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Factors Controlling Germination and Early Survival in Oaks

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FACTORS CONTROLLING GERMINATION AND EARLY SURVIVAL IN OAKS

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FOREWORD

THESE studies were made possible largely as a result of cooperation between the School of Forestry of Yale University and the Appalachian Forest Experiment Station of the Forest Service, U.S. Department of Agriculture. The initial studies were undertaken at the Appalachian Station and were later continued at Yale University as a result of substantial assistance received from a fellowship under the Forest Production Research Endowment of the Vale School of Forestry. The original manuscript was submitted as a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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FACTORS CONTROLLING GERMINATION AND EARLY SURVIVAL IN OAKS

INTRODUCTION

THERE is little information available upon the seed and seedling characteristics of the American oaks. Among the fundamental problems in American silviculture, those which relate to seed efficiency are especially important. The future productiveness of the hardwood forests in which chestnut has been an important element rests largely upon seed and sprout efficiency. Seed efficiency is governed by (1) seed production, (2) seed distribution, and (3) the factors affecting the reproductive value of the seed, such as viability, storage of seed in the litter of the forest floor, and destruction by insects and rodents.

Recent studies by the Appalachian and Northeastern Forest Experiment Stations indicate that the chestnut is being replaced largely by stands funning heavily to various species of oak (Korstian and Stickel, 1927). Other studies by Leffelman and Hawley (1925) emphasize the fact that the future stands on many typical hardwood lands in southern New England promise to be predominantly oak and that among the oaks, redoak[1] and chestnut oak will be prominent; the former particularly on the better sites because of rapid growth, and the latter on the poorer sites because of abundance and of inherent adaptation to these sites. Silviculturists recognize that seedlings are the most desirable elements in a stand and where sprouts are considered those from seedlings are more desirable than sprouts from older trees because of their greater freedom from decay and better root systems. Such facts, together with the outstanding economic importance of the oaks, emphasize the need for thorough investigations of the reproduction of these species.

It has been commonly observed that in nature the white oaks usually germinate in the autumn with heavy losses resulting under certain lions and that the acorns of the black oaks usually do not germinate spring. The relation of this to restocking efficiency, however, is wholly a

1 The nomenclature of the American oaks throughout this bulletin follows that of Sudworth (1927). See list of common and scientific names on page 109.

matter of surmise. Among the specific points which should be investigated in connection with the general problem of oak regeneration are the ways in which seed is best stored over winter, both in nature and artificially, the conditions responsible, in nature, for success or failure of gennination, and methods of securing prompt spring germination. It is evident, therefore, that such investigations should give results of fundamental value in the solution of the silvicultural problems of both natural reproduction and artificial seeding and planting of the oaks.

HISTORICAL REVIEW

THE artificial establishment of forests in Germany in the fourteenth century stImulated an Interest In seed storage, and methods of storing were devised. Many of these methods were forgotten. Others \vere handed down traditionally to succeeding generations.Schwappach (1913) states that as early as the sixteenth century the method of preserving acorns and beechnuts in sand was practiced. Moser (1757) gives precise instructions as to the storage of tree seeds mixed with sand and sawdust and placed where they will not become too dry. Manteuffel (1869) mentions several different methods of preserving acorns. These methods have been followed by recent workers. The problem of storing acorns over winter so that they will retain their viability has received considerable attention during the last quarter of a century, for one finds such methods of storage mentioned frequently in the literature. Cieslar (1896) conducted a preliminary series of acorn storage experiments in 1890-189ı and a more elaborate series in 1892-1893. Acorns preserved over winter covered with moss on top of the ground, in covered pits mixed with sand or soil, and stored in running spring water gave a germination of 71 to 79 per cent. Ciesla! maintains that the storage of acorns in running spring water facilitates retention of viability and' may even delay germination. When acorns are overwintered in moist soil in contact with straw a fungus lowers their viability considerably. Acorns stored over winter in a very shallow pit under a cover of straw and in a dry cellar mixed ,with sand had a viability of only 52 to 53 per cent in the spring. Acorns stored in a sack in a heated room during the winter failed to germinate. The loss of viability in the last three cases was accompanied by a heavy water loss.

Two anonymous papers published in the *Bulletin of the Central Belgian Forestry Society* (1898, 1900) report experiments in which autumn and spring planting of acorns and chestnuts in Belgium is compared. The

autumn plantings were made in two lots; in one the acorns were covered with leaves to a depth of 5 to 6 em., in the other they were planted in trenches to a depth of about 10cm. The seeds for spring planting were preserved as follows: in trenches, piled and covered with soil and with leaves, in baskets submerged in water, and stratified in sand in a dry cave. From the germination and growth of the different lots it is concluded that, where protected against animals, autumn seeding is ordinarily preferable to any of the methods of storing the acorns over winter and planting in the spring. This is because not only higher germination is obtained, but the work can be done at a season when there is less demand for attention to other nursery activities.

Zederbauer (1910) carried out a number of fundamental experiments to aid in the selection of storage methods. He considered the natural conditions under which seed is stored and the various life processes that are active in the resting seed. During the winter of 1906-1907 he stored European turkey oak acorns in tulle sacks hanging in an open wooden shed, also in an unheated room, and in a heated room with the complete loss of their viability. Acorns hanging in small tulle sacks in a cellar had a germination of only 3 per cent in the spring. Acorns sown in a nursery bed on December 11 germinated to the extent of only 25 per cent. He considers it quite possible that, during the 10 days which elapsed between collecting and planting, many of the acorns had dried sufficiently to lose their viability. Another lot of acorns mixed with sand and kept moist in an earthenware vessel in an unheated room gave a germination of 64 per cent in the spring. Those similarly stratified but kept in a cellar had a germination of 87 per cent. He concludes that seeds especially rich in stored food and with thin outer coats, such as acorns, are very sensitive to a low moisture content.

Oppermann (1913) and Hauch (1923) discuss in considerable detail the storage of acorns in Denmark. The latter writer, contending that in his experience the storing of acorns in pits is uncertain and sometimes results in a considerable loss of germination, advocates the use of Alemann's acorn storehouse. This house has a capacity of 800 bushels of acorns. It has a concrete floor and a roof covered with a layer of sod 12 inches thick and is thatched with a thick layer of straw. Hauch states that the temperature in the house must be kept so that it neither goes much below nor much above the freezing point, and that it is well to have fresh air circulating freely in the hut. When the temperature drops below the freezing point the doors are closed and covered with straw to prevent the

loss of the acorns by freezing. Hauch strongly emphasizes the fact that the acorns must be watched with painstaking care so that they do not become too dry and yet not too damp, and furthermore, that they are neither exposed to frost nor temperatures above the optimum. The acorns when first collected must be brought into a dormant state so that they neither sprout nor become so dry that they lose their viability. Frequent stirring of the acorns and weekly germination tests are advocated. Hauch recommends this method of over-winterstorage to make spring planting of acorns possible and thereby reduce the danger of their destruction by mice, deer, pheasants, or pigeons. He also advocates planting the acorns the same day they are removed from storage to prevent drying out and the consequent loss of viability.

Holten (1920) reports that a considerable quantity of acorns which had been stored in the fall of 1918 gave 40 per cent germination in 1920. He concludes that in order to preserve the acorns two years it is necessary to use Hauch's method the first winter and to store them in dry sand the following spring, and at such depth that the temperature will remain fairly constant.

Onlieff (1915) describes a method of storing acorns which is reported to be most satisfactory for Russian conditions. It does not entail all the precautions necessary to prevent heating and rotting and frost injury. A layer of dry oak leaves about 1 inch deep is spread on the ground on a protected north slope, and upon it a 2 to 3-inch layer of selected, dry acorns is placed. They are then covered with more leaves and branches to protect them from the wind. When the winter has set in and the snow no longer melts, it is piled up to a depth of 2 feet on the place where the acorns are buried. The snow is then covered with straw 7 to 10 inches thick and the whole left until spring. The area is surrounded by a I-foot ditch with inclined sides and embankments on the outer side as a protection against rodents. The ditch also drains off surplus water.

In America the method of acorn storage generally followed has been stratification in sand. This method has been advocated by Douglas (1888), Jack (1895), Schenck (1912), Tillotson (1915), Tourney (1916), and Crumley (1926).

Sand, because of its great weight, is generally recognized as unsuited for the storage of acorns being shipped long distances. Heide (1923) advocates packing such acorns in a mixture of powdered dry charcoal and pO'w'dered cocoanut fiber (sphagnum moss may be used) moistened slightly 'vith a 0.1 per cent solution of salicylic acid in water. Galloway

(1924) suggests a mixture of dry coarse charcoal and sifted sphagnum as suitable material for long distance shipments.

In order to obviate the necessity of over-winter storage, Harshberger (1916) advocates the fall planting of immature acorns before they have passed into the dormant period. He contends that the growth of the immature embryos will continue without interruption and that they will develop into normal seedlings ,vithout passing through the resting period. From the standpoint of practical application, the planting of immature acorns is still a very doubtful procedure.

The storage experiments of Delavan (1915) are worthy of special note. He tested three species of the white oak group-white oak, bur oak, and swamp white oak-and two of the black oak group-red oak and black oak. The acorns of each species were divided into four equal lots and stored in closed, but not sealed, glass fruit jars as follows: (I) in the laboratory, without preliminary drying; (2) in the laboratory, after drying until they had lost abouts per cent of their original weight; (3) in a refrigerator; (4) in a pit, buried about 1 foot under the surfa.ce of the ground. The acorns stored in the refrigerator gave the highest germination. Those stored in the pit gave the next highest germination, and, with the black oaks, also a decrease in the period of germination as the season progressed. The acorns artificially dried had a very low percentage of germination, dropping to zero early in the season. It is evident from this experiment that optimum conditions for acorn storage are moist atmosphere and low temperature.

For countries with warm or fluctuating climates the suggestion of Johannsen (192I) seems to offer the most promise in acorn storage. He contends that in order to keep acorns in a condition capable of germinating, constant low temperature is required. In his experiments he found that storing at a temperature between 1 and 2 degrees C. (33.8 to 35.6° F.) gave good results. Temperatures in his cold storage room were maintained by means of a refrigerating machine. He states that, while the temperatures ordinarily were maintained around 2 to 4 degrees C. (35.6 to *39.2°* F.), they went up periodically during the summer months to 9 degrees C. (48.2° F.) and proved injurious to the keeping qualities of the acorns. He contends that another necessary condition is the access of air. By excluding air, the power of germination, even at low temperatures, is lost in about a year. Johannsen was able to keep acorns for more than three years but a gradually decreasing power of germination was evident.

GERMINATION AND SURVIVAL IN OAKS

The literature on acorn storage has been reviewed quite fully because it contains many references to the factors which influence germination. It is evident that the low tenlperature and high humidity in pits preserve acorn viability best, while the temperature and moisture conditions in a dry cellar or heated room reduce viability. Low temperatures, high atmospheric humidity and high soil moisture are factors which favorably influence natural and artificial acorn storage. The influence of these factors in reducing respiration and reducing or preventing transpiration is regarded as important in seed storage.

In many manuals on European silviculture, as those by Bagneris, Beck, Boppe, Biihler, Chancerel, Gayer, Heyer-Hess, and Jolyet, mention is made of the need for protecting acorns against desiccation, high temperatures and destruction by mammals and birds. Manteuffel (1869) emphasizes the necessity of safeguarding acorns against unseasonable frosts and destruction by mice. He also emphasizes failure of natural reproduction on soil too hard for roots to penetrate, so that the roots die as a result of desiccation or freezing. Bagneris (1878) specifically cautions against losses through frost, and destruction by wild pigs and small rodents, mice particularly. Endres (1901), in discussing oak regeneration in the Bavarian Spessart, mentions the large amount of injury which the small oak seedlings suffer from the browsing of game, chiefly deer.

Herrmann (1915) and Knuchel (1919), referring to utilization of acorns as food in Germany, emphasize the necessity of excluding acorn gatherers from cutting areas on which the oak is to be reproduced naturally.

Troup (1921) reports that the acorns of the better known Indian oaks are very subject to the attacks of insects and are also eagerly devoured by birds, bears, monkeys, squirrels, rats, and other animals. These agencies are adverse to natural reproduction. Heavy grazing also prevents oak reproduction. Troup regards grass as quite favorable to the germination of seed and the establishment of the seedling provided the soil is not too dry. He has shown, by an experiment at Dehra Dun, that ban oak acorns lying in the open exposed for any length of time to the sun almost invariably crack open and fail to germinate. The best results were reported as occurring where the acorns had become buried by the action of rain; seed germinating on the surface of the ground was subject to destruction through insects eating the radicle. Troup also stresses the importance of leaf litter as a protective covering for the acorns because of its favorable influence in increasing successful germination.

Watt (1919), in a study of the failure of natural regeneration of oak in Britain, emphasizes the importance of certain animal destroyers of the acorn prior to germination. The following list is given: cattle, deer, wild pigs, rabbits, squirrels, dormice, forest mice, voles, pheasants, wood pigeons, jays, and rooks. The principal offenders are rabbits, mice, voles, pheasants, wood pigeons, and jays. On the basis of his experimental results, he stresses concealment as important in the survival of the acorn and the value of the humus layer or leaf litter for this purpose as well as for protection to the acorns against excessive drying. Watt shows that after the acorns of the European turkey oak have lost a certain amount of water (about 27 per cent under the conditions of his experiments) they lose their viability and will not germinate under any conditions. He also discusses the relation of germination to type of seed bed. No difficulties are met which prevent natural regeneration on moist oak sites but on dry oak sites, largely because of surface cover and soil conditions, unfavorable seed beds are encountered.

The influence of the size of the acorn upon the resulting oak seedling has been studied by a number of investigators. Eytingen (1915) reports upon experiments conducted by Nestorov, who studied the influence of ,veight of acorn upon the weight and length of the top and root. tIe concludes that growth is generally in direct proportion to acorn weight. The acorn weight affects favorably the total weight of the plant, especially the root system, and to a less extent the longitudinal organs. The height of the stem depends more upon the weight of the acorn than does the length of the root. Rodger (1919) reports an experiment with bristletooth oak from which he concludes that the size of the seed in this species has little effect on the size of the resulting trees.

Johannsen (192I), on the other hand, points to a marked correlation between the size of the seedling at the end of the first year and that attained after 10 years' growth. This interdependence, however, is not invariable. Hauch (1923) observes that any given lot of oak seedlings in a closely planted nursery bed will consist of individuals with great differences both as to form and vigor, and that this variation is found to persist throughout the entire life of the oak.

Cieslar (1923) gives the r'esults of an experiment which show that the larger seed generally produces more vigorous seedlings. The seven heaviest lots of acorns (averaging 74 acorns to the pound) produced seedlings averaging 9 inches tall at the end of the first year, while the seven lightest lots (averaging 145 acorns to the pound) produced seedlings

averaging only 6 inches tall at that age. After 7 years the seedlings from the heaviest acorns were still 25 per cent taller, but at the end of 18 years the advantage due to acorn size had completely disappeared and the trees from light acorns were slightly taller than those from the heavy acorns. The oaks that made the most rapid growth were descendants of fast-growing, well-formed trees growing in regions with climates similar to that of Vienna.

For American oaks under native conditions very few experimental results are available concerning the factors which influence germination and early survival. A few purely observational studies have been made. One of the earliest of these is that by Mulford.[2] Later observations by Greeley and Ashe (1907), Foster and Ashe (1908), Schenck (1912), Detwiler (1916), and Crumley (1926) lead these writers to attribute the scarcity of oak reproduction in many of the eastern hardwood forests to destruction of large quantities of acorns by insects, hogs, rodents, and other animals, to forest fires, and to conditions unfavorable for germination, such as hard dry soils. Drying is important among the adverse factors. The beneficial effects of a cover of leaf litter are mentioned. Phillips (1912) reports almost complete failure of seedling reproduction in Emory oak, attributed to fires, grazing, and destruction of the acorns by insects and animals. Similar observations have been made on Oregon white oak.

A review of the literature shows two main groups of factors which influence germination and early survival: (I) biotic and (II) physical factors. The biotic factors include the destruction of the acorns by various mammals, birds, and insect larvae. The physical factors comprise (1) moisture, (2) temperature, (3) compactness of the surface soil, and (4) cover conditions such as effects of leaf litter, grass, and other herbaceous or shrubby vegetation on germination and early survival. Another factor-the influence of the size of the acorn on the resulting seedling-is also worthy of investigation, especially in view of the varying results secured by other investigators.

[2] Mulford, Walter. Forest Conditions in the Southern Appalachians. MS. report in files of U.S. Forest Service. 1905.

STRUCTURE OF ACORN AND PHYSIOLOGY OF GERMINATION

THE gross morphology of the acorn has been described in such works as those of LeMaout and Decaisne (1873), Sachs (1882), Tubeuf (1891), Ward (1892), Lubbock (1892), Sargent (1895), Goebel (1913), and Trelease (1924). The acorn (Fig. 1) consists of the seed and its enclosing fruit coat or pericarp-commonly called the shell-which is the ripened ovary wall. The pericarp (Fig. 2) is a hard, somewhat bony

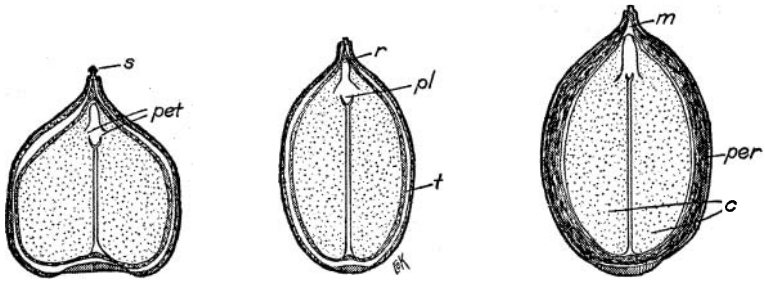

Fig. 1. Longitudinal sections of acorns across the plane of the cotyledons. A, red oak; B, white oak; C, chestnut oak; *c*, cotyledons; *m*, micropyle; *per*, pericarp or fruit coat; *pet*, petioles of cotyledons; *pl*, plumule; *r*, radicle; *s*, remains of stigma; *t*, testa or seed coat.

or coriaceous covering consisting of four tissue layers varying in thickness in the different species: (1) a cutinized epidermal layer of small cuboidal cells with their outer walls much thickened; (2) a single layer of sometimes discontinuous, thin-walled colorless parenchyma cells containing hyaline crystals, presumably of calcium oxalate; (3) several series of very thick-walled sclerotic cells varying from about four times as long as broad at the upper edge to iso-diametric stone cells near the underlying parenchyma layer; (4) numerous layers of parenchyma cells with slightly thickened pitted walls and minute air spaces interspersed with groups of stone cells which comprise the greater part of the thickness of the acorn shell in the species of the white oak group; (5) the inner epidermis, which is usually indistinct in the mature acorn, consists of a single layer of somewhat elongated cells, not much differentiated from the true parenchyma of the pericarp, except that in the red oak group numerous very small hairs arise from this layer, giving a distinctly woolly or felty appearance to the inside of the shell.

The acorn is generally, although not invariably, one-seeded. Coker (1904), has shown that sometimes two or more seedlings may arise from a single acorn. When the ovary is still very young it is 6 celled and contains 6 ovules, all capable of developing into seeds. However, one ovule usu-

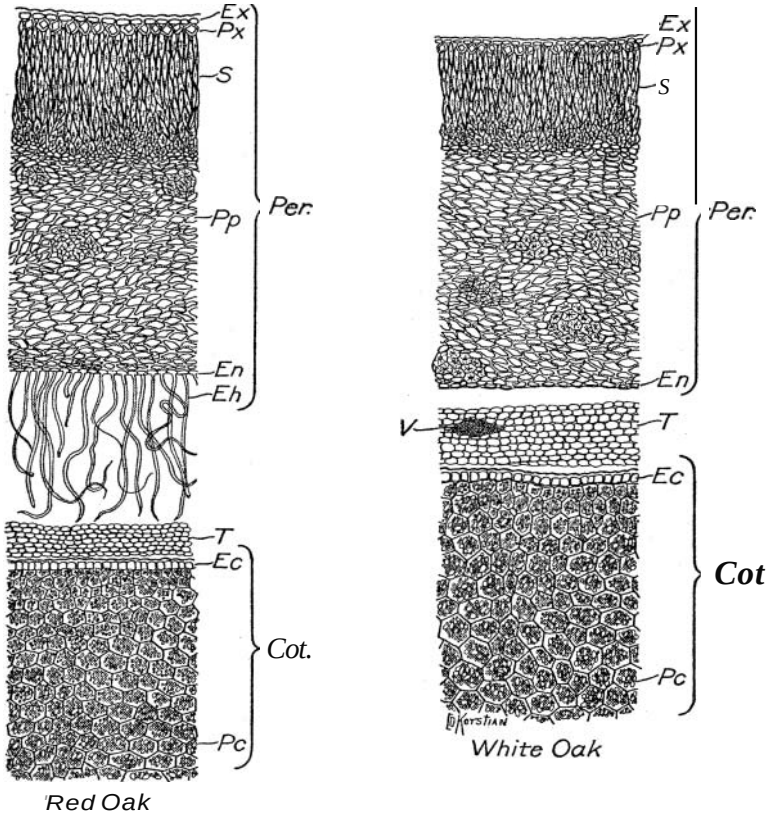

Fig. 2. Semi-diagrammatic transverse sections of the pericarp *(Per.)* and seed of the red and white oaks. *Ex,* exodermis or outer epidermis of pericarp; *Px,* single layer of crystal-bearing parenchyma cells; *S,* sclerotic layer; *Pp,* main parenchyma layer of pericarp with groups of stone cells; *En,* endodermis or internal epidennis of pericarp; *Eh,* epidermal hairs; *T,* testa or seed coat; *V,* vascular bundle; *Cot.,* cotyledon showing epidermis *(Ec)* and storage parenchyma *(Pc)*.

ally takes the lead, absorbing most of the nutrient materials entering the young fruit; the others are arrested in their development and finally become aborted. Trelease (1924) emphasizes the fact that the presence of the

5 aborted ovules is of taxonomic value, since they are found at or near the top of the seed in the black oak group and at or near the base in the white oak group.

The seed proper fills the cavity within the fruit coat. It consists of a very thin seed coat, or testa, and the kernel or embryo. The seed coat in most species is a light brown or yellowish membrane, consisting of only a few rows of thin-walled cuboidal parenchyma cells. This membrane adheres closely to the two cotyledons of the embryo which it encloses, conforming to the various grooves commonly present on the cotyledons of the black oak group; the membrane is usually thickened over these grooves.

The embryo in a ripe acorn is actually a developing plant. Before the mature acorn is shed from the tree this young plant already consists of the radicle, or rudimentary root and foliar structures-collectively termed the plumule—that do not unfold until germination occurs (Fig. I). The radicle is imbedded between the cotyledons near the apex of the seed at the pointed end of the acorn. The plumule lies between two thin narrow pieces of tissue which, on germination, elongate into two short stalks or petioles, one for each cotyledon. Sargent (1895), reports that the radicle in the North American species of the black oak group and in a few of the white oaks is longer than the petioles of the cotyledons, but shorter in most of the white oaks. The petioles are attached to the embryonic seedling at the hypocotyl, which lies between the radicle and plumule. The various tissues in the cotyledons and connecting parts are usually quite clearly differentiated at the time the seed matures.

The cotyledons, however, comprise by far the greater part of the seed. They range in color from pale yellow to colorless and are firm and fleshy in texture and plano-convex in shape. Each cotyledon is composed of a rather delicate epidermis surrounding a mass of cotyledonary tissue, which is made up of very thin-walled, iso-diametric parenchyma cells. Intercellular air spaces occur at the intersections of many of these cells. The reserve food materials required by the young plant during germination are stored in the cotyledons. These materials consist of large quantities of starch, proteins, sugars, and other materials in solution. Tannin is commonly present as is also a considerable amount of oil, particularly in the cotyledons of the black oak group.

Germination in the oaks has been studied or described by the following \vriters: Meehan and Mazyck (1850), Meehan (1871), Engelmann (1880), Stenzel (1877, 1890), Kienitz (1882), Tubeuf (189I), Ward (1892), Sargent (1895), Coker (1912), an anonymous writer in the *American Botan-*

ist (1917), Pammel and King (1917, 1918), and Troup (1921). Germination consists of the development of the embryo into an independent plant. The first visible sign of germination is the splitting of the fruit coat of the acorn at its apex. This is followed closely by the elongation of the radicle, which emerges and forms the tap root (Fig. 3). Meanwhile the petioles of the cotyledons elongate from 1/10 to 1/2 inch, and, carrying

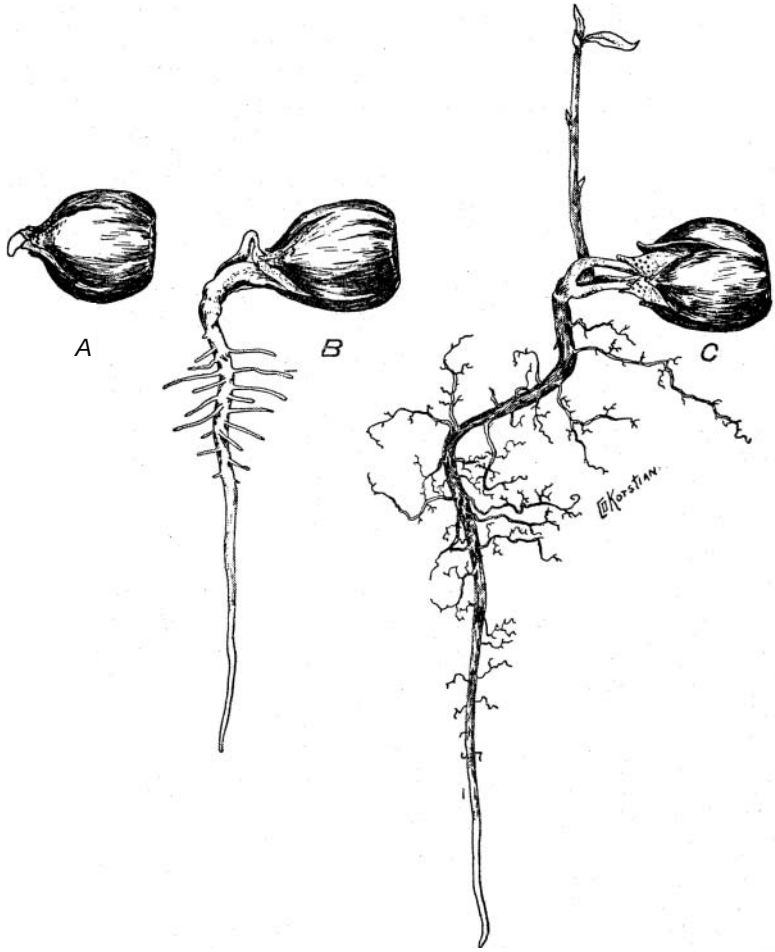

Fig. 3. Successive stages in the germination of after-ripened red oak acorns A, after 10 days, enlargement of embryo confined mainly to elongation of radicle B, after 15 days, enlargement of entire embryo has taken place and plumule is just emerging; C, after 20 days, leaves unfolding.

the plumule outside the cracked fruit coat, they separate, allowing the plumule to emerge and the young shoot to ascend. After germination the cotyledons remain within the fruit coat and are attached to the young seedliIlg, which is nourished by the food stored in them. The cotyledons rot away from the young plant and disappear toward the end of the first growing season after much of their nutrient material has been used by the growing plant. A part of this nutrient material may be translocated to the tap root causing it to become enlarged and s\vollen.

Germination is therefore a growth process coupled with the transfer and assimilation of food materials, and the conditions necessary to cause the germination of a viable acorn are essentially the same as those required for other forms of growth-an adequate supply of food, water, oxygen, and suitable temperatures. Since sufficient food is normally contained in the acorn to last until the developing seedling can rely upon its own photosynthetic activities, an external food supply and corisequently light are not essential for the early stages of germination. The independent life of the plant begins, however, when the first ray of light strikes the unfolding leaves and sets the photosynthetic mechanism in operation.

The vital physiological processes of the plant cannot go on without water. The active protoplasm in the plant cell consists very largely of water. About 80 to 90 per cent of the weight of the physiologically active plant cell is water. The protoplasm of dry seeds, on the other hand, contains relatively little water. For example, Harrington (1923) has shown that the seeds of the common cereals, such as whe'at, oats, and barley, have moisture contents of 10 to 15 per cent. Harrington and Crocker (1918) found that the percentage of germination was not materially changed when wheat, barley, Sudan grass, Kentucky blUe grass, and Johnson grass seeds were dried to less than 1 per cent of moisture.

The water relations of the acorn are very different from those of dry seeds. The acorn contains water equivalent to between 50 and 100 per cent of its dry weight, and Watt (1919) has shown that when English oak acorns lose 25 to 30 per cent of their moisture the embryos die. It is evident, however, that the acor contains sufficient water at the time it is shed from the tree to supply the initial stages of germination. This fact is further substantiated by observations that acorns of the white oak group sometimes begin to germinate before they are shed and that they commonly germinate on the surface of very dry soil, on top of dry leaves, on floors, or on other surfaces from which they can absorb nomoistute.

Additional water is needed to continue the germination process or to

initiate it if the acorns have been subjected to an appreciable amount of drying. Water is important because of the energy it produces in swelling the acorns. This swelling is great enough to actually rupture the fruit coat at the apex. Chemically the water acts as a solvent for the food materials, insures the requisite dilution to the cell contents necessary for the metabolic processes, and serves in the activation of enzymes which render the insoluble foods soluble. Starch is converted into soluble sugar by means of the enzyme diastase. Fats and oils are insoluble in water. Certain enzymes, notably lipase, decompose these during germination into their constituents, fatty acids and glycerin. The latter is readily soluble in water while the fatty acids of higher molecular weight are non-miscible with water, their solubility in water increasing with decreasing molecular weight.

Heat is the regulating factor important in accelerating germination, but on the other hand, if the temperature is reduced the activities begun by the action of water may be retarded or even entirely suspended. The rapidity of germination depends to a large extent upon the temperature, since temperature has the power to modify the absorption of water by the seed, the diffusion of liquids, and enzymic action.

While respiration-the oxidation of the food materials-is the chief source of the kinetic or vital energy required by the plant, it may also release heat. Respiration is sometimes responsible for a material increase in the temperature of germinating seeds and may account for the germination of certain seeds, at very low temperatures. Becker (1912) concludes that oxygen acts as a stimulant in seed germination, ,and many of the conditions under which seeds germinate or do not germinate seem to bear this out. Large quantities of ,oxygen are necessary for germination (Brown, 1925). Unless there is an abundant oxygen supply seeds will not germinate. Most seeds, therefore, fail to germinate in poorly aërated soil, as when buried at a great depth or when the air spaces of the soil are filled with water. However, under natural conditions oxygen is generally present in sufficient amounts.

To summarize, it is evident that water, heat, and oxygen are necessary for the germination of seeds. No two of these factors are sufficient for the germination process; all three must be operative in requisite amounts.

PLAN OF STUDY

DURING the latter part of the summer of 1924 a detailed plan was prepared covering the investigation of the factors controlling germination and early survival in oaks. The conduct of the studies as thus

planned required work in the field, the forest nursery, the greenhouse, and the laboratory. The investigation was undertaken by the writer at the Appalachian Forest Experiment Station in the autumn of 1924. Practical limitations confined the first season's work chiefly to four species; white oak, chestnut oak, red oak, and black oak, although other species were employed occasionally in a limited way. An adequate supply of acorns, consisting of several bushels, was collected during the early part of October for experiments on storage, influence of excessive temperatures, depth of planting in the nursery, influence of size of the acorn on germination and survival, and for field study of natural conditions. Each species was represented by a composite sample of acorns from as many sound, thrifty, middle-aged trees as could be located on the area where the acorns were collected.

In the storage experiments the various lots of acorns were stored over winter in several places in Asheville, N. C., under the different conditions. The following spring these acorns were planted in the Champion Fibre Company's nursery at Canton, N. C., where other lots of acorns had been planted the previous autumn.

Field experiments to determine the natural conditions influencing germination and early survival were conducted on the Bent Creek Experimental Area in the Pisgah National Forest. A field study was made in March and April, 1925, to determine just what actually happened to the acorn crop produced the previous season, and to what extent and under what natural conditions germination occurs.

A preliminary experiment to check field observations of acorn viability as influenced by high temperatures developed in forest fires was conducted in 1924-1925. As a basis for laboratory studies, field data were also obtained on both the amount and duration of excessive heat to which the acorns are subjected in leaf litter fires.

It became evident early in the present investigation that the two most important climatic factors affecting germination and early survival of oaks are moisture and temperature, and that these factors should therefore be studied more intensively than the others. Accordingly in September, 1925, it became possible to continue the investigation in the laboratories and greenhouse of Yale University, where adequate facilities were available.

For use in these studies several bushels of acorns were obtained in the vicinity of New Haven, Conn., early in October, 1925. Since the acorns were collected during rainy weather they were spread out on a barn floor to dry for a few days, after which they were put in baskets and stored in

a cold storage room maintained by refrigeration at a temperature usually between 35 and 40° F. As a check on the Connecticut acorns, smaller samples were collected in the vicinity of Asheville, N. C., by E. H. Frothingham and F. W. Haasis of the Appalachian Forest Experiment Station, and in the vicinity of Raleigh, N. C., by J. S. Holmes, State Forester of North Carolina.

The viability of the different lots of acorns was tested under the controlled greenhouse conditions. A detailed set of experiments on the influence of excessive temperatures on germination was carried out in the laboratory and greenhouse. The influence of temperature on the germination of five common American oaks was studied in five constant temperature chambers.

Germination was studied in the greenhouse under three different controlled soil moisture conditions-dry, moist, and wet. Combined laboratory and greenhouse studies were made to determine (1) the relation of desiccation to germination, and (2) the degree of desiccation as related to the time required for germination.

Preliminary experiments indicated that there was an inherent delayed germination in the black oak group which was not overcome even by optimum conditions for germination. This phenomenon of delayed germination therefore was made the subject of a special study. The effect of acorn position with reference to the soil surface and the influence of various kinds of substrata on germination and early survival of oak seedlings were studied. Special attention was paid to the effects of sad and compactness of the surface soil and to the importance of leaf litter.

RESULTS OF GENERAL GERMINATION TESTS

REPRESENTATIVE lots of acorns collected in october, 1924, and numbered from 1 to 126 according to species and method of treatment, were tested at the Champion Fibre Company's nursery, Canton, N. C. In all tests where depth was not a factor the acorns were planted with the highest point of the acorn uniformly ½ inch below the surface, the acorns being placed crosswise of the nursery beds in rows 3 inches apart. Uniform covering was obtained with the acorn dibble, devised for this purpose (Fig. 4).

All beds received the same general treatment in accordance with the regular practice of the nursery. However, the beds in which germination and survival under ordinary conditions were being tested were screened

against birds and rodents, and were mulched from November 18 to March 28. From that time until April 7 the mulch was removed gradually to avoid sun-scalding the succulent tops which had begun to appear under

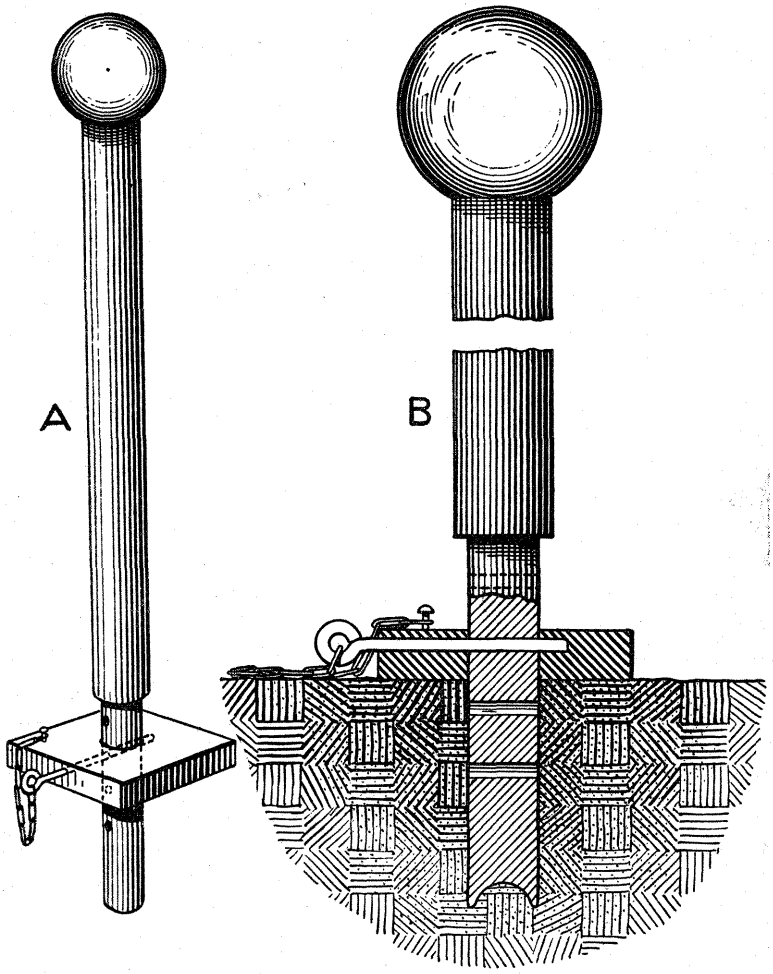

Fig. 4. Acorn dibble. A, perspective; B, vertical section.

the leaves. Screens giving half shade remained on the beds until April 30, when all shade was removed.

The results of these more general tests are summarized in Table I. The salient feature of the summary is the great variation in the germination

of the different lots of acorns. Failure in Lots 69 and 89 was definitely due to insect injury. Lot 70, which was also attacked by insects, had become partially dried before collection and was thereafter kept at room temperature for 10 days or more. Lots 84 and 85 suffered moisture loss in transit or in storage before planting. Subsequent results showed that such drying as has been referred to was sufficient to greatly reduce germination, and failure in the above cases was undoubtedly due to this factor. It is possible that Lots 1, 3, 6, 12, 87, and 92 were the only ones unaffected to any extent by drying.

Studies of the course of germination under controlled conditions in the greenhouse included 14 different species of oak, of which 8 belong to the white oak group and 6 to the black. In benches containing fresh loamy sand the acorns were planted at a uniform depth of ½ inch in crosswise rows. Sprinkling once a day sufficed to prevent drying out at the surface except during April when a second daily watering was necessary.

Continuous records of air temperature and of soil temperature at a depth of ½ to 1 inch-the same depth as the acorns were planted-were taken throughout the entire period with a Friez Soil-Air Thermograph. This instrument was checked against standard thermometers. The march of daily maximum and minimum temperatures of the air and the soil at this depth from October 16, 1925, to May 31, 1926, is shown in Fig. 5. The close correlation between air temperature and that of the soil is probably accentuated to some extent because the pipes of the hot water heating system are situated beneath the benches. The mean maximum soil temperature was between 65 and 70° F. during the first five months, while during the last six weeks it was between 70 and 75°. During the latter period the maximum soil temperature frequently rose to 80° or more. At night the soil temperature generally dropped to between 50 and 60°. Cloudy weather reduced the diurnal variation in temperature by decreasing insolation in the daytime and radiation at night. The diurnal variation in soil temperature ranged from 0 to 30 during cloudy weather and 10 to 20° or rarely 25° during clear weather with cold nights. The diurnal variation in air temperature was generally from 5 to 10° greater than that of soil temperature. In the present study soil temperatures are more important than air temperatures, because they indicate more closely the amount of heat to which the acorns are subjected.

Figures showing the course of germination are more significant and more generally useful than those showing either germinative energy or germinative capacity, as has been pointed out by Fron (1906), Rafn

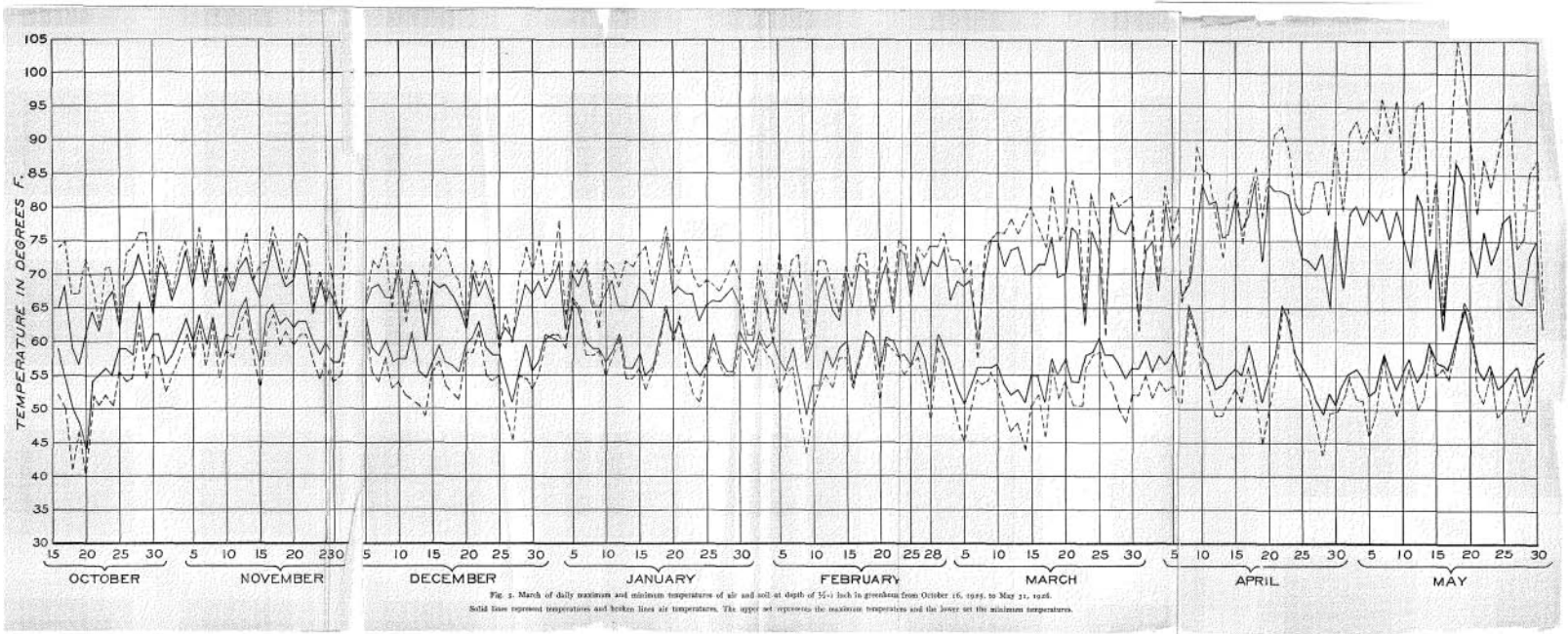

Fig. 2. March of daily maximum and minimum temperatures of air and soil at depth of 3½ inch in greenhouse from October 16, 1925, to May 31, 1926.

Solid lines represent temperatures and broken lines air temperatures. The upper set represents the maximum temperatures and the lower set the minimum temperatures.

(1915), and Toumey (1916). Germination counts were made every five days during the first three months and every ten days thereafter. The results, as given in Table II, were computed on the basis of 10 day intervals between counts, except the last which covers 50 days. In this series of tests an acorn was counted as germinated as soon as the ascending shoot was just visible above the surface of the soil. Table II shows great variability in the germination of the different lots, ranging from 6 per cent in Lot 25, southern red oak from near Raleigh, N. C., to 99 per cent in both Lot 6, swamp white oak, and Lot 12, white oak, each collected near New Haven.

The poor germination in some of these lots cannot be attributed to dryness of the acorns, for they were allowed to dry only slightly to prevent molding while they were in storage. It will be shown later that, particularly in the case of the acorns collected in the vicinity of New Haven, all

TABLE I

NURSERY GERMINATION AND SURVIVAL OF VARIOUS SPECIES OF OAK, SEASON OF 1925

Lot no.	*Species*	*No. acorns planted*	*Date of planting 1924*	*Nursery Germination April 21, 1925*	*Nursery Germination June 2, 1925*	*Survival Aug. 14, 1925*
				Per cent	Per cent	Per cent
1	Chestnut oak	107	Oct. 14	71.0	80.4	76.7
3	Chestnut oak	100	Oct. 14	73.0	82.0	82.0
6	Chestnut oak	100	Oct. 14	65.0	85.0	84.0
12	White oak	100	Oct. 14	41.0	73.0	72.0
14	White oak	100	Oct. 14	49.0	59.0	46.0
69	Red oak*	90	Nov. 7	0.0	0.0	0.0
70	Southern red oak	100	Nov. 7	0.0	0.0	0.0
72	Red oak	48	Nov. 7	68.7	70.8	64.6
79	Red oak	100	Nov. 7	76.0	76.0	74.0
83	European turkey oak	100	Nov. 7	55.0	65.0	65.0
84	Scarlet oak	100	Nov. 18	0.0	0.0	0.0
85	Chinquapin oak	100	Nov. 18	0.0	0.0	0.0
87	Black oak	100	Nov. 18	43.0	91.0	90.0
89	Black oak*	100	Nov. 18	0.0	0.0	0.0
92	Black oak	100	Nov. 18	32.0	88.0	68.0

* All acorns in these lots were weevil-infested, as shown by larvae exit holes.

TABLE II

COURSE OF GERMINATION IN VARIOUS SPECIES OF OAK IN THE GREENHOUSE, DURING WINTER OF 1925-1926*

Lot no.	Species	Locality	Number acorns planted	Percentage of Germination in Greenhouse																
				30 days	40 days	50 days	60 days	70 days	80 days	90 days	100 days	110 days	120 days	130 days	140 days	150 days	160 days	170 days	180 days	190 days	240 days
1	Chestnut oak	Asheville, N. C.	100	16	72	84	86	86	86	86	86	86	86	86	86	86	86	86	...	...	...
2	White oak	Asheville, N. C.	100	12	62	66	66	66	66	66	66	66	66	66	66	66	66	66	...	...	...
3	Post oak	Asheville, N. C.	21	0	33.3	33.3	61.9	61.9	61.9	61.9	61.9	61.9	61.9	61.9	61.9	61.9	61.9	61.9	...	...	...
4	European mossycup oak	New Haven, Conn.	50	0	0	2	6	24	38	44	62	72	80	80	80	80	80	88	...	...	...
5	English oak	New Haven, Conn.	50	0	38	70	92	96	98	98	98	98	98	98	98	98	98	98	...	...	...
6	Swamp white oak	New Haven, Conn.	100	0	2	13	37	58	68	83	85	93	95	96	97	98	98	99	...	...	...
7	Shingle oak	Asheville, N. C.	50	0	0	2	4	4	4	6	6	6	6	8	8	10	10	12	16	26	66
8	Red oak	Asheville, N. C.	100	0	0	0	5	8	8	9	9	10	10	10	11	11	11	11	11	11	...
9	Scarlet oak	Asheville, N. C.	100	0	12	17	20	22	23	23	23	23	23	23	23	24	24	24	24	24	...
10	Black oak	Asheville, N. C.	100	0	9	12	14	18	18	18	22	23	26	26	29	31	32	36	40	44	51
11	Red oak	New Haven, Conn.	250	0	0	0.8	2.0	3.2	5.2	6.4	8.4	9.2	9.6	10.8	10.8	12.8	13.2	13.6	14.0	14.8	28.8
12	White oak	New Haven, Conn.	100	38	93	98	98	99	99	99	99	99	99	99	99	99	99	99	99	99	...
13	Scarlet oak	New Haven, Conn.	100	0	0	1	2	2	3	5	6	8	8	9	9	11	12	13	14	19	31
14	Chestnut oak	New Haven, Conn.	100	23	78	84	86	86	86	86	86	86	86	86	86	86	86	86	86	86	87
15	Black oak	New Haven, Conn.	100	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	3	7
16	White oak	New Haven, Conn.	100	23	90	91	91	91	91	91	91	91	91	91	91	91	91	91	91	91	...
17	Scarlet oak "sinkers"†	Asheville, N. C.	100	0	1	2	2	3	4	6	12	18	22	29	33	40	46	51	51	51	70
18	Shingle oak	Asheville, N. C.	60	1.7	3.3	6.7	8.3	10.0	11.7	11.7	13.3	13.3	15.0	16.7	20.0	20.0	20.0	23.3	23.3	23.3	28.4
19	Southern red oak "sinkers"†	Asheville, N. C.	100	0	5	6	11	13	14	17	20	25	26	29	34	39	40	41	41	41	52
20	Southern red oak, ave.	Asheville, N. C.	100	1	3	6	7	7	8	10	11	12	12	12	12	13	13	14	14	14	20
21	Post oak‡	Asheville, N. C.	100	4	8	10	13	14	18	19	19	20	20	20	20	20	21	21	21	21	25
22	Black oak	Raleigh, N. C.	80	0	0	0	0	2.5	3.8	5.0	6.2	8.8	12.5	28.8	36.2	40.0	51.2	53.7	53.7	53.7	75
23	White oak	Raleigh, N. C.	80	1.2	20.0	25.0	26.2	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	28.8	31.2
24	Scarlet oak	Raleigh, N. C.	80	0	0	3.8	8.8	17.5	28.8	35.0	42.5	42.5	48.8	55.0	56.2	57.5	60.0	60.0	...	...	...
25	Southern red oak	Raleigh, N. C.	50	0	0	0	0	2	4	4	4	4	6	6	6	6	6	6	...	...	...
26	Willow oak	Raleigh, N. C.	50	0	0	0	2	2	4	8	8	8	8	10	10	12	14	14	14	14	22
39	Swamp chestnut oak	Raleigh, N. C.	60	0	3.3	45.0	73.3	80.0	81.7	81.7	83.7	86.7	86.7	86.7	86.7	86.7	86.7	...	...	...	...
40	Overcup oak	Raleigh, N. C.	100	0	0	1	2	20	54	79	82	84	84	84	84	84	84	...	...	...	...
41	Swamp white oak	Raleigh, N. C.	60	0	0	30.0	45.0	60.0	65.0	66.7	66.7	66.7	66.7	66.7	66.7	66.7	66.7	66.7	66.7	66.7	78.3

* Lots 1 to 3, inclusive, were planted October 10; Lots 4 to 16, inclusive, on October 15; Lots 17 to 21, inclusive, on October 28; and Lots 39, 40, and 41 on November 3, 1925.

† By "sinkers" is meant those acorns which sink when immersed in water.

‡ This lot of acorns showed a high percentage of weevil injury as evidenced by a large number of larvae exit holes.

lots contained moisture sufficient to insure retention of their viability until they were planted. The acorns of Lot 2, however, began to germinate while in transit from Asheville, and it is probable that they were injured sufficiently to account for the failure of 34 per cent of the acorns to produce seedlings. After the shells split open at the apex in the early stages of germination, the tender embryos are very easily injured-either by being bruised or through drying out. Considerable insect infestation was noted in the post oak from western North Carolina, particularly in Lot 21, which undoubtedly accounts for the low germination of 25 per cent.

Some of the lots received from North Carolina were large enough to supply material for viability cutting tests. This was possible because the embryos of sound viable acorns are normally light in color, while on loss of viability they darken perceptibly, often becoming brown or black. These tests clarify some of the germination results given in Table II. In Lot 8, red oak from,vestern North Carolina, only 12.4 per cent had living embryos of normal size. Some of these acorns ,vere infested with insect larvae, but the insects had destroyed less than half of the cotyledons at the ends farthest from the radicle and plumule. Insects destroyed 15 per cent of this lot. Forty-five per cent of these acorns had embryos in various stages of abortion from normal-colored and half.·sized embryos to those blackened and shriveled to about 1/20 natural size. This abortion may be due to the extremely great rainfall deficiency for the summer of 1925 in the vicinity of Asheville, N. C., amounting to almost 12 inches less than normal for the months of May to August, inclusive. Scarlet oak, a species common on drier sites, showed 91.8 per cent of the acorns with embryos apparently nor|||al in all respects and yet this lot (No.9) gave a germination of only 24 per cent in 190 days.

Black oak acorns from the same general locality showed 46.5 percent infested with insect larvae, but only 3.9 per cent aborted. Although 47.3 per cent of the acorns in this lot (No. 15) had embryos normal in all respects at the time of planting, a germination of only 7 per cent was obtained in 240 days.

S\vamp white oak acorns from eastern North Carolina showed 22.6 per cent with dead embryos, of which the greater number were the direct result of insect damage. This largely accounts for the germination of only 78.3 per cent in Lot 41.

The very poor results obtained from the white oak acorns from eastern North Carolina (Lot 23) is due almost \vholly to drying and other in-

juries, such as bruising, since 77.6 per cent began to germinate while in transit from Raleigh. The radicles protruding from the acorns were bruised and dried out. This conclusion is substantiated by the results of a cutting test on 233 acorns which showed 85 per cent either germinated (78.1 per cent actually germinated) or with viable embryos. Only 14.6 per cent showed insect injury.

Another lot, No. 11, consisting of red oak from near New Haven, showed 72.8 per cent with normal appearing embryos-only 27.2 per cent being infested with insect larvae. In this lot, as well as in some of the others, the cutting test failed to explain the low germination. This suggests that in some species there may be an inherent condition capable of inhibiting germination or at least of causing delayed germination. The validity of this hypothesis is emphasized when the relative germinative energies for both the black and white oak groups are considered. Lots 8, 21, and 23 are eliminated from this consideration because of the fact that, as already brought out, the poor germination in these lots is due to external factors not inherent in the embryo. If arbitrary periods of 60 and 160 days are considered, it is found that the species of the black oak group have an average germination of 5.9 per cent in 60 days, or only 24.1 per cent of that attained in 160 days, while the species of the white oak group show an average germination of 62 per cent in 60 days, which is 74.2 per cent of that attained in 160 days. After eliminating three species-the European mossycup, swamp white, and overcup oaks—the remainder of the white oak group have an average germination of 81.8 per cent in 60 days, which is 97 per cent of that occurring in 160 days. The three species mentioned first showed an average germination per cent of 22.5 in 60 days, which is only 27.4 percent of that (82.2) obtained in 160 days.

Under the conditions of these tests, an average period of 44 days was required for 75 per cent of the total germination in the group containing the white, post, English, and chestnut oaks, an average of 85 days for the group composed of the European mossycup, swamp white, and overcup oaks, and an average of 163 days for all the species of the black oak group.

These differences suggest that some of the species either possess inherent characteristics which influence the inception and rate of germination, or that they have different temperature requirements for germination. It is quite possible that an interdependence exists between these two conditions. This question, however, will be considered in connection with the study of germination in the constant temperature chambers.

ANALYSIS OF FACTORS INVOLVED

THE results given above emphasize the need for detailed studies to determine the relative importance of the factors controlling germination and early survival of oaks. In many localities and under many conditions one is frequently impressed with the very prolific production of acorns, particularly in good seed years, and also at times one observes the forest floor littered with germinating acorns and yet often must search diligently for established oak seedlings. An early phase of this investigation consisted of a field study in Buncombe County, N. C., to determine what happens to the acorn crop after it reaches the forest floor, and to what extent and under what natural conditions germination and survival occur. Preliminary observations indicated that such a study could best be made by a careful classification of the various forms of injury, kinds of destroying agents, and the condition of all acorns as determined by a cutting test. It was possible to secure records from 37 individual trees: 15 chestnut oaks, 12 white oaks, 9 black oaks, and 1 red oak, selected as to position in the stand, topography, and seed production.

An area typical of the entire crown spread of the tree, but representing one sixth of the crown projection, was selected under each tree. Two men laid out these areas by stretching a tape between the base of the tree and two points on the perimeter of the crown projection. The distance apart of these points was equal to the radius of the crown spread of the tree. All acorns and acorn cups on this area were collected, sacked, and taken to the laboratory for subsequent investigation. It was found that the various animals frequenting the area often carried away sound acorns but that they carried away very few, if any, unsound ones.

The record of the total yield was obtained by counting the cups of the season's crop, and from this number the total acorn production for each tree was approximated by making use of the fact that for each normal cup an acorn was produced, and of the observation that the acorns are normally shed from the tree somewhat in advance of the cups. All cups had fallen from the trees by the time the records were taken. The difference between the total production and the number of acorns found or accounted for was attributed to the animals.

The first data were secured November 3, 1924, from a 19 inch white oak, 65 feet tall, having a crown spread of 30 feet and representing average site conditions on the Bent Creek watershed, southwest of Asheville, N. C.

The results obtained from this tree, on the basis of a calculated total production of 14,075 acorns, are summarized as follows:

			Per cent
Acorns destroyed by animals			83.04
Acorns infested by insects:	weevils	2.35	
	moth larvae	3.45	
			5.80
Acorns with aborted embryos			10.44
Germinated acorns, seedlings dead, dried out			0.31
Germinated acorns, seedlings alive			0.15
Acorns with normal embryos			0.26

During the course of the work on this tree it became evident that since the acorns had been shed but about a month, results obtained in the spring would be much more indicative of the cumulative effect of the factors tending to destroy the viability of the acorns and to preclude natural establishment in the different species. The remainder of this work was therefore deferred until spring, when the records on the other 37 trees were secured between March 23 and April 24, 1925. The significant facts obtained in this study are shown in Table III. It is of interest to note the fair showing in percentage of live seedlings from the germinated white oak acorns and the poor showing of the chestnut oak and particularly the black oak. Notwithstanding the high percentage of acorns destroyed, it is notable that from those trees which produced seed in 1924 a few acorns escaped destruction. The factors responsible for destruction will be considered under the discussion of the specific factors in the following pages.

Further field study emphasized the two factors, animals and drought. In this study small plots, contiguously located on both north and south-facing slopes on the Bent Creek watershed, southwest of Asheville, N. C., were planted with 100 acorns each of several species, chiefly scarlet, black, red, white, and chestnut oaks. The north slope plots were located in a small clearing made for this purpose on the edge of an oak-chestnut forest, while the south slope plots were located in an opening in a pine-oak forest. Different lots of acorns were planted ½ inch deep in well-tilled soil on each aspect; others were placed on the natural soil surface and covered with hardwood leaves. Duplicate sets were screened with ¼ inch mesh hardware cloth tacked to boards which were sunk edgewise into the soil to a depth of 2 inches.

Survival records, as obtained on these plots on May 3 and August 5, 1925, are given in Table IV. A high percentage of acorns in many of the lots was destroyed by rodents before germination. The increases noted in some lots between examinations are due to the fact that germination was still in progress on May 3. The losses in 10 out of the 50 lots were

TABLE III

DISPOSITION OF ACORN CROP UNDER NATURAL CONDITIONS

Based upon the acorn production of 37 representative trees in Buncombe County, N. C.

	Chestnut oak	*White oak*	*Black oak*	*Red oak*
Basis, no. of trees	15	12	9	1
Diameter breast high, inches*	9.9-23.0	10.1-27.0	15.2-23.5	20
	15.5	17.3	18.2	
Crown diameter, feet*	16-36	13-39	25-44	40
	25.7	23.5	33.0	
Computed average no. acorns produced per tree	1,754	4,911	4,930	20,388
Acorns destroyed by animals, per cent	74.78	72.20	66.93	56.51
Acorns destroyed by insect larvae, per cent	9.80	10.57	27.69	24.19
Germinated acorns, dead, drying, per cent	5.37	9.04	....	0.35
Germinated acorns, dead, animals, per cent	0.02	....	....	....
Germinated acorns, dead, insects, per cent	4.50	1.75	....	....
Germinated acorns, seedlings alive, per cent	0.78	4.47	0.01	2.00
Acorns with dead embryos, dark, hard, or moldy, per cent	4.61	1.95	5.01	12.30
Acorns with normal embryos, per cent	0.14	0.02	0.36	4.65
Total	100.00	100.00	100.00	100.00

* In the figures for diameter breast high and crown diameter, given in fractional form, the numerator represents the range from the minimum to the maximum, and the denominator the average.

TABLE IV
SURVIVAL OF OAK SEEDLINGS UNDER VARIOUSLY MODIFIED FIELD CONDITIONS, SEASON OF 1925

Plot no.	*Species*	*Location of acorns*	*Soil tilled or untilled*	*Covered with leaves or not covered*	*Screened or not screened*	*Surviving seedlings**	
						May 3	*Aug. 5*
			North Slope Plots			Per cent	Per cent
1	Sprouted white oak	On soil surface	Untilled	Covered	Not screened	5	4
2	Sprouted white oak	Planted ½ in. deep	Tilled	Not covered	Not screened	13	14
3	Sprouted chestnut oak	On soil surface	Untilled	Covered	Not screened	7	6
4	Sprouted chestnut oak	Planted ½ in. deep	Tilled	Not covered	Not screened	4	15
5	White oak	On soil surface	Untilled	Covered	Screened	80	37
6	White oak	Planted ½ in. deep	Tilled	Not covered	Screened	19	13
7	Chestnut oak	On soil surface	Untilled	Covered	Screened	86	36
8	Chestnut oak	Planted ½ in. deep	Tilled	Not covered	Screened	68	66
9	White oak	On soil surface	Untilled	Covered	Not screened	0	0
10	White oak	Planted ½ in. deep	Tilled	Not covered	Not screened	0	0
11	Chestnut oak	On soil surface	Untilled	Covered	Not screened	0	3
12	Chestnut oak	Planted ½ in. deep	Tilled	Not covered	Not screened	1	1
13	Red oak	On soil surface	Untilled	Covered	Screened	0	0
14	Red oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
15	Black oak	On soil surface	Untilled	Covered	Screened	0	0
16	Black oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
17	Red oak	On soil surface	Untilled	Covered	Not screened	0	0
18	Red oak	Planted ½ in. deep	Tilled	Not covered	Not screened	1	1
19	Black oak	On soil surface	Untilled	Covered	Not screened	0	0
20	Black oak	Planted ½ in. deep	Tilled	Not covered	Not screened	1	6
21	Southern red oak	On soil surface	Untilled	Covered	Screened	0	0
22	Southern red oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
23	Scarlet oak	On soil surface	Untilled	Covered	Screened	0	0
24	Scarlet oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
25	Chinquapin oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
26	Chinquapin oak	Planted ½ in. deep	Tilled and limed	Not covered	Screened	0	0

* Based on original planting of 100 acorns in each lot.

TABLE IV (Continued.)

Plot no.	*Species*	*Location of acorns*	*Soil tilled or untilled*	*Covered with leaves or not covered*	*Screened or not screened*	*Surviving seedlings* May 3*	*Aug. 5*
						Per cent	Per cent
			South Slope Plots				
1	White oak	On soil surface	Untilled	Covered	Screened	2	5
2	White oak	Planted ½ in. deep	Tilled	Not covered	Screened	8	22
3	Chestnut oak	On soil surface	Untilled	Covered	Screened	1	2
4	Chestnut oak	Planted ½ in. deep	Tilled	Not covered	Screened	7	10
5	White oak	On soil surface	Untilled	Covered	Not screened	1	2
6	White oak	Planted ½ in. deep	Tilled	Not covered	Not screened	6	12
7	Chestnut oak	On soil surface	Untilled	Covered	Not screened	0	1
8	Chestnut oak	Planted ½ in. deep	Tilled	Not covered	Not screened	12	16
9	Sprouted white oak	On soil surface	Untilled	Covered	Not screened	5	4
10	Sprouted white oak	Planted ½ in. deep	Tilled	Not covered	Not screened	8	19
11	Sprouted chestnut oak	On soil surface	Untilled	Covered	Not screened	3	4
12	Sprouted chestnut oak	Planted ½ in. deep	Tilled	Not covered	Not screened	6	12
13	Red oak	On soil surface	Untilled	Covered	Screened	38	30
14	Red oak	Planted ½ in. deep	Tilled	Not covered	Screened	24	31
15	Southern red oak	On soil surface	Untilled	Covered	Screened	0	0
16	Southern red oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
17	Red oak	On soil surface	Untilled	Covered	Not screened	0	0
18	Red oak	Planted ½ in. deep	Tilled	Not covered	Screened	7	12
19	Black oak	On soil surface	Untilled	Covered	Screened	22	2
20	Black oak	Planted ½ in. deep	Tilled	Not covered	Screened	16	9
21	Scarlet oak	On soil surface	Untilled	Covered	Screened	0	0
22	Scarlet oak	Planted ½ in. deep	Tilled	Not covered	Screened	0	0
23	Black oak	On soil surface	Untilled	Covered	Not screened	3	9
24	Black oak	Planted ½ in. deep	Tilled	Not covered	Not screened	2	2

* Based on original planting of 100 acorns in each lot.

due chiefly to the summer drought previously noted and to destruction of the seedlings by May beetle larvae. The data given in Table IV, together with that in Tables I to III, inclusive, will be analyzed in greater detail under the appropriate headings.

BIOTIC FACTORS

Consumption of Acorns by Mammals and Birds. The percentage of acorns which may be consumed by mammals is shown in Table III. While these data were being collected, abundant evidence was found that animals had destroyed a large percentage of the acorns from many of the trees. The best evidence was found in the form of pieces of shell lying in little piles or strewn over the ground. Tooth marks of deer and small rodents were observed on these fragments. This, together with the greater accumulation of fecal matter here than elsewhere, leads naturally to the conclusion that the areas under many oak trees are feeding grounds for a large number of such animals.

In Table IV, the poor showing in the survival figures for May 3 is due chiefly to the great activity of rodents. On the unscreened plots the work of squirrels and mice was particularly evident. Scratchings and other evidence indicated the work of wild turkeys. In the screened plots the destruction was caused principally by mice which burrowed under the frames. These screened plots were found to be literally undermined by their burrows. Survival under such conditions is due largely to the chance missing of the acorns by the rodents.

While no consistent attempt was made to segregate animal damage by different kinds of animals, a clear-cut case of the great avidity of deer for acorns was observed in several counted lots which were put out on the forest floor to test over-winter storage under natural conditions. In one group of unscreenedplots the acorns were almost completely consumed, during the first two weeks. Only two chestnut oak acorns and one of white oak remained from 200 acorns of each species put out. One hundred red oak and the same number of black oak acorns put out three weeks later (November 14, 1925) were completely destroyed during the following night. Abundant evidence in the form of tracks, characteristic deer feces, typical tooth marks, and crushed shells, which had not been gnawed as are acorns destroyed by rodents, all unmistakably pointed to deer as the cause of damage.

Another experiment served to emphasize the avidity of rodents for

acorns. One hundred red oak and 140 European turkey oak acorns were seed-spotted in the autumn of 1924, in an open field bordering an oak-chestnut forest. Half the acorns were coated with pine tar, and then rolled in pulverized limestone to make them less sticky and more easily handled. In the spring of 1925 each lot of the European turkey oak showed a germination per cent of 4.3, there being no difference between the two lots in the amount of rodent damage. Thirty-eight per cent of the untreated and 12 per cent of the treated red oak acorns germinated. The destroyed acorns were dug up chiefly by squirrels in the autumn early winter. Since they were selected from the same lot and were planted side by side, it must be concluded that tar is not a satisfactory rodent deterrent.

Rodents have frequently been credited with aiding the natural reproduction of forest trees. They have been repeatedly observed burying viable acorns and likewise recovering and eating them. Only the very small percentage of acorns which are not recovered actually contribute to the quota of established reproduction. Emphasis, therefore, must not be placed on the beneficial effect of rodent work considering the great amount of damage they do to the acorn crop. These studies, together with many other observations, indicate that from 90 to 100 per cent of the available acorn supply may be consumed or otherwise destroyed by animals. Among the mammals and birds known to feed upon acorns, the following may be listed: deer, bears, cattle, hogs, rabbits, squirrels, chipmunks, mice, turkeys, crows, jays, and blackbirds, and there are doubtless many others.

Destruction of Acorns by Insects. Table III shows that the amount of insect injury is variable and infestations are often localized. The extent of injury was found to vary from none with chestnut oak to over 50 per cent in the black oaks. Black oaks were found to be generally more heavily infested than white oaks. Of the 37 trees studied in detail, the black oaks averaged 27 per cent and the white oaks 10 per cent destruction by acorn-feeding insects.

The acorn-destroying insects encountered in the present investigation belong to three main groups: (1) nut weevils or curculios, (2) moth larvae, and (3) gall-forming Cynipids. Murtfeldt (1894) gives notes on all three groups. The nut weevils have been studied by Chittenden (1908), Brooks (1910), and Leng (1920). About 40 species of *Curculio* have already been described, and with the exception of one infesting chestnut and chinquapin, one attacking hazel, and one hickory and pecan, all are believed to be acorn

feeders.[4] According to Packard (1890), there are only two known species of moth larvae infesting acorns in this country-*Valentinia glandulella* Riley and *Melissopus latiferreanus* Walsingham.[5] Weld (1922) described a number of Cynipids, especially several species of Callirhytis which form "stone" galls in various species of acorns. However, the Cynipids encountered in the present study were principally *Callirhytis fructuosa* Weld and *C. lapillula* Weld, according to Weld's determinations.

Additional information on destruction by insects was obtained from cutting tests, summarized in Table V. A striking variation exists between the amount of injury in the different lots. In heavy infestations weevil damage is greatly in excess of that by other insects. In about 75 per cent of the weevil-infested acorns, over half of the cotyledons have been destroyed so that even in the few cases in which the embryos survive they cannot develop normally because of the curtailed food supply. Insect-infested acorns are subject to more rapid decay than uninfested ones. The percentage of normal seedlings developing from weeviled acorns is practically negligible. On the other hand, many of the acorns infested with Cynipids are capable of normal development. They interfere with the germination process only when their galls are formed in the embryonic tissues near the apex.

The old-fashioned water test for separating infested acorns has been advocated by Heyer and Hess (J909), and by Buhler (1922). Its applicability to the elimination of "wormy" chestnuts has been mentioned by Chittenden (1908). Experiments were carried out in the autumn of 1924 to test the efficiency of the flotation test. A preliminary test with white and red oak acorns showed that because of the higher specific gravity of the white oak acorns a solution of greater density is required for these than for the black oak. Accordingly a sugar solution having a specific gravity of 1.05 was used for the white and chestnut oak acorns and water was used for red and black oak. Those tested in the sugar solution were afterward washed in water. All acorns were dried immediately after flotation by means of blotters and the air current of an electric fan. The results of this test are summarized in Table VI.

As a check on the flotation method cutting tests were made on several

[4] Larvae of *Conotrachelus* sp. were also found. All determinations of insects were made by specialists of the Bureau of Entomology, U.S. Department of Agriculture" to whom the writer is under obligation.

[5] Larvae of *Ephestia* sp. were found, but were not considered important in the present study.

lots. One hundred red oak acorns which floated in water were selected at random and examined. Of these 30 per cent were normal in all respects, 55 per cent insect-infested (45 per cent by weevils and 10 per cent by Cynipids), 9 per cent diseased, and 6 per cent had aborted embryos. Twenty-eight out of the 30 normal acorns which floated had an unusually thick, felty layer on the inside of the pericarp and a small air space between it and the seed coat. Another lot of floated acorns on being opened showed 57 per cent destroyed by insects and the remainder sound.

In another lot of 100 red oak acorns which sank in water as many as

TABLE V

PERCENTAGE OF INSECT INJURY IN VARIOUS LOTS OF ACORNS AS DETERMINED BY CUTTING TESTS

Species	*Locality*	*Basis of test*	*Injury by Insects*			*Total amount of insect injury*
			Weevils	*Moth larvae*	*Cynipids*	
		No. of acorns	Per cent	Per cent	Per cent	Per cent
White oak*	Asheville, N. C.	1,944	4.4	6.0	0.0	10.4
White oak	Raleigh, N. C.	233	12.0	2.6	0.0	14.6
White oak*	New Haven, Conn.	400	0.0	0.0	0.0	0.0
Chestnut oak*	New Haven, Conn.	400	0.0	0.0	1.2	1.2
Swamp white oak	Raleigh, N. C.	159	20.8	0.0	0.0	20.8
Swamp chestnut oak	Raleigh, N. C.	126	0.0	0.0	0.0	0.0
Overcup oak	Raleigh, N. C.	273	54.9	0.0	0.0	54.9
Black oak*	Asheville, N. C.	127	29.9	3.9	12.6	46.4
Red oak*	Asheville, N. C.	193	7.8	10.9	0.0	18.7
Red oak*	New Haven, Conn.	400	5.0	0.0	0.0	5.0
Red oak	New Haven, Conn.	199	25.6†	1.5	0.0	27.1
Scarlet oak*	Asheville, N. C.	400	2.2	0.0	0.0	2.2
Scarlet oak*	Asheville, N. C.	160	0.0	0.0	1.9	1.9

* These lots were collected for sound viable acorns. The percentage of infestation, therefore, was lower than if no selection had been made.

† *Curculio baculi* Chttn. and *C. pardalus* Chttn. have thus far been identified from this lot of acorns by Dr. F. H. Chittenden, Entomologist, Bureau of Entomology, U.S. Department of Agriculture.

possible abnormally colored ones were included. The appearance and condition of each acorn was tabulated. Of these 58 per cent were sound and apparently viable, 40 per cent weevil-infested, and 2 per cent diseased. Of the 40 per cent which were abnormal in external appearance, 12 per cent had apparently viable embryos while 28 per cent were insect-infested or diseased. The presence of ovipositor scars and abnormally dark colorations are good indications of insect infestation or a diseased condition in

TABLE VI

RESULTS OF FLOTATION TEST IN VARIOUS LOTS OF ACORNS

Species	*Basis of test*	*Acorns which sank to bottom*	*Nursery germination*
	No. of acorns	Per cent	Per cent
White oak (large-sized acorns)	79	82.3	100
White oak (medium-sized acorns)	67	61.2	48
White oak (small-sized acorns)	202	47.0	16
White oak (small-sized acorns)	204	43.6	. .
White oak (unselected, all sizes)	4,992	63.5	72
White oak (insect-infested acorns)	249	10.1	. .
Chestnut oak (unselected, all sizes)	4,602	74.0	86
Chestnut oak (medium-sized acorns)	400	71.5	82
Red oak (small-sized acorns)	275	39.4	. .
Red oak (unselected, all sizes)	512	26.6	. .
Red oak (unselected, all sizes)	4,568	61.2	. .
Red oak (large-sized acorns)	86	43.0	*
Red oak (medium-sized acorns)	125	38.4	†
Red oak (small-sized acorns)	203	13.8	‡
Black oak (immature acorns)	100	0	. .
Black oak (unselected, all sizes)	968	73.8	. .
Black oak (unselected, all sizes)	2,311	64.0	. .
Black oak (unselected, all sizes)	1,062	23.3	. .
Black oak (insect-infested acorns)	100	5.0	0.

* Those which sank had a germination of 77.8 per cent, while of those which floated only 18 per cent germinated.

† Those which sank had a germination of 68.8 per cent, while of those which floated 52 per cent germinated.

‡ Those which sank had a germination of 60.7 per cent, while of those which floated only 39.4 per cent germinated.

red oak acorns. Of 84 black oak acorns which floated, 45.2 percent were sound" 47.6 per cent insect-infested, and 7.2 per cent diseased. In scarlet oak both sound and insect-infested acorns floated in water.

Noticeably "wormy" acorns, as evidenced by larvae exit holes and loss of weight, generally float, but those which do not also may be infested and require further test to determine their soundness. However, this test is well worth while for the separation of badly infested and aborted acorns from lots which cutting tests show to have an appreciable percentage of infested, aborted, or diseased acorns. In many cases this test will increase the reliability of the results of experimental work and will reduce the cost of seeding operations.

Seedlings in both the nursery and the Bent Creek field tests were affected by May beetle larvae. Mortality caused by these larvae cutting off the roots 1 to 2 inches below the surface of the ground did not exceed 5 per cent in anyone lot.

Fungi. In making the cutting tests, a correlation was noted between insect infestation and the presence of molds. It was not uncommon to find mold, particularly *Pellicillium,* in acorns with ovipositor scars although the insects did not develop. The mold may have entered the acorn through the vascular bundles at the base of the pericarp. Aside from the predisposition of insect-infested acorns to attack by molds, sound acorns stored under temperature and moisture conditions optimum for retention of viability were surprisingly free of mold.

In the field study of the disposition of the acorn crop under natural conditions only 0.48 per cent of the white oak, 0.07 per cent of the chestnut oak, and none of the sound uninfested red and black oak acorns had molded under natural field conditions. The loss due to molding increases slightly in storage under artificial conditions, the maximum amounting to 4 per cent.

Two parasitic fungi were encountered in both acorn storage and in the greenhouse experiments. These fungi killed the root tips or sometimes the entire succulent radicles as they emerged. Fig. 6 shows the effect of these fungi on the subsequent root development where only the tips of the radicles were killed. Similar results are produced when the root tips are injured.

Infection by these fungi occurs during the early stages of germination. The radicles are most susceptible at their growing tips and the injury is confined to the inch nearest the tip. As the roots harden they become

immune to these fungi. This immunity usually becomes pronounced after two to three weeks.

Dr. Florence A. McCormick, Pathologist at the Connecticut Agricultural Experiment Station, determined a species of *Botrytis* to be present on the stored acorns and a *Fusarium* to be responsible for the greenhouse injury. Inoculations on radicles less than 1 inch long were from 50 to 80 per cent successful. With longer and older radicles inoculations were generally unsuccessful. No appreciable difference was observed in the susceptibility of the oaks studied.

INFLUENCE OF MOISTURE ON GERMINATION

The field study to determine the disposition of the acorn crop under natural conditions (Table III) emphasizes the fact that, after the mammals and insects had destroyed the greater part of the crop, the few acorns remaining were influenced by the important physical factors, particu-

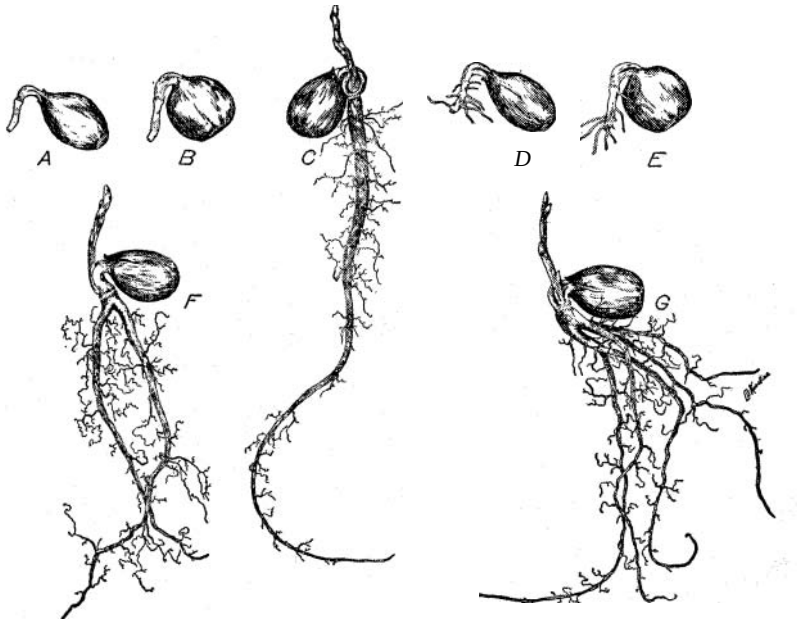

Fig. 6. Recently germinated white oak seedlings; A and B, with newly-injured root tips; D and E, same seedlings a few days later showing development of lateral rootlets; F and G, same seedlings two to three weeks later. Note the greater abundance of fibrous roots as contrasted with C, a seedling of normal development.

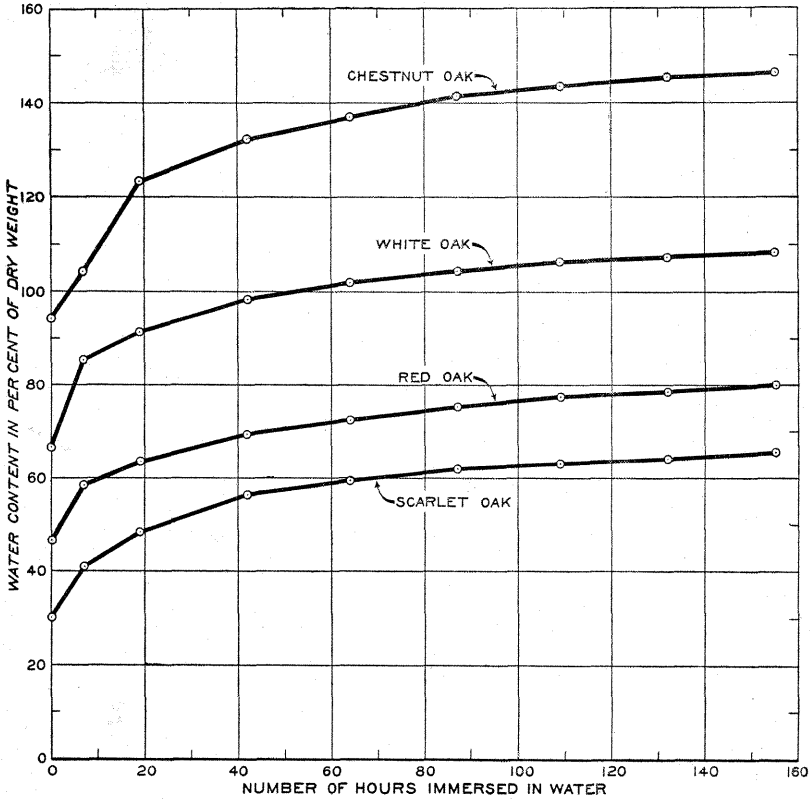

Fig. 7. Water absorption by red, scarlet, white and chestnut oak acorns in 155 hours.

larly moisture and temperature. These are of the utmost importance not only because moisture and heat are necessary for germination and growth but also because they are required in suitable combinations for the retention of acorn viability. Studies of the water relations of the acorn should logically follow two lines: (1) moisture conditions within the acorn, and (2) moisture conditions of the environment.

Critical Range of Moisture Conditions Within Acorns. When acorns become overdry the embryos assume a stony hardness and lose their viability. Those of the white oak group generally turn brown in color. A few figures correlating water loss with germination are given by Watt (1919). As indicated by him, the amount of water loss is an inexact basis

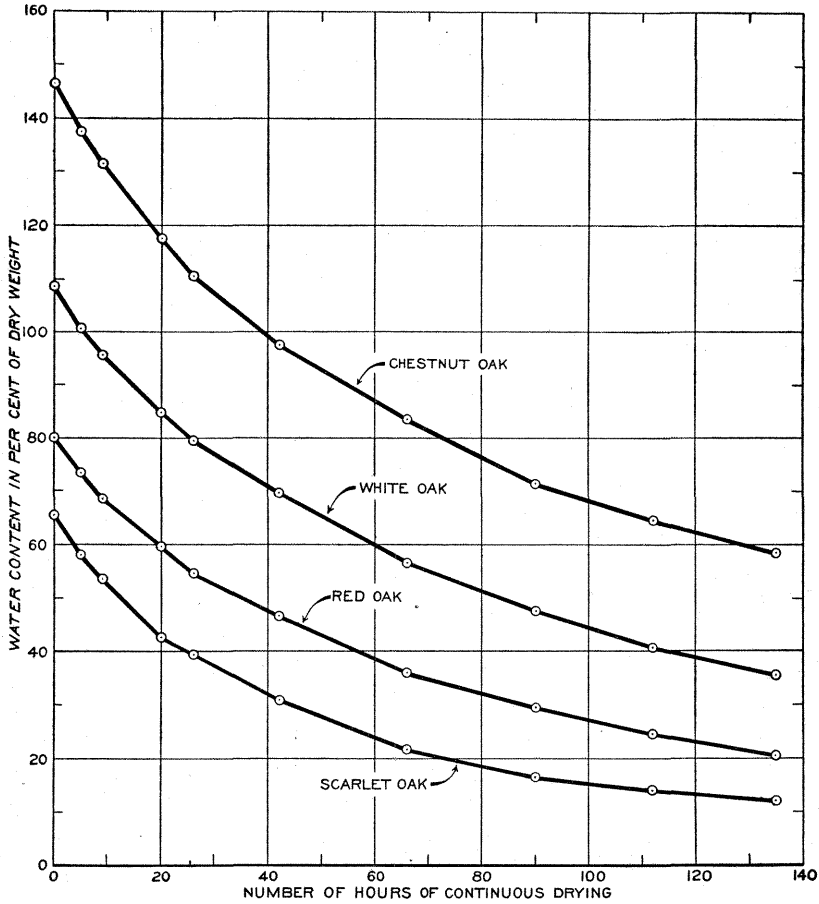

Fig. 8. Water loss in red, scarlet, white and chestnut oak acorns after immersion in water for 155 hours.

upon which to attempt a correlation between germination and the moisture conditions of the acorn, because of the variation in the amount of water in the acorn at different times. The moisture content in per cent of dry weight is a better basis upon which to correlate the moisture conditions within the acorn and viability. The objection to this latter basis has been made that the acorns must be thoroughly dried at 212° F. to bring them to constant weight, and in so doing their viability is destroyed. This objection was easily overcome by using a sufficiently large quantity of acorns

so that after drying for the desired length of time each lot was divided into aliquot parts for the determination of (1) actual moisture content and (2) percentage of germination.

Three preliminary experiments were carried out to provide a basis for the selection of the different time intervals during which the acorn should be dried and to secure information on water absorption and water loss in representative species under laboratory conditions (Figs. 7 to 9). In these graphs each point represents the average of three separate moisture content determinations. In the water absorption experiment (Fig. 7) the acorns were immersed in water at room temperature and at each weighing were taken out and dried for 10 minutes by constantly moving them about

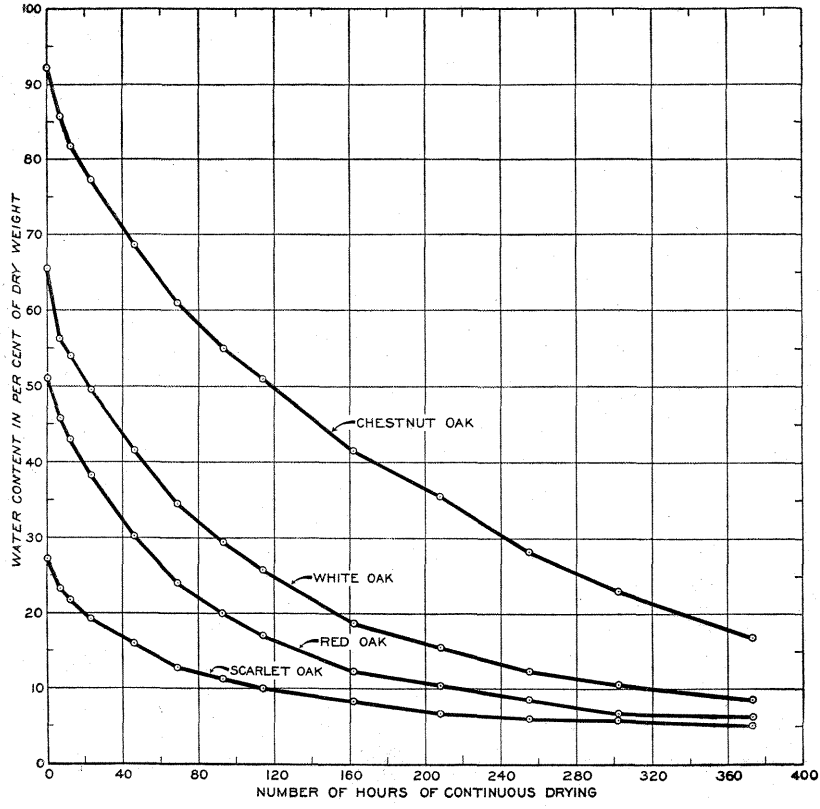

Fig. 9. Rate of water loss in red, scarlet, white and chestnut oak acorns taken directly from cold storage.

in the air current of an electric fan. This drying removed all water from the surface of the acorns. After weighing they were again immersed in fresh water. The greater water-holding capacity of the white oak group is strikingly brought out in Fig. 7. The great water-absorbing capacity of the chestnut oak is due chiefly to the unusually thick layer of parenchyma tissue in the fruit coat. When the rate of water absorption in the acorns of the four different species became very low, at the end of 155 hours of soaking, they were allowed to dry in the laboratory air. The acorns were weighed at intervals during the drying period of 135 hours, their moisture contents determined and figures obtained on water loss and water absorption calculated to a dry weight basis (Fig. 8). The graphs of water loss for each species assume much the same shape and relative position as in Fig. 7.

Since many of the white and chestnut oak acorns used in these experiments began to germinate while immersed in water, and a few of the red and scarlet oak fruit coats split open, the drying experiment was repeated with fresh material taken directly from cold storage. The results of the second drying experiment (Fig. 9), confirm those given in Fig. 8, except

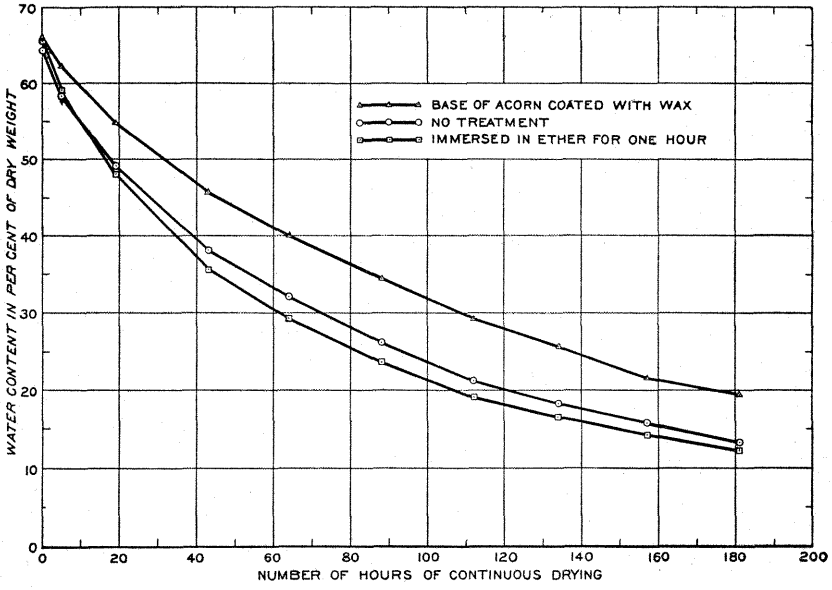

Fig. 10. Rate of water loss in red oak acorns on laboratory table under different kinds of treatment.

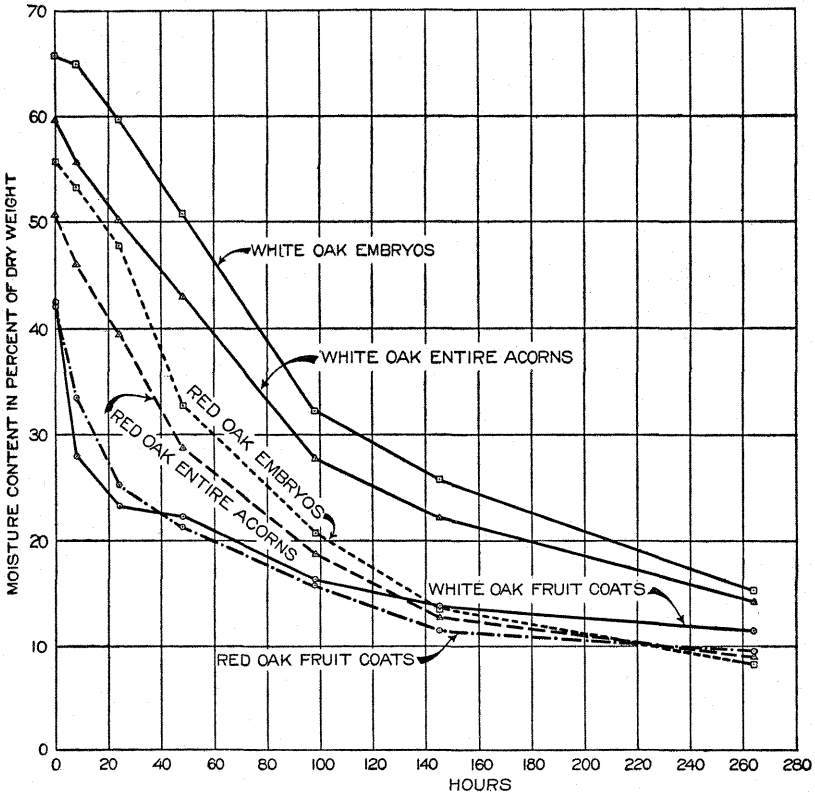

Fig. 11. Rate of moisture loss from the embryos and fruit coats of red and white oak acorns lying on laboratory table.

that the actual water contents naturally differ. The relative rates of water loss are strikingly similar to those shown in Fig. 8 for the same species.

To throw light on the amount of water lost through the vascular bundles in the acorn base and the extent to which the fats deposited in the cuticle retard water loss, the data given in Fig. 10 were taken on three different lots of red oak acorns. Each lot contained 75 acorns. In one lot the vascular bundles in the acorn base were sealed with a wax composed of two parts of paraffin to one of vaseline. Another lot was soaked in ether for one hour, during which time 0.033 gram of fat was extracted from their cuticles. Another experiment showed that longer treatments resulted in a sufficient

TABLE VII

RELATION BETWEEN MOISTURE CONTENT OF THE EMBRYOS AND GERMINATION IN WHITE AND RED OAK ACORNS

Lot no.	*Species*	*Length of drying period prior to planting*	*Moisture content of embryos based on dry weight at time of planting*	*Greenhouse germination**
		Hours	Per cent	Per cent
1	White oak	0	65.6	76
2	Red oak	0	55.8	59
3	White oak	8	65.0	76
4	Red oak	8	53.2	54
5	White oak	24	59.8	65
6	Red oak	24	47.6	56
7	White oak	48	50.6	63
8	Red oak	48	32.7	60
9	White oak	98	32.1	12
10	Red oak	98	20.7	24
11	White oak	145	25.6	0
12	Red oak	145	13.6	3
13	White oak	264	15.3	0
14	Red oak	264	8.7	0

* Based on 100 acorns in each lot.

penetration of the ether through the vascular bundles in the acorn base to kill the adjacent parts of the cotyledons. A third lot of acorns was used in the untreated condition. The results of this experiment are given in Fig. 10. Although the amount of fat extracted was small and the corresponding influence not great, the presence of the fatty substances in the cuticle apparently decreases the permeability of the fruit coat. The experiment shows the extent of water loss through the vascular bundles in the base of the fruit coat; but even with the bundles sealed the acorns still lose a considerable quantity of water through the cutinized exodermal layer.

After definitely establishing the shape of the curve representing water loss from acorns, a series of drying periods was selected. These were

intended to result in decrements of about 10 per cent in water content and to bring out a correlation between moisture content and viability in red and white oak acorns. In this experiment it was considered essential to determine the moisture content of the embryos and fruit coats separately after the various lots of acorns had been dried for different lengths of time at room temperature (Fig. 11). While this experiment was in progress the relative humidity of the laboratory air averaged 25 per cent, ranging from 20 to 40 per cent. One hundred acorns were taken from each lot and planted in the greenhouse. The percentages of germination, together with the other pertinent data, are given in Table VII. The white oak acorns lost their viability between moisture contents of 50 and 25 per cent of the dry weight of the embryos. With a moisture content of 32.1 per cent, a germination of only 12 per cent was secured, while red oak with a moisture content of 32.7 per cent germinated 60 per cent as much as with no preliminary drying.[6] This experiment leads to the conclusion that when the moisture content of white oak seeds (exclusive of the fruit coats or shells) falls to between 50 and 30 per cent of their dry weight, a marked decrease in viability may be expected, while in red oak this marked diminution does not occur until their moisture content has fallen to between 30 and 20 per cent. This difference is probably due to the higher oil content of the red oak acorns, which will be considered in the discussion of delayed germination.

Mention should be made of the relation existing between the hardness of the cotyledons and germination. In Lots 1 to 8, inclusive, the cotyledons were moist and pliable; in Lot 9, 62 per cent of them had become hard, brittle, and dark colored; while in Lot 10, 36 per cent were still pliable and leathery, the others being brittle but not so hard as those of the white oak. The acorns evidently lose their viability at or about the time they become hard and brittle.

An interesting correlation between moisture content and color of the acorns was noted during the drying in the above experiments. The shells of the white oak acorns at the beginning of the experiments were a Vandyke brown-the same color as when the acorns were first shed. Upon drying, the shells became muchlighter in color, passing through various shades of brown from Sayal brown and clay color to cinnamon buff when very

6 Jones (1920) has shown that seeds of silver maple (*Acer saccharinum)* contain about 60 per cent moisture when they fall. They lose their viability if the moisture is reduced to 33 percent before germination.

dry.[7] When red oak acorns contain abundant moisture their color varies from cacao brown to snuff brown and pecan brown, and when very dry from testaceous to cinnamon.

An experiment with white oak acorns showed that color can be used as a convenient index of the water relations of the acorns as far as they affect germination. From two 100-acorn samples selected on the basis of their color from the same lot the dark-colored acorns germinated 94 per cent and the light-colored ones only 66 per cent after 18 days, when germination was complete in both lots. Germination in the light-colored acorns began 5 days later and continued 5 days longer than in the dark-colored ones.

Absorption of water is necessary for germination. On the imbibition of water, the swelling of seeds is caused by the swelling of the cell walls and the water absorption brought about through the osmotic pressure developed by the sugars, acids, and other water-soluble substances in the cells. The results are often very marked. For example, MacDougal (1901) has shown that peas in 30 hours exerted a final pressure of 8 atmospheres or 120 pounds to the square inch. Müller (1914) has pointed out that the presence of water lessens the resistance of dehiscence lines in seed coats.

Cell sap density plays an important rôle in water absorption and the translocation of food materials in plants. Additional information on the water relations of acorns and osmotic pressures developed in them was obtained from two sets of sap density determinations made in the autumn of 1924. The first set was made on September 1 when the acorns were still immature and contained large quantities of water, while the other set was made on October 30 after much of the water had been withdrawn from the acorns and also after they had been shed from the trees but a few days. The same methods and apparatus were used in determining the osmotic concentrations as were used in making similar determinations on the vegetation of the Wasatch Mountains (Korstian, 1924). The results of these determinations are given in Table VIII. Similar determinations on oak leaves are also included for comparison. The densities, expressed in atmospheres of osmotic pressure, show that the cells of the immature acorns are filled with sap of low osmotic concentration. As the acorns mature water is withdrawn and translocated food materials are concentrated in the cotyledons, with the result that in the embryos of mature acorns the cell sap has not only been reduced in volume but has become more highly concentrated. In each case a 100 c.c. test tube was packed full of material and each sample received the same amount of pressing.

[7] Based on Ridgeway's color standards.

The nature and amount of the sap is therefore indicative of the water relations during maturation. All the samples of embryo material yielded abundant sap on September 1, varying between 25 and 75 c.c. for each lot, but by October 30 the amounts were greatly reduced. On the latter date chestnut oak yielded 17 c.c. and white oak 8.4 c.c. of light yellowish brown sap, on the surface of which a thin film of oil collected. In the black oak group the amount of expressed sap was still further reduced until in two species, scarlet oak and southern red oak, no true sap was expressed from the embryos under the same treatment. The liquid expressed from the scarlet oak embryos consisted of 2.3 c.c. of a pale lemon yellow oil, and that from the southern red oak 7.4 c.c. of a deep orange yellow somewhat viscous oil. In the case of black oak it was possible to obtain

TABLE VIII

SAP DENSITIES OF LEAVES, FRUIT COATS, AND EMBRYOS OF VARIOUS OAKS NEAR ASHEVILLE, N. C., AUTUMN OF 1924

	Osmotic Pressure				
	September 1			*October 30*	
Species	*Leaves*	*Fruit coats*	*Embryos*	*Leaves*	*Embryos*
	Atmospheres	Atmospheres	Atmospheres	Atmospheres	Atmospheres
White oak	14.7	9.0	8.8	...	51.2
White oak	...	...	...	...	51.0
White oak (sprouted)	...	...	...	...	17.8
Chestnut oak	14.2	8.6	9.8	14.7	29.3*
Chestnut oak (sprouted)	...	...	...	...	17.6
Post oak	19.1	...	...	...	...
Red oak	26.6	11.7	11.8	17.2	54.0
Black oak	22.6	11.1	10.7	17.6	...†
Scarlet oak	...	...	...	...	...‡
Southern red oak	13.5	11.1	12.5	...	...§

* Not dried as much as unsprouted white oak.

† Not enough liquid expressed for a determination.

‡ A pale lemon yellow oil, would not freeze.

§ A deep orange yellow oil, would not freeze.

only 0.4 c.c. of liquid, of which 30 per cent was a yellowish oil. In red oak 2.8 C.c. of liquid was obtained of which only 10 per cent was a yellowish oiL

These figures, however, do not indicate that embryos of mature acorris contain small amounts afwater (they normally contain from 40 to 80 per cent of their dry weight), but rather the extremely high water percentage which they contain while maturing and the apparently greater ability of the embryos high in oil to retain moisture. The oil may possibly be directly responsible for this phenomenon.

The data in Table VIII emphasize the interdependence of sap density and the water relations of the plant, even while the plant is still in the embryonic stage. As the embryo matures there is a concentration of food materials, the water-soluble substances causing a marked increase in the osmotic concentration of the cell sap. The reverse is true during germination. The cell sap is diluted by the imbibed water and a lower osmotic concentration is the result. This is borne out by the results of determinations on sprouted embryos as contrasted with those from ungerminated acorns.

Moisture Conditions of the Environment. Acorns are unable to maintain a sufficient amount of moisture to insure viability when kept under dry conditions. If they are exposed to dry soil or dry air the moisture will be withdrawn from the acorns and desiccation will continue until an equilibrium has been reached between the moisture in the acorn and that of its environment-generally below the critical range for the acorn. On the other hand, if the acorns are in moist sailor exposed to humid air, the moisture required for the retention of viability is supplied.

Boerker (1916) and Munns (1921) have shown that germination of forest tree seeds varies with the moisture content of the soil. Munns concludes that each species evidently has an optimum range of soil moisture for germination, and that a fluctuation in water content on either side of this optimum results in decreased germination.

In one greenhouse experiment, the writer planted 3 lots of 40 acorns of red, black, white, and chestnut oaks in echard pans containing soils of 7.4 per cent, 20 per cent, and 30.7 per cent moisture content. Judged by the wilting coefficient of 9.5 per cent[8] given by Tourney andLi (1924), these soils were, in the order named, 2.1 per cent below the wilting point, and 10.5 and 21.2 per cent above, at the beginning of the experiment. These percentages were approximately maintained throughout the experiment by waterings at 5-day periods and by a mulch of sifted sphagnum. The

[8] Determined by indirect method of Briggs and Shantz.

moderately moist soil favored white and chestnut oak, while wet soil proved best for red and black oak (Table IX). The fact that the red and black oak acorns were only partially after-ripened before sowing may explain a need for greater soil moisture to hasten the after-ripening process. On the other hand, the excess water in the wet soil may have affected the white and chestnut oak acorns by excluding needed oxygen.

It is notable that all four species germinated to some extent in soil that was constantly below the wilting coefficient. The large amount of water contained by all the embryos when planted made this possible. This moisture amounted to 50 per cent in red and black oak acorns, 63 per cent in white oak acorns, and 94 per cent in chestnut oak acorns. The advantage in this respect possessed by chestnut oak was heightened by the habitual prompt germination of this species and the great moisture-holding capacity of the thick parenchyma layer of the pericarp.

TABLE IX

GERMINATION OF RED, BLACK, WHITE, AND CHESTNUT OAK ACORNS IN DRY, MOIST, AND WET SOILS

Pan no.	*Species*	*Available soil moisture*	*Germination* *On Jan. 29 (45 days)*	*Germination* *On April 29 (95 days)*
		Per cent	Per cent	Per cent
1	White oak	10.8	47.5	92.5
2	Chestnut oak	10.8	45.0	77.5
3	Black oak	10.8	0.0	22.5
4	Red oak	10.8	5.0	20.0
5	White oak	−2.1	0.0	7.5*
6	Chestnut oak	−2.1	0.0	27.5†
7	Black oak	−2.1	0.0	2.5‡
8	Red oak	−2.1	0.0	5.0§
9	White oak	21.5	42.5	80.0
10	Chestnut oak	21.5	25.0	65.0
11	Black oak	21.5	2.5	42.5
12	Red oak	21.5	5.0	27.5

* All seedlings died before leaves unfolded.
† Seedlings developed small leaves, then died.
‡ Seedlings died before leaves unfolded.
§ Seedlings developed leaves, then died.

TABLE X

POSITION OF RED AND WHITE OAK ACORNS IN RELATION TO GERMINATION AND SURVIVAL

Lot no.	*Species*	*Position of acorn*	*Germination**		*Seedlings surviving on June 13*
			Dec. 30 (45 days)	*June 13 (175 days)*	
			Per cent	Per cent	Per cent
33	White oak	Micropyle vertically upward	82	83	10
34	White oak	On side, micropyle at soil surface	89.5	95.8	44.4
35	White oak	Micropyle vertically downward	78.7	90.5	77.7
36	Red oak	Micropyle vertically upward	0	5	0
37	Red oak	On side, micropyle at soil surface	0	24	21
38	Red oak	Micropyle vertically downward	0	28	28

* Based on 100 acorns in each lot, with the exception of Nos. 34 and 35, which had 95 and 94 acorns, respectively.

Position of Acorn in Relation to Germination and Moisture.

An experiment was carried out in the greenhouse where red and white oak acorns were buried in the surface soil to half their length with their long axes vertical, one lot of each species with their micropyles downward and another lot with their micropyles vertically upward. A third lot was buried in the soil to half their thickness and with their long axes parallel to the soil surface. White oak acorns planted with their apical ends in the soil gave not only good germination but also satisfactory survival, while in those with their micropylar ends projecting upward germination began satisfactorily but soon ceased (Table X). Evaporation was doubtless too great from the young succulent radicles, even under the moist conditions in the greenhouse, and the supply of water being inadequate, they wilted and died. With acorns completely covered Kienitz (1882) has shown that the influence of position of acorn on germination and survival became insignificant within two months after planting.

Depth of Cover in Relation to Moisture.

Watt (1919) has shown that acorns placed on the bare soil surface failed to germinate, while those from the same lot put below the surface germinated. He attributes the lack of germination in the acorns on the soil surface to water loss.

An experiment was carried out in the Champion Fibre Company's nursery during 1924-1925 to determine the influence of depth of cover upon germination and early survival (Table XI). Black, red, white, and chestnut oak acorns were placed on top of the soil in somewhat the same way that they lie after falling from the tree; other lots were pressed into the soil flatwise so that the tops of the acorns were flush with the soil surface but not covered; and still other lots were covered with soil to depths of ½, 1, 2, and 4 inches. The beds containing these acorns were mulched with oak leaves throughout the winter. The white and chestnut oak acorns on top of the soil germinated and then dried out to such an extent that the embryos were killed before the leaf litter was put over the beds. The red and black oak acorns did not germinate until February and March, and the leaf mulch afforded sufficient protection to enable some of them to become established before it was removed early in April. A soil covering from ½ inch to 2 inches deep resulted in generally satisfactory germination and survival. The 4-inch depth, however, gave distinctly poorer results. Seedlings from acorns planted to this depth were very slow in appearing above the soil surface, and in the white and chestnut oaks were appreciably smaller. At the greater depths the insufficiency of oxygen is probably a limiting factor, especially since the soil was a rather heavy silt loam. In lighter textured and more pervious soils lack of oxygen would become the limiting factor only at greater depths. Inadequate moisture was the limiting factor at the soil surface, particularly in the white and chestnut oaks. Whenever the surface soil dries out as during dry weather, this factor is effective at even greater depths.

INFLUENCE OF TEMPERATURE ON GERMINATION

Since germination is a vital process and heat is one of the primary requisites for the maintenance of life, it follows that the influence of temperature within the vital range is chiefly as a stimulant. The influence of a change in temperature on metabolism is determined largely by the reactive power of the plant itself, and only slightly by any direct action upon the chemical processes involved in metabolism. It is also well known

TABLE XI

DEPTH OF COVER IN RELATION TO GERMINATION AND SURVIVAL IN RED, BLACK, WHITE, AND CHESTNUT OAKS

Lot no.	*Species*	*Depth of cover*	*Germination**			*Survival on*	*Average height of seedlings*
			April 21	*June 2*	*August 14*	*August 14*	*August 14*
			Per cent	Per cent	Per cent	Per cent	Inches
7	Chestnut oak	On top of soil surface	1	1	1	1	4.80
8	Chestnut oak	Upper edge of acorn flush with soil surface	62	65	65	64	4.49
3	Chestnut oak	½ inch	73	82	82	82	4.85
9	Chestnut oak	1 inch	43	85	85	85	4.36
10	Chestnut oak	2 inches	13	78	83	83	4.57
11	Chestnut oak	4 inches	0	21	58	58	3.40
16	White oak	On top of soil surface	5	5	5	5	4.84
17	White oak	Upper edge of acorn flush with soil surface	25	28	28	24	4.04
12	White oak	½ inch	41	73	73	72	3.07
18	White oak	1 inch	40	76	76	73	3.39
19	White oak	2 inches	3	56	60	57	2.90
20	White oak	4 inches	0	3	37	37	2.38

* Based on 100 acorns in each lot.

TABLE XI (Continued.)

Lot no.	*Species*	*Depth of cover*	*Germination** *April 21*	*June 2*	*August 14*	*Survival on August 14*	*Average height of seedlings August 14*
			Per cent	Per cent	Per cent	Per cent	Inches
77	Red oak	On top of soil surface	37	37	37	36	5.57
78	Red oak	Upper edge of acorn flush with soil surface	76	76	81	81	5.45
79	Red oak	½ inch	76	76	76	74	5.79
80	Red oak	1 inch	71	81	82	81	5.98
81	Red oak	2 inches	54	85	86	86	5.41
82	Red oak	4 inches	0	70	73	72	5.36
90	Black oak	On top of soil surface	28	32	32	25	2.04
91	Black oak	Upper edge of acorn flush with soil surface	83	89	89	75	2.29
92	Black oak	½ inch	32	68	68	67	2.42
93	Black oak	1 inch	11	67	67	67	2.21
94	Black oak	2 inches	0	69	69	68	2.28
95	Black oak	4 inches	0	16	39	38	2.55

* Based on 100 acorns in each lot.

that the temperature requirements for growth are not the same in different species of plants. Intermediate temperatures are the most favorable for plant growth, which ceases with very high and very low temperatures.

The object of the present study has been to determine the influence of temperature on acorn germination.

Optimum Temperature Conditions. Harrington (1923a) has shown that some seeds germinate better under moderate alternations of temperature, while others germinate practically as well at moderate constant temperatures. He has also reviewed the work of other investigators during the 40 years prior to the publication of his paper. These generally report a favorable effect of temperature alternations upon the germination of many kinds of seed. The higher temperature was usually maintained only a small part of the day, never more than nine hours and usually not more than seven. Because of greater ease, simplicity, and uniformity of temperature control, the method of securing temperature alternations by transfer between two germinating chambers maintained at fixed temperatures is preferable to the method of heating and cooling a single chamber.

The influence of temperature on the germination of red, black, scarlet, white, and chestnut oak acorns was studied in five lots of each species collected in the vicinity of New Haven, Conn. An alternation of temperatures, suggestive of the diurnal variation encountered under field conditions, was obtained by shifting the acorns between five temperature chambers. Lot 1 was kept constantly in a cold storage room, the temperature of which averaged 38.5° F. The temperature of this room dropped below the freezing point only once, the minimum being 31.7° F. The temperature went above 45° F. on five different occasions, reaching a maximum of 51.8° F. Thermostatically controlled incubators were used for the other four chambers, and more uniform temperatures were maintained in them. The average temperatures to which Lots 2 to 5, inclusive, were subjected are approximately as follows:

Lot no.	*Temperatures of Germination Chambers*	
	During day	*During night*
2	50	35
3	65	50
4	80	65
5	95	80

These temperatures were maintained with deviations of not more than 2 to 5 degrees. Two hundred acorns each of red and white oak and 100 each of the other three species were used in the experiment. The acorns were kept in wire baskets lined with wet sphagnum moss. These were sprinkled with distilled water when the morning and evening shifts were made. Water squeezed from the moss had a hydrogen-ion concentration of 6.5. Temperature readings were taken at the same time and any necessary adjustments made to the thermostat. In order to supply additional humidity to each chamber and to aid in the maintenance of more uniform temperatures a dish of water was kept in the bottom of each incubator.

The study was begun on November 10 and germination counts were made every five days thereafter. The acorns were considered as germinated when the light-colored tip of the radicle emerged through the ruptured fruit coat. Only those acorns which had lost their viability showed a predisposition to mold, the sound viable ones showing little or no tendency to mold. Those acorns which lost their viability soon fermented and both fruit coats and embryos became noticeably darker in color. The ivory yellow or cream color of the cotyledons of viable acorns changed from brownish olive to sepia when they lost their viability. All insect-infested acorns were deducted from the total number of acorns used in computing the germination percentages.

The course of germination in the five lots of each species at the five different combinations of fluctuating temperature is shown in Figs. 12 to 16, inclusive, for red, black, scarlet, white, and chestnut oaks, respectively. Considering each species separately it is evident that, for Lots 2, 3, and 4, germination begins appreciably later and proceeds more slowly at the lower than at the higher temperatures, but that the final germination percentages are about the same. Similar results were secured by Haak (1909) and Pittauer (1912), in studies on various European species, especially conifers. Although in the present study the highest germination percentages in the black oak group during the first 40 to 50 days were obtained in Lot 5, which was subjected to the highest set of temperatures, this lot actually gave an appreciably lower total germination in all species except chestnut oak. This indicates that the highest combination of temperatures, to which Lot 5 was subjected, are above the optimum for the best total germination. No germination occurred in Lot 1 of any species until the temperature went quite consistently above 40° F. toward the end of the experiment.

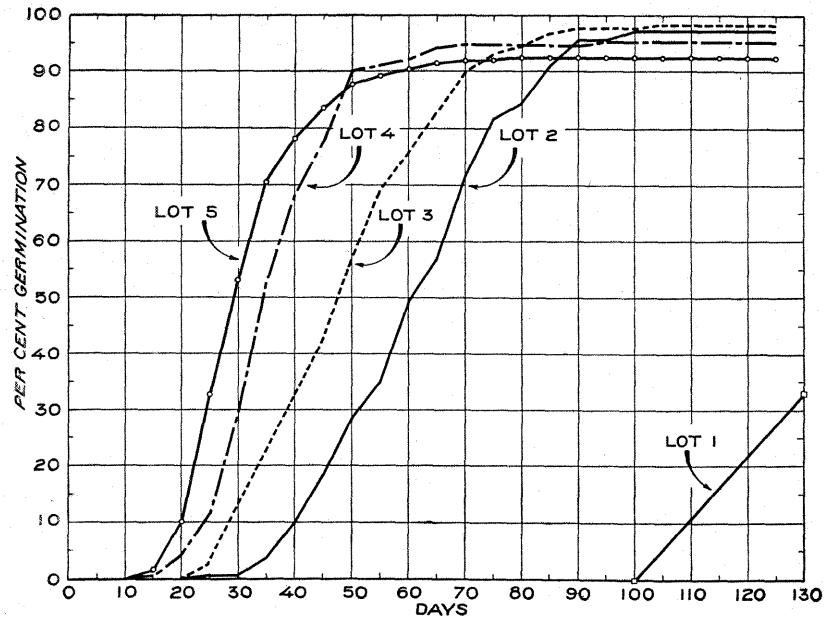

Fig. 12. Course of germination in five lots of red oak acorns subjected to five different sets of temperatures.

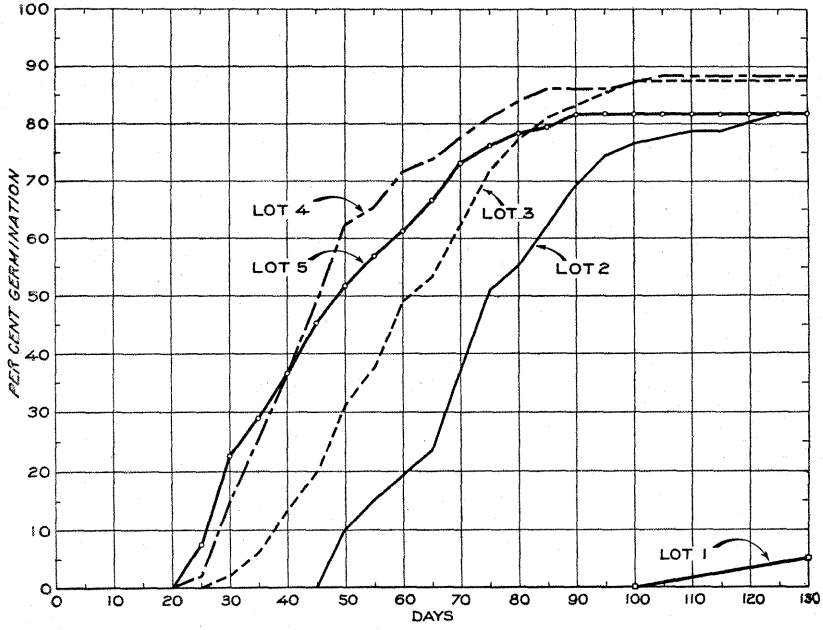

Fig. 13. Course of germination in five lots of black oak acorns subjected to five different sets of temperatures.

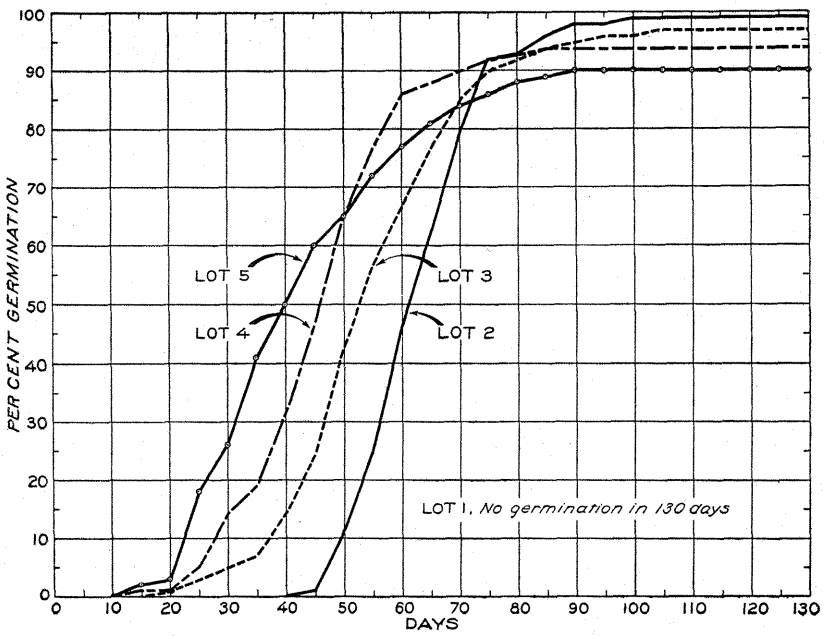

Fig. 14. Course of germination in five lots of scarlet oak acorns subjected to five different sets of temperatures.

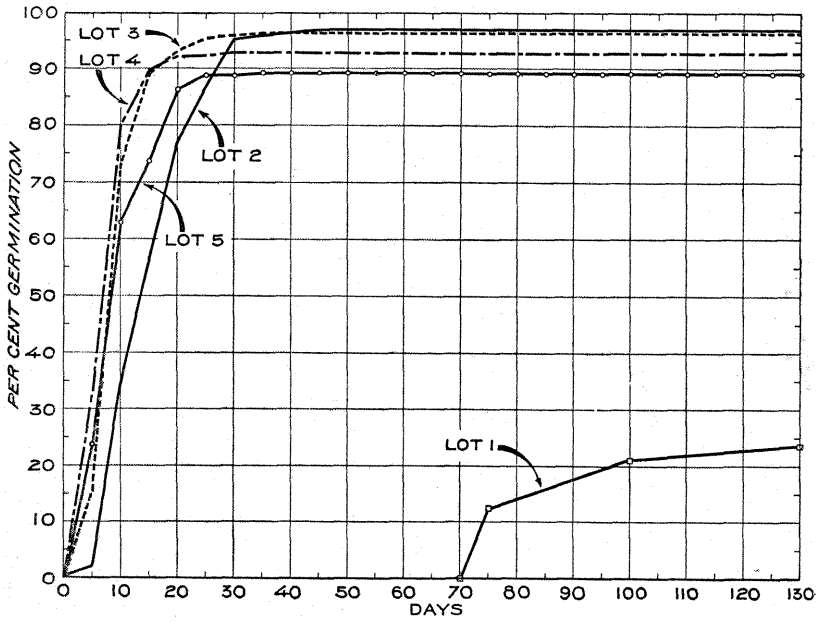

Fig. 15. Course of germination in five lots of white oak acorns subjected to five different sets of temperatures.

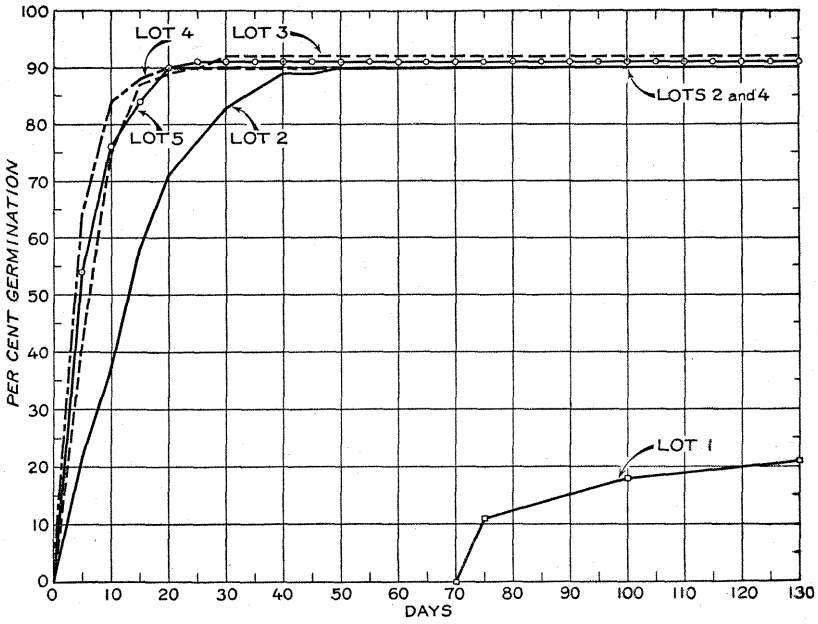

Fig. 16. Course of germination in five lots of chestnut oak acorns subjected to five different sets of temperatures.

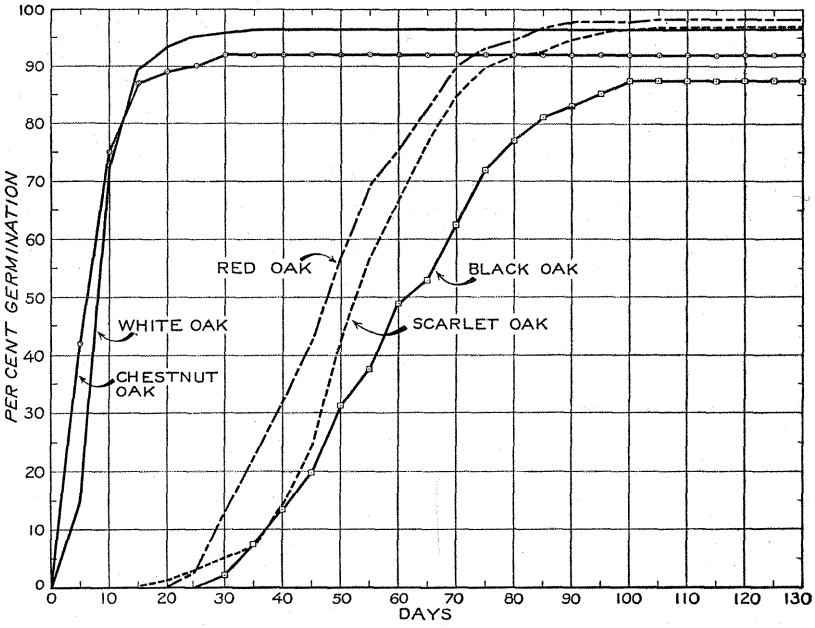

Fig. 17. Rate of germination in five different oaks under identical conditions of temperature and moisture. Lot 3 of each species kept at about 65° F. during the day and close to 50° F. at night during entire period of tests.

From the results of this study it appears that an average night temperature of 50° F. and 65° F. during the day gives the most satisfactory results when both promptness of germination and total germination are considered. The acorns subjected to 80° F. during the day and 65° F. at night are somewhat ahead in promptness of germination but their total germination is lower. Although the acorns kept at an average of 35° F. at night and 50° F. during the day showed good total germination they required a longer time to complete germination. At the optimum temperatures the white and chestnut oaks completed their germination during the first 20 days, while the three species of the black oak group remained dormant during this period and required from 80 to 100 days to complete gennination (Fig. 17).

Variation in Temperature Requirements. Figs. 12 to 17, inclusive, together with the results of the greenhouse germination tests given in Table II, show that temperature alone is often insufficient to bring the embryos in the acorns of the black oak group out of the dormant condition into active growth. Figs. 12, 13, and 14 agree, however, with the general conclusion of Molisch (1909) that, even though the resting period may not be terminated by subjecting the plant to medium temperatures, it can be appreciably shortened by the application of higher temperature.

The greatest difference in the temperature requirements for germination occurs between the white and black oak groups. Relatively little difference was noted between the white and chestnut oaks. The latter showed a somewhat earlier response at the higher temperatures and a somewhat higher germination during the first ten days at all but the lowest temperatures.

Of the three species of the black oak group, black oak itself requires either a longer rest period, or higher temperatures to terminate it in acorns not fully after-ripened. From this study it is evident that red oak requires less heat for germination than either scarlet or black oak. This conclusion agrees with the observed facts that red oak is most abundant and reaches its best development in stands occupying the cool moist coves and slopes in the Southern Appalachian Mountains and that it extends farther north into Canada than the other species.

Influence of Low Temperatures. It has been shown that the growth of the embryo accompanying germination in the acorn ceases at about 40° F. and apparently becomes dormant. When the temperature drops below the freezing point the living tissues are liable to frost injury, the extent of which depends upon the condition of the plant tissue and such environ-

mental factors as humidity and insolation, aside from temperature (Harvey, 1918, and Rosa, 1921).

Cold resistance in plants is associated with the increased water-retaining power of the cells. Because of the presence of hydrophyllous colloids, the cells upon freezing retain a larger amount of *unfrozen* moisture. Thus the susceptibility of living plant tissue to frost injury varies quite directly with the amount of free water in it. The tissue fluids are capable of much undercooling while water on the surface has little of this property. Water on the surface, therefore, freezes before the tissue fluids and ice crystals apparently grow into the tissues through the larger openings. Thus inoculated crystallization starts within the tissue. In tissues with intercellular air spaces crystals form in the air spaces. Thus the water is withdrawn from the protoplasm and the mechanical injuries resulting from the formation of ice crystals are not commonly demonstrated within the protoplast. In the very rapid undercooling of large cells, however, ice crystals probably develop within the cell, resulting in mechanical injury.

Chandler (1913, 1914), Harvey (1918), Rosa (1921), and the writer (1924), in reviewing the extensive literature on this subject, have stressed the relation between cell sap density and resistance to cold. The osmotic concentration of the cell sap may be increased by: (1) increasing the amount of osmotically active solutes in the cell solution, (2) decreasing the total water content, and (3) increasing the amount of unfree water held by colloidal adsorption. Greater resistance to cold is also correlated with the transformation of starch into sugar. This conversion results in an increase in the density of the cell sap which takes place during the hardening process. The maturity of the tissue is important, as is also any other factor which tends to change the constituents of the protoplasm and thus prevent their precipitation as a result of the physical changes incident to freezing.

Field studies showed that the young succulent radicles are sometimes injured as they emerge from the acorn by temperatures only a few degrees below the freezing point. The radicles are much more susceptible while their tissues are still immature and filled with a large amount of sap which has lower concentration than after the tissues have become lignified, lost some of their water, and otherwise become more mature. Thus the germinating acorns are much more susceptible to freezing tem" peratures than the ungerminated ones.

The amount of injury under natural conditions from freezing is much less in normal seasons than that from excessive drying. Unseasonable

temperatures, particularly early fall frosts, can be expected to cause appreciable damage to germinating white and chestnut oak acorns before the radicle has penetrated the soil. Such injury is often completely averted by the protection of a leaf litter cover. The beneficial influence of the leaf litter in this connection can scarcely be overemphasized.

Influence of High Temperatures. High temperatures are pertinent to the present study chiefly in determining the probable damage to the acorn crop by forest fires.

A preliminary experiment was conducted at Asheville, N. C., in 1924-1925. Various lots of red, black, white, and chestnut oak acorns were subjected to different temperatures for varying lengths of time. Duplicate series were run, in one the temperatures were maintained with dry air and in the other with moist air. All the species were treated similarly. All lots were planted ½ inch deep in the nursery where record was kept of germination during the following growing season (Table XII). The ungerminated white and chestnut oak acorns had remained for four weeks in a heated room. This fact is the most likely reason for the marked reduction of their viability. After noting the condition of the acorns in Lots 56 to 68, which were subjected to high temperatures for two hours the time of treatment was reduced to 15 minutes, a period more nearly comparable to the duration of high temperatures resulting from leaf litter fires in the hardwood forests.

Before carrying out the next experiment on the influence of high temperatures information was obtained in the field as to the amount and duration of the excessive heat to which acorns are subjected in forest fires. In the spring of 1925 temperature readings were taken at 35 stations on several different fires by means of a calibrated potentiometer-thermocouple apparatus. The readings were made at intervals of 10 or IS seconds. The thermocouple was located in the leaf litter near the soil surface and often among acorns. The march of the temperature at the point where the thermal junction was inserted is shown in Fig. 18 for a number of typical stations in leaf litter fires. A study of similar graphs for all 35 stations showed that 46 per cent of them had maximum temperatures between 750° F. and 1,000° F., 37 per cent between 500° F. and 750° F., and only 17 per cent below 500° F. By grouping them in this way composite curves representative of the temperatures at the individual stations were obtained. The composite graphs for the three groups of temperatures are shown in Fig. 19. Temperatures above 500° F. do not exist for more than one to three minutes in the majority of cases. Numerous exceptions

TABLE XII

EFFECT OF HEAT TREATMENT ON GERMINATION OF RED, BLACK, WHITE, AND CHESTNUT OAK ACORNS IN THE FOREST NURSERY, 1924-1925

Lot no.	*Species*	*Basis of test No. of acorns*	*Germinated or not germinated*	*Heat Treatment Duration Minutes*	*Heat Treatment Temperature Degrees F.*	*Nursery Germination April 21 Per cent*	*Nursery Germination June 2 Per cent*	*Nursery Germination August 14 Per cent*
			Dry Heat					
21	White oak	45	Germinated	15	140	42.2	71.1	71.1
22	Chestnut oak	37	Germinated	15	140	35.2	54.0	56.8
23	White oak	45	Germinated	15	160	35.5	51.1	51.1
24	White oak	50	Not germinated	15	140	0.0	0.0	0.0†
25	Chestnut oak	50	Not germinated	15	140	38.0	38.0	42.0
26	Red oak	50	Not germinated	15	140	82.0	94.0	94.0
27	Black oak	50	Not germinated	15	140	42.0	74.0	76.0
28	White oak	50	Not germinated	15	160	2.0	2.0	2.0†
29	Chestnut oak	50	Not germinated	15	160	10.0	14.0	14.0
30	Red oak	50	Not germinated	15	160	86.0	86.0	86.0
31	Black oak	50	Not germinated	15	160	44.0	66.0	66.0
32	White oak	50	Not germinated	15	140	0.0	0.0	0.0†
33	Chestnut oak	50	Not germinated	15	140	10.0	10.0	10.0
34	Red oak	50	Not germinated	15	140	48.0	52.0	52.0
35	Black oak	50	Not germinated	15	140	18.0	20.0	22.0

† Viability of all ungerminated white oak acorns greatly reduced as a result of 4 weeks' drying in heated room.

TABLE XII (Continued.)

Lot no.	Species	Basis of test No. of acorns	Germinated or not germinated	Heat Treatment Duration Minutes	Heat Treatment Temperature Degrees F.	Nursery Germination April 21 Per cent	Nursery Germination June 2 Per cent	Nursery Germination August 14 Per cent
			Dry Heat					
36	White oak	50	Not germinated	15	200	0.0	0.0	0.0
37	Chestnut oak	50	Not germinated	15	200	0.0	0.0	0.0
38	Red oak	50	Not germinated	15	200	10.0	18.0	18.0
39	Black oak	50	Not germinated	15	200	0.0	0.0	2.0
			Moist Heat (Air saturated)					
40	White oak	50	Not germinated	15	140	0.0	0.0	2.0†
41	Chestnut oak	50	Not germinated	15	140	6.0	12.0	12.0
42	Red oak	50	Not germinated	15	140	88.0	90.0	90.0
43	Black oak	50	Not germinated	15	140	16.0	30.0	30.0
44	White oak	50	Not germinated	15	200	0.0	0.0	0.0
45	Chestnut oak	50	Not germinated	15	200	0.0	0.0	0.0
46	Red oak	50	Not germinated	15	200	0.0	0.0	0.0
47	Black oak	50	Not germinated	15	200	0.0	0.0	0.0
48	White oak	50	Not germinated	15	220*	0.0	0.0	0.0
49	Chestnut oak	50	Not germinated	15	220*	0.0	0.0	0.0
50	Red oak	48	Not germinated	15	220*	0.0	0.0	0.0
51	Black oak	50	Not germinated	15	220*	0.0	0.0	0.0

* At the temperature of 220° F. a steam pressure of 2 pounds developed.

† Viability of all ungerminated white oak acorns greatly reduced as a result of 4 weeks' drying in heated room.

TABLE XII (Continued.)

Lot no.	Species	Basis of test No. of acorns	Germinated or not germinated	Heat Treatment Duration Minutes	Heat Treatment Temperature Degrees F.	Nursery Germination April 21 Per cent	Nursery Germination June 2 Per cent	Nursery Germination August 14 Per cent
			Moist Heat (Air saturated)					
52	White oak	50	Not germinated	15	240*	0.0	0.0	0.0
53	Chestnut oak	50	Not germinated	15	240*	0.0	0.0	0.0
54	Red oak	50	Not germinated	15	240*	0.0	0.0	0.0
55	Black oak	50	Not germinated	15	240*	0.0	0.0	0.0
56	White oak	50	Germinated	120	120	0.0	0.0	0.0
57	White oak	50	Not germinated	120	120	10.0	12.0	12.0†
58	Chestnut oak	32	Germinated	120	120	0.0	0.0	15.6
59	Chestnut oak	50	Not germinated	120	120	18.0	36.0	36.0
60	Red oak	50	Not germinated	120	120	90.0	90.0	90.0
61	Black oak	50	Not germinated	120	120	0.0	0.0	0.0
62	White oak	50	Not germinated	120	140	0.0	0.0	0.0
63	Chestnut oak	50	Not germinated	120	140	0.0	0.0	0.0
64	Red oak	50	Not germinated	120	140	0.0	0.0	0.0
65	Black oak	50	Not germinated	120	140	0.0	0.0	0.0
66	White oak	50	Not germinated	120	160	0.0	0.0	0.0
67	Chestnut oak	50	Not germinated	120	160	0.0	0.0	0.0
68	Black oak	50	Not germinated	120	160	0.0	0.0	0.0

* At the temperature of 240° F. a steam pressure of 10 pounds developed.

† Viability of all ungerminated white oak acorns greatly reduced as a result of 4 weeks' drying in heated room.

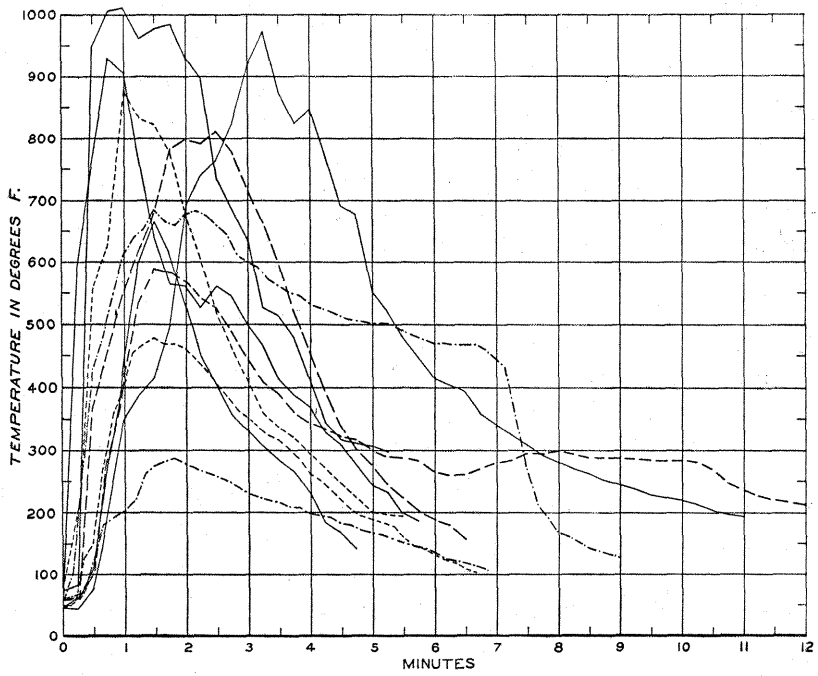

Fig. 18. Ten sets of temperature records selected to show the variability in temperatures of leaf litter fires depending upon such factors as climatic conditions, rate of spread of the fire, inflammability of the litter, and the kind and amount of fuel.

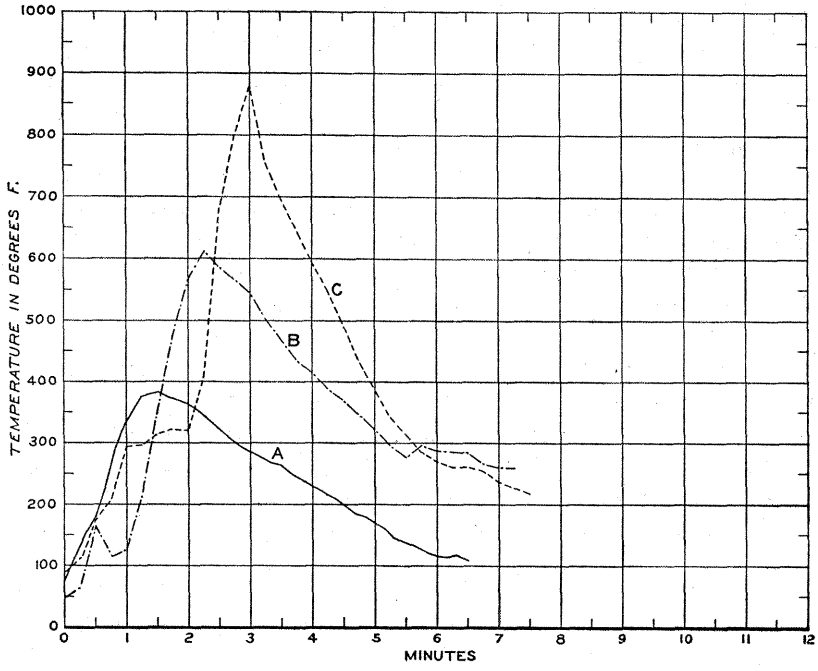

Fig. 19. Temperature behavior in typical leaf litter fires. A, average of two fires, the maximum temperatures of which were below 500° F.; B, average of four fires, the maximum temperatures of which were between 500° F. and 750° F.; C, average of ten fires, the maximum temperatures of which were above 750° F.

were found in which small branches and twigs provided additional fuel or in which smoldering embers were fanned up by the wind.

Most of the acorns found on the ground following such fires had cooked embryos. Only occasionally were viable acorns found in depressions in the soil or partially protected by moist leaf litter or non-inflammable material.

On the basis of these results a more detailed study was made in the laboratory and greenhouse during the winter of 1925'"1926. About 70 different lots of acorns were subjected to a series of heat treatments ranging between 120° F. and 280° F. for 5, 10, and 15 minutes before they were planted in the greenhouse. Dry heat, as generated in an electric incubator, was used. The percentage of water loss was determined for each lot and the acorns were immediately planted in the greenhouse. The results of this experiment are shown in Table XIII. One striking feature is the very low germination percentage obtained in all lots of the black oak group, even at the lower temperatures, chiefly because these acorns had not been after-ripened before planting and the temperatures obtaining in the greenhouse were not high enough to bring them into germination. Hence many of these fermented instead of germinating. At the close of the experiment the acorns were dug up and examined. In some lots the plumules and tips of radicles had been killed; additional roots had been developed but no plumules. T'his suggests that in some cases at least the plumules may be mOre susceptible than the radicles, and that they are less easily replaced.

The results of the two experiments suggest that the species studied may be arranged in the order of the decreasing resistance of their acorns to excessively high temperatures as follows: red oak, chestnut oak, black oak, scarlet oak, and white oak. This is essentially the same order as the decreasing thickness of their fruit coats. White oak acorns are distinctly more susceptible and red oak appreciably more resistant than those of the other species. However, when the fatal temperatures are considered in relation to those encountered in ordinary leaf litter fires, it is evident that the acorns of these oaks have very little chance of surviving unless they are accidentally protected by some non-inflammable material.

Acorns are much less resistant to high temperatures than many agricultural seeds and those of the conifers, according to the work of Burgess (1919), Atanasoff and Johnson (1920), Kienholz (1924), and Hofmann (1925). This striking difference is probably due to the high starch content of the acorns and their greater water content. Waggoner (1917) has

TABLE XIII

EFFECT OF HEAT TREATMENT ON GERMINATION OF RED, SCARLET, WHITE, AND CHESTNUT OAK ACORNS IN THE GREENHOUSE, WINTER OF 1925-1926

Lot no.	Species	Heat Treatment		Water loss during treatment*	Greenhouse Germination†	
		Duration	Temperature		December 30	May 20
		Minutes	Degrees F.	Per cent	Per cent	Per cent
1	Red oak	5	120	0.45	3	56
2	Scarlet oak	5	120	0.40	1	50
3	White oak	5	120	0.40	87	88
4	Red oak	10	120	0.40	5	33
5	Scarlet oak	10	120	0.24	1	54
6	White oak	10	120	0.25	76	80
7	Red oak	15	120	0.42	1	41
8	Scarlet oak	15	120	0.82	4	59
9	White oak	15	120	0.66	83	88
10	Red oak	10	160	0.51	1	52
11	Scarlet oak	10	160	0.58	3	56
12	Chestnut oak	10	160	0.15	73	76
13	White oak	10	160	0.99	63	73
14	Red oak	15	160	0.85	1	50
15	Scarlet oak	15	160	1.44	3	76
16	Chestnut oak	15	160	0.48	55	67
17	White oak	15	160	1.58	47	56
18	Red oak	5	160	0.24	0	38
19	Scarlet oak	5	160	0.53	3	62
20	Chestnut oak	5	160	0.09	55	66
21	White oak	5	160	0.18	63	75
22	Red oak	5	200	0.37	6	38
23	Scarlet oak	5	200	0.27	0	68
24	Chestnut oak	5	200	0.09	55	79
25	White oak	5	200	0.41	67	77
26	Red oak	10	200	0.84	2	38
27	Scarlet oak	10	200	1.00	4	22
28	Chestnut oak	10	200	0.37	62	67
29	White oak	10	200	1.51	20	20

* Computed on basis of original weight.

† Based on 100 acorns in each lot.

TABLE XIII (Continued.)

Lot no.	Species	Heat Treatment Duration	Heat Treatment Temperature	Water loss during treatment*	Greenhouse Germination† December 30	Greenhouse Germination† May 20
		Minutes	Degrees F.	Per cent	Per cent	Per cent
30	Red oak	15	200	0.67	8	34
31	Scarlet oak	15	200	1.13	3	17
32	Chestnut oak	15	200	0.65	26	28
33	White oak	15	200	1.68	0	0
34	Red oak	5	240	0.29	3	48
35	Scarlet oak	5	240	0.77	3	70
36	Chestnut oak	5	240	1.11	18	21
37	White oak	5	240	1.71	6	8
38	Red oak	10	240	0.99	6	21
39	Scarlet oak	10	240	1.71	0	0
40	Chestnut oak	10	240	1.61	3	4
41	White oak	10	240	3.26	0	0
42	Red oak	15	240	1.32	3	13
43	Scarlet oak	15	240	2.01	0	0
44	Chestnut oak	15	240	1.34	0	0
45	White oak	15	240	3.76	0	0
46	Red oak	5	280	4.04	1	13
47	Scarlet oak	5	280	4.67	0	0
48	Chestnut oak	5	280	4.57	6	8
49	White oak	5	280	5.96	0	0
50	Red oak	10	280	5.89	6	21
51	Scarlet oak	10	280	6.81	0	0
52	Chestnut oak	10	280	4.66	27	29
53	White oak	10	280	6.26	5	6
54	Red oak	15	280	6.43	2	4
55	Scarlet oak	15	280	8.17	0	0
56	Chestnut oak	15	280	6.08	0	0
57	White oak	15	280	8.56	0	0
58	Red oak	10	300	6.05	0	14
59	Scarlet oak	10	300	4.13	0	0
60	Chestnut oak	10	300	6.04	0	0
61	White oak	10	300	8.27	0	0
62	Red oak	5	300	5.42	11	24
63	Scarlet oak	5	300	5.70	0	0

* Computed on basis of original weight.

† Based on 100 acorns in each lot.

TABLE XIII (Continued.)

Lot no.	Species	Heat Treatment Duration	Heat Treatment Temperature	Water loss during treatment*	Greenhouse Germination† December 30	Greenhouse Germination† May 20
		Minutes	Degrees F.	Per cent	Per cent	Per cent
64	Chestnut oak	5	300	4.88	6	8
65	White oak	5	300	6.53	3	5
66	Red oak	15	300	9.81	0	0
67	Scarlet oak	15	300	11.44	0	0
68	Chestnut oak	15	300	9.13	0	0
69	White oak	15	300	9.20	0	0

* Computed on basis of original weight.

† Based on 100 acorns in each lot.

shown that the resistance of radish seeds to high temperatures is inversely proportional to the initial water content of the seeds at the time of heating.

A study was undertaken to determine the extent to which insolation may be a factor in the natural regeneration of oak. The temperatures at which stem lesions are commonly formed on oak were compared with the maximum surface temperatures encountered in the field. Records of the temperature of the surface soil on a south-facing slope in the Bent Creek Valley southwest of Asheville, N. C., taken during the extremely hot, dry summer of 1925, were as follows: August 5, 129° F.; August 10, 135° F.; August 18, 132° F., 138° F., 140° F., and 143° F. Toumey and Neethling (1924) have recorded surface soil temperatures in southern New Hampshire up to 152° F.

On the basis of these records six flats of 10 to 20 oak seedlings were subjected to various temperatures ranging well above the maximum recorded in the field. Each flat in turn was placed in the window in full sunlight and the heat from solar radiation was reinforced by heat from an electric heater, placed about 2 feet above the flat. Wire screens were interposed between the seedlings and the heater to control the temperature of the surface soil. The different flats were subjected to different degrees of heat for variable lengths of time. The surface temperatures were recorded by means of a sensitive galvanometer connected with a thermocouple located just below the soil surface. The effect of heat on

the seedlings in each flat was noted. Three flats of two months' old chestnut oak seedlings were subjected to high temperatures as follows:

Flat 1		*Flat 2*		*Flat 3*	
Time	*Surface soil temperature*	*Time*	*Surface soil temperature*	*Time*	*Surface soil temperature*
	Degrees F.		Degrees F.		Degrees F.
10:35 A.M.	112	11:20 A.M.	128	2:05 P.M.	133
10:40 A.M.	117	11:30 A.M.	135	2:15 P.M.	147
11:00 A.M.	133	11:45 A.M.	140	2:30 P.M.	149
11:15 A.M.	149	12:00 M.	144	2:45 P.M.	160
11:30 A.M.	154	12:10 P.M.	133	3:00 P.M.	165
11:45 A.M.	158	12:20 P.M.	138	3:15 P.M.	155
12:00 M.	158			3:30 P.M.	153
				3:45 P.M.	147
				4:00 P.M.	149

All the seedlings in Flat 1 had the cambium killed at the surface of the soil and for about 0.3-0.4 inch above it. In Flat 2 all the seedlings which had the cambium killed at or just above the soil surface were incompletely lignified while all the uninjured seedlings had lignified stems at the soil surface. All the seedlings in Flat 3 were killed.

The three other flats were subjected to temperatures as follows:

Flat 4		*Flat 5*		*Flat 6*	
Time	*Surface soil temperature*	*Time*	*Surface soil temperature*	*Time*	*Surface soil temperature*
A.M.	Degrees F.	P.M.	Degrees F.	A.M.	Degrees F.
9:35	115	2:25	140	9:20	100
9:40	125	2:30	131	9:30	104
9:45	131	2:45	139	9:45	118
10:00	124	3:00	142	10:00	136
10:15	127	3:15	138	10:15	153
10:30	128	3:30	138	10:30	144
10:45	131	3:45	141	10:45	144
11:00	121	4:00	142	11:00	145
11:15	130	4:15	138		
11:25	131	4:30	140		

Flats 4 and 5 contained red oak seedlings varying in size from those coming through the surface soil to seedlings 2 inches tall on which the leaves were just unfolding. The seedlings in Flat 4 showed no injury at or

near the soil surface, while 77 per cent of the seedlings in Flat 5 developed typical heat lesions at the soil surface. Some seedlings had not yet come up. All of these with plumules 1/10 inch or more below the surface of the soil were uninjured. Flat 6 contained scarlet oak seedlings of different ages up to two months. All these seedlings with normally lignified stems were free of heat lesions, while all those with incompletely lignified stems developed typical heat lesions just above the soil surface.

It is evident, therefore, that the maximum temperatures of the soil surface attained under natural conditions are such as to cause injury only to newly germinated oak seedlings. The acorns normally germinate and the seedlings become well developed during the fore part of the growing season. By the time the maximum surface temperatures of the season occur the stems of the oak seedlings are so lignified that injury from excessive heating of the soil surface adjacent to the stems is unlikely. The relatively large leaves, developed early in most oaks, usually shade the soil adjacent to the stems. This renders the probability of injury from this cause still more remote.

RELATION OF MOISTURE AND TEMPERATURE TO ACORN STORAGE

The combined influence of moisture and temperature is an essential consideration in acorn storage. In a preliminary experiment certain storage methods were arranged to simulate natural conditions. The acorns were stored from November 1, 1924, to March 11, 1925, as indicated in Table XIV. At the end of the storage period they were planted in the nursery at Canton, N. C., to obtain records on germination.

This experiment was checked by a more intensive one carried out at New Haven during the winter of 1925-1926 (Table XV). Lots 1 to 4, inclusive, and Lot 34 were placed in storage on October 26, Lots 5 and 6 on November 12, Lots 7 to 10, inclusive, on October 12, and Lots 11 to 31, inclusive, on November 17. All these acorns came from the general supply kept in cold storage since October 7 and which was represented by Lots 31 and 32. In both experiments ungerminated acorns were used.

The best results were secured with those methods of storage in which the acorns were subjected to uniformly low and quite constant temperatures. For best results, however, the temperature should not drop below the freezing point. The relatively poor showing of Lots 107 and 108 in Table XIV and Lots 1 and 2 in Table XV is due to the fact that they had begun to germinate in the autumn after being placed in the storage pit. Germination was arrested by the advent of winter weather, but the young succulent

TABLE XIV

RESULTS OF ACORN STORAGE EXPERIMENT IN NORTH CAROLINA, WINTER OF 1924-1925

Lot no.	*Species*	*Method and place of storage*	*Basis of test*	*Total germination in nursery*
			No. of acorns	Per cent
97	Red oak	Under leaf litter and wire screen, on forest floor	86	80.2
98	Chestnut oak	Under leaf litter and wire screen, on forest floor	85	51.8
100	White oak	Under leaf litter and wire screen, on forest floor	31	64.5
102	White oak	In air-tight glass jar in kitchen refrigerator	100	0.0
103	Red oak	In air-tight glass jar with sphagnum and charcoal moistened with sat. soln. (0.2—0.25%) salicylic acid in unheated outbuilding	100	13.0
104	Red oak	Stratified in sand, buried 1 foot under ground in garden	91	100.0
105	Black oak	Stratified in sand, buried 1 foot under ground in garden	77	100.0
107	White oak	Stratified in sand, buried 1 foot under ground in garden	85	34.2
108	Chestnut oak	Stratified in sand, buried 1 foot under ground in garden	96	39.6
109	Black oak	In atmosphere of carbon dioxide gas in unheated building	97	43.3
110	White oak	In atmosphere of carbon dioxide gas in unheated building	99	0.0
111	Red oak	In atmosphere of carbon dioxide gas in unheated building	100	11.0
112	Chestnut oak	In atmosphere of carbon dioxide gas in unheated building	100	0.0
113	Black oak	In air-tight glass jar in unheated building	95	21.1
114	White oak	In air-tight glass jar in unheated building	98	0.0
115	Red oak	In air-tight glass jar in unheated building	100	7.0
116	Chestnut oak	In air-tight glass jar in unheated building	100	0.0

TABLE XIV (Continued.)

Lot no.	*Species*	*Method and place of storage*	*Basis of test*	*Total germination in nursery*
			No. of acorns	Per cent
117	Black oak	In paper bag in unheated building	95	0.0
118	White oak	In paper bag in unheated building	66	0.0
119	Red oak	In paper bag in unheated building	96	0.0
120	Chestnut oak	In paper bag in unheated building	83	0.0
121	Black oak	In air-tight glass jar in heated building	97	0.0
122	White oak	In air-tight glass jar in heated building	99	0.0
123	Chestnut oak	In air-tight glass jar in heated building	100	0.0
124	White oak	In atmosphere of carbon dioxide gas in heated building	100	0.0
125	Chestnut oak	In atmosphere of carbon dioxide gas in heated building	100	0.0
126	Red oak	In air-tight glass jar in heated building	100	0.0

TABLE XV

RESULTS OF ACORN STORAGE EXPERIMENT IN CONNECTICUT, WINTER OF 1925-1926

Lot no.	*Species*	*Method and place of storage*	*Moisture loss (−) or gain*	*Total germination in greenhouse† to June 5*
			Per cent	Per cent
1	Chestnut oak	Stratified in moist sand, buried 2½ feet under ground in garden	18.2	55.0
2	White oak	Stratified in moist sand, buried 2½ feet under ground in garden	24.4	69.0
3	Red oak	Stratified in moist sand, buried 2½ feet under ground in garden	15.7	88.0
4	Scarlet oak	Stratified in moist sand, buried 2½ feet under ground in garden	17.1	94.0
5	Red oak	Stratified in moist sand, kept in cold storage room*	11.4	80.8
6	White oak	Stratified in moist sand, kept in cold storage room*	− 5.6	45.8
7	Red oak	Immersed in fresh running brook water	33.5	39.0
8	Chestnut oak	Immersed in fresh running brook water	51.3	0.0
9	White oak	Immersed in fresh running brook water	42.2	0.0
10	Black oak	Immersed in fresh running brook water	29.5	16.0
11	White oak	In air-tight glass jar in cold storage room*	− 3.3	0.0
12	Red oak	In air-tight glass jar in cold storage room	− 0.7	33.0
13	Red oak	In air-tight glass jar with calcium chloride, in cold storage room*	−20.8	0.0
14	White oak	In air-tight glass jar with calcium chloride, in cold storage room	−30.5	0.0
15	White oak	In air-tight glass jar with dry sphagnum and charcoal, in heated room	−17.8	0.0
16	Red oak	In air-tight glass jar with dry sphagnum and charcoal, in heated room	− 9.0	27.0
17	White oak	In sodium silicate (1 part to 10 of distilled water) in heated room	19.7	0.0
18	Red oak	In sodium silicate (1 part to 10 of distilled water) in heated room	25.4	3.0

* Chamber 1 used in temperature study, mean temperature 38.5° F., absolute maximum 51.8° F., and minimum 31.7° F.; 10 different times temperature rose above 45° F.

† Lots 1 to 6, inclusive, were based on 500 acorns each while in the other lots 100 acorns were used.

TABLE XV (Continued.)

Lot no.	*Species*	*Method and place of storage*	*Moisture loss (−) or gain*	*Total germination in greenhouse† to June 5*
			Per cent	Per cent
19	White oak	In air-tight glass jar in heated room	− 8.6	0.0
20	Red oak	In air-tight glass jar in heated room	− 3.3	0.0
21	White oak	In air-tight glass jar with sphagnum and charcoal moistened with 0.1% soln. salicylic acid, in cold storage room*	1.4	86.0
22	Red oak	Same as Lot 21	1.6	74.0
23	White oak	Same as Lot 21, except stored in heated room	6.0	0.0
24	Red oak	Same as Lot 21, except stored in heated room	− 1.7	1.0
25	White oak	In sodium silicate (1 part to 10 of distilled water) in cold storage room*	21.9	0.0
26	Red oak	In sodium silicate (1 part to 10 of distilled water) in cold storage room	23.1	4.0
27	White oak	In sodium silicate (1 part to 20 of distilled water) in heated room	20.6	0.0
28	Red oak	In sodium silicate (1 part to 20 of distilled water) in heated room	26.5	0.0
29	White oak	In air-tight glass jar with sphagnum and charcoal moistened with sat. soln. (0.2—0.25%) salicylic acid, in heated room	2.2	0.0
30	Red oak	Same as Lot 29	2.4	45.0
31	Red oak	Same as Lot 29, except stored in cold storage room*	1.6	77.0
32	White oak	In baskets in cold storage room*	−10.2	76.0
33	Red oak	In baskets in cold storage room	− 3.0	59.0
34	Red oak	Stratified in moist sand, buried 2½ feet under ground in garden	. . .	98.0

* Chamber 1 used in temperature study, mean temperature 38.5° F., absolute maximum 51.8° F., and minimum 31.7° F.; 10 different times temperature rose above 45° F.

† Lots 1 to 6, inclusive, were based on 500 acorns each while in the other lots 100 acorns were used.

radicles just protruding through the fruit coats were very susceptible to frost injury when the temperature dropped a few degrees below the freezing point. When the storage pit was opened on April 9 most of the radicle tips of the germinated white and chestnut oak acorns were dead, while those of the ungerminated acorns were uninjured.

The lower germination in Lot 3 as compared with that in Lot 34 which was buried in the same pit can also be attributed largely to frost injury. It was necessary to open one side of the storage pit on a warm day in February. This loosened the soil sufficiently to allow water and frost to reach the acorns on the side that was opened. When opened in April frost \vas still in the ground on this side of the pit, while on the other no frost was encountered. Lot 3 was stored in the side of the pit which was opened in February and some frost injury was noted on the radicle tips while Lot 34 was stored on the undisturbed side of the pit and showed no frost injury. These observations agree with those of Oppermann (1913) and I-Iauch(I923) in that stored acorns are quite susceptible to frost injury. The latter states that the germination is materially lower after ice crystals have formed on the acorns.

Since the white and chestnut oaks germinate in the autunln much smaller percentages of germination were anticipated than with the black oaks. Thus the successful storage of the white oak group is all the more significant and the death of sprouted radicles by freezing was a vicissitude not shared by the black oak group.

The temperatures to which Lots 32 and 33 were subjected in the cold storage room were too variable for the best results. While the temperature for the entire storage period averaged 38.5° F., it rose on ten different occasions to 45 and once to 51.8° F. One night it dropped to 31.70 F., \vhen a few of the acorns were coated with ice.

The atmospheric humidity of the cold storage room was relatively high and was maintained by keeping the cement floor wet. The relative humidity averaged 85 per cent for the entire storage period. It fell below 75 per cent on only six occasions. The minimum relative humidity for the period was 63 per cent and the maximum 96 per cent. That high humidity is suitable for storage is further shown by the results of moisture content determinations made on the embryos and fruit coats of acorns taken from cold storage on various dates during the storage period. Table XVI, \vhich summarizes the results of these determinations, shows that the moisture contents of the embryos, particularly of red, white, and chestnut oak, were sufficiently high during the storage period to maintain their viability. The

failure of Lots 13 and 14 to germinate is attributed to the desiccating influence of the calcium chloride and to insufficient oxygen. The latter factor is probably responsible for the failure of Lot 11 to retain its viability and for the poor showing of Lot 12 and some of the others stored in air-tight glass jars.

The embryo within the acorn requires oxygen for respiration. Respira-

TABLE XVI

MOISTURE CONTENT OF ACORN EMBRYOS AND FRUIT COATS TAKEN FROM COLD STORAGE ON DIFFERENT DATES

	*Moisture Content on Basis of Dry Weight**			
	October 17, 1925	*November 12, 1925*	*January 13, 1926*	*March 8, 1926*
	Per cent	*Per cent*	*Per cent*	*Per cent*
White oak				
Embryos	80.3†	65.4	63.1	65.6
Fruit coats	49.8†	42.8	35.3	42.4
Chestnut oak				
Embryos	90.4	91.2	94.3	. . .
Fruit coats	120.4	77.7	46.8	. . .
Red oak				
Embryos	59.3	49.0	49.9	55.8
Fruit coats	41.5	36.8	36.6	42.0
Scarlet oak				
Embryos	. . .	35.0	30.1	. . .
Fruit coats	. . .	29.0	29.1	. . .

* Each figure represents the average of three separate determinations.

† Freshly collected white oak acorns had 71.7 per cent of moisture in the embryos and 63.6 per cent in the fruit coats, while in acorns of the same species lying on a barn floor for a week the embryos contained 60.6 per cent and the fruit coats 50.6 per cent.

tion, being an oxidation process or one of destructive metabolism, is affected more by temperature than by any of the other environmental factors. It increases with temperature until an optimum is reached and then decreases. Low temperatures decrease respiration and thereby reduce destructive metabolism. If the supply of oxygen is inadequate, respiration is curtailed and this restricts the rate of the vital activities dependent upon the energy released by respiration. These principles are of great importance in connection with the maintenance of suitable conditions for acorn storage.

As a further check on the results of storing acorns in atmospheres of carbon dioxide and to determine the influence of this gas on the dormancy and germination of acorns, another experiment was carried out during the winter of 1925-1926. One hundred white oak acorns and the same number of red oak were stored in sealed glass jarscontaining partial pressures[9] of carbon dioxide varying from the 0.03 per cent in ordinary air up to 46 per cent. The bottom of each jar contained a 1 to 2-inch layer of wet sand. The jars were stored in the heated laboratory. The amount of carbon dioxide in each jar was determined by means of the Henderson-Orsat gas analyser when the experiment was begun on December 21, 1925, and again on April 5, 1926, when the acorns were planted in the greenhouse. The acorns had a very strong odor suggestive of alcoholic-acetic fermentation when the jars were opened. The acorns had abnormally dark-colored embryos indicating that they had lost their viability. None of the acorns germinated by June 19. That drying is not responsible for the loss of their viability is indicated by the fact that all 12 lots showed an increase in weight apparently due to absorption of water, the six lots of white oak showed an average increase of 5.6 per cent and the red oak 4.3 per cent. The acorns were viable when the experiment was begun for they were taken from the general supply kept in cold storage which showed very satisfactory germination. The laboratory temperature was apparently high enough to accelerate respiration, particularly the anaerobic type. This is substantiated by the fact that all the jars showed high partial pressures of carbon dioxide (35.5 to 62.5 per cent) at the close of the storage period, quite independent of the amount of this gas at the beginning.

The results of this experiment are at variance with those which Kidd

[9] The partial pressure of a gas, in a quantity or mixture of gases, is the individual pressure due to anyone of the gases, being the same as if it occupied the whole space alone.

(1914) secured with *Hevea brasiliensis,* ordinarily a very short-lived seed with a high water content. He found that when these seeds were sealed with a definite proportion of air the life processes of the seeds resulted in a carbon dioxide partial pressure of 40 to 45 per cent in the flask and the vitality of the seeds was strikingly prolonged. The marked evolution of carbon dioxide, however, is comparable in both cases. This, together with the results obtained from the other lots stored in air-tight containers, suggests that the uniformly low viability of these acorns was due to two factors-high temperature and an oxygen deficiency-both inimical to the retention of viability in stored acorns.

The poor germination in Lots 7 to 1a, inclusive, which were stored in fresh running water, was doubtless due to the fact that the temperature of the water remained high enough for germination to continue for four or five weeks after they were immersed on October 12 and to the stagnation of the water within the sacks containing the acorns. On October 12 the water had a temperature of 50° F. and by November 11 it had dropped only 3°. By November 29 it had fallen to 36° F. and on January 2 it was 35° F. The sacks containing the acorns swelled and the fabric became sufficiently silted to be fairly water-proof for when they were removed from the brook the foul-smelling water would not drain out of the sacks. These results are in accord with the conclusions of Cieslar (1896), who emphasizes the fact that, in order to result in successful storage, the water must be renewed constantly and not allowed to become stagnant.

The outstanding conclusions to be deduced from all these storage experiments is that low temperature (33 to 38° F.) and high humidity are the most important factors controlling the retention of acorn viability. This is because of their retarding influence on respiration, transpiration, and possibly other physiological activities of the embryo. An ample supply of oxygen must also be available. For the storage of large quantities of acorns and for countries with warm or fluctuating weather the use of a cold storage room artificially refrigerated and under thermostatic control offers the most promise. The ice cellar mentioned by Haack (1909) and Zederbauer (1910) may be used as a substitute. In such cases, if the acorns are not mixed with sand or soil, they must be stirred frequently to prevent heating or the accumulation of mold. For cold climates stratifying in sand or soil and burying deep in the ground well below the lower limit of frost penetration will give very satisfactory results, provided the pits are located on well-drained sites and the acorns are in good condition when put in storage.

FACTORS CAUSING DELAYED GERMINATION IN ACORNS OF BLACK OAK GROUP

In a number of the experiments discussed above, especially those initiated during the autumn and early winter, delayed germination was prevalent in the various species of the black oak group even though the acorns were subjected to moisture, heat, and oxygen ample for germination. Increase in temperature within the vital range, while tending to shorten the rest period, was not alone sufficient to terminate it.

One of the first important contributions to the literature on the causes of delayed germination was made by Crocker (1906), who showed that in certain cases the delay in germination is due to the structure of the seed coat, which excludes sufficient water or oxygen to suppress germination. In a later paper Crocker (1916) summarizes the ways in which dormancy is known to occur in plants, mentioning five primary causes: (1) rudimentary embryos, (2) complete inhibition of water absorption, (3) mechanical resistance of inclosing structures, (4) encasing structures interfering with oxygen absorption, and (5) a state of dormancy inherent in the embryo itself.

Puchner (1922), in studies conducted with hornbeam and ash seeds, showed that piercing the seed coat for the purpose of accelerating germination generally leads to unsatisfactory results, the treated seeds usually decaying before germination. Linden seeds did not germinate until the next year and required over six years to complete a 14 per cent germination. Rose (1919) reports that air-dry seeds of *Tilia americana, Sambucus canadensis,* and *Rubus idaeus* do not germinate on a moist substratum at room temperature, and that water absorption is not the limiting factor. He also states that air-dry seeds planted in soil over winter give low germination percentages. Davis and Rose (1912) have shown that hawthorn seeds will not germinate unless subjected to a season of cold. Exposure of the imbibed seeds to 5° to 6° C. for 75-90 days proved the best for after-ripening. The chemical changes in the after-ripening period of several species of hawthorn were followed microchemically by Eckerson (1913). She found the stored food in the embryo to be a fatty oil with no starch or sugar present. A series of metabolic processes take's place in the embryo during after-ripening. These involve certain physical and chemical changes necessary to germination. At first there is increased acidity accompanied by increased water-holding capacity. Increased production and activity of enzymes then follow and as a result the fats decrease and

sugars appear. The appearance of sugars denotes the beginning of the germination process.

The changes enumerated by Pack (1921) as accompanying after-ripening in *Juniperus,* especially the decrease in stored fats and increase in sugar and amino acids, are similar to those observed by Ives (1923) in the endosperm of *flex* which lead to the further development of the rudimentary embryo.

Jones (1920) has shown that sugar maple seeds after-ripen best at temperatures near 5° C. with a good supply of moisture and oxygen. He states that with after-ripening these seeds show a considerable increase in free reducing sugars. Harrington and Hite (1923) have shown that apple seeds, when taken from the apples at their maturity, are incapable of immediate germination-due also to dormancy inherent in the embryo, for naked embryos fail to germinate normally. These seeds were found to after-ripen in a few months when kept moist at a temperature between 5° and 10° C. They also after-ripen within the fruit in commercial cold storage (0° C.) or in a cold cellar, but not in dry storage or when kept moist at 20°C. or at higher temperatures. Howard (1915) has shown that of those plants requiring a definite rest period the majority are woody species. He states that stratifying these seeds and allowing them to freeze while in the moist sand proved the best treatment which he tried for hastening sprouting and attaining the highest germination. This is contrary to the results of many of the above and other investigators. It is now generally conceded that for most seeds freezing is not necessary and for some distinctly undesirable.

Of the five primary causes of dormancy enumerated by Crocker (1916) two are especially important in connection with seeds in which the embryosare well developed, as in the acorn, and have all the external conditions necessary for germination. (I) In one type of dormancy, enclosing structures, such as seed coats or pericarp, prevent the growth of the embryo by withholding some growth factor or holding some growth inhibitor within the seed. In hard seeds water is entirely excluded, while in many the coats reduce the oxygen supply below the necessary minimum forgerrnination (Crocker, 1916). (2) In the second type the embryo is dormant-that is, incapable of growth when it is naked and supplied with ordinary germination conditions-and must pass through some very fundamental changes preliminary to growth. These changes generally require weeks or months for their completion, and in temperate regions the optimum conditions seem to be a temperature of about 5° C. (41° F.), with a good

supply of water and oxygen. The removal of the enclosing structures distinctly hastens the process, in part at least, by increasing the supply of both water and oxygen available to the embryo. The experiments of Shull (1913, 1914) are significant in showing the complex rôle of oxygen in germination and the importance of water in preceding oxygen through an absolutely dry seed coat. Here again is evidence that both water and oxygen are necessary. Mazé (1900) found that seeds retain their viability but a short time under the considerable reduction in oxygen supply involved in water storage. An excess of water may, therefore, be detrimental through reducing the oxygen supply.

From the above survey it is evident that a search for the causes of delayed germination, prevalent in the black oak group but not in the white oaks, should be directed toward the possible influence of apparent differences in (1) the structure of the acornpericarp and (2) the nature and amount of the food reserve as indicated by chemical analyses made before and subsequent to after-ripening.

Rôle of the Pericarp. Because of the ease with which acorns absorb water, as shown in Fig. 7, the pericarp is considered sufficiently permeable and thus not a primary cause of delayed germination. It seemed desirable, however, to test the validity of this hypothesis.

It has been brought out by Fig. 2 and the discussion of acorn structure, that there exist certain morphological differences in the fruit coats of the black and white oak groups. From 30 to 60 measurements of the thickness of the three main component layers of the pericarp were taken on cross sections of red, scarlet, white, and chestnut oak acorns. The results of these measurements are summarized in Table XVII. The two outer layers, the exodermis and the sclerotic layer (called sclerenchyma by Ward, 1892), are considered most important in excluding growth-promoting factors or the retention of growth-inhibiting ones. While there is not much difference in the thickness of the cutinized exodermal layer, that of the red oak acorns was found to be thickest and that of the white oak thinnest.

The layer of parenchyma tissue on the inside of the fruit coat, being composed of relatively thin-walled parenchyma cells, is considered as playing only a minor rôle in the permeability of the fruit coat. The extreme thickness of this layer in the chestnut oak, however, is undoubtedlyaccountable for the greater water-absorbing capacity of the acorns of this species, as shown in Fig. 7, but because of its spongelike texture it does not indicate a greater capacity to withhold water against loss by drying.

This inner layer of the chestnut oak acorns also accounts for their greater heat resistance over acorns of white, black, or scarlet oaks.

The sclerotic layer, which consists of several series of very thick-walled sclerotic cells, varying from about four times as long as broad at the upper edge, to iso-diametric stone cells near the underlying parenchyma, was found to show more significant differences. In the red oak, for example, this layer of sclerotic tissue is over twice as thick as that in the white oak. If this layer alone were to be considered as the index of imperviousness, then the five species would be arranged, according to their increasing imperviousness, in the following order: white oak, chestnut oak, scarlet oak, black oak, and red oak. It will be seen from Figs. 7 to 10,

TABLE XVII

THICKNESS OF COMPONENT LAYERS OF FRUIT COATS OF RED, SCARLET, BLACK, WHITE, AND CHESTNUT OAKS

Tissue layer	*Species*				
	Red oak	*Scarlet oak*	*Black oak*	*White oak*	*Chestnut oak*
	mm.	mm.	mm.	mm.	mm.
Exodermis					
Minimum	0.017	0.014	0.017	0.009	0.017
Maximum	0.034	0.022	0.035	0.021	0.034
Average	0.025	0.017	0.022	0.015	0.022
Number of measurements	50	40	40	60	50
Sclerotic Layer					
Minimum	0.362	0.224	0.293	0.121	0.172
Maximum	0.603	0.378	0.483	0.241	0.310
Average	0.422	0.317	0.396	0.190	0.244
Number of measurements	50	40	40	50	40
Parenchyma					
Minimum	0.465	0.310	0.517	0.569	0.914
Maximum	0.810	0.724	0.776	0.793	2.620
Average	0.626	0.488	0.629	0.640	1.303
Number of measurements	40	40	40	30	40

inclusive, that the relative capacities for water absorption and the rates of water loss do not fall in this same order. While in general the species of the white oak group with relatively thin sclerotic layers germinate more promptly than those of the black oak group with thicker sclerotic layers, the correlation is not so definite in the individual species.

To determine the extent to which the fruit coats are responsible for delayed germination in red oak, the coats were removed from 100 acorns without injuring the embryos. These acorns, together with another 100 similarly treated white oaks, were planted at a depth of ¾ inch in the greenhouse on November 14, 1925. The first germination appeared in both lots 20 days after planting. The white oak attained its total germination of 84 per cent at the end of 40 days, while at this time only 26 per cent of the red oak had germinated. The latter continued to germinate slowly and did not reach its total of 82 per cent until after 115 days had elapsed. While the total germination is essentially the same in both cases, the red oak required 75 days longer to complete its germination (Fig. 20). This is conclusive evidence that the removal of the fruit coats is alone

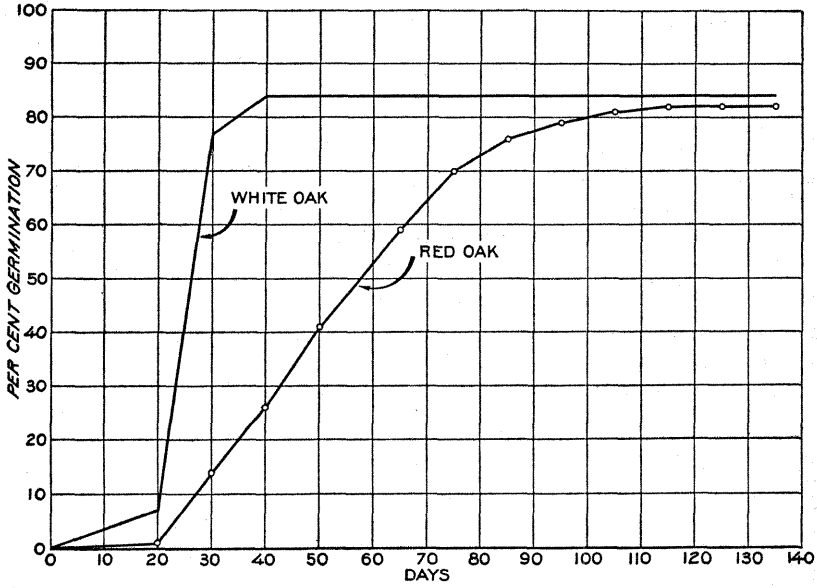

Fig. 20. Course of germination in red and white oak seeds from which fruit coats were removed prior to planting in greenhouse.

insufficient to terminate quickly the period of dormancy in many of the acorns, although it does hasten after-ripening to some extent.

Chemical Differences in Food Reserves. The fact that the cause of delayed germination in the black oak group is inherent in the embryo itself suggests that it may be due to differences in the kind and amount of reserve food materials. Many chemical analyses of acorns have been made in Europe mostly of the English oak or other closely related species of the white oak group. The analyses of the various European workers, which are reviewed and summarized by Wehmer (1911) and Engels (1913), throw little light on the present problem. Two papers published in this country are suggestive in this connection. Shaw (1903), in comparing chemical analyses of valley white oak embryos from California with those of Emory oak from Arizona, shows that the latter (belonging to the black oak group) contains about four times as much fat as the former (white oak group) with a correspondingly lower amount of total carbohydrates. Fraps (1919) gives the results of embryo analyses of several oaks indigenous to Texas. In all cases the embryos of the black oak group have a much higher fat content than the white oaks. Fraps[10] has also shown that post oak embryos which were relatively low in fat contained 6.60 per cent of reducing sugars and a total sugar content of 9.55 per cent and that the embryos of blackjack oak, which are high in fat, contained only 1.70 per cent of reducing sugars and a total sugar content of 5.78 per cent.

Additional information on the delayed germination of the black oak group was obtained through the cooperation of the Chemistry Division of the Connecticut Agricultural Experiment Station. Determinations of the ash, protein, fiber, starch, soluble carbohydrate, and fat content were made of white, chestnut, red, and scarlet oak embryos. The autumn analyses (November, 1925) were made on material taken from the main acorn supply in cold storage and had been collected less than a month, while that used for the spring analyses (April, 1926) came from the same lot that had remained over winter in the storage pit. Immediately after the fruit coats were removed the seeds were ground finely, heated for one-half hour at 95° C. to stop enzymic action, and then dried to constant weight at 70° C. The standard analytical methods of the Association of Official Agricultural Chemists were employed. From Table XVIII it will be seen that the main differences occur in the amount of fat and of direct reducing substances calculated as dextrose. The high fat content of the red and scarlet oaks is in marked contrast to the low fat content of the two white

[10] In a personal communication.

TABLE XVIII

CHEMICAL ANALYSES OF ACORN EMBRYOS BY THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION, AUTUMN OF 1925 AND SPRING OF 1926, ON WATER-FREE BASIS*

	White oak		*Chestnut oak*		*Red oak*		*Scarlet oak*	
	Nov.	*April*	*Nov.*	*April*	*Nov.*	*April*	*Nov.*	*April*
Ash	2.56	2.43	2.26	2.96	2.62	2.87	2.06	2.48
Protein	7.42	7.79	8.50	8.88	7.16	6.90	7.75	7.46
Fiber	1.77	2.51	2.48	3.11	2.37	2.81	2.28	2.49
Carbohydrate:								
Starch†	47.93	51.27	32.20	36.14	23.89	31.94	24.26	26.69
Sol. CHO as dextrose‡	10.47	9.39	14.83	13.00	10.58	6.26	9.41	6.56
Sol. CHO, direct reducing§	(8.01)	(8.80)	(13.40)	(12.27)	(6.41)	(5.47)	(5.32)	(5.56)
Undetermined by diff.	23.04	23.97	35.16	34.04	30.88	29.12	23.41	31.27
Fat	6.81	2.64	4.57	1.87	22.50	20.10	30.83	23.05
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Starch + Sol. CHO	58.40	60.66	47.03	49.14	34.47	38.20	33.67	33.25
Total CHO, nitrogen-free extract	81.44	84.63	82.19	83.18	65.35	67.32	57.08	64.52

* Made under the direction of Dr. E. M. Bailey, Chemist at the Station, to whom the writer is under great obligation for these analyses. The thin membranes or testas enclosing the embryos were included.

† Starch determined by diastase method.

‡ "Soluble carbohydrate as dextrose" includes the substances soluble in 10 per cent alcohol which reduce Fehling's solution after 30 minutes' hydrolysis.

§ "Soluble carbohydrates, direct reducing" includes the direct reducing substances calculated as dextrose; *i.e.*, they reduce Fehling's solution without hydrolysis.

oaks. While the difference is not so striking as the above, the two species of the black oak group-red and scarlet oaks-show a lower content of direct reducing soluble carbohydrates than the t,vo white oaks. Analyses of black oak embryos made in November gave 22.18 per cent of fat and 2.17 per cent of direct reducing soluble carbohydrates. It is also of interest to note that autumn analyses of swamp white oak gave 7.16 per cent of the direct reducing substances and 8.98 per cent of fat. This species showed some delay in germination in the greenhouse as compared with the white and chestnut oaks but not nearly so much as the black oak group (Table II). The delay noted in the germination of European mossycup oak may also be associated with the fat content, for Engels (1913) has shown that the shelled acorns of this species were found to contain 11.52 per cent of fat.

The higher temperature requirements of the black oak group are possibly associated with higher fat content. Since an increase in temperature up to an optimum accelerates the action of catalytic agents, this relation may be due to enzymic action which in turn results in the conversion of the fatty substances into soluble carbohydrates during after-ripening and the early stages of germination.

\Vhen the thickness of the sclerotic layer of the fruit coat is considered another relation is evident. The scarlet oak,which has a higher fat content, has an appreciably thinner layer of sclerotic tissue than the black oak, indicating greater permeability.

Another interesting feature brought out by 1'able XVIII is the lower fat content of the embryos of each species in the spring as compared with that in the autumn. The decrease is more pronounced in the white and chestnut oaks than in the other two species. This may be due to the fact that the germination process was more advanced in the white oaks when the spring samples were taken for analysis. Most of the acorns of these species had radicles protruding about an inch when they were taken from the storage pit on April 9, while those of the red and scarlet oaks were just beginning to crack open. This suggests the probability that the enzymic action connected with the conversion of the fats into soluble carbohydrates continues during the germination process and that the greater part of this conversion takes place after germination begins.

Garner, Allard, and Foubert (1914) have shown that the development of oily seeds is characterized by a progressive accumulation of fat accompanied by a corresponding decrease in carbohydrates, and that under proper conditions this trans.formation takes place in unripe seeds detached

from the plant, indicating that the fat is derived from the carbohydrates. This tends to strengthen the hypothesis that the fats may be reconverted into soluble carbohydrates during after-ripening and the germination process. Onslow (1923) and Priestly (1924) have shown that the metabolism of fatty substances in the plant is still imperfectly understood, although it is known that plants have the power of disorganizing fats and that when fat-containing seeds germinate, lipase, which has the power of hydrolyzing fats, is present in the tissues. The results given in Table XVIII, while very suggestive, should be checked by further studies of the kind and amount of stored foods together with those of the chemical changes and enzymic action incident to after-ripening and germination before final conclusions can be drawn.

Microchemical tests and qualitative determinations were made on the cotyledonary material of several oaks. These, aside from confirming the presence of the substances reported in Table XVIII, showed that fructose and sucrose were also present in the autumn and late Winter. Inulin was tested for but no evidence of its presence could be obtained when the directions given by Onslow (1923) were followed. The presence of tannin was demonstrated.

The great variation in the tannin content of various parts of the acorn of chestnut oak and of the cups of a number of other species reported by Trimble (1896) suggested the desirability of determining whether a difference of sufficient magnitude existed in the embryos of the various species to throw any light on the problem of delayed germination.

Through the courtesy of Mr. Robert W. Griffith, Extract Sales Manager of the Champion Fibre Company, analyses of the tannin content were made on a water-free basis.[11] All samples were prepared as for the other chemical analyses, except that the thin seed coats or testas were removed before the embryos were ground. The acorns were collected between October 5 and 15. The results of these analyses are as follows:

11 Analyses by L. R. Lovelace according to the official method of the American Leather Chemists Association.

Species and part of acorn	*Place of collection*	*Per cent of tannin*
White oak embryos	Buncombe County, N. C.	7.82
White oak embryos	New Haven County, Conn.	4.44
White oak fruit coats	Buncombe County, N. C.	12.48
White oak fruit coats	New Haven County, Conn.	6.52
Chestnut oak embryos	Buncombe County, N. C.	8.89
Chestnut oak embryos	New Haven County, Conn.	7.75
Chestnut oak fruit coats	Buncombe County, N. C.	11.03
Chestnut oak fruit coats	New Haven County, Conn.	8.30
Red oak embryos	New Haven County, Conn.	7.39
Red oak fruit coats	New Haven County, Conn.	1.67
Red oak fruit coats	Buncombe County, N. C.	1.08
Scarlet oak embryos	Buncombe County, N. C.	6.71

There is a consistently greater variation between the high tannin content of the Southern Appalachian acorns and that for the Northeast than there is between the different species; also the fruit coats of the white oak group contain more tannin than those of the black oaks. The amount of tannin contained in the embryos of both groups grown in the same region is so nearly the same that no significance can be attached to the tannin content as a possible explanation of delayed germination in the black oak group.

The most tenable explanation of delayed germination in the black oak group is associated with the much higher fat content of the embryos of these oaks and the time required for the conversion of the fatty substances into soluble carbohydrates. The chemical analyses, in conjunction with the studies of temperature and acorn storage, suggest that the rest period in the black oak group may be terminated when conditions become favorable for the activation of the fat-decomposing enzymes. These convert the reserve supply of fats into more soluble and more readily usable carbohydrates as required by the embryo during its rapid growth in the germination process. In the red oak a very small percentage of the seeds, from which the fruit coats were removed prior to planting, germinated as soon as any of the white oaks and a slow sustained germination occurred throughout the entire period of 115 days (Fig. 20). This indicates that the acorns possess a marked individual variation in the conditions required to bring them into germination, due either to the nature and amount of stored food or to the enzymes present in the embryos.

INFLUENCE OF ACORN SIZE ON GERMINATION AND EARLY GROWTH

The influence of size and weight of seed on germination and development of the plant has been established more definitely for agricultural and garden seeds than for forest tree seeds. During the past 35 years many studies have been made upon small grains and garden plants to determine the comparative value of large and small seed in crop production. The evidence is in favor of large seed, the seeds being otherwise comparable (Cummings, 1914, Kiesselbach and Helm, 1917, Renich, 1921, and Schmidt, 1924). The advantages accruing from large seeds, in addition to higher germination percentage and greater vigor, are a greater number of larger leaves, flowers, and fruits. These facts have been definitely established in practice and adopted as criteria of seed values. Seed weight should also play an important rôle in selecting forest tree seeds.

European foresters have recognized for some time that heavier and larger seeds result in higher germination and seedling survival. Differences in site conditions produce far less variation in the results of sowings of large, heavy seeds.

It is logical from what has been said concerning the general physiology of germination, that large, heavy acorns should be expected to produce the best results. The influence of acorn size upon germination and the oak seedling has been discussed by a number of writers, notably Eytingen (1915), Rodger (1919), Johannsen (1921), Hauch (1923), and Cieslar (1923). Acorn size has also been recognized as a factor in the later development of the tree. In comparing the progeny of heavy and light weight acorns Cieslar (1923) found that the former resulted in larger and more rapidly growing seedlings, but that this advantage entirely disappeared by the end of the eighteenth year. Hauch (1923) contends that the variation in size and vigor of the seedlings persists throughout the entire life of the oak.

An experiment was carried out in western North Carolina during 1924-1925 to determine the influence of acorn size upon germination, survival, and early growth of red, black, white, and chestnut oaks. A correlation was first established between size and weight, indicating that weight can be used as a criterion of size. The frequency distribution, as shown in Table XIX was then determined. For each species a quantity of acorns, sufficient to provide an adequate basis, was taken by "random sampling" from the general stock. These samples were weighed and sorted by weight groups. The groups were combined into five classes

so that the middle, or medium class, included the average weight of the lot used. The intermediate size classes, which were discarded, were selected so that they included about half the total number of acorns. The small, medium, and large classes used in the experiment included the remainder.

Typical lots of these acorn size classes were planted ½ inch deep in the nursery at Canton, N. C. Figures on the germination, survival, and

TABLE XIX

FREQUENCY DISTRIBUTION OF INDIVIDUAL ACORN WEIGHTS OF RED, BLACK, WHITE, AND CHESTNUT OAKS, BUNCOMBE COUNTY, N. C.*

Red oak		*Black oak*		*White oak*		*Chestnut oak*	
Weight group	*Frequency*	*Weight group*	*Frequency*	*Weight group*	*Frequency*	*Weight group*	*Frequency*
Grams	Per cent	Grams	Per cent	Grams	Per cent	Grams	Per cent
2.5-3.0	0.54	0.25-0.50	0.43	0.5-1.0	0.75	0.5-1.5	1.90
3.0-3.5	2.17	0.50-0.75	0.43	1.0-1.5	4.16	1.5-2.5	3.34
3.5-4.0	5.98	0.75-1.00	0.43	1.5-2.0	14.90	2.5-3.5	15.72
4.0-4.5	10.87	1.00-1.25	3.46	2.0-2.5	20.55	3.5-4.5	14.30
4.5-5.0	14.69	1.25-1.50	7.34	2.5-3.0	23.70	4.5-5.5	21.42
5.0-5.5	19.56	1.50-1.75	23.70	3.0-3.5	20.00	5.5-6.5	19.05
5.5-6.0	23.90	1.75-2.00	29.70	3.5-4.0	9.78	6.5-7.5	12.38
6.0-6.5	12.51	2.00-2.25	24.15	4.0-4.5	3.70	7.5-8.5	6.19
6.5-7.0	5.43	2.25-2.50	8.64	4.5-5.0	1.96	8.5-9.5	0.95
7.0-7.5	3.26	2.50-2.75	1.72	5.0-5.5	0.25	9.5-10.5	3.81
7.5-8.0	1.09	.....	....	5.5-6.0	0.25	10.5-11.5	0.47
						11.5-12.5	0.47
	100.00		100.00		100.00		100.00

* Based on individual weighings of 409 white oak and 210 chestnut oak acorns made October 9–11, 1924, and 184 red oak and 232 black oak acorns made November 6–17, 1924.

growth of the resulting seedlings were secured for these lots during the first growing season. The results are summarized in Table XX, which shows an unmistakable advantage in total germination and survival in favor of the large acorns. The difference in seedling growth during the first season, as shown by the average seedling height, average weight of the tops and roots, and the average diameter of the stems and roots, also favors large acorns, with the possible exception of the black oak.

rrhat the highest germination and the largest seedlings came from the large acorns is probably due to the greater food reserve in these acorns. To determine the extent to which the developing seedlings are dependent upon the reserve food stored in the cotyledons an experiment was conducted in the greenhouse in which the cotyledons were removed from typical white and chestnut oak seedlings at various stages of development. In Lot 1 they were clipped off just after the plumule had emerged from the acorn, but before it had elongated perceptibly. All seedlings in this lot died before any additional elongation of the plumule took place. The cotyledons were removed from the seedlings of Lot 2 when the plumules were about ½ inch tall, and those from Lot 3 just after the leaves had unfolded. From Lot 4 the cotyledons were removed 8 days after the leaves had unfolded, and from Lot 5, 10 days later. In Lot 6 the cotyledons were left on the seedlings as a check on the other lots of white oak. The cotyledons were removed from the chestnut oak seedlings in Lot 7 just after the leaves had unfolded.

At the termination of the experiment on June 5, 1926, the average seedling height, and average weight of top and root were determined (Table XXI). The above-ground parts of typical seedlings of Lots 2 to 5 are shown in Plate III. It is evident that in order to survive the seedlings must retain the cotyledons until the plumule has elongated an inch or more. The removal of the cotyledons even after the leaves have unfolded results in smaller seedlings, but this influence disappears during the next 15 to 20 days. This experiment confirms the belief that the greater part of the reserve food of the cotyledons is translocated to the storage tissue of the tap root during the first few weeks following germination and is subsequently used by the seedling in tissue formation.

Information is not available as to the behavior beyond the first year of the seedlings arising from acorns of different sizes. Since heavy acorns possess a greater germinative capacity and the resulting seedlings show greater resistance to injurious environmental influences and are more vigorous due to the greater quantity of reserve food materials deposited

TABLE XX

RELATION OF ACORN WEIGHT TO GERMINATION, SURVIVAL, AND EARLY GROWTH IN NURSERY AT CANTON, N. C.

Species and weight class	*Data based on frequency distribution of weights*					*Growth data at end first season*				*Average diameter of root ½ inch below root collar*
	Inclusive range of weights in class	*Acorns falling in class*	*Basis of tests*	*Total germination*	*Survival first season*	*Average seedling height end first season*	*Average weight of tops*	*Average weight of roots*	*Average diameter of stem at root collar*	
	Grams	Per cent	Number of acorns	Per cent	Per cent	Inches	Grams	Grams	Inches	Inches
Red oak										
Small	2.5-3.5	2.71	28	64.2	60.7	5.19	2.16	2.72	0.166	0.222
Medium	5.0-6.0	43.46	48	68.8	64.6	6.78	3.81	4.93	0.200	0.263
Large	7.0-8.0	4.35	36	77.8	77.8	7.47	5.15	6.76	0.224	0.289
Unselected	.....	100.00	100	74.0	74.0	...	...	...	....	....
Black oak										
Small	0.25-1.25	4.75	100	62.0	62.0	3.02	1.21	1.28	0.123	0.172
Medium	1.50-2.00	53.40	100	85.0	85.0	3.11	1.50	1.54	0.130	0.175
Large	2.25-2.75	10.36	100	91.0	90.0	3.37	1.65	1.70	0.140	0.192
Unselected	.....	100.00	100	68.0	67.0	...	...	...	....	....
White oak										
Small	0.5-1.5	4.91	100	23.0	16.0	3.42	0.96	1.22	0.109	0.164
Medium	2.0-3.5	64.25	100	59.0	57.0	4.45	2.28	3.46	0.143	0.228
Large	4.5-6.0	2.46	65	96.9	96.9	4.94	2.33	4.32	0.152	0.253
Unselected	.....	100.00	100	73.0	72.0	...	...	...	....	....
Chestnut oak										
Small	0.5-2.5	5.24	100	79.0	76.0	4.36	1.34	1.44	0.110	0.166
Medium	4.5-6.5	40.47	100	82.0	82.0	5.48	2.62	3.38	0.147	0.232
Large	9.5-12.5	4.75	100	94.0	94.0	8.17	5.23	4.95	0.179	0.271
Unselected	.....	....	107	80.4	75.7	...	...	...	....	....

in the acorn, it is logical to assume that these results will still be apparent after the seedling stage has passed. The superiority at the start will be especially significant where competition, either between individuals of the same or of different species, is keen from the beginning. In the majority of such cases the dominant trees in the stand will be those which had the better start and, for the most part, have been dominant from their youth.

TABLE XXI

INFLUENCE OF REMOVAL OF COTYLEDONS ON THE DEVELOPMENT OF WHITE AND CHESTNUT OAK SEEDLINGS

Lot no.	*Species*	*Date cotyledons removed*	*Growth Data** *Average seedling height June 5*	*Average weight of top*	*Average weight of root*
		1926	Inches	Grams	Grams
1	White oak	March 21	†	†	†
2	White oak	March 26	1.7	0.17	0.43
3	White oak	April 2	2.4	0.34	0.75
4	White oak	April 10	3.8	0.70	1.24
5	White oak	April 20	3.7	1.03	1.91
6	White oak	Control, cotyledons not removed	4.1	1.02	1.76
7	Chestnut oak	March 24	2.9	0.68	1.24
8	Chestnut oak	Control, cotyledons not removed	4.5	2.12	2.82

* Based on the measurement of 10–20 typical seedlings in each lot, June 5, 1926.
† All seedlings in this lot died as soon as the cotyledons were removed.

Compactness of Surface Soil in Relation to Early Survival

It has been commonly observed that the radicles of germinating acorns fail to penetrate soil which has become excessively compacted as a result of exposure, trampling, or forest fires. Natural regeneration is rendered quite impossible on poor soils and more difficult on soils of better quality by the hardness and dryness of the surface (Henry, 1908, Tansley, 1911).

To study the extent to which the radicles of germinating acorns penetrate various substrata and to determine whether it is possible to secure a

satisfactory measure of the relative penetrability of various types of surface soil, greenhouse experiments were begun on November 7, 1925. Sections of the natural surface soil 4 inches deep were excavated, transferred to flats, and taken to the greenhouse without disturbing the compactness or penetrability of the surface layers. The type of soil used in these experiments is shown in Table XXII. Fifty white oak, and the

TABLE XXII

RELATION BETWEEN PENETRATION OF SURFACE SOIL BY OAK RADICLES AND PENETRABILITY AS MEASURED BY PENETROMETER IN UNIFORM TIME OF 5 SECONDS

Nature of surface soil	*Penetration by oak radicles*	*Load on penetrometer*	*Penetrability by penetrometer**	
			With weight indicated in col. 3	*Reduced to a gram-millimeter basis*
		Grams	mm.	mm.
Natural soil, compacted sandy loam	Not penetrated	200	2.0620	0.0103
Natural soil, compacted sandy loam	Penetrated	200	12.3000	0.0615
Natural soil, bearing sod and moss	Penetrated	200	17.0100	0.0850
Natural soil, bearing moss only	Penetrated	50	11.0320	0.2206
Natural soil, bearing rank growth of blue grass	Penetrated	50	4.4440	0.0889
Sandy loam, artificially packed and baked	Not penetrated	250	1.2075	0.0048
Sandy loam, artificially packed and baked	Penetrated	250	5.7470	0.0230
Sandy loam, artificially compacted, not baked	Not penetrated	250	0.3586	0.0143
Sandy loam, artificially compacted, not baked	Penetrated	250	0.5980	0.0239
Greenhouse potting loam	Penetrated	50	39.9360	0.7987

* Based on the average of 30 to 60 measurements in each case.

same number of chestnut oak acorns, which were just beginning to germinate were placed on the surface of each flat, together with from 50 to 100 red oak acorns. These were kept well watered and covered with bell jars for about two weeks or until the radicles not penetrating the soil had attained a length of 1 to 2 inches.

Those radicles which failed to penetrate the surface soil in some of the flats showed two main types of response: (1) the elongating radicles pressing on the soil raised the acorns, causing them to become inverted with the radicles projecting into the air (Fig. 21, A, B, C, D, E, and F); and (2) the elongating radicles growing along on top of the soil without appreciably lifting the acorn (Fig. 21, G, H, and I). The latter was the most common occurrence.

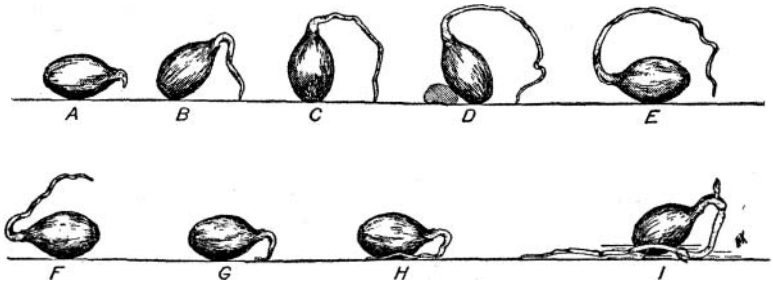

Fig. 21. Various stages in the germination of acorns on the surface of compact, impenetrable soil showing three types of response (1) A, B, C, D and E, the elongating radicle, unable to enter the soil, has pushed the acorn over against a pebble in D, and the acorn has slipped off in E; (2) the elongating radicle unable to enter the soil has pushed the acorn directly over backwards in F; (3) G, H and I, radicles of germinating acorns running along on top of the soil due to their inability to penetrate it-a common occurrence.

Assaon as the fate of the seedlings became apparent penetrability measurements of the surface soil were made with the New York Testing Laboratory penetrometer. This instrument measures the depth to which a standard needle will penetrate during a given time, 5 seconds being the standard. The depth of penetration is measured in tenths of a millimeter, which are indicated on the dial of the instrument. It was found at the outset that, in order to secure measurements within the compass of the scale of the dial, it was necessary to use different loads on the penetrometer in working with the different substrata. To afford a more reliable criterion of the relative compactness of the soil as influencing root penetration the measurements were taken adjacent to the points where the

radicles penetrated the soil or failed to penetrate. To make all the results comparable the measurements were reduceo to the standard basis of the amount of penetration which would have been secured if a load of one gram had been brought to bear upon the point of the penetrometer needle at the soil surface for the standard time of 5 seconds.

The results of this study, summarized in Table XXII, show a great difference in the amount of penetration in the various substrata. On the basis of these measurements and with the instrument and substrata used, the limit of penetration for oak radicles appears to occur in soils, the penetrability of the surface layer of which lies between 0.01 and 0.023 mm. per gram of load applied. The correlation of these results with existing field conditions is a subject for further field study. Soils are not commonly homogeneous so that standards of comparison can only be arrived at through the average of many readings.

The radicles of acorns which germinate on the surface of compact soil are utterly unable to penetrate soil that has become excessively compacted. The pressure of the radicles on the soil throws the acorns out of position. When planted in compact soil the elongating radicles can actually exert much greater pressures. Watt (1919) reports having made similar observations in Great Britain.

It has been shown above that the oak radicles commonly grow along the surface of soils which they cannot penetrate. This is most commonly observed during wet rainy weather, for during dry weather water cannot be replaced as fast as it evaporates from the succulent radicles and they dry up and die.

INFLUENCE OF LXAF LITTER

In the field study reviewed in Table III, which sought to determine what happens to the acorn crop under natural conditions, the importance of leaf litter in preserving the viability of the acorns which escape rodents and insects was' obvious. No sound, viable acorns were found on bare ground under any of the trees studied in the spring of 1925.

A 2o-inch red oak tree having a crown spread of 40 feet afforded a good opportunity to observe the direct influence of the leaf litter as contrasted with that of bare ground, for the litter was 2 to 3 inches thick under half the tree while the ground was bare under the other half. On that part protected by leaf litter 15.7 per cent of the acorns recovered were sound and apparently viable as indicated by a cutting test; 9.3 per cent of the acorns had germinated and had radicles 1 to 2 inches long, the

remainder having been destroyed by rodents and insects. On the bare ground no sound viable or germinated acorns were found. Wherever there is a covering of the leaf litter over the acorns the retention of their viability is favored and the germination of viable seeds is likely to occur.

An experiment was begun October 6, 1925, to show the influence of a leaf litter cover on germination and early survival of red, black, white, and chestnut oaks. Two hundred acorns of each species were put on the bare soil surface in the botanical garden in New Haven and covered with hardwood leaf litter to a depth of 2 inches and screened against rodents. The same number of each species was similarly placed but without any litter cover. Separate lots of germinating white and chestnut oak acorns were also employed in addition to the ungerminated ones. Daily records of the maximum and minimum temperatures to which the acorns were subjected under the two sets of conditions were obtained from the

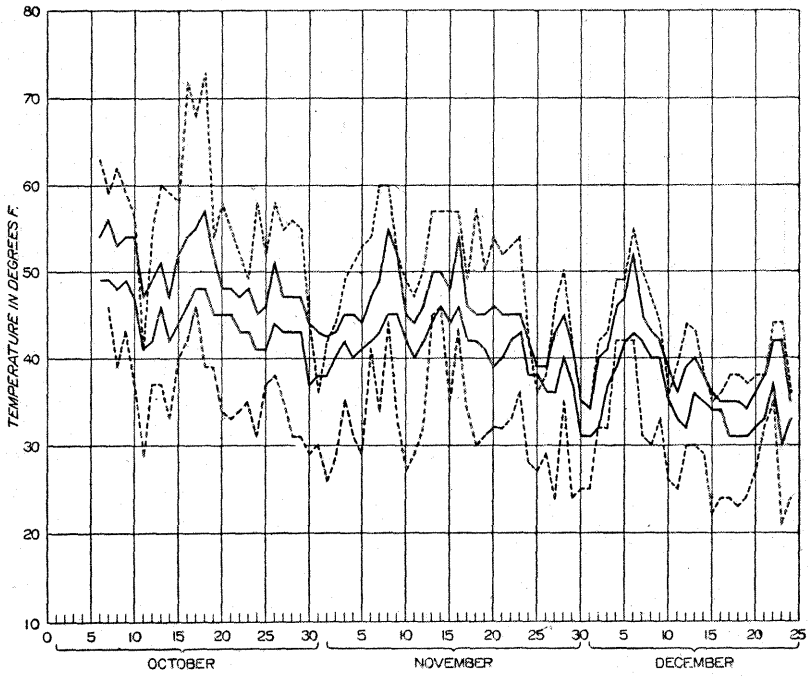

Fig. 22. Effect of leaf litter cover on maximum and minimum temperatures to which acorns were subjected on top of ground. Solid lines represent temperatures under leaf litter and dotted lines those on bare ground. In each pair the upper graph represents the maximum temperatures and the lower the minimum temperatures.

beginning of the experiment to December 24, when 2 inches of snow fell on the beds. These records are shown graphically in Fig. 22, which strikingly shows the extent to which the leaf litter equalizes temperatures by lowering the maxima and raising the minima.

The moisture content of the upper inch of soil was determined at five different times during October and November, generally just preceding rains. Although made at such times the bare soil showed a variation of only 4.5 per cent and that under the leaves 1.5 per cent. Since the minimum moisture content of the upper inch of bare soil was found to be 26 per cent it is evident that the soil contained sufficient moisture at all times, for it varied from this minimum up to 49 per cent when saturated during and just after heavy rains. Dew and frost tended to keep the

TABLE XXIII

INFLUENCE OF LEAF LITTER ON GERMINATION AND EARLY SURVIVAL OF VARIOUS OAKS AT NEW HAVEN, CONN.

Species	*Soil surface (bare or covered by leaf litter)*	*Germination*	*Survival on June 19, 1926*
		Per cent	Per cent
White oak	Bare	97.0	0.0
White oak (sprouted)	Bare	100.0	0.0
White oak	Covered	97.5	80.0
White oak (sprouted)	Covered	100.0	93.5
Chestnut oak	Bare	93.0	0.0
Chestnut oak (sprouted)	Bare	100.0	0.0
Chestnut oak	Covered	93.0	75.0
Chestnut oak (sprouted)	Covered	100.0	77.0
Red oak	Bare	13.0	0.0
Red oak	Covered	98.0	91.0
Black oak	Bare	11.0	1.0*
Black oak (sprouted)	Covered	87.0	64.0

* Acorn partially covered with soil.

moisture of the upper inch relatively high between rains. Although the soil moisture was ample at all times all the germinated white and chestnut oak acorns on the bare soil dried out and the seedlings died before the radicles penetrated the soil. This occurred before freezing temperatures became prevalent.

The total germination and survival of the various lots of acorns on June 19, 1926, are summarized in Table XXIII. No viable acorns or seedlings survived on the bare area, while on that protected by a 2-inch cover of leaf litter not only a high percentage of germination but also a high survival of seedlings occurred in the white and chestnut oaks. Favorable results were also secured with the red and black oaks under the leaf litter, but on the bare soil the acorns of these species lost their viability before germination occurred in the spring.

The results of this experiment were checked by those of another one conducted on the Bent Creek Watershed in Buncombe County, North Carolina. On October 17 and 26, 1925, 500 acorns of white, red, black, and scarlet oak and 100 chestnut oak were put on the surface of the bare soil on both north and south-facing slopes.[12] The same number of each species similarly placed were covered with hardwood leaves to a depth of about 1 inch. All lots were screened against rodents. The total germination and survival of the various lots of acorns on July 7, 1926, are summarized in Table XXIV. When allowance is made for insect infestation and the fact that in several of the lots put on bare soil all the surviving seedlings came from acorns which were buried during heavy rains, it will be seen that the results of this experiment agree with those secured at New Haven. The great importance of the leaf litter in maintaining conditions suitable for acorn germination and seedling survival has also been observed in other localities. The beneficial effects of the leaf litter in protecting Rocky Mountain white oak acorns from drying out and freezing have been observed repeatedly in the semi-arid brushlands of the Intermountain Region.[13]

These experiments and observations emphasize the fact that in all cases where germination and survival occur, environmental conditions are such as to inhibit drying. The figures given by Ebermayer (1876) are significant. He showed that, for the conditions under which he was working, evaporation from forest soil without leaf cover was 47 per cent of that

[12] Carried out by E. F. McCarthy and F. W. Haasis at the writer's request.

[13] Baker, F. S., and C. F. Korstian. The establishment of western yellow pine forests on the brushlands of the Intermountain Region. MS. report, 1926.

from soil in the open, and that from forest soil with a full covering of litter was but 22 per cent.

The studies of Watt (1919) are also significant. He has shown that the drying process begins immediately in those acorns which fall on bare soil and drying inhibits their germination. Table VII above shows that

TABLE XXIV

INFLUENCE OF LEAF LITTER ON GERMINATION AND EARLY SURVIVAL OF VARIOUS OAKS ON THE BENT CREEK WATERSHED, BUNCOMBE COUNTY, N. C.

Species	*Aspect*	*Soil surface (bare or covered by leaf litter)*	*Germination*	*Survival on July 7, 1926*
			Per cent	Per cent
Post oak	North	Covered	91.0	59.2
White oak	North	Covered	92.4	76.0
White oak	North	Bare	98.6	1.0
White oak	South	Covered	69.0*	33.8
White oak	South	Bare	71.2*	4.8
Chestnut oak	North	Covered	85.0	75.0
Chestnut oak	North	Bare	99.0	0.0
Chestnut oak	South	Covered	95.0	86.0
Chestnut oak	South	Bare	85.0	12.0
Red oak	North	Covered	94.0	90.6
Red oak	North	Bare	79.8	47.8†
Red oak	South	Covered	94.4	92.2
Red oak	South	Bare	46.2	1.2
Black oak	North	Covered	85.6	85.6
Black oak	North	Bare	25.6	13.6†
Black oak	South	Covered	84.0	84.0
Black oak	South	Bare	3.6‡	0.8†
Scarlet oak	North	Covered	47.4§	27.8§
Scarlet oak	North	Bare	73.0	16.4†
Scarlet oak	South	Covered	94.4	92.2
Scarlet oak	South	Bare	41.6	1.4†

* These lots of acorns showed 12.2 per cent of weevil infestation.

† All these seedlings came from acorns buried by soil during heavy rains.

‡ Only 10.8 per cent of these acorns were infested with weevils.

§ The poor showing made by this lot of acorns is due to the fact that only those were used which floated in water, thereby including many aborted and insect-infested acorns.

when such acorns have reached a certain degree of dryness they lose their viability and will not germinate, no matter how much moisture they may subsequently take up.

The leaf litter cover of the forest floor is, of course, valuable for other reasons than the protection of acorn viability. It is known to have the capacity of absorbing moisture directly from the air and retaining it. Its beneficial influence in conserving moisture, equalizing temperatures, and in maintaining the fertility and porosity of the soil has been demonstrated by Ramann (1890, 1893) and others. Coville (1914) has shown its importance in harboring earthworms, the larvae of flies and beetles and myriapods, which are beneficial not only in hastening the decay of vegetable matter but also in rendering the soil lighter and more porous. Finally, Ebermayer (1876) has shown that its removal may have a far-reaching influence on the future development of the stand.

That a covering of leaf litter tends to prevent the compacting of the surface soil so that the oak radicles can penetrate, was shown by a greenhouse experiment. Two flats were filled with potting loam. One was left bare and the other covered with oak leaves when the experiment was begun January 2, 1926. On March 25, 58 white oak acorns from cold storage were placed on the soil surface in each flat and covered with bell jars. At this time 40 penetrability measurements were made with the penetrometer on each flat. The soil covered with leaf litter showed a penetrability of 0.593 mm. per gram of load applied, while the bare soil showed only 0.34 mm. Both flats were watered at the same time with a fine spray. By April 9, 60.2 per cent of the acorns had germinated on the bare soil but only 31 per cent had become established, the remainder drying out and dying. Under the leaf litter 89.7 per cent of the acorns germinated with a resulting survival of 82.8 per cent. By comparing these results with those given in Table XXII it will be seen that the failure of the radicles to penetrate the bare soil was not due to its compactness as much as it was to the absence of the leaf litter. The weight of the leaf litter is sufficient to hold the acorns in place while the radicles penetrate the soil.

The results of the above experiments, together with numerous observations by the writer, indicate that too much emphasis cannot be placed on the importance of the leaf litter cover in producing an environment most suitable for acorn germination and survival of the seedlings. This favorable result is due to the influence of the leaf litter in reducing water loss, equalizing temperatures, and facilitating root penetration.

APPLICATION OF RESULTS IN SILVICULTURAL PRACTICE

PLANTING of oak seedlings and direct sowing of acorns in the field will probably find a more or less important place in American silviculture. The artificial storage of acorns is therefore a silvicultural measure of some importance. The relation of moisture and temperature to the success of storage, as brought out in the preceding discussion, consequently has a direct bearing upon silvicultural practice.

In all probability dependence will usually be placed upon natural rather than artificial regeneration. Furthermore, the second-growth stands will be composed of trees of both sprout and seedling origin. A relatively high proportion of seedlings in second-growth oak stands is particularly desirable in silvicultural practice. In mature stands or those suitable for cutting the trees are often so far apart that the sprout growth is not adequate to fully restock the area. Seedling reproduction is desired to fill the gaps and also because the forest will eventually deteriorate if repeatedly reproduced wholly by sprouts.

The pertinent facts are these:

1. The oaks produce a very moderate quantity of seed as compared with many other species.

2. The great bulk of the acorn crop falls under or near the seed trees.

3. Because of their weight the acorns are not disseminated by wind but may roll considerable distances down steep slopes.

4. The chief agents of dissemination are animals, birds, water, and gravity.

5. Acorns of the white oak group germinate very promptly in the autumn, and those of the black oak group in the spring, provided they escape destruction by animals and acorn-feeding insects and at no time become overdry.

6. Satisfactory germination and survival of many heavy-seeded species, including the oaks, does not take place unless the seeds are covered. The covering of leaf litter, which, under natural conditions, falls after the acorns have been shed, usually affords ample protection.

7. The leaf litter on the forest floor, together with the shelter of the older trees in the stand, is therefore extremely important in creating conditions suitable for the retention of acorn viability and for germination and seedling survival.

8. Because of the large food reserve in the acorn a vigorous and rapid development of the tap root follows germination.

9. If the tap root penetrates the soil at all the oak seedling is able to withstand considerable dryness while still in its juvenile form.

These characteristics of acorn germination suggest the following principles to obtain oak seed reproduction.

Suitable seed-bed conditions can be maintained and the natural regeneration of oak by seed most easily secured by a form of partial cutting in which the reproduction becomes established under the protection of the remaining stand before it is cut.

With uneven-aged stands, in which trees of all sizes are represented, the selection system will probably give the best results. In this system the oldest or largest trees, scattered or in groups, are removed and the immature trees are left for subsequent cuts. Cuttings are made at intervals throughout the life of the stand. Natural reproduction starts in the openings created by each cutting, the necessary seed being supplied by the larger trees around the openings.

For even-aged stands, which are more uniform than the uneven-aged ones, the shelterwood system is advocated. This system involves the gradual removal of the stand by a series of partial cuttings, resembling thinnings, that remove the entire stand usually within twenty or thirty years. The new stand starts under the shelter of the older trees and is finally released from their shade and protection when able to endure exposure.

In central Europe, where the shelterwood system has been used extensively for the regeneration of even-aged stands of oak, natural reproduction is commonly secured through three cuttings. The first cutting aims to bring about seeding, the second to strengthen the young growth established, and the third to effect the isolation of the young stand. It is ordinarily considered sufficient to have an acorn crop before the seed cutting or at least within two or three years thereafter. A gradual reduction of the protection afforded the young stand through a number of cuttings is preferable to a single cutting.

In this country the preliminary or seed cutting is likely to be unnecessary because of abundant advance growth. Furthermore, it may be necessary to omit it because of economic limitations (Graves, 1911, Hawley, 1921). It is evident, therefore, that in both the shelterwood and selection methods, as well as in any other, full advantage should be taken of advance reproduction on the area at the time of cutting. This reproduction may vary from a few young seedlings up to considerable areas of saplings.

Where it is abundant the cuttings are made wholly with reference to the special requirements of each group of advance growth.

Because the acorns are unable to withstand high temperatures and the leaf litter cover should be maintained intact, rigid protection of the forest from fire should be insured at all times. Such protection is imperative for all oak forests and especially for cutting areas on which a high survival of oak seedlings is expected.

Under some circumstances the leaf litter might accumulate to an extent prejudicial to the establishment of oak seedlings by mechanical obstruction, smothering or otherwise. However, the decay of forest litter in oak stands is so rapid under normal conditions that there is seldom an excessive accumulation of litter great enough to prevent acorn germination and the establishment of oak seedlings over extensive areas.

SUMMARY

THE results of the investigation of factors controlling germination and early survival in the oaks, which was conducted in Buncombe and Haywood Counties, N. C., and in New Haven County, Conn., are summarized as follows:

1. In many cases, particularly in those of limited seed production, 90 to 100 per cent of the available supply of acorns may be consumed or otherwise destroyed by animals, especially the seed-eating rodents.

2. The extent of insect injury, mostly by nut weevils, was found to vary from no injury on certain chestnut oaks to over 50 per cent on some black oaks.

3. In normally moist white oak acorns moisture comprises 60 to 70 per cent of their dry weight. A marked decrease in viability occurs when the moisture content falls below 25 to 30 per cent. For red oak acorns the normal moisture content is 50 to 60 per cent of their dry weight. A marked decrease in viability is noted when the moisture content falls to 20 to 30 per cent. Loss of viability occurs when the moisture content falls to 10 to 15 per cent.

4. Moisture conditions favorable to acorn germination are determined chiefly by a protective covering of soil or leaf litter.

5. A wide range in temperatures suitable for germination was found for all the oaks studied. No germination occurred in any of the species until the temperature went consistently above 40° F. An average of 80° F. at night and 95° F. during the day was too high for the best total germina-

tion. When both promptness of germination and total germination were considered, an average night temperature of 50° F. and 65° F. during the day gave the most satisfactory results.

6. The prevalence of delayed germination in the black oak group has been clearly shown. An increase in temperature within the vital range, while tending to shorten the rest period, is not alone sufficient to terminate it. That the removal of the fruit coats prior to planting the seeds in the greenhouse failed to terminate quickly the period of dormancy in red oak acorns, although it hastened after-ripening to some extent, is positive evidence that the cause of delayed germination in the black oak group is inherent in the embryo itself. The embryos of this group have a much higher fat content than those of the white oak group, and the need for a rest period and higher temperatures to hasten after-ripening is probably associated with enzymic action and the conversion of the fats into soluble carbohydrates during after-ripening and the early stages of germination.

7. Acorns cannot withstand the amount of heat usually generated in leaf litter fires. The relative susceptibility of acorns to excessively high temperatures in the order of decreasing resistance are: red oak, chestnut oak, black oak, scarlet oak, and white oak.

8. Large, heavy acorns were found to give the highest germination percentage and also the largest and most vigorous seedlings at the end of the first year.

9. A moderately low temperature (33-38° F.) and high atmospheric or high soil moisture are the most important factors controlling the retention of the viability of acorns in either artificial or natural storage. A supply of oxygen sufficient for respiration must also be available.

10. The radicles of germinating acorns are unable to penetrate soil which has become excessively compacted at the surface. On the basis of 630 measurements and with the New York Testing Laboratory penetrometer and substrata used, the limit of penetration for oak radicles appears to occur in soils with the surface layer penetrability falling between 0.01 and 0.023 mm. per gram of load applied. So far as known this is the first effort made to secure actual measurements of the compactness of the surface soil in relation to root penetration. The correlation of these results with existing field conditions is a subject for future field study.

11. The leaf litter cover of the forest floor is of the greatest importance in producing an environment most suitable for acorn germination and the

survival of the seedlings. This is due to the influence of the leaf litter in reducing water loss, equalizing temperatures, and facilitating root penetration.

12. Optimum seed-bed conditions can be maintained and the natural regeneration of oak by seed most easily secured by a form of partial cutting, either by the selection method or by the shelterwood method in which the stand is removed in two or three cuts.

COMMON AND SCIENTIFIC NAMES OF OAKS APPEARING IN THE TEXT

Ban oak (*Quercus incana* Roxb.)
Black oak (*Q. velutina* Lam.)
Blackjack oak (*Q. Marilandica* Muench.)
Bristletooth oak (*Q. serrata* Thunb.)
Bur oak (*Q. macrocarpa* Michx.)
Chestnut oak (*Q. montana* Willd.)
Chinquapin oak (*Q. muehlenbergii* Engelm.)
Emory oak (*Q. emoryi* Torr.)
English oak (*Q. pedunculata* Ehrb.)
European mossycup oak or European turkey oak (*Q. cerris* L.)
Oregon white oak (*Q. garryana* Dougl.)
Overcup oak (*Q. lyrata* Walt.)
Post oak (*Q. stellata* Wang.)
Red oak (*Q. borealis* Michx.)
Rocky Mountain white oak (*Q. utahenis* [A.DC.] Rydb.)
Scarlet oak (*Q. coccinea* Muench.)
Shingle oak (*Q. imbricaria* Michx.)
Southern red oak (*Q. rubra* L.)
Swamp chestnut oak (*Q. prinus* L.)
Swamp white oak (*Q. bicolor* Willd.)
Valley white oak (*Q. lobata* Nee.)
White oak (*Q. alba* L.)
Willow oak (*Q. phellos* L.)

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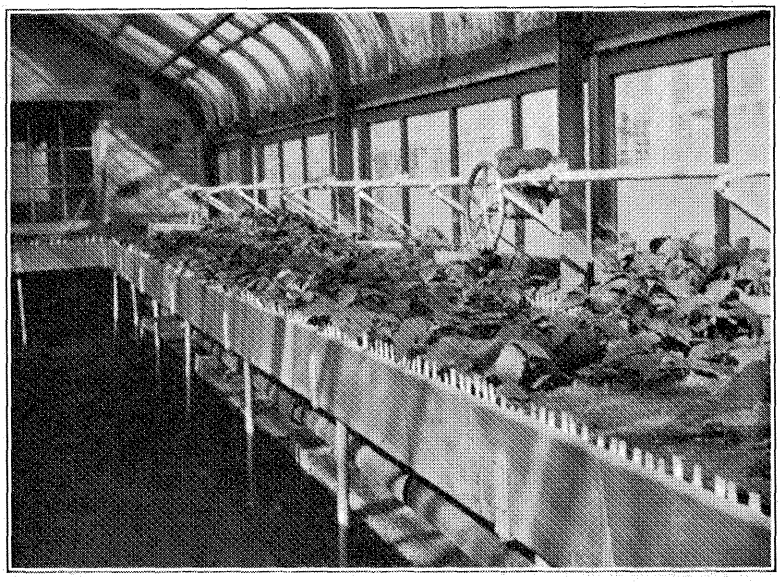
PLATE I

Destruction of acorns by rodents; Fig. 1.—Debris at base of stump resulting from work of squirrels; Fig. 2.—Debris left by field mice adjacent to burrow (indicated by pen knife).



Photos by Dr. Geo. E. Nichols.

PLATE II

Fig. 1.—Greenhouse bench; showing general germination tests. Soil-air thermograph in background.

Fig. 2.—The well-drained hillside where the best results were obtained in acorn storage, location of pit marked by the four stakes.

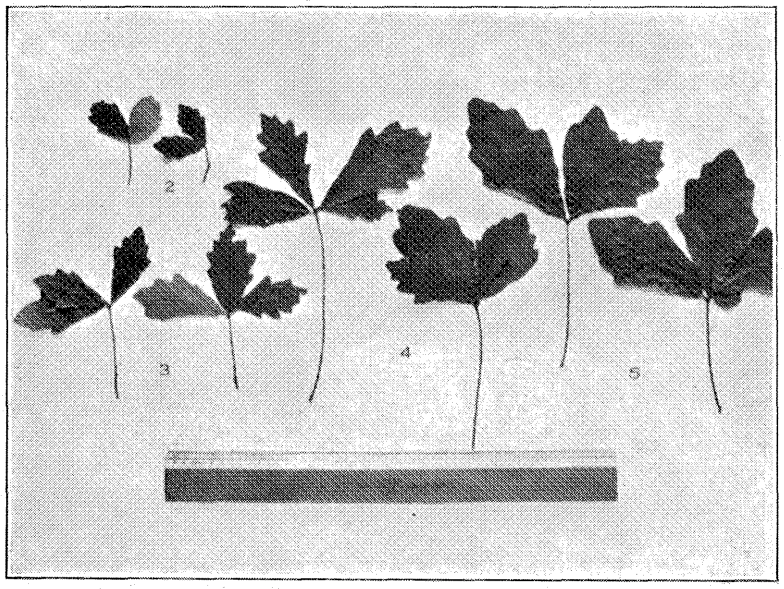
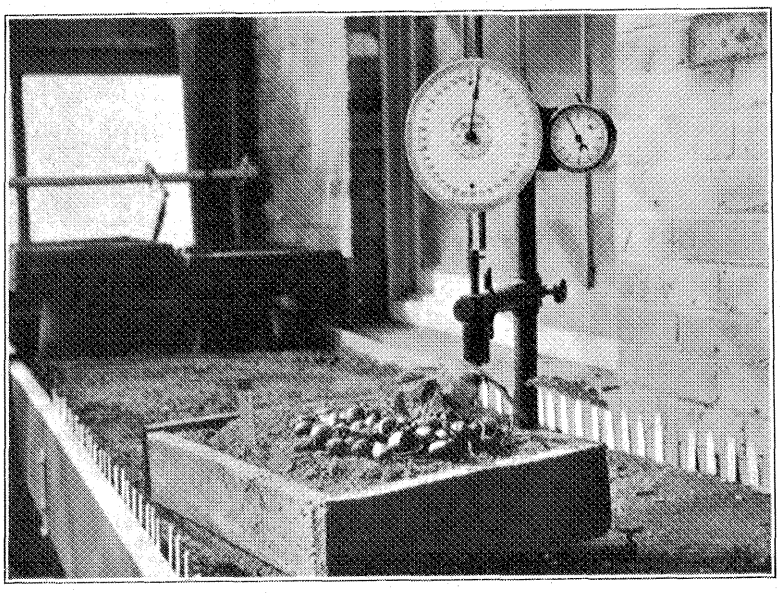
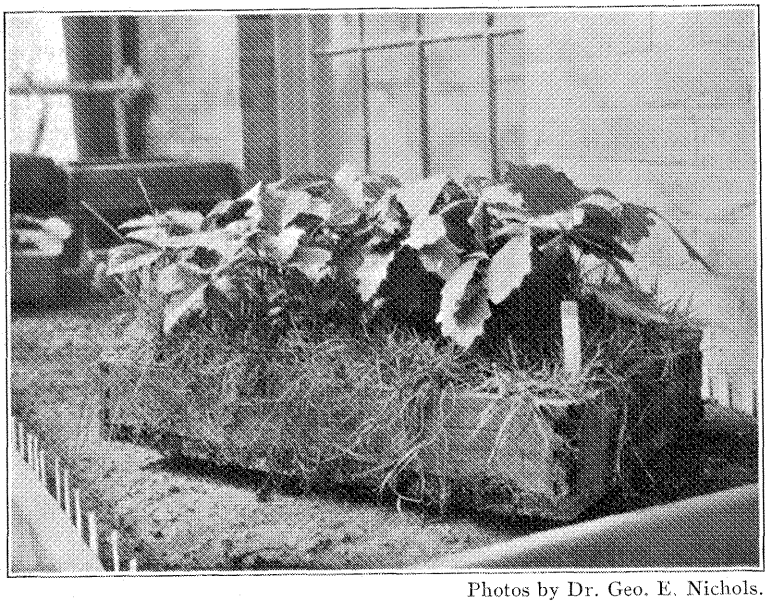


PLATE III

Influence of removal of cotyledons on the development of white oak seedlings:

2. Removed when plumules were about ½ inch tall.
3. Removed just after the leaves unfolded.
4. Removed 8 days after the leaves unfolded.
5. Removed 18 days after the leaves unfolded.





Photos by Dr. Geo. E. Nichols.

PLATE IV

Fig. 1.—Lack of survival in white and chestnut oaks on naturally compacted soil. The flat is in position for making penetrability measurements.

Fig. 2.—High survival of white and chestnut oaks on grass sod, as contrasted with the bare soil shown in Fig. 1.

PLATE V

Fig. 1.—White oak reproduction following partial cutting and protection from fire. Pisgah National Forest, North Carolina.

Fig. 2.—White oak stand carefully managed and protected from fire. Perry County, Tennessee.

PLATE VI

Absence of reproduction on ridge due chiefly to heavy grazing. Browsing and excessive compactness of the soil resulting from trampling by cattle are evident. Near Holden, West Virginia.

PLATE VII

Hardwood stand in which seedling growth of oak and other species has been exterminated by repeated surface fires due to inadequate fire protection. Massanutten Mountain, Va.

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