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Author(s): A. B. Hatch and K. D. Doak

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MYCORRHIZAL AND OTHER FEATURES OF THE ROOT SYSTEMS OF PINUS

A. B. HATCH AND K. D. DOAK

With plates 57-60

The distinctive anatomical and morphological features of mycorrhizal and non-mycorrhizal root systems, as illustrated by those of *Pinus,* are the subject matter of this paper. The discussion, although limited to *Pinus,* considers some features that are common to all ectotrophic mycorrhizal organs of woody plants.

The term ectotrophic mycorrhiza refers to a distinct morphological organ consisting of a "short root" and a fungus that are constantly arranged in an orderly manner with reference to each other. It is a well-defined organ and need not be confused even with its nearest relative the pseudomycorrhiza. Frank (1885) coined the term "mycorhiza"—a compound of Greek terms meaning "fungus root." He described the structure as neither root nor fungus, but rather—analogous to the thallus of the lichen—an association of two differing components to form one morphological organ.[1]

The use of the term mycorrhiza in reference to ectotrophic structures (under which we also include the ectendotrophic forms for con-

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[1] In his first paper on mycorrhiza with reference to the absorbing roots of Oak, Beech, etc., Frank stated that they consist of two kinds of elements—(1) "aus einem Kern, welcher die eigentliche Baumwurzel repräsentiert, und" (2) "aus einer mit jenem organisch verwachsenen Rinde, welche aus Pilzhyphen zusammengesetzt ist." "Der ganze Körper ist also weder Baumwurzel noch Pilz allein, sondern ähnlich wie der Thallus der Flechten, eine Vereinigung zweier verschiedener Wesen zu einem einheitlichen morphologischen Organ, welches vielleicht passend als Pilzwurzel, Mycorhiza bezeichnet werden kann." (Frank, 1885, p. 129.)

The frequent subsequent use of the term mycorrhiza (or mycorhiza) to describe a condition rather than an organ is the result of the absence of such a definite organ in Orchidaceae and Ericaceae, where endophytic infection by one mycelium may occur in roots, stem, leaves and seeds. The usages of the one term to indicate either a condition or an organ are not compatible; consequently it would seem advisable to extend our terminology. One of the difficulties of the dual meaning is the use of the singular noun in the plural sense. Thus the singular "mycorrhiza" is frequently employed in referring to a number of short roots that collectively have been converted into "mycorrhizae." In view of Frank's original definition this is obviously incorrect.

The word mycorrhiza is compounded from the Greek μύκη, a rare variant of μύκης "fungus," and of ῥίζα "root," with ῥῤ (rrh) medially (as usual) and αἱ in the plural (since ῥίζα is a feminine noun of the first declension), which in botanical usage is latinized, becoming *"ae."* Most authors have adopted the plural endings of their respective languages in their writings on ectotrophic mycorrhizae, but in English this is awkward phonetically. Kelley (1931) therefore adopted the latinized Greek plural ending, while retaining the single "r" of Frank. The spelling employed in this paper is the one considered preferable by authorities on the Greek language.

venience) is restricted by most European investigators to such an organ formed from short roots. Elsewhere, the term is frequently used to indicate indiscriminate fungal attacks on "long" as well as on "short roots." McArdle (1932) for example has recently published photographs (Figs. 1 to 6 and plate 2) of root systems of Pine and Spruce grown in open culture synthesis experiments to support his belief that certain fungi investigated form mycorrhizae with the roots of those trees. In figure 5 (ibid.) a dead radicle is illustrated from which three replacement radicles have emerged and grown geotropically. These are labeled "Mycorrhizae on Norway spruce, formed in synthesis with *Lycoperdon gemmatum.*" It is evident from this photograph and from the others mentioned above that long roots are considered to be mycorrhizal organs. Neither these nor any of the visible short roots, however, exhibit the external characters possessed by a typical mycorrhiza. Since conversion of root tips into mycorrhizal structures is probably dependent on slow elongation rates it is improbable that long roots (rapidly growing roots) can be converted into "fungus roots" while the short roots (slow growing roots) of the system remain uninfected. Again, among 21 photographs and drawings of roots of culture plants reported to be mycorrhizal by Masui (1927, figs. 63-84) one drawing only (fig. 83) is included that illustrates a structure characteristically mycorrhizal (ectotrophic). Illustrations of non-mycorrhizal intracellular infection, of cells evidently taken from long roots, are common (figs. 75 and 76).

Further confusion in mycorrhizal studies has resulted from failure to qualify the use of the terms "large root" and "rootlet." The latter evidently has been used to cover all elongating roots (McArdle, 1932). In connection with the former, Masui (1927, fig. 90) and others have used microchemical methods for studying the physiological functions of mycorrhizal roots and in so doing have apparently compared mycorrhizal "short roots" with non-mycorrhizal "large" or "long roots." The impropriety of comparing such roots microchemically may account for the diversity of opinion among these investigators concerning the physiology of mycorrhizal associations.[1]

The profuse surface growth of non-mycorrhizal and probably parasitic fungi on roots has frequently caused such roots to be mistaken for true mycorrhizal structures. Thus abundant and apparently parasitic

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[1] McArdle (1932, p. 292) states that all investigators who have used this technique agree that "mycorrhizal fungi are parasitic upon the associated higher plants, and that there is no evidence of a symbiotic relationship." However, Rexhausen (1920) and Aali (1923) came to views exactly opposite, namely that mycorrhizal fungi are beneficial to the associated higher plant; Weevers (1916) is uncertain of the relationship, and Weyland (1912) and Masui (1927) conclude that parasitism exists.

attacks (with sporophore production) of certain Gasteromycetes on mycorrhizal roots, roots already mycorrhizal through association with Hymenomycetes, have recently been observed in several instances by the authors (further communication by Doak). Recognition of the nature of such secondary attacks is often extremely difficult, a fact which undoubtedly accounts for much confusion in the literature.

Attempts to learn of the abundance of the mycorrhizal roots of trees by reviewing the world's literature of these structures are singularly futile. With few notable exceptions investigators have either neglected to define their use of the term "mycorrhiza," failed to apply it exclusively (and quantitatively) to those roots known as short roots (absorbing roots, "Saugwürzelchen oder Ernährungswurzeln") or omitted a tally and description of the roots they have not listed as mycorrhizal.

In America, McDougal (1928) has reported repeatedly upon the existence of mycorrhizal structures on forest tree roots. One gathers from his papers that although they are widely distributed they are relatively nonabundant and in fact are somewhat infrequent if present at all on some species. For a number of years the authors have devoted their attention, almost exclusively, to the study of the mycorrhizal roots of forest trees both in America and Scandinavia. During this period they have rarely observed short roots (on forest trees over one year in age, growing in good forest soil with pH less than 5.5) that were not mycorrhizal. This is in line with the observations of numerous investigators, including Frank (1885) in Germany who recorded the invariable conversion of short roots into mycorrhizal roots, and also including, Melin (1917, 1923, 1925 and 1927) in Sweden. Kelley (1932) reports similar phenomena for practically all woody plants he has examined in the eastern and middle western United States during the past four years.

The apparent lack of agreement among workers in this field arises in part from failure to distinguish the various root forms. The diagnostic characteristics of the several types of roots occurring on Pine are discussed below.

CLASSIFICATION OF PINE ROOT SYSTEMS

Root systems of conifers exhibit several kinds of roots and are therefore called "heterorhizic" by Noelle (1910). Two broad types are distinguished: (1) long roots ("Bereicherungswurzeln") and (2) short roots or absorbing roots ("Kurzwurzeln, Saugwürzelchen" or "Ernährungswurzeln"). Anatomically these differ in *Pinus* as follows:

1. Long roots are furnished with root caps, while short roots lack

this structure, having a few layers only of cells beyond the plerome apex. (Plate 57, A and B.)

2. Long roots are diarch or polyarch, while short roots are monarch. (Plate 57, D.)

3. The diameter quotient, that is, ratio of stele diameter to total diameter, of short roots is significantly lower than that of all other types of roots (Aldrich-Blake, 1930, p. 24).

4. Long roots exhibit secondary growth, while this condition has never been observed in short roots (Noelle, 1910, reports a questionable observation to the contrary).

5. Root hairs arise from the second or third layer of cortical cells in long roots (Plate 59, D; Noelle, 1910; Aldrich-Blake, 1930) and from the epidermal cells in short roots when the latter possess these structures (Plate 57, B and D).

6. Long roots branch racemosely, while short roots branch dichotomously only. (Text fig. 1 and plate 58, C.)

In addition to anatomical differences these roots have vastly different elongation rates. Finally, barring accidents, long roots, in nature, are permanent structures, while short roots are ephemeral.

It should be mentioned that the monarch structure in uninfected short roots is demonstrated for the first time in this paper (Plate 57, D). Previous workers have apparently considered that the monarch structure resulted from infection by mycorrhizal fungi. Noelle (1910, p. 254), for example, writes—"Die unverpilzten Ernährungswurzeln besitzen dagegen einen wohl ausgebildeten diarchen Protoxylemstrang, . . ." The materials Noelle studied were all from soils. It is probable, therefore, that most of the short roots were converted into mycorrhizal structures, and that Noelle's "unverpilzten Ernährungswurzeln" were in actuality arrested diarch lateral root initials. The latter are described in detail below in the section headed "Types of long roots."

The gross characteristics of long and short roots are illustrated in Text figure 1. The root system of a seedling grown in a mixture of sand and forest humus (the infektionsjord of Hesselman, 1927, p. 361; also Gast, unpublished) is shown. It has 24 long roots (totaling 65 cm. in length) in addition to a 25 cm. radicle or tap root. Including arrested laterals it had 435 short roots (quite a few of which were broken off in transit to America before the photograph was taken). Arrested laterals are to be noted along the radicle and on one uppermost side branch. A slow-growing lateral that was not attacked—as evidenced by absence of swelling and of dichotomy in the basal portion—by a mycorrhizal fungus until it had reached a length of about 1 cm. is marked by the digit "4." The short roots are either mycorrhizal or

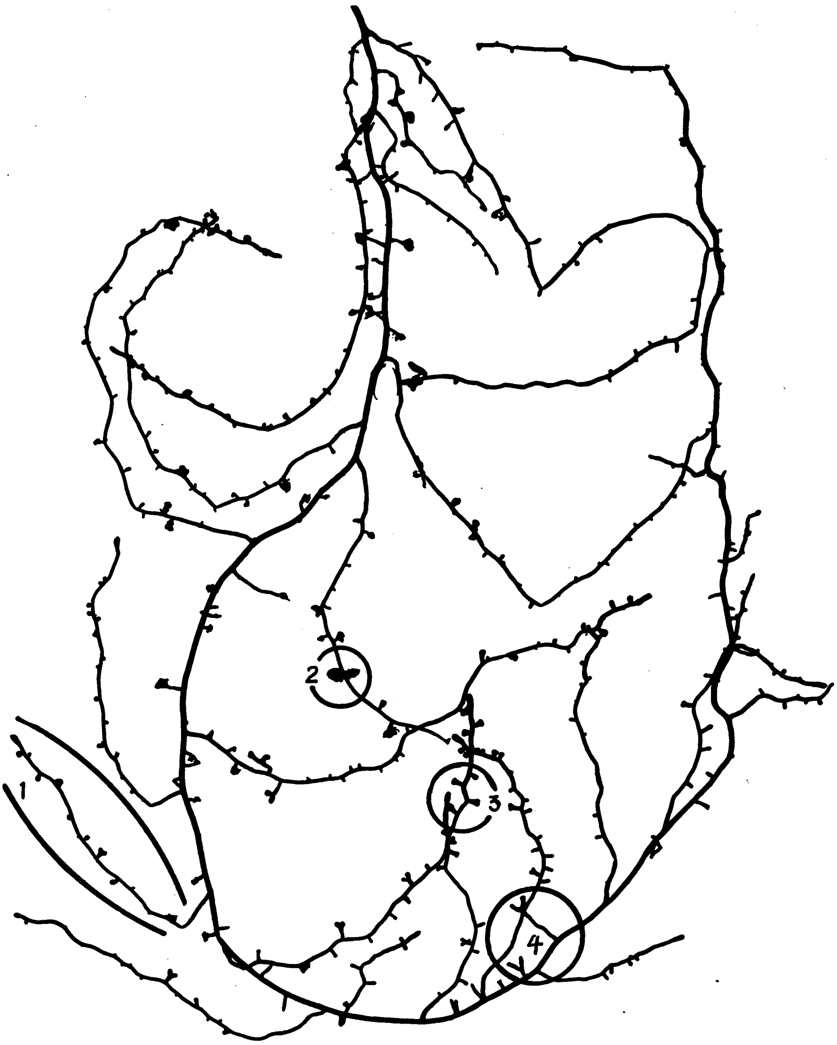

FIGURE 1. ROOT SYSTEM OF PINUS.

Entire root system of a three months old seedling of *Pinus sylvestris* L. grown in sand-mixed humus (infeksionsjord Jönåker, Sweden; unpublished material of P. R. Gast's, Harvard Forest); × 1.58. (1) Mother root, the tip of which is mycorrhizal; (2) short roots attacked by *M. R. atrovirens* type of fungus; (3) dichotomously branched short roots; (4) arrested lateral root initials.

pseudomycorrhizal. Mycelium of the *Mycelium radicis atrovirens* type (Melin, 1923, p. 223) is visible on many of the short roots. The longest true short root on the system does not exceed 3 mm. in length.

The comparative abundance of long and short roots on experimental seedlings is given in Table 1. These seedlings had an average of 19 long roots and 474 short roots per seedling. Thus 96 per cent of the growing root tips are short roots. This is of considerable significance when it is considered that ordinarily these are all mycorrhizal, while the remaining 4 per cent—long root tips—on the other hand rarely acquire this structure.

TYPES OF LONG ROOTS

The term "long root" includes (a) the radicle or tap root (also a replacement radicle should the original radicle be injured), (b) diarch laterals called "mother roots" and (c) polyarch continuations of mother roots termed "pioneers." Of these the radicle is the most strongly developed root in young seedlings. It is polyarch, has a large diameter quotient and a large and well-developed root cap. Lateral roots emerge from the radicle. These either abort (see below) or become mother roots. The latter are diarch and are characterized by a moderate elongation rate and by the production of numerous short roots and secondary laterals. At variable distances from their points of origin mother roots are converted into pioneer roots by augmentation of the number of protoxylem strands. (In Scots Pine, however, all long roots remain diarch, Noelle, 1910). Pioneer roots are the most poorly-branched members of pine root systems, largely because of abortive secondary root initials (Aldrich-Blake, 1930). Pioneer roots elongate rapidly, have an intermediate diameter quotient, and a well-developed root cap. Collectively these roots markedly increase the spread of root systems. They likewise bear lateral and secondary roots in abundance (particularly true of mother roots). To what extent the growing tips of long roots, where the conduction systems are undifferentiated, function as absorbing organs is known by speculation only. The early development of secondary endodermis a short distance back of the tips presumedly soon prevents absorption. Most workers have assumed that absorption is accomplished mainly by short roots. An experimental background for the assumption is lacking. Although a long root is capable of being converted into a mycorrhiza this condition is comparatively infrequent (Melin, 1927).

A knowledge of the behavior of diarch lateral root initials is essential to a proper understanding of the mycorrhizal habit. Three destinies are possible as follows: (1) they may abort before or during emergence or before they have reached an appreciable length; (2)

TABLE 1. ROOT MEASUREMENTS OF 3 MONTHS OLD PINUS SYLVESTRIS L. SEEDLINGS GROWN IN SAND MIXED HUMUS

Seedling number	Number of long roots Total	Number of laterals over 1.5 cm. long	Length of radicle cm.	Total length of laterals cm.	Length of longest lateral cm.	Total length of all long roots cm.	Number of short roots	Number of short roots per 10 cm. of long roots
1	21	16	26	54	6	80	596	77
2	17	12	27	51	5	78	489	74
3	21	12	25	53	10	78	504	70
4	27	18	25	90	11	115	535	55
5	19	10	23	59	7	82	540	72
6	21	18	18	97	11	115	700	70
(Average 6)	21.0	14.3	24.0	67.3	8.3	91.3	560.3	69.7
1	16	12	17	63	11	80	304	47
2	13	9	17	41	7	58	400	76
3	18	13	20	50	6	70	399	57
4	16	8	21	30	4	51	272	78
(Average 4)	15.8	10.5	18.8	46.0	7.0	64.8	343.8	64.5
Average 10	18.9	12.8	21.9	58.8	7.8	80.7	473.7	67.6

Upper six seedlings grown in inoculation earth (infecktionsjord, Hesselman, 1927) in 50% solar radiation minus short ultra-violet (λ 0.31 to 0.30 μ) and infra-red; lower four in good raw humus (ibid.) in 50% solar radiation minus ultra-violet; all were grown at the Royal Institute of Experimental Forestry, Stockholm, Sweden.

they may be attacked by microörganisms with resultant conversion into mycorrhizal or pseudomycorrhizal structures; (3) they may, by continued growth, become mother roots. The latter in turn give rise to initials having the same possible destinies and to monarch short roots.

The distribution of lateral root initials along the radicle in Corsican Pine, their growth and their anatomical features have been studied by Aldrich-Blake (1930). He found that seedlings grown in a sandy soil produced initials opposite any of the four protoxylem points at distances of 1.6 to 2.7 mm. apart. One-half of these became abortive before they grew one millimeter in length and only one-sixth grew beyond the very moderate length of 10 mm. The termination of growth in many initials at an early stage was associated with mycorrhizal formation. The question of whether they were predestined to become mother roots or mycorrhizal roots was therefore examined. Internal as well as external factors were judged to be operative as evidenced by the finding of an abortive initial that had ceased growth while still within the intact endodermis of the parent radicle (l. c., p. 22). It was further determined that the initial size of the roots which became mycorrhizal was distinctly smaller than that of those which continued growth and became mother roots. Aldrich-Blake writes, for example—"The mean protoxylem diameter of the mother roots was 117 ± 6 μ, while that of the diarch basal portion of the dichotomized roots was 73 ± 3 μ; and the probability of significance of the difference between these two measurements was over 100 to 1" (l. c., p. 23). He concluded that the two types of roots were distinct from the very beginning in respect to size and that conversion to mycorrhizal organs was "the response of feeble roots to strong fungal infection" (l. c., p. 24). Melin (1925) also presents convincing evidence that many laterals are "feeble" from the very beginning. It is apparent from photographs (Melin, l. c., pp. 60-62, figs. 23-27) of *Pinus sylvestris* that even in the complete absence of microörganisms and in a uniform substratum the common differentiation of laterals into slow-growing roots and mother roots still occurs. After three years many of the slow-growing laterals on pure culture seedlings had not reached the length of one centimeter (l. c., 1925, p. 61).

During examinations of approximately 2500 seedlings of *Pinus sylvestris* L. and *P. Strobus* L. grown in pot cultures (containing mixtures of forest humus or soil and sand) one of the authors has observed that only in the autumn, after elongation of the rapidly growing long roots has nearly ceased, do the tips of the latter frequently acquire the mycorrhizal structure (Plate 59, A). This leads us to believe, especially in view of the slow elongation rate of short roots which normally are always converted into mycorrhizal organs, that rapid elongation is the primary reason long roots ordinarily escape attack by mycorrhizal fungi. This hypothesis assumes (1) that mycorrhizal fungi can only successfully attack a root in the primary condition, and (2) that in rapidly growing long roots the secondary condition is acquired before mycorrhizal fungi are able to penetrate sufficiently to initiate the characteristic response. Rayner (1927, p. 99) has in part explained a somewhat similar phenomenon, namely, the absence of the endophyte from rapidly growing roots of *Calluna vulgaris* (L.) Salisb. in the early spring, by assuming differential growth rates for fungus and root at low spring temperatures. The same phenomenon is probably operative in tree seedlings, except that root growth rather than fungal growth is assumed to be retarded by low temperatures or other factors. In this connection a seedling of *Pinus resinosa* Ait. grown under very adverse conditions in pure culture has been observed to have all of its roots (long as well as short) converted into mycorrhizal roots (later communication by Hatch). We conclude, therefore, that every root tip in the primary condition is theoretically capable of conversion into a mycorrhiza. That this normally does not occur in nature we attribute to differences in rapidity and character of growth of long and short roots.

Lateral root initials that become mycorrhizal (Plate 59, B) acquire the monarch structure in the dichotomized branches above their diarch basal portion, and they are ephemeral structures. They undoubtedly function in the same manner as true mycorrhizal short roots. For the purpose of our present discussion, therefore, we may include them in the category of short roots.

TYPES OF SHORT ROOTS

Three distinct kinds of short roots may be distinguished: (1) the uninfected short root, (2) the infected short root in which the mycorrhizal structure is absent (pseudomycorrhiza), (3) the infected short root which has acquired the mycorrhizal structure (mycorrhiza).

The first of these, or uninfected short roots, are distinguished by the following features (Plate 57, B):

1. Formation of root hairs from epidermal cells (when grown in a suitable nutrient solution and in a substratum that is adequately aërated).
2. Continuous although slow elongation.
3. Absence of hypertrophy of cortical cells.
4. Complete absence of fungus infection.
5. Frequent but not profuse dichotomy[1] (Melin, 1925, figs. 23, 24).

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[1] It should be noted that dichotomous branching of the short roots is an exclusive habit, so far as is known, of the genus *Pinus* among conifers. The term

This type of short root is exceedingly rare. It appears consistently and probably exclusively in pure cultures and in open, mineral solution sand cultures that are free from organic materials. Root hair production is dependent on the condition of the substratum relative to aëration and chemical composition (Melin, 1925, p. 61). It is notable that root hairs on short roots are elongations of epidermal cells (Plate 57, B and D). Its diagnostic value, considering that all root hairs on long roots of Pine originate from the second or third layer of cortical cells (Aldrich-Blake, 1930, p. 16; Noelle, 1910; and Plate 59, D of the present paper), has not been emphasized. In pure culture short roots exhibit renewed yearly growth in length and have been reported to reach a maximum length of 20 mm. in two years (Melin, 1925, p. 60). The absence of a root cap on mycorrhizal roots is considered to be a natural consequence of attack by mycorrhizal fungi by Laing (1932). McArdle (1932, p. 312) on the other hand attaches physiological significance to the presence of this structure in mycorrhizal roots. That it actually is not present on either uninfected or mycorrhizal short roots in *Pinus* is demonstrated in Plate 57, A, B and C.

The second type of short root exhibits infection, but of a distinctly non-mycorrhizal type. The name pseudomycorrhiza was given to this structure by Melin (1917). Melin applied it to short roots possessing the following features, which likewise are characteristic of American material:

1. Intracellular infection by soil inhabiting fungi that are usually of minute proportions.
2. Absence of root hairs.
3. Absence of hypertrophy in cortical cells of the roots.
4. Complete absence of intercellular net (Hartig's net).
5. Early termination of growth in length (two to three millimeters is usually the maximum length).
6. Occasional dichotomous branching.

The general habit of pseudomycorrhizal roots of *Pinus sylvestris* is illustrated in Plate 58, A. A longitudinal section of one of these is reproduced in Plate 57, A. A common type of infection of the cortical cells is shown in Plate 60, B, C and D, and by Melin (1917, fig. 39). Möller (1902) first called such a structure an "entotrof" mycorrhiza because it was characterized by endophytic infection only. Melin (1917, p. 360) pointed out that it exhibits no similarity to the true endotrophic infection occurring in the *Ericaceae* and *Orchidaceae*.

"Gabelmykorrhiza" was coined by Melin (1923) in his studies on *Pinus* to cover mycorrhizal roots characterized by this type of branching. In this connection McArdle (1932, p. 295) has referred to the coralloid mycorrhiza of Spruce as the "Gabelmykorrhiza" of Melin; but the mycorrhizal short roots of Spruce branch racemosely and should not be confused with the dichotomous type.

Neither may it be confused with an ectotrophic mycorrhiza since the fine endophytic hyphae wander from cell to cell without regard to structure, even occurring in the endodermis and parenchyma cells of the central cylinder (l. c., p. 359). Hyphae never occur in masses in the cells (ibid.). Several species of fungi may be present at once either in abundance or in extreme scarcity. In exterior appearance a pseudomycorrhiza differs from an uninfected short root chiefly in its shorter length and darker color, when the latter does not possess root hairs.

In contrast to the foregoing root types, attack by a mycorrhiza-producing fungus normally results in short roots that possess the following well-known features:

1. Intercellular net between cortical cells (Hartig's net). Plate 59, E; Plate 60, A.
2. Intracellular infection of the cortical cells (which may or may not be discernible; Melin, 1925).
3. A fungal mantle composed of a few to many layers of tightly packed and interlaced hyphae covering the region of cell hypertrophy (Plate 60, A). The mantle has been reported to be almost completely lacking on mycorrhizal short roots of certain experimental seedlings (Melin, 1925).
4. Hypertrophy of the cells of the cortical region.
5. Characteristic profuse dichotomous branching with age (Plate 59, C).
6. Continued elongation of the dichotomous branches under favorable conditions of soil and weather during one growing season.

The external appearance and internal structure of a typical mycorrhiza is illustrated in Plate 57, C; Plate 58, C; Plate 60, A. The cells of the cortical region of an uninfected short root of *Pinus Strobus* grown in pure culture (Plate 57, C) are on the average 29 μ in radial and 61 μ in longitudinal directions. Dimensions of similar cells of a mycorrhizal short root (Plate 57, B) [also pure culture *P. Strobus* and *Lactarius deliciosus* (L.) Fr.] are 43 μ and 40 μ respectively in radial and longitudinal section (average of 15 cells in both cases). Based on the uninfected short root, therefore, the increase in radial size (hypertrophy) of individual cells is 67 per cent. The diameter of the uninfected short root is 300 μ, while the average diameter of the mycorrhiza in this case is 485 μ, an increase of about 62 per cent. Comparative studies of pure culture seedlings indicate that mycorrhizal formation in short roots of Pine is not accompanied by either hyperplasia or hypoplasia. It is evident, therefore, that Laing's statements (1932, pp. 10, 11) that the root cap disappears during the development of a pine mycorrhiza and that the number of cortical cells is less as a result of mycorrhizal formation arose from failure to distinguish between long and short roots. Attack by mycorrhizal fungi, if early in the season, almost invariably results in dichotomous branching of the short root. Judging from the exceedingly slow growth of uninfected short roots (see above), including slow growing laterals, the authors see little basis for the numerous references in the literature to the cessation of elongation of roots following attack by mycorrhizal fungi. Laing (1932), in concluding that mycorrhizal fungi exert a retarding influence on growth in length of "rootlets," evidently failed to make comparisons with uninfected short roots or to include data supporting this view. In this connection McArdle (1932) reports that he observed the formation of what he believed to be "mycorrhizae" through glass plates in sand cultures and that elongation did not proceed after attack by mycorrhizal fungi. McArdle's photographs (ibid., figs. 1-6) as well as his measurements demonstrate conclusively that he was dealing entirely with long root tips. That mycorrhizal short roots do grow after attack by the causative fungus is adequately evidenced by profuse dichotomy which probably never occurs in the absence of true mycorrhizal infection. Likewise the present authors have observed continued growth and branching of typical mycorrhizal short roots, individually, in their own pure cultures on several species of Pines in association with several species of Hymenomycetes. The profuse branching of a mycorrhizal short root of *P. Strobus* is illustrated in Plate 59, C. This short root has approximately 50 individual growing tips; another growing beside it had 84; in fact, all of the short roots on the long root from which these were taken were much branched. We can find no reason to assume that the total length (from the base of the mycorrhiza to the tip) of any of the numerous tips is less than the total length of the short root would have been had it remained non-mycorrhizal. Instead, multiple tip growth represents a greatly accelerated development which increases the absorbing surface many times. In this connection, it is to be noted that by means of hypertrophy of the cortical cells and increase in surface area by means of absorbing fungal hyphae the surface area of a single-tipped mycorrhizal short root seemingly already exceeds that of an uninfected one. A comparative study of the actual absorbing power of mycorrhizal and non-mycorrhizal short roots should yield interesting results.

We have shown that anatomically and morphologically a short root, the organ ordinarily involved in an ectotrophic mycorrhiza, differs markedly from a long root. It seems logical to assume that these root types differ as fundamentally in their physiological functions. In investigations designed to elucidate mycorrhizal nutrition, therefore, it is essential that these differences be recognized and that the types and subgroups of roots be adequately separated. Similarly in ecological studies, when the abundance of mycorrhizal roots is given in percentage or other figures, these data should apply to short roots only; and these should be separated into the three subgroups—mycorrhizal, pseudomycorrhizal and uninfected short roots respectively.

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Laboratory of Plant Pathology, Arnold Arboretum, and the Department of Botany, Harvard University.

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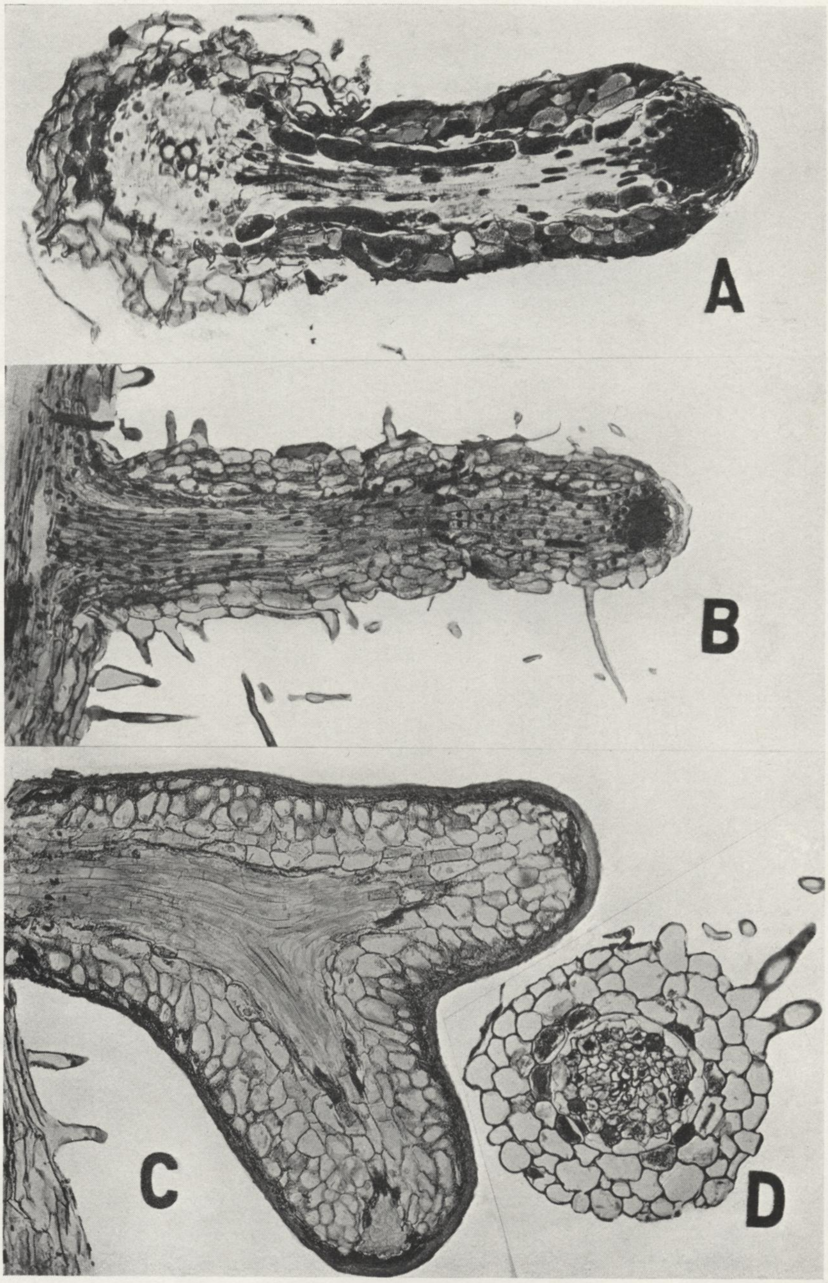
DESCRIPTION OF PLATES

Plate 57. A. Longitudinal section of a pseudomycorrhiza of *Pinus sylvestris;* × 119. (Unpublished results of a growth experiment with Swedish soils of varied carbon nitrogen ratios conducted by Professor E. Melin and the senior author.) See also Plate 58, A.

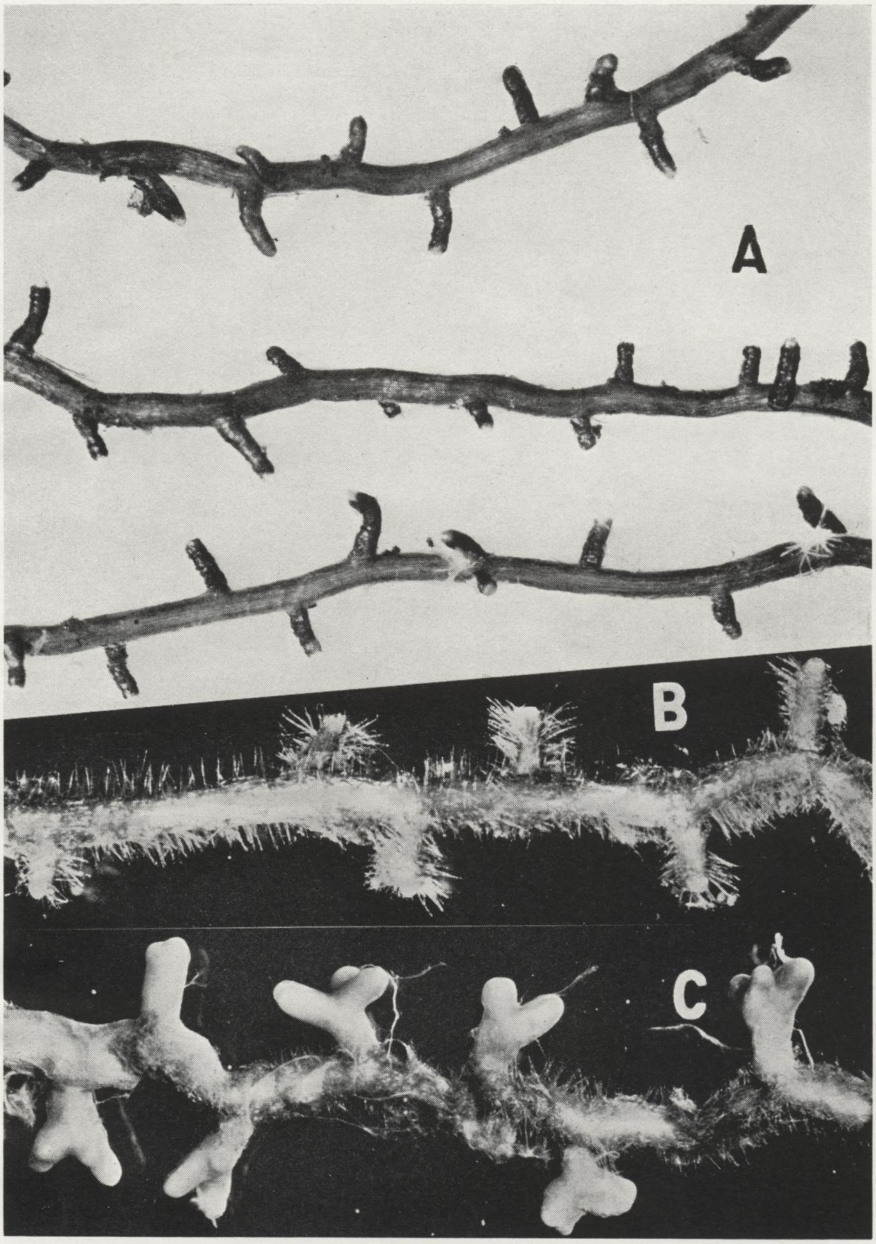
B. Longitudinal (not medial) section of *P. Strobus* short root grown in pure culture, showing absence of hypertrophy and a root hair arising from an epidermal cell; × 69.

C. Longitudinal (not medial) section of dichotomized mycorrhizal short root of *P. Strobus* grown in pure culture with *Lactarius deliciosus* showing mantle, intercellular net and cell hypertrophy; × 67. (Ditto; Plate 58, C.)

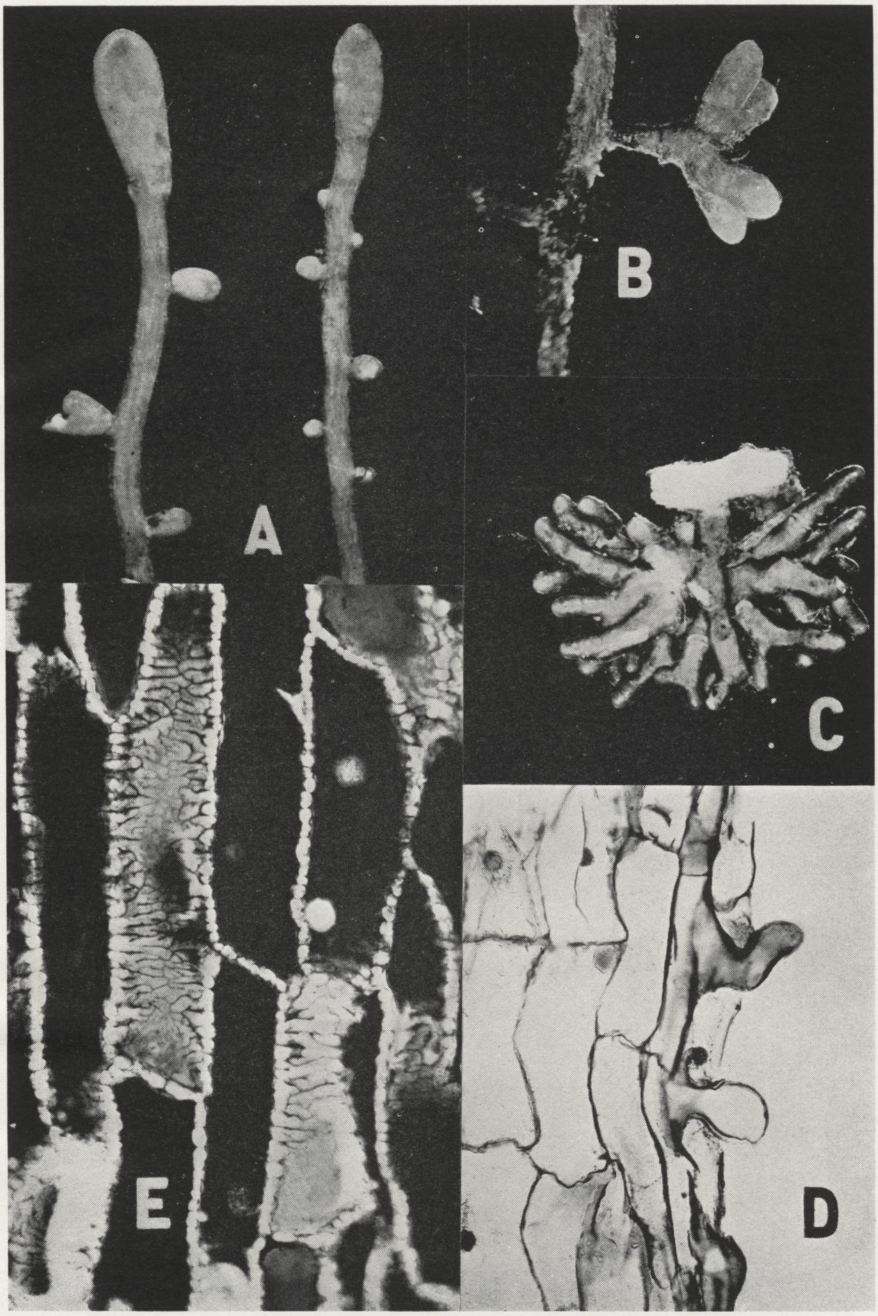
D. Transverse section of monarch short root of *P. sylvestris* grown in open sand culture showing root hairs arising from epidermal cells; × 123. (Nutrient sand culture.)



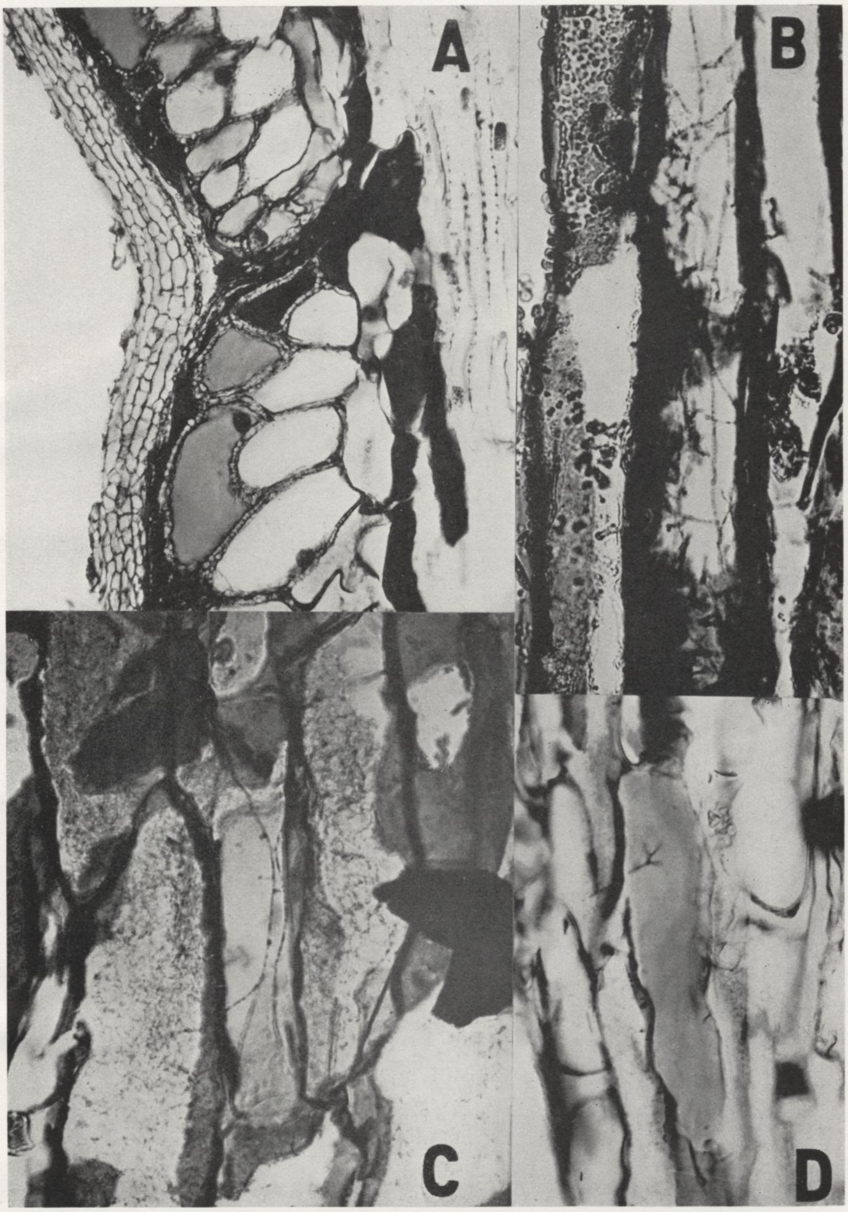
Mycorrhizal and other Features of the Root Systems of Pinus.



Mycorrhizal and other Features of the Root Systems of Pinus.



Mycorrhizal and other Features of the Root Systems of Pinus.



Mycorrhizal and other Features of the Root Systems of Pinus.

Plate 58. A. Pseudomycorrhizal short roots on mother root of *P. sylvestris;* × 12. (Ditto; Plate 57, A; material from unpublished data of Professor E. Melin and the senior author.)
B. Uninfected short roots possessing root hairs on mother root of *P. Strobus* in pure culture; × 12.

C. Mycorrhizal short roots on mother roots of *P. Strobus* grown in pure culture with *Lactarius deliciosus;* × 10.

Plate 59. A. Mycorrhizal mother root tips of *P. Strobus;* plants removed from soil after onset of cold weather, showing also young mycorrhizal short roots; × 8.8. Grown in sand-mixed humus (Infektionsjord from forests in Sweden. See Hesselman, 1927, and Gast, unpublished.)
B. Lateral root initial from radicle of *P. sylvestris* converted into a mycorrhiza; basal portion pseudomycorrhizal; × 12.5.
C. Profusely branched short root of *P. Strobus;* × 8.8.
D. Root hairs on long root of *P. Strobus* originating subepidermally; × 470.
E. Intercellular net (Hartig's net) in a mycorrhiza of *Tsuga canadensis* (L.) Carr.; × 512.

Plate 60. A. Mantle structure and intercellular net of cortical cells in a mycorrhiza of *P. rigida* Mill.; × 330.
B, C and D. Pseudomycorrhizal type of infection in long roots of *P. Strobus;* × 512.