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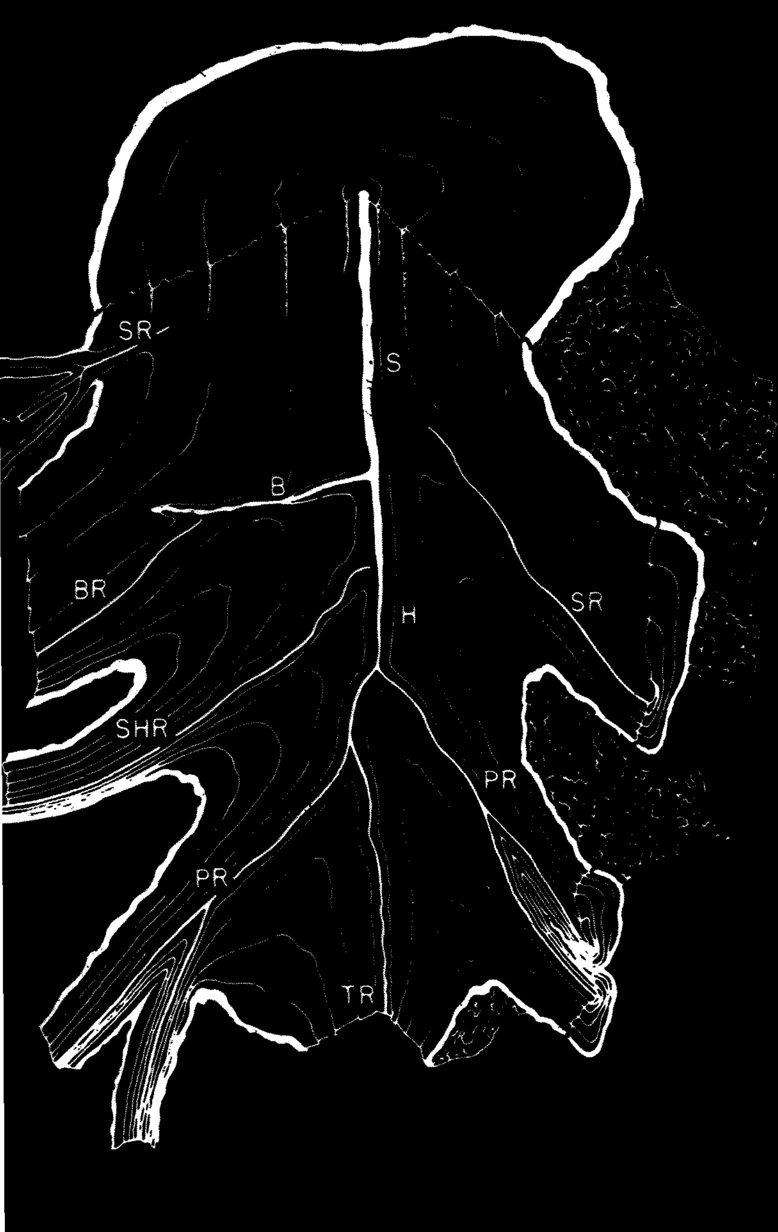

ORIGIN AND DEVELOPMENT OF WHITE SPRUCE ROOT-FORMS

by

J. W. Bruce Wagg

Sommaire en français

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ABSTRACT

Typical root-forms for immature white spruce, *Picea glauca*, in Alberta and the Northwest Territories are an elongated taproot developed on well-drained soils of nearly uniform texture, a restricted taproot on soils with either textural changes between horizons or with compact horizons and monolayered with or without a vestigial taproot on soils with excess moisture near the surface. A fourth multilayered form develops with increasing moss layer and periodic alluvial and lacustrine deposits. Eight variations of the typical root-forms are interpreted according to soils, sites and the spatial organization of roots during morphogenesis. The orientation of roots and the interaction of growth among roots in a system influence form mechanically and physiologically. Secondary roots occur in all root-forms and are a significant part of the restricted taproot and monolayered forms. The multilayered root-form is totally dependent upon the development of secondary roots. The time required to establish individual roots and the interaction between the growth of individual roots within a system are related to the growth of the trunk. Height growth of a tree is small during the period of root establishment and of root replacement.

CONTENTS

ORIGIN AND DEVELOPMENT OF WHITE SPRUCE ROOT-FORMS

by

J. W. Bruce Wagg[1]

INTRODUCTION

The premise that a single root-form is inherent to white spruce[2] is erroneous, as is the concept of a plate-like (monolayered) form of large lateral roots with sinkers to variable depths. While some spruce are monolayered, others vary from a single whorl of laterals with a large elongated taproot to many whorls of superimposed laterals (multilayered) without a taproot. A myriad of intervening forms exist.

To ascribe a single root-form to white spruce is impossible owing to the interaction of different soil properties with changes in site during the life of the tree. Further difficulties arise in explaining root development when soils and sites are considered separately from the spatial organization of roots during morphogenesis.

Variations of root-form which occur among soils with different textural and structural properties and in the presence of excess moisture and anaerobic conditions have been reported often. More recently the role of secondary (often called adventitious) roots has been recognized in the development of the multilayered form after alluvial and lacustrine deposits (Jeffrey 1959; Wagg 1964), growth of mosses (LeBarron 1945; Kosčeev 1953), changes in water tables and soil frost (Krasiljnikov 1956).

Morphogenic variations of root-form result from differences in orientation of individual roots in decayed wood, moss, humus and soil, in numbers and organization of roots at the rootstock and in the growth rates of individual roots.

This paper presents observations on the following aspects of root-form of white spruce:

(1) the occurrence of secondary roots and their role in the development of root-forms;

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[2]Scientific names are listed in Appendix 1.

(2) the influence of (a) soil properties, (b) site modifications during the life of the tree and (c) spatial organization of roots during morphogenesis on the development of form; and

(3) relationships between the development of the root system and the growth of the trunk of the tree.

The illustrated root systems are case histories which show a wide range of root-forms and some variations.

TERMINOLOGY OF ROOTS

Root-form refers to the arrangement of all roots at the rootstock and vertical roots from other roots near the rootstock. The nomenclature of roots attached to the rootstock is expanded from Lemke (1956). Figure 1 shows a composite of white spruce root-forms. Five types of lateral roots are distinguished.

Lateral is applied to lateral roots of the monolayered root-form with a single whorl of laterals, or to lateral roots in general when more precise terminology is not required.

Infralateral is a lateral root in the lowest whorl of lateral roots from the rootstock.

Supralateral is a lateral root in the highest whorl of lateral roots from the rootstock.

Interlateral applies to all roots between the infralateral and supralateral roots. In multilayered root-forms the interlaterals may comprise several whorls of roots and may be further distinguished by numbering the whorls upward.

Bur is a young (1- or 2-year-old) usually secondary root growing from a burl on the rootstock. Bur roots occur in groups and a burl forms from continual die-back and regrowth of roots.

The terminology of oblique and vertical roots is evident in Figure 1. Heart roots originate from lateral roots near the rootstock while proximal roots originate within the rootstock.

The term secondary is used in this paper to describe roots growing from the stems and branches of trees. Primary is used for roots originating below the hypocotyl and adventitious describes roots which develop out of sequence from either primary or secondary roots. Adventitious has been used by various authors to describe roots growing from stem and branches as well as from other roots. Sirén (1950); Veretennikov (1959) *et al.* have retained adventitious in the sense of Büsgen and Münch (1929) by applying the term to roots originating out of sequence from other roots.

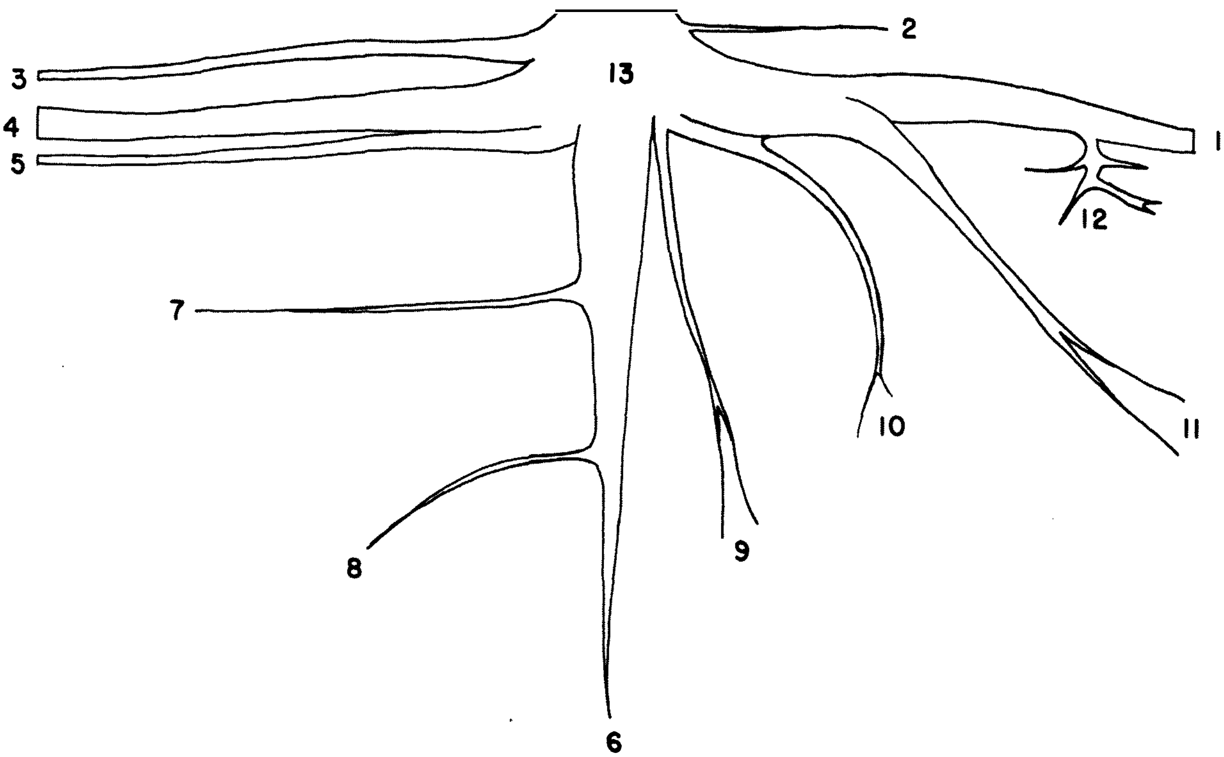

Figure 1. Composite root-form of white spruce showing the following roots: (1) lateral, (2) bur, (3) supralateral, (4) interlateral, (5) infralateral, (6) tap, (7) tap-lateral, (8) tap-oblique, (9) proximal, (10) heart, (11) oblique, (12) sinker, and (13) rootstock.

IDENTIFICATION OF ROOTS

Primary, secondary and adventitious roots are similar in structure and are distinguished only by determining their points of origin. The relation of primary and secondary roots to the seedling stem, hypocotyl and root is shown in Figure 2.

The primary xylem of white spruce roots is usually diarch (Figure 3E) and appears oval in cross section between two large resin canals [Noelle 1910, similar to tamarack (Jeffrey 1917) and black spruce (Stanek 1961)]. Occasionally a root may be triarch (in which the primary xylem is triangular between three resin canals) throughout its length or for a short distance at any place along its length. Tetrarch xylem is rare. No regularity occurs in either the triarch or tetrarch condition.

The diarch xylem usually changes to triarch for a short distance below the base of the hypocotyl [q.v. Norway spruce (Koščeev 1953)]. In some trees it is diarch (Figure 3F) at the base of the hypocotyl.

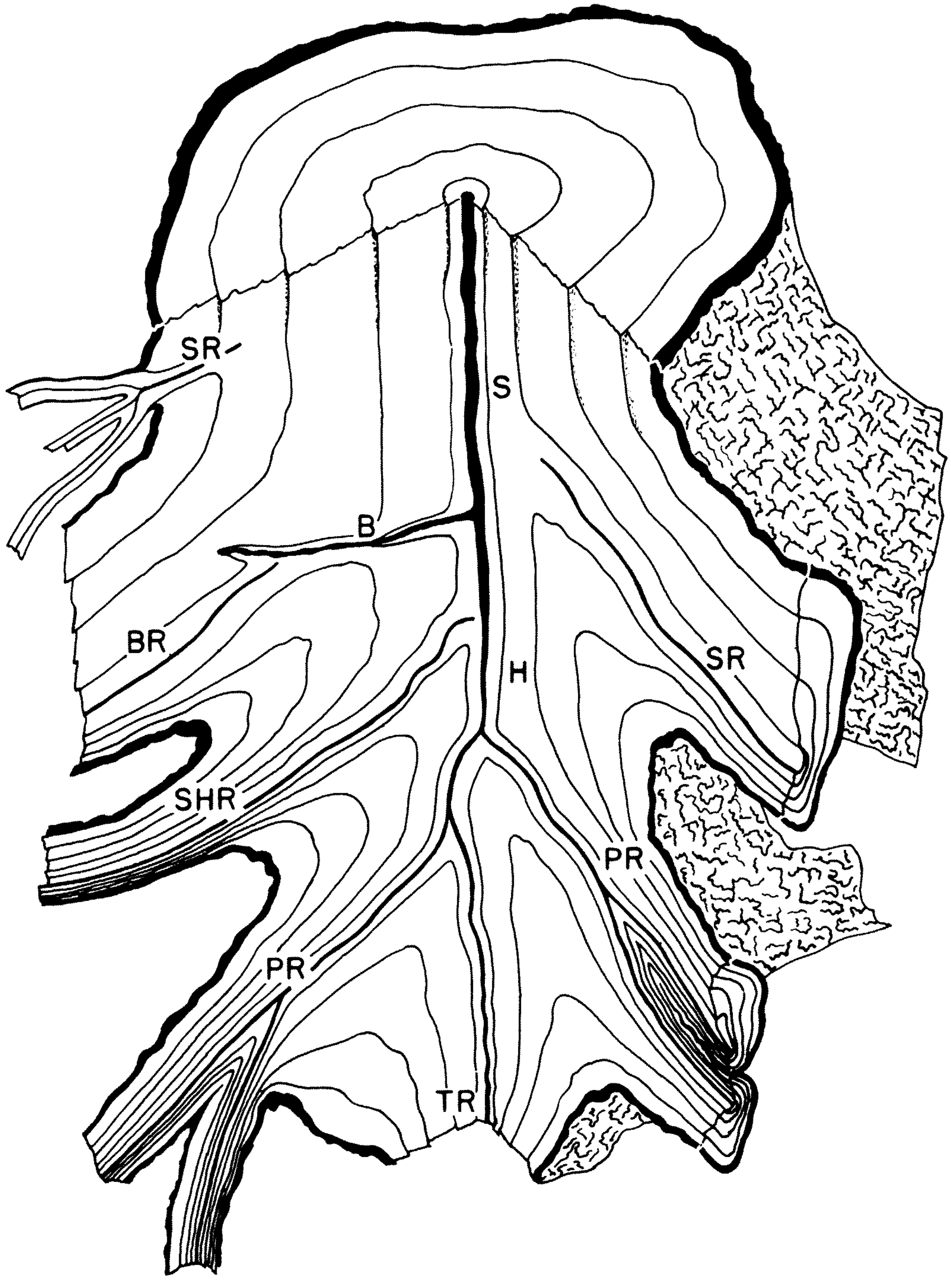

Figure 2. Dissection of rootstock showing roots in relation to hypocotyl (H), *stem* (S) *and branch* (B): *primary root* (PR), *supra-hypocotyl-root* (SHR), *stem-root* (SR) *branch-root* (BR) *and taproot* (TR).

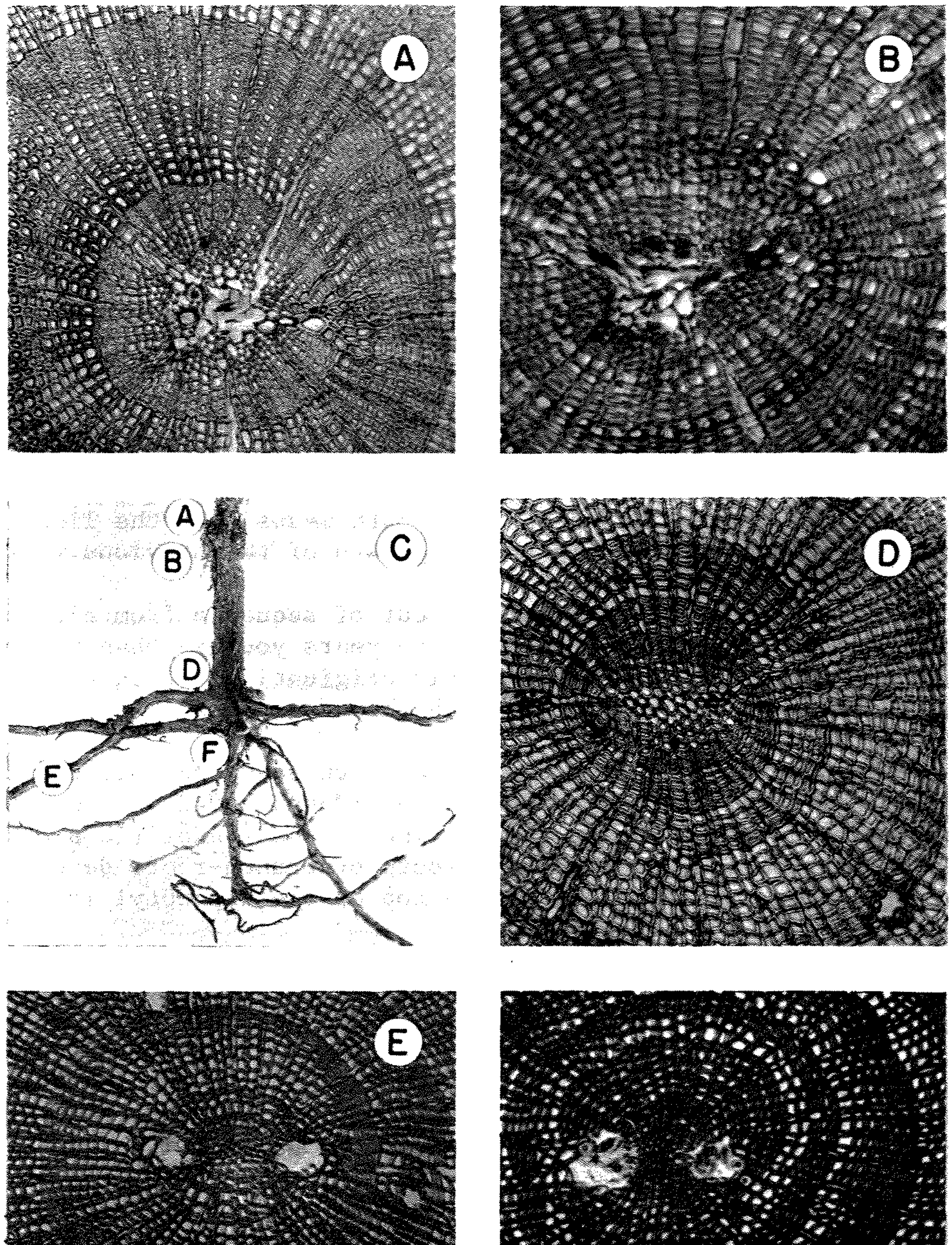

Figure 3. *Cross sections of stem, hypocotyl and roots: A. Stem having small pith (x130); B. Hypocotyl near top with pith-like centre (x110); C. Juvenile tree showing location of photomicrographs (x0.5); D. Hypocotyl near base with diarch xylem devoid of resin canals (x120); E. Lateral root with diarch xylem (x65); F. Tap-root immediately below hypocotyl with diarch xylem, resin canals and indistinct annual rings (x80).*

Within the base of the hypocotyl the resin canals disappear (Figure 3D) and a complicated rearrangement of tissues occurs throughout until (q.v. Dangeard 1892; Hill and de Fraine 1909) a pith-like structure appears (Figure 3B) near the top.

Immediately above the hypocotyl the pith is small and filled with cells (Figure 3A) in contrast to the large pentagonal or polygonal structure found in the upper parts.

When the hypocotyl is overgrown, its upper and lower limits are difficult to ascertain because of the gradation into triarch or diarch xylem at the base and into pith at the top.

Primary roots originate below the hypocotyl and are connected in sequence by two central resin canals to the resin canals of other roots and finally to the taproot. Sequential growth means that the lineal growth of any year is connected directly to the growth of the previous year.

Adventitious roots originate out of sequence from either primary or secondary roots and are two or more years younger than the root to which they are attached. The resin canals originating within the root are connected to those of the root from which they developed.

Secondary roots from dormant buds on stems and branches are connected to the pith by parenchymous tissue (Bannan 1942). Dissections of rootstocks show the resin canals terminating in the annual rings of the wood. Secondary roots are termed stem-roots or branch-roots depending upon the point of origin. A stem-root at the top of the hypocotyl is a supra-hypocotyl-root.

Secondary roots develop on white spruce in many different soils and sites. They develop from the stem and branches of trees when these are covered by humus, moss or soil (Bannan 1940; Jeffrey 1959; Wagg 1964). Secondary roots also occur on other species of spruce (LeBarron 1945; Meyer 1938; Nägeli 1930; Koščeev 1952, 1953; Hustich 1954; Denisov 1960 *et al.*) and root-form differs from white spruce only in degree.

Secondary roots develop throughout much of the life of a tree and have been observed on 2-year-old seedlings and on 135-year-old trees (Figure 4). The most frequent occurrence is probably between 3 and 20 years.

MATERIALS AND METHODS

The 12 root systems were selected from 60 immature trees taken from a variety of sites in Central Alberta and the Northwest Territories. These were supplemented by observation of several hundred root systems exposed on recent burns.

Figure 4. Secondary roots growing from the trunk of a 135-year-old white spruce into moist cone scales.

Sample trees were from the dominants in a stand and the root systems were exposed by removing the L-H and mineral soil layers for a radius of 3 feet from the rootstock. The lateral roots were sawn-off at this distance; taproot, sinkers and obliques were then excavated to a point where their diameter was 0.1 inch; the tree was then winched out.

The trunk was cut from the rootstock and measured for total height. Sections for stem analysis were taken at ground level, 9 inches, 18 inches and every 18 inches to the top. Morphogenesis of individuals was based on dissections of their rootstocks which were compared with seedling and juvenile root systems.

The individual roots of each system were sectioned for age at the rootstock, and at the 6, 12, 18, 24, and 36-inch radii. The rootstock was sectioned horizontally at intervals of 0.75 inch and the age of each section recorded. The origin of the individual roots were traced in the rootstock.

Several techniques were often required to determine the origin of roots, particularly when secondary roots originated at the top of the hypocotyl early in the life of the tree. The resin canals of an individual root were traced, using a chisel and a dissecting microscope, either to the junction of the resin canals of the taproot or to the termination in the annual rings of the rootstock. When there is considerable die-back of a root in the seedling stage and formation of burl tissue, the resin canals lead to other overgrown and contorted resin canals which are difficult to separate and trace to the taproot.

The central core of the rootstock was sometimes sectioned to determine the presence of pith or root structure, as the pith of both stems and branches may show a nodal structure with distinct demarcation of growth between years, a feature not found in hypocotyl or root.

Annual growth rings are usually present in roots, and partial or indistinct rings often occur. However there is great variation in the size of rings which at times makes the determination of the age of some roots difficult, if not impossible. Occasionally growth rings are found near the rootstock, are absent for a distance and present again further along the root.

TYPICAL ROOT-FORMS

Variations in root-form of conifers arising from textural and structural differences among soils and modifications of site by excessive moisture and growth of moss are well documented: Aaltonen 1920; Laitakari 1927; Vater 1927; Pöntynen 1929; Priehäusser 1939; Bannan 1940; Koščeev 1953; Krasiljnikov 1956; Horton 1958; Köstler 1962; Wagg 1964.

Secondary roots account for the many different root-forms of spruce and for changes in form which occur during the life of a tree. The root system of a juvenile tree with four large laterals and a taproot may grow in one of several different ways. Three examples are presented.

1. No change in form occurs when all roots grow at similar rates and secondary roots do not develop. The four laterals form an incomplete whorl around the rootstock and the elongated taproot-form results.

2. Growth of the taproot may be restricted by the development of secondary roots. When two lateral roots are separated by a wide gap on the rootstock and the trunk is connected directly with the taproot, secondary roots may develop in this area. The addition of one or more secondary roots to the four primary roots of the juvenile completes a whorl of lateral roots around the rootstock. This reduces, and may eventually stop, the growth of the taproot. The restricted taproot-form of the immature tree is composed of large laterals and a small taproot.

3. When a build-up of moss or alluvium occurs around the trunk of the juvenile tree, secondary roots develop in this layer above the primary roots. Should the secondary roots grow to a large size, the primary lateral roots and taproot will slow down in growth and may eventually die. With continual re-rooting, the immature tree develops a multilayered root-form of several superimposed layers of lateral roots.

Elongated Taproot-form

The elongated taproot-form of Tree I (Appendix 2 and Figure 5) developed in well-drained aeolian sands. The root system has four large lateral roots (A, B, C and D) and a large taproot (M) which is connected to the trunk between A and D. Young laterals (e.g., F, G, H) occupy the gap on the rootstock between A and D. All roots are of primary origin.

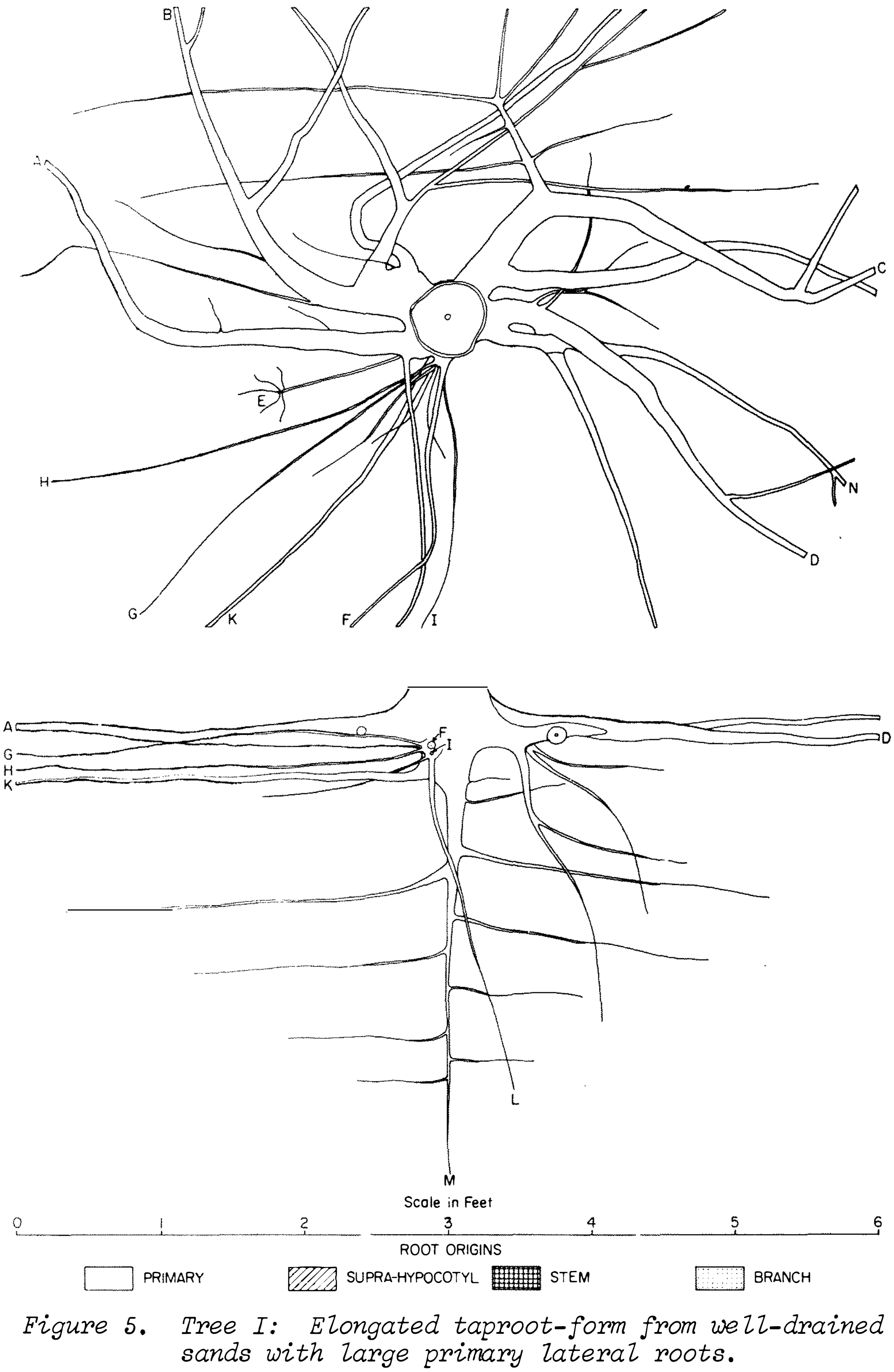

Figure 5. Tree I: Elongated taproot-form from well-drained sands with large primary lateral roots.

The tree was established on mineral soil and developed a long taproot (M), tap-lateral (K) and two laterals (B and C) by the 15th year (Figure 8A). With development of A and D, all large roots except N were present at the 20th year. The young laterals developed from bur roots after the 33rd year. The taproot with numerous tap-laterals grew steadily in length from an early age. It was neither restricted by the aeolian sands or affected radially by an overgrowth of laterals. The taproot was connected, on part of its periphery, to the trunk through a gap between laterals A and D. The young laterals in the gap did not restrict the growth of the taproot as the underlying tap-lateral K was expanding in growth. The thin and dry L-H layer was not suitable for the development of secondary roots.

Spruce with elongated taproots and without secondary roots are uncommon. Usually the taproot is restricted and branched at variable depths. While secondary roots may develop they do not commonly grow to a large size on well-drained soils.

Restricted Taproot-form

As the tree matures the elongated taproot often becomes a restricted taproot. Growth restriction may be owing to either soil texture, structure, moisture and frost (see Dahurian larch and frost, Umkin 1958), or because of rapidly growing lateral roots. Examples below show the influence of soil texture and soil structure on taproot and proximal root growth.

Restricted by Soil Texture

The restricted taproot-form of Tree II (Appendix 2 and Figure 6) resulted from a textural change between soil horizons. The root system has four large laterals (A, B, C and G) and an aborted and distally contorted taproot (N); B and C are secondary roots. A number of bur roots are in the gaps between the large laterals.

Morphogenesis of the system is shown in Figure 8B. The tree, established on mineral soil, developed a large taproot (N). At 15 years the tree had five primary laterals (A, D, G, H and O), two secondary laterals (B and C) and a proximal (E). The primaries A and G grew to become the large roots along with the secondaries B and C in the immature system.

The upper soil layers were favorable for growth of the taproot, particularly tap-laterals. Further vertical development of the taproot was restricted by the mechanical action of the gravel layer. Although secondary roots formed in the feather moss and humus, they did not grow large enough, between laterals C and G, to restrict growth of the taproot.

Restricted by Soil Structure

The restricted proximal roots of Tree III (Appendix 2 and Figure 7) developed in Solonetzic soil. The system of supralateral, infralateral and proximal roots resembles a bilayered and restricted taproot-form. The supralaterals were increasing in growth, and organized into five groups: A, B-C, E, D and P-Q. The infralaterals, K, L, O and F were growing steadily;

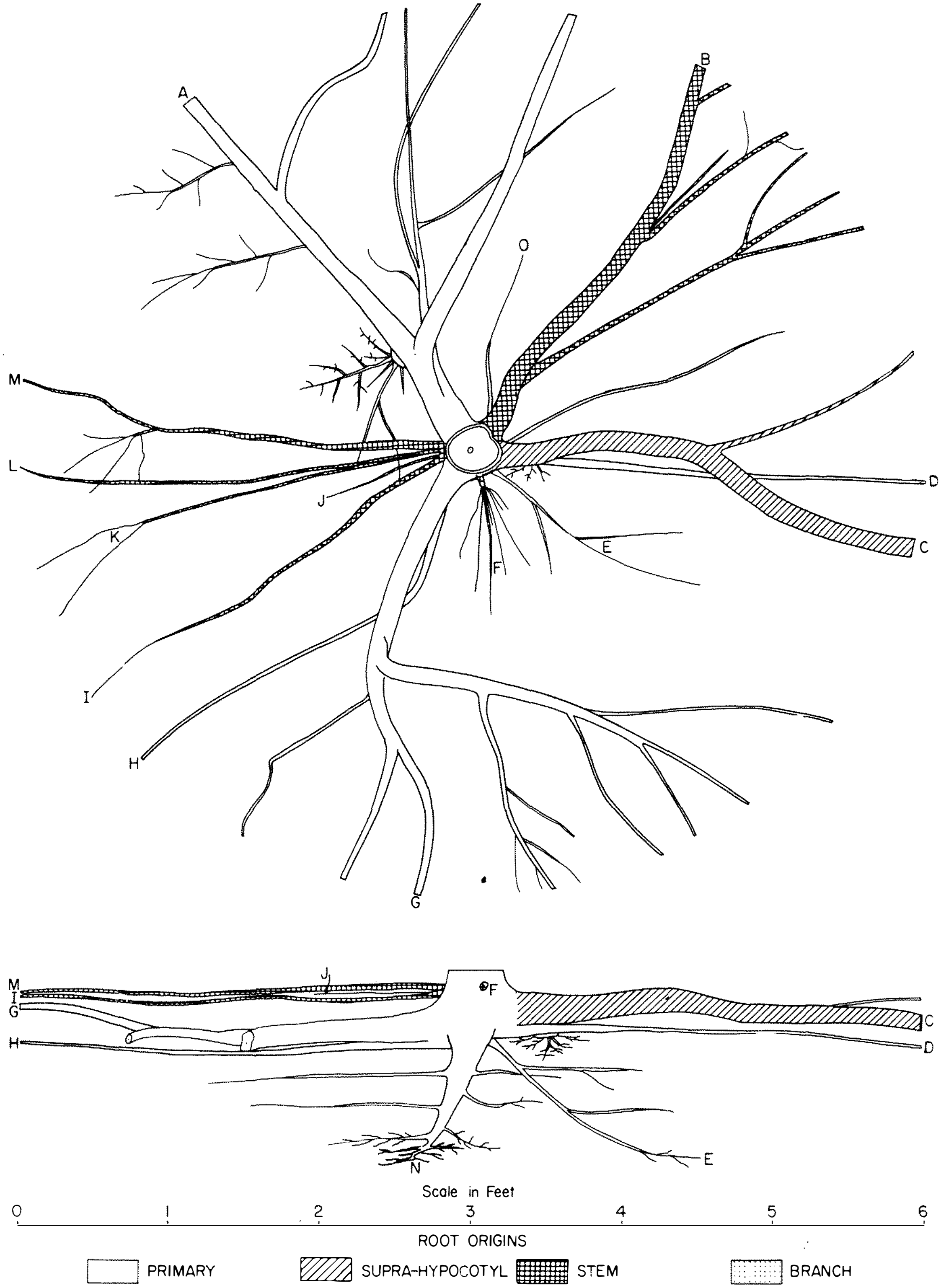

Figure 6. Tree II: Restricted taproot-form caused by a gravel layer with large primary and secondary lateral roots.

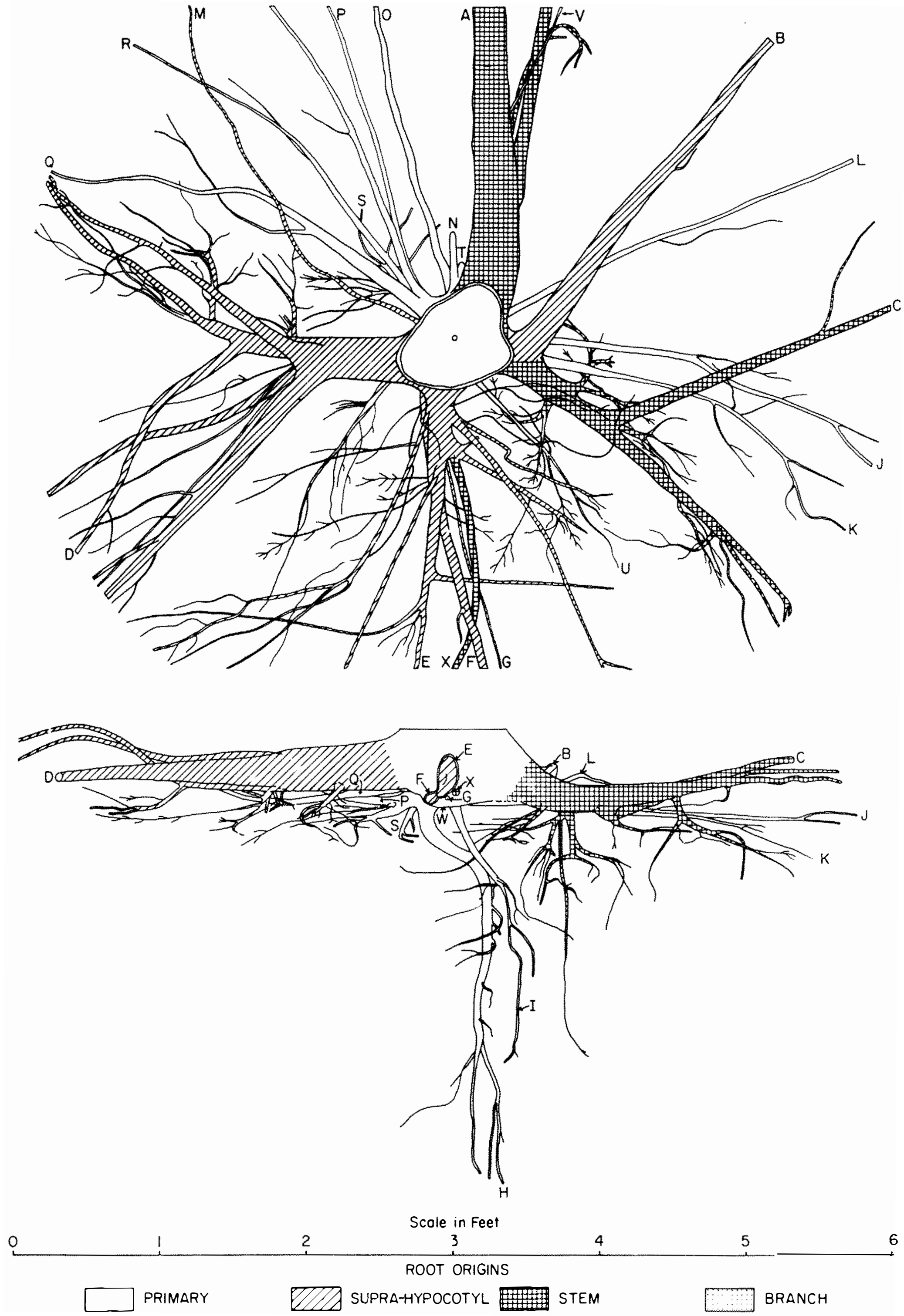

Figure 7. Tree III: Restricted proximal roots from compacted Solonetzic soil with large secondary lateral roots.

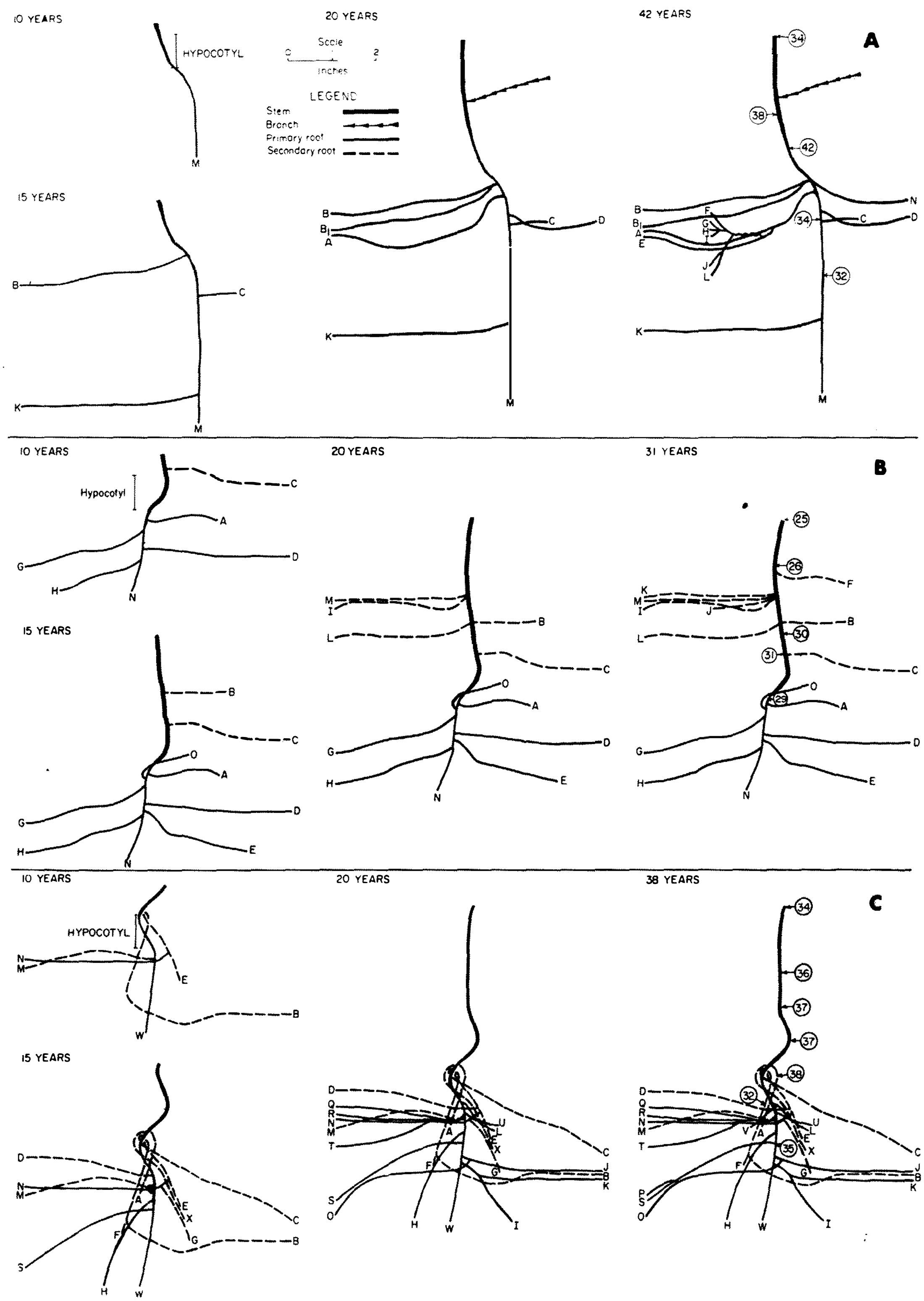

Figure 8. Anatomical origin and chronological development of roots for Tree I(A), Tree II(B) and Tree III(C).

G, J, R and V were decadent; and T, H and N were dead. The proximal roots were contorted proximally and capillaceous distally. The taproot (W) persists as a partially overgrown stub at the base of the rootstock. All large supralaterals are of secondary origin.

Stages in morphogenesis are shown in Figure 8C. The tree developed a taproot (W) and primary (N) and secondary (B, E and N) lateral roots by 10 years. The proximal roots (H, I and S) developed from the taproot between the 11th and 12th years and the taproot died and rotted away. Five secondaries (A, B, C, E and D), which grew into large supralaterals, developed by the 15th year. By the 20th year the primary infralaterals O, Q and R developed in the gap between A and D to close the connection between the proximal roots H and I and the trunk. Later when the proximal roots became decadent they were connected to the trunk through contorted tissue at the rootstock.

Proximal roots, contorted by the blocky B horizon, developed capillaceously distally in the compacted and columnar structured C horizon. A build-up of humus about the seedling stem accounts for the development of secondary roots. The hypocotyl was S-shaped (Figure 8C) bringing the stem in contact with the humus at an early age.

Other Factors

Taproots are often restricted at some period during morphogenesis through either horizontal growth in the seedbed or overgrowth by lateral roots. Seedlings will develop contorted taproots on decayed wood, raw humus and poorly-drained seedbeds. The horizontal growth results from the higher moisture content of decayed logs, the improved nutrient and moisture content of the mineral soil-humus interface, impediments in humus and decayed wood, and anaerobic conditions of poorly-drained soil.

Seedlings with elongated taproots may exhibit a restricted taproot in the immature tree. In such cases, the laterals develop rapidly, encircle the rootstock and retard the growth of the taproot. The laterals and trunk continue to enlarge at a faster rate than the taproot until a restricted taproot-form develops.

Monolayered Root-form

Immature root systems occur without vestigial taproots. These originate from seedling systems in which the taproot is either aborted, contorted and aborted, or degenerate at the rootstock. The lateral roots have either overgrown or outlived the taproot. They are described according to the form in the seedling and dwarf which is an old tree of seedling size.

Developed from Aborted Taproot of Juvenile Tree

The monolayered or partially bilayered root-form of Tree IV (Appendix 2 and Figure 9) resulted from overgrowth of the aborted taproot in the juvenile tree growing in shallow soil. The supralaterals A, C, D, E, F, G and H, which are of primary and secondary origin, form a complete whorl around the root-stock. The infralaterals B and I form a partial second whorl. No taproot is present.

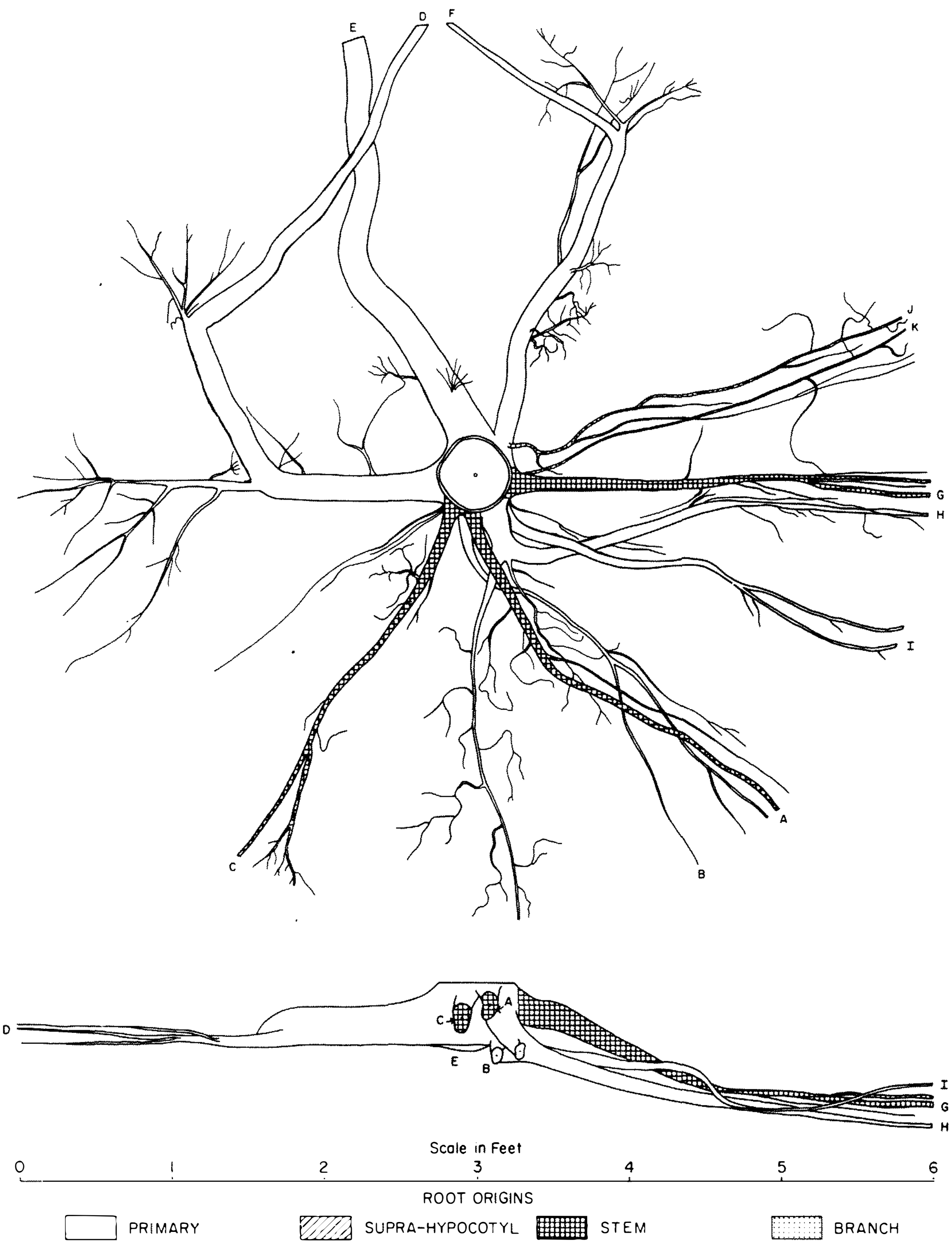

Figure 9. Tree IV: Monolayered (partially bilayered) root-form with large primary and secondary lateral roots which overgrew aborted taproot of juvenile tree.

The monolayered form developed from the restricted taproot-form of the juvenile tree. By the 10th year (Figure 12A) the aborted taproot (L) and the primary laterals D, H and F developed, and by the 15th year the remainder of the primary laterals B, E and I. The primaries constituted the large roots of the immature system. With rapid tree growth between the 15th and 20th years, the primaries overgrew the taproot which aborted due to excessive moisture in the Cg horizon. Later, with an increase in the depth of the feather moss and humus layer, the secondary roots A, C, G, J and K developed.

Tree IV is a compressed variant of the monolayered form and is characteristic of trees growing on shallow soils and depressions in bedrock where vertical penetration of roots is prevented. The proximal portion of lateral roots are rounded or horizontally oblong rather than a vertical I-shape in cross section. Superimposed laterals are compressed and sometimes coalesced; vertical roots are contorted and undulated to follow the contours of the bedrock. The origin of the roots will vary but systems composed of primary and secondary roots are found most commonly.

Developed from Contorted and Aborted Taproot of Seedling

The monolayered root-form of Tree V (Appendix 2 and Figure 10) developed from a contorted and aborted taproot of the seedling growing in humus.

The root system has supralateral, infralateral and proximal roots of primary and secondary origin. Of the five supralaterals which form a complete whorl around the rootstock, A and H are primary roots and C, D and E are secondary roots. The small supralaterals G and J are secondaries. The infralaterals B, I and K and the proximals L and F are primaries. A sinker from H appears on the diagrams as a proximal. The rootstock of another tree caused the bilateral orientation of roots A and D.

Morphogenesis of the root system is shown in Figure 12B. By the 10th year the tree had a contorted and aborted taproot (M) which developed in burned humus of the L-H layer and a single primary lateral root (K). Other primaries (A, B, H and I) and one secondary (C) developed before the tree was 15 years old. The taproot was overgrown by roots A and B. The secondary laterals B and J, of which B grew to a large size, developed in the 17th year and E in the 29th year. The proximal roots L and F developed in the 22nd and 24th years and, with the exception of E and G, were the youngest roots in the system. Proximal and sinker roots were short, terminating in the Ae horizon as a result of fluctuating moisture.

While the monolayered or partially bilayered root-form, without a vestigial taproot, appears uncommonly, the restricted taproot and especially the contorted taproot variant occurs often on Podzols and Gleysols. Wet soil underlying humus precludes vertical growth of roots; sinkers are aborted and branched and taproots contorted and aborted in the humus or upper mineral soils (cf. Norway spruce, Kreutzer 1961). Secondary roots develop at an early age in the moist humus. Typical monolayered forms show rapid growth of primary and secondary roots which either choke the growth or completely overgrow the taproot at an early age.

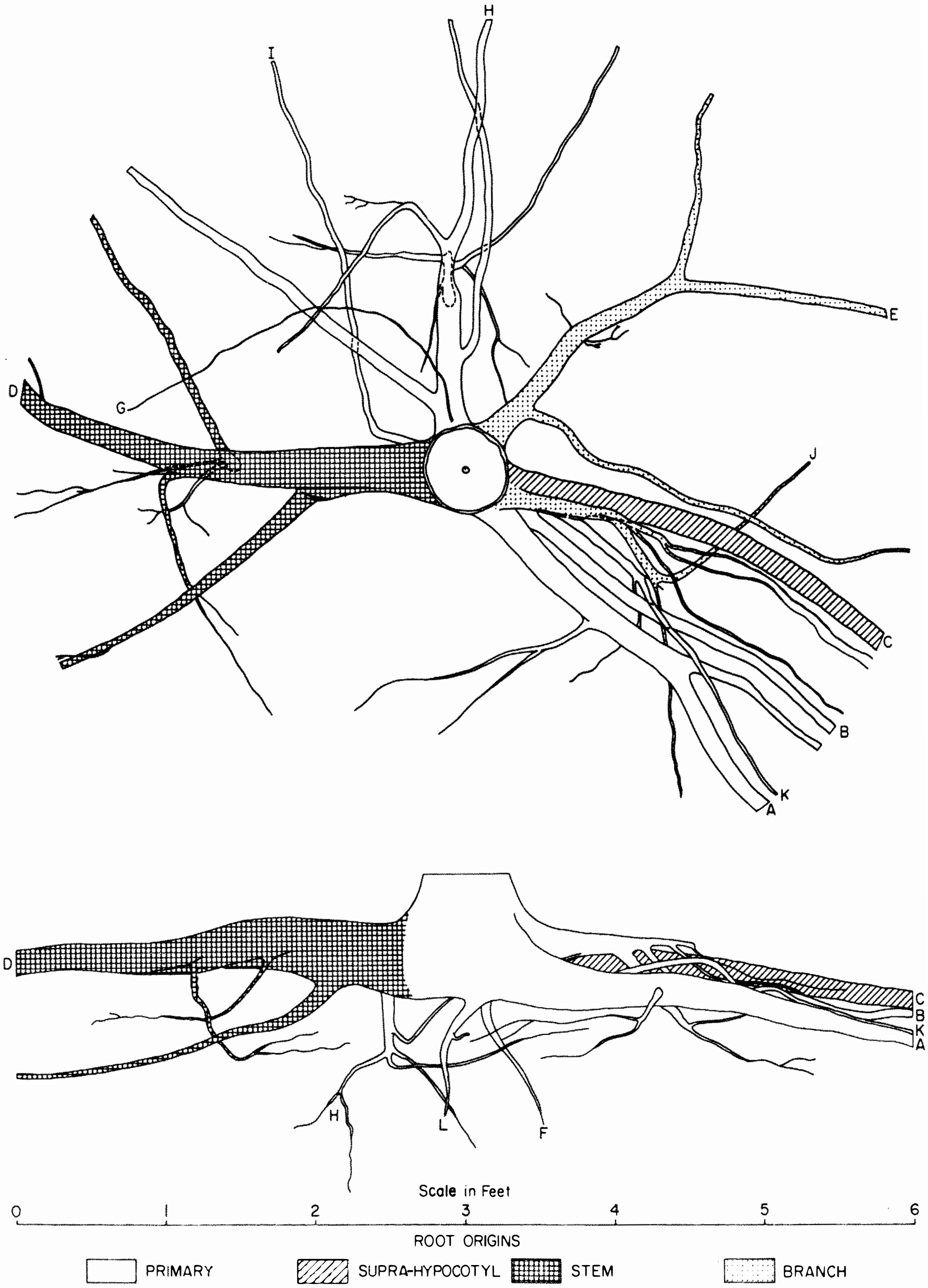

Figure 10. Tree V: Monolayered root-form with large primary and secondary lateral roots which overgrew contorted and aborted taproot of seedling.

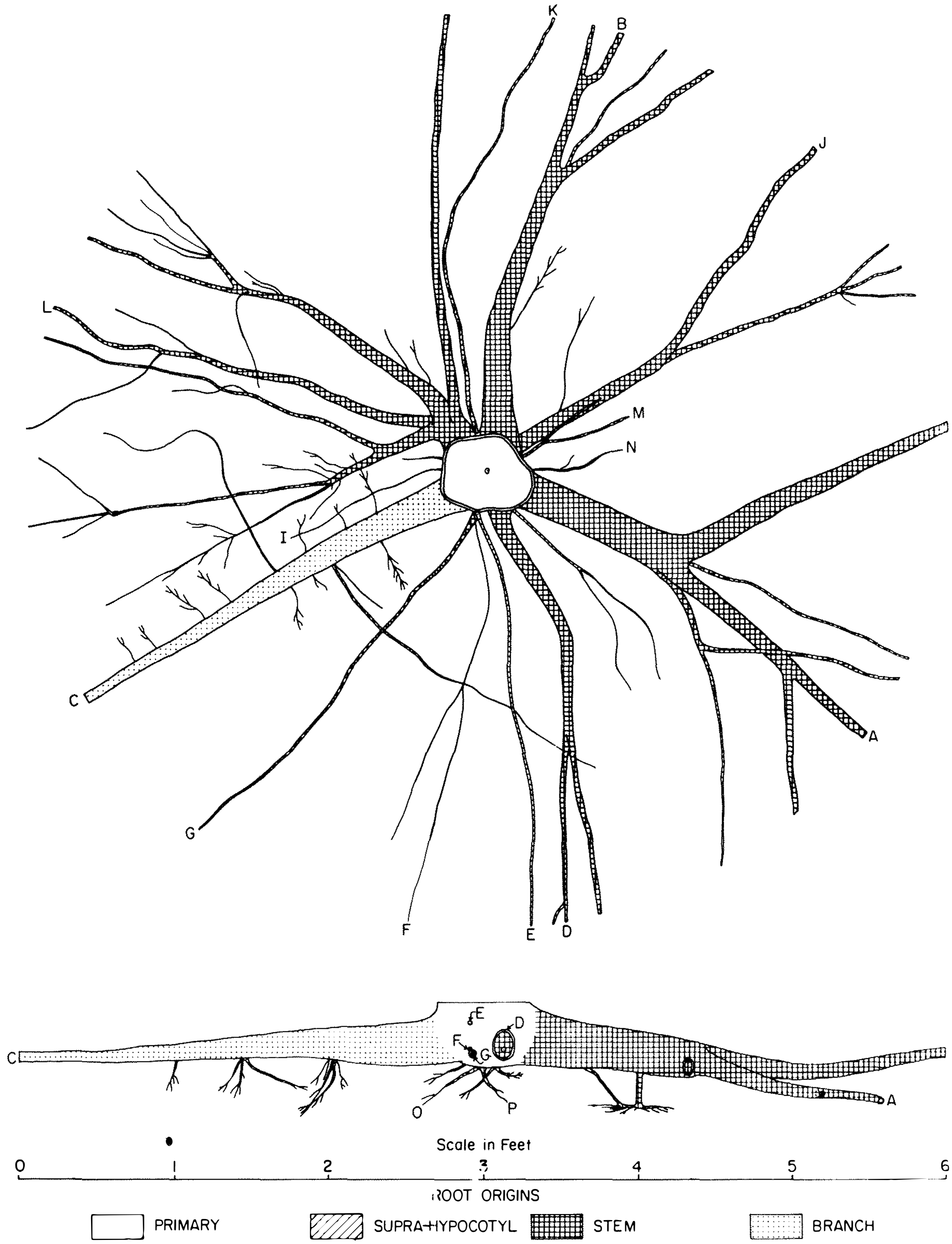

Figure 11. Tree VI: Monolayered root-form with large secondary lateral roots resulted from degeneration of primary roots of dwarf tree in waterlogged soil.

Developed from Degenerate Taproot of Dwarf

The monolayered root-form of Tree VI (Appendix 2 and Figure 11) resulted from the degeneration of the primary root system in the presence of a fluctuating water table. The root system is comprised entirely of secondary roots which include the six large laterals (A, B, C, D, J and L) and a number of small lateral roots. The laterals were monolayered and distributed evenly around the rootstock. The longest sinkers terminate in numerous contorted sinker-laterals.

Seedlings growing on thin burned humus or on the mineral soil horizon of Gleysolic soils develop small primary root systems, (cf. black spruce in sphagnum, Hustich 1954). With growth of feather moss, secondary roots develop at an early age (3-5 years) and the primary roots cease to grow owing to excessive soil moisture. With continued growth of feather moss, successive re-rooting occurs from higher on the stem and the lower roots decay in the zone of fluctuating moisture.

Morphogenesis is shown in Figure 12C. None of the roots, of the immature tree, developed by the 15th year and only two of the secondary lateral roots (C and L) developed by the 20th year. Later the primary roots disintegrated and the taproot (Q) became overgrown and embedded in the rootstock by the growth of the supralateral roots on the surface of the Ae horizon. Sinkers developed in the Ah and terminated on the surface of the gleyed B horizon.

Multilayered Root-form

Modifications in site after seedling establishment have a marked influence on root-form. The previous systems show that the form remained unchanged when secondary roots developed in a small amount of humus around the trunk. The development of secondary roots in conjunction with more pronounced site changes leads to the multilayered form.

Whether the multilayered form is poorly developed or well developed depends upon the amount of change in site and the development of secondary roots upward on the stem of the juvenile tree. Gradual increases in depth of moss and humus produce poorly-developed forms, whereas rapid increases in the depth of the humus layer accompanied by a rise in the water table produce well-developed forms. The well-developed multilayered forms were also found on areas subject to periodic thick alluvial or lacustrine deposits.

Developed with Growth of Sphagnum

The poorly-developed multilayered root-form of Tree VII (Appendix 2 and Figure 13) developed in sphagnum. The system has two vertically distinct whorls of laterals and a contorted and divaricate taproot (J). The supralaterals A, B, C, D, E and I are of secondary origin. The infralaterals G, H and L are primary roots and F and K secondaries. The largest lateral (L) is of primary origin.

The tree was established on decayed wood, and by the 10th year (Figure 15A) the primary laterals G, H and L, taproot J, and secondary root

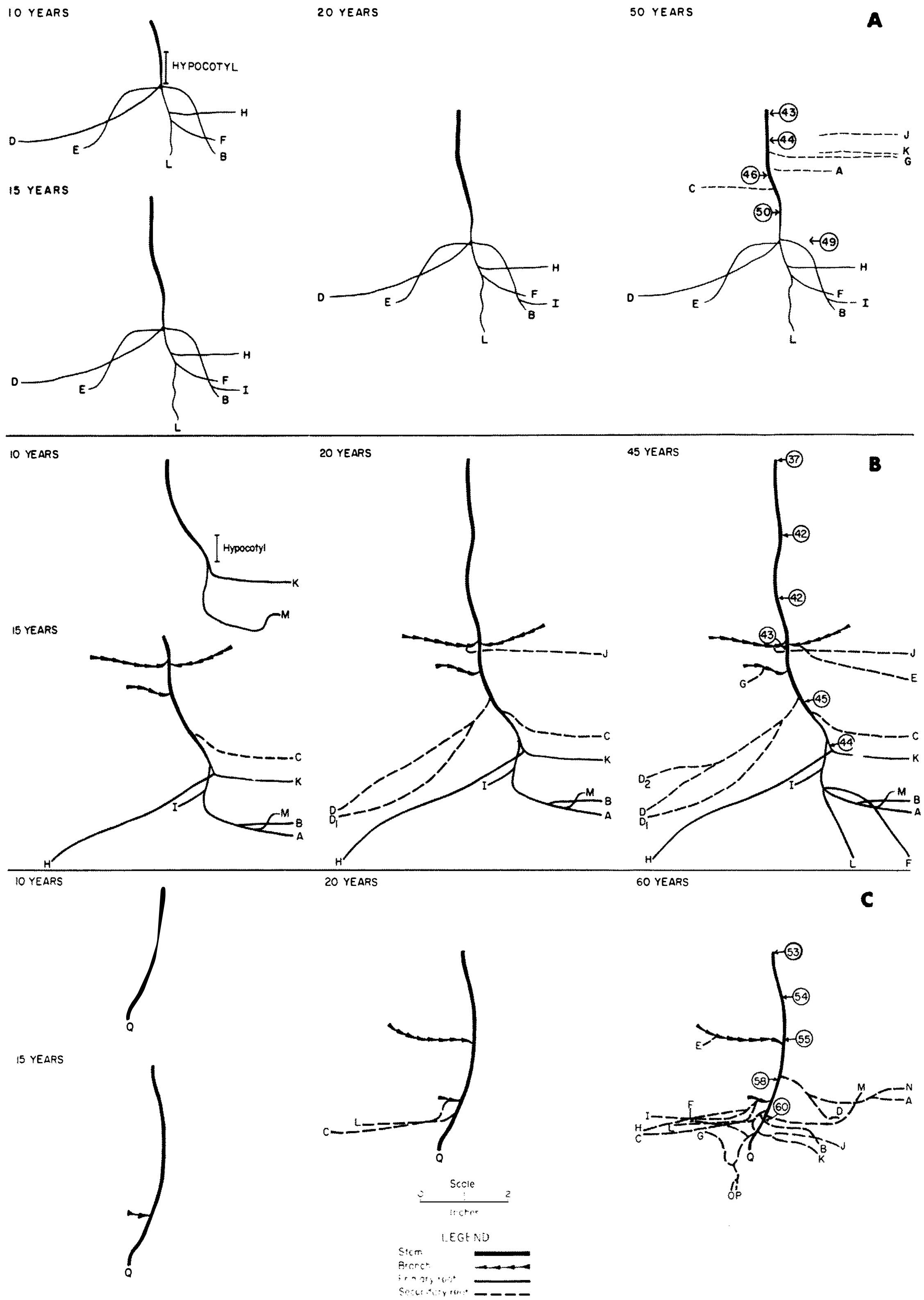

Figure 12: Anatomical origin and chronological development of roots for Tree IV(A), Tree V(B) and Tree VI(C).

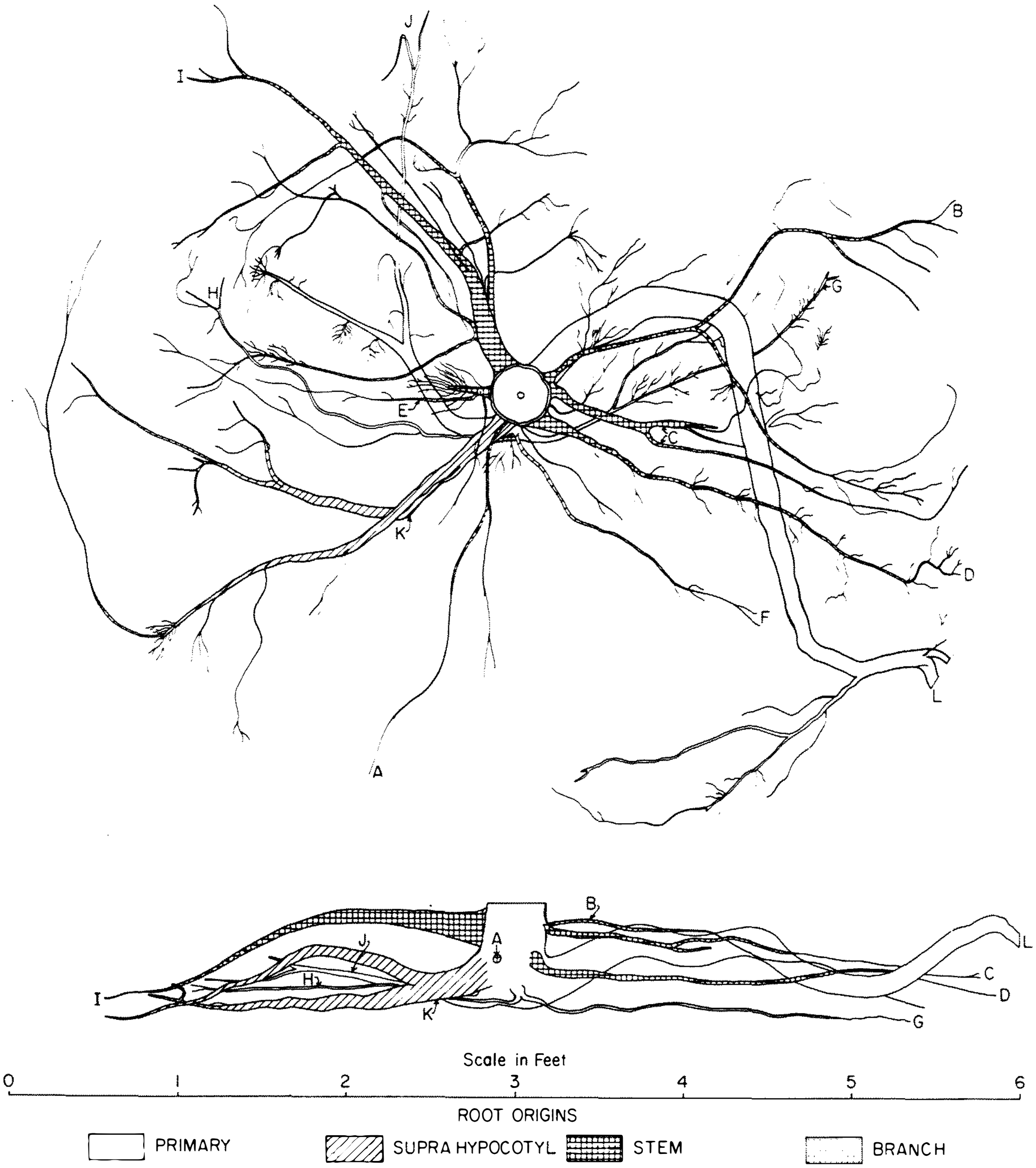

Figure 13. Tree VII: Multilayered root-form with large primary and secondary lateral roots and contorted taproot from sphagnum.

K developed. As sphagnum enveloped the stem, roots D and I developed by the 20th year and small secondaries A, B, C and E after this time. The lateral roots ranged in age from 33 (G) to 8 (A) years. The taproot continued to grow in decayed wood.

Similar root systems are found on feather moss and humus sites except that the supralateral and infralateral roots are vertically overlapped at the rootstock. The multilayered form grades into the monolayered form (Tree IV, Figure 9).

Developed with a Rising Water Table

The multilayered root-form of Tree VIII (Appendix 2 and Figure 14) developed with a gradual rise in the water table and an increase in the depth of the humus and feather moss layer. The vertically compact system has seven whorls of lateral roots. All roots, except W and X, are of secondary origin. The size of roots in each whorl is graded upwards with the infralaterals being the smallest and the supralaterals the largest. The infralaterals and a number of interlaterals are dead. As none of the whorls completely encircle the rootstock, there is a gap between the laterals of one whorl and the whorl below. The live interlaterals show decadence and the supralaterals a steady rate of growth.

Morphogenesis is shown in Figure 15B. The tree became established on mineral soil or thin humus and developed a small primary root system (W and X). As the moss and humus layer grew thicker, the tree rerooted from the stem and branches. The cyclical processes (of re-rooting, growth of moss and re-rooting) continued and secondary roots were still developing from the trunk near the surface of the moss.

Continued growth of feather moss progressively delayed the dissipation of soil frost in the spring and the water table rose nearer the surface. Dead roots persisted on the lower half of the rootstock: the lowest ones, being continually in waterlogged soil, were resin impregnated; and the upper dead roots, in the region of a fluctuating water level, contained in a fibrous decay.

Black spruce and tamarack developed a similar multilayered form on sites with a rising water table and on sphagnum. The form was uncommon to white spruce on sphagnum sites with high water tables and thick layers of moss since most trees, which were rooted on hummocks or decayed logs, had either a poorly-developed multilayered or monolayered form.

Developed after Lacustrine and Alluvial Deposits

The well-developed multilayered root-form of Tree IX (Appendix 2 and Figure 16) resulted from two different lacustrine deposits. The system has six superimposed whorls of lateral roots of which interlaterals A, F, H and B near the top of the rootstock are the largest. All roots are of secondary except the contorted taproot I and the infralateral D.

The tree became established on a 2-inch humus layer. By the 5th year a contorted taproot (I) developed in the underlying sands and an infralateral (D) in the humus. Lacustrine sands were deposited to a depth of 31 inches in the 15th year and several large secondaries developed by the 20th year in the upper part of this deposit. A further 3-inch deposit occurred in the 30th year in which the whorl, composed of R, Q and several bur roots, developed.

The morphogenesis is not typical of multilayered systems in alluvial deposits. Instead of one thick deposit several thin alluvial deposits usually occur during the life of the tree. Secondary roots may develop in each successive deposit. The roots in each superimposed whorl

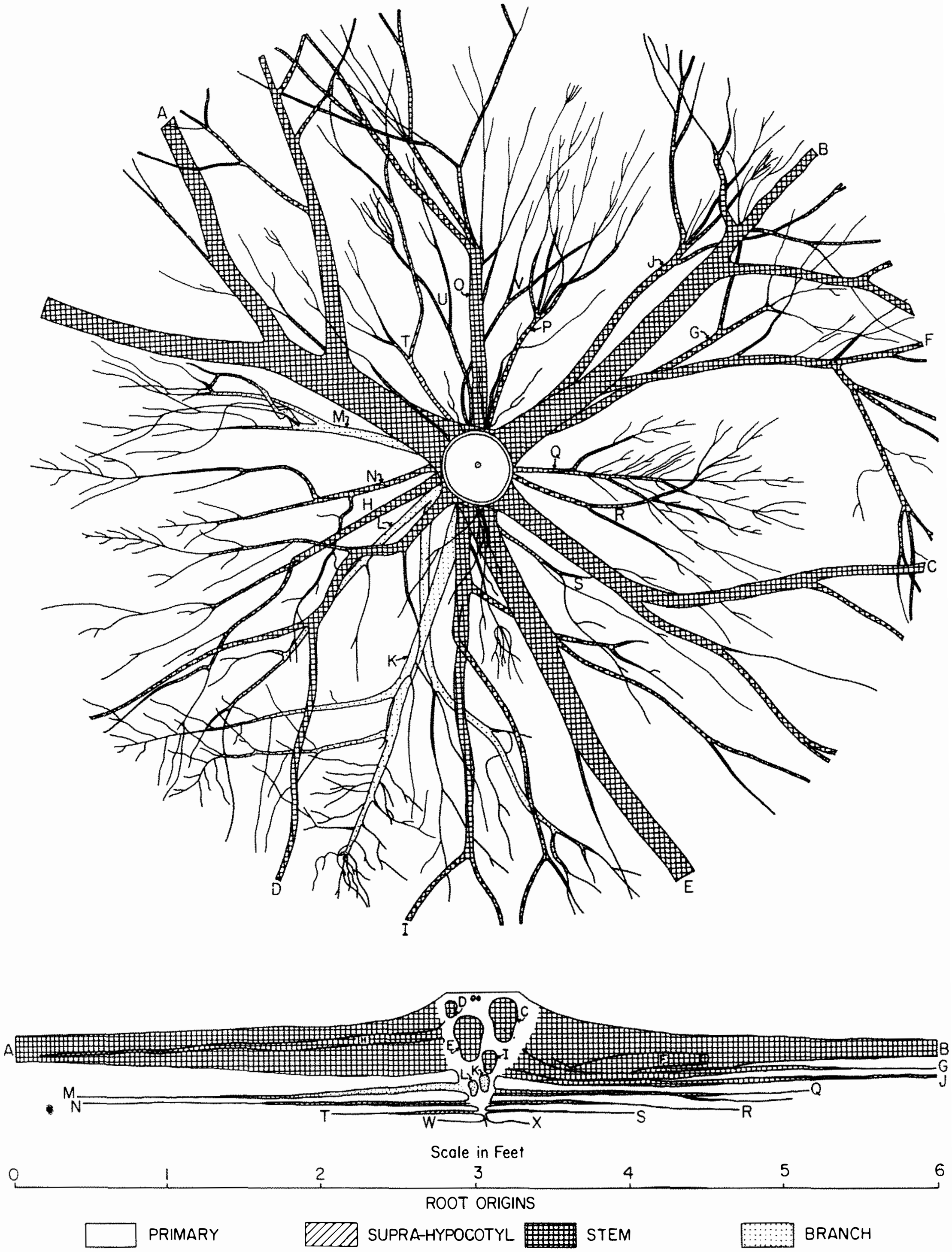

Figure 14. Tree VIII: Multilayered root-form with large secondary lateral roots which developed with a gradual rise in the water table and increase in depth of humus and feather moss.

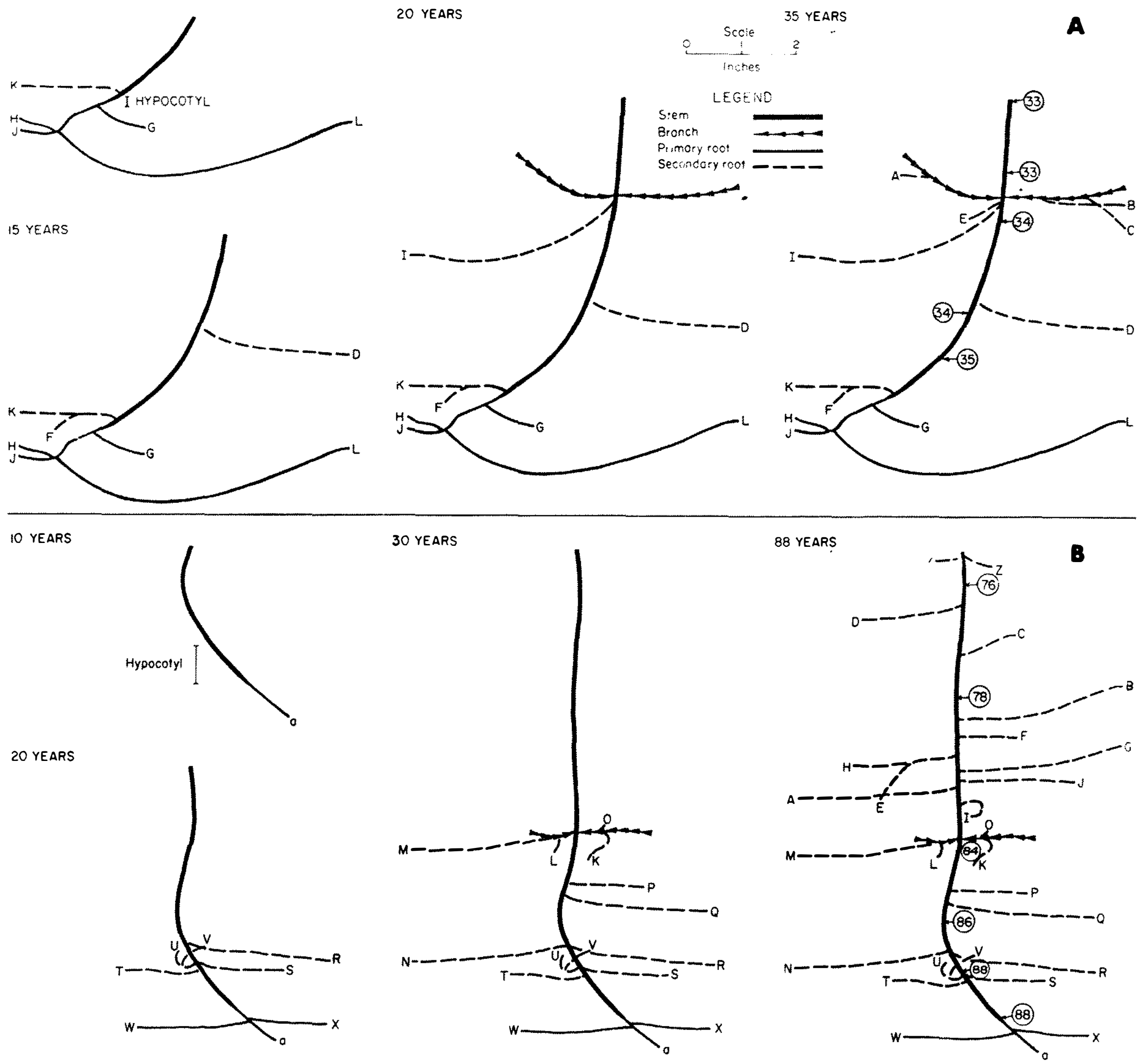

Figure 15. Anatomical origin and chronological development of roots for Tree VII (A) and Tree VIII (B).

are younger and grow to a larger size than those in the whorl below (vid. Tree VIII). The secondary roots of Tree IX developed about the time the 31-inch layer was deposited.

Well-developed multilayered root-forms are common to white spruce and balsam poplar growing on sites subject to periodic alluvial deposits (q.v. Jeffrey 1959; Wagg 1964). They were observed on the alluvial flats of the Peace, Slave and Liard Rivers in the Northwest and Yukon Territories and have been seen throughout Alberta.

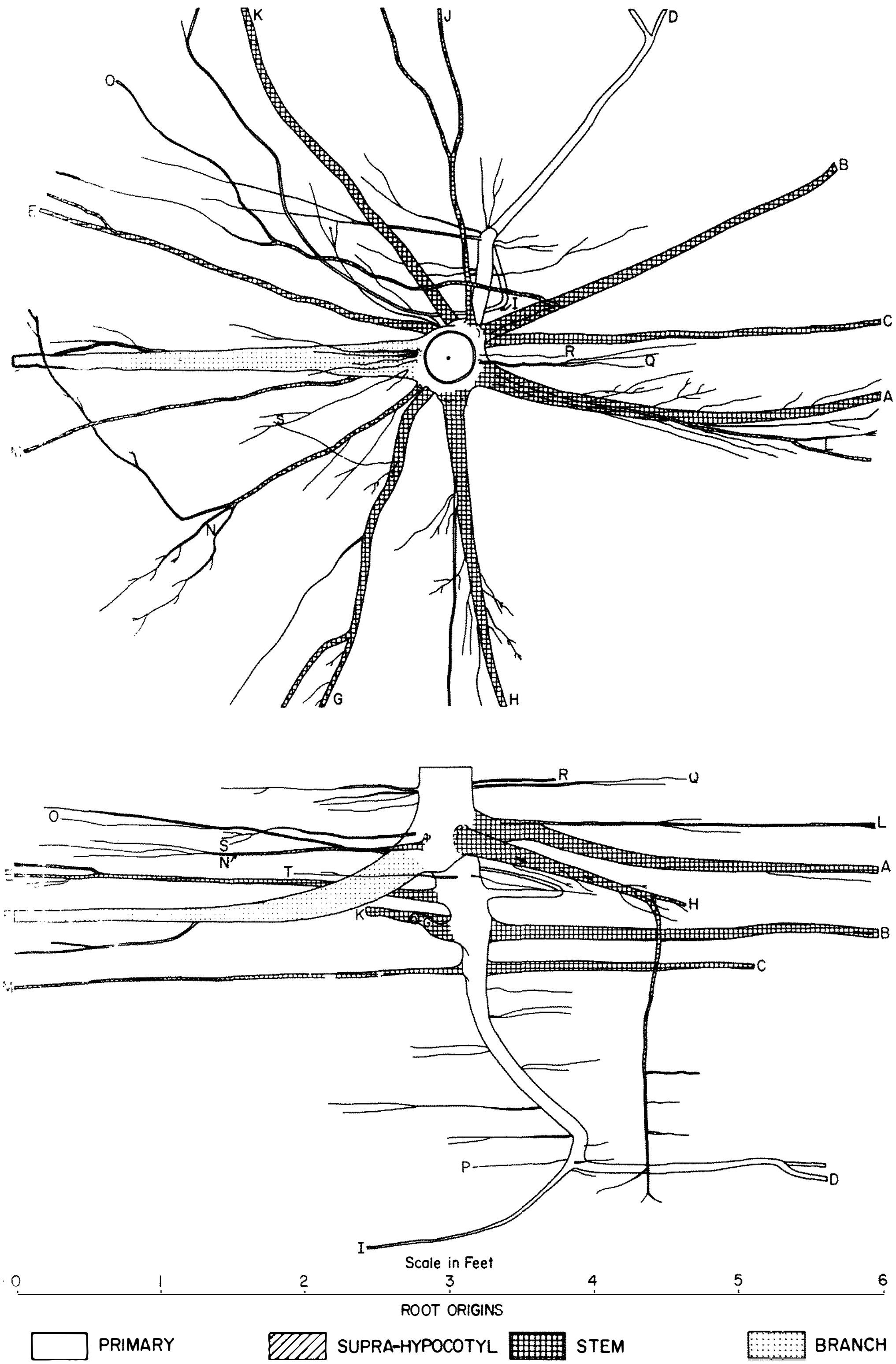

Figure 16. Tree IX: Multilayered root-form with small primary roots and large secondary roots which developed after two lacustrine deposits.

MORPHOGENIC VARIATIONS OF ROOT-FORM

Variations in typical root-forms may occur which are not directly attributable to either soils or sites but to the spatial organization of roots during morphogenesis. Spatial refers to the orientation of roots in the rooting medium (a mechanical influence) and to the interaction of growth among roots (a physiological influence) on form.

Orientation of Roots

The greatest variability in juvenile root systems is found on decayed wood. The variations develop in several ways depending upon the place of seedling establishment and moisture.

On dry areas the seedling roots may be confined to decayed wood until the wood deteriorates and the primary roots enter the surrounding soil. As the wood deteriorates, moss becomes established and humus forms over the wood. Secondary roots grow to a large size in the better moisture and nutrient conditions of this moss-humus layer. A bilayered root-form results.

On wet areas, decayed wood situated above the general soil level is suitable for seedling establishment. The primary roots develop rapidly in the decayed wood and small secondary roots develop in the humus and moss on the wood. The result is an elevated variation of the monolayered form with large primary laterals, grouped asymmetrically around the rootstock. The typical form on such sites would be monolayered or partially bilayered with large secondary roots.

On waterlogged areas, seedlings appear on hummocks and decayed stumps above the level of free water. Primary and secondary roots grow downward around the stump or mound in a stilt root-form.

Three morphogenic variations of root-form are illustrated.

Retarded (Growth of Primary Roots)

The retarded variation of the multilayered root-form of Tree X (Appendix 2 and Figure 17) developed on a decayed log on a dry Bisequa soil. The root system is poorly multilayered since the interlaterals and supralaterals form only a partial whorl around the rootstock. All roots except I are secondary. Only the supralateral D and the interlaterals A and C are large and many small roots terminated capillaceously near the rootstock.

Stages in morphogenesis are shown in Figure 19A. The tree, which was established on a decayed log, developed a primary root system within the log but only the primary root I remained in the immature system. A divaricate stem quickly developed and almost all of the secondary roots developed from one branch. By the 15th year the infralaterals, R and S, grew downward through the log to abort in the top of the Bf horizon. Of the other infralaterals (A, F and X), which grew in the humus on top of the log, only A reached a large size. The supralaterals D and E and the

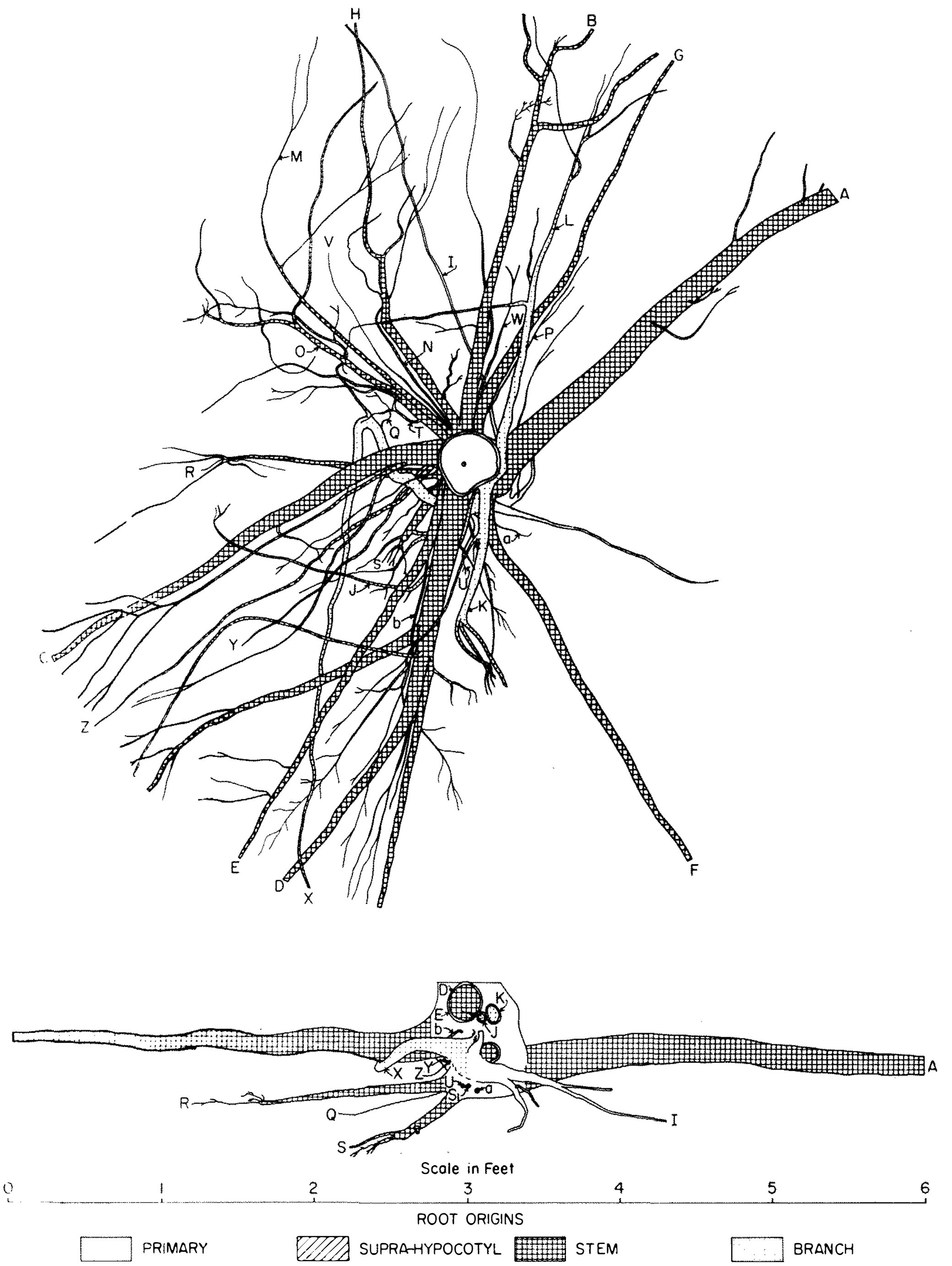

Figure 17. Tree X: Retarded variation of multilayered root-form with large secondary roots in humus and vestigial primary roots confined to decayed wood.

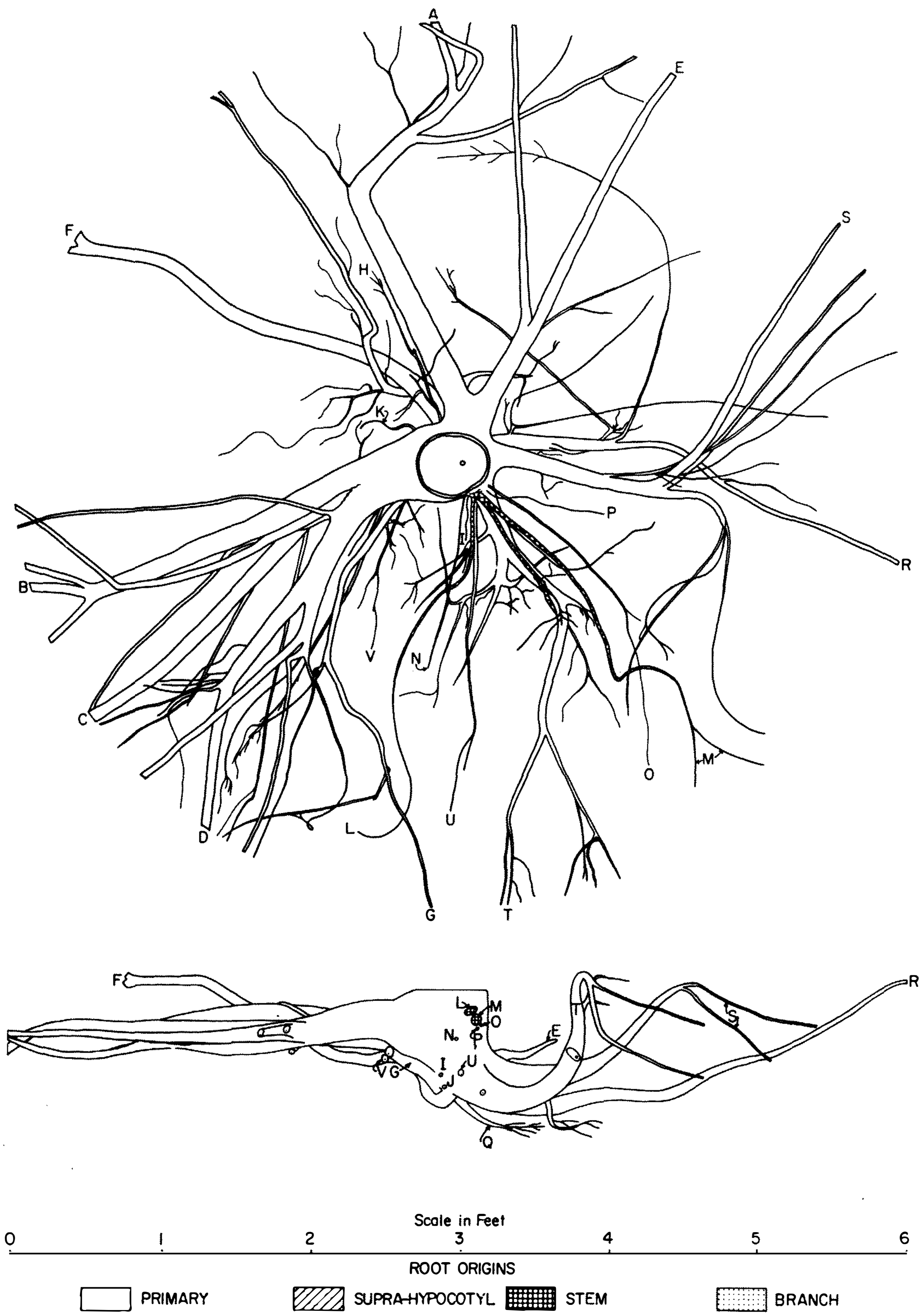

Figure 18. Tree XI: Elevated variation of monolayered root-form with partially bilayered primary roots which developed on the top of a decayed stump in sphagnum.

interlaterals B, G and W developed by the 20th year in the humus on top of the log. The larger interlateral C developed next and then a number of small supralaterals.

The multilayered form resulted from the retardation of primary root growth in the log and the growth of secondary laterals in the humus layer on the log. Typical trees rooted in mineral soil on the site possessed a contorted taproot, owing to the dryness of the Bisequa soil, and a single whorl of large lateral roots of either primary or primary and secondary origin.

Elevated

The elevated variation of the monolayered root-form of Tree XI (Appendix 2 and Figure 18) developed on the end of a decayed log in sphagnum. The system has a unilateral fusion of roots B, C and D near the rootstock. These roots grew along the top of a decayed log. Roots R, S and T show an undulating growth through the depressions and hummocks of the sphagnum. All roots, except the bur roots L, M, N, O and P are primary. The taproot, being degenerate and overgrown in the rootstock, is absent.

The tree was established on a decayed log above the general level of the soil surface. By the 15th year (Figure 19B) roots R, T, F, A and G had grown down the end of the log into the sphagnum. By the 20th year roots B and D had grown along the top of the decayed log. At 40 years the sphagnum covered the rootstock at the end of the log; later, the secondary bur-roots developed.

The root system differs from others in sphagnum with large primary and secondary roots (cf. Tree VII, Figure 13) because the seedling grew on a decayed log above the ground. As it took 40 years for the sphagnum to cover the rootstock, the large roots are primary rather than primary and secondary. A similar or stilt root-form (vid. Rehák 1942) with predominately primary roots may also develop from seedlings established on stumps.

Complex

The variation of the multilayered root-form of Tree XII (Appendix 2 and Figure 20) resulted from complex changes in site.

The system has two whorls of lateral roots of which the secondary supralaterals A, B and H are the largest. The infralaterals are primary and all lateral roots step-down from the rootstock.

The tree became established in living sphagnum and developed a contorted and aborted taproot which was later overgrown by lateral roots. Secondary roots developed early in the live sphagnum and there is only 1 year's difference between the oldest secondary A (33 years) and the oldest primary root C (34 years). The growth of sphagnum caused the multilayered root-form.

Early in the life of the tree, the water table fell and the sphagnum died. This had a threefold effect: (a) no further secondaries

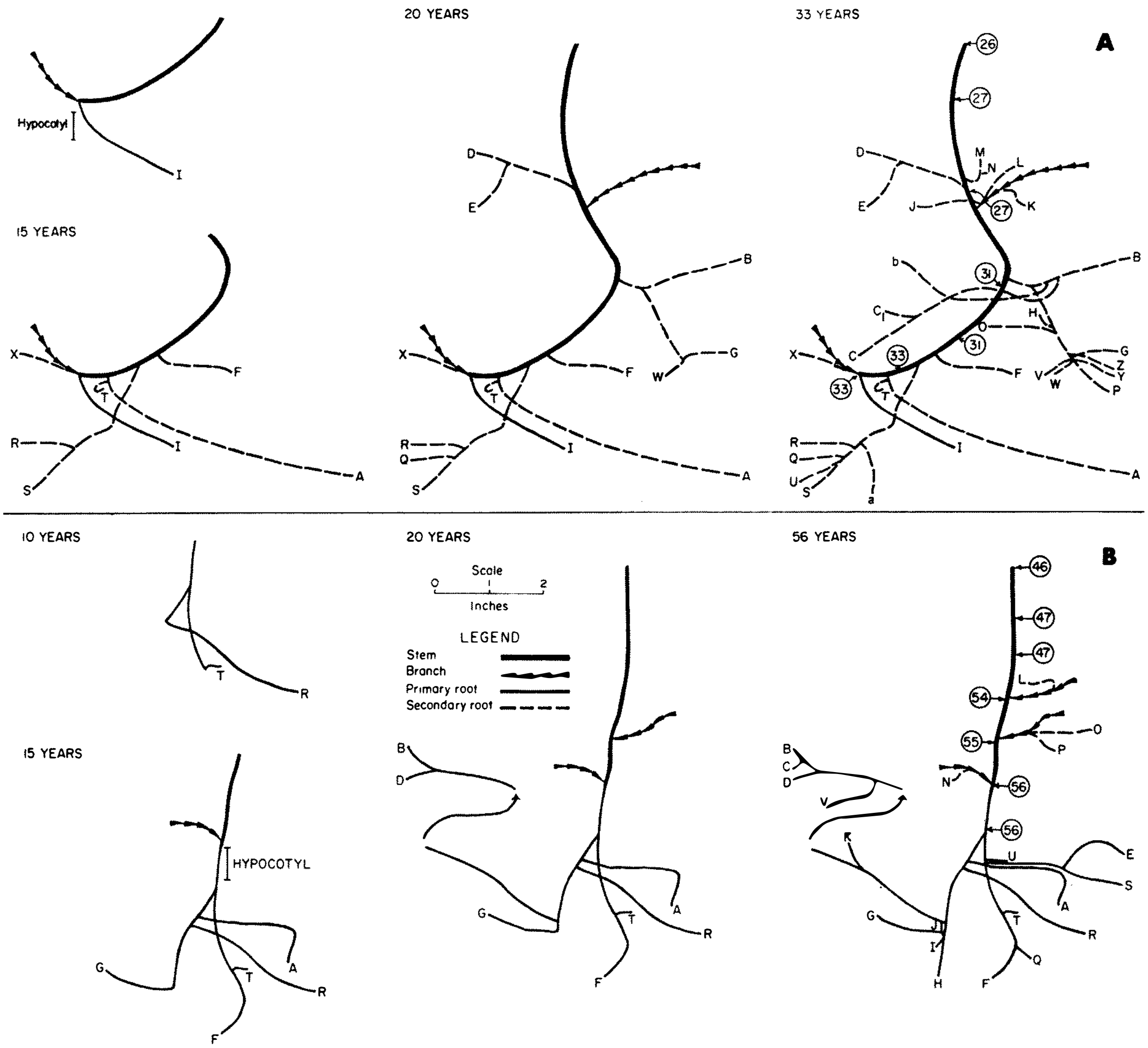

Figure 19. Anatomical origin and chronological development of roots for Tree X (A) and Tree XI (B).

developed above the supralaterals (A, B, H and I); (b) the supralaterals grew obliquely from the rootstock in a stepped-down manner as the sphagnum died, and; (c) the supralaterals terminated near the surface of the dead sphagnum and at the same level as the infralateral roots which would be buried more deeply in live sphagnum.

The complex root-form can be anticipated after alteration of sites by drainage, destruction of the moss cover, or fire. Complex forms require at least two distinct stages in site development, such as the normal development of moss and humus in a stand followed by a destruction of the moss cover.

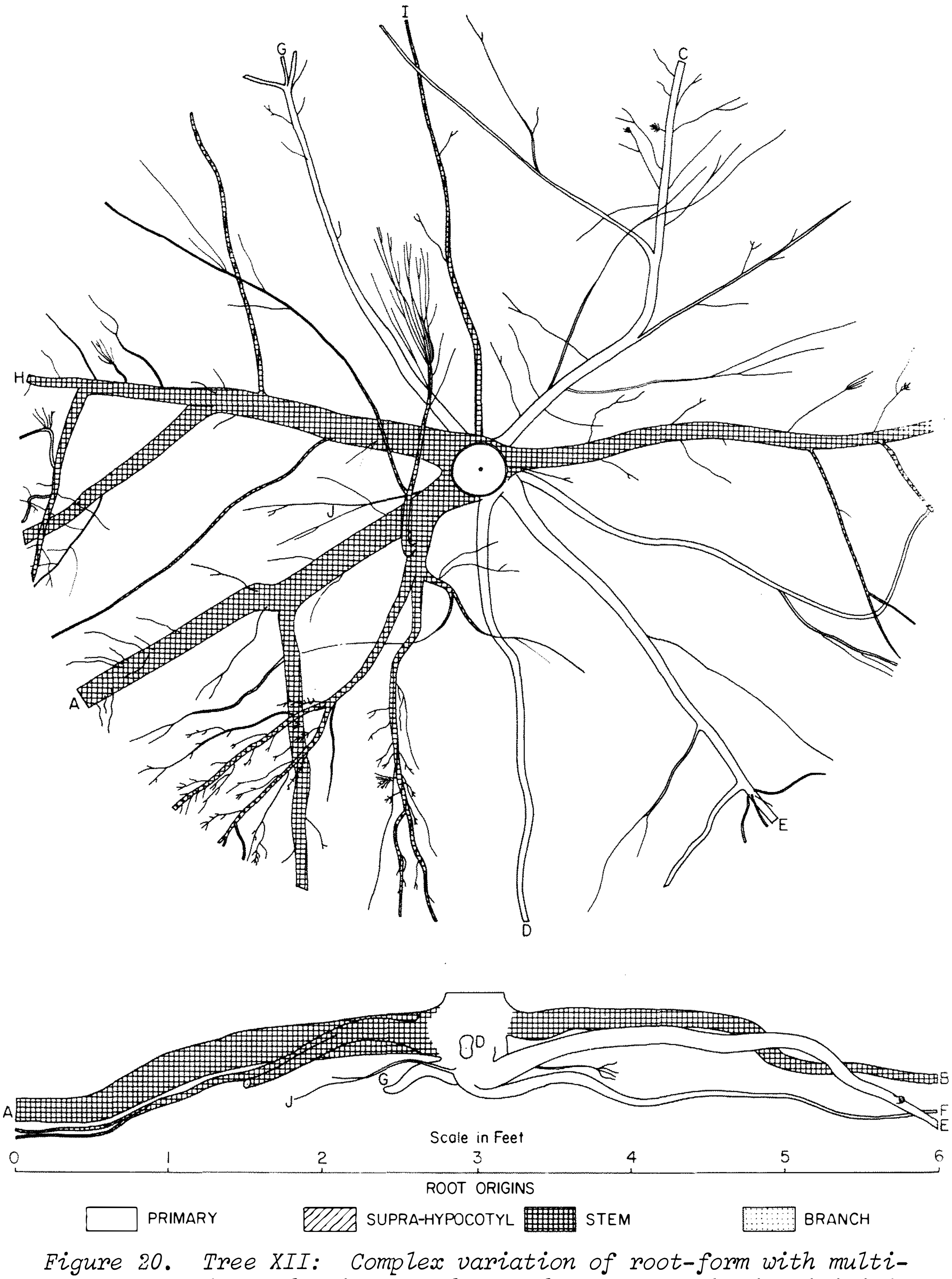

Figure 20. Tree XII: Complex variation of root-form with multi-layered primary and secondary roots showing initial bilayered development in live sphagnum then stepped-down growth in dead sphagnum from a sudden lowering of the water table.

Interactive Growth of Roots

Interactive growth among roots within a system refers to differences in the growth rate of roots of various ages and sizes. This concept may be clarified by a review of some of the previous root-forms.

Restricted Taproot

While the restricted taproot-form develops on certain soils, it also occurs when a complete whorl of laterals develops above the taproot. This is interactive growth between laterals and taproot.

Neither Tree I nor Tree II shows suppression of taproot growth by the laterals. In Tree I (Figure 5) the taproot is connected directly to the trunk through a gap between laterals A and D. Similarly, the taproot of Tree II (Figure 6) is connected to the trunk between laterals G and H. In neither case did lateral roots completely surround the rootstock, and therefore growth of the taproots was not restricted.

When lateral roots completely encircle the rootstock, the taproot is connected to the trunk through contorted tissue and both radial and lineal growth is suppressed. Suppression of the taproot may occur at any age; the earlier it begins the smaller the taproot will be in relation to the diameter of the rootstock.

Multilayered Roots

Interactive growth is characteristic of all multilayered forms but unlike in taproot-forms it is more dependent upon changes in site and orientations of roots. The multilayered form develops from the replacement of one group of roots by another (cf. Veščikova 1964).

Tree VIII (Figure 15B) is an example. As a whorl of laterals replaced the lateral roots below, the upper roots grew more rapidly and became larger than the roots below; this replacement occurred six times. However this type of growth depends upon the rootstock being completely surrounded by lateral roots and the lower roots being unable to continue to grow.

In Tree VII (Figure 13) the replacement of one whorl of roots by a whorl above was not complete as in Tree VIII (Figure 14). This resulted in large roots occurring in both the upper and lower whorls. The infralateral L, the largest root developed before the 10th year, maintained a direct connection with the trunk between the supralaterals B and I. It was not suppressed in any way.

STRUCTURE OF ROOT SYSTEM AND TRUNK GROWTH

The structure of the root system has many relationships with growth of the trunk. Two of these, the chronological development of roots and interactive growth among roots within a system are examined. Since the root systems are taken from a wide variety of sites, only qualitative comparisons of trees are possible.

Chronological Development of Roots

Roots in all systems develop over varying periods of time which is determined by the nature and amount of change in site. On dry sites, with little humus to promote secondary roots, the root system of the immature tree is established early. On wet and cold sites with much humus there is considerable die-back of roots and replacement of primary roots with secondaries and secondaries with other secondaries. The roots became established later than on dry sites and these differences influence the height growth of trees.

Compare the times of rooting in the monolayered systems of Tree V (Figure 12B) and Tree VI (Figure 12C) with their respective height growth (Figure 21). Tree V had seven roots and was 33 inches high by the 15th year, whereas Tree VI was 11 inches high and had no roots which were to form the immature root system. The roots of Tree VI continually died-back prior to the 15th year and it took nearly 20 years for permanent roots to develop. Tree V grew rapidly after 10 years, but Tree VI did not show any appreciable growth increase until after 30 years. Growth of the trunk is associated with the time of development of permanent roots rather than with their anatomical origin since secondary roots can develop in the second year.

Interactive Growth of Roots

When a tree reaches the immature stage, the root system may have undergone considerable change from its original form. Such changes result from modifications of site and a reorganization of the system. The amount of change depends upon the rate and chronology of site development and is reflected in the amount of trunk growth.

Site alteration has the greatest influence on changes in the root system, and Trees VIII and IX show extremes. Both developed multilayered systems -- Tree VIII in presence of a rising water table and increase in moss growth, and Tree IX after successive lacustrine sand deposits buried part of the trunk. Figure 15B (vid. Figure 14) shows the interactive growth of the root system of Tree VIII. As the water table rose and moss became deeper, new lateral roots formed above the older ones. The older and lower lateral roots died as replacement occurred. This change occurred gradually throughout the mid-life of the tree (20-50 years).

The interactive growth of root systems and its relation to trunk growth can be broadly interpreted. Several things are involved: comparative physiology of taproot and lateral root, time of the individual root development within the system, interaction between replacement roots and original roots and organization of a root system at the rootstock for the greatest growth potential.

Interaction among roots may be seen by comparing development of the root systems of Trees III and VIII (Figures 7 and 14). Little replacement of roots occurred in Tree III whereas roots were continually replaced in Tree VIII. At the same time Tree III grew more rapidly in height than

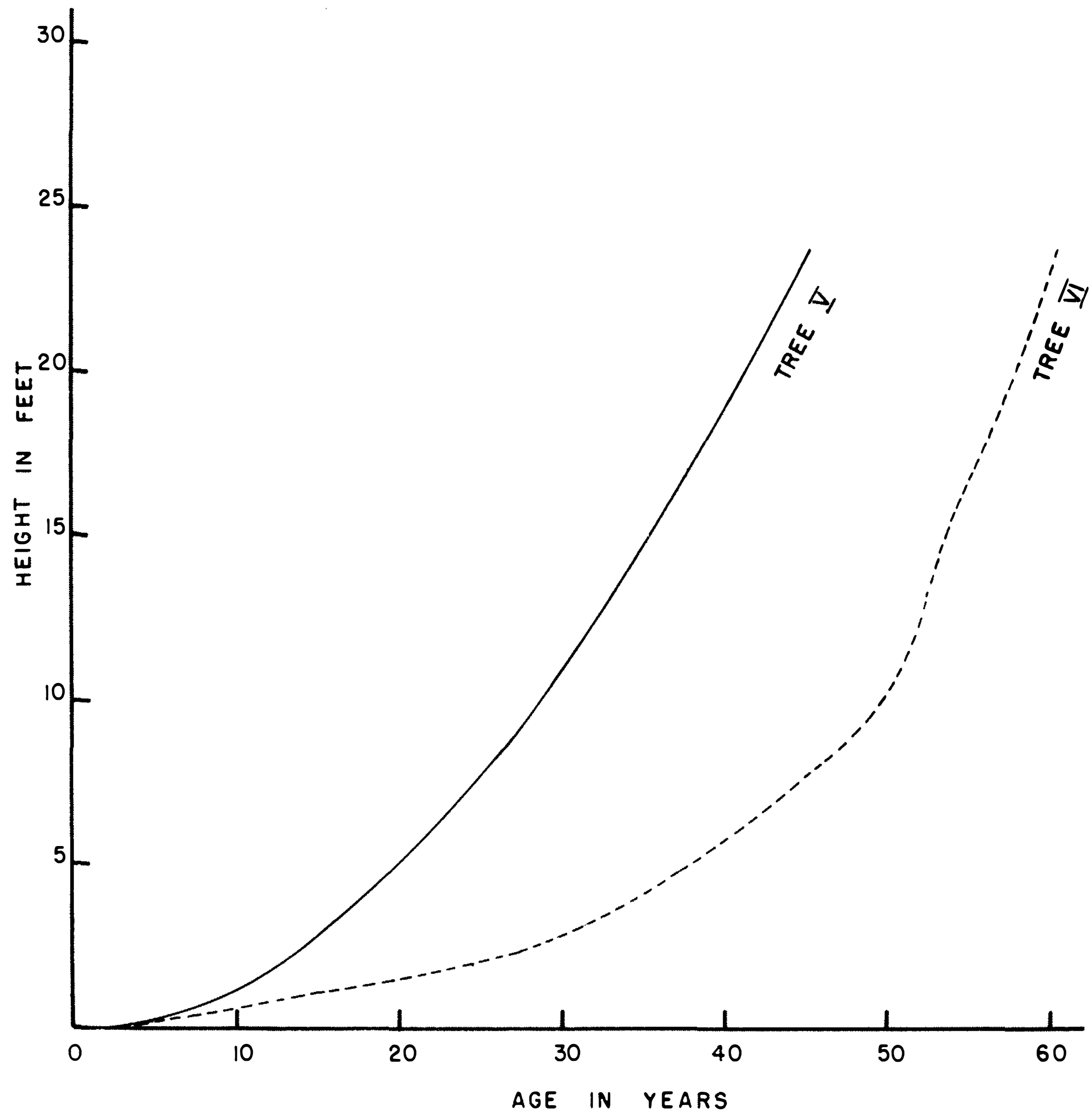

Figure 21. Differences in height growth and age between Tree V, which established roots at an early age, and Tree VI, which established roots at a later age.

Tree VIII (Figure 22). This variation in height increment must be accounted for partially by differences associated with the established root systems.

The replacement of one system of roots with another does not appear to be consistent with maximum growth although, on some sites, this is the only way a tree can maintain itself. The trunk growth of a tree with a young expansive root or one with an older decadent root does not equal the growth of one with an old established root. A replacement of roots leads to a fairly uniform rate of trunk increment.

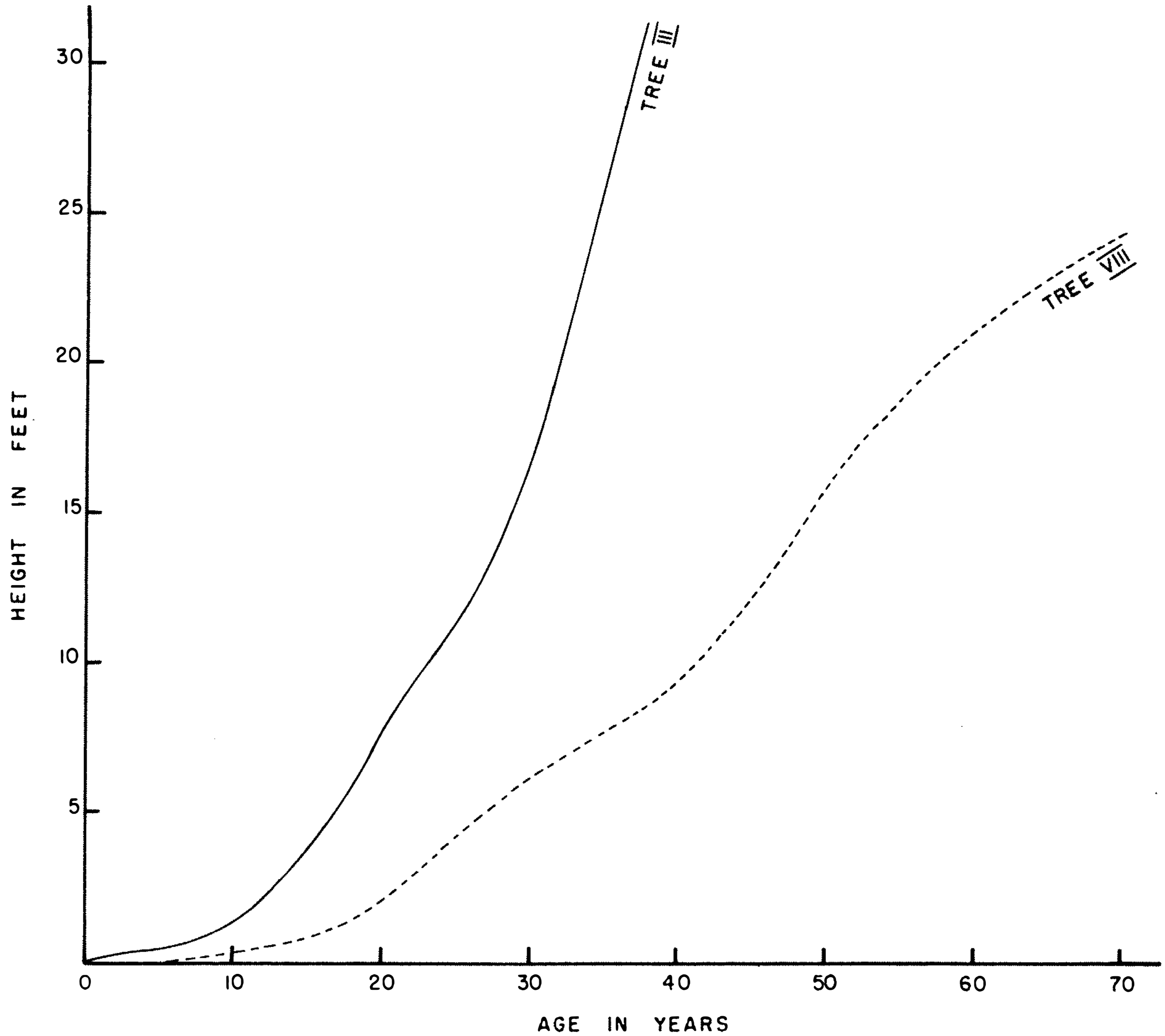

Figure 22. Differences in height growth and age between Tree III, which developed a restricted taproot-form, and Tree VIII, which developed a multilayered form.

SUMMARY

A single root-form is not inherent to immature white spruce growing on a wide variety of soils and sites in west-central Alberta and the southern part of the Mackenzie District of the Northwest Territories.

Twelve trees were selected to show the influence of soil properties, site modifications during the life of the tree, and the spatial organization of roots during morphogenesis on the development of root-form. The occurrence of secondary roots was determined and their role in development is presented.

Four root-forms are found in the region.

The elongated taproot-form occurs on well-drained Podzolic soils where taproot growth is not restricted by soil texture, structure or drainage. The taproot maintains a direct connection with the trunk through a gap between the laterals at the rootstock. Usually the elongated taproot consists of primary roots since it is found on soils with a thin L-H layer in which secondary roots do not develop readily.

The restricted taproot-form, which occurs on well-drained Podzolic, Regosolic and Solonetzic soils, has several origins. The growth of the taproot and proximal roots may be aborted and contorted by textural changes between horizons or restricted by compaction of the underlying soil. The taproot may be restricted by rapid development of a complete whorl of secondary lateral roots around the rootstock. A contorted variant occurs early in growth through horizontal orientation of the taproot in decayed logs, humus and wet soils. Restricted taproot-forms are composed of both primary and secondary roots.

The monolayered root-form, with or without a vestigial taproot, is found in imperfectly-drained to poorly-drained Podzolic and Gleysolic soils. The lateral roots form a single whorl around the rootstock; sometimes a partial second whorl exists (bilayered form); and the taproot is vestigial or overgrown in the rootstock. The form may develop from an aborted or degenerate taproot in the seedling, from restriction by a rock or gley layer, or from degeneration of the lower part of the root system in the presence of a fluctuating water table. The root system, depending on the mode of development, consists of either primary and secondary roots or all secondary roots.

The multilayered root-form is common on well to imperfectly-drained Regosolic soils and very poorly-drained Gleysolic soils. The well-developed form occurs in the presence of thick lacustrine and alluvial deposits. The form develops on sites where the water table is rising or soil frost is rising, accompanied by growth of moss and humus accumulation. Poorly-developed forms that grade into the monolayered root-form are found on poorly-drained Podzolic soils with a thick feather moss and humus layer. Development of the multilayered form is dependent upon the formation of secondary roots, and all large roots are of secondary origin.

Variations of the typical root-form can be found on any area; these result from the spatial organization of roots during morphogenesis. Differences in the orientation of seedling roots in the rooting medium (a mechanical influence) and the interaction of growth among roots (a physiological influence) produce variations of form.

Two variants of the multilayered form resulted from a retardation of growth of primary roots by a decayed log and from two different and opposite (complex) changes in site. A monolayered form of primary roots instead of secondaries developed in sphagnum because of elevation above the general soil level. Interactive growth, occurring in all root systems, is most pronounced in systems which change form during morphogenesis as some restricted taproot and multilayered forms.

The structure of the root system is related to the growth of the trunk. The duration of retarded growth in the trunk corresponds to the length of time required for roots to become established. The effect of the interaction of growth among roots of a system on trunk growth is most pronounced in the multilayered form. The replacement of a decadent whorl of lateral roots with a whorl of expanding laterals tends to maintain a uniform rate of trunk growth which is slower than for trees that did not replace roots.

SOMMAIRE

Les racines des jeunes Épinettes blanches (*Picea glauca* (Moench) Voss) qui croissent dans plusieurs types de sol et de Station écologique, en Alberta ouest-central et dans le secteur sud du district de Mackenzie (Territoires du Nord-Ouest), n'ont pas toutes la même forme générale.

Douze arbres ont été étudiés. Le but de la recherche était de connaître le rapport entre le développement de la forme générale des racines d'une part et les propriétés du sol, les modifications de la Station écologique du vivant de l'arbre et la répartition des racines au cours de leur développement morphologique d'autre part. De plus, l'auteur a noté la présence des racines secondaires et le rôle qu'elles jouent dans le développement global de la racine.

Il existe quatre formes générales de racine dans cette région.

La <u>racine pivotante allongée</u> se voit dans les sols podzoliques bien drainés, où elle croît facilement. Elle part directement du collet, malgré la présence, à côté, de grosses racines latérales, et elle est formée surtout de racines primaires: dans ce type de sol, à horizons L-H minces, les racines secondaires ne se développent pas facilement.

La deuxième forme, dite <u>pivotante courte</u>, a plusieurs origines. Elle se rencontre dans les sols podzoliques, régosoliques et solonetziques, et son mode de croissance est affecté par des changements de texture d'un horizon à l'autre; dans certains cas, sa profondeur est limitée par un sous-sol très compact. Elle est d'autant plus courte qu'un verticille complet de racines latérales se développe tout autour du collet. Parfois, elle dévie au début de sa croissance pour suivre la direction horizontale du bois pourri gisant ou se maintenir dans un horizon d'humus ou de sol mouillé. Cette forme générale se compose de racines primaires et secondaires.

La <u>racine fasciculée</u>, avec ou sans racine pivotante peu développée, pousse en sols podzoliques ou gleysoliques peu ou pas drainés. Un seul fascicule existe et il vient du collet; on voit parfois un fascicule sous-jacent (forme bi-fasciculée). Cette forme provient de la dégradation ou de l'avortement hâtif de la racine pivotante quand l'arbre n'était

qu'un jeune plant; elle peut aussi avoir sa source dans la présence d'une strate de roc ou de gley près de la surface, ou dans la dégradation de la partie inférieure du système radiculaire à cause de la présence d'une nappe phréatique fluctuante. Dans cette forme, se rencontrent soit des racines primaires et secondaires, soit uniquement des racines secondaires, selon le mode de développement qui existe.

Enfin, la racine multifasciculée est fréquente dans les sols régosoliques mal drainés et dans les sols gleysoliques mouillés. C'est dans les épais dépôts d'alluvions ou lacustres qu'elle se développe bien, plus particulièrement aux endroits où la nappe phréatique a tendance à s'élever et où le sol gèle plus profondément qu'auparavant; de tels endroits sont couverts de mousse et d'humus. Les formes intermédiaires (entre la racine multifasciculée et la racine fasciculée) arrivent en des sols podzoliques mal drainés couverts d'une épaisse couche d'humus et de mousse. Toutes les grosses racines de cette forme générale sont d'origine secondaire.

Les racines de chaque forme générale se trouvent dans chaque Station: leur formation dépend du lieu précis où elles poussent. Au nombre des diverses influences, signalons l'orientation des racines des jeunes plantes dans le sol (c'est une influence mécanique); signalons aussi l'interaction des racines au cours de leur croissance (influence physiologique).

Parmi les variétés de racines multifasciculées, l'une résulte du retard dans la croissance des racines primaires causé par un tronc de bois pourri gisant; l'autre a pour origine la présence de sol différent et complexe situé dans le chemin des racines. Une racine fasciculée à membres primaires (sans racines secondaires) se développait dans la tourbe à sphaigne qui s'élevait au-dessus du sol adjacent. L'interaction de la croissance, présente dans toutes les formes, est plus prononcée lorsque la forme évolue, au cours de son développement morphologique, en une racine soit multifasciculée ou pivotante réduite.

La forme qu'adopte la racine influe sur la croissance du tronc: celle-ci est retardée aussi longtemps que prennent les racines pour bien se développer. Ce cas est le plus évident lorsque la racine devient multifasciculée: pendant qu'un nouveau fascicule de racines latérales se forme pour remplacer celui qui se dégrade, le tronc croît à un taux comparativement plus lent, bien que régulier.

LITERATURE CITED

AALTONEN, V. T. 1920. Über die Ausbreitung und den Reichtum der Baumwurzeln in den Heidewäldern Lapplands. (On the development and abundance of tree roots in the Lapland heath forests). Acta Forestalia Fennica 14 (1) : 1-55.

BANNAN, M. W. 1940. The root systems of northern Ontario conifers growing in sand. American Journal Botany 27:108-114.

BANNAN, M. W. 1942. Notes on the origin of adventitious roots in the native Ontario conifers. American Journal Botany 29(8):593-598.

BÜSGEN, M. and E. MÜNCH 1929. The structure and life of forest trees. John Wiley and Sons, Inc., New York. xi + 436 pp. (English translation by T. Thomson).

DANGEARD, P. A. 1892. Recherches sur les plantules des Conifères. (Investigations on the germinants of the Conifers). Le Botaniste, Series 3: 126-204 + plates XIII-XVII.

DENISOV, A. K. 1960. Razvitie pridatočnyh kornej v pesčanom alljuvii drevesnymi i kustarnikovymi porodami južnoj tajgi. (Development of adventitious roots in a sandy alluvium by trees and shrubs of the northern taiga). Izdatelĭstvo Akademii Nauk, S.S.S.R., Botaničeskiĭ Žurnal 45(10): 1516-1522.

HILL, T. G. and E. de FRAINE 1909. On the seedling structure of gymnosperms II, III. Annals Botany 23(90): 189-227 and 23(91): 433-458.

HORTON, K. W. 1958. Rooting habits of lodgepole pine. Canada, Department Northern Affairs and National Resources, Forestry Branch, Tech. Note 67. 26 pp.

HUSTICH, I. 1954. On forests and tree growth in the Knob Lake area, Quebec-Labrador peninsula. Acta Geographica 13(1): 1-60.

JEFFREY, E. C. 1917. The anatomy of woody plants. The University of Chicago Press. X + 478 pp.

JEFFREY, W. W. 1959. White spruce rooting modifications on the fluvial deposits of the lower Peace River. Forestry Chronicle 35(4): 304-311.

KOŠČEEV, A. L. 1952. Lesovodstvennoe značenie pridatočnyh korneĭ drevesnyh porod. (The silvicultural significance of adventitious roots in woody species). Lesnoe Khoziaistvo 5(9): 48-50.

KOŠČEEV, A. L. 1953. Lesovodstvennoe značenie pridatočnyh korneĭ drevesnyh porod v uslovijah zabolačivanija lesosek. (The silvicultural significance of adventitious roots on tree species in waterlogged clear-felled areas). Trudy Instituta Lesa, Izdatelĭstvo Akademii Nauk, S.S.S.R. 13 (9): 116-129.

KÖSTLER, J. N. 1962. Untersuchungen zur Wurzelbildung. (Investigations on root formation). Allgemeine Forstzeitschrift 17(28): 413-417.

KRASILJNIKOV, P. K. 1956. Pridatočnye korni i kornevaja sistema u kedra v centraljnyh Sajanah. (Adventitious roots and the root system of *Pinus sibirica* in the central Sayan Mts.). Russkoe Botanischeskiĭ Obschestvo, Izdatelĭstvo Akademii Nauk, S.S.S.R., Botaničeskiĭ Žurnal 41(8): 1194-1206.

KREUTZER, K. 1961. Wurzelbildung junger Waldbäume auf Pseudogleyböden. (Root formation by young forest trees on pseudogley soils). Forstwissenschaftliches Centralblatt 80 (11/12): 356-392.

LAITAKARI, E. 1927. Männyn juuristo. Morfologinen tutkimus. (The root system of *Pinus sylvestris*. A morphological investigation). Acta Forestalia Fennica 33(1): 1-380.

LeBARRON, R. K. 1945. Adjustment of black spruce root systems to increasing depth of peat. Ecology 26: 309-311.

LEMKE, K. 1956. Untersuchungen über das Wurzelsystem der Roteiche auf diluvialen Standortsformen. (Investigations concerning the root system of red oak on diluvial site types). Archiv für Forstwesen 5(1/2): 8-45 and 5(3/4): 161-202.

MEYER, E. 1938. Adventivwurzeln der Fichte. (Adventitious roots of spruce). Forstwissenschaftliches Centralblatt 60(9): 290-295.

NÄGELI, W. 1930. Adventiwurzelbildung an „ubererdeten" Baumstämmen. (Adventitious root growth by "above the earth" tree-trunks). Mitteilungen der Schweizerischen Centralanstalt für das forstliche Versuchwesen 16(1): 129-147.

NOELLE, W. 1910. Studien zur vergleichenden Anatomie und Morphologie der Koniferenwurzeln mit Rucksicht auf die Systematik. (Studies on comparative anatomy and morphology of coniferous roots with regard to taxonomy). Botanische Zeitung 68(10/12): 169-266.

PÖNTYNEN, V. 1929. Tutkimuksia kuusen esiintymisestä alkiasvoksina Raja-Karjalan valtionmailla. (Investigations on the presence of spruce as underwood in the Finnish State Forest of Raja-Karjalan). Acta Forestalia Fennica 35(1): 1-235.

PRIEHÄUSSER, G. 1939. Bodenfrost, Bodenentwicklung und Flachwurzeligkeit der Fichte. (Ground frost, soil development and shallow rootedness of spruce). Forstwissenschaftliches Centralblatt 61(11): 329-342 and 61(12): 381-389.

REHÁK, J. 1942. Chůdové kořeny. (Stilt roots). Lesnická Práce 21(4/5): 200-208.

SIRÉN, G. 1950. Alikasvoskuusten biologiaa. (On the biology of undergrown spruce). Acta Forestalia Fennica 58(2): 1-90.

STANEK, W. 1961. Natural layering of black spruce in northern Ontario. Forestry Chronicle 37(3): 245-258.

UMKIN, A. I. 1958. Nekotorye osobennosti rasprostranenija kornevyh sistem drevesnyh porod v holodnyh počvah. (Some features of the distribution of root systems of tree species in cold soils). Soobščeniya Instituta Lesa, Izdatelǐstvo Akademii Nauk, S.S.S.R. 9: 64-71.

VATER, H. 1927. Die Berwurzelung der Kiefer, Fichte und Buche. (The root-form of pine, spruce and beech). Tharandter Forstliches Jahrbuch 78(3): 65-85.

VERETENNIKOV, A. V. 1959. Otmiranie i regeneracija kornevoj sistemy *Pinus sylvestris* L. v zavisimosti ot uslovij snabženija korneobitaemogo sloja počvy kislorodom vozducha. (The dying and regeneration of the root system of *Pinus sylvestris* L., as related to oxygen supply in the rooting zone). Izdatelǐstvo Akademii Nauk, S.S.S.R., Botaničeskiǐ Žurnal 44(2): 202-209.

VEŠČIKOVA, T. V. 1964. Sezonnyǐ rost i formirovannie kornevoǐ sistemy eli obykiovennoǐ v taezioi zone Europeǐskoǐ Chastǐ S.S.S.R. (Seasonal growth and formation of the root system of *Picea abies* in the taiga zone of European Russia). Bjulletenǐ M.o-va Obšc. Ispyt. Prirody (Otd. Biologii) 69(1): 74-85.

WAGG, J. W. B. 1964. White spruce regeneration on the Peace and Slave River lowlands. Canada, Forest Research Branch, Department of Forestry Publication 1069: 35 pp.

APPENDIX 1

Scientific Names of Trees, Plants and Mosses*

Alpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Aspen	*Populus tremuloides* Michx.
Balsam poplar	*Populus balsamifera* L.
Black spruce	*Picea mariana* (Mill.) BSP.
Bog cranberry	*Vaccinium vitis-idaea* L. var *minus* Lodd.
Canadian buffalo-berry	*Shepherdia canadensis* (L.) Nutt.
Bunchberry	*Cornus canadensis* L.
Cladonia	*Cladonia* spp.
Creeping juniper	*Juniperus horizontalis* Moench
Dahurian larch	*Larix gmelini* (Rupr.) Litvin
Dwarf birch	*Betula glandulosa* Michx.
Feather moss	*Hylocomium splendens* (Hedw.) BSG.
Fireweed	*Epilobium angustifolium* L.
Kinnikinnick	*Arctostaphylos uva-ursi* (L.) Spreng.
Labrador tea	*Ledum groenlandicum* Oeder
Meadow horsetail	*Equisetum pratense* Ehrh.
Mooseberry	*Viburnum edule* (Michx.) Raf.
Norway spruce	*Picea abies* (L.) Karst.
Paper birch	*Betula papyrifera* Marsh.
River alder	*Alnus tenuifolia* Nutt.
Sedge	*Carex* spp.
Sphagnum	*Sphagnum* spp.
Stiff club-moss	*Lycopodium annotinum* L.
Tamarack	*Larix laricina* (Du Roi) K. Koch
Twin-flower	*Linnaea borealis* L. var *americana* (Forbes) Rehd.
White spruce	*Picea glauca* (Moench) Voss
Willow	*Salix* spp.
Woodland horsetail	*Equisetum sylvaticum* L.

* Taken from: Moss, E.H., Flora of Alberta. University of Toronto Press, Toronto, 1959.

APPENDIX 2

Description, Location and Site Characteristics of Selected Trees

Tree I (Figures 5, 8A)

The tree, 42 years old, 20.7 feet high and 3.7 inches d.b.h. grew in an open stand of white spruce near Brulé Lake, Alberta. Buffalo-berry, kinnikinnick, creeping juniper and grass were abundant on the site. The well-drained nearly uniform textured and loose structured Podzolic (Dark Gray Wooded) soil, which developed on the deep aeolian fine sands, has an L-H horizon less than 1-inch thick, a 2-inch Ah, 8-inch Ae and a 12-inch B horizon.

Tree II (Figures 6, 8B)

The tree, 31 years old, 21.3 feet high and 2.5 inches d.b.h., grew in a small opening in a mature white spruce stand beside the Waskahigan River in Alberta. The shrubs were paper birch, willow, and the herbs were woodland horsetail and grass. The well-drained Regosolic (Mor Regosol) soil of alluvium had a 5-inch L-H horizon of feather moss and humus, thin Ah and a textural change from sand to gravel at 16 inches.

Tree III (Figures 7, 8C, 22)

The tree, 38 years old, 30.5 feet high and 4.9 inches d.b.h., grew in a mixed stand of balsam poplar and aspen near Grande Prairie, Alberta. The ground vegetation consisted of willow, fireweed, grasses and some feather moss. The imperfectly-drained Solonetzic (Gray Wooded Solodized Solonetz) soil developed on glacio-lacustrine clay. A profile showed a 2-inch L-H horizon, a 2-inch Ah and a 4-inch Ae overlaying a 5-inch blocky B and a compact and columnar structured C horizon at 13 inches.

Tree IV (Figures 9, 12A)

The tree, 50 years old, 25.7 feet high and 3.6 inches d.b.h., grew with black spruce and tamarack in a small depression on the limestone escarpment east of Kakisa Lake, Northwest Territories. Feather moss, cladonias, dwarf birch and sedge were predominant associates. The poorly-drained Gleysolic (Carbonated Gleysol) soil had a 3-inch L-H horizon of feather moss and humus, 1-inch Ah of silty clay loam, 4-inch Cg of silty clay overlaying calcareous rock at 9 inches.

Tree V (Figures 10, 12B, 21)

The tree, 45 years old, 23.7 feet high and 4.7 inches d.b.h., grew in a stand of pure white spruce near Entrance, Alberta. Feather moss was present under the shade of the trees while willow, grasses and sedges occupied the openings. The imperfectly-drained Podzolic (Gleyed Gray Wooded) soil, developed on aeolian sands, showed a 2-inch L-H horizon of feather moss and humus, a 7-inch Ae and a B with a gley layer at 15 inches.

Tree VI (Figures 11, 12C, 21)

The tree, 60 years old, 23.1 feet high and 3.9 inches d.b.h., grew in a pure stand of white spruce south of Grande Prairie, Alberta. The feather mosses, *Hylocomium splendens* and *Pleurozium schreberi*, were dominant under the trees, and willow, mountain alder and grasses were in the openings. The very poorly-drained Gleysolic (Orthic Humic Gleysol) soil, having a 5-inch L-H horizon of feather moss and humus, 6-inch Ah and a gleyed B horizon at 11 inches, developed on glacio-lacustrine clay.

Tree VII (Figures 13, 15A)

The tree, 35 years old, 18.0 feet high and 2.5 inches d.b.h., grew in a sparse stand of black and white spruce near Fox Creek, Alberta. The vegetation was paper birch, Labrador tea, grasses, bunchberry and twin-flower. The very poorly-drained Gleysolic (Peaty Rego Humic Gleysol) soil, formed on lacustrine clay, had a 6-inch L-H horizon of sphagnum and decomposed peat and a 4-inch Ah which was underlaid with gley.

Tree VIII (Figures 14, 15B, 22)

The tree, 88 years old, 32.9 feet high and 4.1 inches d.b.h., grew in a dense stand of white and black spruce and tamarack on a high terrace near the mouth of Hay River, Northwest Territories. The vegetation was paper birch, sedge and an almost continuous carpet of feather mosses (*Hylocomium splendens, Pleurozium schreberi* and *Ptilium crista-castrensis*). The waterlogged Gleysolic (Rego Humic Gleysol) soil, developed on lacustrine sand, had a 5-inch L-H horizon of feather moss and humus and 12-inch Ah underlaid with a mottled C Horizon. Free water was present at the surface in the middle of July.

Tree IX (Figure 16)

The tree, 35 years old, 20.3 feet high and 3.0 inches d.b.h., grew in a mixed stand of balsam poplar and mountain alder on the shore of Great Slave Lake at Vale Island, near Hay River, Northwest Territories. The only vegetation was woodland horsetail. The well-drained Regosolic (Orthic Regosol) soil was coarse lacustrine sand deposited on a levée. The profile showed a 3-inch deposit on a 31-inch deposit both of which overlay a 2-inch humus layer on top of sand.

Tree X (Figures 17, 19A)

The tree, 33 years old, 23.7 feet high and 3.4 inches d.b.h., grew in a dense stand of white spruce on the Simonette River south of Valleyview, Alberta. The ground cover was willow, stiff club-moss, mooseberry, twinflower, grasses and feather moss. The well-drained Podzolic (Bisequa Gray Wooded) soil, developed on very fine aeolian sand, had a 6-inch decayed log on top of a 3-inch Ae, 6-inch Bf and a deep C/B+ horizon.

Tree XI (Figures 18, 19B)

The tree, 56 years old, 18.8 feet high and 3.8 inches d.b.h., grew in a sparse stand of white spruce near Goodwin, Alberta. The ground cover included willow, Labrador tea, sphagnum, *Pleurozium schreberi* and bog cranberry. The very poorly-drained Gleysolic (Peaty Orthic Humic Gleysol) soil, which developed on alluvial deposits, had a 6-inch L-H horizon of partly decomposed sphagnum and sedges overlaying a 4-inch Ah and a 16-inch gleyed sandy clay B horizon.

Tree XII (Figure 20)

The tree, 43 years old, 24.1 feet high and 3.1 inches d.b.h., grew in an open stand of white spruce mixed with tamarack and black spruce in an abandoned alluvial channel north of Fort Providence, Northwest Territories. The vegetation was mountain alder, paper birch, Labrador tea, grasses and sphagnum. The sphagnum was dead except in occasional moist depressions. The imperfectly drained Organic soil has partially decomposed sphagnum overlaying decomposed sphagnum and sedges and a gleyed mineral horizon at 14 inches.

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