations:

"Nitrification in forest soils is stimulated by burning and the liberation of the basic ash materials.... Burning and the increased nitrification
increase the soluble mineral nutrients in the soil, probably for some time after burning...Burning destroys not only the organic matter on top of the soil but may destroy some of that in the immediate soil surface...The temporary effect of burning may be helpful at least in some respects but, since the productivity of the forest soil depends upon gradual mineralization of the fallen litter, it does not appear reasonable to expect continuous and often repeated burning to improve forest soil fertility."

Cary (9) found that fire had a distinct effect upon the growth output of the soil in the longleaf pine. "Young trees up to the time they are 15 feet high may be burned hard enough in the winter to check height growth for the following year to a half or a third of its normal amount, and that more than once in all probability, and yet may resume the normal rate of growth the second or third year...The most careful protective burning that was observed (that is to say, light winter burning annually conducted with the idea of protecting the areas from severe summer fires) checked height growth of the young timber affected by between 20 and 25%." The article does not state whether these effects are due to direct physical injury to the tree or indirectly through injury to the soil. We may assume the latter since the trees evidently continued to live.

Pearson (45) found that in the southwest ponderosa pine "Burning the brush favors reproduction on grassy areas, but not where herbaceous vegetation or litter is absent. Under the latter conditions burning may become detrimental, particularly on compact soils."
Ecological Effects of Burning

Isaac has recently made a study of vegetative succession on logged areas following the slash fire (29). His comments follow. "The plant association in the Douglas fir region, when destroyed by fire, goes through four distinct stages of succession before it reaches the climax type, unless again interrupted by fire or logging. These stages are the "moss-liverwort", "weed-brush", "intolerant even-aged Douglas fir", and the "tolerant all-aged hemlock-balsam fir"; the last named so far as is known will persist. The weed-brush stage is most subject to fire, and successive fires do prolong and can perpetuate this stage."

The vegetative cover averaged 35% the first year after the slash fire, 79% the third, and 73% the fifth after which it gradually increases. "Light cover is beneficial to coniferous seedlings but heavy cover is detrimental, and the weed-brush stage often develops a density that practically prohibits forest regeneration."

Competition of tree seedlings with weeds starts as cover density approaches 24% and becomes increasingly detrimental to seedling growth and establishment to 85% cover. It is almost impossible for seedlings to become established under a cover of 85% and greater.

It is indicated that the intolerant even-aged Douglas fir type is not climax. This would indicate that an interruption of some sort in the order of climax is necessary to the perpetuation of the type. This point of view is borne out by Maissurow (33) in light of his experiments with the role of fire in perpetuating the forests of Wisconsin. "Although fire may be looked upon, from the silvicultural point of view, as a factor inimical to the normal development of the forest, it has been and
and is, from a broad ecological viewpoint, a normal, beneficial and necessary factor in the perpetuation of virgin forests."
chapter x

MEASUREMENT OF FACTORS AFFECTING
SEEDLING ESTABLISHMENT AND GROWTH

* * *

General

"The plant cover, if properly interpreted, can be used as an indicator of the climatic conditions under which it was produced, of the soils on which it grew, and of the practices of grazing or other use to which it has been subjected. It is of value in the rapid classification of land as to climatic conditions, soil types, soil texture, soil chemical composition, the value of soil for crop production under natural rainfall or under irrigation, the value of the land for grazing with domestic stock or wild animals, and the value for wildlife food production. It may also indicate the amount of overuse to which vegetation has been subjected, the kind of animal responsible for this overuse, and the degree of destruction of the soil profile on which the vegetation is growing."

"The great plant communities (formations and associations) are relatively independent of such factors as physical composition of the soil, while the smaller or minor communities are often directly affected by such factors. Soil provinces are relatively independent of such factors as physical composition of the parent material, but the soil types are often affected by this factor. In other words, soil units are closely associated with small vegetation communities (societies) and soil provinces with great communities (formations and associations)." Shantz (52)
Weaver and Clements (67) present the story of indicators from the ecological angle. "Forest indicators are of three chief types, namely, those that have to do with the existing forests, those that indicate former forests, and those that indicate the possibility of establishing new forests. Obviously, every forest climax indicates a forest climate although of different degrees.

"Indicators of Former forests -- Such indicators are either actual relics of the forest itself or seral communities that mark particular stages of succession toward reforestation. After the forest cover has disappeared because of fire, lumbering, lack of reproduction due to overgrazing, or other factors, the area is freed from the competition of climax species and conditions made favorable for the growth of many subdominants. As a result of excessive seed production, the ability to produce root sprouts, or the opening of cones by fire, these rapidly and often completely occupy the ground.

"In the cedar-hemlock forests of the Pacific Northwest, Douglas fir, the most valuable of lumber trees, forms a remarkably permanent subclimax over an enormous extent due to repeated burns. Such seral communities not only indicate the possibility of reforestation, but they also make it clear that artificial means, such as periodic removal of the forest, must be resorted to where it is desirable to maintain the subclimax as a relatively permanent type.

"Indicators of sites for planting are of two kinds, namely, those that indicate the former presence of a forest, and those that suggest the possibility of developing forest in grass-land or scrub areas. These are indicators of reforestation, respectively... Where there is no direct evidence of the original forests, indirect evidence is often furnished
by indicator communities which bear a direct relation to forest. Such are seral and subclimax communities that show a successional relation to the forest climax and societies of shrubs or herbs which formed layers in them....Indicators of afforestation are either savannah, i.e. isolated trees or clumps of trees in grassland, chaparral, or tall-grass prairies in which the water requirements are very near those of trees, such as subclimax prairie.

"The indicators of sites for planting or sowing serve also to indicate the preferred species. In reforestation, for example, the general rule is to employ the species of climax trees that were in possession, unless reasons of management make it desirable to employ a subclimax dominant....Where the virgin timber has nearly or altogether disappeared, as a result both of severe burns and of grazing, and has been replaced by shrubs, herbaceous vegetation, and wide stretches of aspen extending over an area originally occupied by several forest types, the question of deciding what species to plant on a given site becomes very difficult. But even in such cases a study of the existing vegetation furnishes the most valuable guide, as has been repeatedly demonstrated in forest practice."

Plant Cover Indicators

Coile (12) when reporting on forest classification, pointed out the following in regard to site classification through the use of indicator plants. "The belief that ground-vegetation is essentially uninfluenced by the nature of the forest cover under which it may be growing is questionable." The condition of the soil is greatly influenced by the type of litter deposited upon it. Coniferous litter is acid and un-
favorable to the growth of nitrogen fixing bacteria while the litter from such species as white ash and basswood are rich in calcium and encourage the break down of organic compounds to usable form through action of rich microorganic growth. "Differences in the lesser vegetation found under the cover types mentioned above are related to differences in the effects of forest trees on fertility and physical characteristics of the upper part of the soil mass.

"The application of forest (site) types, the vegetation of which is developed under stands of timber, to deforested land which may be greatly influenced by cutting, repeated fires, and the strong influence of relatively unimpeded solar radiation, requires a considerable amount of applied imagination on the part of a field man." Plantings of a certain species on denuded areas though favorable conditions are indicated by indicator plants, may fail due to the difference in microclimate between the forested and open sites.

"That broad relationships exist between ground-vegetation and productive capacity of land is agreed." In many instances the ground cover vegetation is directly conditioned by the forest cover type rather than being dependent upon the same site characteristics as the tree overstory. Certain ground-vegetation types have been found to be associated with certain fertility conditions of forest soil. These ground-cover types are "treatment" types and are not directly related to the inherent quality of the site.

"It is felt that in general if a classification of forest sites is desired, it should be based on fundamental and permanent features of site, namely soil and relative topographic position of the soil mass. Characteristics of the soil mass, the substratum, and topography, which
are related to the total volume and availability of water present for use by forests, should be the primary criteria in any classification of site. Markedly different chemical characteristics of soil may be a secondary criteria of classification." The features of site that should be measured are permanent features.

In Wisconsin, Maisurow (29) found that due to the fire history of Northern Wisconsin stand composition and species distribution have become mixed to such an extent that all attempts to establish a definite relation between soil types and composition have failed.

Writing on reforestation research, Chapman (10) states: "In choosing the species to be planted on a denuded area, it may be profitable to study succession of vegetative covers on abandoned areas in various stages of deterioration. Every cover is a dynamic complex, and the rate of progressive composition change is an expression of site recovery and when properly observed may manifest a site quality index.

"It need not be emphasized that there is little interdependence between distribution of original forest types and soil types. It has been definitely demonstrated...that forest types traverse soil phases, types, series, and occasionally soil provinces or regions. Rather, these forest types are correlated with drainage, physiographic features, and climatic gradients."

Hickock, Morgan, and others (22) studied the soil type as a possible factor in determining the composition of natural, unmanaged mixed hardwood stands in Connecticut but found it very difficult to make any correlation between soil type and tree species, and had even less success in attempting to correlate ground cover species with soil type and in finding indicator plants.
Chapman (1939) brings out the thought that a certain cover type in itself may not be a great help as an indicator of site, especially on denuded lands. The study of these indicators is a study in dynamics, not in statics. The original stand which was removed represented a certain degree of climax for the particular micro-climate. When it was removed, the order of climax was interrupted. Because of the presence of the forest itself and its predecessor types, it was quite probably more mesophytic than the same area when denuded could possibly sustain. It is for this reason that in various localities, the building back to the original stand may be required in a series of steps.

Soil Composition Indicators

As has been pointed out by several of the above quoted investigators, the soil itself may be the controlling factor of vegetative type at any sere. In previous chapters we have read how the various chemical and physical characteristics of the soil were very important to plant growth. Some of these characteristics have been measured in attempted correlations of soil factors with site quality. Varied successes are found.

Haig (18) investigated soil colloidal content and other related factors as possible indicators. His findings for the brown and weakly podsolized forest soils of southern Connecticut and adjacent territory were as follows:

1 'A' layer soil values appear superior to similar values of the B and C layers as measures of soil conditions. It is relatively easy to sample this surface layer.

2 Colloidal content and a closely allied measure, silt-clay content, are both definitely correlated with site quality...Site index
values predicted from the silt-plus-clay content will fall...Within about one broad site class of the actual site index. Colloidal content and silt-plus-clay content are fair measures of site index.

3 Organic matter varies between 2 and 10 per cent and its influence on soil fertility is relatively negligible.

4 Soil reaction, measured in pH values, varies between 4.5 and 5.5 pH and its influence on soil fertility is also negligible.

5 The value of soil type as an indicator of site quality cannot be accurately estimated with the data available.

6 A knowledge of the soil class (the textural quality of the A horizon or surface soil permits classification of soil quality within approximately one broad site class. Considering the relative ease with which this factor can be estimated by a trained investigator, it offers an excellent method for determining the site quality of forest soils."

Hicock, Morgan, and others also investigated the relation of soil factors to the growth of red pine in plantations (23). Their results included the following points: "It was impossible to discover any relation between the acidity of any horizon of the soil, as expressed by its hydrogen ion concentration, and the site index of red pine. The total nitrogen content of the $A_{1-2}$ horizon showed a better correlation with site index than any other factors analyzed. The moisture equivalent of the $A_{1-2}$ horizon also exhibited a fairly high correlation with site index although less than that for total nitrogen content of the same horizon." These two factors were found to correlate better with each other than with site index. "The silt-plus-clay content of the $A_{1-2}$ horizon showed a very good correlation with site index for values up to 25%, but above 25 per cent there was no correlation. Colloidal content of the
A$_{1-2}$ horizon showed practically no correlation with site index.

"There is no consistent relation between site index and the transformation of nitrogen to available nitrates and ammonia in the A$_0$ or A$_{1-2}$ horizon for site indices of 16 feet or more. Low site indices were associated with low nitrogen transformation and low total nitrogen content with but one exception among 10 samples studied." Better correlation was found between low site quality and low value of factor in question than for high site quality and high value of factor in question.
SYNOPSIS AND CONCLUSIONS

Now that we have explored more or less thoroughly the subject of forest seedling establishment from its many viewpoints, it may be advisable to record the general observations made and conclusions reached in the light of the present status of our information. Certainly this subject is not of the static type, characterized by a complete and unchanging knowledge. Throughout the entire assemblage of data have arisen many contradictory statements of observations and conclusions drawn therefrom. Certain aspects of the problems involved that are as yet outstanding and unsolved have come to the attention of the authors whose works have been quoted. Other problems have suggested themselves and many more lie dormant in this mass of semi-organized observations and will be brought out by more careful processes of sorting out the salient points on one side or the other from this resume of our present knowledge. Some of these problems are listed below.

Problems for Research

From his intensive studies of the problems of light, heat, and moisture as they influence the establishment of reproduction in the southwest pine region, Pearson recommend "to future advocates of sunless forestry" the following experiments. Grow seedlings of recognized intolerant species in different degrees of shade down to about 5 percent of full sunlight using natural sunlight away from any artificial
factors such as glass. Eliminate competing vegetation. Repeat these set ups under 3 or 4 air temperatures ranging from near the minimum to the optimum for the species. It might be desirable to stage experiments in mountainous regions where different altitudes afford the range of temperatures desired. Distinction should be based on the effective temperatures rather than on the daily mean, i.e. the maximum and minimum. Repeat the set-ups again varying moisture and light conditions. He states that this "experiment should be continued at least five years and preferably longer in order to furnish information on the influence of light upon rate of growth, form, and general development as well as upon survival." (46)

Romell (51) suggests that there should be additional study of the effect of killing a luxuriant mor vegetation on the forest soil and its growth supporting potential. It is evident from the disagreement we have found among authorities that the surface layers of the forest soil present a myriad of opportunities for really important research.

Other problems have suggested themselves as a result of reviewing the previous findings. It might be very enlightening to study the root competition factors of various common cover types as they influence the factors governing the establishment of seedlings. For example an enlightening study could be made of the effect of a fern cover, supplemented with certain brush, weed, and grass species, on the water content of the various soil layers at critical periods during the summer for various exposures, soil types, and areas of previous annual burning, grazing, etc. It would be necessary to determine the wilting coefficient and rate of root penetration for Douglas fir or other seedlings on each habitat measured. Results might indicate a means whereby it
could be known whether certain areas would or would not reseed naturally without requiring the usual period of waiting for nature to take its course before the success of natural reproduction could be determined.

A problem similar to this would be the determination of the relation of colloidal content in the soil to the duff covering of the soil, to the moisture holding capacity and wilting coefficient of the soil, and to concentration of humus and clay content in the soil. This study would be very important due to the relation of the soil colloidal faction to solute and water intake. Similar studies have been made but not in the Douglas fir region.

Another problem of interest might be that of the influence of nutrient concentration in the soil layers after a slash fire on seedling root penetration. It will be recalled that investigators have found that roots will have a tendency to reach their greatest development in areas of favorable moisture and nutrient concentration. If this area is on or near the surface of the soil, root penetration would therefore seemingly be retarded. Concentrations of solutes liberated by slash fires might tend to produce this sort of condition.

It has been suggested by Isaac that the Shelterwood Method of cutting and regeneration is the best method for the Douglas fir where the residual stand is wind firm. To better substantiate or disprove this theory it would be interesting to determine the rapidity of growth of the various brush and herbaceous species which would be competing with Douglas fir seedlings under various percentages of crown canopy removed. It is thought that although Douglas fir seedlings can remain alive in 1% of sunlight, considerably more light is required for them to surpass in growth the many brush and weed species offering competi-
A comparison of the growth rates, moisture requirements, aerial space occupied, root development, etc. between Douglas fir seedlings and competing vegetation for various lighting conditions might give a clear picture of the ability of the tree seedlings to outgrow other species which would be offering competition in Shelterwood stands.

A Final Word

It is obvious that of reforestation there is still much to learn and that the path of experimentation toward this eventual knowledge is long and tedious. It is hoped that the portion of the present known facts herein presented and the problems suggested for further research will be of some value in pointing the way toward an original piece of valuable research such as the many herein quoted.
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