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The Compound Mycorrhiza of Quercus pausidentata Fr.

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With 1 Plate and 41 Text-figures.

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Contents.

Introduction.

In August, 1925, I found a considerable number of tubercles attached to the roots of *Quercus pausidentata* (= *Q. sessilifolia*) (Japanese name: Tsukubane-gashi) at Takayashiro, about two miles west of Tajimi, Gifu-Prefecture. Other specimens of the same were found then also at Kasuga-yama, Nara-Prefecture. After a careful investigation I found that they were a kind of compound mycorrhiza, quite different in structure from those hitherto reported. In Octoberof the same year I found another kind of the compound mycorrhiza on the roots of the same plant at Takayashiro.

The occurrence of such mycorrhizas has not yet been reported, as the distribution of *Quercus pausidentata* is limited only to some parts of Japan. MIMURA mentions in his paper ('17) only that this plant possesses ectotrophic mycorrhizas, but no further description is given.

The compound mycorrhizas have been described by FRANK ('88). BÜSGEN ('01), MÖLLER ('03), MÜLLER ('03), TUBEUF ('03), McDOUGALL ('22) and MELIN ('23) all in *Pinus*. But their descriptions are brief and confined to the morphological characteristics, the development of the mycorrhiza being almost neglected.

The present paper deals chiefly with the structure and development of two kinds of the compound mycorrhizas, denoted as Forms A and B, of *Quercus pausidentata*.

I. The compound mycorrhiza Form A.

A. The external characteristics.

The compound mycorrhiza Form A is found in clusters or dispersed, slighthy deeper than the other kinds of mycorrhizas of *Quercus pausidentata* in raw humus[1] (Fig. 1).

1) *Quercus pausidentata* has several kinds of mycorrhizas. They are found usually in the superficial layer of raw humus, except in the case of the compound mycorrhiza Form A.

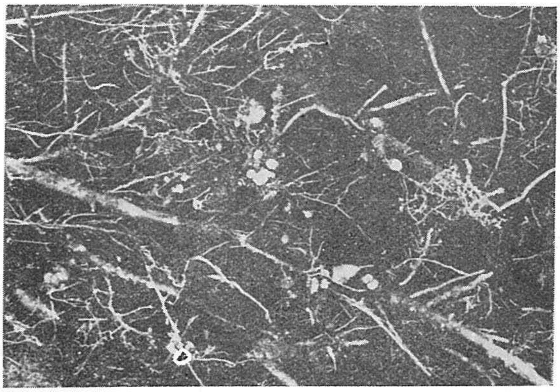

Fig. 1. The compound mycorrhiza, Form A, of *Quercus pausidentata*. The photograph was taken at Takayashiro after removal of the superficial layer of raw humus. × ca 1/3.

When young it is pure white. but turns brownish with age. It is a spherical, ovoid or clavate body attached to the side of the mother root. Sometimes it develops at its termination (Fig. 2).

The length of it is usually 4—10 mm., sometimes more than 15 mm. In this respect this is the largest compound mycorrhiza hitherto known. Superficial examination with pocket lens reveals a smooth surface with dull wrinkles. Small pieces of raw humus are found abundantly clinging to it. In the older tubercles, as their cortex goes off, the internal body, made up of numerous entangled mycorrhizas, comes out as shown in Fig. 3. The tubercles in a very old stage are dark brown and the surface is very rough (Fig. 4).

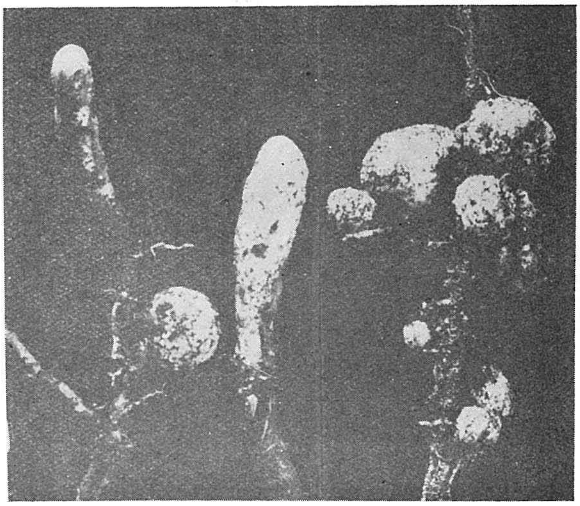

Fig. 2. Compound mycorrhiza, Form A. × 2.5.

The rhizomorpha-like hyphal bundles or ozonia (BULLER '24) are

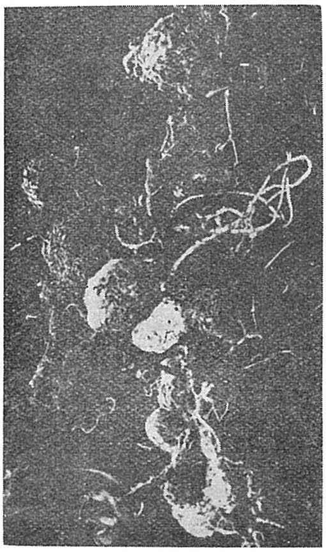

Fig. 3. Rather old compound mycorrhiza, Form A whose cortex is already dead. × 2.5.

Fig. 4. Very old compound mycorrhiza, Form A. ×2.5.

usually given rise to, from the surface of the tubercle, when it becomes old (Fig. 3).

B. The internal structure.

The material in various stages of development were fixed with FLEMMING'S weaker solution, and microtomic paraffin sections were made. An alcoholic solution of acid fuchsin and DELAFIELD'S haematoxylin were used for staining. Sometimes material fixed with FLEMMING'S solution were stained with the fuchsin solution before being imbedded in paraffin.

The structure is a cluster of numerous mycorrhizas, developed around an axial mother root, with the parts all bound together in one mass by the cortex of the tubercles (Fig. 5). A novel thing about this tubercle is that among these mycorrhizas there exist a few or several rootlets which have been demolished by the infecting fungus.

1. *The cortex of the tubercle.*

This is a thick mycelium (70—320 μ), enveloping all the internal mycorrhizal mass. It is differentiated into two layers (Fig. 6). The outer layer is made up of rather loosely associated thin filaments, measuring 1.3—3.2 μ in diameter. There are mycelial protuberances on its surface. The inner layer is more or less denser in texture than the outer, and almost homogeneous when the tubercle is young, as shown in Fig. 6. Frequently fragmentation of the inner layer is carried on in tubercles in a much advanced stage of development. At the same time, large swollen hyphae, measuring 20—30 μ in diam., come out in large numbers in the protuberances of the outer layer, so that they become more protrusive.

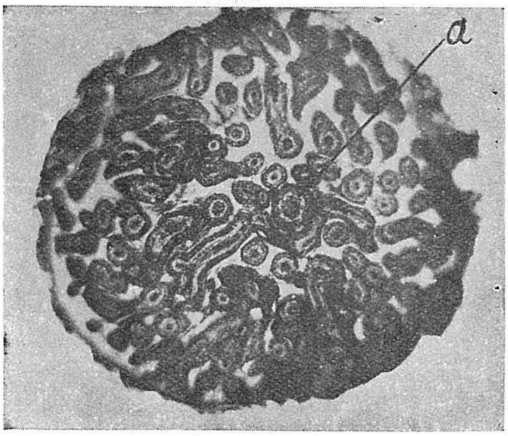

Fig. 5. A cross section of the compound mycorrhiza Form A, showing an axial root, *a*, in the central portion. × 14.

2. *The axial root.*

Each tubercle possesses one axial root. It is a thick, spiral nodose root, indicating shortened internodes (Fig. 7—8). The side-branches are usually given rise to in two to four rows from its surface (Fig. 7). Sometimes the termination of the axial root is found growing out from the tubercle, though in general it is entirely enclosed within the latter. The protruding portion is

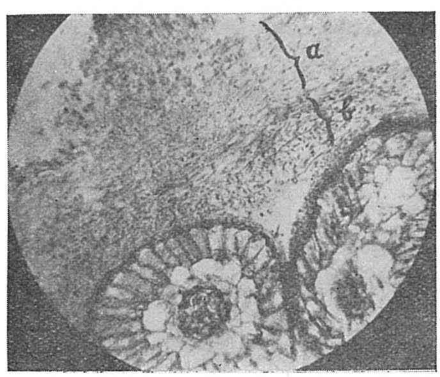

Fig. 6. Section of young compound mycorrhiza, showing the cortex of the tubercle differentiated into two layers, *a* and *b*. × 140.

usually free from the mycelium.

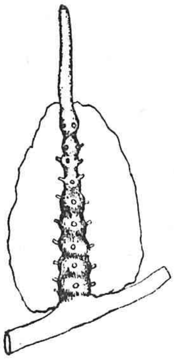

Fig. 7. The axial mother roots. ×2.6

Fig. 8. A longitudinal hand-section of an old tubercle, showing an axial root spirally twisted and with entangled mycorrhizas around it. ×5.

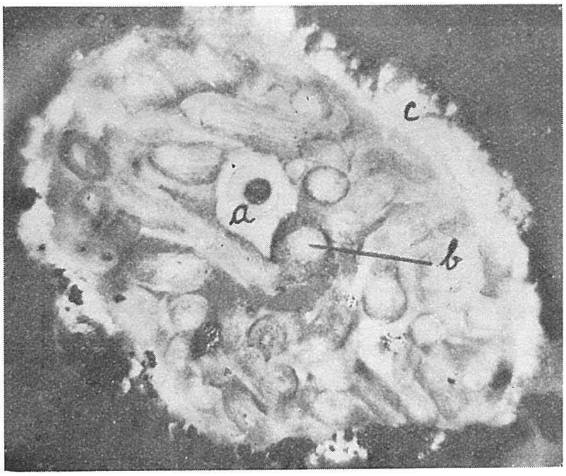

Fig. 9. Cross-section of a fresh tubercle, showing a heavily infected rootlet, *a*. *b*, an axial root; *c*, the cortex of the tubercle.

The photograph was taken with reflex light in order to show the mycelium white. × 27.

3. *The mycorrhizas.*

A considerable number of slender, irregularly bent, monopodially branched mycorrhizas are found filling up the internal space of the tubercle (Fig. 5 and Pl. XIV, Fig. 4.). They are all branchlets divided directly or indirectly from the axial root and transformed into mycorrhizas. These mycorrhizas are composed of the following parts, beginning at the outer portion :—

a. The fungous mantle. The fungous mantle is usually 6—20 μ in thickness, composed of closely interwoven thin filaments, measuring 1.5—3.2 μ in diamater. The connection of the fungous mantles with each other and between the cortex of the tubercle is fully realized by the numerous filaments projecting out from their surfaces. They frequently unite into one at the point of contact (Fig. 6). There is found a layer of demolished cells inserted between the fungous mantle and the epidermal layer.

Fig. 10. Cross section of a tubercle, showing the axial root and mycorrhizas. × 45.

They are those which have been derived from the root-cap cells.

b. The epidermal layer. The epidermal tissue is made up of a row of anticlinally elongated cells. The fungous filaments penetrating in between these cells form a well-developed HARTING's network (Fig. 20). Sometimes thin fungous filaments, measuring 1—1.5 μ in diam., enter into the cell-cavity as if they were endotrophic filaments (Fig. 11). They seem very much like the haustorial hyphae in the mycorrhiza of *Betula* described by MELIN ('23).

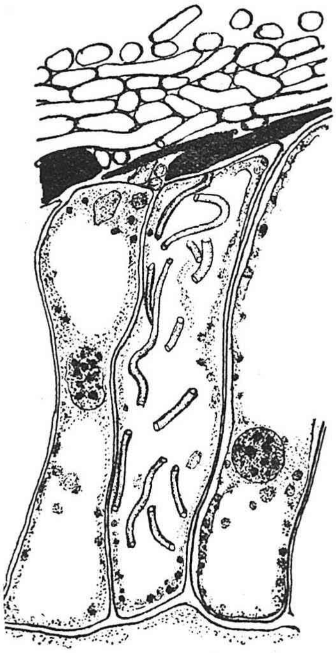

Fig. 11 A longitudinal section of a mycorrhiza, showing intracellular hyphae in epidermal cells. × 1300.

c. The cortical layer. Beneath the epidermal layer, there is a cortical tissue made up of three to five rows of cells. The fungous filaments are not found within or between these cells. They contain tannic substances; and an exceptionally large amount of it occurs in the endodermis.

d. The central cylinder. This is not much changed as compared with the normal root.

4. *The heavily-infected rootlets.*

In each tubercle there are found a few or several rootlets heavily infected by the fungus, embedded in the mycelial mass (Fig. 13). In fresh material they appear as white mycelial bodies with dark central portion (Fig. 8, *a*).

Its chief difference from the normal mycorrhiza is that it has (1) a very thick fungous mantle measuring 14—36 μ in width, (2) an inwardly-developed very thick mycelium, attaining to 60—80 μ in width, a little behind the apex, and (3) an entirely suppressed tissue of epidermis and cortex around the central cylinder at that portion.[1]

Such a mycorrhiza is found in the young tubercles with exceptionally thick fungous mantle (Pl. XIV, Fig. 7). Near its apex, then, the fungous

1) In the section, it seems, at first sight, as if the mycorrhiza has curved off and disappeared from the figure, but the investigation of successive sections shows immediately that it is not really so.

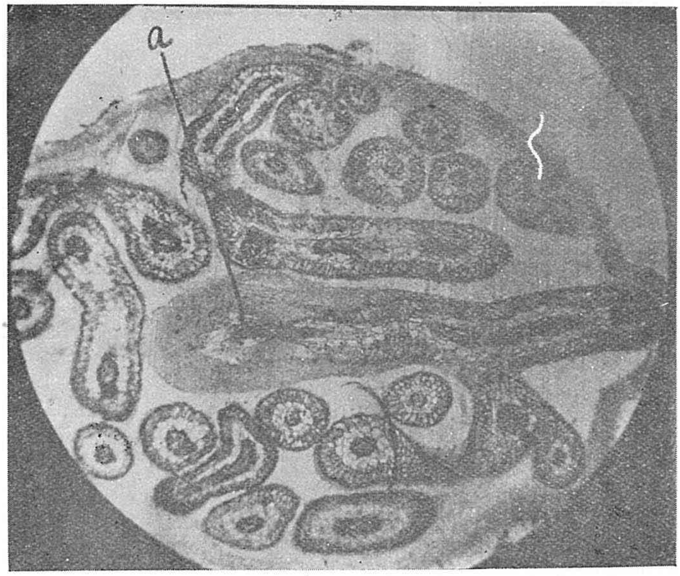

Fig. 12. A longitudinal section of the compound mycorrhiza, showing a demolished rootlet, *a*. × 45.

filaments which constitute the inner portion of the fungous mantle begin to grow inward in a mass, pushing on the rootlet, and forming a new inner layer within the mantle. They continue their growth further until the epidermis, as well as the cortical tissue, and even the layers of the central cylinder are ultimately pressed down (Figs. 13—14). They are clavate filaments provided with a large amount of plasmic substances and granules which are easily stained with haematoxylin. The apices of the filaments are radiated more or less perpendicular to the depressed host cells (Fig. 15). There are pieces of tannic substances

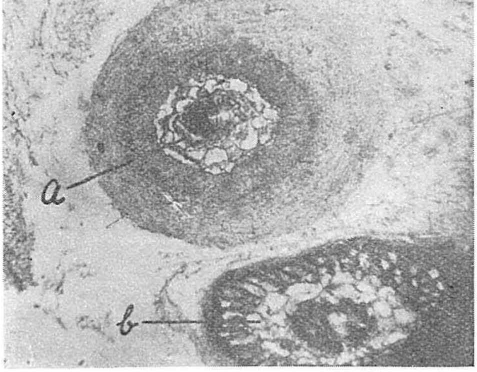

Fig. 13. A cross section of a heavily infected rootlet, *a*, in contrast with a usual mycorrhiza, *b*. × 100.

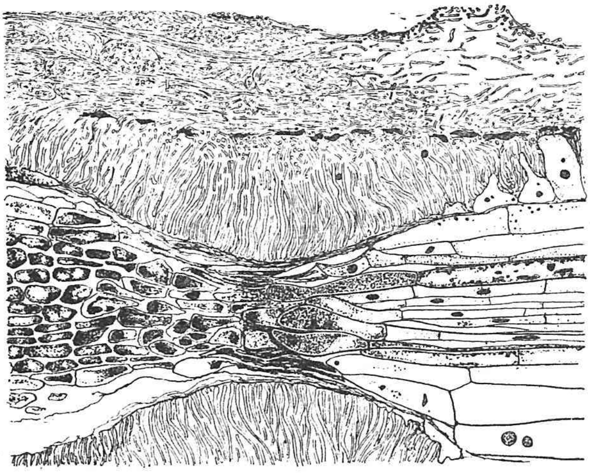

Fig. 14. A longitudinal section of a heavily infected rootlet, showing luxuriant mycelial growth around it. × 240.

dotted in a line between the base of these filaments and the fungous mantle (Fig. 14). They represent the demolished remnant of the calyptral layer. As the mass of filaments grows inward, surrounding the root, the middle portion of the root is tightly constricted, so that, on the one hand, these clavate filaments, approaching to the central cylinder, suck off food substances directly from it, and on the other hand, the nutrient supply to the growing apex of the mycorrhizal root, being interrupted by the tight constriction, becomes insufficient. It follows, then, that the cells of the distal portion of such a constriction begin to lose their vitality, their protoplasmic membranes

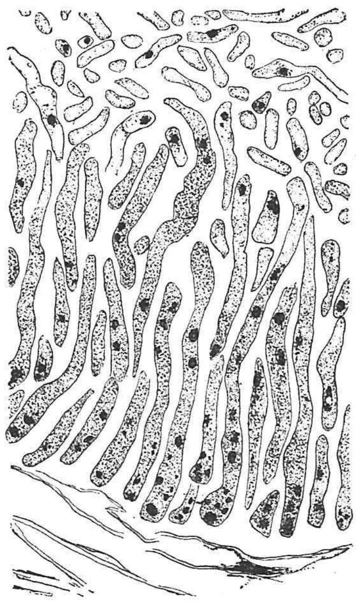

Fig. 15. A mass of filaments, growing in, pushing away the host tissue. × 1080.

separate from the walls and die away (Fig. 14). Through this procedure the apices of some mycorrhizas are entirely demolished.

C. The morphological difference between the normal and the mycorrhizal root.

The root of *Quercus pausidentata* is tolerably modified in its structure by the fungous infection, due perhaps chiefly to the chemical stimulation and also to the mechanical obstruction caused by the fungous mantle to the cells of its growing point. The chief difference between the normal root and the mycorrhiza is as follows:—

1. Dimension of cells: All the cells of the mycorrhizal root, especially those of the calyptral and epidermal layers are shortened longitudinally and elongated transversely as compared with the normal root. Measurement shows that the dimensions (longitudinal × transversal) of epidermal cells of the normal root are 35—160 μ × 8—15 μ, while those of the mycorrhizal root are 14—22 μ × 35—58 μ (Figs. 16—20).

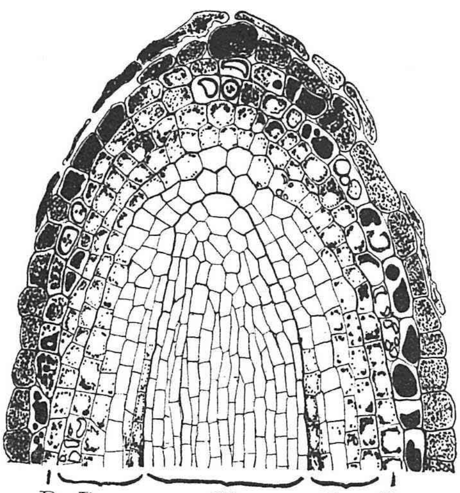

Fig. 16. A median longitudinal section of the growing point of a normal root. *D*, Dermatogen; *Per*, periblem; *Pl*, plerome × 240

2. Number of cell-layers: The number of cell-layers, especially in the root-cap and periblem, is more or less reduced in the mycorrhizal root.

The normal root possesses six or more rows of calyptral layers at its apex (Fig. 16), while in the infected one only 3—5 layers are to be seen (Fig. 17).

The initial cells are situated therefore much nearer to the surface of the root-tip. In the periblem or cortex the mycorrhizal root has also a smaller number of layer,

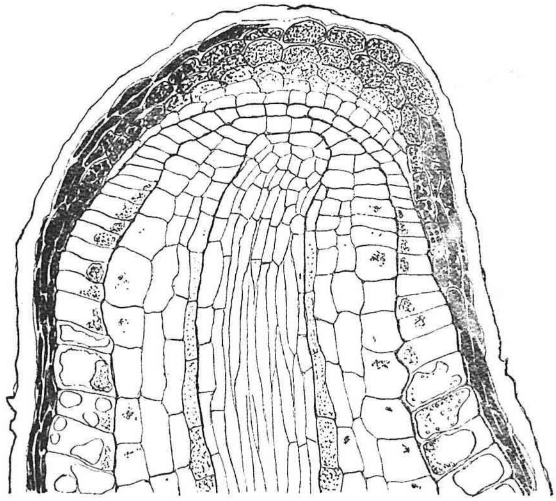

Fig. 17. A median longitudinal section of the apex of a mycorrhizal root. *F*, Fungous mantle; *D*, dermatogen; *Per*, periblem; *Pl*, plerome. × 380.

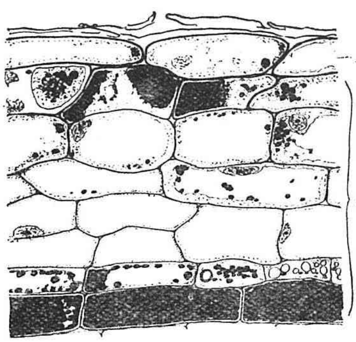

Fig. 18. A longitudinal section of a normal root. *Ep*, Epidermis; *Cort*, cortex. ×430.

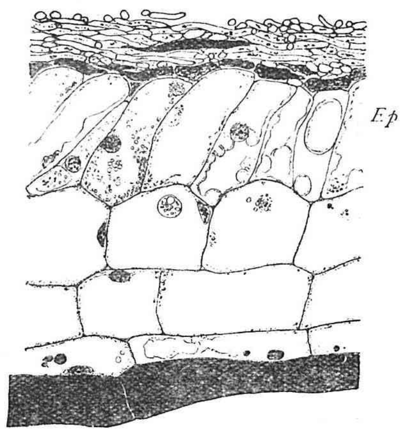

Fig. 19. A longitudinal section of a rather young mycorrhizal root. *Ep*, Epidermis. × 867.

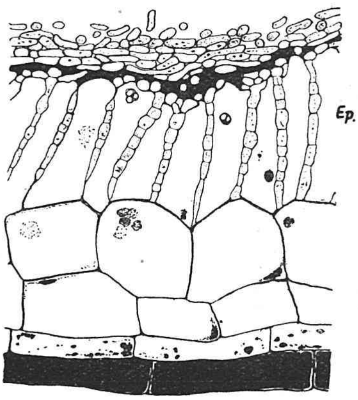

Fig. 20. A longitudinal section of the mycorrhiza in a much advanced stage of development. *Ep*, epidermis. × 430.

but the cells in them are larger. The number is only 3—5, while in the normal one it is five or more (Fig. 18—20).

3. Contents of the cells: In the epidermal cells of a mycorrhizal root, the protoplasmic membrane separates from the cell-wall at a certain stage of development, large vacuolar bodies frequently appearing in it. This fact indicates that the root has been much affected chemically by the infecting fungus. These bodies disappear however in a much advanced stage of development when HARTIG's network is fully formed (Figs. 19—20). In the normal root such a feature is never seen (Fig. 18).

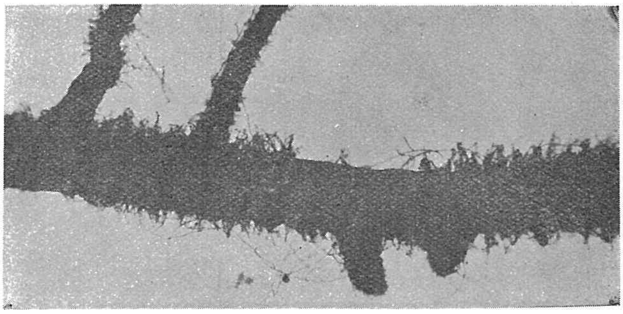

Fig. 21. A branched normal root, showing root-hairs given off from its surface. × 20.

4. Root-hairs: The epidermis of the normal root gives off root-hairs from its surface (Fig. 21), while the mycorrhizal root completely lacks them.

D. The development of the compound mycorrhiza Form A.

Frequently the growing apices of large, vigorous roots are transformed into ectotrophic mycorrhizas. They attain sometimes 2.3 mm. in diam., taking a clavate form without exception. Such clavate mycorrhizas are the primordia of the compound mycorrhizas Form A. They have a very thick fungous mantle attaing sometimes 0.44 mm in width (Fig. 22). The fungous mantle is differentiated usually into two layers. The outer layer is composed of a closely interwoven fungous filament including sometimes humus particles within it, while the inner layer is very wide and looser in texture than the former (Fig. 23). The innermost portion of the latter is somewhat compact in texture and includes numerous crowded host-cells isolated as islands. The fungous filaments penetrate slightly in between the epidermal cells.

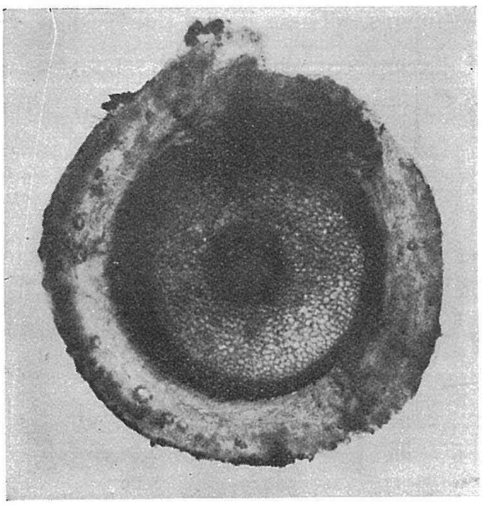

Fig. 22. A cross section of a clavate mycorrhiza, the primordium of the compound mycorrhiza Form A. ×26.

The development of the compound mycorrhiza Form A, starting from such a single mycorrhiza, is diagrammatically demonstrated in Fig. 24.

In spite of the injury from the infecting mycelium, these vigorous roots grow further and give off branches. The branches continue their growth turning more or less to the direction of the axial root, interrupted perhaps by the fungous mantle or the cortex of the tubercle (Pl. XIV, Fig. 2). The side-branches are usually infected and transformed into mycorrhizas, as soon as they come out. Such a young mycorrhiza has not yet a HARTIG'S network in the epidermal tissue (Fig. 19).

As the first branch elongates a little, the second branch is given off from the next node. In the same way, the third, the fourth and the following branches come up in turn in a spiral order acropetally

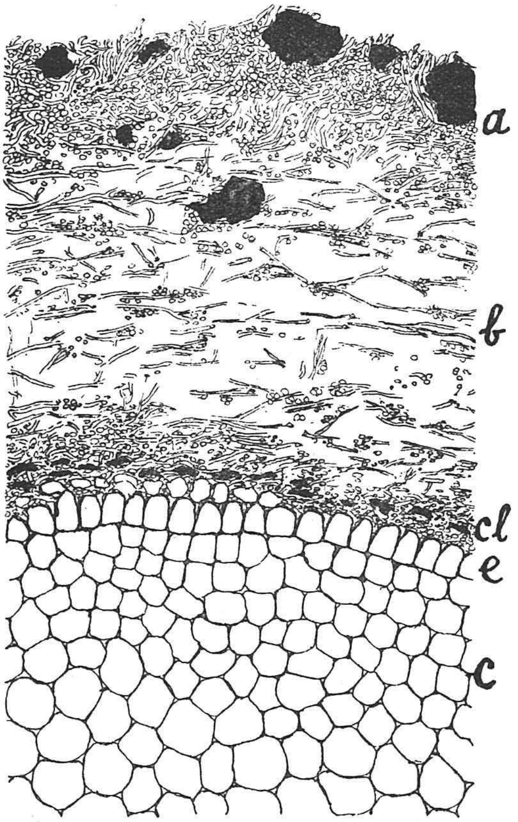

Fig. 23. A cross-section of the clavate mycorrhiza, *a*, *b*, outer and inner layers of the fungous mantle; *cl*, demolished calyptral layer; *e*, epidermis; *c*, cortex. ×200.

(Pl. XIV, Figs. 1—4, and Text-fig. 24, A–D).

The axial root continues its elongation, giving off the side-branches, while each branch, which has come up meanwhile, gives off branchlets, one after another, until it has been so seriously invaded by the fungus that HARTIG's network is formed (Fig. 20).

As the axial root divides into many side-branches, the total number of the rootlets given off from it is innumerable. The cortex of the tubercle, though it was once the fungous mantle of the primordial mycorrhiza, is gradually pushed aside by the increasing side-branchlets, and pushed forward by the further growth of the axial root. Thus the compound mycorrhiza with the cortex is completed.

An important thing about this mycorrhiza is that a l a r g e p r i m o r d i u m d e v e l o p s i n t o a l a r g e c o m p o u n d m y c o r r h i z a, a n d a s m a l l p r i m o r d i u m i n t o a s m a l l m y c o r r h i z a. As a larger axial root seems to give off more side-branches than a smaller one.

In the completed tubercles I found the mycorrhizas not only irregularly bent, but also adhering to one another, indicating that each of them had

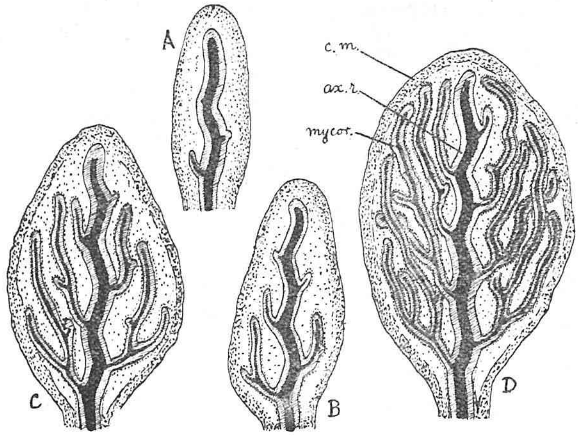

Fig. 24. Diagrammatic representation of the development of the compound mycorrhiza Form A. *c. m.*, the cortex of the tubercle; *ax. r*, the axial root; *mycor.*, the mycorrhiza.

made its way, only turning aside under the strong tension of the strong cortex of the tubercle (Fig. 25).

When the tubercle becomes old, the mycelium perishes, so that large interspaces are formed among the numerous mycorrhizas (Pl. XIV, Fig. 5.). In tubercles in an older stage of development, each mycorrhiza shrinks except the axial root (Pl. XIV, Fig. 6,).

Fig. 25. A longitudinal section of a tubercle, showing one mycorrhiza turning off from the cortex of the tubercle. ×50.

E. The hyphal bundles.

The microtomic section of the hyphal bundles or ozonia shows clearly their internal structure. They are made up of numerous hyphae adhering fast to one another in compact bundles. Among the elements of the bundle there are several food-storage hyphae, whose contents have a strong affinity for haematoxylin and fuchsin.

II. The compound mycorrhiza Form B.

A. The external characteristics.

The compound mycorrhiza Form B occurs in clusters in the superficial layer of raw humus. It is a spheroidal or botryoidal body measuring 2—6 mm. in diameter (Figs. 26, 27). Its colour is whitish when young, though it changes to brownish with age. A superficial examination with low-powered microscope reveals its smooth surface and the rhizomorpha-like hyphal bundles which are given off from it.

Fig. 26. The compound mycorrhiza Form B. ×1.3

Several mycorrhizas which have been tightly bound up into a mass, may be fully demonstrated in the total preparation, if the compound mycorrhiza is treated with chromo-acetic solution (MASUI '26,). Such a preparation shows clearly that each mycorrhizal branch has been much deformed by the restriction of the enveloping mycelium. The chief deformations are that (1) the mycorrhizas are flattened on the sides where they come in contact with one another and that (2) their apices come near together and give the compound my-

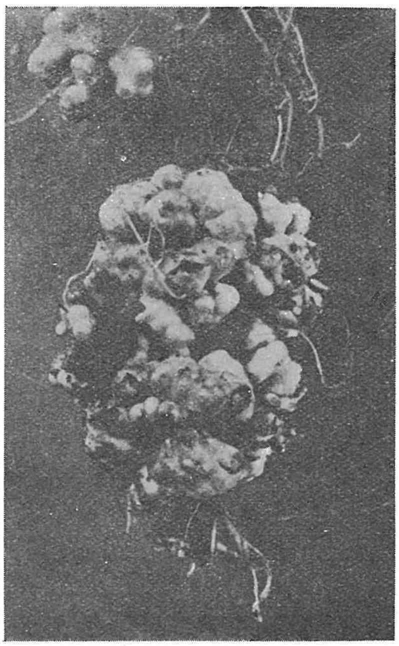

Fig. 27. The compound mycorrhiza Form B and rhizomorpha-like hyphal bundles. ×7.

corrhiza a flat apex as shown in Fig. 28.

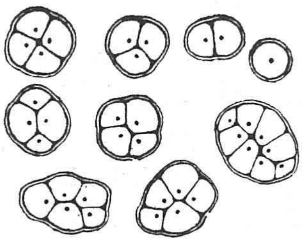

Fig. 28. The apical view of the compound mycorrhiza Form B, showing the apices of the mycorrhizas (indicated by the points) coming near together.

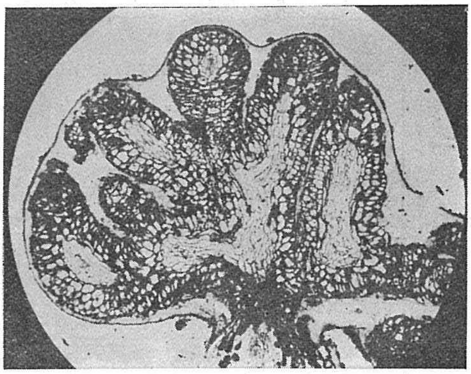

Fig. 29 a. A longitudinal section of compound mycorrhiza Form B. ×29.

B. The internal structure.

The mycorrhiza Form B is a coral cluster of a few, or many, mycorrhizas all bound together in one mass by the common cortex of the tubercle. The chief difference from Form A, in respect of internal structure, is that it lacks the axial mother root.

1. *The cortex of the tubercle.*

This is a thick mycelium (21—88 μ), enveloping all the internal mycorrhizal mass (Figs. 29a, 29b). Its outer portion is made up of closely interwoven filaments measuring 3.1—4.7 μ in diam., while the inner portion is frequently composed of rather roughly associated filaments. When two or more

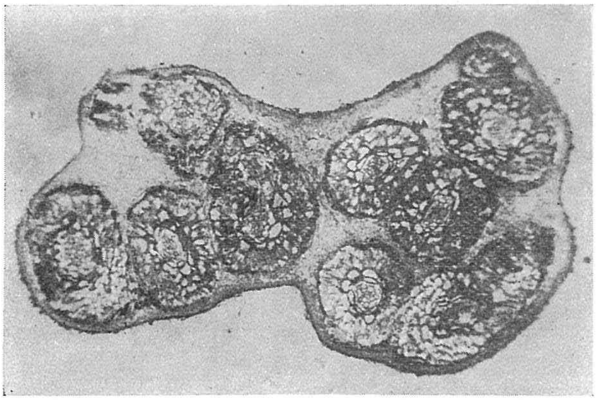

Fig. 29 b. A cross section of a compound mycorrhiza Form B. ×45.

compound mycorrhizas develop close together, their cortices unite at the point of contact (Fig. 30).

Fig. 30. A section of three compound mycorrhizas, showing the cortices united at the point of contact. ×45.

2. *The mycorrhizas.*

The mycorrhizas are very large, as compared with those of Form A, and give off branches dichotomously. The mycorrhiza is composed of the following parts, beginning at the outer portion :—

a. The fungous mantle. The fungous mantle is usually 10—30 μ in thickness. It is composed of rather closely interwoven filaments. The union of mycorrhizal mantles with one another and with the cortex of the tubercle is fully realized by the numerous filaments projecting from their surfaces. They frequently unite into one at the point of contact (Fig. 31). Tannic substances are found in a large mass or in a filamentous body included in the mycelium (Fig. 32).

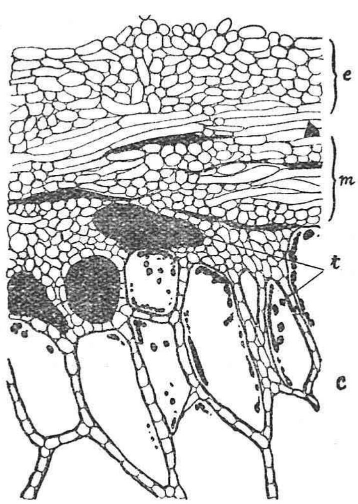

Fig. 32. Longitudinal section of the mycorrhiza. *e*, cortex of the tubercle ; *m*, fungous mantle ; *c*, cortex; *t*, tannic substance. ×430.

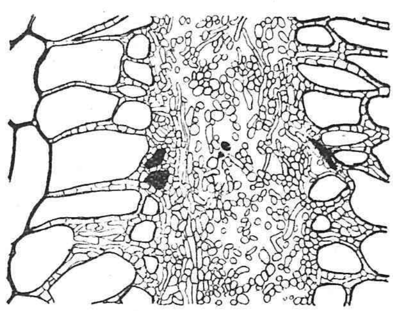

Fig. 31. A united portion of two fungous mantles shown by longitudinal section ×190.

b. The cortical layer. The

fungous filaments penetrate deep in between the cortical cells and form the so-called HARTIG's network (Fig. 32). Frequently the fungous filaments of this network increase greatly in number and elongate in a mass inwards pushing aside the cells until they attain the endodermis (Fig. 33). Intracellular filaments are frequently found in such a case. In this respect, this is truly an ectoendotrophic mycorrhiza.

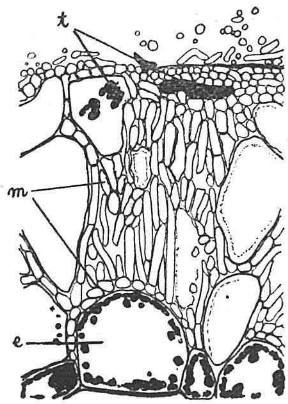

Fig. 33. A cross-section of a rather old mycorrhiza, showing luxuriant filaments, *m*, in the cortical tissue. *e*, endodermis ; *t*, tannic substances. ×ca 350.

C. The morphological difference between the normal and the mycorrhizal root.

1. Mode of branching. The mycorrhizas divide dichotomously (Fig. 34), while the normal root branches monopodially (Fig. 35).

2. Meristematic portion. The most significant difference between the mycorrhizal root and the normal one is that at its apex the former is completely lacking the epidermal initial cell and nearly all of the root-cap cells, as shown in Fig. 36. Accordingly, initial cells of the periblem and the plerome are situated close to the fungous mantle. When a very young mycorrhiza, just infected by the fungus, is examined, the initial cell of the dermatogen can be clearly seen.

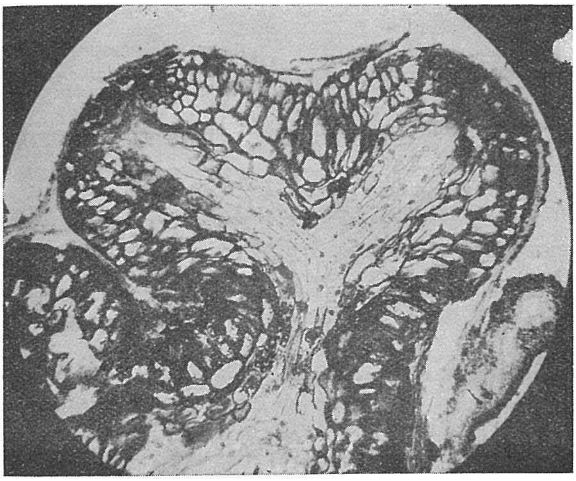

Fig. 34. Dichotomously branched mycorrhiza. ×100.

Its absence in the mycorrhiza may be concluded, therefore, to be a result of the chemical or mechanical influence of the fungus while the root is growing in length.

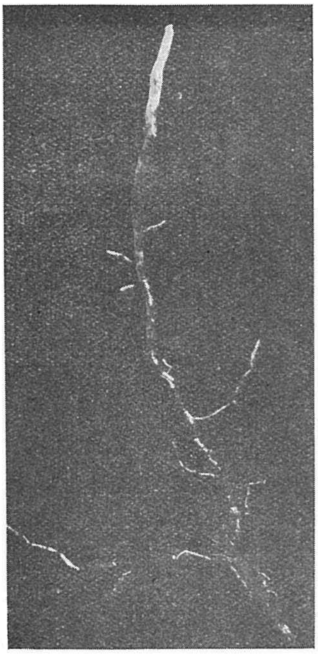

Fig. 35. Normal root of *Quercus pausidentata*, showing monopodially branched rootlets. ×7.

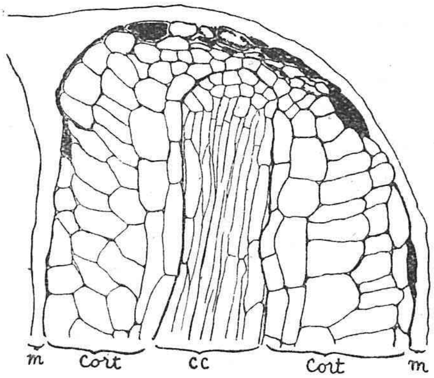

Fig. 36. Median longitudinal section of the mycorrhizal root. *m*, Cortex of the tubercle + fungous mantle; *cort*, cortex; *cc*, central cylinder. ×270.

D. The development of the compound mycorrhiza Form B.

There are often growing roots which bear many compound mycorrhizas arranged in the order of development as shown in Fig. 37. In such a specimen, it is easy to follow the successive stages of development of the mycorrhiza. The material were fixed with FLEMMING'S solution, imbedded in paraffin and sectioned microtomically. Sometimes the free-hand sections of fresh material were favourable for investigation.

The mother root has numerous root-hairs on its surface, indicating that it has no fungous mantle. After a detailed observation, however, I found very roughly interwoven fungous filaments and sometimes small hyphal bundles along its surface (Fig. 37). As soon as the primordium

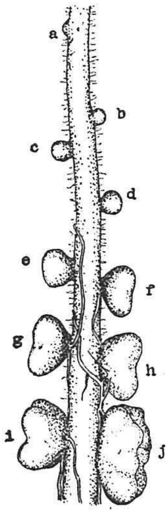

Fig. 37. A root having the compound mycorrhizas in their successive stages of development. × 10.

of the side root comes up, the hyphae begin to increase in number exceedingly on that portion until its surface is covered up completely by a rather compact network (Figs. 37, a and 38, A). As the primordium grows, the mycelium becomes more compact in texture, and presents the characteristics of an ectotrophic mycorrhiza. The primordial root does not then grow much in length, but divides dichotomously, so that it increases its dimensions transversely (Fig. 38, C—D). These first branches then divide into second sets (Fig. 38, E) and so on, all the while pushing their way against the strong tension of the fungous mantle as well as that of the cortex of the tubercle, and grow hand in hand with them until the total complex attains a certain size. After maturity the colour changes brown.

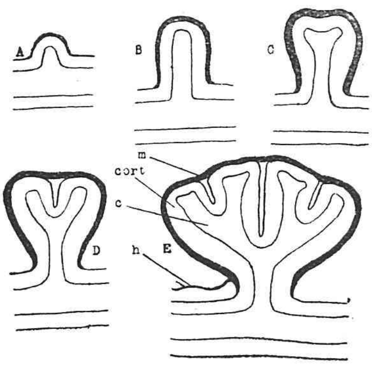

Fig. 38. A diagrammatic representation of the mode of development of the compound mycorrhiza Form B. *c*, central cylinder; *cort*, cortex; *h*, hyphal bundle; *m*, cortex of the tubercle.

E. The mycorrhizal fungus—Boletus luteus?

I found fungous fruiting bodies actually attached to the mycorrhizal roots of *Quercus pausidentata* at Takayashiro (Fig. 39). The connection between the compound mycorrhiza Form B and the mushroom was so fully realized that many of the hyphal bundles produced from the surfaces of the former were united into a large mycelial mass or the basal portion of the mushroom (Fig. 40).

The fruiting bodies which I found there were all rather old. But the following diagnosis was obtained by the detailed observation: The mushroom is 15 cm. high, the cap 3 cm. in diam., and the stem 7 mm.

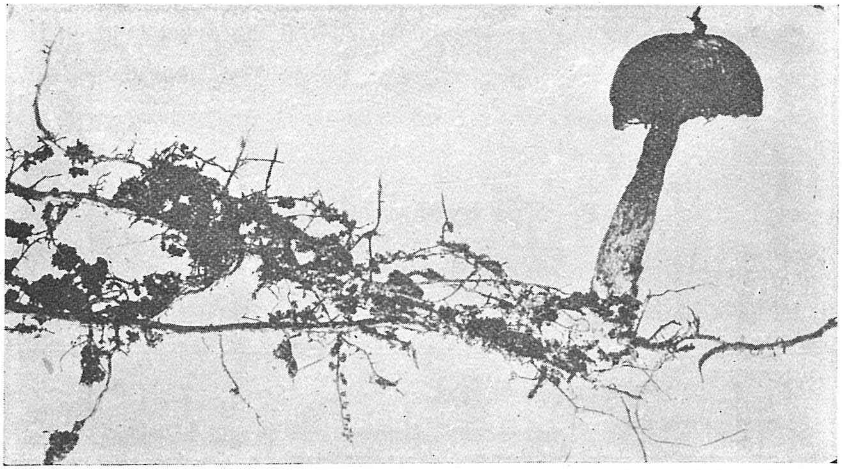

Fig. 39. *Boletus* attached to the mycorrhizal roots (Form B) of *Quercus pausidentata*. ×4/5.

in thickness. The pileus is convex, viscid, yellowish brown in colour. The flesh is whitish. The tube surface is almost plane and the tubes are small, with small, nearly rounded mouths. The colour of the tubes is yellow. The stem is yellowish, covered with granular black dots. The spores are fusiform, $3.2-3.8 \times 8.5-10.7\ \mu$. In these respects this mush-

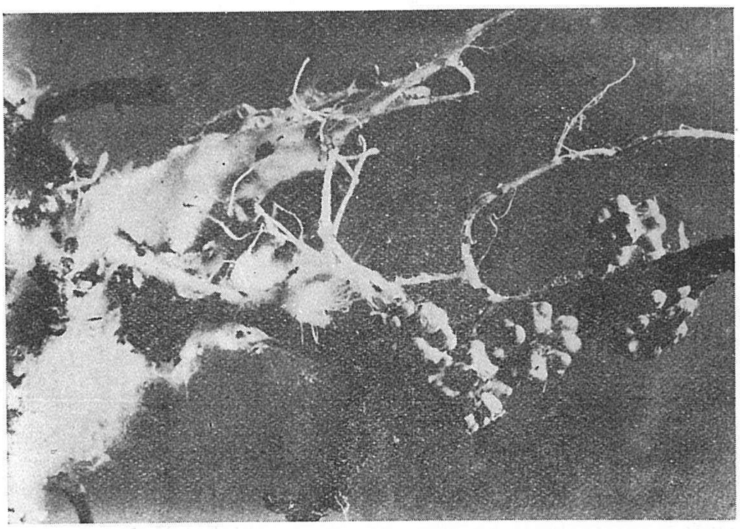

Fig. 40. A mycelium formed by the union of the hyphal bundles produced from the compound mycorrhizas. ×6.

room may be identified as *Boletus luteus*, L.

MELIN stated that the mycorrhizal fungus of the compound mycorrhiza of *Pinus silvestris* is *Boletus*. It seems, therefore, that some species of *Boletus* have a tendency to form compound mycorrhizas with the roots of various trees.

F. The hyphal bundles.

The hyphal bundles are found numerously connected with the compound mycorrhizas as above mentioned. Their structure is much alike to that of the "Knollenmykorrhiza" of *Pinus silvestris* described by MELIN. They are bundles made up of numerous small filaments, 2—3.5 μ, including in their central portion a few or several number of very large filaments, attaining sometimes 15 μ in diameter (Fig. 41). The function of the bundles seems to serve, on the one hand, for the further infection of the remote rootlets, and, on the other hand, for the formation of the fruiting body, as described by BULLER ('24).

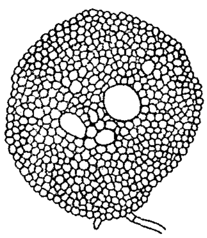

Fig. 41. A cross section of the hyphal bundle. In the central portion there are some very thick filaments. ×430.

III. The compoud mycorrhiza in general.

The compound mycorrhizas hitherto known are all clusters of dichotomously branched stubby mycorrhizas. The Form B of *Quercus pausidentata*, mentioned above, is somewhat like them in its construction, while the Form A is a particular one differing greatly from them.

Considering the compound mycorrhizas in general, it may be convenient to classify them into the following two groups according to their mode of development.

1. The dichotomously branched type. This type of tubercle develops at first from a dichotomously branched mycorrhiza, only increasing in number by repeated branching and forming an aggregate. (a) Thus a mycorrhizal cluster, the most primitive tubercle, is formed. That of *Pinus Cembra* described by TUBEUF ('03) is an example of this

stage. (b) In the more advanced form of the tubercle the cluster thus formed provides a common mycelial envelope formed by numerous hyphae projected from each mycorrhiza, not only binding them up entirely, but also including soil particles existing closely within it. The tubercle of *Pinus silvestris* described by FRANK ('88) and MELIN ('23) clearly belongs to this form. The tubercles of *Pinus montana* described by MÜLLER ('03) seem also, in general, to be of this form, though in sandy soil they show little of it, indicating that the environmental conditions may also affect the formation of the envelope. Judging from MCDOUGALL's ('22) description and illustration, that of *Pinus strobus* seems to be a slightly more advanced one than the former. (c) In the case of Form B here, the mycelial envelope is developed from the first as a proper wrapping with its clearly differentiated outer portion. It contains therefore no soil particles within it. Presumably this form is the most advanced one in this type.

In short, the compound mycorrhizas of this type have a range of differentiation, from a single bifurcated mycorrhiza to the most complicated form, Form B, with at least two intermediate forms between them.

2. The monopodially branched type. In the second type of tubercle, only one complicated form, Form A of *Quercus pausidentata*, is before us and no intermediate stages between this and the monopodially branched single mycorrhizas are known, even though these latter are quite common. The Form A represents therefore, at least, at present a monotypic form of the second case.

It seems at first rather curious, that the roots of the same plant should produce two kinds of mycorrhizas, monopodial and dichotomous, so greatly contrasted in their development and structure, although it is a well known fact that different fungi may cause different mycorrhizas on the same plant. Such a contrast is due undoubtedly at first to the difference in the growth reactions of each fungus to the chemical stimulation of the host roots, which results in the dissimilarity of the mycelial distribution accompanied by difference in the mechanical obstructions to the roots.

IV. Summary.

1. *Quercus pausidentata* has, besides some simple mycorrhizas, two kinds of compound mycorrhizas, Forms A and B.

2. The compound mycorrhiza Form A.

a. It is a cluster of numerous mycorrhizas, developed around an axial root, with the parts all bound together in one mass by an enveloping mycelium or by the cortex of the tubercle.

b. It developes from a large clavate primordium which is only a single ectotrophic mycorrhiza. This primordial mycorrhiza, on the one hand, continues its own growth longitudinally, and, on the other hand, gives off numerous side branches monopodially, each of which is then transformed into a mycorrhiza, all the while pushing forward and aside the fungous mantle of the primordium or the cortex of the tubercle. Thus the compound mycorrhiza Form A is formed.

c. Some of the mycorrhizal roots within the tubercle are entirely demolished by the infecting mycelium.

3. The compound mycorrhiza Form B.

a. It is a cluster of stubby mycorrhizas enveloped by a common cortex forming the tubercle as a whole.

b. Its primordium is at first a single short ectotrophic mycorrhiza, and develops by repeated dichotomous branching to a conspicuous size pushing aside its primordial mantle or the cortex of the tubercle. Each mycorrhiza assumes then an ecto-endotrophic structure.

c. The mycorrhizal fungus of this tubercle is *Boletus*.

In conclusion I wish to express sincere thanks for many helpful suggestions to Professor K. KORIBA, under whose direction this study was undertaken.

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Explanation of plate.

Plate XIV.

Fig. 1. Median longitudinal section of a primordium of the compound mycorrhiza Form A. ×45.

Fig. 2. Median longitudinal section of very young compound mycorhiza Form A. ×45.

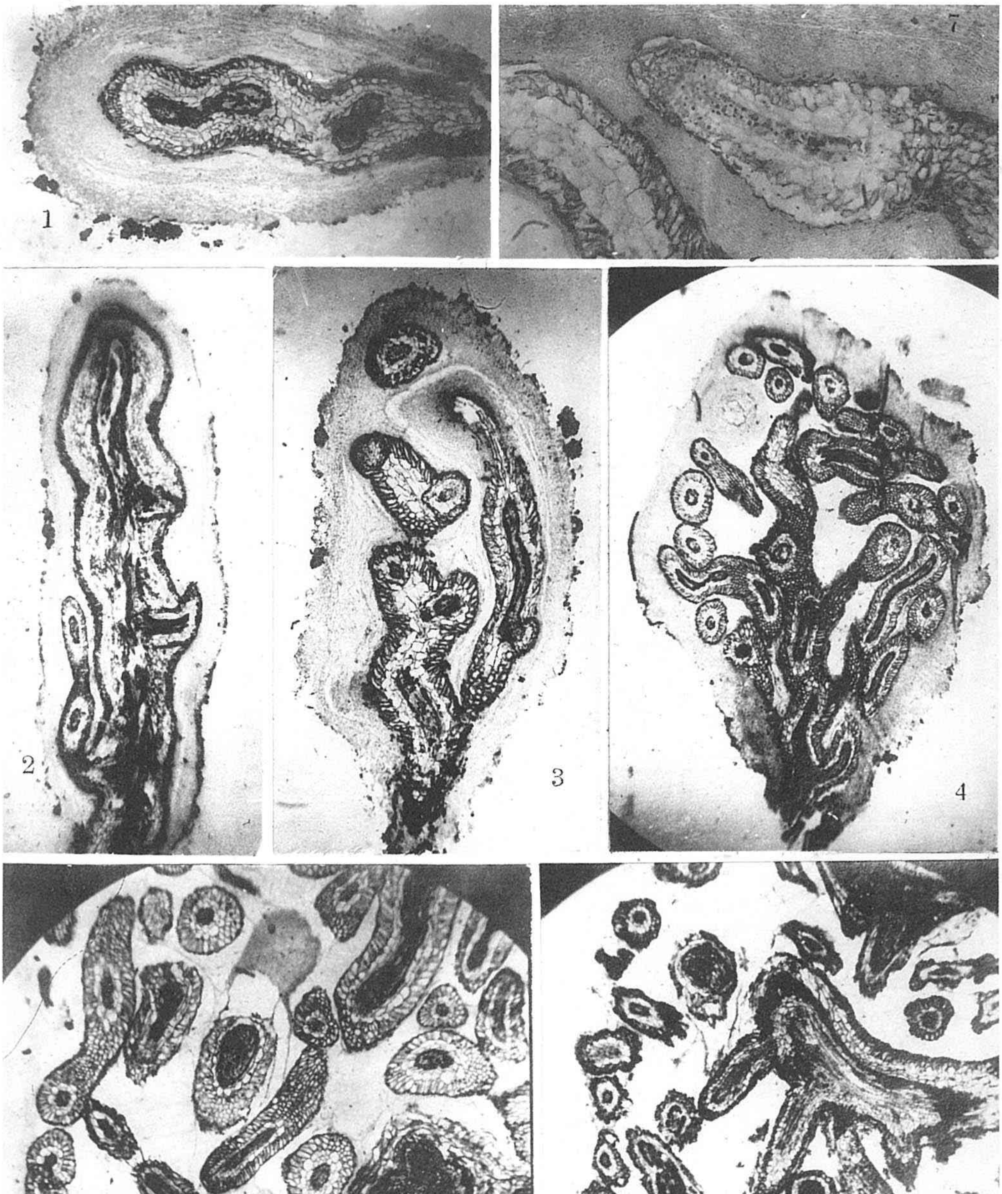
Fig. 3. Median longitudinal section of the same in a slightly advanced stage of development. ×45.

Fig. 4. Median longitudinal section of the same in an advanced stage of development. ×45.

Fig. 5. A section of a rather old compound mycorrhiza, Form A. ×45.

Fig. 6. A section of a very old compound mycorrhiza, Form A. ×45.

Fig. 7. A longitudinal section of a mycorrhiza (Form A) which has been imbedded in a mycelium. ×100.



MASUI phot.

MASUI: Compound Mycorrhiza.