

DEVELOPMENT OF THE ROOT SYSTEM OF  
NORTHERN RED OAK (*QUERCUS RUBRA* L.)

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Walter H. Lyford was Soil Scientist at the Harvard Forest from 1960 until he retired in 1976. The studies described in this paper covered several years and, although the manuscript was written before Walter's retirement, he kept "polishing" it afterward. With the exception of a few editorial adjustments suggested by his colleagues who read it, the paper is just as Walter left it when he died March 11, 1979. It contains a wealth of information about red oak root systems, painstakingly gathered as only Walter had the patience to do. It is a fitting addition to the Harvard Forest Paper series that contains so much of Walter's work.

## DEVELOPMENT OF THE ROOT SYSTEM OF NORTHERN RED OAK (*QUERCUS RUBRA* L.)

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### ABSTRACT

Root systems of mature red oak trees are dominated by 5-10 first order, woody major framework laterals that arise from the taproot near the soil line. These extend horizontally through the B horizon for distances up to 17 meters. Injury is almost immediately followed by development of replacement roots. This leads to forking and to the coarsely branched woody root systems of the forest-grown tree. Laterals on uninjured roots emerge acropetally about every 1-2 mm. Many laterals grow upwards, rising from woody horizontal laterals into the A1 and forest floor horizons. These laterals elaborate into an enormous number of 0.1-0.2 mm diameter root tips, most of which are ectomycorrhizal.

### INTRODUCTION

Northern red oak (*Quercus rubra* L.) is a commercially important tree in many parts of the United States (Fowells, 1965). Although root systems of seedlings and saplings have been studied in considerable detail (Auchmoody, 1972; Biswell, 1935; Carpenter and Guard, 1954; Garin, 1942; Holch, 1931; Korstian, 1927; Larson, 1970, 1975; Lyr and Hoffmann, 1967; Phares, 1971; Richardson, 1953; Toumey, 1929), not much attention has been paid to the root systems of mature trees. In the United States, only Stout (1956) has described the root systems of older red oaks. He washed out the entire root system of two 17-year-old trees and representative roots of two mature trees, 73 and 84 years of age. Stout was concerned primarily with the distribution of the woody portions of the root system and made only a few observations on small-diameter roots and root tips. Several studies of the red oak root system have been made in Europe where red oak is an introduced species. Köstler, Brückner and Bibelriether (1968) devoted one section of their book to the root systems of red oak, paying particular attention to the central part. By far the most detailed study of red oak root systems, either in the United States or Europe, was made by Lemke (1956) who worked on all ages of red oak at eleven different sites in East Germany. As in many studies of the root systems of trees, a large part of his study was with the woody root system and particularly its central portion.

During studies of red maple (*Acer rubrum* L.) root systems in forest stands at the Harvard Forest in central Massachusetts (Lyford and Wilson, 1964, 1966) the root systems of the closely associated red oaks were found to differ considerably from red maple in depth of laterals, return of roots to the surface, character of root tips and several other features. These observations were the impetus for further studies. This report is concerned with the development and morphology of the root systems of seedlings, saplings and mature red oaks growing in forest stands and also observations of the growth or replacement roots in a root cellar. Some discussion of the non-woody roots of red oak was included in a previous paper (Lyford, 1975).

#### TERMINOLOGY

The following root terminology is used in this paper. Taproot - the single root which emerges from the acorn, initially designated the radicle and later, the taproot. Adventitious root - any root originating from the shoot. Lateral root - any root originating from another root. Alternative terms are branch or side roots. Replacement root - any lateral root formed as a result of injury to the parent root. Most replacement roots continue elongation in much the same direction as the parent root. Forked root - portion of the root where two or more replacement roots have continued forward elongation. Generally, forked root members are separated from each other by smaller angles than those between uninjured parent roots and their normal laterals. Order - degree of branching, first order laterals originate from the taproot or, in the case of adventitious roots, from the shoot; second order laterals originate from first order laterals and so on. Replacement roots are designated by the same order as that of the injured parent root from which they originate. Order terminology is useful primarily for the younger non-woody portions of the root system. Root tip - that portion at the end of the root containing live cortical tissue and extending from the terminus of the root cap back to either the first lateral or, if laterals are lacking, back to the parent root. Root tips may be non-mycorrhizal (uninfected) or mycorrhizal. Longitudinal spacing - distance between laterals along the root axis. Radial position - arrangement (ranking) of laterals around the root axis. Woody roots - roots stiffened and thickened by secondary xylem (wood). Woody red oak roots generally are 2 mm or more in diameter and have distinct annual rings in the xylem. Non-woody roots - thin, flexible roots lacking enough secondary xylem to make them stiff. Generally they are less than 1 mm in diameter and seldom have distinct annual rings. Several terms have been used to differentiate thin, flexible roots from stiff roots. None of these are completely satisfactory or connotative; for example, rootlets, fibrous roots and thin roots are names often used for thin, flexible roots. The terms long and short roots are connotative for many root systems, particularly those of conifers, but for red oak the terms woody and non-woody roots and small diameter and large diameter root tips are more descriptive than length terms. Framework roots - the long, woody roots in a mature root system that radiate horizontally from the base of the trunk.

#### MATERIALS AND METHODS

Studies were made of red oak in mixed hardwood stands, ranging from 40 - 70 years of age, in the Prospect Hill Tract of the Harvard Forest. Ten or

more hardwood species grew in these stands; red maple (*Acer rubrum* L.) was generally the most common but red oak was dominating, especially in older stands. There were also a few white pines (*Pinus strobus* L.) and hemlock (*Tsuga canadensis* [L.] Carr.).

The soil in these stands is stony, well-drained Gloucester sandy loam. Classed in the sandy-skeletal, mixed, mesic family of Typic Dystrochrepts, this soil was formed on stony, sandy glacial till of Wisconsin Age derived principally from relatively unweathered granite and gneiss. The soil parent material itself has a low-cation exchange capacity and is strongly acid. Most of the natural fertility of the soil lies in the forest floor and A1 horizons. Fertilization is necessary for economic yields of agricultural crops.

Most seedling and sapling root systems of trees up to 8-10 years of age were excavated with shovels inasmuch as interest in these younger ages was primarily on the initial development of the several first order laterals that later make up the main framework portion of the root system of mature trees. Single roots of mature trees were excavated both by hand and hydraulic methods. Hand methods were used on most roots as many small-diameter roots were broken or debarked by the high pressure necessary in hydraulic washing. Small-diameter roots in the forest floor were examined by removal of the surrounding organic matter with tweezers, needles and other small tools.

Controlled studies of red oak replacement roots were made on roots of three red oak trees that extended into the same root cellar (rhizotron) used previously for controlled studies of red maple roots by Lyford and Wilson (1966). These red oak roots were broken when the trench within the root cellar was originally excavated and for two years they protruded 15-30 cm from the face of the trench and remained uncovered during this period. When studies of red oak roots began in May 1967, the broken ends were sawed off about 15 cm behind the break and the surrounding moist soil near the front of the trench was removed leaving about 50 cm of the 2-5 cm diameter woody roots exposed. These freshly cut ends were then covered with moist soil. Within 2-3 weeks new root tips grew through the rather thick bark, 1-3 cm behind the cut. These replacement root tips were 2-3 mm in diameter and elongated at the rate of 5-mm per day. They grew equally well in moist soil, between moist paper towels, in water, or in gravel nutrient culture. When grown on horizontal flat trays in a thin layer of soil, their character and growth could be observed after careful removal of the thin layer of soil from short portions of the root tips. A stereoscopic microscope was used to examine exudation, rate of root hair development, influence of drying and other short term changes. The roots were not noticeably injured by exposure to short periods of artificial light or dry air.

## ROOT GROWTH IN NATURAL STANDS

### Seedlings and Saplings

#### Taproots

At the Harvard Forest red oak acorns commonly sprout before the snow is completely melted in the spring. Elongation of the radicle is rapid and the taproot penetrates vertically downward through the forest floor and mineral

soil. The taproot may reach a depth of 45 cm by the end of the first season (Figs. 1,2). The strong white radicle is 2-3 cm in diameter when it emerges from the acorn and the tip remains about this same diameter during the entire life of the taproot. Downward extension is hindered by stones, pieces of wood, or other hard objects, but unless the object is large the root diverges only for a cm or two and then resumes almost vertical penetration.

The external diameter of the fleshy, young taproot tip is about three times that of the central cylinder so about 90 percent of the tip volume consists of epidermal and cortical tissue. Secondary xylem production starts soon after laterals emerge, the central layer then enlarges and a cork covering develops. The enlargement results in the death of the epidermal and cortical tissues which shrink away and reveal the thinner, cork-covered root beneath. This marked contrast in diameter between the thin, proximal root and fleshy root tip gives the latter its characteristic swollen appearance.

By the end of the first season of growth the upper part of the taproot, free of its encircling mantle of cortical and epidermal tissue, is about 4 mm in diameter and covered with cork. This portion of root now has an appreciable amount of secondary growth and, when dry, is longitudinally corrugated. By contrast, the younger lower portion of the taproot has little or no secondary xylem and, when dry, has the shape of a hexagonal prism due to its inner hexarch vascular anatomy. This shape is revealed when the shriveled mantle of dried cortical tissue is removed (Figs. 3,4).

By the time a young tree is 3-5 years old the upper part of the taproot is about 1 cm in diameter; it may reach a depth of 70 cm or more if the soil is well drained and friable. At 6-8 years of age the taproot is nearly 3 cm in diameter in the upper part and 1-1.5 cm in diameter at depths of 30-40 cm (Fig. 2).

The taproot of seedlings grown in the forest is often injured near the soil surface; one or more replacement roots then develop just behind the injury. These continue elongation in much the same direction as the parent root. If only one replacement root persists it can hardly be distinguished from the original taproot after a few weeks. Carpenter and Guard (1954) called attention to the lack of persistence of the taproot and thought that an uninjured red oak taproot in the forest might be very rare. Korstian (1927) and Holch (1931) also noted injuries of the very young taproot and Larson (1970) showed five replacement roots growing from the injured end of a one-year-old taproot.

#### First Order Laterals

Up to 20 first order laterals per cm occur on red oak taproots with a normal range of 12-18. They emerge acropetally and are spaced fairly regularly along each of 6 rows (Fig. 4). Diameters of the newly emerged root tips vary from a minimum of 0.07 to about 1.5 mm with a striking lack of regularity in this characteristic. For example, central cylinder diameters - about one-third of external diameters - of a typical sequence of first order laterals along one of the 6 rows was 0.30, 0.46, 0.27, 0.20, 0.27 mm.

Some of the tips along adjacent rows are very close together when they emerge from the taproot (Fig. 4); this pairing is common and distinctive on

most red oak roots (Fig. 30). Many radial pairs persist on old woody roots although they are not especially obvious on the large roots as the pair members are then radially separated by a considerable distance.

At the end of the first year a large proportion of the first order laterals are still less than 1 mm in diameter. Lyr and Hoffmann (1967) indicated that 85.7 percent of the total length and 16.8 percent of the total weight of one-year-old red oak seedlings were in roots of less than 1 mm in diameter. Most first order laterals persist during the entire first year so that a young taproot seems very heavily rooted (Figs. 1,2). A few laterals are 2-3 mm in diameter but there is little evidence at this age as to which, if any, of the many laterals will enlarge and become the 5-10 large woody framework laterals at the base of the mature tree. At the end of the first year the larger laterals may extend outward 50-60 cm and have several orders of branching. Smaller diameter laterals extend outward 15 cm or so and may not be branched at all or have only one or two orders of branching. Even first order root tips on these small laterals can be mycorrhizal (Fig. 5). Carpenter and Guard (1954) noted mycorrhizae on first order laterals of one-month-old seedlings.

By the time the young tree is 3-5 years old many laterals have disappeared (except for their stumps) and live laterals along the taproot are spaced 5-10 mm apart. Of the persistent roots about half are smaller than 1 mm in diameter and are flexible, tough and fibrous. A few of the larger laterals are 3-5 mm in diameter. Some 6 to 8 year old forest-grown trees have laterals up to 1 cm in diameter and apparently have a good start toward a large and vigorous woody framework root system.

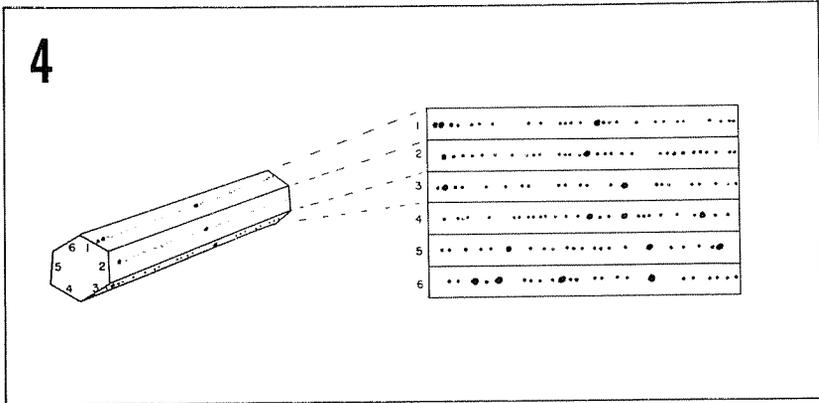
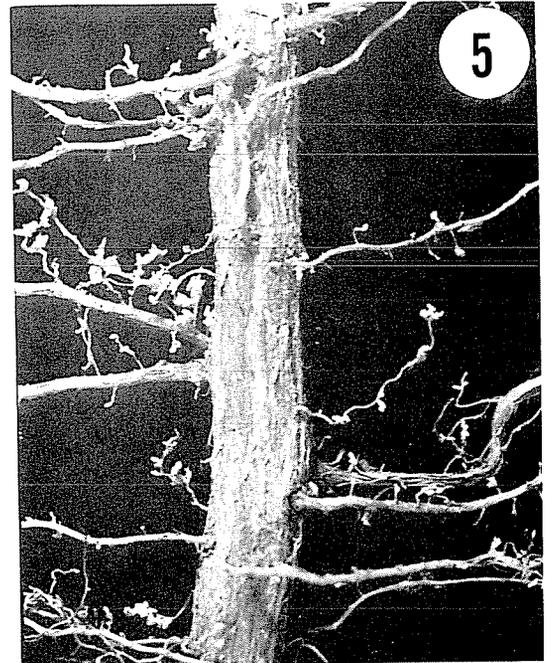
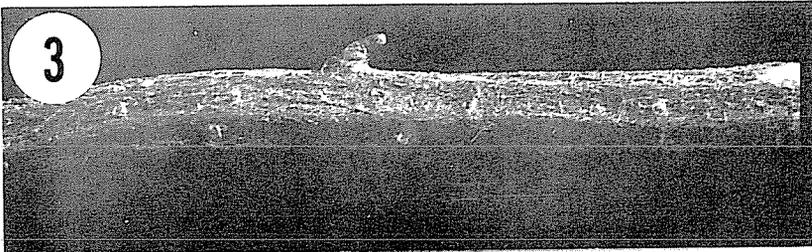
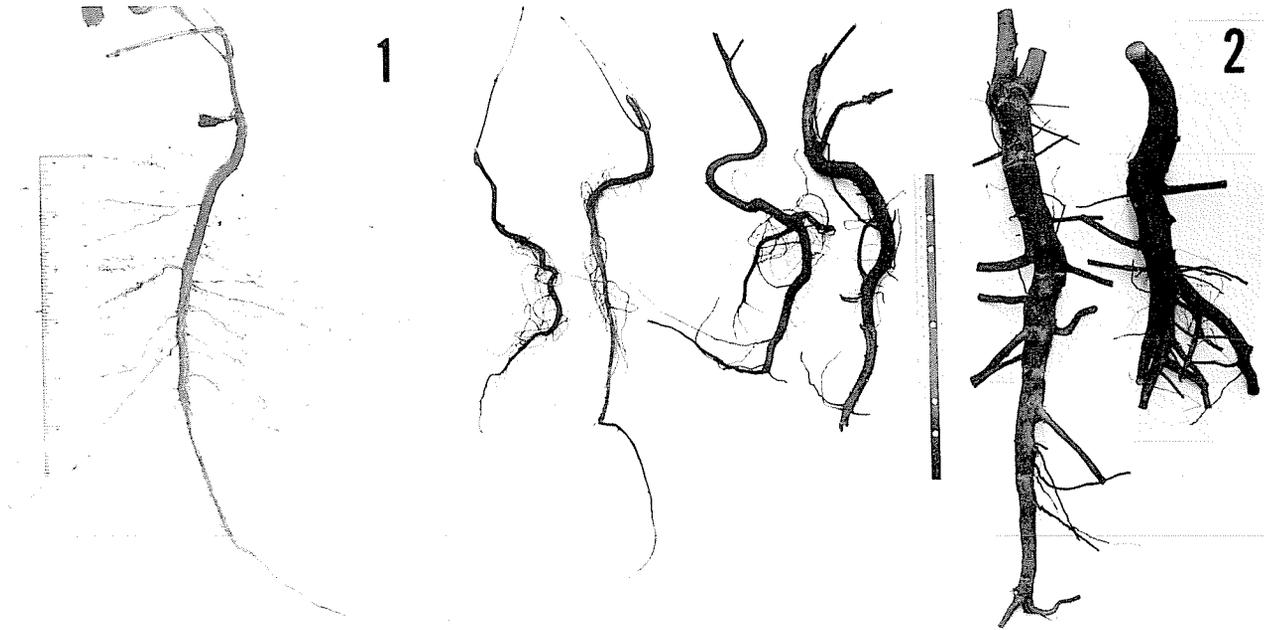
#### Second Order Laterals

These root tips emerge acropetally from first order laterals and are also variable in diameter, ranging from 0.07 to 1.0 mm, with a relatively small proportion in the larger diameter class. Because of this variability, some of the second order tips are actually larger than some of the first order tips. Spacing along the parent root is fairly regular; laterals average about 0.8 mm apart. Length of second order roots at the end of the first season of growth varies from about 5-20 cm.

#### Third and Higher Orders

Third and fourth order laterals are spaced about 0.5-0.8 mm apart. Many are mycorrhizal and have a minimal diameter of 0.07 mm. Fifth order laterals are uncommon as most of the fourth order roots are of minimal size and do not form laterals. Absolute maximum order of branching on a forest-grown seedling is not known; the maximum observed was fifth order.

Root hairs occur on most third and higher order non-mycorrhizal root tips. They do not occur on the mycorrhizae.



## Mature Trees

### Central Root System

By the time red oak trees are 10-12 cm in diameter and 30-40 years old the root system can be conveniently divided into a central and a peripheral or outer root system (Lyr and Hoffmann, 1967). The central root system is at the base of the tree and extends away for a meter or two. It consists of the taproot, main laterals, and numerous vertically and obliquely descending and ascending woody and non-woody roots (Figs. 6,7). Five to ten first order woody roots at the base of the tree make up the framework of the central root system and provide much of the support and anchoring system for the tree. These large roots descend obliquely from the soil line to a depth of 20-40 cm at a distance of 1-1.5 mm from the tree. From here they extend horizontally into the outer root system for several to many meters. These first order roots are eccentric and 30 cm or more in diameter at the base where they join the trunk. They taper rapidly and become cylindrical at about a meter from the tree. This junction of the zone of rapid taper with the 2-5 cm diameter cylindrical root is where roots lose a good deal of their rigidity and strength and where they tend to break when the tree is overturned by a storm.

Other woody first order roots arise from the taproot below the topmost large framework roots. These are rarely as large in diameter, as eccentric, or as long as the ones above. Some of these lower first order roots extend horizontally for 25-30 cm and then turn abruptly and descend vertically parallel to the taproot. However, most extend horizontally and it is the second and third order roots that descend vertically.

The taproot is not a prominent feature of the root system of mature red oak trees and generally it is eclipsed by woody laterals that descend vertically and penetrate the soil as deeply as the taproot. Biswell (1935) pointed out that first order laterals growing from the lower part of the taproot tend to descend vertically almost as soon as they start to elongate and these particular roots, even in young trees, soon are as large and deep as the taproot.

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Fig. 1. One-year-old seedling of red oak with cotyledons still attached. Scale is 15 cm long. Fig. 2. The two roots at the left are of 1-2 year-old-trees; the two in the middle are 3-5 years of age; the two on the right are 6-8 years. Scale is 30 cm long. Fig. 3. Hexagonal shape of the lower part of a dry taproot. Root diameter is about 2 mm. Stumps of eight first order laterals are visible along the middle of the facing plane. Fig. 4. Longitudinal spacing and radial position of first order lateral roots in each of the six planes on a 5 cm long section. Fig. 5. Close up of a 3 cm long portion of the taproot showing varying size and spacing of the first and second order laterals. Many of the small diameter second order laterals are mycorrhizal. Figs. 6 and 7. Red oak roots in the central root system. Large first order laterals originate near the soil line, taper rapidly and descend obliquely to a depth of 20-50 cm at about one meter from the tree. From there on they extend horizontally for several to many meters.

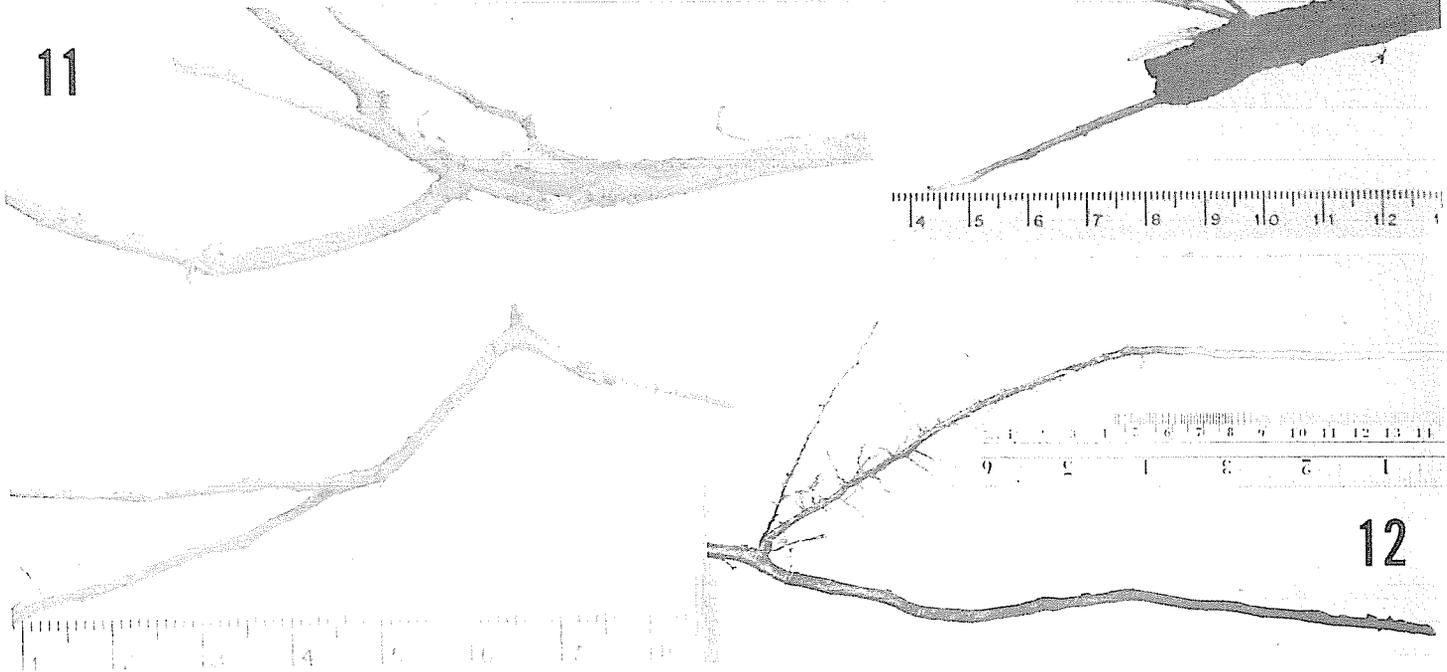
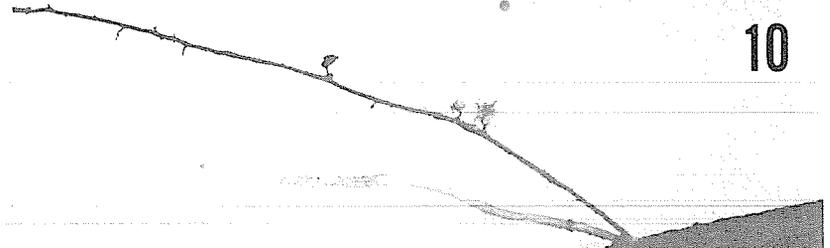
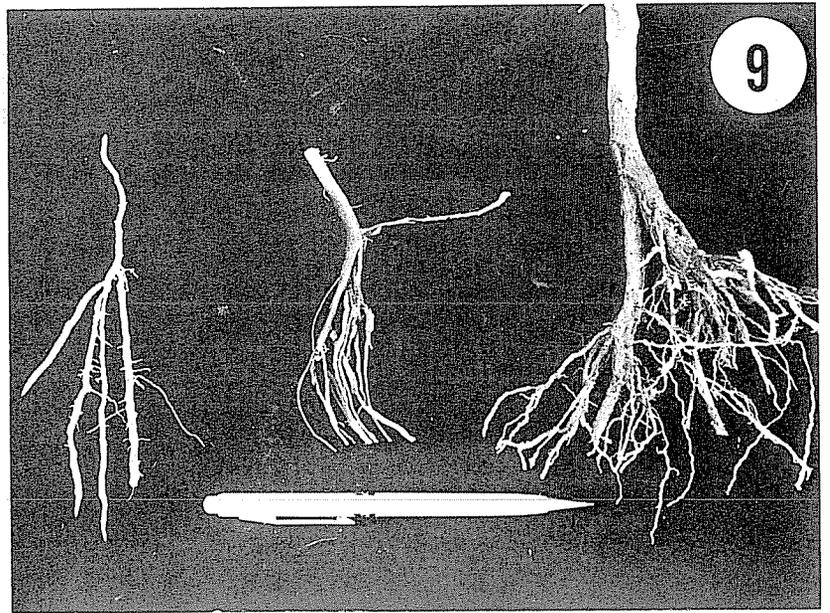


Fig. 8. Grafts between red oak roots of the same tree or between invading roots of an adjacent red oak tree are common in the central root zone. Fig. 9. When a large root tip is unable to penetrate the C horizon it dies and replacement roots form behind the dead tip. They in turn die, more roots form, and so on until finally a splayed root results. Fig. 10. Three new replacement root tips were growing from a woody root cut when the soil pit was dug. The upper root in

Some second and third order laterals are themselves 7-10 cm in diameter and as large as some first order roots. This is particularly true of large, woody second and third order roots that originate from the large first order framework laterals at the base of the tree. These second and third order roots also have eccentric growth, rapid taper and extend horizontally as far as some of the first order roots. In some instances it is difficult to distinguish first and second order roots with certainty if both arise close to the base of the tree.

Large diameter woody roots in the central root system occupy so much space and are so large that it is easy to overlook the many small first to fourth order laterals that are there. These small diameter roots remain 1-2 mm in diameter for their entire life and never become stiff and woody. For example, second order, 1-2 mm diameter, non-woody roots are persistent near the base of the tree on large, woody first order framework laterals yet, even though small, they were initiated only a few days later than the much larger woody parent roots from which they arose acropetally.

Root grafts are common in the central root system where roots are close together and where they cross each other (Fig. 8). Many woody roots are held so tightly together they cannot move when they themselves, or other roots that cross them, enlarge. As a result there is considerable intergrowth and grafting in, or immediately adjacent to, the central root system. When grafts and intergrowths are numerous the central root system becomes a three-dimensional rigid network. When such a rigid system overturns it moves as an entity and carries with it a large mass of soil. Grafting between roots on the same tree is common in red oak. There is also grafting between roots of neighboring red oak trees. Grafting is uncommon in the outer root systems.

Red oak roots penetrate only rarely more than a meter below the surface of the Gloucester soils, either in the central or outer root systems. The Gloucester soils have friable A and B horizons but the C horizon is firm and rigid. Only where root tips happen to find some weakness in the C horizon, such as former root channels, or where the C horizon has been loosened by treethrow of some previous generation of trees can the roots penetrate into the C horizon. Similar observations of root depths of forest trees were made during a study of soils along a 12 mile segment of a cable line trench through glacial till in central Massachusetts and of soils on stratified sands along a 10 mile segment of a gas line trench in eastern Massachusetts.

As a result of soil rigidity most root tips on the vertically descending roots that reach the junction of the B and C horizons either turn to the horizontal or die. In those that die, within about two weeks, several new replacement tips of about the same diameter as the injured tip develop just behind the dead tissue and elongate rapidly. These in turn either become horizontal or

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this photo is non-woody and it showed no response to the injury. Note the corralloid clusters of mycorrhizae on the non-woody root. Fig. 11. Two forks from near the end of one of the main laterals. Fig. 12. The upper root, cut when a soil pit was dug, died back about 20 cm when the soil in the face of the pit dried (lower stub). The upper root is a replacement and its 10 cm long, 3 mm root tip is typical of those on woody roots.

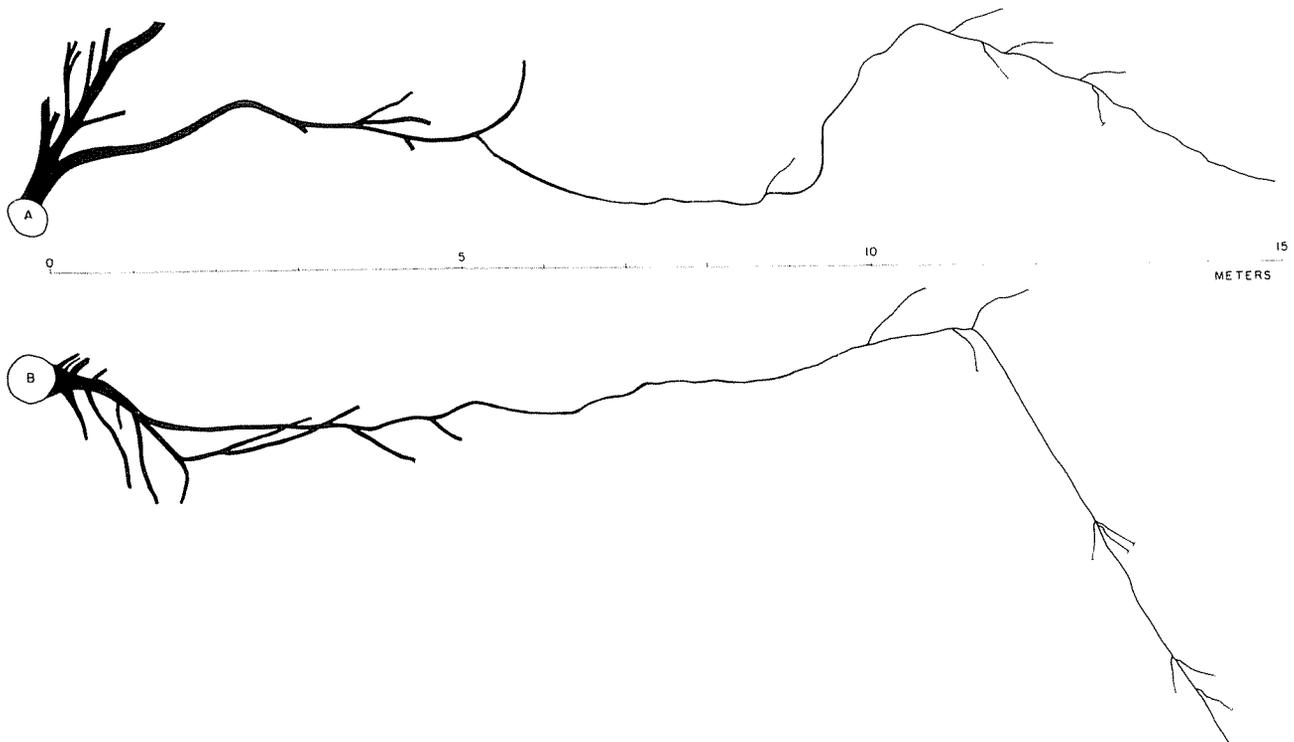


Fig. 13. Scale diagram of two horizontal laterals. Locations of the forks are shown prominently to illustrate the irregular spacing along the woody laterals.

die and thus cause more replacement tips to be formed. Soon the root has a flattened, splayed shape (Fig. 9). Some of the injury at the junction of the B and C horizons may result when the tree is swayed by heavy winds. Hintikka (1972) has shown that movement may be appreciable throughout the central root system of red pine, especially if the root system is a rigid three-dimensional mass as a result of intergrowth and grafting. Root cellar studies show that large diameter red oak tips are very sensitive to movement of any kind.

Some of the roots diverted from the vertical to the horizontal at the junction of the B and C horizons rise obliquely to the middle of the B horizon and continue growth horizontally into the outer root system. Others ascend obliquely all the way to the surface and elaborate into small-diameter roots in the A1 or forest floor horizons.

#### Outer Root System

The outer root system extends from the central root system outward for several to many meters. At the junction of the two systems - one or two meters from the base of the tree - the large first order framework laterals are a meter or two apart and from here outward they can be excavated individually without much interference from other large roots. Two such large roots, one from each of two nearby 60 year-old 30 cm diameter trees, were excavated for their entire length (Fig. 13). When this was done, the largest fork member at each junction was chosen for continuous excavation as it was not possible to excavate each and every branch completely. One root was 17 m long, the other 16.6 m, both terminating at a distance of 15 m from the base of the tree. These roots grew at an

average depth of 30 cm but along their course the depth varied from 5 - 50 cm. Red maple woody roots in the same area grew in the top 10 cm of soil, usually above the red oak roots (Lyford and Wilson, 1964).

### Forks

Along each of the two roots the main root forked at intervals of 1 - 5 m into two or more smaller diameter fork members which then extended forward in much the same direction as the parent root. This forking on red oak is similar to that described in red maple by Wilson (1970). Examination of forks on young portions of red oak roots show that, as in red maple, injury caused forking (Fig. 11).

Forks were irregularly spaced along the parent root, in contrast to the regular spacing of second-order laterals on the younger portion of the root system. The irregular distribution of forks presumably reflected the randomness of injury to the root tips. On the two framework roots studied, all large woody laterals more than 1 - 2 m from the base of the tree seemed to be fork members resulting from injury. Large "second" and "third" order laterals near the base of the tree may have been either fork members or normal laterals that became woody. Their large size masked their exact origin.

From one fork junction to the next, the parent root had little taper; if the fork junctions were far enough apart the portion of root between fork junctions had a rope-like appearance because of the uniform diameter.

### Second Order Laterals

Spacing and diameter of all second order laterals on one of the long excavated framework roots was determined (Table I). On the young portion of the long root there were 365 second order laterals per meter (spacing of 2.7 mm between laterals). This short distance between laterals suggests that distance from the base of the tree had little influence on the number of laterals produced. In fact, this spacing is about the same as that on a young replacement root grown under nearly ideal conditions in the root cellar. Many of the 365 second order laterals were represented only by stumps so there is the likelihood of considerable death of young laterals in the first two or three years of life. Horsley and Wilson (1971) suggested that lateral roots less than one fourth of the diameter of the parent root tip are likely to be ephemeral.

Closer to the base of the tree, on the oldest portion of the roots, the second order laterals were much less numerous and were spaced 3 - 5 cm apart. Second order laterals presumably had an initial spacing of about 0.3 cm on this older portion of the root but many later died and their stumps were overgrown.

Radial location of second order roots emerging from the long parent root is more or less uniform around the root, although a few more may grow from the top and sides than from the bottom. Roots that emerge from the sides generally continue growth parallel to the surface of the soil and angle forward 5 - 10 degrees from the perpendicular. These roots extend a meter or more away from the parent root and are profusely branched with third and fourth order laterals. Roots that emerge from the bottom tend to orient horizontally and only a few descend vertically and then only for a few centimeters. Large-diameter vertically descending roots, termed sinkers, are found only within a meter or two of the base of the tree in the central root system.

Table I

Number and size of second order laterals on a long, first order framework lateral.

| Distance<br>from base<br>of tree<br>m | Diam. of<br>first order<br>lateral<br>mm | No. of second order laterals (stumps and persistent<br>roots) by diameter classes |       |           |           |         | Total |
|---------------------------------------|--|---|-------|-----------|-----------|---------|-------|
|                                       |  | <0.5 mm   | 0.5-1 | 1-2       | 2-10      | >10 mm  |       |
| 0 (base)                              | 254                                      |   |       |           |           |         |       |
| 1                                     | 90                                       | 4   | 15    | 14        | 8         | 9       | 54    |
| 2                                     | 42                                       | 1   | 22    | 6         | 6         | 1(fork) | 36    |
| 3                                     | 35                                       | 7   | 15    | 13        | 7         | 0       | 42    |
| 4                                     | 18                                       | 13  | 10    | 5         | 2         | 1(fork) | 30    |
| 5                                     | 12                                       | 4   | 12    | 8         | 5         | 1(fork) | 30    |
| 6                                     | 11                                       | 5   | 7     | 6         | 2         |         | 20    |
| 7                                     | 11                                       | 10  | 5     | 8         | 1         |         | 24    |
| 8                                     | 11                                       | 9   | 2     | 5         | 2         |         | 18    |
| 9                                     | 11                                       | 4   | 6     | 1         | 1         |         | 12    |
| 10                                    | 10                                       | 7   | 16    | 13        | 1         |         | 37    |
| 11                                    | 9  | 8   | 33    | 11        | 2(1 fork) |         | 55    |
| 12                                    | 6  | 13  | 39    | 6         | 2(forks)  |         | 59    |
| 13                                    | 5  | 18  | 12    | 8         |           |         | 38    |
| 14                                    | 3  | 28  | 48    | 2         |           |         | 78    |
| 15                                    | 2  | 86  | 25    | 3(1 fork) |           |         | 114   |
| 16                                    | 2  | 297   | 24    | 1(fork )  |           |         | 322   |
| 17                                    | 2  | 350   | 13    | 2(forks ) |           |         | 365   |

Many roots that emerge from the upper quadrant of horizontal parent woody roots grow upwards. Some rise almost vertically to the surface and elaborate into many higher order small-diameter non-woody roots in the A1 or forest floor horizons. Others ascend obliquely forward and reach the soil surface a meter or more away from their point of origin (Figs. 14-17). The roots that grow upward seldom are over 4-6 mm in diameter and apparently live for many years without increasing appreciably in size. They may arise from almost any order of horizontal woody laterals. The ascending laterals are easily overlooked when digging a pit but are readily visible when the soil is removed in successive thin layers. The upwards orientation of these roots provides the tree with some measure of protection from root injury by minor surface soil disturbances such as those caused by rodents, pasturing or lumbering because the parent woody horizontal laterals lie 30-50 cm below the surface.

### Third and Higher Order Laterals

Most of the statements made for second order also apply to third, fourth and higher order roots. Roots continue to branch until the root tips reach a diameter of 0.07 mm, the minimum size observed for red oak. Some first order laterals are at minimum diameter when they emerge from the taproot and so they never branch unless they increase in diameter. On the other hand, the first order laterals with large tips may branch and rebranch until minimal size is reached with the highest order of roots. On uninjured root systems of young

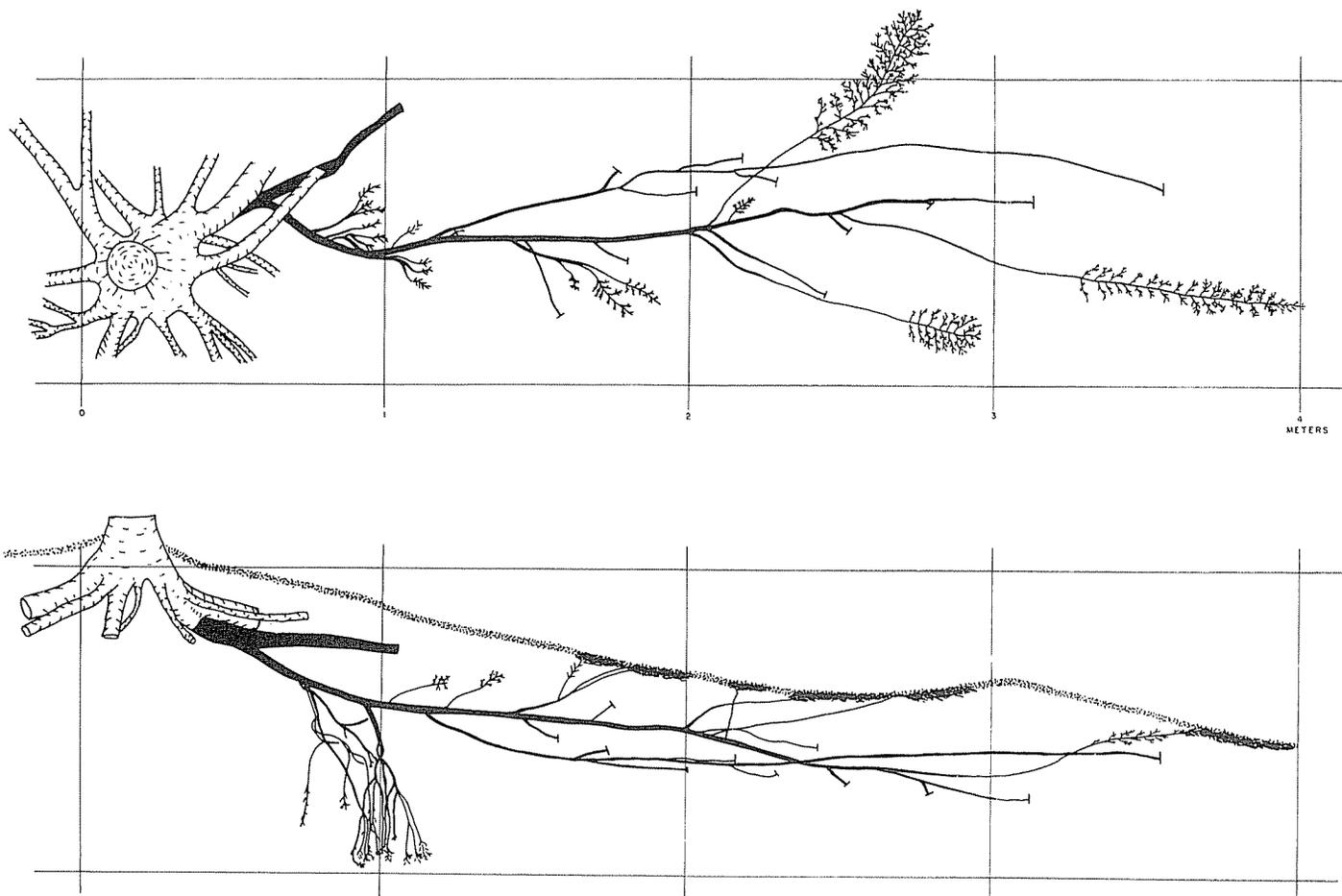


Fig. 14. Scale diagrams of a horizontal woody third order lateral with particular emphasis on the roots that return to the surface and elaborate into many small-diameter non-woody roots in the forest floor. Top view (above), side view (below). The squares are 1 m on a side.

trees the majority of the minimal size root tips are third, fourth or fifth order. On older root systems the maximum order could not be determined.

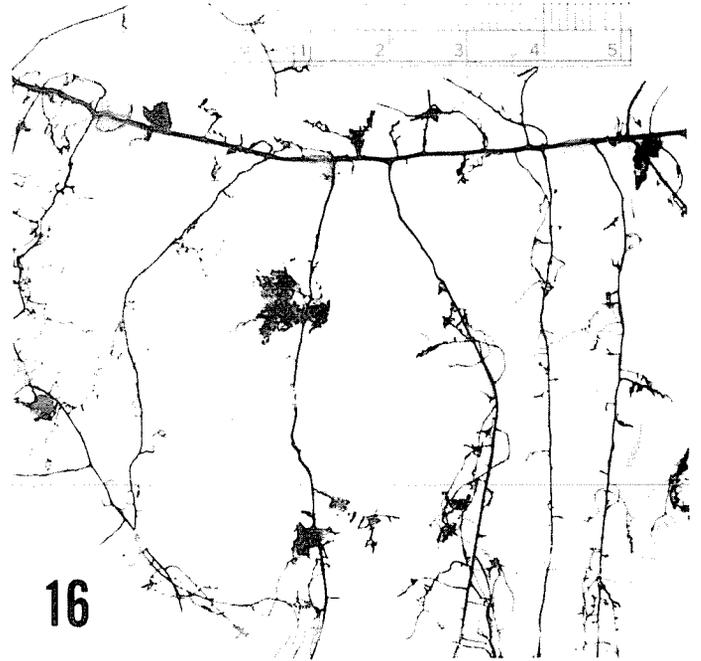
#### Root Tips

Red oak root tips range in diameter from 0.07 to 4.0 mm. Most of those larger than 1 mm occur as terminal root tips on roots that become woody, whereas, those smaller than 1 mm are more likely to be terminals of non-woody roots. For discussion purposes the two size categories of root tips are designated as large-diameter and small-diameter root tips.

Large-diameter root tips on forest-grown red oak trees range from 1-4 mm in diameter with most in the 2-3 mm range. They are pointed, brittle, swollen in appearance, nearly white, and 5-10 cm long before the first laterals appear. During the growing season they elongate at an average rate of 5-10 mm per day.



15



16



17

Fig. 15. Roots painted white are those that returned to the surface from large horizontal laterals in the B horizon. Fig. 16. Non-woody roots in the forest floor such as those into which the upward-growing roots elaborate. Fig. 17. Terminal portion of a non-woody root in the forest floor. It was only 0.2 mm in diameter yet it had a total of 1230 root tips (see Table II) most of which were mycorrhizal.

Size and color are masked somewhat by adhering soil particles especially in the region where the 0.25 mm long root hairs are attached. Shape also may be somewhat distorted by the imprint of soil particles. The fleshy root tip appears to be swollen because the older cortical tissue shrinks as previously discussed for the taproot. None of the large-diameter root tips show external evidence of infection by mycorrhizal fungi. All have root hairs, elongate rapidly and do not have mycelial mantles.

Considering the whole root system of a mature red oak tree, it is probable that there are several thousand times more small-diameter root tips than large diameter root tips. Small diameter red oak root tips range from 0.07 to 1.0 mm and most are 0.1-0.2 mm. They are exceedingly numerous in the A1 and forest floor horizons and newly formed tips are readily observed within the two- or three-year-old layers of partially disintegrated leaves (Figs. 14-21). Many of the rapidly elongating root tips are 5 mm or more in length, have root hairs and probably are non-mycorrhizal. At least they are so weakly infected that they do not have the characteristic hypertrophy, mantle and slow elongation rate of most mycorrhizae. But a very high proportion of small diameter tips are mycorrhizal. Most of the mycorrhizae are 0.1-0.2 mm in diameter and 0.1-1.0 mm long. There are several kinds of red oak mycorrhizae. One kind is conspicuous because it has a black surface and long black hair-like hyphae radiating out into the surrounding soil. These black hyphae are strong and are not broken when the soil is washed away (Figs. 20,21). This particular mycorrhiza is the common one on many forest tree root systems and is caused by infection with *Cenococcum graniforme*. The other kinds are yellow, cream colored, gray, white or brown and these are covered completely with a smooth, shiny, dense parenchyma-like fungal mantle. These types are caused by other fungi. In many instances the root tips are covered by wefts of loose mycelium. Shape of red oak mycorrhizae varies from monopodial to pinnatifid to corralloid. All red oak mycorrhizae examined so far have been ectotrophic.

Some idea of the number of root tips in the forest floor of a 70-year-old stand where red oak was the dominant species was obtained by counting the intact mycorrhizal and non-mycorrhizal root tips in several 1 cm cubes cut from the mid portion of a 6 cm thick sample of forest floor. These cubes were teased apart and examined by means of a stereomicroscope. Each cube contained an average of 1000 intact root tips, most of which were mycorrhizal. At first thought it would seem impossible for this many root tips to be enclosed within a 1 cm cube. Calculation shows that if each root tip is 0.2 mm in diameter and 1 mm long - perhaps a high estimate of average size - only 3 percent of the volume of the cube is occupied. More important from the standpoint of absorption of nutrients and water is that these same 1000 root tips have a surface area of more than 6 cm<sup>2</sup>, not counting the surface of the mycorrhizae, and not counting the surface area of any root hairs.

Another example of the enormous number of root tips on the root system of a mature red oak tree is provided by a count of the root tips on a small portion at the very end of a non-woody root system. This portion, carefully removed from the forest floor, was 0.2 mm in diameter at the broken end and when spread out covered an area about 6 cm wide (Fig. 17). There were 1230 root tips on this very small portion of the root system (Table II). More than 80 percent of the tips were mycorrhizal and the majority were of the black hairy kind (Figs. 20,21). Noteworthy is the fact that many of the mycorrhizae were as large in diameter as the broken end of the root on which they were growing.

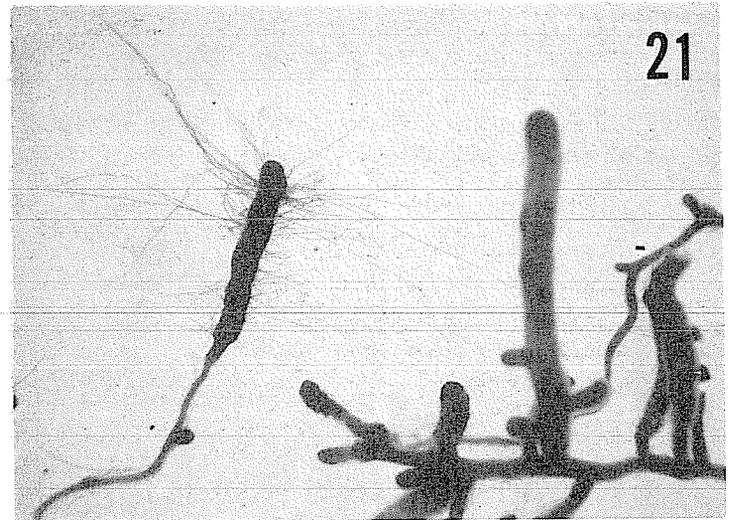
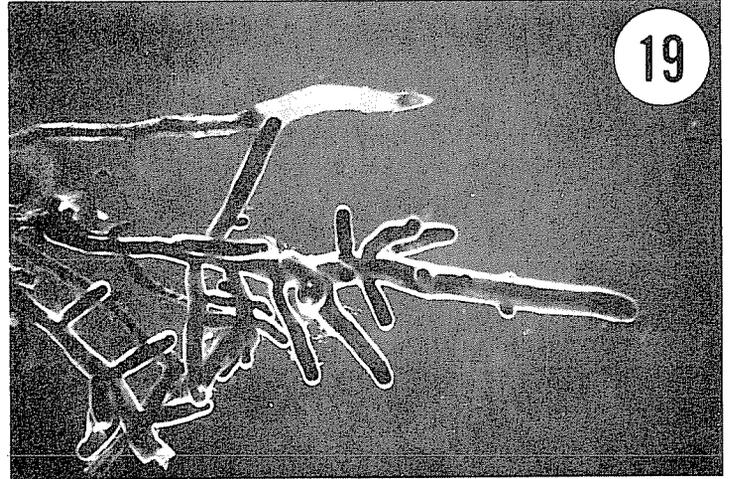
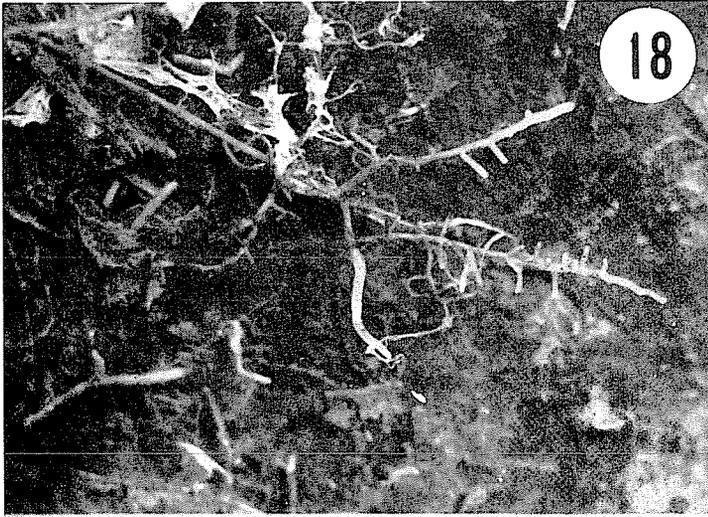


Fig. 18. Red oak roots growing among leaves in the upper part of the forest floor. Most tips shown are ectomycorrhizal and a smooth dense mycelial mantle covers the tips completely. Also visible are loose mycelial wefts enmeshing some mycorrhizae. Fig. 19. Rounded mycorrhizal tips and a pointed (uninfected) root tip on the same root segment. Fig. 20. Close-up of a portion of the terminal root section shown in Fig. 17. Fig. 21. Close-up of a black, hairy mycorrhizal root, 0.2 mm in diameter and 1.5 mm long. The hairs are up to 2 mm long.

Non-woody roots in the B horizon generally are not as vigorous or as branched as those in the forest floor. Most root tips are mycorrhizal but of the cream colored variety. The black hairy mycorrhizae seem most prevalent in the forest floor or where there is a large amount of organic matter.

Table II

Number and kinds of root tips on a 0.2 mm diameter, 8.2 cm long, terminal portion of a non-woody red oak root from the forest floor.

| Branching Sequence* | Number of root ends             |                       |                    | Avg. no. tips per cm of parent root |
|---------------------|---------------------------------|-----------------------|--------------------|-------------------------------------|
|                     | Broken roots or stumps of roots | Mycorrhizal Root tips | Non-mycorrhizal ** |                                     |
| First (main root)   | 1                               | 0                     | 0                  |                                     |
| Second              | 42                              | 32                    | 29                 | 13                                  |
| Third               | 93                              | 416                   | 121                | 18                                  |
| Fourth              | 9                               | 379                   | 67                 | 17                                  |
| Fifth               | 0                               | 147                   | 4                  |                                     |
| Sixth               | 0                               | 28                    | 0                  |                                     |
| Seventh             | 0                               | 7                     | 0                  |                                     |
| Total               | 145                             | 1009                  | 221                |                                     |

\*

Branching sequence is used inasmuch as the absolute order of branching is not known because the root was not traced back to its origin and some of the branching, even on this small root, seemed to be the result of injury.

\*\*

Count of the non-mycorrhizal root tips may include some dead tips from which the mycorrhizal mantle was torn away during cleaning.

#### GROWTH OF REPLACEMENT ROOTS IN A ROOT CELLAR

##### Formation of New Replacement Tips

If a woody red oak root is severed and the cut end, still attached to the tree, is kept continually moist, replacement tips emerge from just behind the injury. Replacement roots may be initiated in this way during the early or middle portion of the growing season; they grow best after the middle of July when most leaf growth has ceased. This is the well-known response to root pruning utilized for centuries by all those who transplant shrubs and trees. Examples of this response of red oak roots in a dark root cellar are shown in Figs. 22-26. Replacement roots grow as those in forest stands with the exception that mycorrhizae were never noted on the roots in the root cellar.

Eighty percent of injured woody red oak roots in the root cellar developed replacement root tips if kept continually moist by encasement in moist soil, moist paper towels, or otherwise. Up to 30 tips will grow from the periphery of woody roots 3-5 cm in diameter whereas 3-5 root tips grow from roots 1 cm or less in diameter. My observations suggest that the tips growing from 3-5 cm roots originate in ray callus and those from small diameter roots originate from the pericycle. Pre-existing small-diameter laterals just behind the injury do not respond by increased growth. Horsley (1971) also noted this on paper birch.

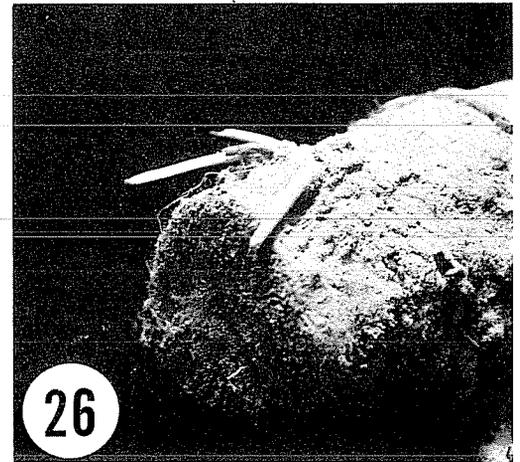
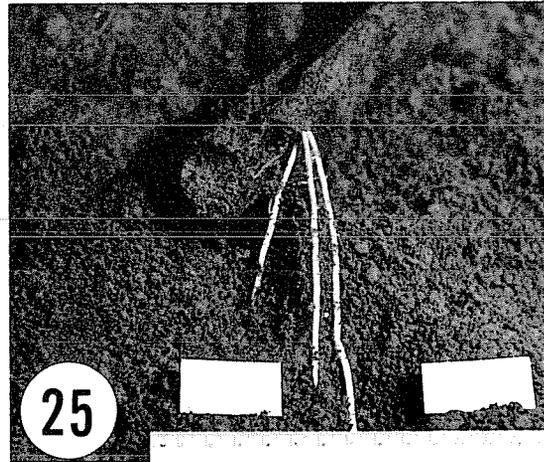
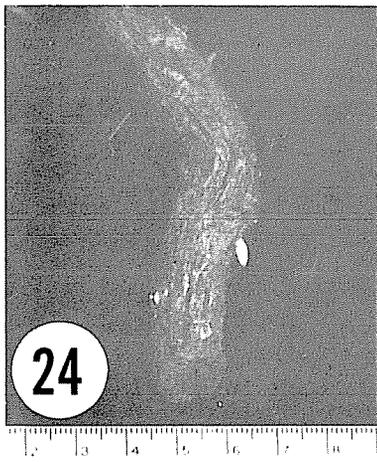
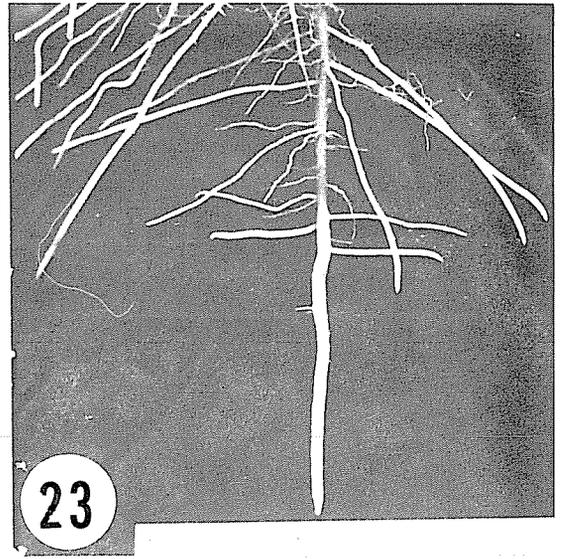
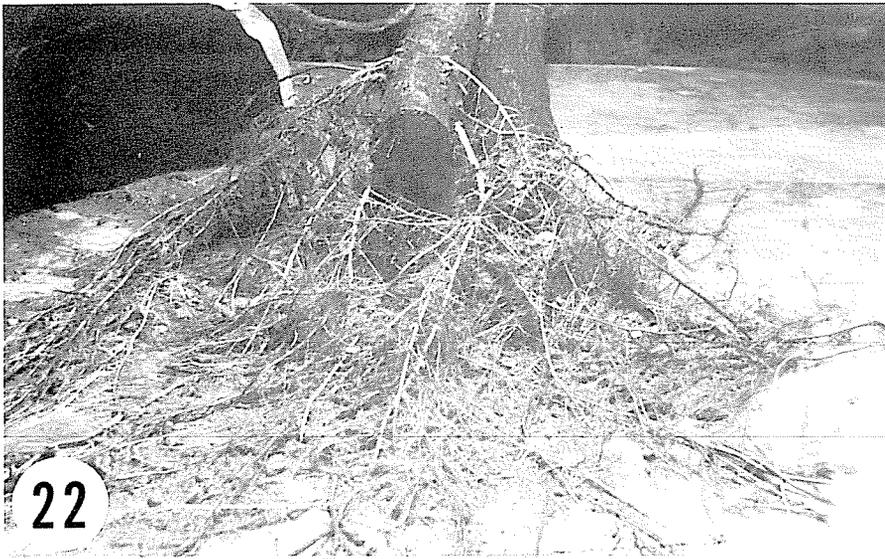


Fig. 22. Root system after one month's growth in B horizon soil material. Fig. 23. Portion of one of the roots illustrated in Fig. 22, showing a 3 mm root tip, the varying diameters and lengths of second order laterals, and the suberization behind the first order laterals. Fig. 24. Two emerging root tips. The one on the left, located above the 4.5 cm mark is barely visible as it is just penetrating the bark. Figs. 25 and 26. Emerging replacement roots at a later stage of development.

#### Color and Diameter of Replacement Root Tips

The root cap of a 1-3 mm diameter first order replacement tip is pointed, wet, mucilaginous, transparent, flexible and about 0.3 mm in length. When the mucilaginous root cap is touched, it readily moves from side to side without causing movement of the root behind. Immediately behind the almost needle-sharp root cap the root increases abruptly in diameter and full diameter is reached within a distance of 1 mm. Behind the root cap the root is brilliant red over a distance of 1-3 mm and this portion, as well as the portion behind, is firm and brittle. Behind the short, brilliant red section the color is generally

creamy white and the boundary between the red and white colors is sharp. In some instances there is a yellowish transitional color between the red and white. Root tips less than 1 mm in diameter, whether of first, second or higher order, lack the brilliant red color and tend to be pale yellow just behind the root cap. Root tips 0.2 mm in diameter are nearly white.

First order replacement tips are rather uniformly 2-3 mm in diameter. By contrast the second order tips growing from these replacement tips vary considerably in diameter, and there is no readily apparent relationship between diameter and distance from the apex of the parent root or distance from other second order tips (Fig. 27). These same variations in diameter hold also for third and higher order tips. It was pointed out earlier that laterals on seedlings show the same variation in diameter.

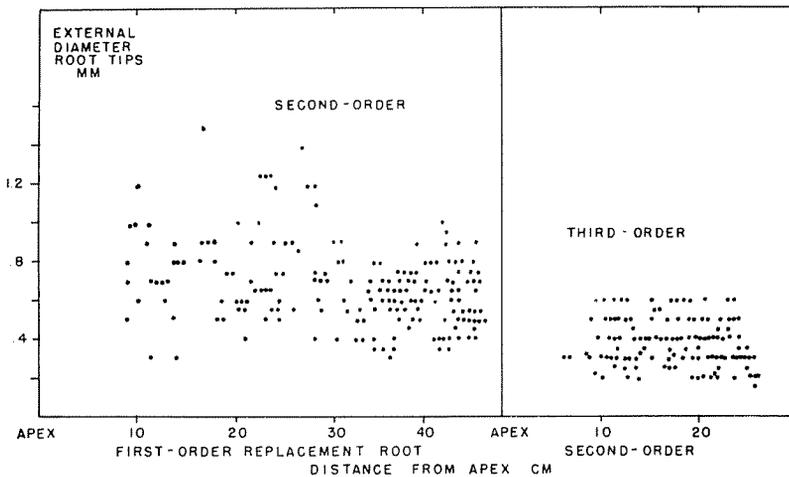


Fig. 27. Variation in spacing and diameters of second and third order root tips

Most root tips become cylindrical 1 mm or less behind the root cap and thereafter remain uniform in diameter until secondary xylem is formed. Some second and higher order tips less than 0.5 mm diameter become smaller as the root grows giving the root tip a tapered appearance. In these tapered tips the diameter of the central cylinder remains essentially the same for the entire length.

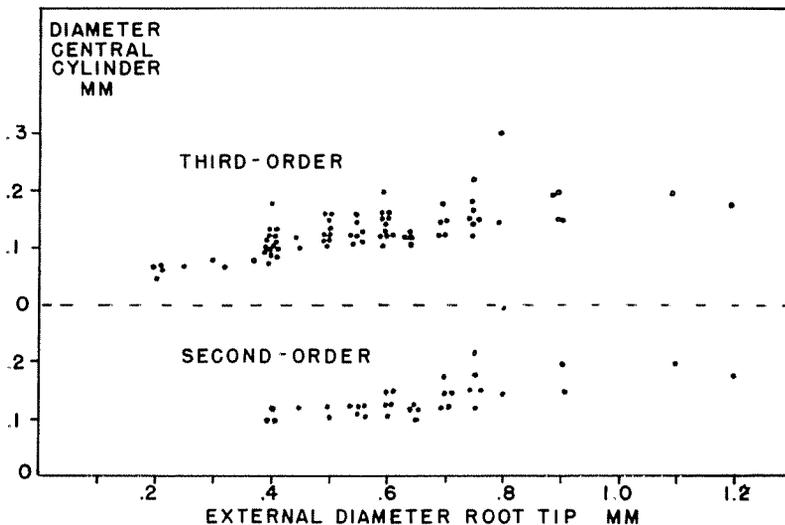


Fig. 28. Relationship between external and central cylinder diameters of second and third order root tips.

Table III

Length of fully elongated, uninfected replacement root tips by orders and diameter classes\*

| Order and diameter class | No. of root tips measured | Length in mm |         |         |
|--------------------------|---------------------------|--------------|---------|---------|
|                          |                           | Minimum      | Maximum | Average |
| First Order              |                           |              |         |         |
| 2 - 3 mm                 | 22                        | 55           | 100     | 78      |
| Second Order             |                           |              |         |         |
| 1 - 2 mm                 | 16                        | 4            | 70      | 41      |
| 0.5 - 1 mm               | 38                        | 2            | 49      | 16      |
| 0.25 - 0.5 mm            | 18                        | 1            | 36      | 14      |
| 0.10 - 0.25 mm           | 4                         | 4            | 9       | 6       |
| Third Order              |                           |              |         |         |
| 0.5 - 1 mm               | 13                        | 1            | 13      | 7       |
| 0.25 - 0.5 mm            | 39                        | 1            | 9       | 4       |
| 0.10 - 0.25 mm           | 9                         | 1            | 5       | 2       |

\* Fully elongated root tips are those long enough and old enough to have a newly emerged lateral. The length of the fully elongated root tip is the distance from the terminus of the root cap to the newly emerged lateral.

Table IV

Longitudinal spacing of laterals along replacement roots

| Order        | Number of roots per cm |         |         | Avg. distance apart (nearest mm) |
|--------------|------------------------|---------|---------|----------------------------------|
|              | Minimum                | Maximum | Average |                                  |
| Second Order |                        |         |         |                                  |
| Root 1       | 0                      | 13      | 4       | 2                                |
| Root 2       | 3                      | 8       | 4       | 2                                |
| Third Order  |                        |         |         |                                  |
| Root 1       | 2                      | 13      | 8       | 1                                |
| Root 2       | 4                      | 10      | 4       | 1                                |
| Root 3       | 3                      | 15      | 9       | 1                                |
| Fourth Order |                        |         |         |                                  |
| Root 1       | 3                      | 15      | 9       | 1                                |

The relationship between external and internal diameters of second and third order root tips is shown in Fig. 28. Diameter of the central cylinder averages about one-fourth that of the external diameter but there is considerable variation.

#### Tip Length and Elongation Rate

The length of root tips depends to some degree on diameter and order (Table III). For any given diameter class, root tips are generally shorter as the order number increases. First order replacement tips elongate rapidly. Average daily elongation for six newly emerged tips was 7 mm during a 20-day period in July, so that within about 7-14 days the root tips were 5.5-11 cm long and second order laterals were emerging. Average elongation rate for three second order roots growing in gravel from 5 September to 6 October was 5 mm per day with a range of 1-14 mm. There were noticeable day to day variations in growth rate among the three roots (Fig. 29). These differences in growth rate among seemingly identical laterals growing from the same parent root and in exactly the same environment were noted many times in the root cellar.

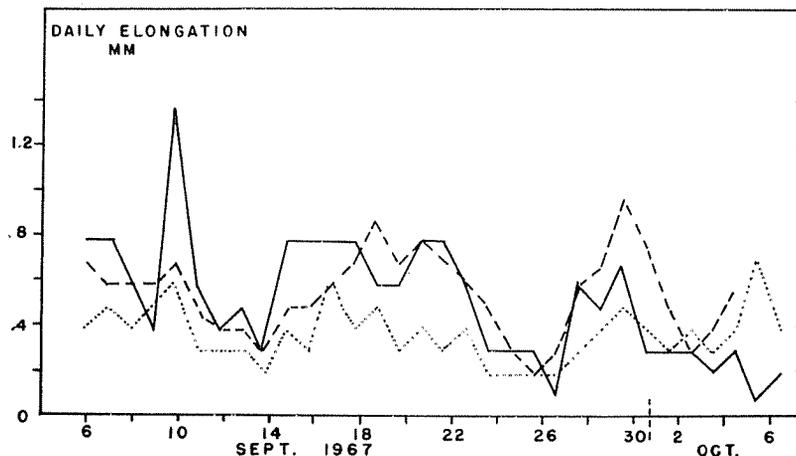


Fig. 29. Daily elongation of three second order roots growing in a shallow tray.

#### Spacing and Branching

Longitudinal spacing of lateral roots along first order replacement roots tends to be irregular, even for those roots that grow under ideal conditions (Table IV). Second order laterals are about 2 mm apart on the average; third and fourth order laterals are about 1 mm apart. In places individual laterals may be several mm apart.

The "twinning" habit of red oak roots provides an example of irregular spacing. It is common for two root tips to be almost touching as they emerge from the parent root. These twin roots may be in line along the root axis or side-by-side radially (Fig. 30). The in-line twins consist of a large and a small lateral and the small lateral does not persist for long. The side-by-side twins consist of equal sized laterals which diverge at an acute angle, giving a distinctive V-shaped appearance. Side-by-side laterals tend to persist on woody roots but gradually become less noticeable because they become separated as the parent root increases in diameter.

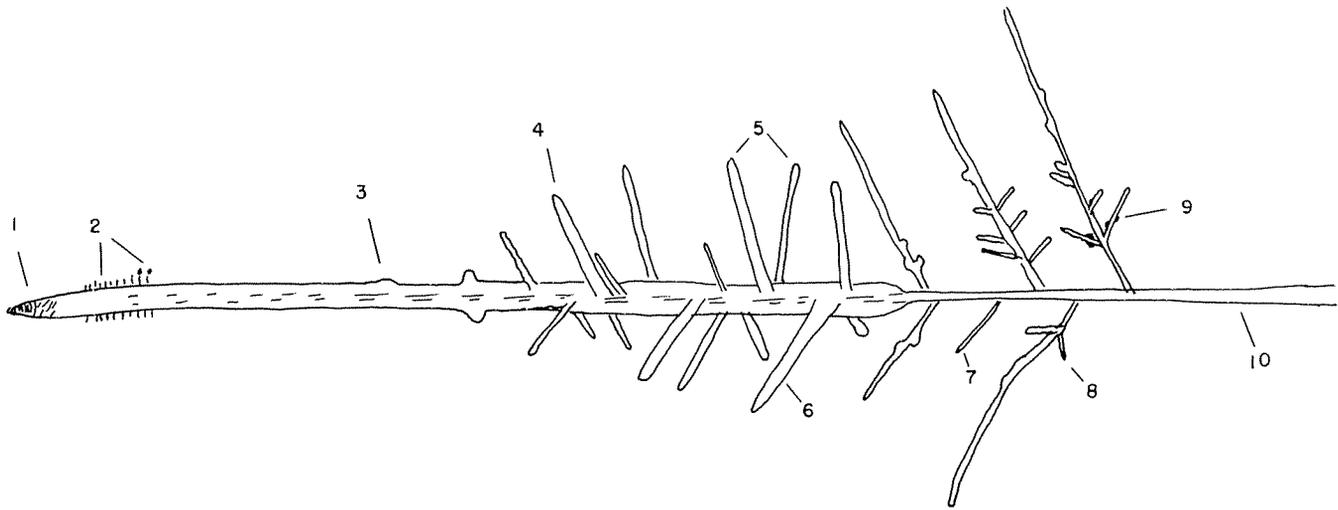


Fig. 30. Idealized terminal portion of a 2-3 mm diameter replacement root. 1. Brilliant red pointed apex and mucilaginous root cap. 2. Root hairs, some of which show exudation. 3. Second order root tip just emerging through the epidermis. 4. Longitudinal-twin (in line) root tips. 5. Radial-twin (side-by-side) root tips. 6. Tapered root tip. 7. Small-diameter lateral. 8. Third order root tip. 9. Fourth order root tip (just emerging). 10. Cork-covered woody root from which cortex and epidermis has disappeared, showing gradual increase in diameter as a result of the production of secondary xylem.

Laterals on replacement roots emerge from several positions around the root axis. The number of protoxylem poles was not determined but most of the small-diameter non-woody roots in the forest floor are known to be triarch. Lemke (1956) noted some red oak roots with as many as eight protoxylem poles.

Most replacement roots in the root cellar branched during the first season until fourth order laterals had formed. These had a diameter of 0.07 mm, the minimum diameter noted for red oak roots. In only one instance were fifth order laterals observed.

Branching in the root cellar is rapid, especially after second order laterals appear. For example, on July 3rd two replacement root tips 60 and 28 mm long had no second order laterals but by July 23rd they had 52 and 49 second order and 300 and 90 third order laterals, respectively.

## Root Hairs

The first evidence of root hairs on the large diameter first order replacement roots is a slightly roughened, pimply surface 3-7 mm behind the root cap. These root hairs become full length (about 0.25 mm) in about 24 hours and are located 7-10 mm behind the root tip.

Occurrence of root hairs is variable. In July, in one instance, only one of many second order laterals had root hairs. In August there were profuse root hairs on all orders. In another instance there were no root hairs on a second order lateral but all fourth order laterals on this same root were profusely covered. Richardson (1953) noted the absence of root hairs on some larger laterals on red oak seedlings grown in gravel and soil. He found a few root hairs on some of the smaller laterals and, in some instances, root hair development did not occur until the root stopped elongation. Then they extended to the very apex. Root hairs, when present, are profuse and regularly spaced. They are fairly thick and strong, and, in some instances, are strong enough to push soil particles away rather than growing around and clasping the particles.

## Exudation

Exudation, the formation of tiny drops of liquid at the tips of root hairs, can be seen on red oak replacement roots by using a stereomicroscope; earlier, it was also observed on red maple replacement roots. On a 3 mm diameter first order replacement root of red oak, spherical drops of liquid were observed at 9:00 AM, August 21, 1967, on about five percent of the root hairs. At 1:00 PM about one percent of the root hairs had drops of liquid at their tips and more could be seen on isolated tips among soil particles just behind the exposed part of the root hair zone. On August 26 this same root at 9:30 AM had liquid on about one of every 500 root hairs.

## Arching, Suberization and Cessation of Growth

There are times when large-diameter replacement roots elongating on horizontal surfaces arch until only the apex touches the surface (Fig. 31). Several days later these same roots may be appressed closely to the surface and show no tendency for arching. Arching was also noted on root tips of other species of trees growing in the root cellar. In a few instances roots turned obliquely for no apparent reason.

Suberization of the large first order replacement roots is not initiated during the early part of the growing season until the root has elongated for several cm (Figs. 23,30). For example, a first order replacement root 26 cm long on July 24 was brown 13.5 cm behind the apex. During the later part of the season roots are suberized closer to the apex and the entire tip is brown when elongation ceases.

In a few instances tips stopped growing suddenly and then resumed growth after a period of two or three weeks. On the same root system other tips continued active growth during the entire period. Cessation of growth took place without any known injury.

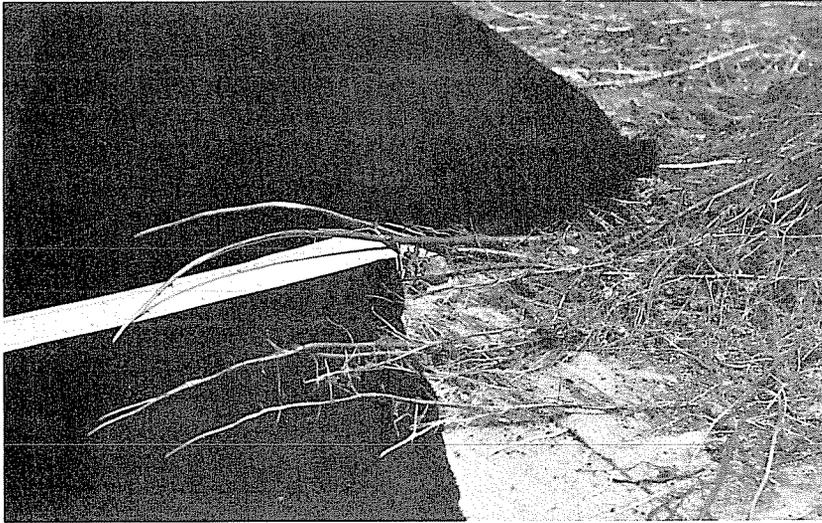


Fig. 31. Arching root tips on a level surface. Later these root tips flattened and were closely appressed to the surface.

### Response to Injury

Young, rapidly growing root tips are subject to many kinds of injury and this can be observed at first hand on roots growing in the root cellar. Drying and decay are major hazards. Both can be kept under control rather easily by growing the roots in moist soil or between paper towels kept moist by a wick system. Decay of small-diameter third and fourth order roots exposed to continuously moist warm air is rapid. This decay is especially common during the warm part of the growing season if the trays are covered solely by polyethylene sheeting with no paper towels between the sheeting and the roots. Decay of the small-diameter roots is confined to those outside the soil covering and does not seem especially detrimental to growth of the young root system as a whole. Death of the larger tips by decay is followed by development of replacement roots behind the dead portion.

In the root cellar rodents were sometimes a problem, although the major injury was caused by slugs, millipeds and crickets that got under the protective coverings. In some instances these grazed the cortex of the root tip and growth was slowed but not stopped (Fig. 32). In other instances the entire root tip was consumed.

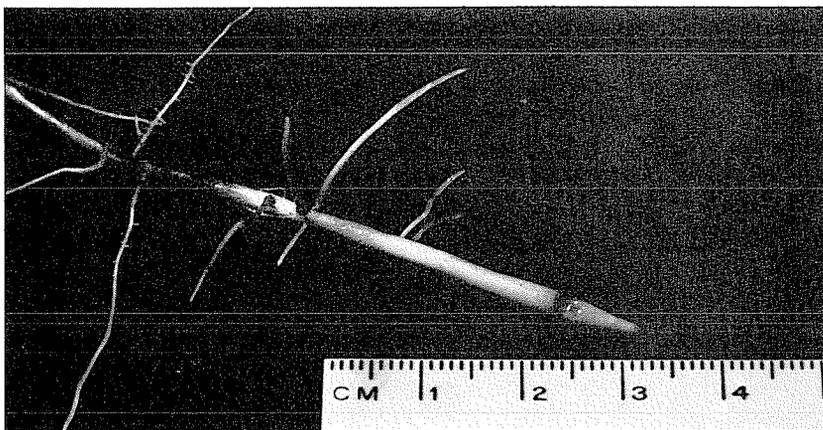


Fig. 32. Milliped injury. The cortical tissue in the narrow dark area just behind the apex has been eaten.

Moving the root tips from side to side or touching the growing tip near the apex often caused a temporary cessation of growth.

Short exposures to light had no noticeable effect. Growing root tips were kept in the dark except when uncovered briefly for measurement or photography. At these times no special effort was made to keep the light at low intensity.

Another response, which perhaps can be attributed to a kind of injury, is the production of new root tips on short, stubby woody roots that are barely living because they are in very dry soil. These stubby roots are replacement roots and were grown in thin layers of soil in shallow trays covered with plastic sheeting in the root cellar. When studies in the root cellar were discontinued the soil was no longer watered and so all growth on these roots seemed to cease. Yet each year, about mid-July, new root tips emerged from the side of the woody roots, elongated for about two or three weeks and then died. This period of growth was long enough for the woody parent root to become a little larger.

#### Growth in Soil Horizon Materials

Several replacement roots were grown in materials from the A, B, and C horizons of the same soil in which the parent tree was growing. The end of the rapidly elongating first order replacement root was placed on a paper towel kept moist by a wick system and the soil material was placed over the root. No differences in growth habits were noted, even for small-diameter roots or for root hair development. Considering the fact that first order replacement roots will grow out into moist air for distances of 10-20 cm, and will grow on moist paper towels for even greater distances, it is possible that the growth of rapidly elongating replacement roots depends more on photosynthate availability from the tree itself than on substances obtained from the immediate surroundings. This may, in part, explain why red oak laterals are able to grow readily in the relatively infertile B horizon.

#### Mycorrhizae

No mycorrhizae were noted on replacement roots in the root cellar either on red oak, red maple, sugar maple or yellow birch. These roots were grown in forest soil so there was ample opportunity for inoculation with causative fungi. A possible explanation is that the root systems were in soil kept at about field capacity so there was no moisture stress.

#### DISCUSSION

The taproot is an important feature of the young red oak root system. From this source all other roots originate (adventitious roots have not been observed). In older trees the taproot is overshadowed by the 5-10 large woody horizontal framework laterals that originate near the soil line.

Just how or why only a few large woody roots develop from the hundreds of small-diameter first order laterals that emerge acropetally along the taproot is not known. Possibly the few that eventually become large do so as a result of increased size of primary tissue after they emerge (Horsley and Wilson, 1971). Another possibility is that some roots develop from root tips that emerge from

the taproot out of acropetal sequence when the seedling is several years of age.

Once established, the large first-order framework laterals elongate at a maximum rate of 5-10 mm per day and some eventually extend outward horizontally 15 m or more from the base of the tree. They grow mostly in the B horizon at depths of 20-50 cm.

As many as 350 second order laterals per meter arise acropetally along the large first order laterals. Many of these die within a few years and only 10-20 per meter persist on older portions of the parent root. They emerge from several positions around the horizontal parent root and most finally extend horizontally away from the parent root for a meter or two. A very few grow vertically downward for a few centimeters. A fairly large number grow upward into the forest floor where they elaborate into an enormous number of small-diameter, non-woody roots.

Second order roots that grow upward into the forest floor never become large in diameter and there is some question whether any true second order laterals ever become long, large and woody. Forking as a result of injury is so prevalent on large first order laterals that many woody forked members may be designated erroneously as woody second order laterals whereas, more properly, they should be considered as forked continuations of the first order root. Indeed it is extremely doubtful if any red oak root of any order lives in the forest for more than a few years without injury and resultant formation of replacement roots or forking. Conceivably, if there were an entire lack of injury to the first order laterals, the resultant root system might end up as a rather narrow feather-like system rather than the coarsely branched system that seems to typify red oak in natural stands.

The extremely numerous small-diameter, non-woody roots in the forest floor elongate at a maximum rate of 2-3 mm per day and branch and rebranch until they eventually reach a minimum diameter of about 0.07 mm. Most small-diameter tips become infected with ectomycorrhizal fungi and, in contrast to uninfected tips, the mycorrhizal tips do not elongate for the year or two they remain alive. Thus the relatively few uninfected tips explore the soil over a moving front whereas the numerous mycorrhizae remain in one place but exploit a rather large volume of soil continuously by means of their radiating hyphae.

Red oak systems differ in several conspicuous ways from red maple root systems with which they are often closely associated. Red oak taproots are long, strong and descend vertically deep into the soil; red maple taproots are weak, turn aside easily and become horizontal roots. Red oak woody laterals are mostly within the B horizon at depths of 20-50 cm; red maple woody laterals tend to be close to the surface of the mineral soil. Red oak roots are polyarch and the laterals emerge from several positions around the root; red maple roots are diarch and the laterals have a fan-like appearance. Red oak root tips in the forest floor range from 0.07 to 0.2 mm in diameter and the mycorrhizal root tips are ectotrophic, of several colors and shapes, and not easily seen with the naked eye; red maple root tips in the forest floor are seldom less than 0.5 mm in diameter and the mycorrhizal root tips are endotrophic, smooth, bead-like and readily visible.

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