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Ecological Investigations upon the Germination and Early Growth of Forest Trees

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I.—ECOLOGICAL INVESTIGATIONS UPON THE GERMINATION AND EARLY GROWTH OF FOREST TREES

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PREFATORY NOTE

Almost every national industry makes provision for investigative work. Millions of dollars are spent annually to develop both human and mechanical efficiency. It is immaterial whether the investigations are for the purpose of utilizing certain products hitherto considered waste, or to make workmen more efficient, or to employ the latest processes and inventions to better survive in the competitive struggle—the results of this class of work are

considered a great, indispensable business asset, warranting wholesome moral and financial support.

The history of our country reveals the fact that material industrial progress is largely in direct proportion to scientific research and invention. This is especially true in the agricultural pursuits. The various governmental bureaus, our state universities and agricultural colleges, and our many agricultural experiment stations are intimately connected with and responsible for the progressive agricultural development of our country. These institutions form a vast ganglionic intellectual organization; they are rapidly becoming the centers of a new agricultural system and, working from these centers outward, they are gradually touching every phase of agricultural activity.

Forestry has joined the ranks of the great industries in developing the investigative side of the business and the establishment of forest experiment stations and a forest products laboratory by the Forest Service of the United States Department of Agriculture has been the first step in this direction. It has become the business of these stations and this laboratory to study the fundamental laws governing the life of the forest and their effect upon the final product—wood. That vast complex of environmental factors—the habitat—is beginning to be analyzed to discover in what ways man can help nature to produce more and better timber, in a shorter length of time and at less cost than nature has produced in the ages past. While perhaps, on account of economic conditions, industrial investigations have been given preference to purely silvicultural research, yet investigations in establishing and growing forests have received no small amount of attention.

Outside of these governmental endeavors very little has been done along the lines of silvicultural research. State forest experiment stations are practically unknown. It is true that the foresters as well as the ecologists connected with some of our agricultural experiment stations are contributing to this field, but a beginning has scarcely been made. There is a great need for state forest experiment stations or at least for foresters upon the staffs of some of the agricultural experiment stations to help

solve local forestry problems. Finally, there is no reason why forest experiment stations established and maintained by private endowment on the plan of the Desert Botanical Laboratory of the Carnegie Institution would not be able to do a great service along these lines.

The importance and need of silvicultural investigations scarcely needs comment, yet it might be well at the outset to emphasize certain fundamental concepts. Forests are one of our greatest natural resources. Unlike coal, iron, oil, etc., they can be *grown* to insure a continuous supply. *Forests are not huge warehouses of standing logs from which we can take our annual supply ad infinitum; they are not merely aggregations of individual trees; they are complex communities of living organisms capable of response to environmental factors not unlike human beings.* It follows then that in order to replace what we take from the forest, in other words, in order to *grow a neverfailing supply of timber intelligently and economically, we must understand these complex living organisms and communities, must study their behavior and requirements and ascertain the conditions under which they grow best.* This domain is forest ecology or silvics.

It has been asked, Does forestry in its present stage of development need this kind of work? Is not this work ahead of the times? Is it not of too little practical value to demand our attention at present? It will be my purpose to show at this point of my paper that, while this class of work is not absolutely essential to forestry at the present time, it is *extremely desirable* that it be begun in a *scientific* manner at the earliest possible moment, in order to put American forestry upon a firm scientific basis. The present status of forestry in the United States emphasizes the necessity of beginning soon. A brief word as to our present stage of development may be in order.

Forestry either of an intensive or an extensive nature is being practised in many parts of the country to-day. Both private and public corporations are engaged in one or more of the main phases of it, viz.: silviculture, forest protection, forest administration, or forest utilization. In the field of forest protection gigantic

strides have been made in the last ten years on both public and private holdings, and obviously this is the first step towards forest management. Such intensive silvicultural operations as planting and thinning are being practised principally in the east, while extensive forestry involving the selection and shelterwood systems of management is almost the rule in the west. As might be expected, in the west forest planting is still in its experimental stage. On the whole economic conditions in the east have favored the development of both public and private forestry and hence this activity has been on a more intensive scale there than in the west. That forestry in some sections of the country is not developing as fast as some conservationists might wish is due to the fact that it is being held back by certain conditions and elements of environment which by their very nature belong to a new country with enormous natural resources like ours and over which human endeavor has no control. It must be realized that forestry never developed in any country in the world as fast as it has in the United States in the last twenty-five years, and that at the present time it is proceeding as fast as is consistent with sound principles and existing economic conditions.

While the practice of forestry is making rapid strides, silvicultural investigations are still in the infancy of their development. In other words the practice of forestry and the science of forestry have not developed in a ratio which would make them mutually helpful. The greater development of the applied phases of forestry is due partly to economic conditions and partly also to a lack of appreciation of the value of purely scientific research. The tendency has always been to magnify the industrial branch of a science at the expense of the main body from which it had its origin. Purely scientific botany has been largely lost sight of in the face of such of its branches as bacteriology, plant breeding, pathology, etc. Similarly the science of silvics has had to give way to seemingly more important phases concerned with the utilization of forests. In these days of commercial ideals when the value of most things is gauged by what they will bring on the market, I fear that undue emphasis has been placed upon the economic or applied phases of a science. Hence it is not strange

that we should measure the value of purely scientific work in dollars and cents rather than in terms of scientific advance and intellectual satisfaction. The test nowadays applied to any science by the large majority of people is, How much money does it influence? What industries has it created? What has it added to the wealth of the world?

If purely investigative work in forestry must give a *raison d'être,* it might be well to call to mind the following facts: that many of its problems strike the foundations of national prosperity and their value cannot be measured in dollars and cents; that some of its problems must be gauged by the future returns they bring rather than by the present; and that it is the avowed purpose of scientific work to solve those problems in which the so-called practical worker has failed to produce results. History bears witness to the fact that those fields which have seemed furthest removed from utility have often yielded the most fruitful results. What seems of only scientific value to-day very often turns out to be of great practical utility later. It is comparatively easy to estimate the value of a piece of work when it is possible to base that estimate upon what has been actually gained; but how hopeless is very often the task when we must base our estimate upon the loss which it prevented. In such silvical investigations as the influence of forests upon stream flow, upon the water supply of communities, and upon the health and prosperity of our people *money values fade into insignificance.*

Silvicultural investigations as well as forestry business are long time propositions. The value of such work is very often measured not so much by the immediate financial returns it brings as by the principles it helps to establish, which in turn may affect our management and hence the financial returns many years hence. It is the *time* element more than any other that emphasizes the need for beginning the solution of some of our silvicultural problems soon. It is believed by many that it will be at least twenty-five years before intensive operations such as planting, thinning, and other silvicultural measures will be economically possible in some parts of the country. Granted that this is true. Is this too much time to devote in preparation for this work? If

we keep on getting results in the next twenty-five years in the same proportion as we have done in the past ten, will many of our important problems be solved? Most silvicultural investigative problems take many years to solve. Some nursery and planting problems can be solved in from three to five years (if nothing interferes), but most of even these take longer. In many cases it takes from two to four years merely to raise stock let alone experiment with it. It usually takes six months or more to determine whether the stock set out will live, let alone establish principles in planting. The element of time is the largest factor in this work; we will need much of it, for failures will be numerous and this will mean the loss of many years. Only long time and carefully planned investigations can lead to stable and economic forest management.

With the development of forestry it cannot be doubted that a great deal of exact silvical and silvicultural knowledge is necessary, and we must admit that a great deal of data is needed to-day which cannot be furnished. We have unsystematic and indefinite knowledge about many phenomena which await experimental proof. In fact, forestry is loaded down with a vast weight of *undigested* facts, and pure science has only begun to relieve forestry of this burden. The quickest and surest way for purely forestry research to gain recognition is to show how to attain practical results which years of blind groping along applied lines have failed to accomplish.

Our task is a gigantic one, greater than any investigative problems that have confronted or will confront European nations. We have more species of trees important in forestry than all European nations combined. Our varied topographic and climatic conditions make our problems infinitely more complex and numerous. But that should not discourage us. Big problems concerning the forest have been solved in the past and are being attacked to-day. We have worked out our problems in logging and have developed machinery and methods unique in the history of forest industry; we have developed a system of forest fire protection unlike anything ever attempted by forestry-practicing nations; it remains for American ingenuity and enterprise to solve the silvicultural problems which confront the American forester.

Briefly stated the purpose of the present investigation is to inquire into the effect of the more important habitat and seed factors upon the germination and early development of certain American forest trees in control cultures in the greenhouse for the purpose of obtaining data that may be used in the silvicultural management of these species.

This investigation has been conducted under the direction of Professor Raymond J. Pool and I am indebted to him for his friendly advice and counsel. I am especially grateful to him for having read the first draft of this paper and for offering valuable criticisms and suggestions. I wish to further acknowledge my indebtedness to Professors P. B. Barker and H. J. Young of the department of agronomy of the College of Agriculture for the mechanical analyses of the soils used in these experiments and to various members of the departments of botany and geology for the many courtesies extended to me. Thanks are due to the various district foresters, forest supervisors, and rangers, also members of the Washington office of the Forest Service for their kindness in furnishing so much of the seed used in these investigations. Without this material assistance a large part of this work would have been impossible. Grateful acknowledgment is also due to my wife for much valuable assistance in counting seeds, in compiling the final data and in reading proof. Also, I cannot fail to acknowledge the guidance and inspiration of the late Dr. Charles E. Bessey throughout the course of these studies.

PRELIMINARY CONSIDERATIONS

Historical

The literature of the work done upon this problem is meager and widely scattered. As has been noted before, both botanists and foresters have worked in this field, so that papers from widely different sources had to be considered. General observations were found to be much more numerous than results based upon exact investigations. Too often one finds opinions and views upon these questions with but very little data to substantiate

them. Foresters and botanists, in general, have proceeded on the assumption that light and soil moisture are necessary for germination. They have also noted that germination is accelerated in sand as against a heavier soil like loam or clay. Little has been done to inquire further into these relations. On the whole the effect of habitat factors upon the early development of plants has received more attention than their effect upon germination. In the following historical summary, light in relation to germination and early development of plants will be considered first, since probably more work has been done upon that particular phase of the problem than any other.

One of the oldest notions regarding light and its relation to plant growth is the one concerning the effect of artificial or natural shade upon atmospheric and soil moisture conditions. The forest experiment stations of Europe have long since worked out this relation in the forest, so that to-day these results are more or less well known to all foresters and botanists. Several Americans, working on the effect of artificial shading upon the growth of tobacco, have brought out results similar to those secured in connection with forests. Hasselbring (3) has shown that the transpiration of plants grown in the open is nearly 30 per cent. greater than the transpiration of plants grown under cheese-cloth shade. The transpiration per unit of leaf surface was nearly twice as great in the sun plants as in the shade plants. Stewart (4) records the results of observations made in the course of tobacco experiments in Connecticut on the climate and soil conditions as affected by tents in producing a certain kind of tobacco. He concludes that under the shade of tents the soil retains more moisture, there is a greater relative humidity, and there is a reduction in wind velocity, all resulting in plants which are larger and of more rapid growth as compared to those grown without tents. To sum up the effect of shade it might be stated tersely: it lowers the air and soil temperatures and breaks the action of the wind; these factors increase the humidity of the air and this increased humidity results in less evaporation from the soil and less transpiration from the plant; the final consequence is a greater soil moisture content with its correspondingly good effect upon the growth of the plant.

The effect of light upon the height growth of forest trees has been used as a basis for determining the relative tolerance of these trees. As early as 1866 Kraft (2) planted a number of different species in the shade of older trees and measured their heights and diameters several years later. Upon this basis Kraft arranged the species according to their tolerance. Nikolsky (2) in 1881 carried on similar experiments with pine and spruce and showed that the greatest length of stem was found in the trees which grew in the shade; the length of the entire plant above ground increased with increase in shade; the length of the main root as well as the number and total length of the lateral roots, however, diminished with increase in shade, while the total length of all roots of plants which grew in great light intensity was greater than the total length of all the roots in the shaded rows. At the Swiss experiment station in 1893 Badoux (2) carried on experiments on eleven tree species with different degrees of shading to determine their behavior in different light intensities and thus determine their tolerance. Fir and spruce had almost the same average height growth. at different degrees of shading. With pines, larch, beech, and ash the growth on the contrary decreased in proportion to the shading. In the case of basswood, blue beech, and elm the growth in height was but little affected. The work of Wiesner (2) from 1905 to 1909, in various parts of the world, and of Clements and Pearson in the United States (2) between 1907 and 1909 was only for the purpose of determining the minimum light requirements of species as a basis for scales of tolerance. The last two investigators took numerous readings in the Rocky Mountains and noted the condition of seedlings under various light intensities.

Burns (9) experimenting with white pine under lath shade in the nursery found that shading delayed the time of germination but that the final germination per cent. was about the same in both cases. He likewise raised white pine seedlings in full shade, half shade, and no shade and (at an age which he does not state) measured the length of the hypocotyls, tap roots and lateral root branches. He found the greatest length of hypocotyl in the plants that had been grown in the full shade, the greatest length

of tap root in plants that had been grown in no shade and the greatest length of lateral roots and total root system in the no-shade plants. This bears out Nikolsky's experiments along the same line. An interesting conclusion reached by Burns is that shade reduces the temperature of the soil and delays the time of germination.

The work of Atterberg (9) which is quoted by Burns is given here for completeness. Atterberg studied the relation of light and temperature to the germination of pine seedlings. He found that at a constant temperature of 23° C. 80 per cent. of the seed germinated in the absence of light and 87 per cent. in the presence of light during practically identical germination periods. Burns concludes from this: "Apparently a high and changing temperature, light, and a moist seedbed are essential to satisfactory germination."

The investigations of Haak (5) and Pittauer (6) have very little bearing upon the problem at hand. The former at the mycological laboratory at Eberswalde studied the influence of season, moisture, temperature, light days and dull, artificial and natural light, color of light, intensity and duration of light, and the influence of chemicals upon the germination of Scotch pine seeds. He found that in lower temperatures germination begins considerably later and proceeds much more slowly that in higher temperatures, but that the final germination per cents. are about the same in either case. He found that certain rays of light were beneficial and certain harmful to germination. Pittauer studied the effect of different degrees of light and extreme temperatures upon the germination of tree seeds of certain European species, viz.: beech, black locust, and various conifers. He found that germination proceeds more rapidly in light than in shade and is most satisfactorily accelerated in diffused light.

Undoubtedly considerable work has been done in the United States by the various forest experiment stations of the Forest Service but these results have not been, as far as my knowledge goes, published. In a very recent article in *Science,* Graves (7) speaks of such work being carried on at the Wind River Forest Experiment Station in Oregon. A recent discovery at this sta-

tion showed that the seed of *Pinus monticola* of Idaho lies in the duff and litter beneath the mature stands for years and then germinates when the ground is exposed to direct lighting. This is mentioned here, merely as another instance of the many of record in which it is assumed that light is to a large degree responsible for the germination of certain tree seeds.

Practically the only work of any importance on record concerning the effect of soil moisture and soil texture upon the early development of forest trees is that of Tolsky (8). He studied the relative effect of sandy and black soils upon the structure of the root system of Scotch pine. He found on black soils that pine developed principally vertical roots while on sandy soils superficial roots predominate. In rich soils roots are guided in their development by moisture, while in poor soils like sand, activity is directed mainly towards extracting nutrition from the soil. In poor soils nutrition is spread over a large area and in order to get it in sufficient quantities trees need numerous roots. Whatever the cause might be, Tolsky found more lateral roots and more superficial roots in the case of trees grown in sand, and this may be taken as the most significant part of his work.

Before discussing the present investigations, I feel that it would be profitable to briefly summarize the edaphic factors of the habitat with special reference to the physical properties of the soil which play a physiological rôle in the germination of the seed.

Classification and Résumé of Habitat Factors

The complex of climatic, edaphic, and biotic factors which influences the life, growth, and reproduction of a plant is known as its habitat. The study and investigation of habitats as entities avails us very little unless we analyze a habitat into its component parts and investigate each of these parts by itself.

Clements (1) classifies habitat factors into physical and biotic. The former have to do in general with inanimate objects and the latter with human beings and animals. He further divides physical factors into climatic and edaphic. Climatic factors are atmospheric in their nature and the edaphic factors are concerned with

the soil. He further subdivides climatic factors into humidity, light, temperature, wind, pressure and precipitation. The edaphic factors are subdivided in a similar way into water content, soil composition, soil temperature, altitude, slope, exposure, and surface.

In glancing over this classification it becomes at once obvious that all of these factors cannot affect the plant directly. Many of those enumerated are in themselves very complex in their nature. For example, slope, aspect, altitude, and surface could each be subdivided into component factors, but if this is done it will be seen that they resolve themselves into those factors mentioned above which are not divisible. In other words there are about three master factors which are able to affect plant life directly, and all others are combinations of these. There is no better way to bring out this idea than to give Clements' (1) classification based upon the influence which each of these factors may exert on plant life. He classifies factors into those that have a direct bearing upon plant life, those that have an indirect bearing, and those that have a remote bearing. Direct factors are only those which produce qualitative structural changes in the plant itself. Furthermore, the classification of habitat forms and plant formations is based upon them, which fact merely emphasizes that they are fundamental. Indirect factors are those that affect a formative function of the plant through another factor; and remote factors are those which are physiographic or biotic in nature and must operate through at least two other factors in order to produce a structural change in the plant. This classification is as follows:

Direct Factors	*Indirect Factors*	*Remote Factors*
Water content	Temperature	Altitude
Humidity	Wind	Slope
Light	Pressure	Exposure
	Precipitation	Surface
	Soil composition	
	Soil temperature	

The germination of seeds depends principally upon edaphic factors, hence climatic factors will receive little attention here except in so far as they condition the former. It is taken for granted that the morphological and the physiological significance of water, light and heat to plant life are too well known to require discussion here, especially since that phase of botany is fundamental in all ecological work.

The water content of the soil is by all odds the most important edaphic factor in determining germination, for while other factors may condition this process to a certain extent, none but water, within certain limits, can prevent it altogether. In a synoptical manner I will briefly call to mind the significance of this master factor in germination and then briefly inquire into the important soil factors and properties that bear directly on the investigations at hand.

The amount of water in the soil has no direct relation to the amount of water which plants can use. At the outset distinction must be made between the different kinds of water in the soil and which of these are available to plant roots. Usually three kinds of water are distinguished, namely: hygroscopic water, capillary water and free water. Hygroscopic water is that water which plants cannot get owing to the enormous film pressure which holds it. It is also known as the amount of water in an air-dry soil. Capillary water is that water, most of which is available to plants and is held against gravity around the soil particles by capillary forces. Free water is that which is not held either as hygroscopic or as capillary water. It is water influenced in its movements by gravity and is therefore called gravitational or hydrostatic water. Clements (1) calls these echard, chresard, and holard respectively. It will be seen then, that the only water available to plants is a part of the capillary water which surrounds every soil particle and fills every small pore space.

The principal factors which influence the amount of soil moisture available (capillary water) to plants are:

1. The amount of water reaching the soil.
2. The catchment of water by the soil.
3. The water-holding capacity of the soil.

4. The amount of evaporation from the soil.
5. The amount of water withdrawn by other plants.
6. The replacement of loss by capillary movement.
7. The amount lost by seepage, percolation, etc.

Of these factors, only four are important in the present investigations. These are the water-holding capacity of the soil, the evaporation from the soil, the replacement of loss by capillary movement, and the amount lost by seepage and percolation. The water-holding capacity of a soil is determined by soil depth, soil texture, and the amount of organic matter present. In soil texture two factors are important, namely, the size of the soil particles, which affects the surface area of the particles and the amount of pore space in the soil, and the density of arrangement of these particles. It is largely for these reasons that loam will hold more capillary water and will contain more air space than sand or gravel. Evaporation from the soil naturally affects greatly the amount of water available to the plant. This is affected by climatic factors such as temperature, relative humidity, and wind; and by soil factors such as texture, color, depth and the character of the surface. The replacement of the loss of soil water by capillarity depends upon the rise of water from the water table. This rise is conditioned by the degree of saturation of the lower soil layers, the texture of the soil, the height to which the water must be raised and the character of the intervening soil layers. A fine-textured soil like loam or clay is much more favorable in this respect than a coarse-grained soil like sand or gravel, principally on account of its great ability to obtain water from the lower soil layers. The amount of water lost by seepage and percolation depends largely upon the texture of the soil. The coarser the soil the greater is the amount of water that percolates through it and the less is the amount held by capillary forces.

As far as it determines the amount of soil moisture available to plants, soil texture is certainly the most important physical property of the soil and it deserves a foremost consideration in all problems that pertain to the germination of seeds.

The Germination Process (10, 11, 12, 13)

This period in the life history of the green plant is unique in that the organism is independent of an external food supply and also of all luminous energy. Germination may be called a period of growth without photosynthetic activity, and it terminates at the time the accumulated food in the endosperm is more or less exhausted. During all this time it is without light; it does not require it, but lives in total darkness beneath the surface of the soil. While the seed has no use for light, it does require water, oxygen, and a certain amount of heat in order to germinate successfully. The dependent life of the plant begins at the termination of the process of germination, when the first ray of light strikes the spreading cotyledons. Light sets the photosynthetic mechanism in motion and this marks the beginning of the plant's manufacture of food; henceforth it is dependent upon its environment.

The rôle of water in the germination process is to aid in the transformation of the accumulated nutrient material into food that can be used by the germinating embryo. In other words, this factor is instrumental in taking this sunken capital and transforming it into specie for circulation. But water cannot do this directly; it must act through the agency of certain catylists or enzymes. These enzymes transform insoluble and indiffusible foods into soluble and diffusible ones which in turn move from the endosperm to nourish the embryo.

Water is important to the seed for two reasons; its absence determines the seed's power to live in a dormant condition, which is one of its most important properties. If a seed is not dry it cannot be preserved; we cannot secure good seed in a wet autumn. The second reason why water is important is because of its chemical and mechanical action in germination. Hales at the beginning of the eighteenth century showed that the absorption of water by seeds is generally accompanied by a considerable manifestation of energy, which takes the form of swelling. Chemically water acts as a solvent for the enzymes which render the accumulated foods soluble.

Practically all the accumulated foods in the endosperm must be transformed by the action of enzymes, which in turn must first be dissolved by water. Starch, which is insoluble in water, is converted by means of the enzyme diastase into a soluble sugar. Throughout germination the quantity of starch in the seed decreases; the starch grains at first corrode and finally dissolve completely. Many albuminoids (simple proteins) are likewise insoluble in water and certain soluble albumens cannot diffuse through membranes. A pepsin-like enzyme which develops during germination acts upon the albuminoids, transforming them into soluble and diffusible forms. Others are changed to crystalloids which after solution diffuse very readily. Fats and oils are likewise insoluble. Certain enzymes during germination decompose oil into its constituents, fatty acids and glycerin, the latter easily soluble in water. It is well known that fatty acids when set free assist the breaking up of oil in water into very fine drops with the formation of an emulsion.

Heat is important in the germination of the seed in that it may accelerate, retard, or even entirely stagnate the processes begun by the action of water. It might well be said that the rapidity of germination depends to a large extent upon heat, since it has the power to modify the action of enzymes. Temperature likewise affects the diffusion of liquids. A considerable part of the heat used in germination is generated by respiration. This process sometimes raises the temperature of the seed as much as 40–50° F. above the surrounding temperature. Certain seeds owe their ability to germinate at very low temperatures (below freezing) to the heat generated during respiration. Certain arctic and alpine plants are able to blossom in the snow for this same reason.

Seeds in water, seeds buried too deep, or seeds surrounded by air deprived of oxygen do not germinate even if other conditions are favorable. In other words, water and heat are of little avail without oxygen. Even before water and heat can act through the agency of the enzymes, in many cases another factor must come into play to release the enzymes. The latest investigations show that the formation of diastase is intimately connected with respiration. In a similar manner respiration supplies the energy

which oxidizes the fats and oils of the endosperm. It has been noted that the quantity of oxygen absorbed is much greater in the case of fatty seeds, like those of the pines and birches, than in the case of the starchy ones.

It has been known for a long time that seeds lose weight during the process of germination although no solid matter is lost as near as can be determined. If we take a certain quantity of seeds and weigh them both before and after germination, being sure to get the dry weight both times, we find that although the seeds have increased in size, they have lost weight. This is due to the loss of certain elements like carbon and hydrogen. In the process of respiration the carbohydrates in the endosperm are broken down, carbon and hydrogen are lost while the quantity of nitrogen remains practically constant. In the process of respiration, the products of combustion are carbon dioxide and water.

Respiration in the seed is quite different from that in the case of leaves and other green parts of the plant. Seeds are generally not provided with intercellular air spaces, but oxygen penetrates to their interior chiefly by diffusion from cell to cell. Thus it will be seen that the supply of oxygen to the deep-seated cells of the seed is most liable to become insufficient. This of course retards germination. If the supply of oxygen is reduced materially, due to lack of soil aeration, germination may be prevented. The best aerated soils are those that have comparatively large interstitial spaces, like sands and gravels, and the poorest ventilated soils are the heavy loams and clays which are small grained and compact and have minute interstitial spaces. The seeds of different tree species naturally vary as to their soil requirements in this respect. This explains why tree species of sandy habitats germinate so poorly on clay soils.

From what has been said, it will be seen that water, heat, and oxygen are the essentials for germination, and that the lack of any of these factors is sufficient to retard, if not entirely to inhibit the process.

It is a well-known fact that seeds have a power of remaining dormant for a period without affecting their vitality. The power to retain this vitality is due largely to the nature of the seed-coat

which insulates the embryo from heat, water and air and protects it from mechanical injury. Cottonwoods, willows, elms, soft maples, and white oaks have a very short period of rest. Usually the period is not over six months, but basswood and hornbeam lay over from fifteen to eighteen months. It has likewise been noted that some tree seeds must lay over for a certain period before germination can take place. The common experience of attempting to germinate seeds in mid-winter which have been gathered during the previous fall is proof of this phenomenon. This leads me to a brief discussion of the process of after-ripening as it is called.

Many seeds we know require a long time for germination in spite of the fact that they are surrounded by the proper conditions. During this period it has been found that certain chemical and physical changes take place which are necessary before the seed can germinate. The length of delay is apparently determined by the persistence of the structure of the seed-coat and to the conditions under which the seed is exposed. The term "after-ripening" has come into use to designate the changes in the seed during this period. Eckerson (17) concludes that most cases of delayed germination are due to the exclusion of water or oxygen by the seed coats. But some seeds do not germinate after all coats have been removed and the seed put into germinating conditions, indicating that the delay is due to embryo conditions. It is now certain that some changes within the embryo are necessary for germination. In the case of *Crataegus* used by Eckerson it was found that food is stored in the embryo in the form of fatty oils; neither starch nor sugar is present. A series of metabolic processes takes place in the embryo during the period of after-ripening. At first there is increased acidity accompanied by increased waterholding capacity. There follows an increased activity and production of enzymes and as a result the fats decrease and sugars appear. The appearance of sugars which are soluble and diffusible marks the beginning of the germination of the seed.

All recent investigations both in America and abroad show how extremely complex is the rôle of oxygen in germination. A set

of conclusions based upon one species of plant apparently may or may not hold for others. Shull's investigations (14, 15, 18) are based mostly on *Xanthium* seeds. In his experiments he finds no evidences of the diffusion of oxygen through an absolutely dry seed coat. This is significant in that it shows an important rôle of water in preceding oxygen in penetrating seed coats. Experimenting with *Crataegus mollis* Davis and Rose (16) find that seeds treated dry or those placed under water do not go through the process of after-ripening. Here again is evidence that both water and oxygen are necessary. These investigators, working on the effects of temperature upon the period of after-ripening, conclude that favorable moisture conditions and temperature conditions shorten the period. Atwood (19) confirms almost all of the conclusions drawn by Eckerson although working on *Avena fatua*. Crocker and Davis (20, 21) worked with water plants and their results totally different than those described for land plants need not be given.

Unfortunately these conclusions are not based upon forest tree seeds. Such investigations have not been undertaken. This phenomenon will probably explain many of the cases of delayed germination which are well known to foresters. It is reasonable to assume that the conclusions based on *Crataegus* would also hold for such fatty seeds like the birches, spruces, hard maples, etc. It is also reasonable to suppose that most tree seeds pass through this period of after-ripening during the winter months; if this is true it explains why it is often impossible to germinate certain tree seeds immediately after they have been gathered.

Method of Attacking the Problem

There are two general methods of determining the causes influencing the behavior of seeds or plants growing under natural conditions. These are the observational and experimental methods. In the observational method we observe the kind of vegetation produced in response to a certain complex of physical factors and seek to find constant relations of one to the other in order to draw conclusions. In the experimental method we may

either synthetize an artificial environment and proceed to study the plant under definitely measured differences of light and water, or we may measure the physical factors influencing the same plant under various natural conditions. The observational method is ill suited for most work on habitat relations because the habitat involves an extremely variable array of uncontrolled physical factors, and it is practically impossible to determine without actual measurements which factor has the controlling influence and what the relative importance of the others are. The most desirable method for problems which will allow its application is the one in which we synthetize an artificial environment. In this case we keep certain factors constant and measure the variable one; in this way, it is quite obvious, the environment is comparatively easy to analyze. This method, of course, presupposes a greenhouse and on this account is only of limited application.

There is no question that all these methods have their value in their proper places; the choice of one must vary with the problem and the circumstances. The method of measuring the factors influencing the same plant under various natural complexes is the one probably of widest application in the field. The purely observational method, for work on the determination of habitat factors, while of some value when other methods are impossible of application has unsurmountable objections. Observers in various parts have no common basis or standard; their mental equipment and fund of ecological knowledge vary greatly and they may even have very different points of view. Some of these objections might be summed up in the term "personal equation." Another danger in this method is that of applying local observations to large areas, in other words, in generalizing on the basis of too meager observations. The conclusions drawn in the observational method are largely in the nature of opinions modified as indicated above by the personal equation, while the experimental method produces conclusions based upon actual figures which are indisputable and carry the weight of scientifically proven facts.

Another objection to the observational method in determining the effect of habitat factors is that this method studies the effect

and not the cause of the factors. It is a most significant fact that the same habitat factors do not always produce the same effects upon vegetation even under apparently the same set of conditions. The effect of two habitat factors or groups of factors may be the same so far as the structure and behavior of the plant is concerned, yet upon inquiry into the causes concerned we might find in one case it was due to temperature and in the other to soil moisture. In a similar manner it is known that other factors besides light determine tolerance. In other words the study of the effect of habitat factors upon plants does not always lead us to safe assumptions as to what the underlying cause is. The only safe method in this kind of work is to measure the cause, thus employing a direct method instead of an indirect one.

Methods and Apparatus Used in These Investigations

The investigations herein described were carried on in the middle room of the west greenhouse of the botany department of the University of Nebraska. For the germination studies three series of cultures were used, namely, the light, soil-moisture, and soil-texture series. For the experiments and measurements in connection with the early development of roots and stem a fourth series was added, namely, the soil-depth series. In each series three degrees were used. In the light series open light, medium shade, and dense shade were used; in the soil-depth series shallow, medium deep, and very deep soil was used; in the soil-moisture-content series, dry soil, medium wet soil, and wet soil was employed; and in the soil-texture series loam, sand, and gravel were used. The values of each degree in each case will be given later. As the experiments progressed it was found that the amount of greenhouse space assigned to the work was not sufficient, so that the open light culture, the wet soil culture, and the loam culture were combined into one since these were being run under identical conditions. (For arrangement of cultures see page 33.)

The seeds for these experiments were obtained from any source it was possible to get them. Large orders were sent to almost all large commercial seed houses at one time or another. On the whole the response from these orders was very discouraging. At

the time the seed was wanted (early fall) many of the seed crops had not been collected. Likewise it took time to determine whether there would be any crops at all in the case of some species. This resulted in delay in getting the work started. By the middle of January eighteen species had been obtained from commercial seedmen and of these only seven produced results that were in any way satisfactory. On the other hand, through the kindness of various members of the Forest Service throughout the United States, twenty-six species were secured and practically all of these produced good results. Due to these facts anyone undertaking experiments of this kind in the future must look a long ways ahead for a good seed supply. The following series of tables gives the source of the seed obtained together with what information was available as to date and place of collection. The nomenclature used here and throughout this report is that used by the Forest Service and is according to Forest Service Bulletin No. 17 by G. B. Sudworth.

Species Supplied by the United States Forest Service

Species	Place Collected	Date
Pinus ponderosa	California	?
Pinus ponderosa	Pecos N. F., New Mexico	1913
Pinus ponderosa	Weiser N. F., Idaho	1912
Pinus ponderosa	Harney N. F., South Dakota	1912
Pinus ponderosa	Bitterroot N. F., Montana	1912
Pseudotsuga taxifolia	Pecos N. F., New Mexico	1913
Pseudotsuga taxifolia	Caribou N. F., Idaho	1912
Pseudotsuga taxifolia	Madison N. F., Montana	1911
Pseudotsuga taxifolia	Western Washington and Oregon	1911
Pinus Jeffreyi	Kern N. F., California	1912
Abies concolor	Durango N. F., Colorado	1913
Tsuga heterophylla	Olympic N. F., Washington	1911
Pinus lambertiana	Lassen N. F., California	1910
Libocedrus decurrens	Eldorado N. F., California	1914
Pinus palustris	Florida N. F., Florida	?
Pinus coulteri	Monterey N. F., California	1910
Abies magnifica	Sequoia N. F., California	?
Sequoia washingtoniana	Sequoia N. F., California	1912
Pinus divaricata	Minnesota N. F., Minnesota	1910
Pinus contorta	Arapaho N. F., Colorado	?
Pinus resinosa	Minnesota N. F., Minnesota	1910

Larix occidentalis	Colville N. F., Washington	1911
Abies lasiocarpa	Priest River, Idaho	1913
Abies grandis	Priest River, Idaho	1913
Picea sitkensis	Coast of Washington	1911
Pinus monticola	Priest River, Idaho	1914

SPECIES SUPPLIED BY COMMERCIAL SEEDMEN OR COLLECTED

Species	Place Collected	Date
Pinus strobus	Canada	1913
Larix europea	Europe	?
Pinus ponderosa	Black Hills, South Dakota	1913
Pinus divaricata	Northern Minnesota	1914
Robinia pseudacacia	Europe	?
Catalpa speciosa	Indiana	1913
Quercus rubra	Michigan	1914
Acer saccharum	Illinois	1914
Liriodendron tulipifera	Ohio	1914
Betula papyrifera	Pennsylvania	1914
Abies balsamea	Maine	1914
Pseudotsuga taxifolia	Colorado	1913
Pinus taeda	Southern states	?
Taxodium distichum	Southern states	?
Liquidamber styraciflua	North Carolina	1914
Acer saccharum	Canada	1914
Acer rubrum	New Hampshire	1914
Fraxinus americana	Indiana	1914
Juniperis virginiana	Missouri River, Nebraska	1914
Gleditschia triacanthos	Lincoln, Nebraska	1915
Pinus monticola	Glacier Park, Montana	1914
Catalpa speciosa	Lincoln, Nebraska	1915

In the body of this report, in order to distinguish the climatic varieties of a species, the name of the state in which the seed was collected is given with the name of the species.

The first planting was done on October 28, 1914. From that time on plantings were made as the seed arrived. The last seeds were planted March 21, 1915. All experiments were conducted between the first date mentioned and May 1, 1915, a period of 184 days. In all cases ample time was allowed for the completion of the process of germination. This time naturally varied with the species. For most species three months was allowed but in the

case of certain Pacific coast species four months was apparently necessary. Three months ordinarily is plenty time enough; usually if a seed in the forest fails to germinate in that time, it usually does not germinate at all, especially in the west where the dry period sets in after the spring is over.

Ten of the species mentioned in the foregoing tables failed to germinate. These species were *Larix europea, Acer saccharum* (both), *Liriodendron tulipifera, Taxodium distichum, Liquidamber styraciflua, Fraxinus americana,* all of which were supplied by commercial seedmen. If the data regarding the collection of these seeds is bona-fide, their failure to germinate must be explained by the fact that they had not completed their resting period. In the case of *Juniperis virginiana, Gleditschia triacanthos,* and *Pinus monticola,* whose place and date of collection is known absolutely there can be very little doubt as to why they failed to germinate.

The soil used in all cultures (except the sand and gravel) was a garden loam of excellent quality with a mixture of about 25 per cent. of white sand. The mixture was prepared in the greenhouse. This made a very good soil for experimentation purposes. The sand used was common white, quartz sand with but a very small per cent. of hornblende and magnetite. The gravel was the kind used by the large construction companies around Lincoln for concrete work. Mechanical analyses of representative samples of these soils are given elsewhere.

All seeds were planted in rows at a depth which was 2½ times the shortest diameter of the seed as near as this was determinable by the unaided eye. The rows averaged 3 inches apart and about 24 inches in length. In general 200 seeds were used of each species when the seeds were of medium size or smaller; for some of the western pines only 100 were used because of their large size.

The Control of Habitat Factors

As has been pointed out, the only safe way to study the effect of the factors of the habitat upon the life of the plant is to measure one variable factor while all the rest are kept constant.

This principle is fundamental in mathematics; a single algebraic equation with two unknown quantities cannot be solved. In each of the series used in these investigations it was the intention to have only one variable habitat factor. In this way the study of cause and effect was much more clearly brought out.

The soil moisture determinations were made for four different purposes:

1. As a check upon daily watering in similar cultures.
2. To show the effect of shading on soil moisture content.
3. To show the minimum content in the soil moisture series.
4. To compare soil moisture content in loam, sand, and gravel.

The samples were taken in certain cultures and at intervals varying with the purpose. The samples for the moisture content series of cultures were taken once a week, all others once a month. Each sample consisted of from 50–100 grams of soil, and was taken at depths varying with the development of the plants in the culture. In order to provide against error each sample consisted of from two to five portions taken from spots several decimeters apart, care being exercised that no soil was dug near holes where previous samples had recently been obtained. The samples were always dug between the rows of seedlings. The samples were immediately weighed and dried at a temperature of 95–105° Centigrade to constant weight (24 hours). The per cent. of water was computed upon the dry weight of the soil.

All the cultures except the dry soil and the medium wet soil cultures were watered every evening. As was noted above, when the amount of room for the germination tests became insufficient the number of cultures was reduced from 12 to 10 by eliminating two duplicate cultures. The only check moisture samples which will be considered here are those that have to do with the three cultures which were being operated under identical conditions. Samples taken and recorded hereafter will take care of the other cultures and series. During the time (three months) that these duplicate cultures were run, one set of soil samples was taken as a check to determine whether they were being watered equally. These figures follow:

CHECK SOIL MOISTURE SAMPLES 11/14/14

Depth 5.0 cm.

Name of Culture	Moisture Per Cent.
Open light	27.9
Wet soil	24.1
Loam	27.7
Deep soil	28.2
Medium depth	28.5
Shallow soil	31.4

These figures, obtained after more than two weeks of daily watering, pretty well indicate the small amount of variation in moisture content which results in a number of cultures under the same conditions.

Light was controlled in the greenhouse by means of shade tents. The east bench of the room was divided into three parts and the portions at the ends of the bench were covered with cheese cloth. The central compartment of the three was not used on account of the shading influence of the tent to the south of it. (See page 33.) The tent intended to develop medium shade was made of a medium grade of cheese cloth, while the tent intended for the dense shade was constructed of a double layer of heavy cheese cloth. The light values developed in these tents and in the full light of the greenhouse as determined by a Clements photometer are given below:

TABLE OF LIGHT VALUES

Date	Time	Open Light	Medium Shade	Dense Shade	Number Readings	Weather
11/21/14	11:30 A.	0.4250	0.1775	.....	5	Clear
11/27/14	12:00 A.	0.4040	0.1467	0.0216	3	Clear
Average.......	.....	0.4145	0.1621	0.0216	.	.....

These values are based upon full sunlight just outside of the greenhouse. These tables indicate that full greenhouse light is approximately ½ of full daylight and that the medium and dense shade tents have values approximately ⅙ and 1/50 of full daylight respectively.

It is quite natural to wonder how these values compare with values that have been obtained in the woods. Probably the comparison of the light values obtained in the dense shade with some of the lowest values obtained in the woods would be most interesting. Clements (2) found light values from 0.12 to 0.05 under mature lodgepole pine in Colorado. He observed that Douglas fir occurred very rarely in densities below 0.05. Wiesner found the same value in this case. Pearson in Arizona found that western yellow pine seedlings grow fairly well in a light intensity from 0.309 to 0.414. White fir was found in good condition in light intensities of from 0.027 to 0.068 and healthy young growth of Engelmann spruce was found in intensities of from 0.033 to 0.062. In Oregon Pearson found such tolerant species as alpine fir, Engelmann spruce, western hemlock, and Lowland fir growing in light intensities from 0.021 to 0.029. The western larch however showed only poor development in a light intensity of 0.353. This will be sufficient to indicate that the light in the dense shade tent compares with some of the lowest light intensities that have been measured in our western forests. In this connection it is interesting to note that white pine, black locust, red oak, and western yellow pine lived for two to four mouths in the dense shade tent, as is evidenced by the fact that stem and root measurements were taken on these species during the last days of these investigations.

In connection with the light experiments a very important fact soon became evident. In spite of the fact that all three cultures were watered every evening at the same time and in the same degree, it soon became evident from mere observation that the top layer of soil by the following evening had dried out to very different degrees in the three cultures. The open light culture was noticeably the driest and the dense shade culture the moistest so far as the top layer was concerned. This fact led to taking systematic moisture samples to determine the exact difference in moisture content. These samples were taken once a month, three evenings in succession and these readings were averaged into one reading. The table of soil moisture contents is given below:

TABLE OF SOIL MOISTURE CONTENT IN LIGHT CULTURES IN PER CENT.
Depth 2 cm.

Dates	Open Light	Medium Shade	Dense Shade
11/10–12	12.3	15.3	19.8
12/13–15	12.0	19.0	19.3
1/4 –6	6.1	15.7	18.0
2/14–16	14.0	16.6	21.3
3/14–16	14.4	17.0	21.3
4/15–17	10.3	17.2	19.7
Average	11.5	16.8	19.9

Soil depth was comparatively easily controlled, either by only partially filling the flats with soil or by using deeper boxes. This was done and the depths used were as follows:

Shallow soil	4.0 cm.
Medium deep soil	9.0 cm.
Very deep soil	30.0 cm.

The depth of the medium soil was the depth of all the other cultures used in the light, soil moisture, and soil texture experiments. No attempt was made to measure the soil moisture content periodically in the soil depth cultures, except as noted in checking up the watering of the cultures.

Soil moisture was controlled in the soil moisture experiment by watering the cultures at different intervals. The wet culture was watered every evening, the medium wet culture was watered every Wednesday noon and Saturday evening and the dry soil culture was watered only every Saturday evening. The soil samples that were taken were secured just before watering and were taken at first every Wednesday noon and every Saturday evening and later only every Saturday evening. Thus the soil samples represent the minimum water content of the soil at the end of one day, at the end of three and one half days, or at the end of seven days. In the following table are given the soil moisture per cents as taken at various depths according to the stage of development of the majority of the seeds or plants in the cultures concerned.

MINIMUM SOIL MOISTURE CONTENT IN SOIL MOISTURE CULTURES

Date	Depth, Cm.	Dry Culture, Per Cent	Medium Wet Culture, Per Cent	Wet Culture, Per Cent
11/4	0–5	6.4	10.5	23.0
11/7	0–5	4.0	13.7	30.0
11/11	0–5	4.6	5.0	25.0
11/14	0–5	7.2	14.1	24.1
11/21	0–5	7.7	17.1	21.1
11/28	0–5	6.7	13.8	22.3
12/5	0–5	6.1	12.4	24.3
12/12	0–5	8.5	16.6	23.3
12/19	0–5	5.2	12.1	26.5
12/26	0–9	4.3	9.4	27.5
1/2	0–9	6.8	11.8	24.7
1/9	0–5	5.7	15.7	40.0
1/16	0–5	5.1	12.5	36.6
1/23	0–5	3.0	6.3	17.9
1/30	0–5	3.2	7.1	18.8
2/6	0–9	4.7	12.4	20.7
2/13	0–5	4.3	....[1]	19.0
2/20	0–5	6.3	13.8	23.3
2/27	0–5	5.4	14.1	38.3
3/6	0–5	4.0	9.4	27.7
3/13	0–5	3.1	6.7	19.8
3/20	0–5	3.5	9.3	19.6
3/27	0–5	4.5	15.6	21.7
4/3	0–5	4.5	12.4	19.8
4/10	0–5	5.9	14.0	30.8
4/17	0–5	3.5	8.0	23.8
4/24	0–5	4.0	12.4	20.7
Average	....	5.1	11.8	23.9

Soil texture was controlled by the use of cultures of loam, sand, and gravel. Soil texture affects principally the moisture content and the air content of the soil, hence careful analyses to determine both relations were made. The following moisture determinations were made for sand, loam and gravel, which show the amount of hygroscopic water, the volume of pore space, and the amount of capillary water in each of these soils:

TABLE OF SOIL DETERMINATIONS

Texture of Soil	Hygroscopic Water, Per Cent	Volume of Pore Space in Per Cent	Capillary Water, Per Cent
Gravel, fine		36.54	5.4
medium	0.14	39.34	5.0
coarse	....	41.14	2.8
average	....	39.04	4.4
Sand	0.11	33.51	16.6
Loam	0.92	53.32	38.0

[1] Lost by accident in the soil oven.

The per cent. of hygroscopic water in the soils was the amount of moisture the soils held at room temperature. The amount of pore space in the soils was equivalent to the total amount of water the soils would hold. This would also be the amount of air in the soil when air dry. In determining the amount of pore space the soil used was air dry, hence the amount of hygroscopic water in the soil had to be added to the amount of pore space. The amount of capillary water was the amount of water the soils held against gravity. The same soils were used in all three experiments and the samples consisted of about 150 grams each except in the volume determinations in which 100 cubic centimeters of soil were used in each case. This table shows very strikingly the water and air relations in these soils. The great amount of air in gravel when it is at its maximum capillary water content is also shown approximately.

The mechanical analyses of representative samples of these soils which were kindly furnished by the department of agronomy of the University of Nebraska are given below:

MECHANICAL ANALYSIS OF SOILS

Separate	Diameter, Mm.	Loam	Sand	Gravel
Stones	Above 3	.....	.....	38.639
Coarse gravel	3–2	.....	.....	40.382
Fine gravel	2–1	7.936	21.045	14.051
Coarse sand	1–.5	11.771	29.418	4.245
Medium sand	.5 –.25	8.197	21.709	1.062
Fine sand	.25 –.1	11.392	25.708	0.770
Very fine sand	.1 –.05	6.182	1.074	}
Silt	.05 –.005	21.704	} .346	} 0.268
Clay	.005 and less	26.566	}	}
Volatile matter	....	6.252	0.700	0.583
Total	....	100.000	100.000	100.000

Besides these determinations soil samples were taken once a month to determine how much moisture these soils held at the end of a day in the cultures in the greenhouse. These results bear out the findings in regard to capillary water held by the soils shown in a preceding table. These moisture contents are given below:

SOIL MOISTURE CONTENT TWENTY-FOUR HOURS AFTER WATERING
Depth 5.0 cm.

Date	Loam, Per Cent	Sand, Per Cent	Gravel, Per Cent
11/14	27.7	4.3	2.4
12/15	25.6	5.4	2.1
1/15	25.1	4.8	2.5
2/15	26.1	5.0	2.0
3/15	28.7	5.1	2.4
4/15	27.4	4.9	1.9
Average	26.8	4.9	2.2

The temperature and humidity of the air were determined by a hydrothermograph which was checked every Monday morning by means of a cog psychometer and humidity tables (the barometric pressure used was 29 inches). The record sheets were summarized and the results for the entire period are given below by weekly averages:

Week Ending		Temperature, Degrees Fahr.				Relative Humidity, Per Cent		
		Min.	Max.	Weekly Range	Weekly Mean, 2 Hr.	Min.	Max.	Weekly Mean, 2 Hr.
November	1	60	100	40	71.7	18	78	49.0
	8	53	99	46	67.9	34	93	69.4
	15	52	94	42	67.8	20	90	64.0
	22	49	90	41	66.6	29	75	54.9
	29	54	90	36	67.2	21	75	55.9
December	6	59	89	30	70.2	32	84	60.7
	13	59	87	28	69.7	37	66	55.0
	20	52	83	31	67.8	38	62	48.9
	27	51	88	37	67.0	35	57	48.8
January	3	56	93	37	72.9	34	69	52.8
	10	52	89	37	67.3	41	79	64.7
	17	54	85	31	64.6	30	76	64.1
	24	47	96	49	65.4	39	75	58.5
	31	53	88	35	64.6	43	82	65.7
February	7	53	98	45	70.4	33	68	54.5
	14	57	98	41	68.4	38	78	62.2
	21	52	95	43	61.5	35	85	71.7
	28	55	98	43	64.9	25	65	54.0
March	7	57	100	43	63.2	21	60	53.7
	14	54	98	44	65.5	28	65	54.6
	21	59	100	41	67.4	22	63	50.5
	28	54	100	46	63.7	28	83	62.0
April	4	53	100	47	66.6	23	88	55.7
	11	55	100	45	64.5	23	61	47.2
	18	47	100	53	64.6	18	85	49.9
	25	49	100	51	73.2	24	90	68.3
May	2	61	100	39	75.0	18	92	63.0

Soil temperature was not measured. With the air temperature at an optimum point during the entire experiment it is reasonable to assume that the soil temperatures were likewise always at an optimum, at least they were never at such a low nor at such a high point so as to affect materially the germination of the seeds or the growth of the seedlings.

Notes on Damping-Off

No special investigations were conducted to determine what species were most affected and what conditions of light, moisture, and soil were most favorable for the development of this group of fungous diseases. This part of nursery practice is a problem of no small importance in itself and the only data here given is that which had to be taken in connection with this series of investigations. Therefore these are merely notes and suggestions, which, while conclusive as far as they go, must be substantiated in the future to be of any permanent value.

It was found that the pines were most affected. *Pinus divaricata* at the end of five weeks was affected most. About 15 separate cultures of 200 seeds each of this species were started and most of these showed more or less serious effects of the disease. Several cultures of *Pinus resinosa* failed after six weeks. *Pinus palustris* damps off in loam before it really gets its crown above ground. In this case the loss was reduced in the sand and gravel cultures. Both the New Mexico and South Dakota varieties of *Pinus ponderosa* after five weeks damped off considerably, leaving only from 10–25 per cent. of the original stand. The following is a list of species in the order in which they were affected in loam under normal conditions of light and water. The first mentioned were affected most:

Pinus divaricata
Pinus resinosa
Pinus palustris
Pinus ponderosa (S. D.)
Pinus ponderosa (N. M.)
Robinia pseudacacia
Pinus strobus
Pinus taeda

It appears that the seeds of trees of certain habitats when germinated in soils or under conditions different from those obtaining in their natural environment are affected worst. These habitats are:

1. Sandy soils
    Pinus divaricata
    Pinus resinosa
    Pinus palustris
    Pinus taeda
2. Dry habitats
    Pinus ponderosa (S. D.)
    Pinus ponderosa (N. M.)
3. Poor soils
    Robinia pseudacacia.

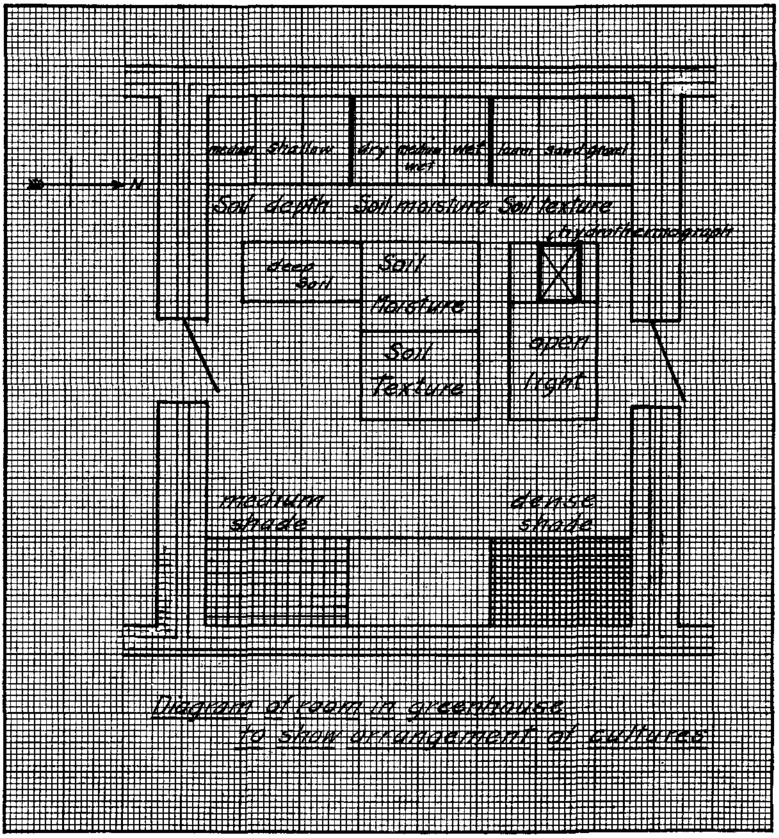

Diagram of room in greenhouse to show arrangement of cultures

Species that seemed to be affected most were those from the Black Hills and New Mexico and those affected least were those from the Pacific coast. Intermediate between these were those species obtained from Montana and Idaho. The coast species affected most was *Sequoia washingtoniana*. *Pseudotsuga taxifolia* was much less affected than *Pinus ponderosa* taking into account all the varieties of each.

The conditions and cultures which were favorable to damping-off are of interest in that they emphasize many points already known about this part of the subject. Loam is more dangerous than sand or gravel due to its moisture retentiveness. The shade cultures were more affected than the open light due to a greater soil moisture content in the upper layers of soil. The moist cultures were affected more than the dry ones and the shallow soil cultures more than the deep soil ones due to a greater amount of soil water per unit of volume of soil. Humous soils, soils with decaying vegetable matter, and manure soils should be avoided because they contain myriads of fungus spores. The data for *Pinus divaricata* is given as representative of the three worst affected species. The per cents. given below are those of the number of plants killed (out of the total number that germinated) within five weeks after planting the seed. Two hundred seeds were planted in each culture:

Pinus divaricata Killed by Damping-off

Light Cultures		Soil Moisture		Soil Depth		Soil Texture	
Open	35%	Dry soil	0%	Deep	8%	Loam	35%
Medium	26%	Medium soil	24%	Medium	35%	Sand	1%
Dense	90%	Wet soil	35%	Shallow	61%	Gravel	0%

THE EFFECT OF HABITAT FACTORS UPON GERMINATION

This problem was undertaken because it was felt to be of fundamental significance not only to silviculture but to ecology as well. Not only was it desired to throw more light upon some of the phases of this problem that had already been partly worked out and to modify, if necessary, some conclusions that have been drawn, but it was my intention to throw some light upon phases

of it that had never been attacked. Some of the questions that are immediately called to mind by a mere statement of the problem are: Does light affect germination in any way? Does light affect the germination of tolerant and intolerant species differently? How does soil moisture content affect germination? Do drought-enduring species and moisture-loving species behave alike in this respect? What is the effect of soil texture upon germination? Has the amount of air or oxygen in the soil any significance in germination? Since soil texture affects mainly the moisture content of the soil, does soil texture affect drought-enduring species in the same way as moisture-loving species?

The data collected upon the effect of habitat factors on germination will be presented in four parts. The effect of light, soil moisture, and soil texture will be taken up in the order named and following this there will be given a résumé of the relative effect of all habitat factors. The three most important points to be noted in germination, are the number of days it took until germination began, the total number of days in the germination period, and the final germination per cent. The rate of germination is shown by curves for certain representative species. The length of the germination period was taken as the total number of days during which any seeds germinated. Records were kept long after germination ceased, so that the germination period was ended at the time the last seed germinated. To give data as to the period of greatest activity involves certain arbitrary standards and this method, though tried in compiling the present data, was abandoned. The effect of light, soil moisture, and soil texture upon the periods of greatest activity is best shown by the curves offered for certain representative species.

The original data was taken by two-day periods. Every other day the number of seeds that germinated were counted and recorded. In most cases these were immediately pulled up; but where growth measurements were to be taken later the seedlings were allowed to grow.

The first three tables show the effect of light upon the germination of eastern species, Rocky Mountain species, and Pacific coast species respectively. Three sets of figures are given under each

degree of light, namely, the number of days which elapsed before germination began, the number of days in the germination period, and lastly the final germination per cent.

The number of seeds used of each species in each culture made was as follows: 100 seeds each of *Catalpa speciosa, Acer rubrum, Gleditschia triacanthos, Pinus taeda, Pinus ponderosa* (Idaho), *Abies grandis, Abies lasiocarpa, Pinus ponderosa* (Mon.), *Pinus ponderosa* (Harney), *Pinus ponderosa* (Calif.), *Pinus jeffreyi, Pinus lambertiana, Pinus coulteri, Abies magnifica,* and *Pseudotsuga taxifolia* (Wash.); 25 seeds of *Quercus rubra,* 400 of *Betula papyrifera,* and 200 seeds of all other species.

When a number of check cultures were combined as was noted previously it became necessary to average the results obtained in several cultures under the same set of conditions. Thus the check cultures used in each series show the same data in every case. Three cultures of each of the following species were averaged together: *Catalpa speciosa* (Ind.), *Pinus strobus, Quercus rubra, Pinus divaricata, Robinia pseudacacia, Betula papyrifera, Pinus ponderosa* (S. D.), *Pseudotsuga taxifolia* (N. M.), *Pinus ponderosa* (N. M.), and *Pinus ponderosa* (Calif.). Two cultures of each of the following species were averaged together: *Pinus palustris, Pinus resinosa, Pinus jeffreyi, Pinus lambertiana,* and *Pinus coulteri.* All other species in the check cultures were planted but once.

In Table I 10 species out of a total of 14 germinated in the dense shade before they did in the open light culture. Only one species, *Pinus palustris,* germinated first in the open light, one species, *Gleditschia triacanthos,* did not germinate in the open light at all, and two species germinated simultaneously in all three cultures. *Pinus strobus* germinated 8 days earlier in the dense shade than in the open light, *Pinus divaricata* 2 to 4 days, *Pinus resinosa* 10 days, *Pinus taeda* 2 days, *Catalpa speciosa* 2 days, *Quercus rubra* 14 days, *Robinia pseudacacia* 2 days, and *Acer rubrum* 4 days.

In 9 cases the germination period is longer in the dense shade than in the open light and, considering the shade cultures together,

11 species show a longer germination period in the shade than in the light. The other three species did not germinate sufficiently to make a conclusion possible.

TABLE I

THE EFFECT OF *Light* ON GERMINATION

Eastern Species

Species	Open Light			Medium Shade			Dense Shade		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus strobus.........	22	50	10.7	16	54	11.5	14	26	8.0
Pinus divaricata.......	12	32	54.5	10	26	63.5	10	38	73.5
Pinus divaricata (F. S.)	14	20	39.5	14	26	37.0	10	24	46.5
Pinus resinosa........	24	16	30.5	16	24	50.0	14	14	74.5
Pinus palustris.......	31	53	10.5	32	82	12.0	32	62	5.5
Pinus taeda..........	34	6	19.0	34	6	33.0	32	8	33.0
Abies balsamea.......	18	30	11.0	18	38	10.0	18	36	8.0
Catalpa speciosa.......	18	1	1.0	0	0	0.0	16	1	1.0
Catalpa speciosa (Neb.)	16	12	91.0	14	20	92.0	14	14	88.0
Quercus rubra.........	40	28	28.0	30	18	12.0	26	42	12.0
Robinia pseudacacia...	8	16	28.8	6	18	29.0	6	18	33.5
Betula papyrifera......	34	1	1.0	34	1	2.0	34	1	1.0
Acer rubrum..........	18	30	17.0	16	34	15.0	14	34	16.0
Gleditschia triacanthos .	0	0	0.0	6	2	2.0	6	2	2.0

Three species had a higher germination per cent. in the open light than in either of the shade cultures. Four showed the highest per cent. in the medium light and six in the dense shade. The greatest difference was shown in the case of *Pinus resinosa* whose germination per cent. was almost two and one half times greater in the dense shade than in the open light culture.

The germination curves of *Pinus resinosa* and of *Pinus divaricata* are given on page 38. These are representative of the effect that light has upon germination. These curves show a greater germination per cent. in the dense shade culture, a more rapid rise of the germination curve in the dense shade and that germination begins sooner in the shade than it does in the light.

THE EFFECT OF *Light* UPON GERMINATION

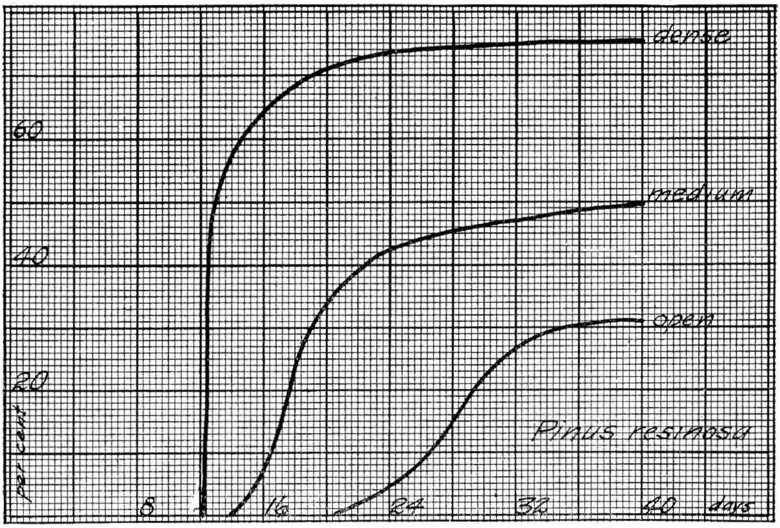

FIG. 1. The germination curves of *Pinus resinosa*.

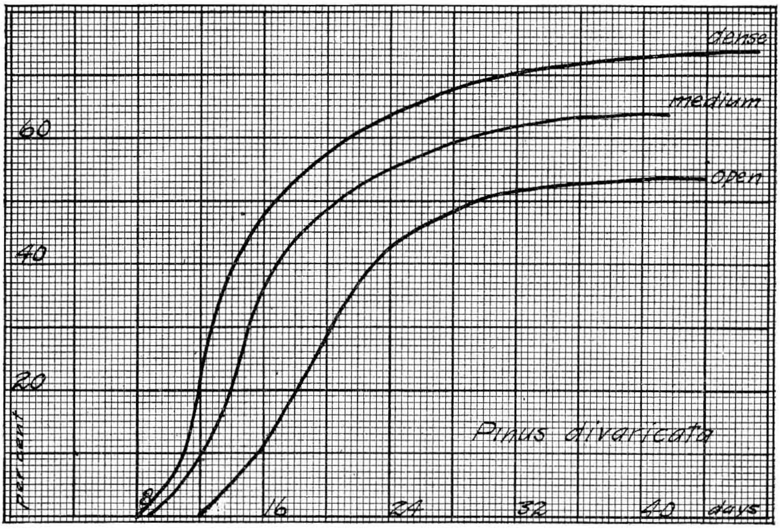

FIG. 2. The germination curves of *Pinus divaricata*.

TABLE II

THE EFFECT OF *Light* ON GERMINATION

Rocky Mountain Species

Species	State	Open Light			Medium Shade			Dense Shade		
		Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa	S.D.	10	32	58.0	10	22	56.5	10	34	58.5
Pinus ponderosa	Harney	14	14	52.0	8	26	58.0	8	26	63.0
Pinus ponderosa	N.M.	14	40	56.0	12	32	82.0	10	12	79.0
Pseudotsuga taxifolia	N.M.	12	26	63.0	10	12	69.0	10	16	65.0
Pseudotsuga taxifolia	Colo.	12	42	91.0	12	36	73.5	8	36	82.0
Abies concolor	Colo.	24	50	38.0	18	56	54.0	14	60	56.0
Pinus contorta	Colo.	14	80	22.0	16	70	7.5	14	72	3.5
Pinus ponderosa	Mon.	18	12	10.0	18	54	15.0	10	8	9.0
Pseudotsuga taxifolia	Mon.	14	34	20.5	12	32	15.5	12	44	35.0
Pseudotsuga taxifolia	Idaho	18	30	20.5	16	64	49.0	10	64	50.0
Pinus ponderosa	Idaho	36	52	42.0	24	66	52.0	14	82	43.0
Abies grandis	Idaho	36	36	4.0	22	62	16.0	22	60	10.0
Abies lasiocarpa	Idaho	30	30	6.0	26	50	7.0	22	28	6.0
Pinus monticola	Idaho	24	50	22.5	16	58	20.0	14	60	36.5

In Table II 12 species out of a total of 14 germinated first in the dense shade, the other two germinated simultaneously in the dense shade and open light. The number of days difference between the two cultures varied from 2 to 22 days. *Pinus ponderosa* (Harney) germinated 6 days earlier in the dense shade than in the open light, *Pinus ponderosa* (N. M.) 4 days, *Pseudotsuga taxifolia* (N. M.) 2 days, *Pseudotsuga taxifolia* (Colo.) 4 days, *Abies concolor* 10 days, *Pinus ponderosa* (Mon.) 8 days, *Pseudotsuga taxifolia* (Mon.) 2 days, *Pseudotsuga taxifolia* (Idaho) 8 days, *Pinus ponderosa* (Idaho) 22 days, *Abies grandis* 14 days, *Abies lasiocarpa* 8 days, and *Pinus monticola* 10 days. The medium shade cultures in most cases represent a condition intermediate between the open light and dense shade.

In 10 species out of 14 the germination period was longer in the shade than in the light. In 6 species the germination per cent, was higher in the dense shade than in either of the other two cultures and in 12 cases out of 14 the highest per cent. was in either of the two shade cultures as against the light culture. In other

THE EFFECT OF *Light* UPON GERMINATION

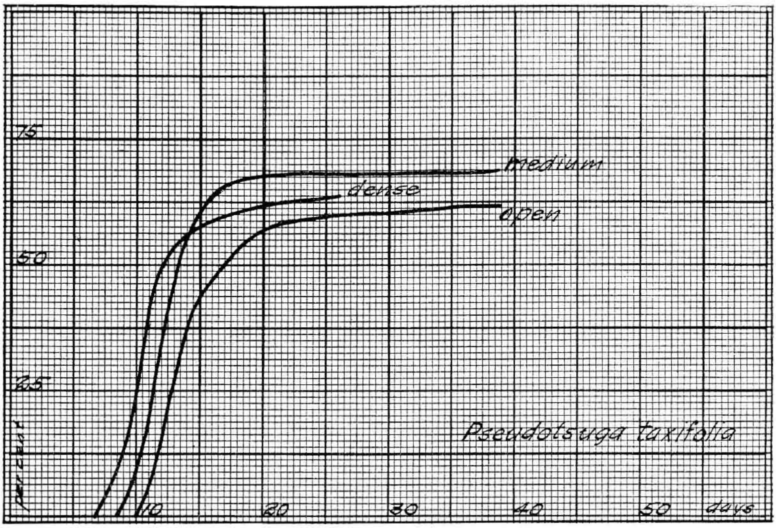

FIG. 1. The germination curves of *Pseudotsuga taxifolia* (N. M.).

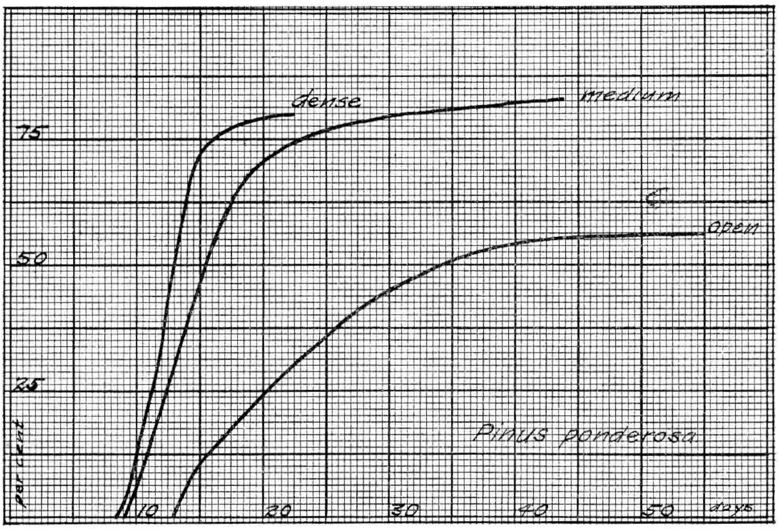

FIG. 2. The germination curves of *Pinus ponderosa* (N. M.).

words, only 2 species had a higher germination per cent. in the open light than in the shade.

On page 40 are given the germination curves of the two New Mexico species, *Pinus ponderosa* and *Pseudotsuga taxifolia*. While these do not show a higher germination per cent. in the dense shade than in the open light they show the characteristic rapid rise of the shade curves and the fact that germination begins earlier in the shade than in the light.

TABLE III

THE EFFECT OF *Light* ON GERMINATION

Pacific Coast Species

Species	Open Light			Medium Shade			Dense Shade		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa (Calif.)	42	67	61.0	22	92	62.0	22	62	42.0
Pinus jeffreyi	31	77	22.0	22	84	14.0	20	54	17.0
Pinus lambertiana	70	36	2.5	76	20	4.0	70	24	7.0
Pinus coulteri	52	41	15.5	54	30	18.0	52	62	23.0
Abies magnifica	44	52	18.0	24	54	30.0	36	54	10.0
Libocedrus decurrens	29	73	6.0	24	18	4.0	16	52	9.0
Sequoia washingtoniana	16	18	7.0	16	6	5.5	14	14	8.5
Tsuga heterophylla	66	1	0.5	0	0	0	0	0	0
Picea sitkensis	22	60	22.5	18	64	34.0	14	36	38.0
Larix occidentalis	0	0	0	72	1	0.5	70	1	0.5
Pseudotsuga taxifolia (Wash.)	22	28	6.0	22	54	13.0	14	62	22.0

Out of the 11 Pacific coast species listed in Table III, 7 germinated in the dense shade before they did in the open light culture, 2 germinated simultaneously in the light and shade and 2 species did not germinate sufficiently to warrant conclusions. *Pinus ponderosa* (Calif.) germinated 20 days earlier in the dense shade than in the light, *Pinus jeffreyi* 11 days, *Abies magnifica* 8 days, *Libocedrus decurrens* 13 days, *Sequoia washingtoniana* 2 days, *Picea sitkensis* 8 days and *Pseudotsuga taxifolia* (Wash.) 8 days.

Six species showed longer germination periods in the shade, three in the open light, and two species did not germinate sufficiently to be considered. Only one species, *Pinus jeffreyi*, showed a higher germination per cent. in the open light, two species showed

THE EFFECT OF *Light* UPON GERMINATION

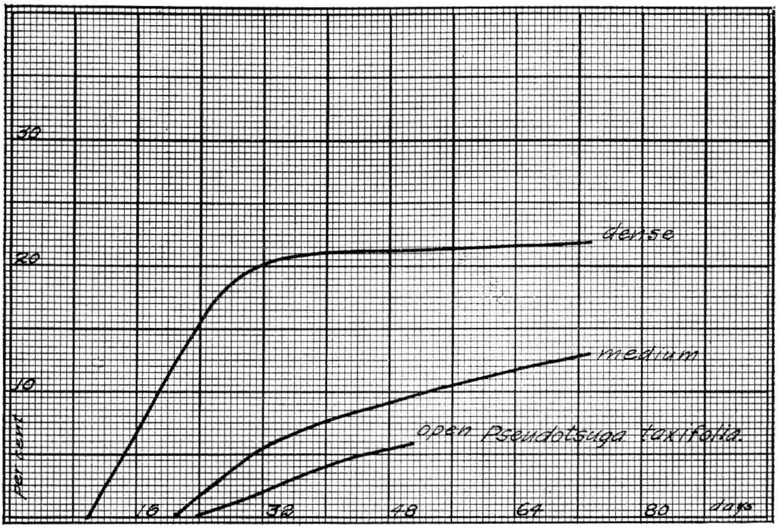

FIG. 1. The germination curves of *Pseudotsuga taxifolia* (Wash.).

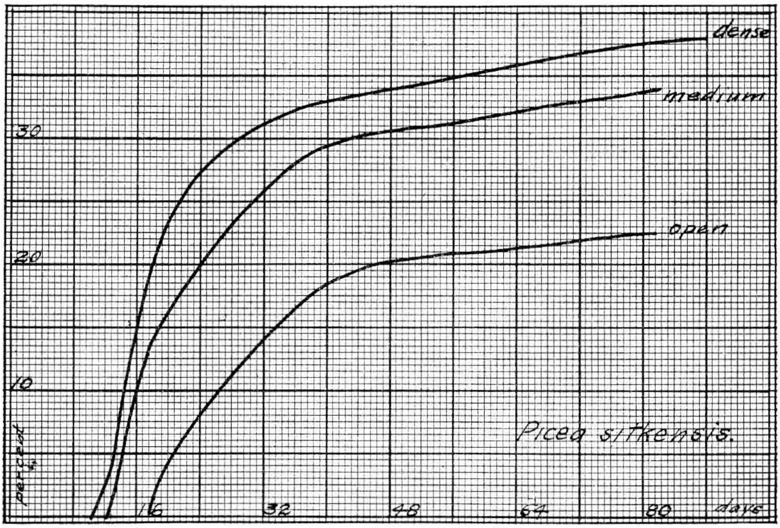

FIG. 2. The germination curves of *Picea sitkensis*.

a higher per cent. in the medium shade, and six a higher per cent. in the dense shade than in the other cultures.

On page 42 are given the germination curves of *Pseudotsuga taxifolia* (Wash.), and *Picea sitkensis.* Both sets of curves show that germination begins sooner, the curve rises more rapidly and the final germination per cent. is higher in the case of seeds germinated in the shade as compared to light.

TABLE IV

THE EFFECT OF *Soil Moisture* ON GERMINATION

Eastern Species

Species	Dry Soil			Medium Wet Soil			Wet Soil		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus strobus	—	—	—	30	34	8.0	22	50	10.7
Pinus divaricata	40	24	10.0	14	50	53.5	12	32	54.5
Pinus divaricata (F. S.)	28	12	7.5	22	18	4.0	14	20	39.5
Pinus resinosa	68	1	2.5	24	40	49.0	24	16	30.5
Pinus palustris	—	—	—	36	50	6.0	31	53	10.5
Pinus taeda	—	—	—	—	—	—	34	6	19.0
Abies balsamea	—	—	—	22	22	12.0	18	30	11.0
Catalpa speciosa	—	—	—	—	—	—	18	1	1.0
Catalpa speciosa (Neb.)	—	—	—	22	6	4.0	16	12	91.0
Quercus rubra	—	—	—	—	—	—	40	28	28.0
Robinia pseudacacia	10	30	15.0	8	32	32.0	8	16	28.8
Betula papyrifera	—	—	—	—	—	—	34	1	1.0
Acer rubrum	24	1	3.0	24	26	12.0	18	30	17.0

Tables IV, V, and VI consider the same species as the three preceding tables from the standpoint of soil moisture instead of light.

In Table IV in practically every case where a comparison is possible germination started in the wet soil culture, and was delayed as the soil moisture content was reduced. Also the germination period is shortened with decrease in soil moisture. The final germination per cent. in every case but one was highest in the wet soil. *Pinus resinosa* showed the highest per cent. in the medium wet soil.

This table separates the species into classes based upon their ability to germinate in dry soil, medium wet soil, or wet soil.

THE EFFECT OF *Soil Moisture* UPON GERMINATION

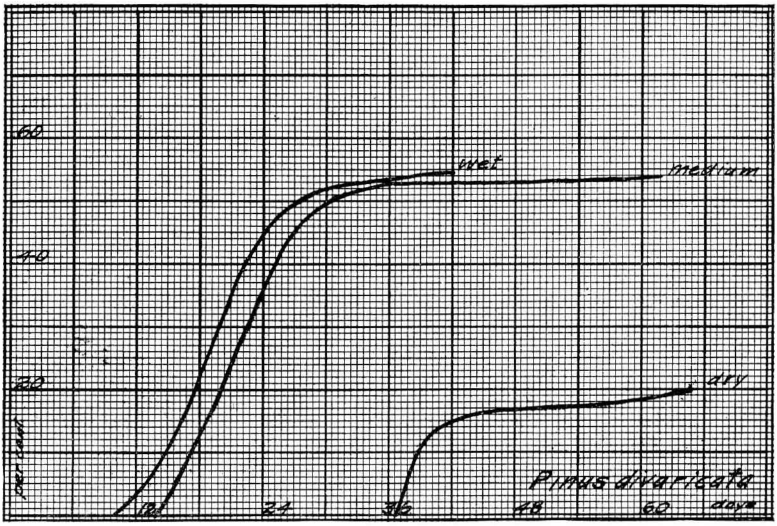

FIG. 1. The germination curves of *Pinus divaricata.*

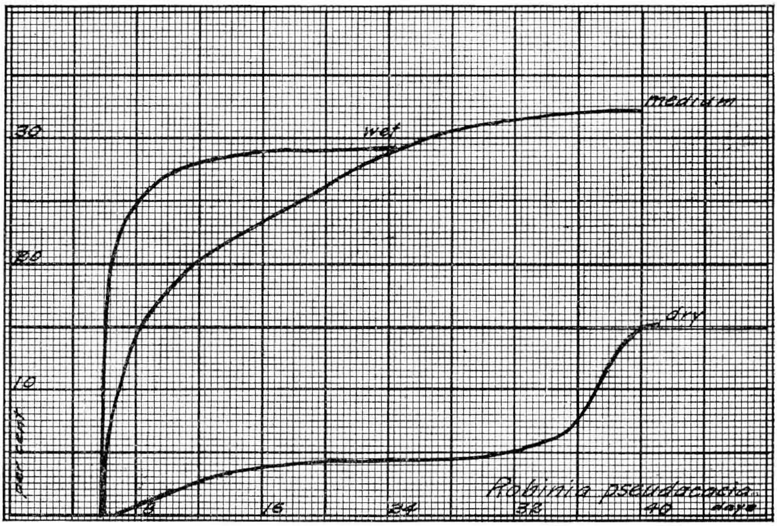

FIG. 2. The germination curves of *Robinia pseudacacia.*

According to that classification the most drought enduring are *Pinus divaricata, Pinus resinosa, Robinia pseudacacia,* and *Acer rubrum.* It is rather unusual to find *Acer rubrum* in this category but the seed has such a thin seed coat that water absorption is easier than in the case of a thick-coated seed. The intermediate species are *Pinus strobus, Pinus palustris, Abies balsamea,* and *Catalpa speciosa* (Neb.). Among what might be called the moisture loving species are found *Pinus taeda, Catalpa speciosa* (Ind.), *Quercus rubra* and *Betula papyrifera.*

On page 44 are given the germination curves of *Pinus divaricata* and *Robinia pseudacacia.* These sets of curves show that as soil moisture decreases the beginning of germination is delayed, the germination curve rises less rapidly and the final germination per cent. is decreased.

TABLE V

THE EFFECT OF *Soil Moisture* ON GERMINATION

Rocky Mountain Species

Species	State	Dry Soil			Medium Wet Soil			Wet Soil		
		Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa	S.D.	26	26	26.0	12	36	48.0	10	32	58.0
Pinus ponderosa	Harney	34	6	8.0	22	18	17.0	14	14	52.0
Pinus ponderosa	N.M.	22	18	39.5	20	16	61.0	14	40	56.0
Pseudotsuga taxifolia	N.M.	12	6	5.5	12	44	54.0	12	26	63.0
Pseudotsuga taxifolia	Colo.	14	24	9.5	12	42	60.5	12	42	91.0
Abies concolor	Colo.	—	—	—	80	26	12.0	24	50	38.0
Pinus contorta	Colo.	—	—	—	20	66	3.5	14	80	22.0
Pinus ponderosa	Mon.	—	—	—	18	58	6.0	18	12	10.0
Pseudotsuga taxifolia	Mon.	—	—	—	18	26	12.0	14	34	20.5
Pseudotsuga taxifolia	Idaho	24	1	0.5	20	32	6.5	18	30	20.5
Pinus ponderosa	Idaho	90	8	5.0	14	72	21.0	36	52	42.0
Abies grandis	Idaho	—	—	—	66	10	3.0	36	36	4.0
Abies lasiocarpa	Idaho	—	—	—	84	1	1.0	30	30	6.0
Pinus monticola	Idaho	48	1	0.5	18	38	9.0	24	50	22.5

As in the preceding table, Table V shows that the beginning of germination is delayed in most cases and that the germination period is considerably shortened with the decrease of soil moisture content. Only 1 species, *Pinus ponderosa* (N. M.) showed a higher germination per cent. in the medium wet soil than in the wet soil, all other species show a higher per cent. in the wet soil.

THE EFFECT OF *Soil Moisture* UPON GERMINATION

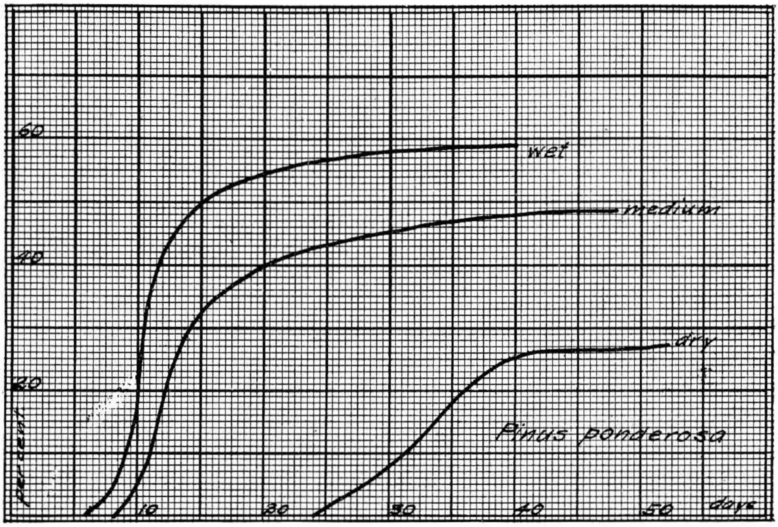

FIG. 1. The germination curves of *Pinus ponderosa* (S. D.).

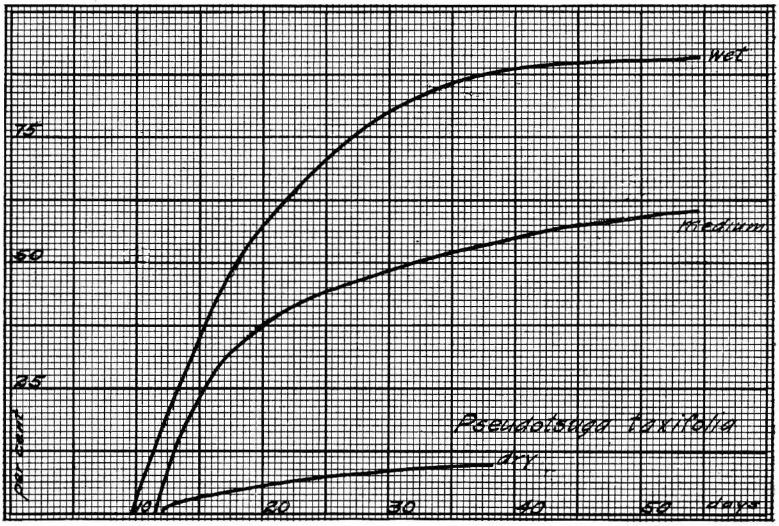

FIG. 2. The germination curves of *Pseudotsuga taxifolia* (Colo.)

It is evident from this table that the two most drought enduring species are *Pinus ponderosa* (S. D.) and *Pinus ponderosa* (N. M.). While other species germinated in the dry soil their germination per cents. were very small. Among the intermediate species, as far as soil moisture goes, are *Abies concolor, grandis,* and *lasiocarpa, Pinus contorta, Pinus ponderosa* (Mon.), and *Pseudotsuga taxifolia* (Mon.). It is interesting to see that with one exception the only species that germinated in the dry culture were either *Pinus ponderosa* or *Pseudotsuga taxifolia.* The former from the Black hills, New Mexico, and Southern Idaho and the latter from New Mexico, Colorado, and Idaho. The line is evidently drawn between Southern Idaho and Montana as to whether these species will germinate in the dry culture or not, since both species from Montana did not germinate in the dry culture. Another interesting fact is that there are no moisture-loving species in the Rocky Mountains so far as this classification and these species are concerned, since there are no species that germinated only in the wet soil.

On page 46 are given the curves of *Pinus ponderosa* and *Pseudotsuga taxifolia* in their relation to soil moisture. These curves show that germination is delayed, the curve rises less rapidly, the period is shorter, and the final per cent. lower with a decrease in soil moisture.

TABLE VI

THE EFFECT OF *Soil Moisture* ON GERMINATION

Pacific Coast Species

Species	Dry Soil			Medium Wet Soil			Wet Soil		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa (Calif.)	—	—	—	68	12	6.0	42	67	61.0
Pinus jeffreyi	—	—	—	80	6	12.0	31	77	22.0
Pinus lambertiana	—	—	—	—	—	—	70	36	2.5
Pinus coulteri	—	—	—	90	8	3.0	52	41	15.5
Abies magnifica	—	—	—	—	—	—	44	52	18.0
Libocedrus decurrens	20	1	0.5	—	—	—	29	73	6.0
Sequoia washingtoniana	—	—	—	—	—	—	16	18	7.0
Tsuga heterophylla	—	—	—	—	—	—	66	01	0.5
Picea sitkensis	—	—	—	—	—	—	22	60	22.5
Larix occidentalis	—	—	—	—	—	—	—	—	—
Pseudotsuga taxifolia	—	—	—	—	—	—	22	28	6.0

CLASSIFICATION OF SPECIES BASED UPON THE EFFECT OF *Soil Moisture* UPON GERMINATION

Xerophilous Species	Xero-mesophilous Species	Mesophilous Species
	Eastern Hardwoods	
Robinia pseudacacia	*Catalpa speciosa* (Neb.)	*Catalpa speciosa* (Ind.)
Acer rubrum		*Quercus rubra*
		Betula papyrifera
	Eastern Conifers	
Pinus divaricata		
Pinus divaricata (F. S.)	*Pinus palustris*	
	Abies balsamea	
Pinus resinosa	*Pinus strobus*	*Pinus taeda*
	Rocky Mountain Species	
Pinus ponderosa (S. D.)	*Abies concolor*	
Pinus ponderosa (N. M.)	*Abies grandis*	
Pinus ponderosa (H.)	*Abies lasiocarpa*	
Pinus ponderosa (Id.)	*Pinus contorta*	
Pseudotsuga taxifolia (N. M.)	*Pseudotsuga taxifolia* (Mon.)	
Pseudotsuga taxifolia (Id.)		
Pseudotsuga taxifolia (Colo.)	*Pinus ponderosa* (Mon.)	
Pinus monticola		
	Pacific Coast Species	
Libocedrus decurrens	*Pinus ponderosa* (Calif.)	*Tsuga heterophylla*
	Pinus jeffreyi	*Picea sitkensis*
	Pinus coulteri	*Pseudotsuga taxifolia* (Wash.)
		Pinus lambertiana
		Abies magnifica
		Sequoia washingtoniana

In Table VI in every case where conclusions were possible it was noted that the beginning of germination was delayed and the germination period was shortened with the decrease of soil moisture. In every case the germination per cent. was highest in the wet soil culture.

For some unaccountable reason *Libocedrus decurrens* germinated in the very dry and wet cultures but not in the medium wet one. However, the four drought resistant species stand out

conspicuously: *Pinus ponderosa, Pinus jeffreyi, Pinus coulteri,* and *Libocedrus decurrens.* This table shows that the Pacific coast species are predominantly moisture-loving.

The foregoing table is a classification of all species used in the soil moisture experiments upon the basis of whether they germinated in all three soil moisture cultures, in two of them or in only one of them. These three groups are called by the terms xerophilous, xero-mesophilous, and mesophilous. Xerophilous species are those that germinated in all three cultures; xero-mesophilous species are those that germinated in the medium wet and the wet soil cultures; and mesophilous species are those that germinated only in the wet soil culture.

TABLE VII

THE EFFECT OF *Soil Texture* ON GERMINATION

Eastern Species

Species	Loam			Sand			Gravel		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus strobus	22	50	10.7	18	34	11.0	34	38	7.0
Pinus divaricata	12	32	54.5	12	38	72.0	10	40	45.5
Pinus divaricata (F. S.)	14	20	39.5	16	18	32.5	16	18	28.0
Pinus resinosa	24	16	30.5	20	54	85.0	16	8	16.5
Pinus palustris	31	53	10.5	26	54	12.5	22	62	9.5
Pinus taeda	34	6	19.0	28	12	41.0	40	1	1.0
Abies balsamea	18	30	11.0	14	34	18.5	16	40	7.0
Catalpa speciosa	18	1	1.0	0	0	0.0	0	0	0.0
Catalpa speciosa (Neb.)	16	12	91.0	16	12	92.0	16	1	9.0
Quercus rubra	40	28	28.0	38	46	24.0	30	54	16.0
Robinia pseudacacia	8	16	28.8	8	18	39.5	8	18	11.5
Betula papyrifera	34	1	1.0	34	1	3.0	34	1	0.5
Acer rubrum	18	30	17.0	24	18	13.0	18	8	8.0
Gleditschia triacanthos	0	0	0.0	34	1	1.0	0	0	0.0

Tables VII, VIII, and IX show the effect of soil texture upon the same species.

Table VII shows that for the 12 species considered in the final results only one germinated first in the loam culture. Three germinated simultaneously in all cultures, three first in the sand, and four germinated first in the gravel. Three species had the longest germination period in loam, two in sand and 5 in gravel.

THE EFFECT OF *Soil Texture* UPON GERMINATION

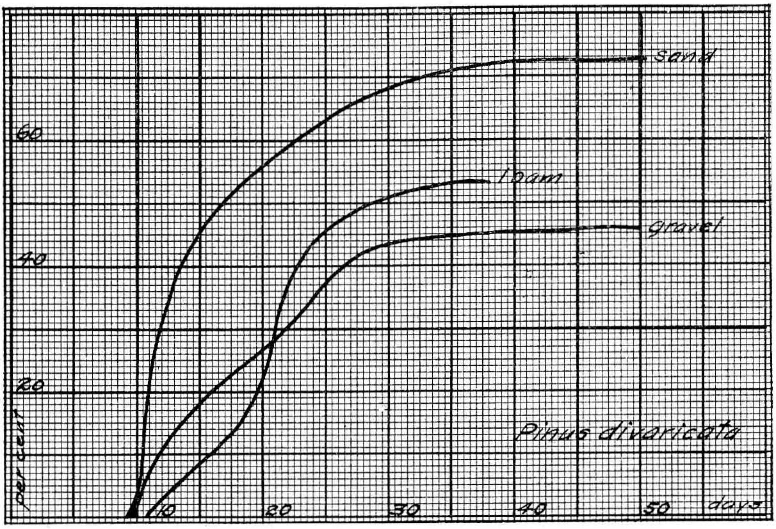

FIG. 1. The germination curves of *Pinus divaricata*.

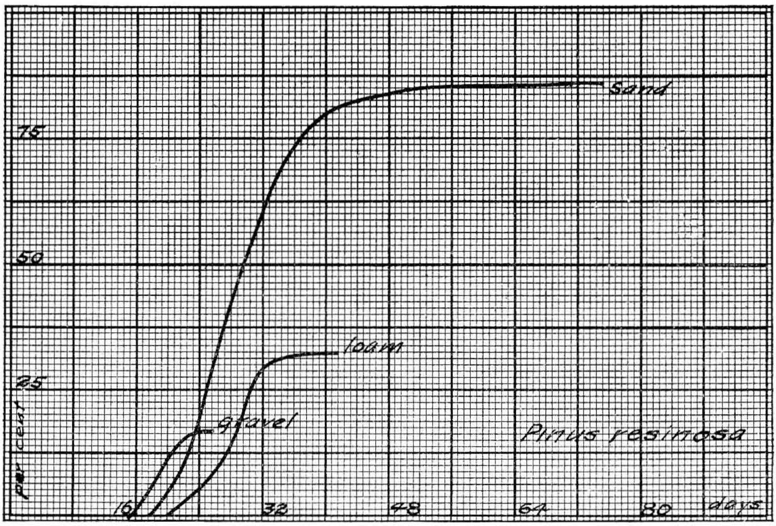

FIG. 2. The germination curves of *Pinus resinosa*.

The two species that stand out as having the greatest germination per cent. in the loam are *Quercus rubra* and *Acer rubrum*. Nine species reached their highest germination per cents. in the sand and in this group the following stand out most conspicuously: *Pinus divaricata, Pinus resinosa, Pinus palustris, Pinus taeda,* and *Robinia pseudacacia*. Being species of sandy habitats it is quite easy to see why they should germinate better in the sand. In the gravel, which is a poor moisture retainer, it is interesting to compare such a drought enduring species like *Pinus divaricata* and such a moisture-loving species like *Pinus taeda*.

On page 50 are given the curves for *Pinus divaricata* and *Pinus resinosa*.

TABLE VIII

THE EFFECT OF *Soil Texture* ON GERMINATION

Rocky Mountain Species

Species	State	Loam			Sand			Gravel		
		Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa	S.D.	10	32	58.0	8	20	57.5	8	38	44.0
Pinus ponderosa	Harney	14	14	52.0	14	26	45.0	14	8	13.0
Pinus ponderosa	N.M.	14	40	56.0	10	26	71.5	12	12	57.5
Pseudotsuga taxifolia	N.M.	12	26	63.0	10	22	70.5	10	14	63.5
Pseudotsuga taxifolia	Colo.	12	42	91.0	10	38	83.5	10	44	80.0
Abies concolor	Colo.	24	50	38.0	18	66	51.0	20	48	34.0
Pinus contorta	Colo.	14	80	22.0	20	66	19.5	16	70	40.5
Pinus ponderosa	Mon.	18	12	10.0	18	48	11.0	18	1	4.0
Pseudotsuga taxifolia	Mon.	14	34	20.5	12	44	43.0	12	42	44.5
Pseudotsuga taxifolia	Idaho	18	30	20.5	20	54	11.0	16	70	43.0
Pinus ponderosa	Idaho	36	52	43.0	44	52	59.0	20	78	71.0
Abies grandis	Idaho	36	36	4.0	46	6	2.0	36	36	3.0
Abies lasiocarpa	Idaho	30	30	6.0	0	0	0	0	0	0
Pinus monticola	Idaho	24	50	22.5	24	50	11.5	24	50	13.5

Table VIII gives the results for the Rocky Mountain species. Out of 13 species, 8 germinated first in sand or in gravel, only one germinated first in loam, and four germinated simultaneously in loam and in sand or gravel. Eight species show a longer period of germination in sand or gravel than in loam, and 5 species show the same length of period in either sand or gravel and in loam. Six species show a higher germination per cent. in

THE EFFECT OF *Soil Texture* UPON GERMINATION

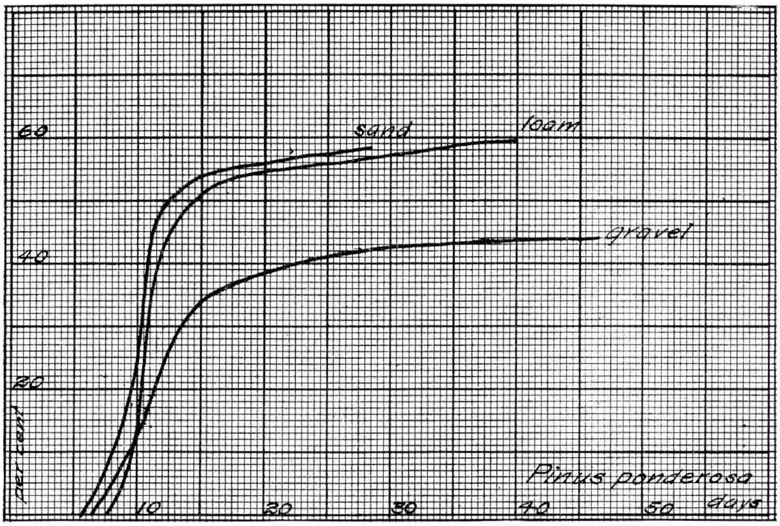

FIG. 1. The germination curves of *Pinus ponderosa* (S. D.).

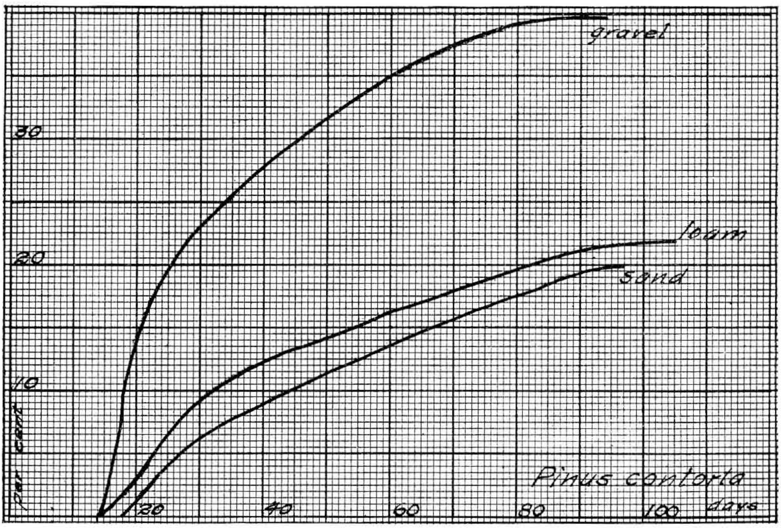

FIG. 2. The germination curves of *Pinus contorta.*

THE EFFECT OF *Soil Texture* UPON GERMINATION

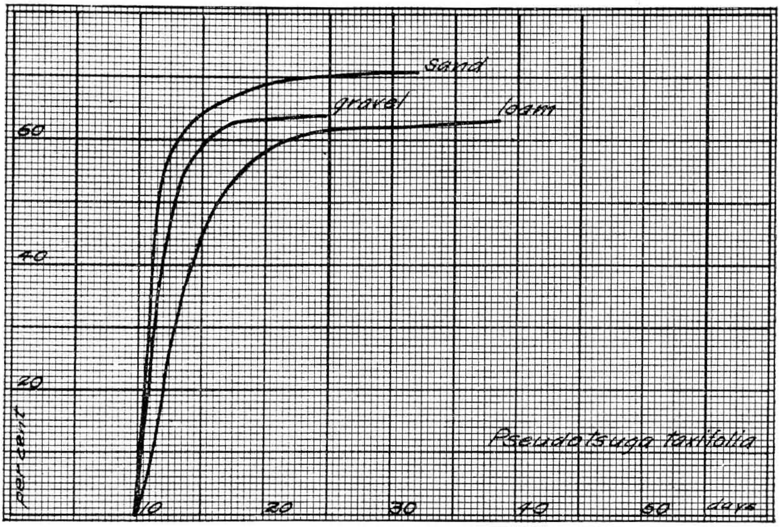

FIG. 1. The germination curves of *Pseudotsuga taxifolia* (N. M.).

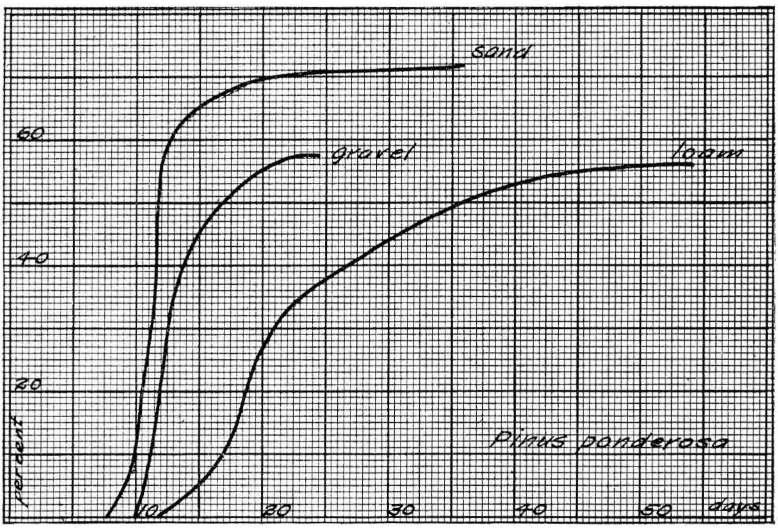

FIG. 2. The germination curves of *Pinus ponderosa* (N. M.).

loam, four in sand, and four in gravel. It is significant to note the large number of species in this table that germinate well in the gravel.

On pages 52 and 53 are given the germination curves of *Pinus ponderosa* (S. D.), *Pinus contorta, Pseudotsuga taxifolia* (N. M.) and *Pinus ponderosa* (N. M.). These curves show that the germination usually begins earlier in the sand or gravel, that the curve rises more rapidly for these soils and that the germination per cent. is usually higher.

Table IX gives the results for the Pacific coast species. Out of 9 species, two germinated first in the loam, the others germinated first in either the sand or gravel. Three had longest germination periods in the loam and six in either the sand or the gravel. Only one species, *Libocedrus decurrens,* showed the highest germination per cent. in the gravel, while six species germinated highest in the sand.

On page 55 are given the germination curves of *Pinus ponderosa* and *Pinus jeffreyi* both from California. These curves show substantially the same facts as those for the Rocky Mountain species. These curves show that *Pinus ponderosa* does not germinate so well on gravel as does *Pinus jeffreyi* a fact which is significant when it is remembered that the latter will grow on much poorer soil than the former.

TABLE IX

THE EFFECT OF *Soil Texture* ON GERMINATION

Pacific Coast Species

Species	Loam			Sand			Gravel		
	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent	Began, Days	Period, Days	Final, Per Cent
Pinus ponderosa (Calif.)	42	67	61.0	20	82	68.0	30	30	17.0
Pinus jeffreyi	31	77	22.0	26	80	33.0	20	86	19.0
Pinus lambertiana	70	36	2.5	52	16	9.0	80	18	9.0
Abies magnifica	44	52	18.0	96	2	3.0	50	48	5.0
Libocedrus decurrens	29	73	6.0	28	58	13.5	28	68	22.0
Sequoia washingtoniana	16	18	7.0	16	24	16.5	22	1	0.5
Tsuga heterophylla	66	1	0.5	44	42	3.0	56	8	1.5
Picea sitkensis	22	60	22.5	18	64	31.0	18	64	24.5
Larix occidentalis	—	—	—	—	—	—	—	—	—
Pseudotsuga taxifolia	22	28	6.0	38	44	5.0	36	48	6.0

THE EFFECT OF *Soil Texture* UPON GERMINATION

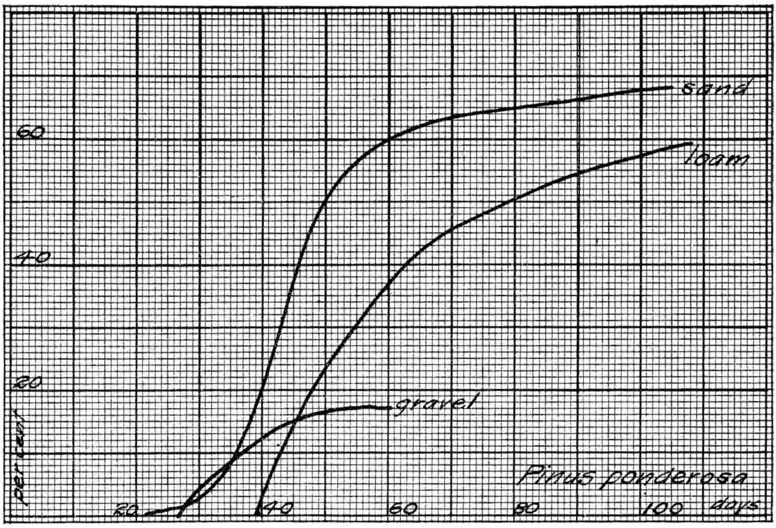

FIG. 1. The germination curves of *Pinus ponderosa* (Calif.).

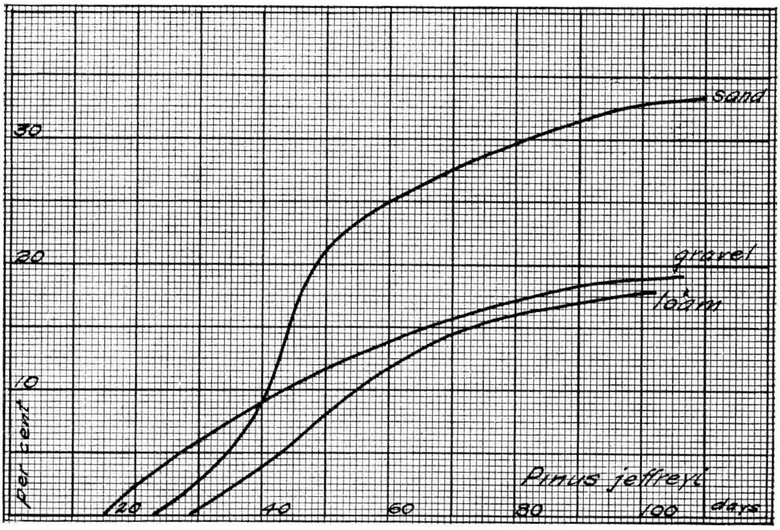

FIG. 2. The germination curves of *Pinus jeffreyi*.

Tables X, XI, and XII give the results of the effect of light, soil moisture, and soil texture upon certain groups of species as they were classified on page 48. While the foregoing tables group the species and the final results on the basis of the geographical distribution of the species, these tables divide all species into three groups based upon the amount of soil moisture necessary for germination. The tabulation of the final data on this basis is probably more significant than any other that could be offered.

The data for the xerophilous species are given in Table X. The average figures given at the bottom of the table show that germination begins first in the dense shade, next in the medium shade, and last in the light; that the germination period is longest in the dense shade; that germination begins last in the dry soil; that the germination period is shortest in the dry soil; that germination begins first in the gravel and that the shortest germination period is in the loam and gravel. Of the 14 species given in this table, 13 germinated in the dense shade before they did in the open, 9 showed longer germination periods in the dense shade than in the open light, 12 germinated in wet soil before they did in dry soil, 13 had shorter germination periods in the dry soil than in the wet, and 9 germinated in gravel before they did in loam.

Table XI gives the results for the xero-mesophilous species. The average figures given in this table show that germination begins first in dense shade, next in medium shade, and last in open light; that the germination periods are longest in the medium and dense shade; that germination begins last in the medium dry soil; that the germination period is shortest in the medium dry soil; that germination begins first in the sand or in the gravel; and that the germination period is shortest in the gravel. Out of 13 species listed in this table 9 germinated in dense shade before they did in the open, 7 showed longer germination periods in the dense shade than in the open light, 12 germinated in the wet soil before they did in the medium dry soil, 12 showed shorter germination periods in the dry soil and 9 out of 11 germinated first in either sand or gravel.

The data for the mesophilous species are given in Table XII. The average figures at the bottom of the table show that germination began in dense shade, followed by medium shade and open light; that the germination period is longest in the case of the dense shade; that germination began first in the loam and last in the gravel; and that the germination period was shortest in loam. Out of the 10 species listed in this table 7 germinated in the dense shade before they did in the open light, 4 out of 8 species showed longer germination period in the dense shade than in the open light; and 7 showed shorter germination periods in the loam and sand than in the gravel.

These three groups show exactly the same results so far as light and soil moisture go. From the standpoint of soil texture there are some interesting results. In the xerophilous species germination usually begins in the gravel, in the xero-mesophilous species it usually begins in the sand; and in the mesophilous species it usually begins in the loam, as the average figures and number of species in each case testify. In the xerophilous species the germination period is shortest in the loam and gravel, in the xero-mesophilous it is shortest in the gravel, and in the mesophilous species the period is shortest in the loam. That xerophilous species germinate sooner in the sand and gravel than in the loam is due undoubtedly to the amount of oxygen in these soils. This suggests that oxygen is more necessary for the germination of xerophilous species than is the case in mesophilous ones. In the mesophilous species germination begins sooner in the loam indicating that soil moisture is more necessary to them than oxygen. In the case of the light and the soil moisture experiments it has been shown that favorable moisture conditions lengthen the time of germination. In these cases it was found that the shortest periods were in the open light and in the dry soil. This same theory is proven in the case of the soil texture experiments. It is well known that loam is favorable for germination on account of its moisture-retaining properties and that gravel is favorable on account of its great amount of aeration. Sand is intermediate between these and combines enough of the soil moisture property of the loam with the aeration of the gravel

TABLE X

THE EFFECT OF *Light, Soil Moisture,* AND *Soil Texture* ON THE GERMINATION OF *Xerophilous* SPECIES

Species	Light						Soil Moisture						Soil Texture			
	Check Culture		Medium Shade		Dense Shade		Dry Soil		Medium Wet Soil		Check Culture		Sand		Gravel	
	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days
Pinus divaricata..........	12	32	10	26	10	38	40	24	14	50	12	32	12	38	10	40
Pinus divaricata (F. S.)	14	20	14	26	10	24	28	12	22	18	14	20	16	18	16	18
Pinus resinosa...........	24	16	16	24	14	14	68	1	24	40	24	16	20	54	16	8
Acer rubrum.............	18	30	16	34	14	34	24	1	24	26	18	30	24	18	18	8
Robinia pseudacacia.......	8	16	6	18	6	18	10	30	8	32	8	16	8	18	8	18
Pinus ponderosa (S. D.) ...	10	32	10	22	10	34	26	26	12	36	10	32	8	20	8	38
Pinus ponderosa (Harney)..	14	14	8	26	8	26	34	6	22	18	14	14	14	26	14	8
Pinus ponderosa (N. M.)...	14	40	12	32	10	12	22	18	20	16	14	40	10	26	12	12
Pseudotsuga taxifolia (N. M.)	12	26	10	12	10	16	12	6	12	44	12	26	10	22	10	14
Pinus ponderosa (Id.)......	36	52	24	66	14	82	90	8	14	72	36	52	44	52	20	78
Pseudotsuga taxifolia (Id.)..	18	30	16	64	10	64	24	1	20	32	18	30	20	54	16	70
Pseudotsuga taxifolia (Colo.)	12	42	12	36	8	36	14	24	12	42	12	42	10	38	10	44
Pinus monticola (Id.)......	24	50	16	58	14	60	48	1	18	38	24	50	24	50	24	50
Libocedrus decurrens.......	29	73	24	18	16	52	20	1	0	0	29	73	28	58	28	68
Averages...............	17.5	33.7	13.8	33.0	11.0	36.4	33.0	11.4	17.0	36.0	17.5	33.8	17.7	35.0	15.0	33.8

TABLE XI

THE EFFECT OF *Light, Soil Moisture,* AND *Soil Texture* ON THE GERMINATION OF *Xero-mesophilous* SPECIES

Species	Light						Soil Moisture				Soil Texture			
	Check Culture		Medium Shade		Dense Shade		Medium Wet Soil		Check Culture		Sand		Gravel	
	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days
Pinus strobus	22	50	16	54	14	26	30	34	22	50	18	34	34	38
Pinus palustris	31	53	32	82	32	62	36	50	31	53	26	54	22	62
Abies balsamea	18	30	18	38	18	36	22	22	18	30	14	34	16	40
Catalpa speciosa (Neb.)	16	12	14	20	14	14	22	6	16	12	16	12	16	1
Abies concolor	24	50	18	54	14	60	80	26	24	50	18	66	20	48
Pinus contorta	14	80	16	70	14	72	20	66	14	80	20	66	16	70
Pseudotsuga taxifolia (Mon.)	14	34	12	32	12	44	18	26	14	34	12	44	12	42
Pinus ponderosa (Mon.)	18	12	18	54	10	8	18	58	18	12	18	48	18	1
Abies grandis	36	36	22	62	22	60	66	10	36	36	46	6	36	36
Abies lasiocarpa	30	30	26	50	22	28	84	1	30	30	—	—	—	—
Pinus ponderosa (Calif.)	42	67	22	92	22	62	68	12	42	67	20	82	30	30
Pinus jeffreyi	31	77	22	84	20	54	80	6	31	77	26	80	20	86
Pinus coulteri	52	41	54	30	52	62	90	8	52	41	—	—	—	—
Averages	26.7	44.0	22.3	55.5	20.4	45.2	48.8	25.0	26.7	44.0	21.3	48.0	21.8	41.3

so as to make it an ideal soil for germination. Hence we might expect to find the longest germination periods in the sand. The average figures show that this is the case in each group of species. The shortest periods in every case are either in the loam or the gravel because loam is unfavorable from one standpoint and gravel from another.

In comparing the check cultures of the three groups of species it will be seen that xerophilous species germinate first, xero-mesophilous next, and mesophilous last. In other words the drier the habitat the sooner germination starts, granting that the conditions are favorable.

TABLE XII

THE EFFECT OF *Light* AND *Soil Texture* ON THE GERMINATION OF *Mesophilous* SPECIES

Species	Light						Soil Texture					
	Check Culture		Medium Shade		Dense Shade		Check Culture		Sand		Gravel	
	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days	Began, Days	Period, Days
Pinus taeda	34	6	34	6	32	8	34	6	28	12	40	1
Catalpa speciosa (Ind.)	18	1	0	0	16	1	18	1	0	0	0	0
Quercus rubra	40	28	30	18	26	42	40	28	38	46	30	54
Betula papyrifera	34	1	34	1	34	1	34	1	34	1	34	1
Pinus lambertiana	70	36	76	20	70	24	70	36	52	16	80	18
Abies magnifica	44	52	24	54	36	54	44	52	96	2	50	48
Sequoia washingtoniana	16	18	16	6	14	14	16	18	16	24	22	1
Tsuga heterophylla	66	1	0	0	0	0	66	1	44	42	56	8
Picea sitkensis	22	60	18	64	14	36	22	60	18	64	18	64
Pseudotsuga taxifolia (Wash.)	22	28	22	54	14	62	22	28	38	44	36	48
Averages[2]	35.9	28.6	31.7	27.9	30.0	30.1	38.7	25.5	40.4	27.9	40.7	27.0

Tables similar to X, XI, and XII were constructed showing the effect of these habitat factors upon the germination per cent. of the species. This table is not given but the most significant facts which it shows are given here and in a later table. It is interesting to note that of the 37 species used in the experiments the highest

[2] *Catalpa speciosa* and *Tsuga heterophylla* not included in averages of light cultures. *Catalpa speciosa* not included in soil-texture averages.

germination per cent. did not always occur under the influence of the same conditions. Considering all factors and all degrees of these factors the highest germination per cents. occurred as follows:

In open light	3
In medium shade	7
In dense shade	11
In sand	12
In gravel	4
Total	37

The distribution of these species in the three groups as determined by soil moisture is not significant. The only interesting fact to be found is that no mesophilous species germinated highest in the gravel.

TABLE XIII

SUMMARY OF THE *Beginning of Germination* BY NUMBER OF SPECIES

Light

Germinated First in	Number of Species			Total
	Xerophilous	Xero-meso-philous	Mesophilous	
Open light	0.33	2.33	0.50	3.17
Medium shade	2.33	2.33	1.00	5.67
Dense shade	11.34	8.33	5.50	25.16
Total	14.00	13.00	7.00	34.00
Soil Moisture				
Dry soil	1.33	....	....	1.33
Medium wet soil	3.83	0.50	....	4.33
Wet soil	8.83	12.50	....	21.34
Total	14.00	13.00	....	27.00
Soil Texture				
Loam	2.50	2.17	2.50	7.17
Sand	4.00	5.17	3.00	12.17
Gravel	7.50	3.66	1.50	12.66
Total	14.00	11.00	7.00	32.00

Tables XIII, XIV, and XV take the same data as presented in previous tables but the results are given by number of species rather than by average numbers. The number of species in each group which performed certain things under certain conditions are given without respect to the name of the species. This is perhaps a better way of drawing conclusions than to use average figures. Each species is counted in its proper column; if a species, for example, germinated simultaneously in two cultures it counted one half in each column.

TABLE XIV

SUMMARY OF THE *Length of the Germination Period* BY NUMBER OF SPECIES

Shortest Germination Period in	Number of Species			Total
	Xerophilous	Xeromeso-philous	Mesophilous	
Light				
Open light	7.00	5.00	2.50	14.50
Medium shade	4.50	3.00	3.50	11.00
Dense shade	2.50	5.00	1.00	8.50
Total	14.00	13.00	7.00	34.00
Soil Moisture				
Dry soil	12.00	....	....	12.00
Medium dry soil	1.00	12.00	....	13.00
Wet soil	1.00	1.00	....	2.00
Total	14.00	13.00	....	27.00
Soil Texture				
Loam	3.83	4.00	3.00	10.83
Sand	4.33	3.00	2.00	9.33
Gravel	5.83	4.00	2.00	11.83
Total	14.00	11.00	7.00	32.00

Out of 34 species 31 germinated first in either of the two shade cultures and only 3 began their germination in the open light. The tendency to germinate first in the shade is more marked in the case of the xerophilous and the mesophilous species and less marked in the xero-mesophilous. Out of 27 species,

over 21 germinated first in the wet soil. In both the xerophilous and the xero-mesophilous species the tendency is to germinate first in the wet soil. In the experiments on soil texture the tendency is for the xerophilous species to germinate first in the gravel and sand, for the xero-mesophilous to germinate first in the sand, and for the mesophilous species to germinate first in the sand and loam. This is a most interesting result, in view of the moisture and air conditions in these soils. On the whole the tendency is for most of the species to begin germinating in the sand and gravel; about 25 out of 32 species began germinating in either of these two kinds of soils. In the soil texture data it is interesting to compare the germination of xerophilous and mesophilous species in the gravel. Such a comparison shows 7.50 xerophilous species germinated first in the gravel and only 1.50 mesophilous species.

From Table XIV it is apparent that out of 34 species 14.5 showed the shortest germination period in open light and that the number of species of this kind decreases as the intensity of the light decreases. In other words shade increases the length of the germination period. In the soil moisture experiments the shortest periods were in 25 species out of 27 found in the dry or the medium wet soil. In the soil texture experiment the species are very evenly distributed. Loam and gravel, the two extreme soils from the standpoint of soil moisture and soil aeration, show the greatest number of species and the sand culture shows the least. This fact is in harmony with the idea that favorable conditions, such as we found in the light and the soil moisture experiments, lengthen the period of germination.

Table XV shows that out of 14 drought-enduring species 12 reached their greatest germination per cent. in the shade; out of 13 xero-mesophilous species 10 reached their highest per cent. in the shade; and out of 8 mesophilous species 7 reached their highest per cent. in the shade cultures. Out of a total of 35 species, 29 germinated highest in the shade cultures. Out of 27 species tried in the soil moisture experiments 23 germinated highest in the wet soil and 4 highest in the medium soil. None reached their highest per cent. in the dry soil cultures. Among

the xerophilous species the highest per cents. are in the loam and sand, among the xero-mesophilous species the highest per cents. are in the sand while in the mesophilous species the highest per cents. are in the sand and loam. Out of 34 species, 18.5 germinated highest in the sand, thus showing the value of this class of soil for seed germination.

TABLE XV

SUMMARY OF THE *Final Germination Per Cent.* BY NUMBER OF SPECIES.

Greatest Germination Per Cent in	Number of Species			Total
	Xerophilous	Xeromesophilous	Mesophilous	
Light				
Open light	2.00	3.00	1.00	6.00
Medium shade	3.00	7.00	2.50	12.50
Dense shade	9.00	3.00	4.50	16.50
Total	14.00	13.00	8.00	35.00
Soil Moisture				
Dry soil	0.00	....	....	0.00
Medium wet soil	3.00	1.00	....	4.00
Wet soil	11.00	12.00	....	23.00
Total	14.00	13.00	....	27.00
Soil Texture				
Loam	6.00	1.00	2.50	9.50
Sand	5.00	8.00	5.50	18.50
Gravel	3.00	2.00	1.00	6.00
Total	14.00	11.00	9.00	34.00

THE EFFECT OF HABITAT FACTORS UPON STEM AND ROOT DEVELOPMENT

Following the experiments upon germination, some of the species were grown for several months for the purpose of obtaining root and stem measurements. Since damping-off reduced materially the number of seedlings as time went on, the number of plants upon which final measurements could be taken was naturally reduced. Hence the results are not based upon as many measurements as was originally intended.

The species retained for this work were *Pinus ponderosa* (S. D.), *Robinia pseudacacia, Quercus rubra,* and *Pinus strobus.* Stem and root measurements were taken upon the first three of these species and stem measurements only upon the last one. Each measurement represents the average of 10 representative plants, except in case of *Quercus rubra* where from 3 to 14 plants were used depending upon the number available. The measurements of the stems of *Pinus ponderosa* and *Robinia pseudacacia* were taken at two different ages, namely at the age of two and three months, but the plants used at the age of three months were not the same ones used at the end of two months. Hence in the data the three months' old plants are not necessarily larger than the two months' old plants, although they usually are. Root measurements of *Pinus ponderosa* and *Robinia pseudacacia* were taken at the end of three months. Both stem and root measurements for *Quercus rubra* were taken at the age of five months.

The effect of light on stem and root development is shown in the following table:

THE EFFECT OF *Light* ON STEM AND ROOT DEVELOPMENT

Conifers

Degrees	Stem Measurements			Root Measurements	
	P. ponderosa		*P. strobus*	*P. ponderosa* (3 Mos.)	
	2 Mos., Cm.	3 Mos., Cm.	2 Mos., Cm.	Tap, Cm.	Laterals, Cm.
Open light	2.76	2.59	4.31	5.93	1.11
Medium shade	2.90	3.13	5.50	5.80	.62
Dense shade	3.50	...	6.35	...	...

Hardwoods

Degrees	Stem Measurements			Root Measurements (Tap)	
	R. pseudacacia		*Q. rubra*	*Rob. pseud.*	*Q. rubra*
	2 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.
Open light	6.00	7.02	9.40	9.64	13.8
Medium shade	5.80	5.95	7.30	7.16	10.2
Dense shade	5.00	5.52	8.00	5.69	10.2

From these tables it will be seen that *Pinus ponderosa* increases its length of stem with a decrease in light intensity both at the age of two and at three months. This is likewise true for *Pinus strobus*. For *Robinia pseudacacia*, however, both at the age of two and three months, there is a striking decrease in stem height with a decrease in light intensity. *Quercus rubra* behaves the same way, except that the length of stem is greater in the medium shade than in the dense shade. This development is shown very well by the accompanying photographs.

In the case of all species it is strikingly shown that the length of the tap root and the total length of the laterals decrease with decrease in light intensity.

In so far as the stem and its relation to light is concerned it is quite evident that hardwoods behave differently from conifers. As has been pointed out conifers tend to increase their height growth with decrease in light intensity while hardwoods tend to decrease this growth with decrease in light intensity. Evidently conifers can adapt themselves to these unfavorable light conditions better than hardwoods. In the hardwoods the reciprocal relation of roots and stem in their dependence upon light is strikingly shown.

THE EFFECT OF *Soil Depth* UPON STEM AND ROOT DEVELOPMENT

Conifers

Degrees Soil Depth	Stem Measurements			Root Measurements	
	Pinus pond.		*P. strobus*	*P. ponderosa* (3 Mos.)	
	2 Mos., Cm.	3 Mos., Cm.	2 Mos., Cm.	Tap, Cm.	Laterals, Cm.
Deep	2.85	2.69	4.35	9.51	.47
Medium	2.76	2.59	4.31	5.93	1.11
Shallow	2.60	2.68	4.25	3.97	4.61

Hardwoods

Degrees Soil Depth	Stem Measurements			Root Measurements (Tap)	
	R. pseudacacia		*Q. rubra*	*Rob. pseud.*	*Q. rubra*
	2 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.
Deep	6.45	7.20	6.50	15.55	20.4
Medium	6.00	7.02	9.40	9.64	13.8
Shallow	5.70	6.04	5.90	3.30	6.9

The foregoing tables show the effect of soil depth upon root and stem development for the same species and ages of stock.

In the case of stem development in all species except *Quercus rubra,* the height of the stem increases with increase in soil depth. The increase in length between the deep soil and the shallow soil is not very great, *i. e.,* in the pines it is never over 0.25 cm. and in *Robinia* it is never over 1.16 cm. In *Quercus rubra* the smallest height growth is in the shallow soil but the greatest height growth is in the medium deep soil. It is interesting to note that in all cases the greatest total length of stem and root together is in the plants grown in deep soil.

As is to be expected the length of the tap root is materially decreased as the soil depth decreases. In *Pinus ponderosa* the tap root is 2½ times longer, in *Robinia* it is 5 times longer and in *Quercus* it is 3 times longer in the case of the deep soil than in the shallow soil. The length of lateral roots was taken only in the case of *Pinus ponderosa* and this species is representative of what took place in all the other species. In this species the total length of lateral roots increased with decrease in soil depth. In the case of *Robinia* this is strikingly shown in the photographs. This indicates that whether a tree has deep-seated roots or superficial roots depends largely upon the depth of the soil in which the tree grows. The terms "deep-rooted species" and "shallow-rooted species" have therefore only limited significance and the real basis for these terms is in most cases the environment.

In the following table are given the data upon the effect of soil moisture upon root and stem development:

THE EFFECT OF *Soil Moisture* UPON STEM AND ROOT DEVELOPMENT
Conifers and Hardwoods

Degrees	Stem Measurements					Root Measurements[3]		
	Pinus ponderosa		*Robinia pseud.*		*P. strobus*	*P. pond.*		*R. pseud.*
	2 Mos., Cm.	3 Mos., Cm.	2 Mos., Cm.	3 Mos., Cm.	2 Mos., Cm.	Tap, Cm.	Lat., Cm.	Tap, Cm.
Dry	..	..	2.60	..	..	..	..	6.00[4]
Medium	1.80	2.02	4.35	3.80	3.90	7.33	2.65	7.54
Wet	2.76	2.59	6.00	7.02	4.31	5.93	1.11	9.64

[3] Age, 3 months.

[4] Age, 2 months.

In connection with the soil moisture experiments a very interesting fact was noted. Both *Pinus ponderosa* and *Robinia pseudacacia* wilted on January 1, just exactly two months after the seeds were sown. The soil moisture at the time was determined to be 6.6 per cent. It happens that at three different times the moisture content was far below this figure. On October 28 the seeds were sown, on November 7 the moisture content was 4 per cent., on the 11th it was 4.6 per cent. and again on December 5 it fell to 6.1 per cent. *Robinia pseudacacia* germinated first on November 9 and the *Pinus ponderosa* on November 26. It is evident from this occurrence that more moisture is needed for the early development of the seedlings than is necessary for germination. On the 9th of January this fact was further emphasized. While taking root and stem measurements and digging up the seedlings two germinating seeds of *Robinia* were found. The moisture samples taken on this day show 5.7 per cent. moisture in the dry culture. As a result of this condition no stem and root measurements appear in the dry column at the age of three months.

In all species measured the length of the stem decreases with diminishing moisture supply and the fact is noted that this decrease is greater in the case of *Robinia* than it is in the case of *Pinus ponderosa* or *Pinus strobus*. This indicates the greater drought resistance of the conifers as compared to the hardwoods.

In the case of the root development of *Pinus ponderosa* it is shown that both the tap root and the total length of lateral roots increase with diminishing moisture supply. For *Robinia* the result was quite different, for it was found that the length of the tap root decreases with diminishing moisture. While *Pinus ponderosa* seems to be able to develop roots to reach the lower moisture layers of soil, *Robinia* is unable to do this.

The following table gives the results on the effect of soil texture upon the development of the stem and roots of these species.

The greatest length of stem in *Pinus ponderosa* was found to be in the case of the two-months-old seedlings in the loam and the next greatest length in the gravel. In the case of the three-months-old trees the greatest length was in the gravel and the

next greatest in the loam. In the case of *Pinus ponderosa* clearly the greatest length is either in the loam or in the gravel and the shortest length of stem is in the sand. Loam and gravel are, as we have seen, quite opposite when it comes to moisture retentiveness, hence the good development of plants grown in gravel must be attributed to other properties of gravel, namely, the amount

THE EFFECT OF *Soil Texture* UPON STEM AND ROOT DEVELOPMENT

Conifers

Degrees	Stem Measurements			Root Measurements	
	P. ponderosa		*P. strobus*	*P. ponderosa* (3 Mos.)	
	2 Mos., Cm.	3 Mos., Cm.	2 Mos., Cm.	Tap, Cm.	Laterals, Cm.
Loam	2.76	2.59	4.31	5.93	1.11
Sand	2.15	2.06	4.80	6.22	.94
Gravel	2.65	2.70	4.10	7.83	4.01

Hardwoods

Degrees	Stem Measurements			Root Measurements (Tap)	
	R. pseudacacia		*Q. rubra*	*Rob. pseud.*	*Q. rubra*
	2 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.	3 Mos., Cm.	5 Mos., Cm.
Loam	6.00	7.02	9.40	9.64	13.80
Sand	4.75	4.75	5.90	10.85	15.70
Gravel	3.80	4.25	5.70	10.11	16.00

of air in the soil. *Pinus strobus* shows the greatest height growth in the sand. *Robinia* shows the greatest length of stem in the loam and the least in the gravel. This is in peculiar contrast to *Pinus ponderosa.* For growth *Robinia* is evidently more particular about soil moisture than about the amount of air in the soil. *Quercus rubra* shows the greatest height growth in the loam and the least in the gravel.

The tap root of *Pinus ponderosa* is of greatest length in the gravel and least in the loam, and the total length of lateral roots is greatest in the gravel. This naturally follows from the fact that, as has been pointed out before, gravel allows water to percolate rapidly and the top layers dry out very soon, hence the

plant has to go deep for its moisture. In the cases of *Robinia* and *Quercus* the greatest length of laterals and the greatest length of the tap root was found in the sand or gravel, again bearing out the fact that sands and gravels are poor soils for retaining moisture.

THE RELATION OF SIZE AND WEIGHT OF SEED TO GERMINATION PER CENT. AND EARLY DEVELOPMENT

During the process of counting between 100,000 and 125,000 seeds of various kinds for these experiments the fact that seeds of the same species varied considerably in size came to the author's notice very forcibly. In his experience in the woods as well as in seed extracting it was often noted that many factors may affect the size of seeds. In general, it may be said that the size of the seeds of any one species depends upon one or more of the following factors:

1. The size of the cone.
2. The position of the seed in the cone.
3. The development of the cone.
4. The age of the tree.
5. The physiological condition of the tree.
6. The site upon which the tree grew.
7. The climatic variety of the species.

It is an old experience that large cones produce large seeds and small cones small seeds. The seeds at the extreme base and the extreme apex of the cone are very often very much smaller than in other parts of the cone. External conditions such as temperature and moisture, may affect in no small degree the seed while it is maturing, thus retarding its morphological development. It has been observed that middle-aged trees produce the largest cones and the largest seeds, while very young or very old trees usually produce small cones and small seeds. The physiological condition of the tree may affect the size of the seed. Since seed crops are dependent upon the accumulated food in the tree, it is reasonable to suppose that a paucity of such food ma-

terial will produce smaller seeds than in cases where there is a great accumulation. It has been repeatedly shown that after a seed year the amount of accumulated food in the medullary rays and other food accumulation centers is reduced to a minimum. The site upon which the tree grew, naturally, is intimately connected with the amount of food material available for the embryo of the seed. For the same reason the climatic variety of the tree probably affects the size of the seed. At least, it is common knowledge that the California variety of *Pinus ponderosa* has seeds which may weigh from three to four times as much as those of the South Dakota variety. While most of these points remain to be proven experimentally, they have been indicated to the writer by various experiences and are put forth as interesting hypotheses awaiting experimental proof. Whatever the cause of the varying size of seeds is, it is quite evident from the amount of literature on the subject that this phenomenon has attracted considerable attention in recent years both in silviculture and agriculture.

That heavier and larger seeds furnish a better germination per cent. than light ones has been recognized for a long time by European silviculturists. The physiology of germination indicates that large seeds should succeed better, and repeated experiments by Bühler, Friedrich, Haack, Eisenmenger, and others establish this beyond much doubt. In fact forestry practice throughout Europe and especially in Prussia shows that smaller seeds produce fewer plants per hectare than larger ones in broadcast sowing. Favorable and unfavorable site and season conditions produce far less variation in the final results in cases where heavy seeds are sowed.

In 1904 Blumer (22) conducted at the seed laboratory of the United States Department of Agriculture a series of tests upon certain American species of tree seeds. *Pinus ponderosa* from the Rocky Mountains and *Pinus divaricata* showed the highest germination but *Pinus ponderosa* from Oregon germinated exceedingly slowly, a feature which also characterized *Pseudotsuga taxifolia* from the Pacific Coast. He noted great variation in the number of seeds per pound for the same species, especially

for *Pinus ponderosa*. In the case of this species the difference was often as much as 100 per cent.; usually the difference in other species did not exceed 50 per cent. Schotte (23), of the Swedish Forest Experiment Station, has shown that the size of the seed and the size of the cones decrease with increasing age of the tree in the case of Scotch pine. The work (24) done on seeds by certain forest experiment stations in Europe in 1907 with spruce showed that seeds from large cones germinate earlier than those from small cones; that the largest cones produce the largest and heaviest seeds and hence the largest plants; and that the effect of the size of seed upon the life of the plant has been noticed only in the first two years of its growth.

In Busse's (25) experiments pine seeds were graded by means of a Kayser centrifuge into three grades according to weight. The heaviest seed made up 68 per cent. of the stock seed, the medium weight seed 27 per cent. and the light seed 5 per cent. He recommended the first grade for field sowing but said that the third grade should not be used. Sprout tests did not show any differences in germination results. Centgraf (26) examined 247 tests of pine seed as to the relation of the weight of 1,000 grains to their germination. He failed to find a relation between weight and germinative energy or germination per cent. In fact he found that the heavier seed averaged a smaller germination per cent. than the light ones. He concluded that the slower germination of big seed is probably due to a thicker seed coat of the heavier seed which determines in part its weight and which takes up water more slowly than thin coats of light seed. Some of these results do not agree with the many experiments made by foresters in Europe. These tests being made for commercial purposes cannot therefore be taken as conclusive.

While the size and weight of seed has been recognized as a factor in germination it also has been recognized as a factor in the early development of the seedling as has been indicated in a few instances above. One finds statements in regard to this relation quite common in silvicultural works but very little material to substantiate these opinions. The view held by many writers is summarized very well by Schlich in his *Manual of Forestry* (27):

In the case of one and the same species large, heavy seed are better than light ones. The former generally possess a greater power of germination and the resulting seedlings show a greater power of resistance against injurious external influences and a more vigorous development which in many species is due to the greater quantity of reserve food materials deposited in the seed. This superiority at the first start should not be underestimated because it is recognizable long after the seedling stage has been passed. In many cases the dominant trees grow out of the seedlings which had the better start.

The relation of size and weight of seed to germination per cent. and later development has been worked out to a much greater degree of certainty in the case of agricultural and garden seeds than in the case of forest-tree seeds. These facts have already been quite firmly established in practice and already adopted as a criterion of seed values. There is no reason why weight of seed should not play as important a part in selecting forest tree seeds as well as agricultural and garden seeds in the future, as the source and germination per cent. of those seeds.

A considerable amount of work has been done by investigators upon cereals, regarding the comparative value of heavy and light seed used in planting. Most of the work has been done with wheat, oats, and barley and the preponderance of evidence is in favor of the large seed. The hypothesis upon which this work has been based was the fact that, since the weight and size of the seed determines largely the amount of food material immediately available for the plantlet at the time of germination, it is reasonable to assume that these factors might have some influence upon the life of the plant and even upon the final crop.

Early experiments by Hellriegel, Wollny, Marek, and others (28) were favorable to the view that seeds of greater size and weight generally give more vigorous plants than those smaller and lighter. Hellriegel was of the opinion that differences at maturity between the product of heavy and light seeds are intensified when the conditions are unfavorable. Hicks and Dabney (28) have made a test of the relative effects of weight upon vigor, using many kinds of seeds. In the case of radish, vetch, sweet pea, cane, Kafir corn, rye, and oats the total weight of the seedlings in each case favored the heavy seed. The differences in germination per cent. of light and heavy seed was not

conclusive. Only in the case of the corn was there a sufficient difference to warrant a conclusion in favor of the heavy seed. From the results of these experiments it seems logical to conclude that in general more vigorous growth and consequently a better stand in the field is secured by employing only the heavier seed. The effect of the size and weight of seed on production has been with no other plant so extensively studied as in the case of the wheat. The majority of results seem to favor the view that large and heavy seed are preferable. Zavitz (28) showed that the yield in bushels per acre was in favor of the large plump seed.

Trabut (32) found in the case of tobacco seeds that it was possible to affect a separation into heavy and light sorts through the capacity of these two kinds respectively to sink and float in water. It was found that the heavy seed produced plants which were greener, more vigorous, and of larger size. The yield from plants from the heavy seed was almost double that of the yield from the light seed. Shamel (31) secured results similar to these. Careful comparative tests of the light and heavy seeds of tobacco have proved that the best developed and most vigorous plants are always produced from the large, heavy seed while the light seed produce small, irregular and undesirable plants. In an experiment with Cuban tobacco seed Shamel found the germination of heavy seeds almost perfect while less than five per cent. of the light seeds sprouted. The plants from the heavy seed grew more rapidly than those from the light seed and reached the proper size for transplanting seven to nine days earlier than the plants from the light seed.

In the case of cotton seed, comparative production tests of the value of the heavy seed over the usual farm product have been made by the U. S. Department of Agriculture (30). The yields in pounds on equal areas in South Carolina show the gain from the use of heavy seed in two different cases to be 10.9 per cent. and 8.25 per cent. respectively.

Bolley (29) selected large and small grains from the same heads of wheat and found that the large grains generally produced the largest yields. Waldron (29) found that short wheat culms, shortheads, and those with a smaller number of grains

bear on the whole grains of a greater weight. Walls (37), working upon the size of the grain and the germ of corn, concludes that the heaviest grains do not necessarily have the best germinating qualities and that plants from the heaviest grains attain the greatest weight, other conditions being favorable. Concerning the size of the germ he finds that the germinating properties of the kernels containing different sizes of germs may be equal; that the largest, hardiest, and most vigorous plants come from the kernels with the large germs; and that the plants from the kernels with the largest germs withstand the drought best. He says in the selection of corn, in order to insure a good stand and a large yield none but the large germed kernels should be used.

Harris (33, 34, 35) working on the differential mortality with respect to seed weight of beans and peas secured similar results, though in a different way. In the case of peas about 1,000 seeds from each of ten early varieties were weighed and planted. In seven cases out of ten the total weights of the seeds which germinated was higher than the total weights of the seeds which did not germinate. Cummings (38) worked with numerous kinds of garden seeds. He quotes numerous investigators who worked on corn, oats, wheat, sugar beets, cotton, and beans and practically all the results show an increased yield through the use of large seeds. He himself worked with squash, pumpkin, lettuce, spinach, parsley, radishes, beans, garden peas, and sweet peas. Here too the results were almost without exception in favor of the large seeds. Not only were the resulting yields larger and heavier but in most cases the yield was earlier. In the case of the radishes the large seeds produced more uniform crops one week earlier than the small seeds. Sweet peas showed earlier blossoming, a larger total yield of blossoms and a larger number of blossoms of good quality. On the whole the permanent advantages accruing from large seeds are a larger and greater number of leaves, flowers and fruits.

Present Investigations

Having on hand several climatic varieties each of *Pinus ponderosa* and *Pseudotsuga taxifolia*, I was prepared to determine

the effect of size upon germination per cent. for many varieties of the same species. This study would also bring out some interesting relations between these varieties, as for example, correlating the size and weight of the seed with the site upon which the trees grew.

The largest and the smallest seeds were separated from the stock seed and counted, weighed, planted and carefully labelled. Of each variety of *Pinus ponderosa* 500 seeds were used except in the case of the California varieties. Due to the scant supply of these only 200 seeds of each of these were used. In the case of the *Pseudotsuga taxifolia* 200 seeds of each variety were used. After germination began counts were taken every other day. The tables below give the size of the seeds, weight of 500 seeds, the number of seeds per pound, the final germination per cent., and

Size AND *Weight of Seed* IN RELATION TO GERMINATION PER CENT.

Pinus ponderosa

Source or Variety	Size	Size, Mm.	Total Weight 500 Seeds, Gm.	Seeds Per Lb.	Final Germ, Per Cent	Per Cent in Favor of Large Seeds
South Dakota.........	Small	3–5	10.065	22,530	50.6	
	Large	5–9	20.720	11,000	53.6	3.0
Harney, N. F., S. D. ..	Small	4–6	10.845	20,900	25.0	...
	Large	6–9	20.720	11,000	40.2	15.2
Bitterroot, N. F., Mon.	Small	5–8	19.050	11,900	7.6	...
	Large	8–11	30.400	7,450	8.0	0.4
Weiser, N. F., Idaho...	Small	4–7	17.100	13,250	60.0	...
	Large	7–10	29.540	7,650	84.8	24.8
Pecos, N. F., N. M. ...	Small	4–7	16.150	14,000	65.2	...
	Large	7–9	23.470	9,650	73.4	8.2
California............	Small	7–11	35.500	6,350	63.5	...
	Large	11–14	67.000	3,385	73.5	10.0
P. jeffreyi............	Small	7–10	26.000	8,725	8.0	...
	Large	10–14	77.600	2,900	84.0	76.0

Pseudotsuga taxifolia

Source or Variety	Size	Size, Mm.	Total Weight 500 Seeds, Gm.	Seeds Per Lb.	Final Germ, Per Cent	Per Cent in Favor of Large Seeds
Caribou, N. F., Idaho...	Small	..	6.040	...	32.5	...
	Large	..	8.290	...	42.5	10.0
Pecos, N. F., N. M.....	Small	..	5.450	...	65.0	...
	Large	..	7.850	...	69.0	4.0
Washington	Small	..	3.780	...	16.5	
	Large	..	6.450	...	16.0	—0.5
Colorado.............	Small	..	3.750	...	79.0	...
	Large	..	6.980	...	88.0	9.0
Madison, N. F., Mon...	Small	..	3.350	...	43.5	...
	Large	..	6.630	...	50.0	6.5

the per cent. in favor of the large seeds. In converting grams to pounds it was assumed that 453.6 grams equals one pound. The germination period for *Pinus ponderosa* was 120 days and for *Pseudotsuga taxifolia* 100 days.

From these tables it will be seen that in every variety of *Pinus ponderosa* the final germination per cent. is in favor of the large seeds. In the case of *Pseudotsuga taxifolia* every variety except one shows a final per cent. in favor of the large seeds.

It is well known that there are definite climatic differences between the Rocky Mountains and the Pacific coast. The most conspicuous proof of this is in the flora of these regions. In general the Pacific coast is inhabited by relatively mesophilous vegetation, especially near the coast, while the vegetation of the Rocky Mountains is more xerophilous in nature. Again, the Rockies themselves show marked differences in this very respect in travelling from south to north and from east to west.

Probably the best way of studying the effect of great climatic variations upon vegetation is to use polydemic species such as we are considering here. *Pinus ponderosa* and *Pseudotsuga taxifolia* are conspicuous examples of this class of species. It is well known that both these species reach a better development on the Pacific coast than in the Rocky Mountains. It is likewise well known that they reach a far better development in the northern Rockies than in the southern. As a proof of this we have but to go to volume tables of these species in the *Woodsman's Handbook* by Graves and Ziegler. In the case of *Pinus ponderosa* three tables are given, one for the Black Hills, one for Arizona, and one for California and Montana. In studying these tables it will be seen that the maximum heights and maximum diameters and the average and maximum heights for a given diameter increase steadily in going from the Black Hills to California. In the case of the Douglas fir the same thing is true in considering the volume table for Idaho and Wyoming and that for Washington and Oregon. In the order of their favorability for tree growth, as manifested by these species these regions arrange themselves in the following order, the least favorable being given first:

Black Hills
Arizona and New Mexico
Colorado and Wyoming
Idaho and Montana
Washington, Oregon, and California.

It is a striking fact in the case of *Pinus ponderosa* that the size and weight of the seed and their manner of germination follow exactly this same order. The smallest seeds come from the Black Hills and New Mexico and the largest from California; the total weight of 500 seeds is least in the case of the Black Hills variety and greatest in the California variety, hence the number of seeds per pound is greatest in the former and smallest in the latter variety. Furthermore, germination begins sooner, the germination period is shorter and the germination curve rises more rapidly in the case of the South Dakota and New Mexico variety than in the case of the Pacific coast variety. Some of these striking relations between seeds and site are also shown by *Pseudotsuga taxifolia.* This species shows all these relations except those of weight of seed and number of seeds per pound. There seems to be no definite relation in this respect.

On page 79 the germination curves of the climatic varieties of *Pinus ponderosa* and *Pseudotsuga taxifolia* are given and they illustrate very forcibly what has been said above concerning the behavior of these curves.

In order to determine the effect of the size of the seed upon the size of the seedling shortly after germination, the seedlings were dug up very carefully as they were counted and taken to the laboratory and measured. The total length of the hypocotyl and tap root was taken in each case, the seed being excluded from the measurement. These measurements were kept separate for the small and large seeds and the results are given below:

Pinus ponderosa (Idaho)—Age, 2 Days

200 seedlings from small seeds averaged	3.07 cm.
200 seedlings from large seeds averaged	3.90 cm.

These 400 seedlings were classified according to their total length as follows:

THE EFFECT OF *Climatic Varieties* UPON GERMINATION

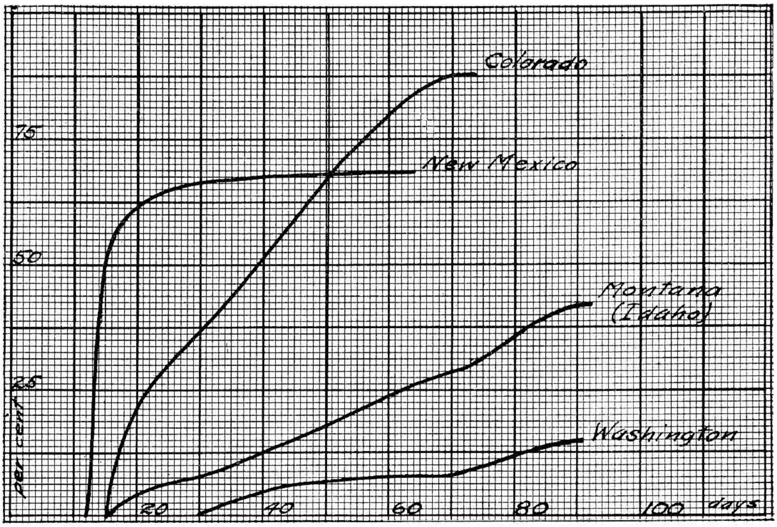

FIG. 1. The germination curves of *Pseudotsuga taxifolia.*

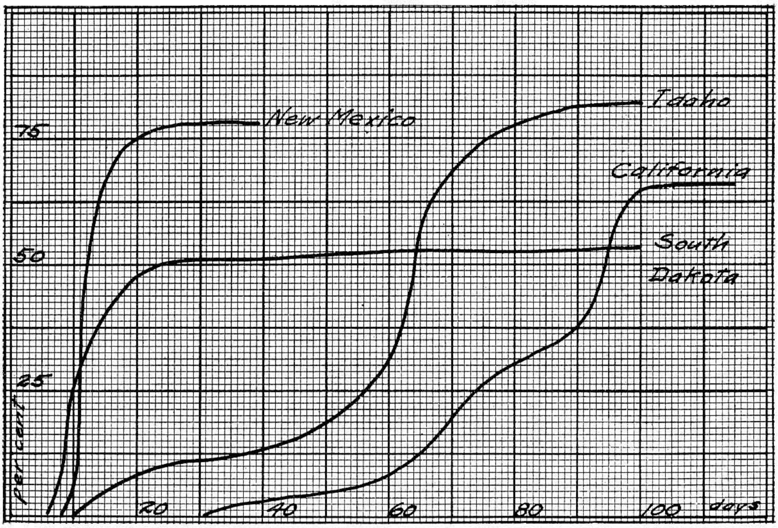

FIG. 2. The germination curves of *Pinus ponderosa.*

Size, Cm.	Seedlings from Seeds Small	Large
0–0.5	2	0
0.6–1.0	10	0
1.1–1.5	17	6
1.6–2.0	26	14
2.1–2.5	24	19
2.6–3.0	25	25
3.1–3.5	30	26
3.6–4.0	23	31
4.1–4.5	15	17
4.6–5.0	11	15
5.1–5.5	8	13
5.6–6.0	4	12
6.1–6.5	3	9
6.6–7.0	0	8
7.1–7.5	0	2
7.6–8.0	1	2
8.1–8.5	1	0
8.6–9.0	1	1
Total	200	200

It will be seen that most of the plants from the small seeds fall between the limits 0.6 and 5.0 while most of the plants from the large seeds fall between the limits 1.6 and 6.0. In other words a greater per cent. of small plants were found among the plants that germinated from the small seeds. The average difference in size of 200 plants of each kind was 0.84 cm. in favor of the plants from the large seeds.

The measurements taken for another climatic variety of *Pinus ponderosa* were as follows:

Pinus ponderosa (South Dakota)—Age, 4 Days

35 seedlings from small seeds averaged	4.6 cm.
51 seedlings from large seeds averaged	5.6 cm.

Here there is a difference of 1.0 cm. in favor of the seedlings from the large seeds.

Similar measurements were taken in the case of *Pseudotsuga taxifolia:*

Pseudotsuga taxifolia (New Mexico)—Age, 4 Days

100 seedlings from small seeds averaged	3.58 cm.
100 seedlings from large seeds averaged	4.27 cm.

These 200 seedlings were classified according to their total length as follows:

Size, Cm.	Seedlings from Seeds Small	Large
0–0.5	0	0
0.6–1.0	0	0
1.1–1.5	1	0
1.6–2.0	9	3
2.1–2.5	7	9
2.6–3.0	20	8
3.1–3.5	19	12
3.6–4.0	12	12
4.1–4.5	10	17
4.6–5.0	11	12
5.1–5.5	5	11
5.6–6.0	5	7
6.1–6.5	1	6
6.6–7.0	0	2
7.1–7.5	0	1
Total	100	100

It will be seen from this table that most of the seedlings from the small seeds fall between the limits 2.6–5.0 while most of the seedlings from the large seeds fall between the limits 3.1–5.5. Just as in the case of *Pinus ponderosa* above we see that the greater per cent. of small seedlings are found among the seedlings that germinated from small seeds. The average difference in size of 100 plants of each kind is 0.69 cm. in favor of the plants from large seeds.

The measurements taken for another climatic variety of *Pseudotsuga taxifolia* were as follows:

Pseudotsuga taxifolia (Colorado)—Age, 4 Days

31 seedlings from small seeds averaged	3.4 cm.
76 seedlings from large seeds averaged	3.9 cm.

Here again there is a difference of 0.5 cm. in favor of the large seeds. In comparing *Pseudotsuga taxifolia* with *Pinus ponderosa* it is found that the size of the seed makes a greater difference in the case of the latter species than in the case of the former. Also,

the difference in both cases is greater for the variety that comes from the drier climate, that is, the South Dakota variety of *Pinus ponderosa* shows a greater difference than the Idaho variety and the New Mexico variety of *Pseudotsuga taxifolia* shows a greater difference than the Colorado. The data here presented upon this phase of the problem, however, are not sufficient to warrant conclusions.

GENERAL SUMMARY AND CONCLUSIONS

I. *The Effect of Habitat Factors upon Germination*

1. *Shade decreases evaporation* and *transpiration* and thereby *increases* the *soil-moisture content* of the superficial soil layers. This increase in soil moisture content is best shown by the accompanying diagram. This conclusion agrees with the results obtained by Stewart and Hasselbring who grew tobacco in shade tents.

2. *Shade accelerates germination,* that is seeds germinate sooner in the shade than in the light. This *acceleration* is *due* to the *increase* in *soil-moisture content* spoken about above.

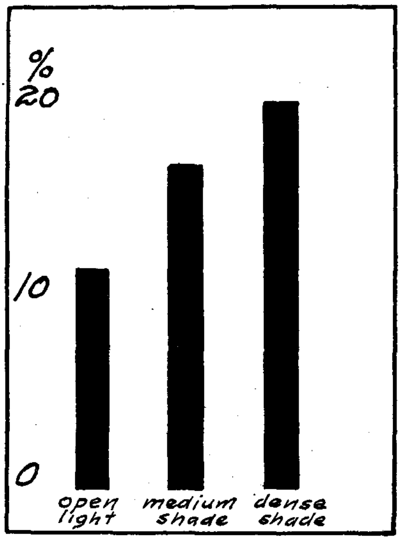

Diagram showing soil moisture content in the three light cultures.

Burns reached the conclusion that shade reduces the temperature of the soil and delays germination. Evidently there is a delicate balance between soil moisture and soil temperature, so that a slight deficiency in either might delay the germination process. In Burns's case the temperature of the soil was so low, that in spite of the fact that there was sufficient soil moisture, germination was delayed. In the present investigations soil temperature was kept at an optimum and measured differences in soil moisture were sufficient to result in an acceleration of germination in the shade cultures. One unfortunate fact about Burns's work was that he failed to take into account soil moisture. In his experiments it must be assumed that there was sufficient soil moisture for germination. But there is nothing in his report which does not indicate that there was too much soil moisture. The reciprocal relation between soil temperature and soil moisture is well known. Furthermore there is an intimate relation between soil moisture and soil aeration and germination. Such factors as these were evidently not taken into account to explain the delay in germination in the experiments cited.

3. *Shade increases* the length of the germination period. This bears out to a certain extent Pittauer's experiments which showed that germination proceeds more rapidly in the light than in the shade.

4. The *germination curve* of seeds sown in the shade rises *more rapidly* than the curve of seeds sown in the light. This conclusion does not agree with the results obtained by Pittauer.

5. The *final germination per cent.* is usually *higher* in the case of seeds sown in the shade than those sown in the light. This conclusion, based upon abundant evidence, is not in accord with some work done by Atterberg which showed a greater germination per cent. in the presence of light than in the absence of it.

6. *Light plays absolutely no part in the germination of tree seeds;* in fact shade has been found to be exceedingly beneficial to germination, other factors being equal. In the work carried on by Burns already referred to, there are at least two statements that a certain amount of light is necessary for satisfactory germination. Whether he means to imply by the term "light"

merely the luminous energy or the heat energy of the sun or both is difficult to say. As a general thing it is impossible to have light energy without a certain amount of heat energy, but heat and light affect plants so differently that the final effect of these factors is easily recognized. It is important to keep these two concepts separate in order to avoid confusion. Graves also makes the statement that light is necessary for the germination of Western White pine. It is inconceivable how luminous energy can play any part in germination, especially when the seeds are below the ground; it is likewise difficult to conceive what possible effect light could have if it did reach the seed.

7. An *inadequate* supply of soil moisture *delays* germination.

8. An *inadequate* supply of soil moisture *decreases* the length of the germination period.

9. A *lack* of soil moisture *decreases* the final germination per cent.

10. The germination curves of seeds sown in wet soil rises much *more rapidly* than that of seeds sown in dry soil.

11. Xerophilous species begin germination *first,* xero-mesophilous germinate *later,* and mesophilous germinate *last.*

12. The germination period of xerophilous species is *shorter* than that for either the xero-mesophilous or the mesophilous species.

13. In xerophilous species germination is *accelerated* in the gravel and sand; in mesophilous species it is *accelerated* in loam and sand. In general germination is accelerated in sand and gravel due not to the amount of soil moisture in these soils (see accompanying diagram) but to the amount of oxygen in the soil.

14. The germination period is *longest* in the sand.

15. The germination per cent. is usually *highest* in the sand.

16. The rise of the germination curve of seeds sown in sand is usually *more rapid* than of seeds sown in loam or gravel.

17. According to the table on page 29 of this report the volume of air space in a given volume of soil is about 39 per cent. for gravel, 33 per cent. for sand, and 53 per cent. for loam. In the accompanying diagram is shown the amount of capillary water in these soils at the time of watering and twenty-four hours later.

This diagram shows very strikingly the water retaining capacity of these three soils. Not only do sand and gravel hold less moisture at the time of watering but they lose a much greater per cent. of it in the course of twenty-four hours than does loam.

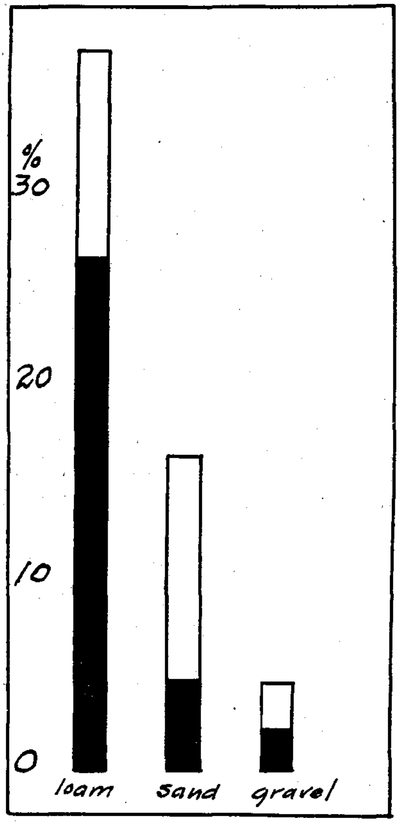

Diagram showing:

☐ soil moisture per cent. at time of watering;

■ soil moisture per cent. twenty-four hours later.

When we consider the amount of air space in these soils and the amount of soil moisture each retains, the fact that loam usually contains a great deal of moisture and very little air space and that gravel contains very little moisture and a great volume of air space is very strikingly shown.

II. *The Effect of Habitat Factors upon Stem and Root Development*

1. *Pinus ponderosa* and *Pinus strobus* show *increased* height growth with *diminishing* light intensity. This conclusion bears out the results secured by Nikolsky who worked with pine and spruce and Burns who worked with *Pinus strobus.* On the other hand Badoux showed that pines decrease their height growth with increasing shade; but these trees were grown to a height of about six feet while Nikolsky and Burns experimented with much smaller stock.

2. *Robinia pseudacacia* and *Quercus rubra* show a *decrease* in height growth with *diminishing* light intensity.

3. *Pinus ponderosa* shows a *decrease* in length of tap root and in total length of laterals with *diminishing* light intensity. These results again bear out the conclusions of Nikolsky and Burns.

4. *Robinia pseudacacia* and *Quercus rubra* show a *decrease* in length of tap root and total length of lateral roots with *decreased* light intensity.

5. *Pinus ponderosa, Robinia pseudacacia, Pinus strobus,* and *Quercus rubra* show *increased* height growth with an *increase* in soil depth.

6. *Pinus ponderosa, Robinia pseudacacia, Pinus strobus,* and *Quercus rubra* show an *increase* in length of tap root but a *decreased* development of lateral roots with *increased* depth of soil.

7. *Pinus ponderosa, Robinia pseudacacia,* and *Pinus strobus* show a *decrease* in height growth with a *decrease* in the soil moisture supply.

8. *Pinus ponderosa* shows an *increase* in length of tap root and an *increase* in total length of lateral roots with diminishing soil moisture content.

9. *Robinia* shows a *decrease* in length of tap root with a *decrease* in soil moisture supply.

10. *Pinus ponderosa* shows the *greatest* height growth in the loam and gravel, but *Pinus strobus* shows the *greatest* height growth in the sand.

11. *Robinia pseudacacia* and *Quercus rubra* show the *greatest*

height growth in the loam and the *least* in the gravel. Comparing this conclusion with No. 10 it is interesting to see that the conifers do well in either sand, loam or gravel, but that the hardwoods do best in loam only.

12. *Pinus ponderosa,* and *Quercus rubra* show the *greatest* length of tap root and *greatest* length of lateral roots in the gravel and the *shortest* length in the loam; *Robinia pseudacacia* shows the *greatest* length of tap root in the sand and least in the loam. In other words, root development is usually *greatest* in the gravel, and *least* in the loam. This conclusion agrees in part with Tolsky's results that pine in black soils develop vertical roots but in sand develop a greater spread of lateral roots.

13. As far as height growth goes it is evident that pines, on account of their greater drought resistance, may grow as well in sand or gravel, or even attain a greater height in sand or gravel than in loam; while hardwoods which prefer moister soils grow best in loam. That root development is greatest in gravel is due undoubtedly to the fact that water quickly percolates through this soil and hence the roots have to go deep for the moisture. Reference to the diagram on page 85 will bring out these relations more clearly.

III. *The Relation of Size and Weight of Seed to Germination and Early Development.*

1. Large seeds of *Pinus ponderosa* and *Pseudotsuga taxifolia* produce a *higher final germination per cent.* than small seeds. This conclusion contradicts the results of Busse and Centgraf who found no relation between size of seeds and germination per cent., but it proves the contentions of many old silviculturists that large seeds produce a higher germination per cent.

2. At the age of from 2 to 4 days large seeds of *Pinus ponderosa* and *Pseudotsuga taxifolia* produce *larger* seedlings than small seeds. This conclusion proves at least in part Schlich's statement on page 73 concerning the use of large seeds in planting and nursery work and bears out the contentions of practicing foresters in Europe that large seeds should be used in field sowing. This conclusion likewise agrees with the mass of evidence collected in connection with many cereal and garden vege-

table seeds, namely that the use of large seeds results in a better all round later development and a greater final crop.

3. The Rocky Mountain varieties of *Pinus ponderosa* produce *smaller* seeds, their germination begins *earlier*, their germination period is *shorter*, and their germination curves rise much *more rapidly* than in the case of the Pacific coast varieties of this species.

4. Except for the size of the seed, the same relations hold for the Rocky Mountain and Pacific coast varieties of *Pseudotsuga taxifolia*. Blumer noted the slow germination of *Pinus ponderosa* and *Pseudotsuga taxifolia* from the coast and he also noted the great difference in size of the seed of *Pinus ponderosa*. These observations are corroborated.

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PLATE I

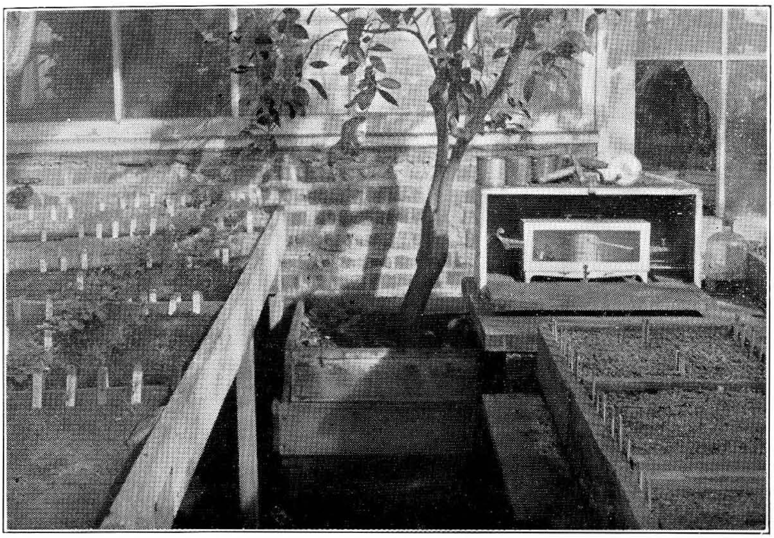

FIG. 1. View of the interior of the greenhouse, showing cultures and hydrothermograph.

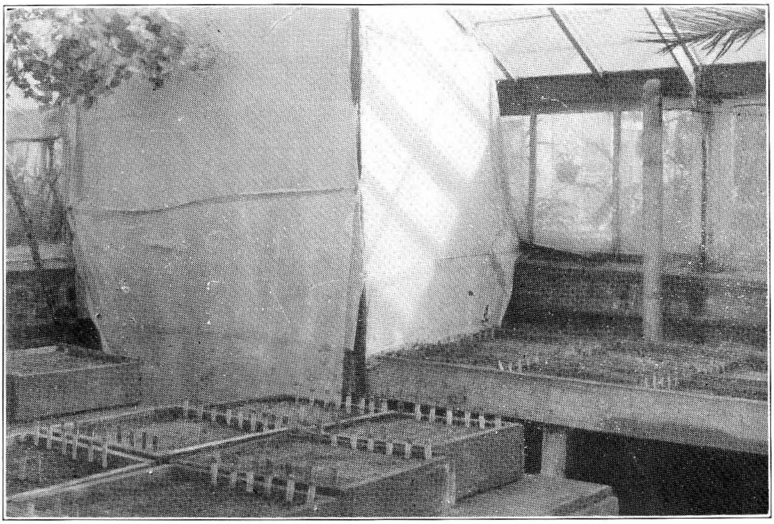

FIG. 2. View of the interior of the greenhouse, showing cultures and the cheesecloth tent used for the dense shade experiments.

PLATE II

The Effect of *Light* upon Early Development

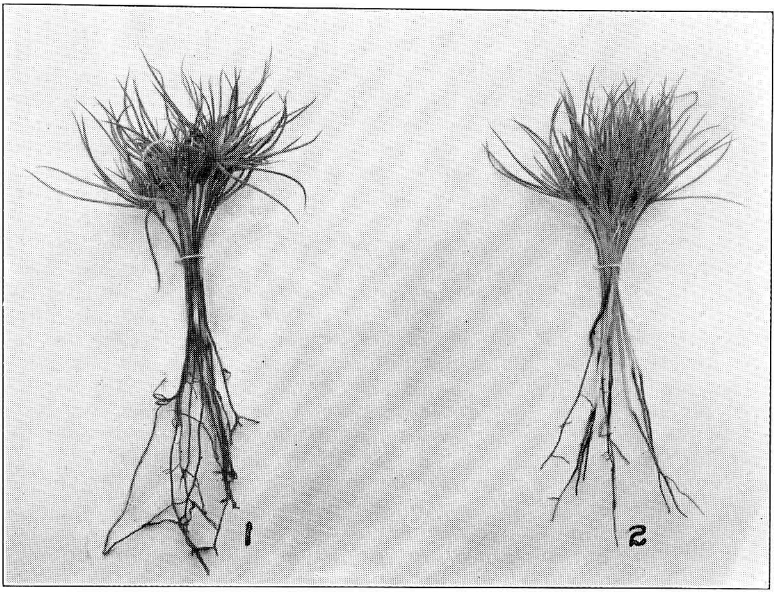

Fig. 1. The effect of *light* upon the development of *Pinus ponderosa* (S. D.). Ten plants each (1) grown in open light, (2) grown in medium shade. ⅝ natural size.

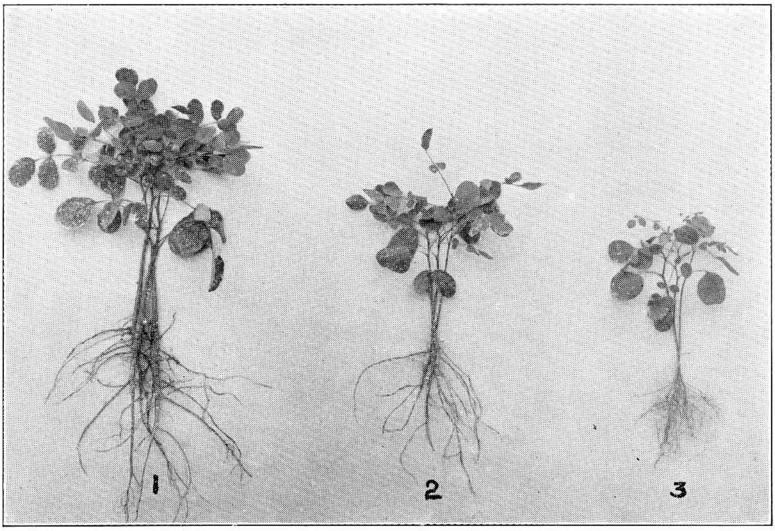

Fig. 2. The effect of *light* upon the development of *Robinia pseudacacia*. Three plants each (1) grown in open light, (2) in medium shade, (3) in dense shade. ⅜ natural size.

PLATE III

THE EFFECT OF *Soil Depth* UPON EARLY DEVELOPMENT

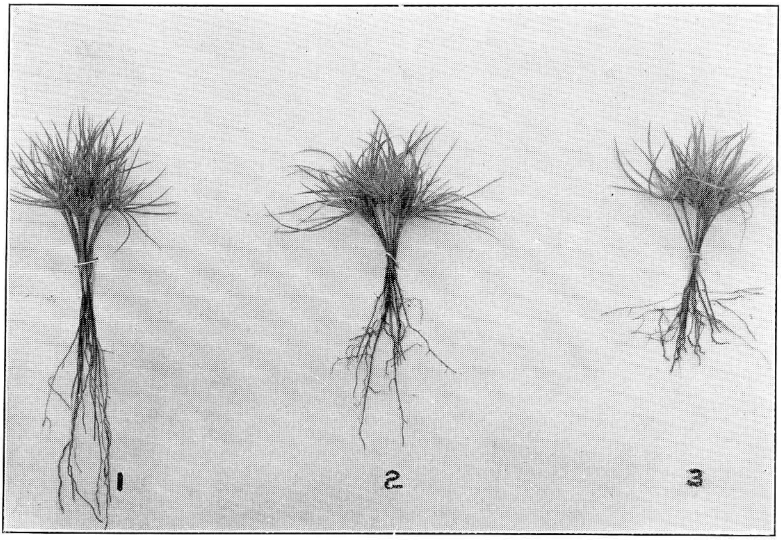

FIG. 1. The effect of *soil depth* upon the development of *Pinus ponderosa* (S. D.). Ten plants grown (1) in deep, (2) in medium, and (3) in shallow soil. ½ natural size.

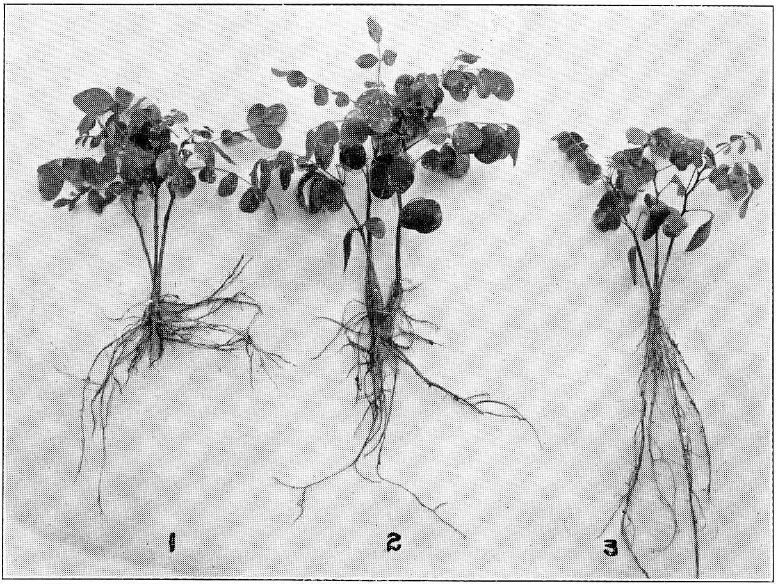

FIG. 2. The effect of *soil depth* upon the development of *Robinia pseudacacia*. Three plants each (1) grown in shallow, (2) in medium, (3) in deep soil. ⅓ natural size.

PLATE IV

THE EFFECT OF *Soil Moisture* UPON EARLY DEVELOPMENT

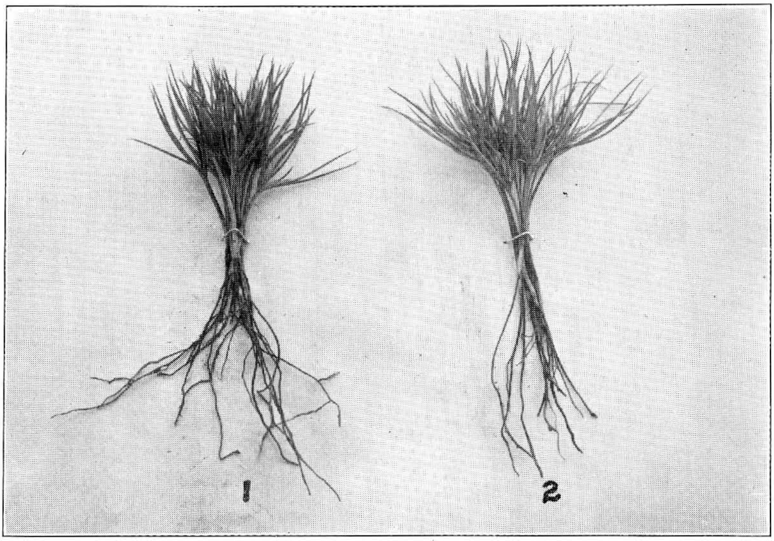

FIG. 1. The effect of *soil moisture* upon the development of *Pinus ponderosa* (S. D.). Ten plants grown in (1) medium dry soil, (2) wet soil. ½ natural size.

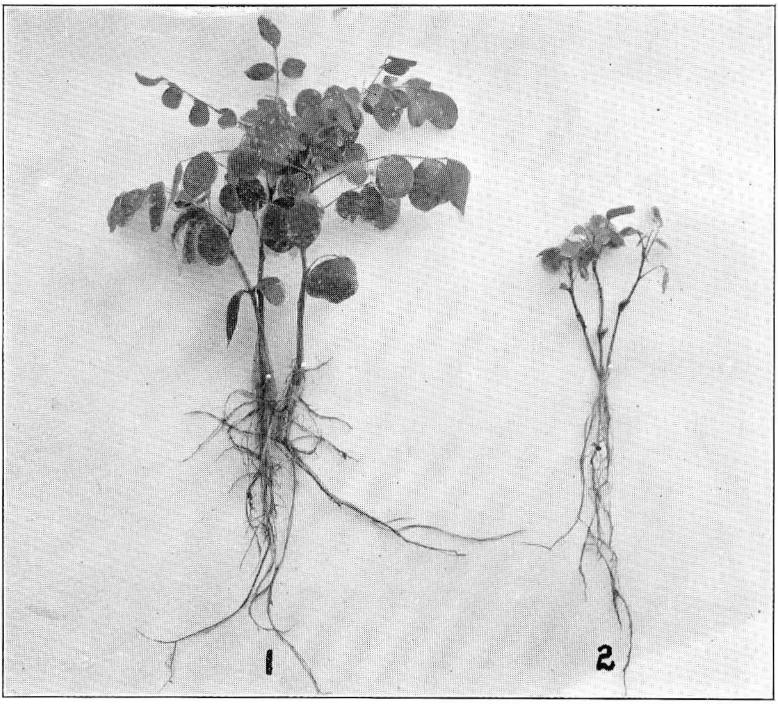

FIG. 2. The effect of *soil moisture* upon the development of *Robinia pseudacacia*. Three plants grown (1) in wet soil, (2) in medium dry soil. ½ natural size.

PLATE V

The Effect of *Soil Texture* upon Early Development

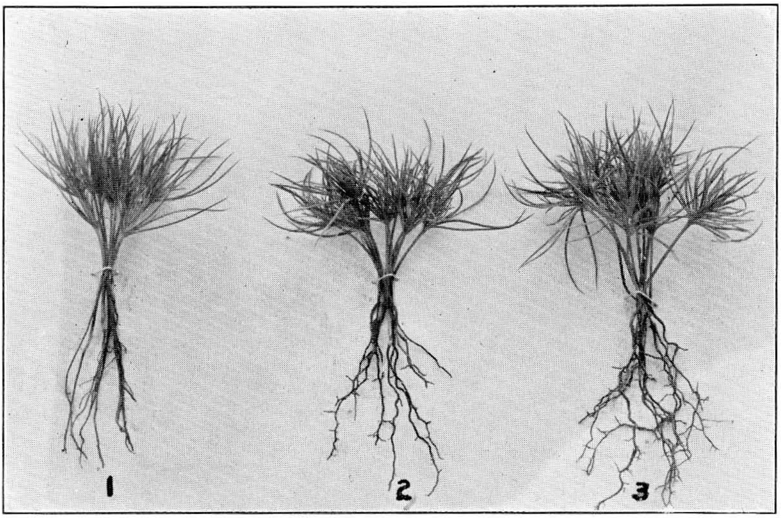

Fig. 1. The effect of *soil texture* upon the development of *Pinus ponderosa* (S. D.). Ten plants each (1) grown in loam, (2) grown in sand, (3) grown in gravel. ½ natural size.

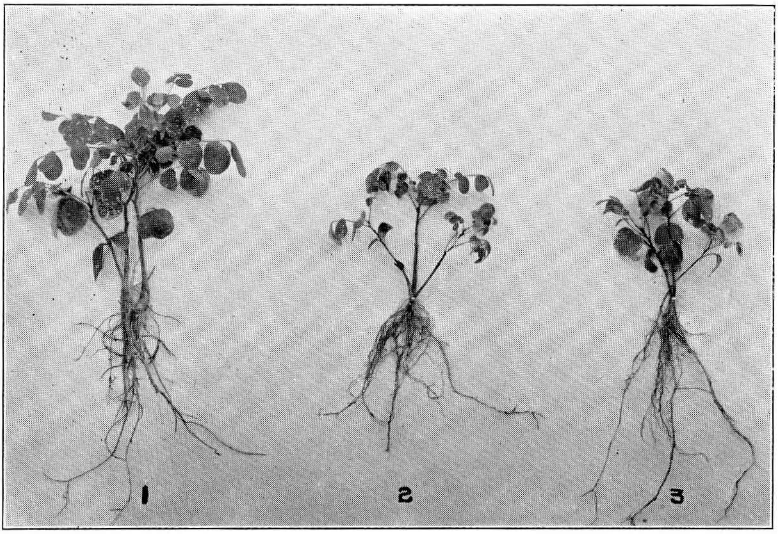

Fig. 2. The effect of *soil texture* upon the development of *Robinia pseudacacia*. Three plants each (1) grown in loam, (2) grown in sand, (3) in gravel. ⅓ natural size.

PLATE V

The Effect of *Soil Texture* upon Early Development

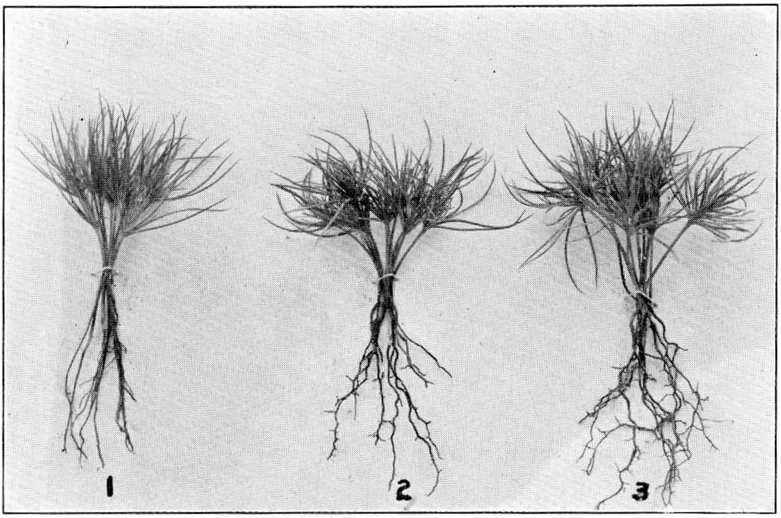

Fig. 1. The effect of *soil texture* upon the development of *Pinus ponderosa* (S. D.). Ten plants each (1) grown in loam, (2) grown in sand, (3) grown in gravel. ½ natural size.

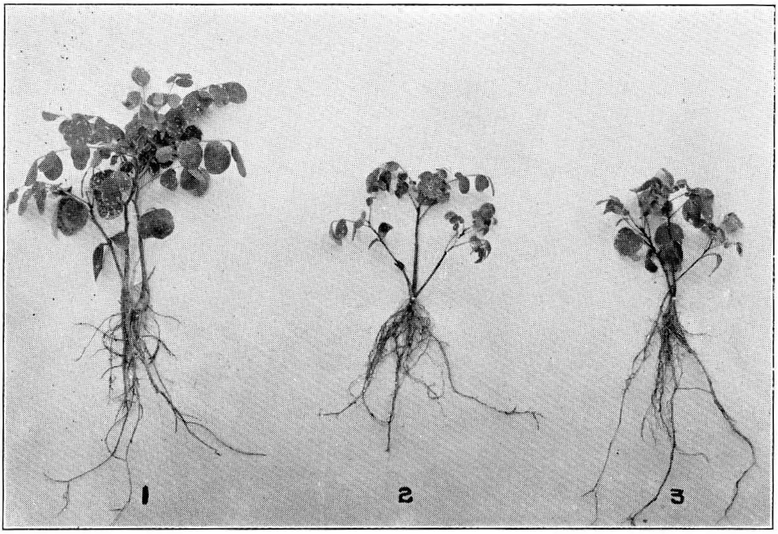

Fig. 2. The effect of *soil texture* upon the development of *Robinia pseudacacia*. Three plants each (1) grown in loam, (2) grown in sand, (3) in gravel. ⅓ natural size.