1964 HARVARD FOREST PAPER No. 10

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ABSTRACT

Roots of Acer rubrum L. (red maple) at the Harvard Forest are primarily horizontal and in the upper 25 cm of soil. Woody roots are up to 25 meters long, relatively straight, infrequently branched, rope-like, and increase in diameter by annual production of secondary xylem. Non-woody first order roots emerge from opposite sides of the woody roots, at 1 cm intervals, grow upward into the forest floor and develop into multiple-pinnate fans about 20 cm long with up to 6 orders of branching. Non-woody roots lack annual increments of secondary xylem, seldom are larger than 1 mm in diameter and are relatively short-lived. Each full grown root fan bears from 1 to 5 thousand, 1 mm long, bead-shaped endotrophic mycorrhizae and these probably are the major absorbing organs. Vigorous adventitious woody roots develop near the stem of older trees or on injured larger woody roots and re-occupy the area once filled with the root system of the young tree. The distribution of the root types and the implications for sampling the root system are discussed briefly.

INTRODUCTION

Root systems of trees seldom receive the attention given crowns and stems partly because they are concealed in the soil and partly because the interrelationships of roots seem hopelessly complicated. The purpose of the study reported here was to examine the developmental relationships and distribution of the root types within the root system of Acer rubrum L. in order to provide a valid basis for sampling and for interpretation of the information obtained from the samples. Sampling a root system is not much more difficult than sampling the soil; the problem is to determine what measurements and observations are relevant. Red maple was chosen because this species has a wide geographic range (Hutnik and Yawney, 1961), and because it grows well on either wet or dry soils. From these standpoints the species can serve as a good frame of reference for comparisons of root systems in different sites.

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2 We thank our associates, both at Petersham and at Cambridge, for helpful discussion during the course of the study. Funds for this publication have been supplied from generous gifts by the Friends of the Harvard Forest.

REVIEW OF LITERATURE

Remarkably little has been published on the root systems of red maple. Stout (1956) charted the root systems of three mature trees, Toumey (1929) and Duncan (1941) examined the root systems of seedlings, adventitious roots were grown from vegetative cuttings by Snow (1941) and by Bachelard and Stowe (1962), and were noted in a mature stem by Westing (1959). Excised seedling roots have been grown in vitro by Bachelard and Stowe (1963).

Root systems of some other forest tree species, especially conifers, have been studied intensely, however, in the last 50 years both in Europe and North America (Dunning, 1949). The thorough studies made in Finland on pine, spruce, and birch are reviewed briefly here to call attention to the gradual shift in emphasis from one part of the root system to another. Similar changes in emphasis have occurred in root studies made in other countries.

The classic studies of Laitakari (1929, 1935) on pine and birch emphasized the length, size and distribution of the larger horizontal and vertical roots, particularly those at the base of the tree. He barely mentioned fine roots less than about 2 mm in diameter except to note they are short-lived and often mycorrhizal. Kalela (1950) sampled the roots in known volumes and depths of soil from between trees. These roots were separated into diameter classes of less than 1 mm, 1-2, 2-5, and over 5 mm and the length, weight, and volume of the roots in each diameter class were determined. Because known volumes and depths of soil were sampled the results could be expressed in many different ways. Kalela pointed out, for example, that the roots smaller than 1 mm in diameter made up more than half the total length of the root system. Sirén (1951) stressed the growth of roots in addition to root morphology and distribution, and subsequently Kalela (1957) studied the rate of root growth by sampling at intervals during the growing season. In addition to diameter classes Kalela counted the number of root tips. Heikurainen (1957) not only counted the root tips, but also classified them into several categories. Thus in the period from 1935 to 1957 the emphasis in Finland shifted from large roots, particularly those near the base of the stem, to small roots of less than 1 mm diameter and to root tips.

METHODS AND MATERIALS

The root systems of red maple trees were investigated in detail at two locations within Compartment I of the Prospect Hill tract of the Harvard Forest, Petersham, Massachusetts. Most of the study was made on 40 to 60 year old trees growing at the edge of a former plowed field on Scituate fine sandy loam, a moderately well drained Brown Podzolic soil developed from acid, stony, sandy glacial till derived mostly from granite and schist. The surface and subsoil is very friable to a depth of about 60 cm and offers little resistance to root penetration, but below 60 cm a brittle, hard layer called a fragipan restricts root growth. Young seedling red maple trees 10 to 15 years old were examined in an area cleared of forest about 1940. The soil here is Gloucester fine sandy loam, much like Scituate soil, but well drained and friable throughout.

Horizontal woody roots were exposed by removal of the 2 to 8 cm thick forest floor and the upper 2 to 8 cm of mineral soil by hand digging (Fig. 1). A geological hammer with a pick head was used to minimize root damage. This method of root examination although laborious, is simple, requires little equipment, and can be used for any tree at any location.

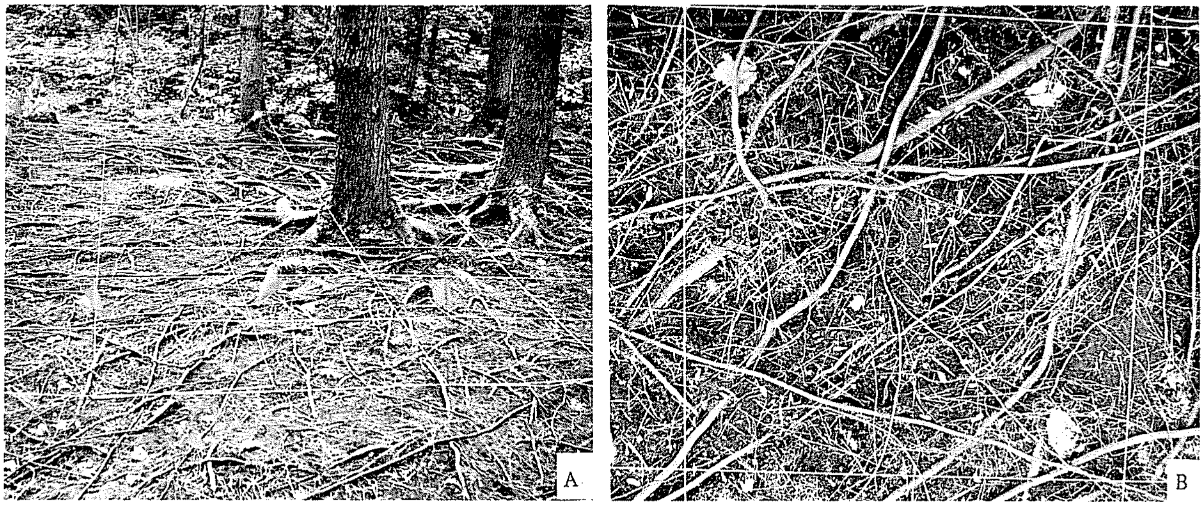

Figure 1. A. Roots of several closely spaced red maple trees exposed by removal of the forest floor and the upper centimeter or two of mineral soil. The squares are 2 feet (61 cm) on a side.

B. Close-up view of the exposed woody roots within one of the squares.

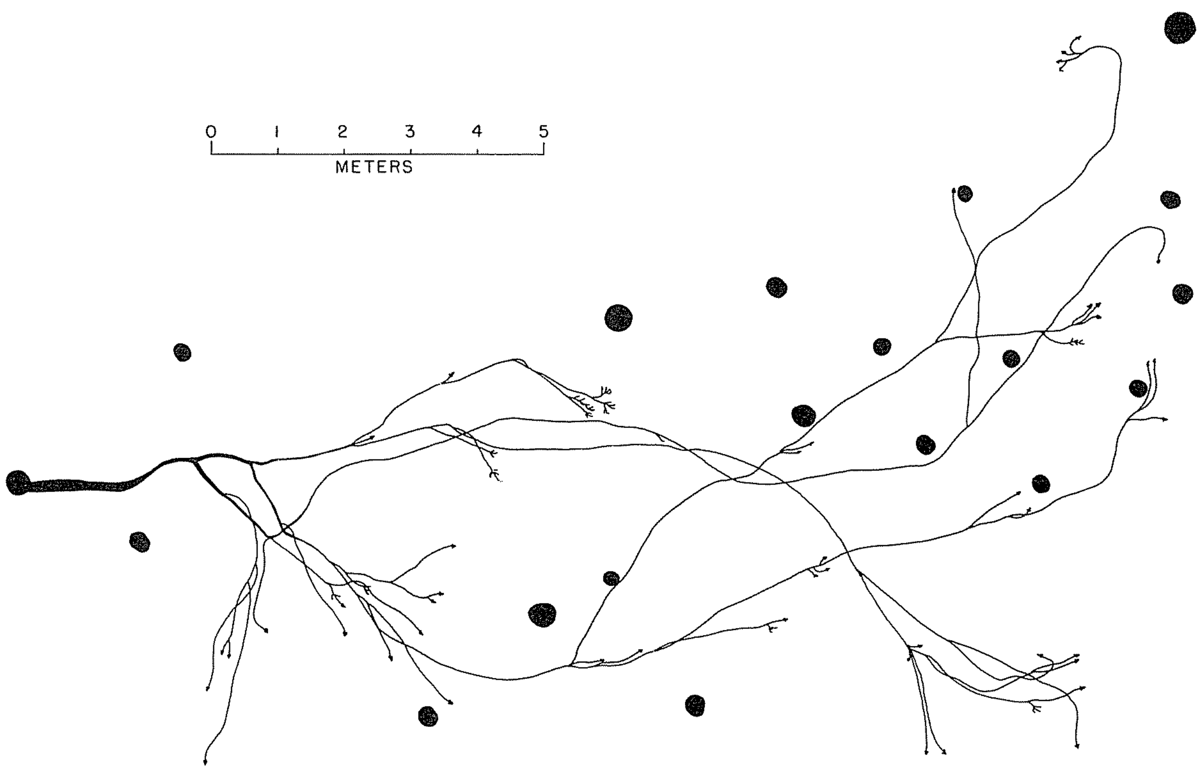

Figure 2. Plan view diagram of the horizontal woody root system developed from a single lateral root of a red maple tree about 60 years old. Solid circles show the location of other trees in the stand. Arrows indicate that root tips were not found and therefore these roots continue somewhat farther than is shown.

Photographs were made of representative portions of the root systems and a few roots were excavated completely and diagrammed. Non-woody roots were examined microscopically after removal from the forest floor. Vertical roots were examined in soil pits.

ROOT TYPES

Classification of the root types of conifers commonly is based on differences between long and short roots (Aldrich-Blake, 1930; Wilcox, 1964). This classification has been found inadequate for roots of intermediate size such as those commonly occurring in root systems of Fagus sylvatica L. (Clowes, 1950) and of red maple. In the present study, a basic dichotomy between woody and non-woody roots has been found more useful for classifying red maple roots.

Woody and non-woody roots are distinguished primarily by the presence or absence of annual production of secondary xylem (wood). In red maple, only one root type, a type comparable to that designated as pioneer roots in conifers, develops appreciable secondary xylem from annual periods of cambial activity. All other root types, including those previously designated as short or intermediate roots, have little or no cambial activity and most are short-lived.

Woody roots have been described in detail by Wilson (1964) and only a brief résumé of their character is given here. Woody roots extend outward from the base of the tree in a more or less straight line (Fig. 2), taper rapidly near the stem, and from then on are rope-like with a small diameter (up to 2.5 cm) relative to their length (up to 25 m) (Fig. 5A). At about 1 to 5 meter intervals lateral woody roots branch off the main root. Tips of woody roots are white, swollen, about 2 mm in diameter and up to 15 to 20 cm long.

The relationship of woody to non-woody red maple roots is shown in Figure 3. The first non-woody roots emerge at 1 to 3 cm intervals just behind the swollen root tip of a woody root. They are in two ranks on opposite sides of the woody root and at approximately right angles to the woody root (Fig. 4). These first non-woody roots are named first order non-woody roots in this paper. Lateral to these grow second order non-woody roots smaller in diameter than the first order roots. Third order non-woody roots grow from opposite sides of second order non-woody roots and so on. These related first and higher order non-woody roots form a multiple-pinnate fan-like structure about 20 to 40 cm long with the first order non-woody root as the midrib (Fig. 3). Such a structure of non-woody roots, commonly designated a "root-fan" (Laitakari, 1929), when occurring in the forest floor and when full grown, consists in idealized form of a first order non-woody root, about 40 second order roots and 5000 or more mycorrhizae. Root-fans are less conspicuous in the lower B horizon because there are fewer higher order non-woody roots and only a few scattered mycorrhizae. Root-fans are relatively short-lived, become less frequent on the older thicker roots, and are virtually absent from roots 2 cm in diameter.

Most mycorrhizae occur lateral to second or higher order non-woody roots. Single mycorrhizae are shaped like small 1 mm long beads (Fig. 4D), but fully half of the mycorrhizal roots consist of a series of end-to-end beads named "necklace-beaded mycorrhizae" by Kelley (1950). As many as seven or eight beads with a total length of nearly a centimeter are formed by constrictions in the cortex. Lateral root primordia develop within the beads rather than at the constrictions. These primordia may remain dormant within the cortex or they may elongate to form new mycorrhizae which grow out the side of the older mycorrhizae. In general mycorrhizae are terminal; but occasionally as in other species (Harley, 1959; McMinn, 1963) a root tip resumes active elongation and continues to grow as an uninfected root. This resumption of active elongation occurs frequently just behind areas that are injured or diseased.

The classification scheme proposed in this paper, based on woody and non-woody roots, takes into account both morphological and physiological similarities and also the developmental relationships among roots. In red maple all woody roots fall into a single broad class because in addition to secondary xylem they also have root tips approximately 2 mm in diameter. These are consistently larger than root tips of non-woody roots that are 1 mm or less in diameter. Even the root tips of small lateral woody roots are about as large as those of the parent woody roots. In this respect, therefore, the woody roots

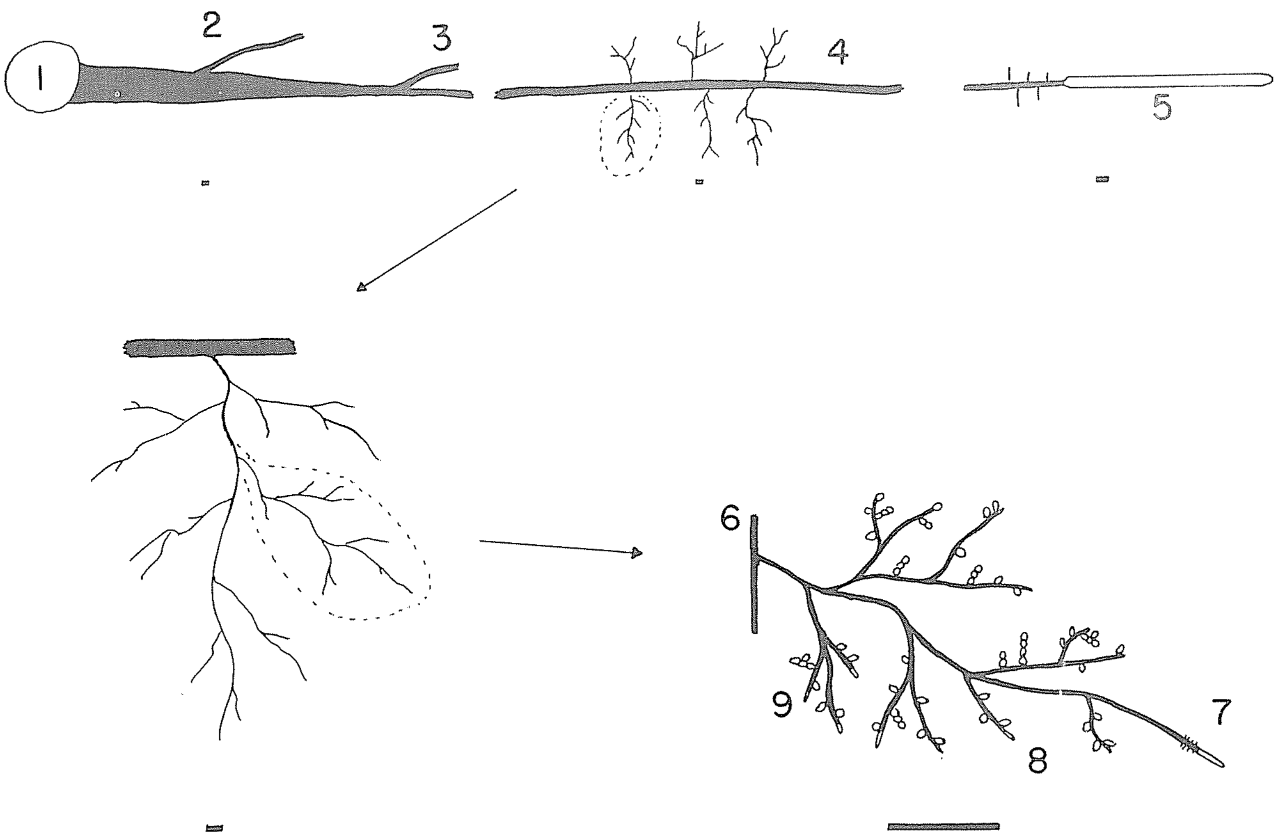

Figure 3. Schematic diagram showing woody and non-woody root relationships. 1, stem. 2, adventitious roots in the zone of rapid taper. 3, lateral root. 4, non-woody root fans growing from opposite sides of a rope-like woody root. 5, tip of woody root and emerging first order non-woody roots. 6, second and higher order non-woody roots growing from a first order non-woody root. 7, uninfected tip of second order non-woody root with root hairs. 8, third order non-woody root with single bead-shaped mycorrhizae. 9, fourth order non-woody root with single and necklace-beaded mycorrhizae. The horizontal bar beneath each root section represents a distance of about 1 cm.

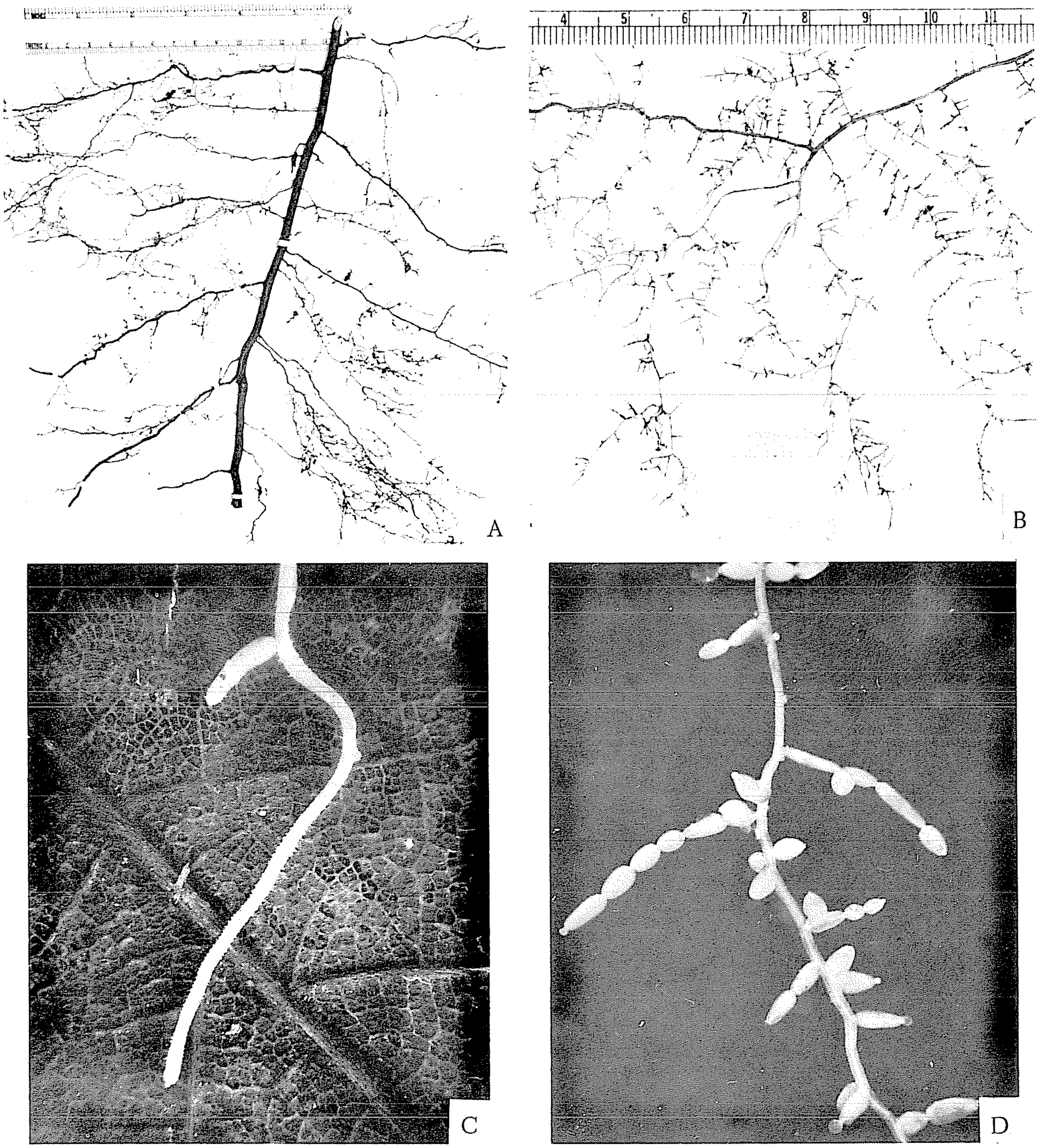

Figure 4. A. Root fans growing from opposite sides of a woody root.
B. Detail of a root fan showing second and higher order non-woody roots growing from a first order non-woody root.
C. Uninfected root tip, with numerous root hairs, growing on the surface of a leaf within the forest floor. The small knob-like protruberance at the very end of the root tip is common on dormant uninfected root tips and mycorrhizae. The root tip shown is approximately 1 cm long.
D. Single and necklace-beaded mycorrhizae on a root fan within the forest floor. The single bead-like mycorrhizae are about 1 mm long.

differ significantly from the non-woody roots which tend to have smaller and smaller root tips as the roots become successively smaller from branching (Table 1). Non-woody roots therefore fall in several classes on the basis of size of root and relationship to woody roots. This comes about primarily because non-woody roots do not increase in diameter as a result of cambial activity. This relationship between the various orders of non-woody roots is shown in Table 1. Diameters of root tips and maximum lengths of non-woody roots decrease in successively higher orders, whereas frequency of mycorrhizae and lateral roots increases. Injured roots of any type may develop replacement tips, more than one of which retains the characteristic of the mother root. A branched or forked non-woody root under this system, is considered to be of the same order as the parent root. This aspect of the classification implies, though in no sense proves, that there is a developmental relationship between the order of a non-woody root and its morphological and physiological characteristics.

Special attention is called to the designation of orders of roots used in this paper because the numbering system commonly used in root studies has been modified to provide a separate numbering system for non-woody and woody roots. Orders of roots generally are numbered with the taproot as the starting point. By this system of numbering, all roots, whether woody or non-woody, growing from the taproot are first order roots; all those from first order roots, whether woody or non-woody, are second order, and so on. Thus, although this numbering system provides information about the complexity of branching, it masks the dichotomy between woody and non-woody roots. In this paper woody and non-woody roots have been given separate numbering systems. Non-woody roots are numbered starting from their origin at the woody root as was explained previously. These two systems of numbering will not be confused if the complete name is always given, for example, first order woody root or first order non-woody root rather than simply first order root.

Briefly then, a mature red maple root system may be visualized as a framework of woody roots bearing many fans of non-woody roots. This concept of the major absorbing portion of the root system grouped into root-fan units considerably simplifies the interpretation both of the morphology of a large root system and of its development over time.

TABLE 1

SOME CHARACTERISTICS OF RED MAPLE ROOTS

Root type	Approx. tip diameter (mm)	Approx. final length	Frequency of laterals per cm of length	Frequency of mycorrhizae
Woody	2.0	10-25 m	0.3-1	None
Non-woody				
First order	0.5-1.0	20-40 cm	2-3	None
Second order	0.5-1.0	10-15 cm	3-10	Low
Third order	0.3-0.5	1-2 cm	3-10	High
Higher than third order and mycorrhizae	0.2-0.3	1-10 mm	---	Almost all

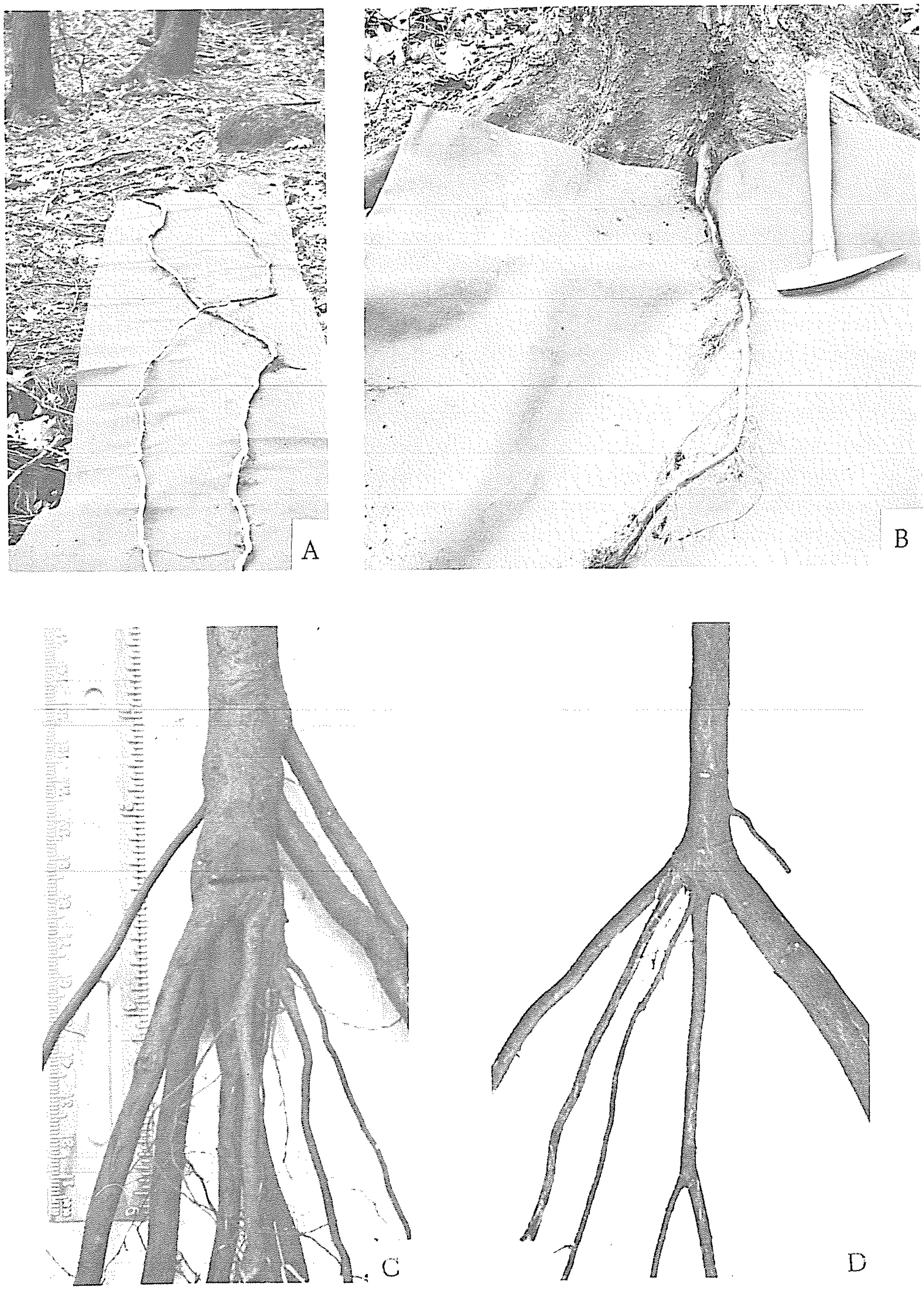

Figure 5. A. Long rope-like horizontal woody roots. These roots (painted white to make them conspicuous) originate from the tree in the center background and are a portion of the root system drawn to scale and shown in Figure 2.

B. A vigorous young adventitious root, with many fairly evenly spaced root fans, growing from the root collar of a large red maple tree.

C. Replacement roots of about equal size developed after injury to the root tip of a woody root.

D. Replacement roots, one much larger than the others, developed after injury to the root tip of a woody root.

Although woody and non-woody roots are distinguished in this study primarily on a morphological basis, the two groups can be distinguished also on the basis of their major physiological roles. Woody roots are permanent structural and conducting members of the system, while the relatively short-lived non-woody roots take up most of the water and minerals used by the tree.

GROWTH OF WOODY ROOTS

Lateral root primordia, normally formed 10 to 15 cm behind the tips of woody roots, develop into first order non-woody roots, yet every 1 to 5 meters along the woody roots lateral woody roots develop (Wilson, 1964) so there must be conditions in which either the development of these primordia alters, or different primordia are formed. An indication of these conditions is that less frequent branching and greater extension of woody roots are usually associated with poor tree vigor and poor soils, and more frequent branching occurs in fertilized areas or areas of high organic matter content (Busgen and Munch, 1929). In red maple the longest woody roots found were from the least vigorous trees and branching of woody roots was, in some cases, enhanced in areas of deep litter accumulation. In two situations it seems clear that woody roots develop from different root primordia than non-woody roots. One of these is where a woody root is injured and a group of replacement tips form just proximal to the injury. These replacement tips are of the same diameter class as the normal tips of woody roots. In some cases all these tips develop into roots of comparable size (Fig. 5C), in other cases one root becomes dominant and the others are left as a tuft of small woody roots marking the point of injury (Fig. 5D). Injuries to red maple roots by small rodents, nematodes, frost heaving, fungal infection, and other agencies are common, so that the formation of replacement roots appears to be a quantitatively important type of branching.

A second situation, particularly noticeable in older or suppressed trees, is where adventitious roots are formed from the stem (Fig. 5B), the zone of rapid taper, or on woody roots at a considerable distance behind a severe injury. Following is an example of the latter kind of growth. A red maple root about 1 cm in diameter was severed early in July and one short section about a meter back from the injury toward the tree was encased in moist surface soil and another in moist sphagnum. Adventitious roots developed in these moist materials and extended to a length of 20 cm producing many laterals. The tips of these roots were larger than 1 mm in diameter, but by the end of the summer had not yet undergone extensive thickening. Transverse sections through the woody roots showed that these adventitious roots were always connected to a protoxylem pole. There was no suggestion that primordia had formed de novo on the outside of the woody root. Induced laterals probably develop from dormant primordia persisting after the loss of the root fans, a situation comparable to the production of epicormic branches in stems. Dead first order non-woody roots were never found grown over by wood the way branch stubs are grown over in stems, so there must have been a mechanism for maintaining primordia at the positions of root fans.

A third possible way for the formation of woody branch roots is for non-woody roots to change to woody roots. Changes from mother roots (diarch) to pioneer roots (triarch) seems to be common in pine (Aldrich-Blake, 1930), so that a change from a first order non-woody root with severely limited cambial activity to a woody root is conceivable. On the other hand we have not observed such a change and once a woody branch root is established it is difficult to determine whether it originated adventitiously or from a pre-existing non-woody root. The formation of adventitious or replacement tips might account for all the branching of the woody root system; injuries to tips could be more frequent in soils that have rather large populations of injurious fauna or flora while the formation of adventitious roots could occur preferentially in moister soils. The possibility of a natural change from non-woody to woody roots does exist, however, particularly in vigorous trees, and should be further investigated.

Most woody roots are remarkably straight and appear to be oriented both with respect to the surface of the soil and with respect to a direction radiating from the stem. These roots are usually found 10 to 20 cm from the surface of the soil, although occasionally they originate from the stem at depths of up to 40 cm. The inherent stiffness of the tips of the woody roots permits them to extend horizontally for some distance independent of support from the soil, so that they can extend across spaces several centimeters in diameter. Those roots which are forced to grow upwards or downwards because of obstacles tend to return to the same depth at which they have been growing. Roots which deviate to the right or left around an obstacle generally return to their original direction although some of these roots may continue to grow in the new direction. In fact, Stout's (1956) diagrams of red maple root systems show a few roots that have taken a circular path. Although Laitakari (1935) states that the direction of a root away from the stem is "seldom maintained," his detailed maps of birch (Betula verrucosa, B. odorata) root systems show that, despite changes in direction, most roots tend to resume the original direction away from the stem. In so far as woody roots do maintain a general direction away from the stem they may be exhibiting the phenomenon of "exotropy" described by Noll (1894) for similar behaviour of the lateral roots from Lupinus and Vicia faba seedlings. The growth of replacement root tips in the same general direction as the injured root is presumably a separate phenomenon.

Vertical woody red maple roots are infrequent and usually less than 1 cm in diameter. They are most numerous within 2 to 3 meters of the base of the stem where they occur as downward growing branches of horizontal roots. In sandy Gloucester soil, lacking a fragipan, the vertical roots extend downward into the C horizon to depths of 1 to 1.5 meters, but in Scituate soil vertical roots penetrate only 50 to 75 cm to the hard fragipan. The roots penetrate the fragipan only where vertical cracks are filled with tongues of friable B horizon material.

GROWTH OF NON-WOODY ROOTS.

First order non-woody roots initially grow at various orientations to the surface of the soil because the woody roots from which they emerge are twisted (Wilson, 1964), but most of them seem to be negatively geotropic so that they reorient to extend upwards into the 2 to 8 cm thick forest floor. Within the forest floor non-woody roots grow horizontally between 2 to 3 year old fallen leaves. The various orders of roots of a root fan all tend to grow on the same or between closely appressed leaf surfaces and thus within the forest floor the members of a root fan tend to be in approximately the same plane (Fig. 4). One or two year old leaves are occasionally penetrated by the root tips, and this is one of the means by which the roots invade successively younger layers of leaves.

Root fans permeate and hold together the litter of a considerable area of the forest floor above the woody root from which they originate. Each full grown root fan occupies a thin horizontal layer 300 square cm or more in area where the roots are growing between and through the leaves. Adjacent root fans from the same woody root or those from different roots occupy overlapping areas so that in a 300 square cm sample of the forest floor there may be more than 10 different intermingled root fans and thousands of root tips. Despite this large population of roots, examination with a dissecting microscope shows that the roots seldom, if ever, touch. Rather, they seem to completely occupy an area until some minimal distance between the roots is reached, a distance of the magnitude of 0.1 mm to 1.0 mm.

ROOT SYSTEMS OF DIFFERENT SIZE TREES

SEEDLINGS:

New seeds fell June 5 and 6, 1963. They germinated within 10 to 12 days wherever they fell on bare, moist mineral soil and the radicles grew rapidly for 5 to 10 mm along the surface and then directly downward into the soil. The first laterals emerged from the radicles about two weeks after germination, about when the first pair of leaves expanded. After formation of lateral roots, the plant could not be pulled from the soil without breaking either the stem or some of the roots. Soon after the first laterals appeared the tap root, now at a depth of 2 to 5 cm, turned at the first small obstacle and subsequently grew horizontally. By the end of the first year, even for seedlings grown in small containers, the radicle was about 10 to 15 cm long and the major laterals were 5 to 10 cm long. Toumey (1929) showed a penetration of 10 inches (25 cm) for the tap root of a red maple seedling after a season's growth. None of the seedling roots exhibited distinct cambial activity and all seemed to be more like the non-woody roots of root fans than like woody roots. In some instances even the first order laterals on the taproot were mycorrhizal.

Root systems of two and three year old seedlings have lateral roots only about 1 mm in diameter. There is no clear indication that these original laterals become the woody laterals of the mature root system. New roots emerged from the tap root of the older seedlings, so it is conceivable that the large root tips of woody roots develop only from adventitious primordia.

YOUNG TREES:

Red maple trees 10 to 15 years old have essentially the same type of roots and root systems as mature trees. Woody roots are up to one centimeter in diameter and are morpholigically similar to the rope-like roots of older trees. Usually several woody laterals are distributed more or less evenly around the stem. In some trees the root system is one sided because there are no laterals extending from the stem on the side opposite the horizontal tap root. Root fans are evenly distributed along most of the length of these young horizontal woody roots. Apparently there has not been time for the root fans to be broken or lost through soil movement, burrowing animals or rot. The longest roots on these trees are about 5 meters and the root systems cover an area of approximately 50 square meters.

MATURE TREES:

Root systems of mature red maple trees at the Harvard Forest exist mostly in a thin horizontal layer in the upper 25 cm of the soil and downward growing tap roots are lacking. Infrequent vertical branches growing downward from horizontal woody roots probably made up no more than 2 percent of the whole root system.

The horizontal root system can be divided into three main portions (Stout, 1956). At the base of the tree, extending out for about one meter, are several large, rapidly tapered roots (Fig. 1). These roots commonly have a diameter of 10 to 15 cm at the base of the tree and less than 3 cm at a distance of one to two meters. Taper in some instances results from branching, but in other cases there is appreciable taper without any branching. Beyond the zone of rapid taper and extending outwards in a broad zone for many meters, depending on the age and vigor of the tree, are sparsely branched, rope-like woody roots (Fig. 5A). Root fans grow from the smaller, distal portions of the woody roots to form the outermost portion of the root system.

Although most of the rope-like roots arise a meter or more from the stem as branches of a main lateral, a few arise adventitiously from the zone of rapid taper, the root collar (Fig. 5B), or even the stem itself (Westing, 1959). Adventitious roots are smaller, have fewer growth rings, are more orange than the older reddish-brown rope-like roots, and have healthy root fans along their entire length. In wet sites, where water levels are commonly high, these roots are found high on the root collar. On well drained soils adventitious roots seem to develop when the larger roots have been injured or diseased, or possibly when their growth rate and physiological activity slow down.

Although most rope-like roots are only 5 to 15 meters long, three rope-like roots about 25 meters long were exposed during our study. Figure 2 shows a scale diagram of one of these roots. These long roots were remarkable for their scarcity of branches, paucity of root fans, small change in diameter over long distances (Wilson, 1964), marked tendency to grow straight, and the apparent poor vigor of the stems from which they grew.

RELATIONSHIPS AMONG ROOTS

Exposed woody roots of red maple trees form fairly regular patterns when viewed from above. The pattern of an individual root system seems to be much the same whether or not it is intermingled with the roots of other systems. In the zone of rapid taper several thick roots radiate outward. Within 2 to 3 meters of the stem a radiating pattern of roots 2 to 3 cm in diameter is formed as a result of frequent branching and from here on the woody roots generally are 20 to 25 cm apart. Beyond 3 meters from the stem the woody roots are seldom larger than 1/2 to 1 cm in diameter and are progressively further apart. When several red maple root systems are intermingled an intricate pattern of interwoven roots is formed (Fig. 1), but even so there are few woody roots which grow side by side. Most of the roots which cross each other are separated by thin layers of soil.

The sites chosen in the study included species other than red maple and a few preliminary observations were made on other root systems. Where red maple and red or white pine (*Pinus resinosa* Ait., *P. Strobus* L.) were growing together, woody maple roots were within the upper 8 cm of the mineral soil, whereas the woody horizontal pine roots were found at depths of 8 to 30 cm. Woody red oak (*Quercus rubra* L.) roots were even deeper, usually below 25 cm. Woody horizontal roots of black cherry (*Prunus serotina* Ehrh.), grey and yellow birch (*Betula populifolia* Marsh., *B. lutea* Michx. f.), and trembling aspen (*Populus tremuloides* Michx.), were intermingled with or even occurred nearer the surface than woody red maple roots.

In the mixed hardwood stands dominated by red oak practically all the non-woody tree roots in the forest floor were red maple. Rootlets of the red oak did not seem to be competing for this portion of the soil. Thus distribution of non-woody red maple roots in the forest floor apparently was not affected greatly by interrelationships with roots of other tree species.

DISCUSSION

Although red maple root systems are similar in overall characteristics to the root systems of many other tree species, examination from the standpoint of morphogenesis has led to an increased awareness of the importance of differences between woody and non-woody roots, the character of the root fans, and the common occurrence of replacement and adventitious roots. The observations made in this study suggest a generalized pattern for the development of mature red maple root systems composed of non-woody roots that absorb water and minerals from the forest floor and woody roots that bear the non-woody roots and serve as channels for movement of materials between the non-woody roots and the stem. There seem to be three relatively distinct phases in this developmental pattern: (1) the development of the seedling root system; (2) the differentiation and radiating extension of woody roots that bear non-woody roots grouped as root fans; and (3) the slowing of extension of the original woody roots, and the formation of adventitious roots near the stem. These phases are illustrated diagrammatically in Fig. 6. The seedling root system is largely confined to the forest floor and, although the basal portion of the radicle becomes woody, the system as a whole is not differentiated into woody and non-woody roots. Further investigation is needed to provide a detailed description of the transition from phase 1 to phase 2. The second phase is characterized by large diameter root tips developed either adventitiously, as in spruce (Sirén, 1951), or from pre-existing non-woody roots. Once formed, 5 to 8 woody roots extend in a radiating pattern away from the stem in what may be interpreted as a preferred orientation maintained by exotropy (Noll, 1894) at depths of 10 to 20 cm. This depth may be maintained either by some geotropic response or as a response to some gradient in the soil such as light or carbon dioxide. Non-woody roots grow from younger portions of woody roots up into the forest floor, possibly because they are negatively geotropic. Between the partially decayed leaves they develop into root fans, each composed of a first order non-woody root, a hundred or so higher order roots and several thousand mycorrhizae. The root fans are relatively short-lived, so that as the woody roots become older and longer they bear root fans only toward their tips (Fig. 6). Thus, the area of forest floor permeated by root fans moves progressively further away from the stem as the woody roots elongate. At the same time that this area moves away from the stem it also increases in size because branching increases the number of woody root tips from the original 5 to 8 per tree to more than 100 in a large tree. As shown in Figure 2, all the branches derived from one original root tend to grow in the same direction so that in surface view they occupy a wedge-shaped area. As the tree increases in size the woody roots near the stem develop a zone of rapid taper and root grafts. The third developmental phase occurs in older trees, or severely damaged trees, where it is marked by the formation of vigorous adventitious roots at the base of the stem and a general decline in vigor of the original woody roots. Adventitious roots re-occupy the area near the stem (Fig. 6), while the older roots eventually die. The behavior of roots during the final stages in the death of red maple has not been investigated.

Measurements made on the root systems of trees as a means of evaluating their characteristics depend on the objectives of the study. For studies such as pulpwood or turpentine production from roots the major concern will be with the larger woody roots 2 or 3 meters from the base of the tree where more than half the root volume occurs. For most studies of site the major emphasis will be on non-woody roots where most of the absorption of water and minerals occurs.

Identification and sampling constitute the major problems of root study in forest stands. Identification of the parent tree, even in pure stands of a single species, is possible only by tracing the root back to the tree by time consuming methods such as hand digging, use of dyes or radioactive substances. Identification of the species can be made from the anatomy of woody roots, but non-woody roots are difficult to identify and root keys are available for only a few species (Gilbertson et al., 1961; McDougall, 1921).

Sampling to enable measurement of roots involves much the same principles as those for the above-ground portions of the tree. Our studies show that the root system of an individual tree is little or no more complicated in morphology than the crown.

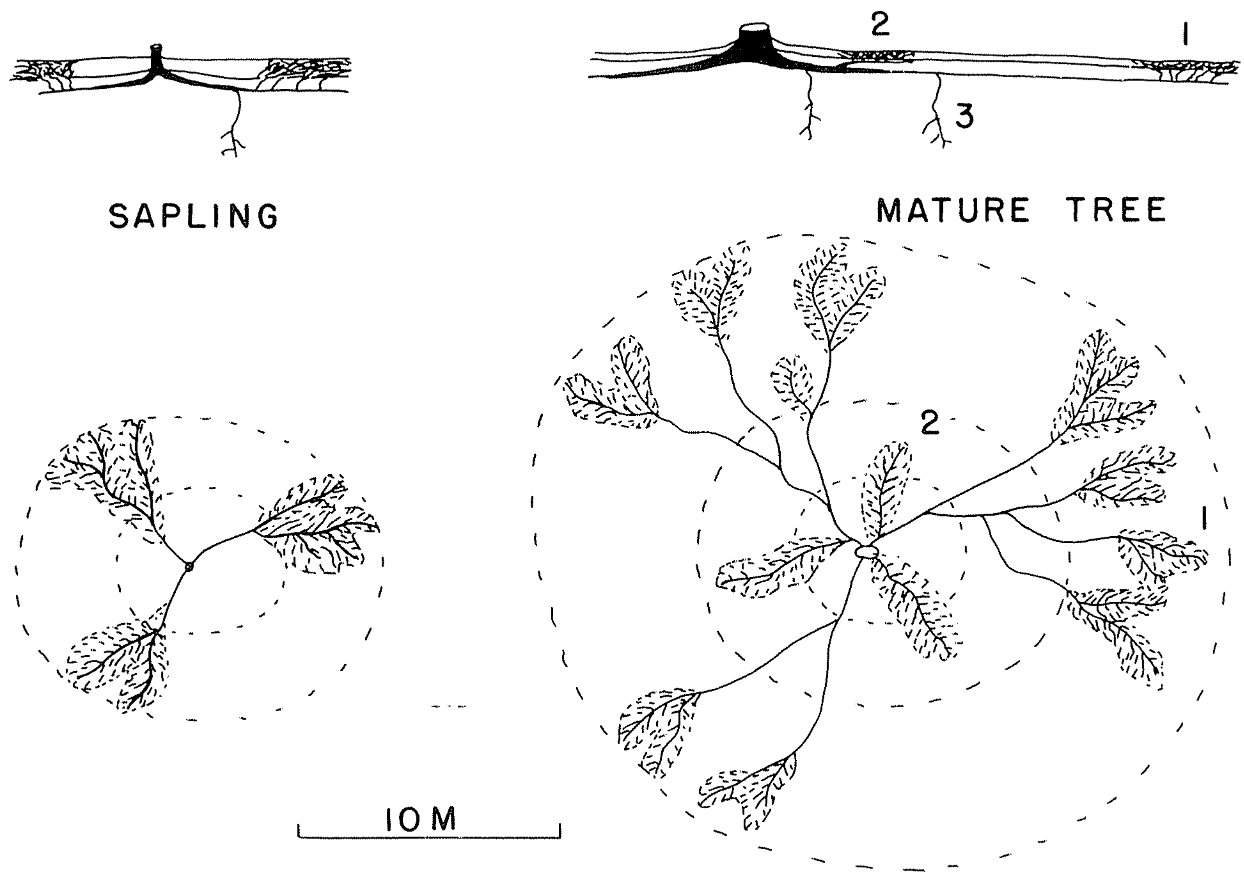

Figure 6. Schematic diagram showing reoccupation of the soil area near the base of a mature tree by the growth of adventitious roots. 1, root fans growing from the younger portions of the woody roots which have extended to a distance of several meters from the tree. 2, root fans on adventitious roots only recently emerged from the zone of rapid taper or root collar and now occupying the area near the base of the tree. 3, vertical roots.

The major difference is that the root systems of trees in a stand intermingle far more than the crown portions of trees, and in addition are concealed in the soil. The soil varies considerably more from foot to foot than does the air that surrounds the crowns, and this variation needs to be taken into account in root studies.

The initial stimulus for this red maple root study was a desire to work out a sampling system for roots that could be used for comparison of tree growth on different sites. For this particular purpose the major emphasis should be on the non-woody roots where absorption of moisture and minerals takes place. The method used to sample non-woody roots probably will involve study of roots in known volumes of soil, and sampling will be patterned to some degree at least after that of Kalela (1957) who used 10 cm diameter cores. It seems likely, therefore, that soil and root sampling can be coordinated and one set of samples will suffice for both. Important root measurements will include number and kind of roots, lengths of non-woody roots by orders, distance between mycorrhizae, frequency of root fans along the woody root, and percent of dead or decayed roots. The size and number of random samples needed for adequate characterization of the red maple root system will depend on the objective. If only mycorrhizae are to be studied the individual samples can be relatively small in size, perhaps cores as small as 2-5 cm in diameter, because there are many mycorrhizae in a small volume of soil and they seem to be fairly uniformly distributed throughout the area occupied by the tree root system. On the other hand if the objective is to obtain an idea of the length and volume occupied by the various orders of non-woody roots a larger volume of soil may be needed. This particular objective might require that each individual sample contain portions of woody roots to obtain some idea of the spacing of root fans along woody roots. In this event the core samples should be at least 20 to 30 cm in diameter because the woody roots tend to be spaced about this distance apart.

The distribution patterns of the thousands of non-woody roots in a small areas of the forest floor deserves further study, because our observations suggest that there is some mechanism that keeps roots from getting close to each other. Büsgen and Münch (1929) observed this characteristic in tree roots, and Garrett (1963) discusses similar mechanisms in hyphae of soil fungi. A direct result of this avoidance may be that even though roots seldom exceed 5 percent of the volume of the soil, there is no "room" for other roots. Whatever the mechanism, presumably some rhizosphere effect (Norman, 1961), it has important consequences in terms of root competition and site utilization.

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