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STRUCTURE AND GROWTH OF WOODY ROOTS OF ACER RUBRUM L.

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ABSTRACT

A. rubrum L. (red maple) has horizontal woody roots up to 25 m long. These roots are characteristically eccentric in cross section, twisted, and only slightly tapered. A study of transverse sections showed that the eccentricities resulted from depressed, often discontinuous, cambial activity opposite the diarch protoxylem poles and that the twisting apparently occurs in the root tips while they grow through the soil. Examination of successive sections from woody roots showed that some growth rings were longitudinally discontinuous, disappearing toward the stem. The presence of both circumferentially and longitudinally discontinuous growth rings makes age determination virtually impossible. It is suggested that woody branch roots emerging opposite the protoxylem poles divert materials moving from the stem down the main roots and thus decrease cambial activity further toward the root tip. This reduction could result both in discontinuous growth rings and in the diameter decreases observed after branching. Major factors causing the lack of taper between branch roots may be the relatively rapid rate of extension of the root tips (0.5-1.5 meters per year) and the presence of longitudinally discontinuous growth rings.

INTRODUCTION

Most studies of the structure and growth of woody tree roots limit themselves to the zone of rapid taper, that portion of the root system within one or two meters of the stem. Yet the portions of the roots beyond the zone of rapid taper have interesting features quite different from those near the stem. Horizontal woody roots of Acer rubrum L. (red maple) are up to 25 m long and slightly twisted. They appear rope-like because they are quite straight and do not taper. These roots in transverse section are usually oval, eccentric or grooved, with frequent discontinuous growth rings. The present study tries to describe the development of these characteristic features of long woody roots through study of the growth rings in the wood and of the external morphology of the roots.

Previous investigations seem to show that the characteristics of the zone of rapid taper are caused by mechanical and physiological stimuli from the adjacent stem. Many investigators have commented on the "I" beam, or "T" girder shape of roots next to the stem; they have interpreted the shape in terms of its mechanical efficiency in supporting

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and anchoring the stem (Haberlandt, 1914; Büsgen and Münch, 1929; Rigg and Harrar, 1931; Fegel, 1941; Stout, 1956). Jacobs (1939) has presented data showing that in Pinus radiata swaying of the stem in the wind stimulates diameter increment of roots in the zone of rapid taper; he had previously reviewed the general aspects of root shape in relation to wind sway (Jacobs, 1936). Both Laitakari (1935) in two species of Betula and Stout (1956) in several hardwood species including A. rubrum, have observed that beyond the zone of rapid taper roots are essentially round, which Stout interpreted to mean that they were relatively unimportant mechanically. Riedl (1937) and Bannan (1941) have observed that with respect to wood anatomy the zone of rapid taper is essentially stem-like, while Liese (1924) showed that the proportion of mechanical tissue (fibers) decreases with increasing distance from the stem, and indeed Wight (1933) even considered the zone of rapid taper to be physiologically part of the stem. Cockerham (1930) distinguished a "typical root cambium" from the cambium of the stem and of the zone of rapid taper. The illustrations of the zone of rapid taper and of root buttresses in Haberlandt (1914), Büsgen and Münch (1929) and Richards (1957) suggest that the central growth rings formed by the root cambium when the stem was small are usually concentric, while the later rings formed as the stem grew larger and its influence presumably reached further out the roots, are progressively more eccentric.

Observations of the specific characteristics of woody tree roots beyond the zone of rapid taper are fragmentary, many of them made in connection with general descriptions of root systems. Hugo von Mohl (1862) described the discontinuous rings and eccentric growth in several coniferous and hardwood species; remarkably little has been added since. Von Mohl pointed out that the inner growth rings of a root are often regular and relatively wide, while the outer rings are narrow, poorly defined, and frequently discontinuous. He thought that discontinuous rings were annual, that they resulted from the failure of part of the root to grow in certain years. After describing the thickening on the upper side of the roots near the stem, he suggested that further from the stem the lower side grows more than the upper. Kny (1908), however, studied the effect of gravity on branches and roots and stated that conifer roots did not grow eccentrically on the lower side unless they were exposed. Brown (1915) found eccentric, false and double annual rings in Pinus strobus roots. The widest part of the eccentric rings was on the lower side in the zone of rapid taper, but beyond the zone the widest part was irregularly distributed with no apparent relation to position in the ground or to gravity.

MATERIALS AND METHODS

The excavation of root systems of A. rubrum trees at the Harvard Forest during the summer of 1963 permitted easy observation and sampling of the horizontal woody roots. Aspects of the morphogenesis of these root systems are reported in a companion paper (Lyford and Wilson, 1964). In the present study the longest (up to 25 m) roots of these systems were investigated most intensively. These long roots were generally from suppressed trees and may have some features not characteristic of the woody roots from vigorous, dominant trees.

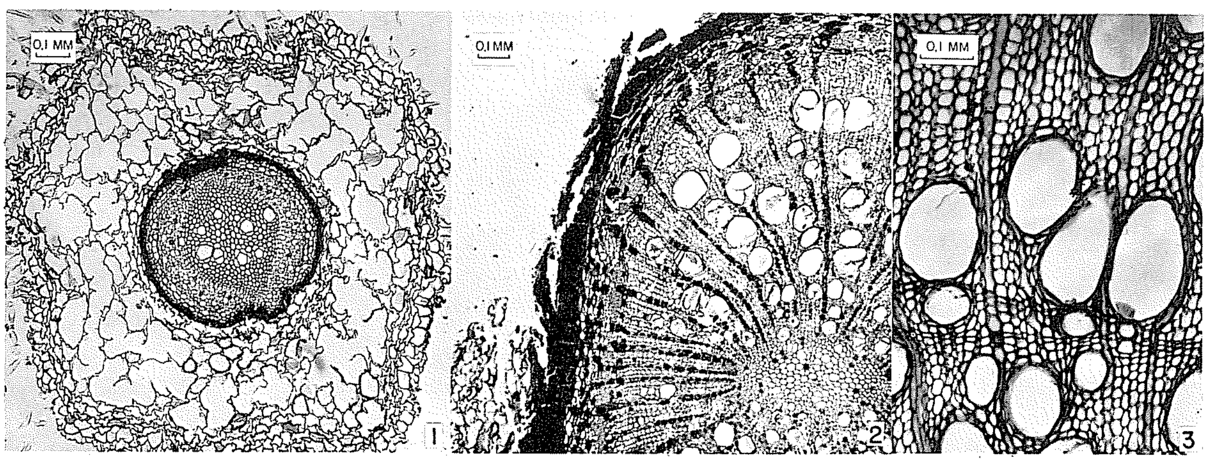
Minimum and maximum root diameters were measured in the field to 0.1 mm with a vernier caliper. It was not possible to measure from the inside of longitudinal grooves, so when grooves were present they were disregarded.

Samples were taken at intervals from the long roots of five different trees, and at particular points of interest such as branching, twisting or marked eccentricities from the roots of other trees. Some shorter woody roots were successfully excavated to the tips. Two such tips were fixed in formalin-acetic acid-alcohol, embedded in paraffin and sectioned on a rotary microtome. The woody samples were boiled in water and, after removal of the bark, sectioned on a sliding microtome and stained with safranin. All sections were prepared as permanent microslides.

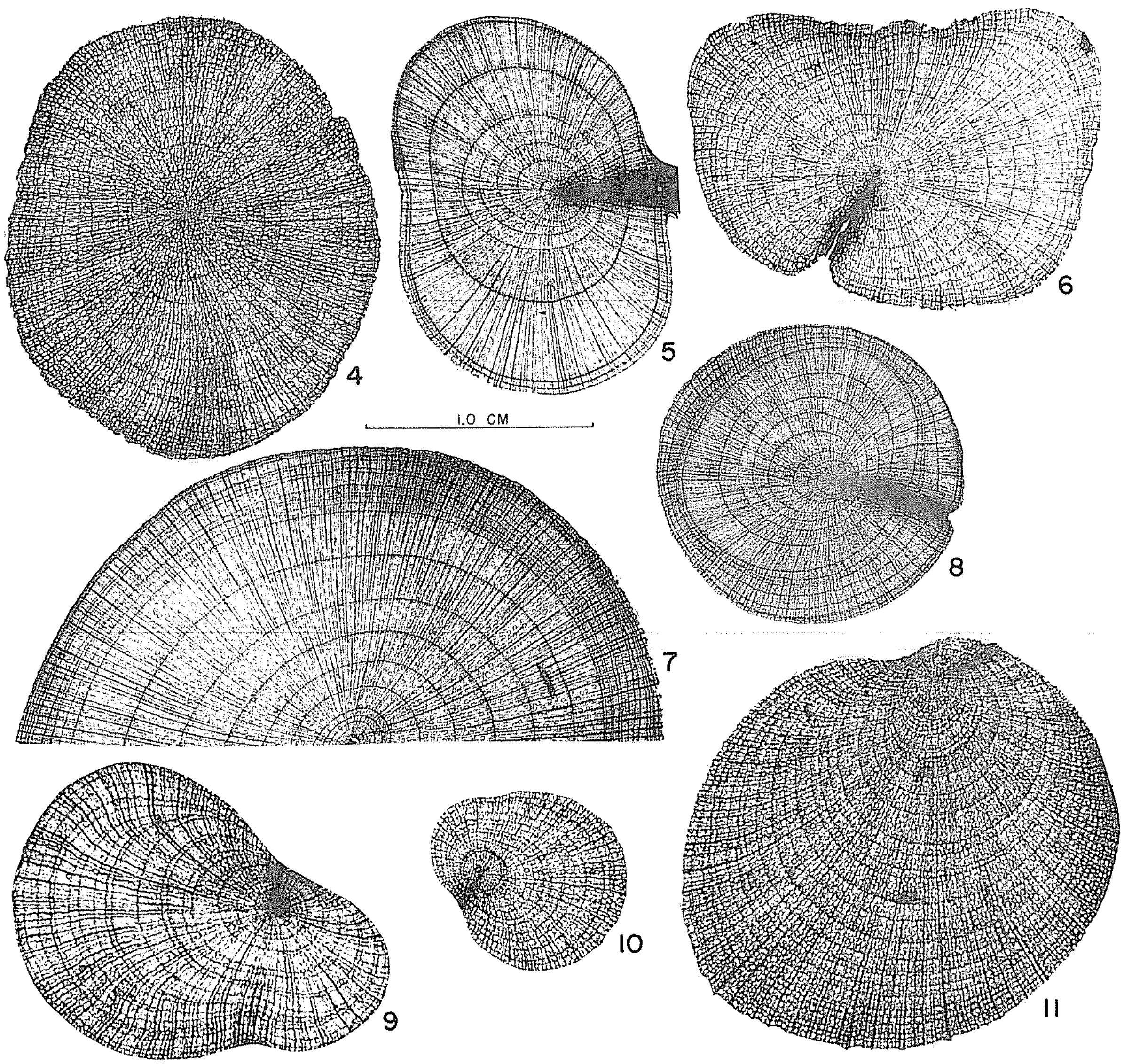
RESULTS

CAMBIAL ACTIVITY

Woody roots of *A. rubrum* have white tips about 2 mm in diameter and 10 to 15 cm in length, that are comparable in morphology to the tips of woody roots in *Pinus sylvestris* (Laitakari, 1929) and comparable in pattern of vascular differentiation to the tips of woody roots in pear and apple (Esau, 1943; Riedhardt and Guard, 1957). The root cap extends about 150 μ beyond the apical initials and 1.5 mm behind the initials. Thus, most of the root tip is made up of cortex, about 0.6 mm thick radially, and the central cylinder, with a radius of about 0.3 mm. Lateral root primordia develop from the pericycle opposite the diarch protoxylem poles about 15 cm behind the apical initials. The cambium is initiated between the primary xylem and phloem about 19 cm behind the initials. It is soon completed around the protoxylem poles, but most cambial activity occurs between the primary xylem and primary phloem until the core of xylem becomes approximately round (Fig. 1). A cork cambium forms from the pericycle about 20 cm behind the apical initials. Behind the cork cambium the cortex shrinks and most of it is sloughed off, though some cortical cells may remain attached to fairly large roots (Fig. 2). These cells often resemble a lacy white net external to the red cork cells.



Figures 1-3. Figure 1. Transverse section through the tip of a woody root 20 cm behind the apical initials where the cambium has just been completed around the protoxylem poles.
Figure 2. Transverse section through a woody root 200 cm behind the apical initials where the cambium has produced three growth rings. The cork is well developed, but some cortical cells still remain attached to the root in the lower left hand corner of the photograph.
Figure 3. Transverse section through the wood of a large root showing the size of the vessels and the edge of a discontinuous growth ring.



Figures 4-11. Transverse sections through woody roots to show the patterns of growth ring widths and the distribution of discontinuous rings. All sections are at the same magnification; all sections have had the bark removed.

The new cambium initially produces at least 2, and up to 10, relatively wide concentric growth rings (Fig. 2, 4-11). Occasionally a discontinuous ring is present among these central wide rings. Toward the outside of larger roots the width of the growth rings usually decreases, in many cases abruptly (Fig. 4-8). These abrupt changes occur along the entire length of a root and seem to reflect a change in vigor of the whole root. Discontinuous rings are common among these narrow outer rings.

The wood produced directly opposite the protoxylem poles does not have vessels during the first one or two years of growth; later, however, vessels are produced around the entire circumference of the root (Fig. 2, 4-11). These vessels have large diameters relative to those in the zone of rapid taper or in the stem (Fig. 3), as has been found in other species (Von Mohl, 1862; Riedl, 1937; Fegel, 1941). Within the same growth ring of A. rubrum the vessels in the zone of rapid taper are slightly larger than those in the stem; in the root 2 m from the stem the vessels are 2 to 3 times larger than in the stem; in the root 10 m from the stem the vessels are still 2 to 3 times larger than in the stem (Table 1).

Some growth rings that are discontinuous in a cross section disappear entirely closer to the stem (longitudinally discontinuous rings). The two prominent ridges on the outside of the cross section in Fig. 6 are formed by 5 to 6 narrow discontinuous rings. These extra rings are not present, however, in cross sections cut 2 m closer to the stem. It was not possible to determine whether or not these rings were present all the way to the tip of the root. One longitudinally discontinuous ring in the central wide rings (Fig. 6) was traced in sections from successive samples. Its development with increasing

Tree Number	Stem	Zone of Rapid Taper	Root (2m from stem)	Root (10m from stem)
	Avg. radial vessel diameter in μ for 1962 growth ring			
1	64.4	68.5	137.0	--
2	52.0	64.5	93.9	--
3	75.1	89.1	241.7	196.4
4	68.5	95.7	202.1	193.9

Table 1. Comparative vessel diameters from the stem, zone of rapid taper and roots in the same growth ring from 4 different trees. Each diameter is the average of the radial diameter of 50 vessels in the earlywood of the 1962 growth ring.

distance from the stem (Fig. 12) was as follows: it first appeared as a crescent-shaped "cap" perpendicular to the primary xylem plate, on the outside of the third growth ring; a second cap appeared opposite the first 1.0 m further away, also on the third ring; an additional 1.5 m toward the root tip these two caps had enlarged and fused circumferentially to form a continuous ring; 0.5 m further toward the tip a small additional cap had formed on the new ring, then fused with it, and 3 m from the first appearance of the cap, the ring was continuous, relatively wide, and now constituted the second instead of the fourth ring.

ECCENTRICITIES AND TWISTING

Beyond the zone of rapid taper many woody roots of A. rubrum are eccentric in cross section. They may be oval (Fig. 4), flattened (Fig. 5), or grooved (Fig. 6); if two grooves are opposite each other the root is "I" shaped, if they are close together on opposite sides of the root it is skull shaped (Fig. 9, 10). Most grooves are continuous along the root, some are discontinuous, and a few are only a series of shallow depressions (Fig. 13). In general a root has the same level of eccentricity along its entire length down to about 5 mm in diameter.

The areas of minimal cambial activity, as shown by the narrowest part of a growth ring or by a discontinuity, are opposite the diarch protoxylem poles so that non-woody lateral roots emerge from grooves or the flattened sides of the roots (Fig. 4-11, 13). Exceptions to this general observation are common only in the narrow outer rings of large round roots near the zone of rapid taper (Fig. 7). Where there is a series of depressions along the root, non-woody lateral roots emerge from the depressions (Fig. 13) suggesting that the laterals had depressed cambial activity of the woody root (Fig. 13).

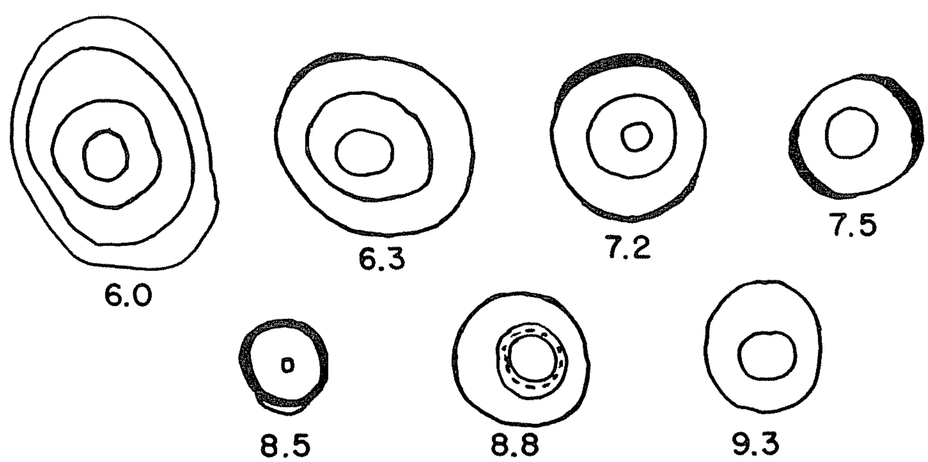


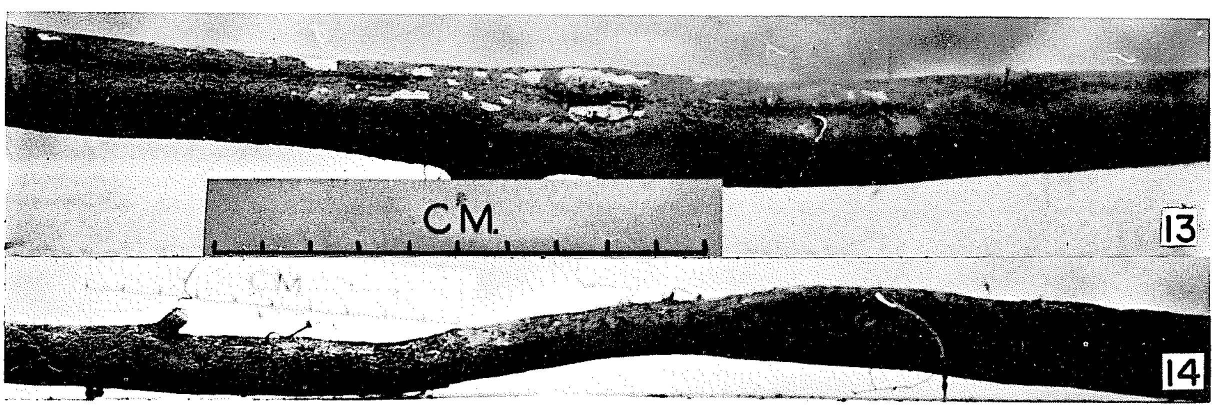
Figure 12. A series of diagrams taken from transverse sections, in each diagram the number indicates the distance from the stem in meters. See text for a description of the longitudinally discontinuous ring shown in black in these diagrams.

The orientation of the eccentricity in most woody roots continually changes because the roots are twisted in a clockwise direction going away from the tree (Fig. 14). One root was twisted a full 360 degrees 4.5 times in a distance of 22 meters. The rate of twisting, judged by following the grooves or a line of lateral roots, was variable; sometimes a root was twisted 180 degrees in less than a meter and occasionally a root was twisted slightly counter-clockwise, but it later twisted back and continued clockwise. There was no obvious connection between obstructions in the soil and the rate of twisting. Sections cut through greatly twisted parts of roots showed that grooves were always opposite protoxylem poles. Since the orientation of the primary xylem plate is determined within a few mm of the root apex, the external twisted appearance of the roots is apparently only a record of the twisting of the root tip as it grew through the soil, not a secondary twisting produced by cambial activity.

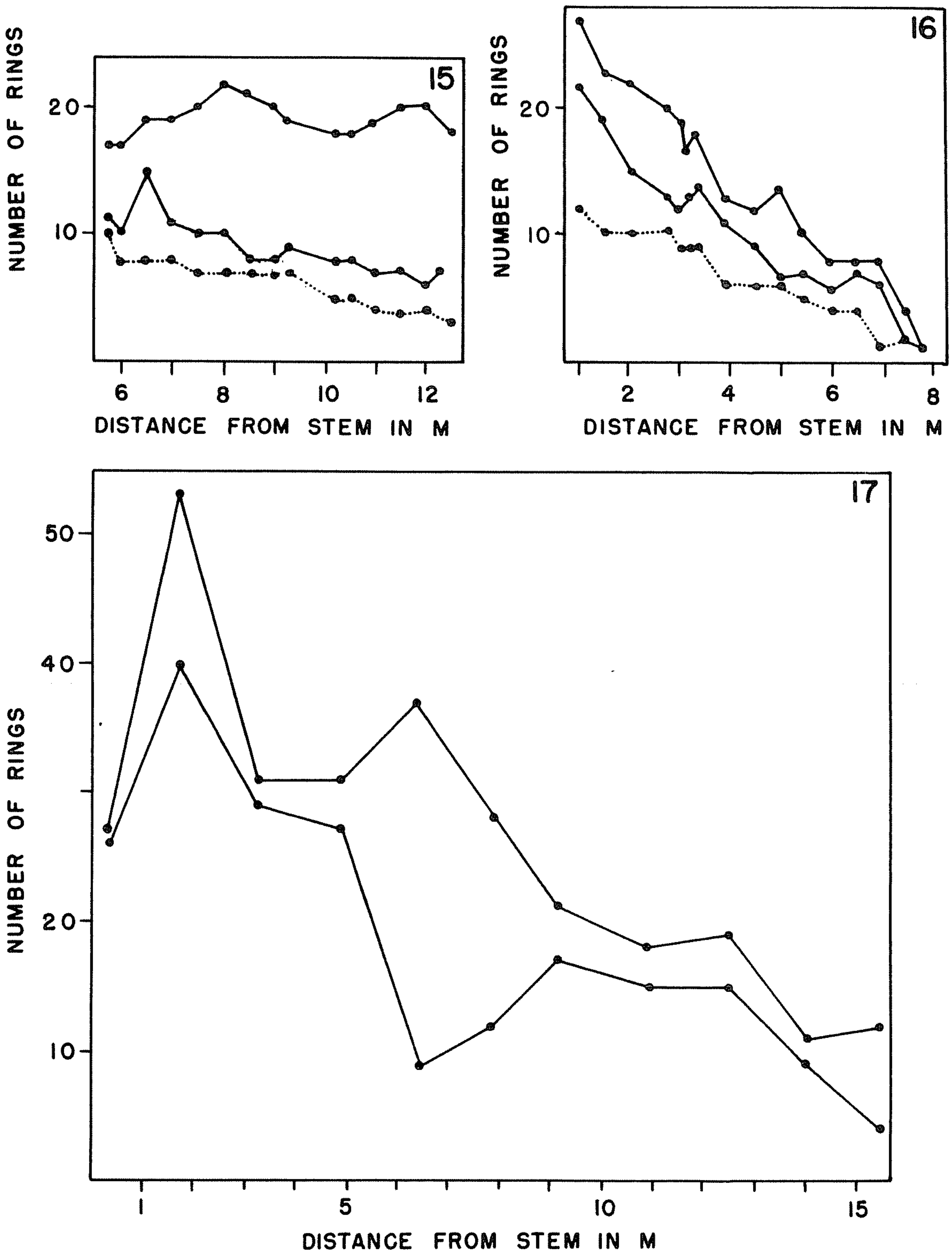
GROWTH RINGS FOR AGE AND LENGTH INCREMENT DETERMINATION

Age determination in *A. rubrum* woody roots is difficult because the frequent discontinuous rings permit both a maximum and a minimum ring count in most cross sections and longitudinally discontinuous rings may increase the ring number with increasing distance from the stem. The ring counts taken at intervals along three roots are shown in Fig. 15-17. In general the minimum ring count is opposite a protoxylem pole and the maximum number is perpendicular to the plane of the primary xylem plate. The difference between minimum and maximum ring counts tends to increase as the external eccentricity increases, particularly when grooves develop.

In most cases the age of an *A. rubrum* stem cannot be used as a basis for determining the age of the roots, either because the stem is of sprout origin and younger than the root system, or because the roots are of adventitous origin and are younger than the stem. The ring counts for one adventitous root are shown in Fig. 17. Although the stem was 70 years old, the maximum ring count 30 cm from the stem was 26 and the absolute maximum ring count was 51, 2 m from the stem. Sirén (1951) has suggested that all horizontal woody roots in undergrown spruce originate adventitously because they are all younger than the stem.



Figures 13, 14. Figure 13. A woody root with the bark on showing a longitudinal groove on the left and a series of depressions on the right. Note the lateral roots emerging from some of the depressions.
Figure 14. A rapidly twisted, much flattened root. The root is twisted 90 degrees in 12 cm.



Figures 15-17. Graphs showing the change in number of growth rings in three woody roots with increasing distance from the stem. Upper solid line = maximum number of rings, lower solid line = minimum number of rings, dotted line = number of wide central rings (not present in Fig. 17).

Lateral woody roots may not have the same number of growth rings as their parent root (also noted by Sirén (1951) for spruce). Laterals which form near injured tips have the same number of rings as the parent root, but others that have originated adventitously or from pre-existing non-woody roots (Lyford and Wilson, 1964) may be much younger than the parent root.

The annual length increment of horizontal woody roots of A. rubrum was estimated at from 45 cm to 150 cm. Three different methods were used. (1) In three roots the number of wide central rings decreased consistently with increasing distance from the stem, despite variations in the minimum and maximum number of rings (Fig. 12, 15, 16). In these cases the average annual length increment, assuming that the central rings are annual, is equal to the length of the root segment divided by the decrease in number of central rings over that length. The average annual increments were calculated for Fig. 12 to be $\frac{300\text{cm}}{2\text{ yr}} = 150$ cm/yr ; for Fig. 15 to be $\frac{650\text{ cm}}{7\text{ yr}} = 93$ cm/yr ; for Fig. 16 to be $\frac{690\text{ cm}}{11\text{ yr}} = 63$ cm/yr. (2) The longest roots of a tree were consistently 1.5 to 2 times longer than the height of the stem. Since the average annual height increment of comparable A. rubrum trees is 30 to 50 cm/yr, the average annual length increment must be at least 45 to 100 cm/yr, and even more if the roots are of adventitous origin and younger than the stem. Laitakari (1935) calculated an average annual rate of extension for the woody roots of birch of 1.0 to 2.0 m/yr using the first method and up to 42 cm/yr using the second method. (3) the position of the root tip of one woody root was marked in November, 1962, then uncovered and re-marked at intervals during the summer of 1963. The tip extended throughout the period of height growth of the stem at a rate of 3 cm/week. This rate is similar to that of A. rubrum seedling roots and excised roots in culture of 4.0 to 4.6 cm/week (Bachelard and Stowe, 1963). In late July the tip was injured, but continued to grow to a total length increment of 42 cm by November, 1963. In view of the injury to the tip, this increment is presumed to be minimal.

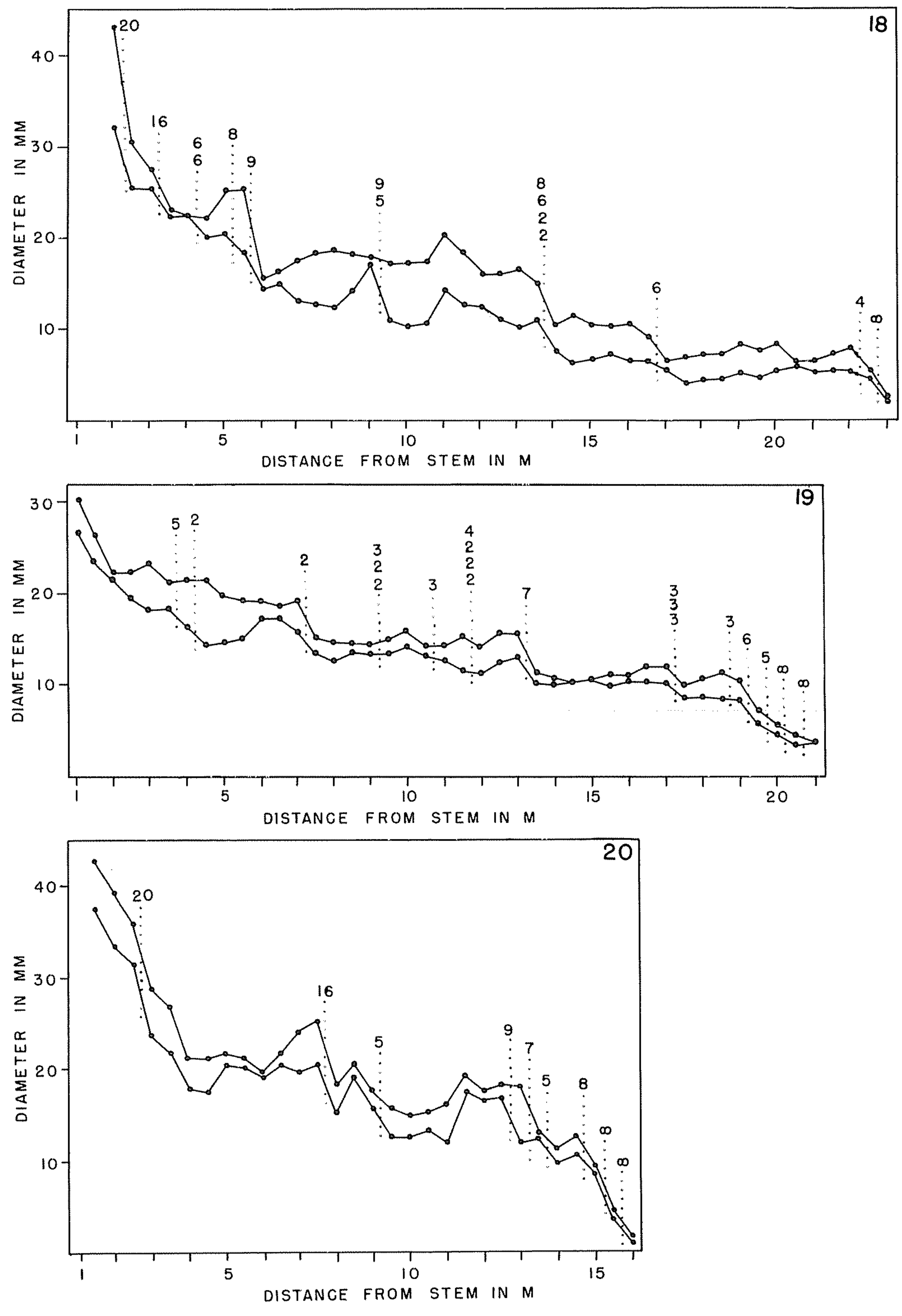
LACK OF TAPER IN WOODY ROOTS

Woody horizontal roots, once beyond the zone of rapid taper, decrease in diameter by sudden steps immediately beyond woody branch roots. Within the first 1 to 2 m from the stem the roots are eccentric, but basically conical so that they taper down to a diameter of 2 to 2.5 cm. Further from the stem the roots are basically cylindrical for distances of up to 5 m between branch roots (Fig. 18-20). The magnitude of the decreases in diameter following branching did not appear to be correlated well with the size of the branch root; indeed not all branchings were followed by a diameter decrease.

Sections taken at each end of a 5 m cylindrical segment of a root showed that toward the stem there was a maximum of 13 and a minimum of 7 growth rings, while at the end toward the root tip there was a maximum of 12 and a minimum of 8 growth rings. The root tip had either grown through this segment at a rate of more than 2.5 m/yr, about twice the estimated normal rate, or there were longitudinally discontinuous rings present. It could not be determined, however, which of these possibilities was correct.

DISCUSSION

The growth of the root tip determines the position, length and orientation of woody roots. The woody portion of the root is restrained by the soil so that its convolutions record the path of the root tip through the soil. This path is presumably the resultant



Figures 18-20. Graphs showing the change in outside diameters of three woody roots with increasing distance from the stem. Upper solid line = maximum diameter, lower solid line = minimum diameter. Each number above a dotted line represents the diameter of a woody lateral root coming off the main root at the point marked by the dotted line, ∞ = more than 5 woody laterals each 2 mm or less in diameter.

of tropisms which maintain the tip at particular depths in the soil and direct it away from the stem (Lyford and Wilson, 1964). Just as the path of the root tip is recorded by the position of the woody root, so is its twisting recorded by the twists of longitudinal grooves and the changing orientation of successively emerging lateral roots. The question of how the root tips undergo these movements, and under what conditions, can be answered only by observation and experimentation with the root tips themselves.

The distribution of cambial activity along and around the root produces the discontinuous growth rings, the eccentricities in cross section, and the rope-like form of long woody roots in A. rubrum. One characteristic of this distribution is the change in overall rate of cambial activity over time. During the first 2 to 10 years of cambial activity growth rings are concentric and relatively wide. Rings produced later, however, are narrow (Fig. 4-11). The decrease in ring width, which may be quite abrupt, seems to be caused by a general slowing of growth because it occurs in the same ring along the whole length of the root. The other characteristic of the distribution of cambial activity in long woody roots is the high frequency of discontinuous rings. They are most common among the narrow outer rings, but they also occur within the central zone of wide rings. In both cases however, and also when cambial activity is depressed in some areas but still continuous, the area of minimal cambial activity is opposite the diarch proxylem poles where the lateral roots emerge from the parent root (Fig. 5, 6, 8-11). Thus, when the general level of cambial activity decreases, discontinuous rings are produced more frequently; the root becomes oval in cross section; longitudinal grooves may develop opposite the protoxylem poles. Because the growth of the whole root slows, the level of eccentricity is about the same throughout the entire length of these roots (Fig. 18-20).

Discontinuous growth rings represent periods when only part of the cambium was active. Unfortunately, using trees from natural stands with no roots of known age, it was not possible to determine whether discontinuous rings were annual. There seem to be two types of discontinuous rings in A. rubrum roots, both of which may also be absent closer to the stem and therefore longitudinally discontinuous. Those discontinuous rings found in the narrow rings of the outer parts of large roots, where all cambial activity seems limited, may well be annual; those within the central wide rings, where cambial activity is generally high, are probably not annual and should not be counted for age determination. The technique of matching growth ring patterns used to detect "missing" growth rings in stems (Block and Agerter, 1962) cannot be used with longitudinally discontinuous rings because there is no such pattern in A. rubrum roots.

Several factors contribute to the rope-like form of long woody roots. Perhaps most important is the small diameter of these roots relative to their great length. The largest roots increase in diameter so slowly, because they produce such narrow growth rings, that beyond the zone of rapid taper they seldom exceed 2.5 cm in diameter. In contrast the diameter of a stem 25 m tall would be at least 25 cm and probably much more. A second factor is that lateral woody roots occur only every 1 to 5 m along these long roots. The types of branching in A. rubrum are discussed in Lyford and Wilson (1964). The third factor is the lack of taper between branch roots, apparently associated with, or balanced by, decreases in diameter just after the point of branching (Fig. 18-20). These latter features are found in other species. Stout (1956) noted that some woody roots are larger in diameter 20 feet from the stem than they are 10 feet from the stem. Sirén (1951) attributed the drop in diameter after branching to pathological injury to the root tip at the point of branching which halted its growth for 8 to 30 years (comparable "rests" were not found in A. rubrum). In A. rubrum the age difference of only 1 to 2 years between branchings and the possibility of longitudinally discontinuous rings which are present only toward the end of a segment, both contribute to the cylindrical shape of the root. Another possibility is that woody laterals have a slight girdling effect and thus stimulate diameter growth toward the end of each segment. Some possible reasons for the drop in diameter following branching will be discussed below.

Most studies show that root elongation, the formation of a cambium in a root and its later activity are all controlled by the stem. Excised pea roots growing in culture, which normally do not form a cambium, are induced to to so only by adding auxin to the proximal, or "stem", end of the root (Torrey, 1964). Although excised roots of A. rubrum have been grown in culture (Bachelard and Stowe, 1963), they have not yet been induced to form cambium in culture. Richardson (1957) found that root initiation and elongation in A. saccharinum seedlings was controlled by the stem. Laitakari (1929) and Lyford and Wilson (1964) have stated that maximum length of woody roots was achieved in trees with the slowest growing stems. Studies of the initiation of cambial activity in the spring show that activity starts later in the root than in the stem, and moves from the stem out to the end of the root. (Hartig, 1878; Cockerham, 1930; Brown, 1935; Wight, 1933; Knight, 1962). Cessation of activity in the autumn occurs in the same sequence. Both Riedl (1937) and Bannan (1941) have reported that the amount of latewood in growth rings of roots decreases with increasing distance from the stem, so apparently the differentiation of wood in the roots, as well as in the zone of rapid taper, is affected by proximity to the stem.

A few studies have shown that root elongation and cambial activity can proceed at reduced rates even though the stem is dormant and the roots are, in a sense, autonomous. Morrow (1950) has found that "surface" roots (presumably not the tips of woody roots) of A. saccharum elongate all year (as judged by the color of the root tips), although the amount of elongation was reduced after the stem cambium became dormant. Ladefoged (1939) has shown that although Fagus sylvatica roots may elongate slightly during a mild winter, the roots of other species he investigated stopped even during such a mild winter. He found that there was considerable variation between species in whether root elongation begins before or after leaf production. Both von Mohl (1862) and Cockerham (1930; in A. pseudoplatanus) have reported that the cambium in the portions of woody roots far from the stem may be active throughout the winter, even when the stem cambium is inactive.

Thus it seems that materials necessary for root growth, hormones and photosynthate, move out the woody roots where they may accumulate in sufficient quantities to allow cambial activity to continue after the supply of materials from the stem is shut off. Apparently in roots of A. rubrum this flow of materials may be stopped or decreased opposite the protoxylem poles, resulting in decreased ring width in these areas. The major structural features which would seem to be able to interrupt the flow are the woody branch roots which are opposite the protoxylem poles and for their growth divert some of the materials which would normally flow down the major root. Such a diversion would result in a relative starvation of the areas opposite the poles after the branch roots, and might also account, in part, for the observed drop in diameter after branch roots. It could therefore be expected that the more numerous and vigorous the lateral roots the more marked would be the eccentricity. It would also be predicted, and was observed in this study, that in suppressed trees producing less materials for the roots, competition between the main root and the woody laterals would be more severe, eccentricities more marked, and discontinuous rings more common.

Longitudinally discontinuous rings may form when the root cambium is active and the stem cambium inactive. The whole question of the duration of cambial activity in roots, however, needs further study to establish this possibility. In addition, other hypotheses seem equally tenable at present. There may be localized production of hormones by the root cambium itself, or the root tip may provide some factor necessary for cambial activity. These questions can only be answered by more observation and perhaps manipulation of longitudinally discontinuous rings.

LITERATURE CITED

BACHELARD, E.P. and B.B. STOWE. 1963. Growth in vitro of roots of Acer rubrum L. and Eucalyptus camaldulensis Dehn. Physiol. Plantarum 16:20-30.

BANNAN, M.W. 1941. Variability in wood structure in roots of native Ontario conifers. Bull. Torr. Bot. Club 68:173-194.

BROWN, A.B. 1935. Cambial activity, root habit and sucker development in two species of poplar. New Phytologist 34:163-179.

BROWN, H.P. 1915. Growth studies in forest trees 2. Pinus strobus L. Bot. Gaz. 59:197-241.

BÜSGEN, M. and E. MÜNCH. 1927. The Structure and Life of Forest Trees. John Wiley and Sons. New York. 436pp.

COCKERHAM, G. 1930. Some observations on cambial activity and seasonal starch content in sycamore (Acer pseudoplatanus L.). Proc. Leeds Philos. Soc. (Sci. Sect.) 2:64-80.

ESAU, K. 1943. Vascular differentiation in the pear root. Hilgardia 15:299-324.

FEGEL, A.C. 1941. Comparative anatomy and varying physical properties of trunk, branch, and root wood in certain northeastern trees. Tech. Publ. N.Y. State Coll. For. No. 55.

GLOCK, W.S. and SHARLENE R. AGERTER. 1962. Rainfall and tree growth. In. T.T. Kozlowski (ed.) Tree Growth. Ronald Press. New York. 442pp: pp23-56.

HABERLANDT, G. 1914. Physiological Plant Anatomy. MacMillan and Co. London. 436pp.

HARTIG, T. 1878. Anatomie und Physiologie der Holzpflanzen. Julius Springer, Berlin. 412 pp: pp363-368.

JACOBS, M.R. 1936. The effect of wind on trees. Australian Forestry 1:25-32.

JACOBS, M.R. 1939. A study of the effect of sway on trees. Comm. For. Bureau (Australia) Bull. No. 26.

KNIGHT, R.C. 1961. Taper and secondary thickening in stems and roots of the apple. Ann. Report East Malling Res. Sta. for 1960: 65-71.

KNY, L. 1908. Über das Dickenwachstum des Holzkörpers der Wurzelin in seiner Besiehung zur Lotlinie. Ber. Dtsch. Bot. Ges. 26:19-50.

LADEFOGED, K. 1939. Untersuchungen über die Periodizität im Ausbruch und Längenwachstum der Wurzeln. Forstl. Forsøgsv. Danm. 16:1-256.

LAITAKARI, E. 1929. The root system of pine (Pinus sylvestris): a morphological investigation. (In Finnish with 75p. English summary). Acta Forestalia Fennica 33:1-306.

LAITAKARI, E. 1935. The root system of birch (Betula verrucosa and odorata). (In Finnish with 47 p. English summary). Acta Forestalia Fennica 41 (2): 1-216.

LIESE, J. 1924. Beiträge zur Anatomie und Physiologie des Wurzelholzes. Ber. Dtsch. Bot. Ges. 42:91-97.

LYFORD, W.H. and B.F. WILSON. 1964. Development of the root systems of Acer rubrum L. Harvard Forest Paper No. 10.

MOHL, H.V. 1862. Einige anatomische und physiologische Untersuchungen uber das Holz der Baumwurzeln. Bot. Zietung 20: 225-230, 233-239, 269-278, 279-287, 289-295, 313-319, 321-327.

MORROW, R.R. 1950. Periodicity and growth of sugar maple surface layer roots. J. Forestry 48: 875-881.

RICHARDS, P.W. 1957. The Tropical Rain Forest. Cambridge University Press, Cambridge. 450 pp.

RICHARDSON, S.D. 1957. Studies of root growth in Acer saccharinum L. VI. Further effects of the shoot system on root growth. Koninkl. Akad. Weteinsch. Amsterdam, Ser. C. 60: 624-629.

RIEDHARDT, J.M. and A .T. GUARD. 1957. On the anatomy of the roots of apple seedlings. Bot. Gaz. 118: 191-194.

RIEDL, H. 1937. Bau und Leistungen des Wurzelholzes. Jahr. Wiss. Bot. 85: 1-72.

RIGG, G.B. and E.S. HARRAR. 1931. The root systems of trees growing in sphagnum. Amer. J. Bot. 18: 391-397.

SIRÉN, G. 1951. On the biology of undergrown spruce. (In Finnish with 8 p. English summary). Acta Forestalia fennica 58 (2): 1-90.

STOUT, B.B. 1956. Studies of the root systems of decidious trees. Black Rock Forest Bull. No. 15.

TORREY, J.G. 1964. Cellular patterns in developing roots. Symp. Soc. Exp. Biol. 17: 283-314.

WIGHT, W. 1933. Radial growth of the xylem and the starch reserves of Pinus sylvestris: a preliminary survey. New Phytologist 32: 77-96.