

MYCORRHIZA BEARING SPECIES IN THE VICINITY
OF LAFAYETTE, INDIANA.¹

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Accounts of mycorrhiza investigations up to the present time have been reviewed by Rayner (1926, 1927) and Waksman (1927). The distribution and extent of development of mycorrhiza in plants has been recorded more completely for native species in Europe than in America. In the United States the investigations of McDougall (1914, 1916, 1927), Lohman (1926), Jones (1924), and Coville (1910) indicate that mycorrhiza-producing fungi are widely distributed. While the European workers: Gallaud (1905), Janse (1897), Magrou (1921, 1925, 1927), Bernard (1910, 1911), Demeter (1923), Bjorenheim (1904), Constantin (1924), Magnus (1901), Frank (1885, 1887, 1888, 1891), Melin (1922, 1925), Melin and Helleberg (1925), Peklo (1909), Reyronel (1921, 1923), Nicholas (1924), Woronin (1885), Wolff (1926), Stahl (1900), Tubeuf (1903), Weyland (1912), Rayner (1915), McLennan (1926), and Ternetz (1904) have arrived at conclusions regarding the physiologic effects of mycorrhiza-producing fungi on roots, the evidence has often been so conflicting or insufficient as to demand further investigation. In many cases this was due to a lack of knowledge concerning the identity of the fungi or the methods of isolation. According to a classification of symbiotic phenomenon set up by McDougall (1918), the works of McLennan (1926) on the fungus of *Lolium temulentum*, and Rayner (1915, 1922) on that of *Calluna vulgaris* indicate that reciprocal, nutritive, conjunctive symbiosis occurred. The fungi were not only found in parts other than the roots but were also thought to be seed transmitted. A similar obligate symbiosis observed by Ramsbottom (1924), Kusano (1911), Constantin (1926), Burgeff (1909), and Bernard (1911) between a fungus and the bulbs of orchids during germination and early growth stages, has been found by Knudson (1924, 1925) to be due to a carbohydrate transition, possible to be produced by fungi other than the one previously supposed specific. Normal germination and growth was obtained by adding the proper carbohydrates without the fungus. Under natural conditions, however, it is apparent that these plants depend upon fungus activities. A possible increased nitrogen obtaining power of *Vaccinium corymbosum* due to the action of the ever-present root fungus has been suggested by Coville (1910), while in other members of the *Ericaceae* the fungus has been considered active in a similar capacity by Ternetz (1904, 1907) and in an entirely different manner by Christoph (1921) and Dufrenoy (1917). Jones (1924) found some

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evidence that mycorrhizas formed in the roots of leguminous plants were detrimental.

The fungi producing mycorrhizas in roots of forest trees have been considered by McDougall (1922, 1927) as antagonistic nutritive conjunctive symbionts acting as parasites. A similar parasitic nature of the mycorrhizas of *Alnus* and *Quercus* in Japan has been described by Masui (1926). As a result of extensive cultural experiments with European forest mycorrhiza-producing fungi, Melin (1925) concluded that the hosts or higher plants derived some benefit. It is evident that the physiological processes in roots bearing mycorrhiza is not completely understood.

Types of mycorrhiza. The term "mycorrhiza" has been used to designate the condition of a fungus-root system in which the fungus forms a specialized structure either around or upon the root surface, between the cells (inter-cellular), or within the cells (intra-cellular). Used by Frank (1885) to describe the mass of filamentous strands surrounding the tips and passing between the outer cell layers of forest tree roots, it has since been applied to the intra-cellular structures often found in the same roots and wrongly to the entire fungus-root or to the fungus itself, regardless of the structure formed.

The division of mycorrhizas into two general types has been based upon the position assumed by the fungus with respect to the root cells. The term "ectotrophic" has been used to describe the type forming external mantles and intercellular structures, while those forming intra-cellular structures have been termed "endotrophic." It has been observed by Masui (1926), Lohman (1926) and McDougall (1927) that some fungi produce mycorrhizas having both an intercellular and an intracellular structure. First described in *Tilia americana* as an heterotrophic form by McDougall (1914), these dual forms have since been termed "ecto-endotrophic." Fungi producing the respective forms are thus called endophytes, ectophytes or ecto-endophytes. While they have served to distinguish known forms, it is evident that the earlier terminology did not always describe the structures produced.

The identity of fungi producing mycorrhizas has been more often definitely determined in the ectotrophic forms. Kauffman (1921) identified *Amanitopsis*; McDougall (1914, 1916), *Russula*, *Boletus*, *Scleroderma*, and *Laccaria*; and Masui (1926), *Cantharellus*. Endophytes have been found by Ternetz (1907) as *Phoma*; Kusano (1911), *Armillaria*; Bernard (1911) and Demeter (1923), *Rhizoctonia*, and Pennington (1908), *Boletus* and *Tricholoma*.

Conditions for development. The production of mycorrhizas in various plants has been found dependent on the environment of both root and fungus. Growing roots and the presence of the proper fungus have been given by McDougall (1916) as essential requirements. It is evident, however, that these may be in turn modified by additional factors. Paulson (1924) considered moisture essential and found the most extensive development of tree mycorrhizas in the lower layers of the moss carpet, apparently due to a chemotoxic action of decay. While

mycorrhizas of the deciduous trees have been found in greater numbers when roots were growing in leafmold or decaying organic material, McDougall (1927) reported mycorrhizas of *Pinus flexilis* in soil composed largely of volcanic cinders. Endotrophic forms have been found by Rayner (1915) and Coville (1910) in acid soils. Lohman (1926) found mycorrhiza-like fungi more common and developing better in soils with a pH value below 6.5, although many occurred in neutral and alkaline conditions. The wide distribution of mycorrhiza in plants makes it increasingly evident that the present knowledge of physiology, length of life, and relative development of the fungi producing them under different soil conditions is insufficient to draw conclusions regarding the degree of parasitism.

Local Survey. A study of plants known in the other regions to possess mycorrhizal root structures was begun in the vicinity of Lafayette in 1925 and continued as a root-fungus survey of all possible native plants and trees in 1926 and 1927. The present paper is a list of the species bearing mycorrhizas in this locality, including a detailed description of forms not previously described and a summary of observations concerning the apparent nature of the fungus-root association. While the identification of fungi producing the mycorrhizas here studied has not been undertaken, it is hoped that the records of distribution, types, and extent of formation may serve as a basis for further physiological investigations.

The region included in this survey lies between West Lafayette and Battle Ground, Indiana, extending one mile west from the Wabash River. A series of steep wooded slopes, moist lowlands and sod-covered, pastured woods is included within this area. The predominating soil types are Miami silt loam and Wabash sandy loam with occasional narrow strips of fine sandy loam near the creeks. While these soil types are distinct in most cases many mixtures with gravel out-crops on the steeper slopes and sandy deposits near creeks are found. Soils of the wooded slopes are mostly covered by a heavy leaf-fall accumulation.

Methods of Collection and Identification. In a study of this type, accuracy in identifying the source of rootlets from a large number of species and the later determination of types of mycorrhiza from collected material was found to require special precautions. A definite method of collection was followed. Roots found upon examination with a hand lens to possess external signs of fungus association were traced to their respective plants before removal. If a field identification of the higher plants was not possible, collections of these were made for later identification.

Rootlets removed from the known plants were placed in the field into each of two fixing solutions and a solution of formalin. Formalin acetic alcohol and Schaffner's chromo-acetic fixing solutions were used. Formalin solution (1 part commercial formalin in 14.5 parts distilled water) was used for preservation of material for immediate free-hand sectioning. It was found convenient to carry about 50 vials of the three reagents, each supplied with a blank label in a portable typewriter carry-

ing case. By giving each vial and plant collection a corresponding number and placing the plant species name on each vial it was not found necessary, after recording the soil conditions and extent of development, to duplicate the results of later examination in the field records.

Fagus grandifolia Ehr. Roots collected in November 1926, April, May and from July to October 1927 have shown the presence of three distinct forms, distinguished by the character of mantle, and extent of extrance into roots.

A brown, waxy, smooth surfaced mantle and extreme hyper-enlargement of rootlets, together with the absence of filamentous strands, characterizes the least common form found in this vicinity. (Fig. 1.) Rootlets in a hard clay soil have been observed to possess this form, while in moist leafmold the other forms have been found upon each collection.



Fig. 1.—Mycorrhizas of beech (*Fagus grandifolia*). Left. Form 1, producing a brown, waxy, compact mantle Terminal root-tip of form 1, showing extreme enlargement, containing short laterals within same mantle. Form 2. Yellowish mantle, showing coarse filamentous strands attached. Form 3. White mantle, numerous fine filaments produce a woolly surface.

The second form found has a bright yellow mantle from which many stiff rhizomorph-like strands arise. (Fig. 1.) It has been observed most frequently on roots growing in rotting wood, frequently in dead stumps of oak.

Most widely distributed in this region is the third form, which produces a white, finely filamentous mantle. (Fig. 1.) It has been collected from both a moist and dry situation but develops to greatest extent in moist leafmold. Of these three forms, the first seems in some cases to live for two years, especially on terminal, strongly growing roots. While this form seems to produce a small amount of intercellular growth, the root tips were found to have several laterals which apparently turned forward into the same enclosing mantle. Paulson

(1924) described a brown, waxy form on *Fagus sylvatica* in England but, since this character is not mentioned, it is probably produced by a different fungus.

Populus tremuloides Marsh. An ectotrophic form producing thick, white mantles and intercellular growth closely resembling that found in white oak was collected in this section. While identical in all characters to the form on *P. deltoides* it has not been found on all trees examined. McDougall and Jacobs (1927) described a form closely resembling this one, which was collected in a western region where it occurred only in rotten wood. The lack of extensive mycorrhiza development on this plant cannot be attributed to lack of moisture in the situations most commonly found. It has been observed, however, that it occurs in sandy wash soil which is seldom permanently covered by leafmold.

Populus deltoides Marsh. Densely filamentous mantles were found during July and August, 1927, on trees growing in a wet, sandy soil near the mouth of a creek. The absence of leafmold on the surface did not seem to hinder development. Lohman (1926) described both an ectotrophic and an endotrophic form for this species but did not mention the mantle color of the former. Numerous dead roots and mantles found among the living ones collected in late summer indicates an annual development of this form. It has been found in this section only in a continually moist situation.

Carya cordiformis (Wang.) K. Koch. A white ectotrophic form was collected August 1, 1926, and repeatedly until December 1 the same year. Sections made during the fall and from material collected in April the following year showed groups of fungous strands passing beyond the first layer of slightly radially elongated cells and in contact with the first cortical layer. It was observed during intervals of collecting that mantles of this form became completely developed within a period of 10-12 days and did not become larger during the remainder of the season. Aside from the lack of decidedly radially elongated cells of the first layer, this form agrees with the form 3 described by McDougall (1914) on *C. ovata*. In this section it was found on all roots growing in and several inches below moist leafmold.

Carya ovata (Mill.) K. Koch. An ectotrophic form producing yellow mantles was found in late September, 1927. In removing roots from loose soil it was observed that many soil particles adhered to the mantle surface. The filamentous character of the mantle resembles the form 1 described on this species by McDougall (1914). While it has been collected in this locality from trees growing in sod and in all excepting very dry conditions, the mycorrhizas always occurred in clumps of decomposing grass roots near the surface and occasionally in portions of dead roots deeper in the soil. From a collection made on May 10, 1927, living roots having fully developed mantles apparently formed in the previous growing season were obtained. Since in the two attempts to collect during late June only brown mantles on dead roots were available, this form is probably always annual.

Tilia americana L. Dense, smooth, gray mantles were found in groups whenever they had access to surface accumulation of moist

organic matter. In 1927 they were found in leafmold above dry gravel subsoil from late July until October. This was apparently the heterotrophic form 6 described by McDougall (1914) as having, in addition to a mantle and intercellular growth, occasional intracellular strands. Since roots collected August 15 did not show the latter development, it is probable that it occurs only late in the season or under adverse conditions. Living mantle-covered roots were not found during June.

Cercis canadensis L. Two types of mycorrhiza development were found. The first, a yellow, compact mantle covering entire root tips was found in moist leafmold in two collections. In the second type a mantle-like pseudoparenchymatous mass of yellow mycelium was found tightly attached to the roots 4-5 millimeters back from the tips. Occurring as a modified mantle, it was found in some cases passing entirely around and in others compactly appressed to one side or partially enclosing the root. This condition was found most commonly in the more moist soils. While it is apparently due to the rapid root growth at the time the mantles are being formed, this plant is known to show a less rapid root development than other forest trees. The reasons, however, for the affinity of the ectotrophic forms for root tips are not clearly

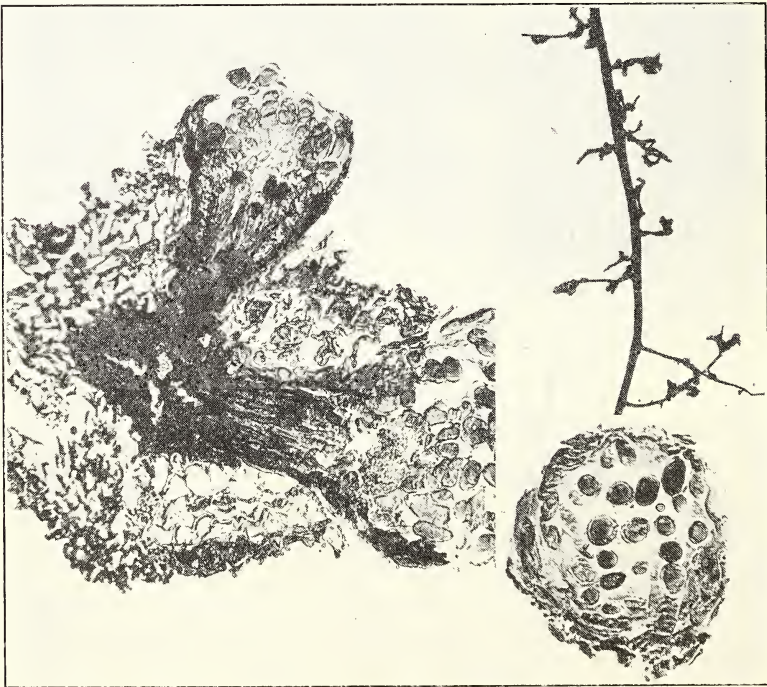


Fig. 2—The mycorrhiza of ironwood (*Ostrya virginiana*). Left. Transverse section of root near tip, showing intercellular development of fungus in growing points of laterals. Transverse section of short lateral, showing separation of cells by groups of fungous strands. Roots fresh from soil, showing profuse branching near tips.

understood, and it is probable that the condition here observed was due to a difference in the rate of development of the fungus or to a toxic root exudation at the tips.

Ostrya virginiana (Mill.) Will. The ectotrophic form occurring in this vicinity was found upon sectioning and staining to bear a peculiar relation to root laterals. The white mantles usually found in late July to produce only slight intercellular growth were found in roots collected October 7 and 8 to extend between the outer cell layers of short laterals. (Fig. 2.) Entry occurred at the tips. These were apparently produced on roots having the early formed mantles. Rapid entry of the filamentous strands between the cells inhibited all further growth of laterals, while in some roots disintegration had resulted. Lohman (1926) reports a thick mantled ectotroph for this species and in one collection an endotroph. This mycorrhiza has been found under all soil and moisture conditions favorable for growth of the plant.

Carpinus caroliniana Walt. The ectotrophic smooth white or gray mantle and compact structure of strand groups passing from the mantle surface into the leafmold, distinguish the most common form on this species from another which develops uniformly on the surface. The first has been found abundant in leafmold. A collection made September 20 and again from the same tree on October 1 and 2, 1927, showed the first form only. The second form has been observed on roots growing deep in the edge of a moist clay bank. An ectotrophic form was found on this species by McDougall (1914).

Erythronium albidum. Nutt. The root system of this species was found divided into a many-beaded structure resembling the endotropic mycorrhizal roots of *Acer rubrum*. Free-hand sections from roots taken in July, 1927, showed slightly clouded, gray glomerulus strands in cells of the first cortical layer and direct intercellular connections with a dark brown mycelium on the root surface. In a second group of roots collected, this same type of structure was found in one case, a dark colored root tip Lohman (1926) described a phycomycetoid endotroph in this species from roots collected in April.

Rumex Acetosella L. Roots taken during the summer of 1927 were found to contain intracellular strands terminating in a knob-like structure. Entered cells were not darkened. Since only free-hand sections of this form were made, the nature of the attachment to external mycelium is not known. It is apparently a true endotroph growing directly from the soil and producing thick hyphae which become brownish in color after entering roots.

Adiantum Pedatum. Two collections taken in May, 1927, showed an endotrophic form in all shortened lateral root tips. These were from a shaded, moist location, apparently most favorable for the plants. Root cells entered by the fungus were in all cases dark in color and entire roots were often found dead. In describing an endotrophic form in this species, Lohman (1926) concludes that the distorted, darkened thick root branches apparently associated with entrance by the fungus indicates true parasitism. As in case of many ferns, the limiting of plants to moist situations causes a continual infection by the endophyte.

Acer rubrum L. The bead-like chains of rootlets associated with the endotrophic form described by McDougall (1914) have been found most common in this vicinity when the roots have contact with abundant, moist organic matter. Evidence of surface growth of the fungus or direct connections with the inner hyphae were not found in roots collected during July and August, 1927. Disintegration of bead-like chains of rootlets was observed, but it is not certain that this condition is always associated with drying of leafmold as occurred during two weeks recorded in August. If the beaded rootlets always indicate the fungus development, this form is present wherever the species occurs in this timbered area.

Acer negundo L. An endotrophic form producing beaded rootlets as in *A. rubrum*. Since this condition was found only on trees growing in heavy sod or leafmold it is probable that the same or a closely related fungus produces it.

Quercus palustris L. Two ectotrophic forms have been found in this region. The first has been found only in moist leafmold and is distinguished by the dense masses of coral-like rootlets which appear to be in no way connected with each other by fungous filaments. The surface of these mantles was, however, covered by uniformly distributed, protruding strands. (Fig. 3.) Free-hand and stained sections showed



Fig. 3—Mycorrhizal roots of pin oak. (*Quercus palustris*). Left. Form 1. Group of coral-like roots, showing few strands passing between grayish-brown mantles. Form 2. White mantles, showing rhizomorph-like strands passing between mantles and into a decomposing leaf.

an outer layer of radially elongated cells and a compact mantle. The second form produces white mantles from which groups of strands may pass into the soil, decomposing leaves, or to other mantles. (Fig. 4.) The mantle surface was found smooth and dense. This form was found most abundantly in this vicinity.

Quercus Macrocarpa Mich. White, compact mantles similar to those produced on *Q. alba* were collected and sectioned in July and August,

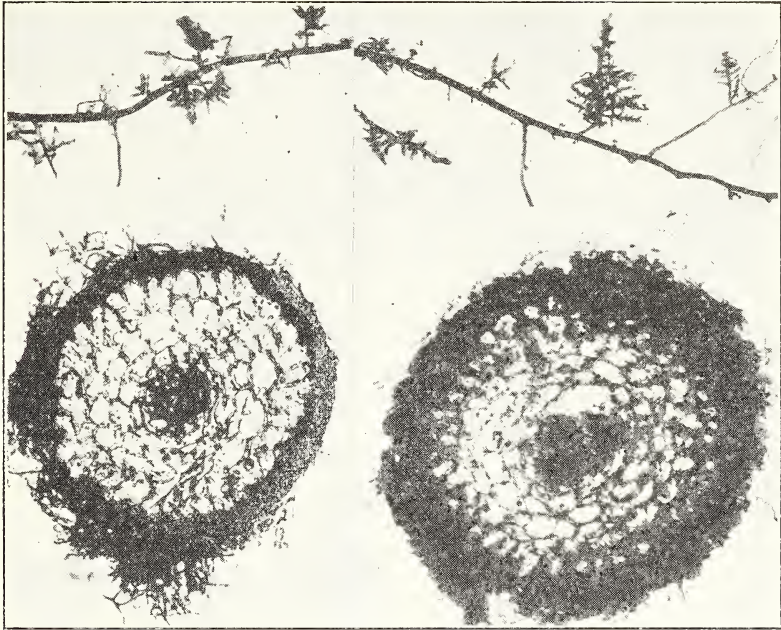


Fig. 4—Left. Mycorrhiza of white oak (*Quercus alba*). Group of white mantle-covered roots, showing development of long mantles. Transverse section of root, showing darkly stained fungous mantle and strands between radially elongated cells. Right. Compound mycorrhiza of swamps white oak (*Quercus bicolor*). Fresh roots, showing brown mantles overlapping the loosely constructed white ones. Transverse section of compound mycorrhizal root, showing fungus between cells of third cortical layer on side of root having two mantles. Easily separated outer mantle does not send strands through the inner.

1927. Cells of the outer layer were found surrounded by the fungus filaments and the usual growth passed between cells of the first cortical layer. (Fig. 5.) The surrounded cells were apparently not discolored, but distortion, rounding of edges and a reduction in size was observed. While some cells were radially elongated, this did not occur in a regular manner. Found on this plant whenever the roots grow in leafmold, it seems to be widely distributed. An ectotroph in roots of this tree has been described and figured by Lohman (1926).

Quercus bicolor Will. The development of compound or dual-fungus mantles was found frequently in this region. The inner filamentous mantle characterizes the common form on this species. This is filamentous and white or gray in late fall. The secondary brown mantle, which develops outside the first, becomes highly appressed. While the strands of the outside mantle were not found intermingling or passing through the inner, an attraction either to the root or the other fungus is evident. A condition almost identical to this has been described by Masui (1926) on the roots of *Q. paucidentata* Fr. The secondary or outer fungus has not been found existing alone on roots.

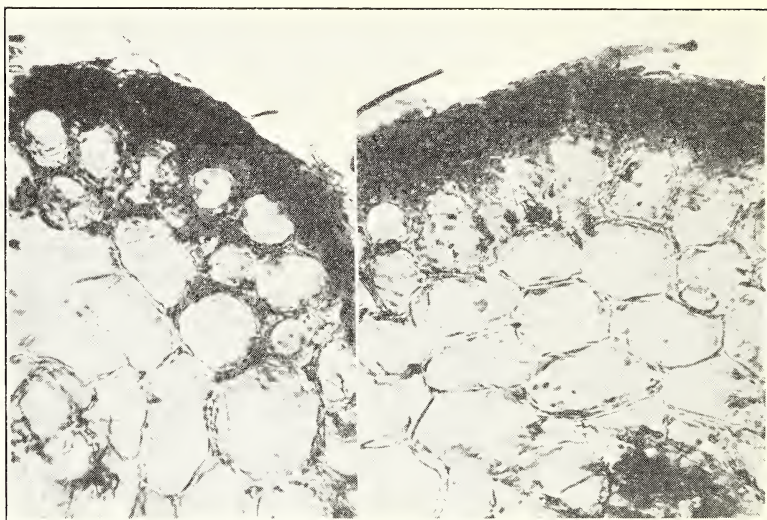


Fig. 5—Left. Transverse section, mycorrhizal root of bur oak (*Quercus macrocarpa*), showing dense, compact mantle and strands between cells of second cortical layer. Right. Transverse section, mycorrhizal root, (form 2) of pin oak (*Quercus pulstris*), showing loose mantle and strands between radially elongated cells.

Quercus alba L. An ectotropic form was found on all roots examined. Groups of white filamentous loose mantles occurred most frequently between the lower layers of moist leafmold. It is apparently the form 4 described by McDougall (1914) on this species.

Fraginus americana L. An examination of roots in August showed the production of a brown mantle. This seemed to consist of a thin web of mycelium, which served to prevent further growth of the enclosed roots in the same manner as thicker mantles. Since it has not been found in large groups of shortened roots or on parts of every root system even in a most favorable condition, the association is probably not so important in the life of the tree. An ectotroph and endotroph apparently due to the same fungus has been described by Lohman (1926) in *F. pennsylvanica*, var. *lanceolata*.

Rubus Flagellaris Will. The presence of bead-like structures among roots taken in July and until August 15, 1927, indicated that an endotroph similar to that of *Acer rubrum* might be present. While the roots sectioned later did not demonstrate the presence of a true endotroph, mycelia were found in the outer and dark colored epidermis of young roots. Apparently a parasite, the intracellular growth did not appear unlike that of a true endotrophic form after seasonal development.

Corylus Americana Walt. Two conditions of mycorrhiza development were found. An endotrophic white mantle was found on roots growing in moist locations. It cannot be considered common in this vicinity. The arrangement of young roots into a bead-like structure resembles that described for *Acer rubrum* by McDougall. Since sections

of roots did not reveal the fungus, it was probably a normal habit of root growth.

Summary. The ectotrophic forms of mycorrhiza found most commonly on forest trees are in general favored in development by the presence of leafmold or other surface organic deposits. The fungi producing mycorrhizas on species of *Quercus* are more nearly dependent upon this condition.

While the production of mycorrhizas by several fungi on the same plant has been observed in case of *Fagus* and *Quercus*, there are indications that an even greater number of fungi may be involved.

A compound mycorrhiza of *Quercus bicolor* gives some evidence that the attraction forces of certain fungi toward young growing roots of trees is greater than the inhibiting forces between two fungi.

An incompletely formed mantle found frequently on roots of *Cercis canadensis* indicates that the rate of growth of the fungus may be a determining factor in mantle formation.

The true endotrophic forms here observed have been previously described.

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