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A Study of the Ectotrophic mycorrhiza of Alnus.

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With one Plate and 31 Text-figures.

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Contents.

Introduction.

The ectotrophic mycorrhiza of *Alnus* has hitherto engaged little attention. So far as I know, only FRANK ('88) and MIMURA ('17) have reported it. Among many other kinds of mycorrhizal plants, the former mentioned *Alnus viridis* as having an ectotrophic mycorrhiza, and the latter stated that *A. japonica* S. et Z., *A. incana* WILD *var. sibilica* SP. and sometimes *A. firma var. multinervis* REGEL have one, though they gave neither the structural details nor their causal organisms.

During my researches into various mycorrhizas in Japan I often met with those of *Alnus*, which have many characteristics not yet well known. So I may introduce them in detail here.

In the vicinity of Kyoto, there are two kinds of ectotrophic mycorrhiza in *A. japonica* S. et Z., three in *A. firma* S. et Z. *var. Sieboldiana* WINKEL and one in *A. firma* S. et Z. *var. multinervis* REGEL. They differ greatly in colour, structure and in some other features, and one of them produces the fruiting body, *Cortinarius sp.* (a), on the roots of *A. japonica* S. et Z.

It has been reported by a few authors that several species of *Cortinarius* cause mycorrhizas on higher plants. According to NOAK ('89), *Cortinarius callisteus* FR. causes mycorrhiza on *Picea*, *C. coerulescens* SCH. on *Fagus* and *C. fulmineus* FR. on *Quercus*. According to KAUFMANN ('06), *C. rubipes* is a mycorrhizal fungus of *Quercus rubra*, *Acer saccharum* and *Celastrus scandeus*. McDOUGALL reported in 1914 that *Cortinarius sp.* is a mycorrhizal fungus of *Betula*, and in 1922 that another species of *Cortinarius* is connected with *Picea rubra* and *Abies balsamea*.

In Japan no *Cortinarius* has hitherto been reported as a mycorrhizal fungus of *Alnus*.

I. The mycorrhiza of Alnus japonica S. et Z.

The mycorrhizas of *Alnus iaponica* are found abundantly in the superficial layer of soil, and are easily recognized by white, abnormally thickened rootlets. After detailed investigation, I could distinguish in the rootlets two types of mycorrhizas, which I may denote Forms A and B.

Form A.

The mycorrhiza: This form is pure white in colour when fresh. Its particular character is that the numerous white hyphae given off from its surface grow densely together in the surrounding soil or on the rotten leaves, as shown in Text-figs. 1 and 2.

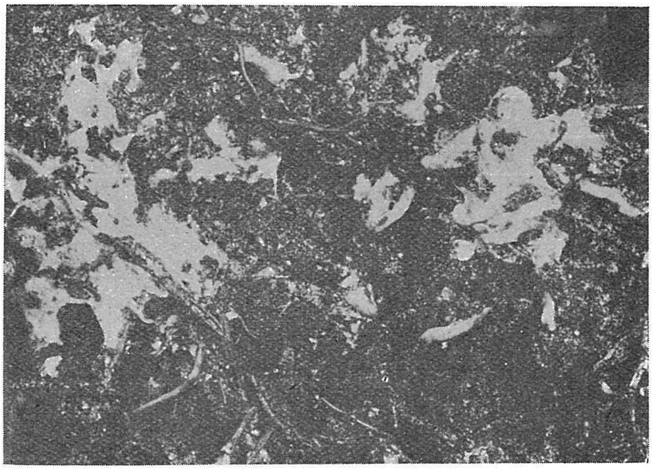


Fig. 1. Mycorrhiza Form A of *Alnus japonica* S. et Z. Numerous mycorrhizas are found on the surface of humid soil. ×2·2.

Microtomic sections of the mycorrhiza stained with pianese III b, DELAFIELD's haematoxylin, aniline blue, fuchsin-iodine green or FLEMMING's safranin-gentian- violet-orange show clearly its internal structure.

Fig. 2. Mycorrhizas Form A of *Alnus japonica* S. et Z., showing numerous hyphae given off from their surfaces. ×2.3.

The fungous mantle is very thick, measuring 60--90 μ in thickness, and differentiates into three layers (Fig. 1, Pl.XV). The outer layer is usually thinner than the middle, and composed of small binucleated filaments, measuring 2.8—4.5 μ in thickness. Hyphae, grown out from its surface and interwoven into a loose network, are the same in thickness as the elements of this layer, binucleated and provided with abundant clump-connections (Figs. 3 and 4, Pl. XV). The clumps appear constantly in connection with the branching of the main filaments as well as between the branches. Hyphal anastomoses also occur occasionally. There are chromatic granules along both sides of the septum, as shown in Figs. 3 and 4, Pl. XV.

The middle layer is composed of large undistinguishable binucleated filaments, measuring 8.9—20 μ in thickness. They contain a dense accumulation of a substance which is coloured deep red by FISCHER's tannin-safranin-stain, indicating it to be glycogen.

The inner layer is comparatively thin, composed of filaments with denser contents than those of the outer layers.

One of the most striking characteristics of this mycorrhiza is that there is a marked contrast between the hyphal structure of the young apex and that of the fully developed portion of the mantle, though the number of hyphal layers is almost the same (Fig. 2, Pl. XV). The former is very thin, measuring 11—17 μ in thickness, and composed of undifferentiated thin hyphae, 2.3—4.3 μ in diam., while the latter is formed of tolerably thickened unseparable filaments, as mentioned above. The secondary thickening of the hyphae of the middle and inner layer of the mantle, due perhaps to the nutritive supply, is therefore quite clear, while those of the apex and the outer layer remain undifferentiated. (Compare MASUI '26, b, p. 90).

The epidermal tissue of the mycorrhizal root is composed of one layer of small cells. Beneath the epidermis there are several cell-layers of cortical tissue. These layers, as well as the root-cap, usually contain in their cells granular bodies which have a strong affinity for anilin blue, fuchsin and haematoxylin. These bodies, however, are not the special product of the mycorrhiza, as they are found also in uninfected roots.

From the inner part of the mantle, hyphae penetrate inwards between the epidermal cells and form the so-called HARTIG'S network (Text-fig. 3 and Fig. 1, Pl. XV). Further inwards, they do not extend intercellularly,

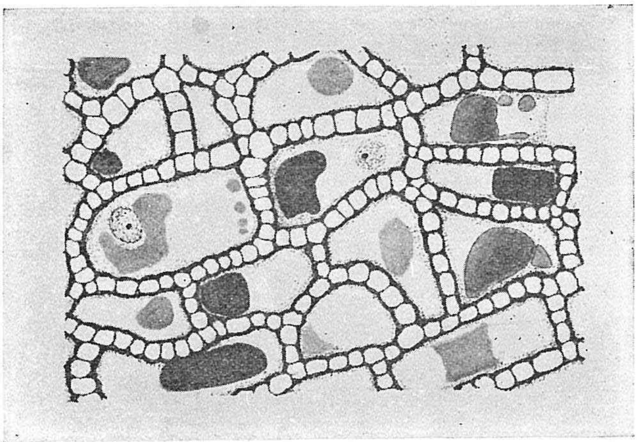


Fig. 3. Tangential section of a mycorrhiza, showing HARTIG'S network. ×867.

but invade intracellularly the outermost layer of the cortex, so that they appear very much like endotrophic filaments (Figs. 5 and 6, Pl. XV). The intracellular hyphae are sooner or later transformed into granulated filaments embedded in a kind of mucilage (Fig. 5, Pl. XV). In one case, I observed in cell cavity a large mass resembling the "sporangiole" of GALLAUD (Fig. 7. Pl. XV), formed of membranous walls of the mycelium.

The mycorrhizal fungus: Cortinarius sp. (a) (Text-fig. 4). This mushroom occurs in this locality during summer and autumn on the ground, where *Alnus japonica* and *Castanea vulgaris var. jap nica* grow. It is 4—7 cm. high, the cap 1.3—2 cm. broad, and the stem is 1.5—3 mm. in thickness. The pileus is conical and the margin incurved when young, then bell-shaped, and, as the margin of the cap expands, appears more or less umbonated. The surface is smooth with innate fibrils. The colour is grey or yellowish grey and the umbo is much darker than the marginal portions.

The gills are grey or dark brown in colour, adnate, sometimes sinuate.

The stem is very slender, cylindrical, hollow, with loose threads in

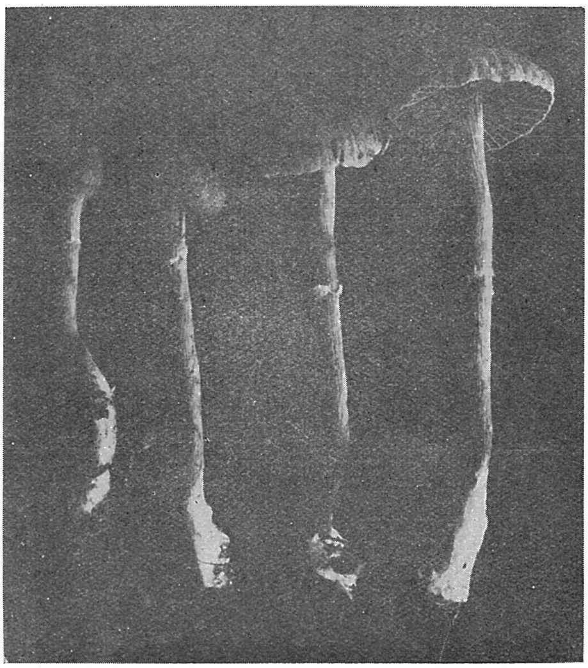


Fig. 4. Cortinarius sp. ×1.

the cavity, fibrous, yellowish brown or greyish brown in colour. Its lower portion is much thicker than the upper portion and is clad with white mycelium.

The veil is yellowish brown, and an arachnoidal network extends from the margin of the pileus to the stem when the plant is young. As the stipe elongates, a part of it forms a delicate ring around the stem.

The spores are brown in mass, eliptical, 7.7—10.8 × 4.7 μ.

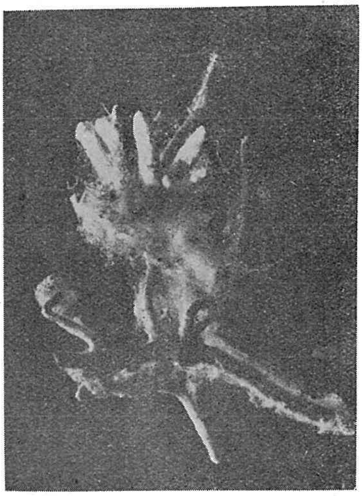
The seasonal development of the mycorrhiza and the fruiting body of the mycorrhizal fungus, Cortinarius sp. (a). MÖLLER ('03) and McDOUGALL ('14) have reported on the seasonal variation of mycorrhizas. The latter stated that "they reach their fullest development in late autumn, and persist in this condition through the winter. In late spring they die. They are, therefore, annual." In the case of the mycorrhizas Form A of *Alnus japonica*, on the contrary, they begin to develop in spring, and reach their climax in the middle of August.[1] The renewed growth of mycorrhizal roots also goes on during these periods.[2]

1) The habit of trees and the climatic conditions especially the rainfall, may play some role in the seasonal variation.

2) Compare Masui '26, (b).

Fungous filaments sent out from each of the clustered mycorrhizas, form then a rather compact network over the surface of the surrounding soil as shown in Text-fig. 5. In late August numerous primordia of the basidiocarp are formed as minute knots in the mycelium. They are slender, and tapering towards the apex. In every case the actual connection between the primordium and the mycorrhiza is easily recognized even with a pocket lens (Text-figs. 6 and 7).

Fig. 5. Two young fruiting bodies (×) arising on the mycelial network. ×2.



Fin. 6. Four primordia of the basidiocarp originated on a mycelial network woven by the hyphae projecting fiom a few mycorrhizas. ×4.

Fig. 7. On the side of a mycorrhiza two small mycelia knots have originated. ×4.

At this stage of development, the primordia consist of a homogenous weft of slender threads. They develop gradually and attain their fullest maturity in one or two weeks (Text-fig. 8).

The mycorrhizas begin to decay in late autumn and most of them die in winter. But they may be found all through the year sporadically, since the formation of new mycorrhizas usually begins before all of the old ones are dead. McDOUGALL ('22) stated in the case of *Picea rubra* and *Abies balsamea* that "the relatively thin and loosely constructed fungous mantle may be somewhat characteristic of mycorrhizas caused by a species of *Cortinarius*." But in the case of *Alnus japonica* the mycorrhiza caused by this *Cortinarius* has a very thick and compact fungous mantle as above mentioned. It seems therefore that not all the species of *Cortinarius* always cause a similar mycorrhiza on the root of higher plants.

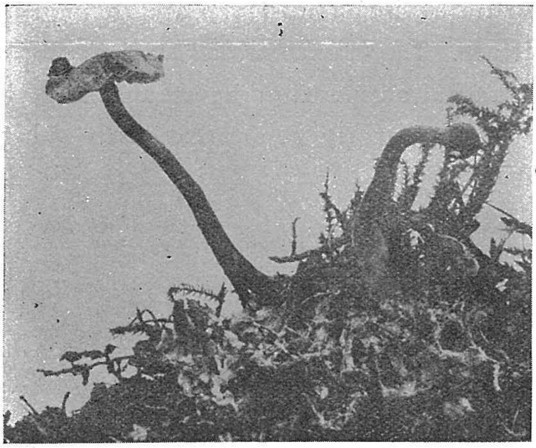


Fig. 8. *Cortinarius Sp.* (a) originated on a mycelial network. ×1.

Form B.

The mycorrhiza: This from is whitish when young, changing to brownish with age, and is easily distinguishable by its slender, sometimes irregularly bent form. They occur usually in clusters during spring and summer (Text-fig. 9). Occasionally it is found mixing with Form A. In rare cases both forms of the mycorrhiza develop on a common mother root as shown in Text-fig. 10.

A superficial examination with a low-powered microscope reveals a rather smooth surface

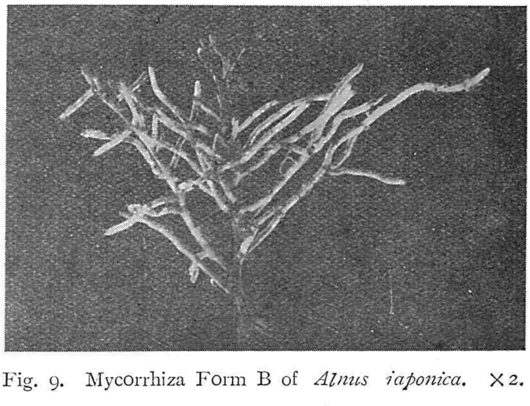


Fig. 9. Mycorrhiza Form B of *Alnus iaponica*. ×2.

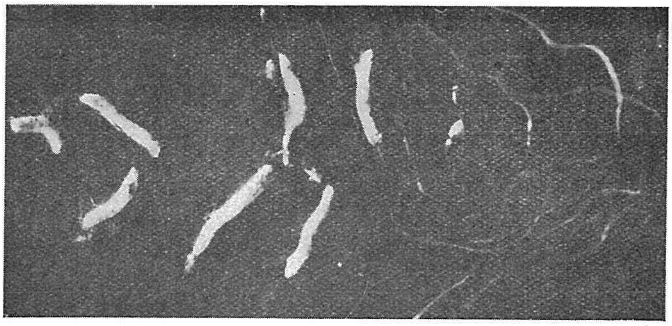


Fig. 10. Mycorrhiza Forms A and B attached to a common mother root. ×2.2.

and rhizomorpha-like hyphal bundles which are given off from its surface.

The mode of develapment of the fungous mantle is, in this case, very interesting. In the earliest stage of development, the fungous filaments, which grow apically along the surface of the root, are found, partly scattered outside of the already perished calyptral layer, partly along the epidermis. These intercalar filaments begin to increase in size and some of them penetrate in between the epidermal cells, preparing to form the so-called HARTIG's network (Text-fig. 11, *A*).

They enlarge then more rapidly and the inserted filaments penetrate deeper and deeper, pushing aside the epidermal cells, until they reach the cortical cells, so that the epidermal cells are separated from each other. Text fig. 11, *B* shows the well developed HARTIG's network between the epidermal cells and also a considerable number of fungous filaments lying on the outside of the dark-coloured calyptral layer. The latter increase more in number until they interweave a rather compact network as an outer layer of the fungous mantle (Text-fig. 11, *C*). To put it shortly, the most interesting characteristic of this mycorrhiza is that the filaments lying immediately outside of the epidermal layer not only increase in size but also are provided with copious contents, while those outside of the calyptral layer become a compact mycelial layer so as to form the outermost layer of the mycorrhiza.

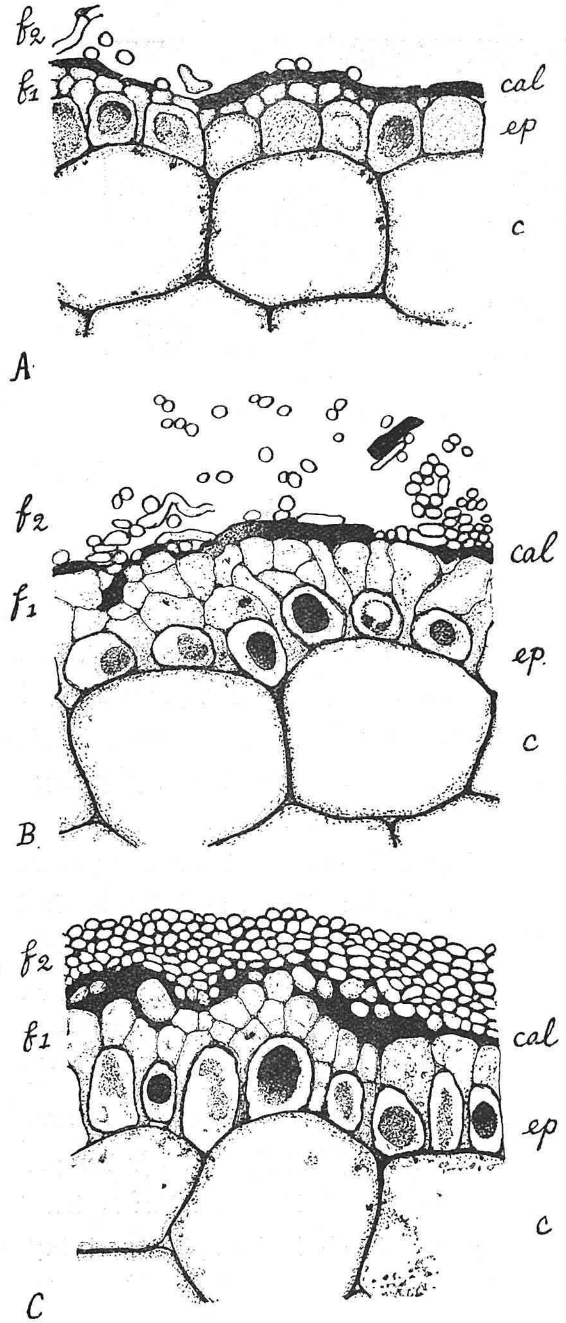


Fig. 11. A—C, Successive stages of development of mycorrhiza. Cross sections. *cal*, calyptral layers; *ep*, epidermis; *c*, cortex; *f1*, inner layer: *f2*, outer layer of mantle. ×867.

The rhizomorpha-like hyphal bundles:

The rhizomorpha-like hyphal bundles are found in large numbers among the mycorrhizas Form B of *A. japonica*, as in the case of the other mycorrhizas (FRANK ('85 and '88), MÜLLER ('86), MELIN ('23) and MASUI ('26). They are whitish or brownish in colour, 0.04—0.23 mm. in thickness and send off branches as shown in Text-fig. 12. In these respects, they resemble "ozonia" which was described by BULLER ('24).

A superficial examination with low-powered microscope reveals a rather smooth surface and numerous long filaments projecting out from it. The latter are irregulary bent thin filaments, 3.3—4 μ in thickness, provided with clump connections.

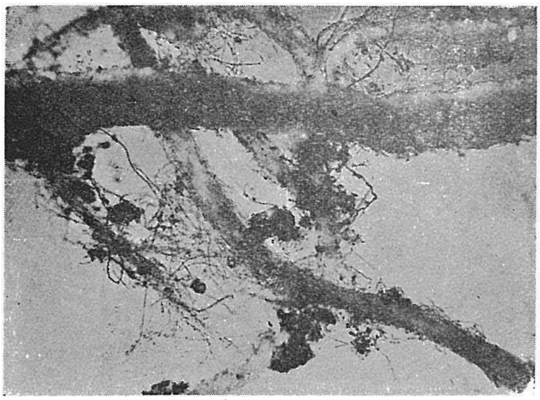


Fig. 12. Rhizomorpha-like hyphal bundle. × 50.

The occurrene of such a bundle may be important in connection with the spreading of the infection of the mycorrhizal fungus to newly elongated rootlets of the host plant, as described already in my previous paper. Old mycorrhizas always produce bundles of filaments. These bundles elongate along the mother root (Text-fig. 13) or in any other direction, as if they were searching for new host roots (Text-fig 14). When the bundle comes in contact with the surface of young rootlets, the projected filaments expand all over the surface until a new mantle is completed (Text-fig. 15). The bundles are often found not only connected with mycorrhizas, but also with rotten leaves or humus particles, as described by FRANK ('88). When the strands are lying on rotten leaves, usually the projected filaments penetrate deep into their dead tissue through the cell-walls. These filaments are usually provided with a large amount of proteinous substances as shown

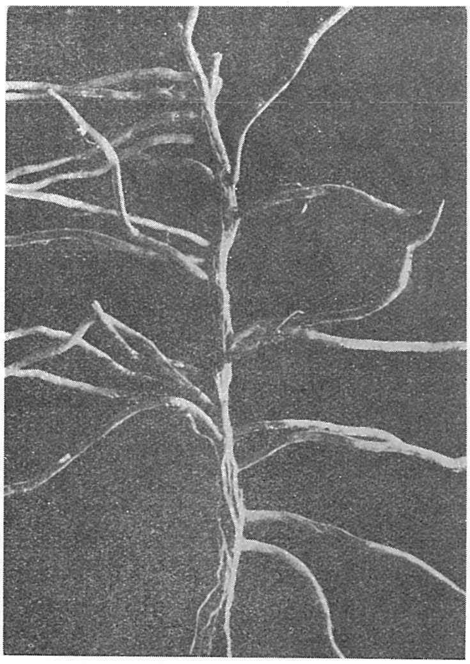


Fig. 13. Rhizomorpha-like hyphal dundles elongated along the surface of an axial root. × 3.

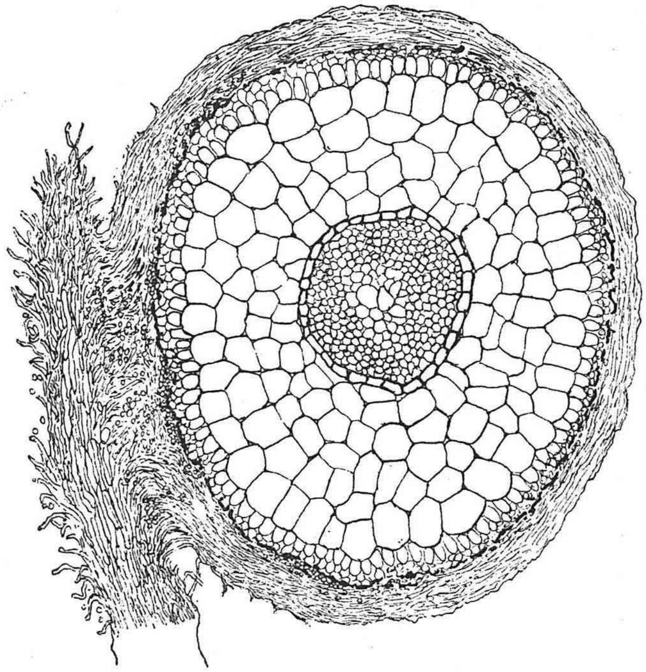


Fig. 15. A cross section of the mycorrhiza, showing the relation between its fungous mantle and the hyphal bundle. ×ca 80.

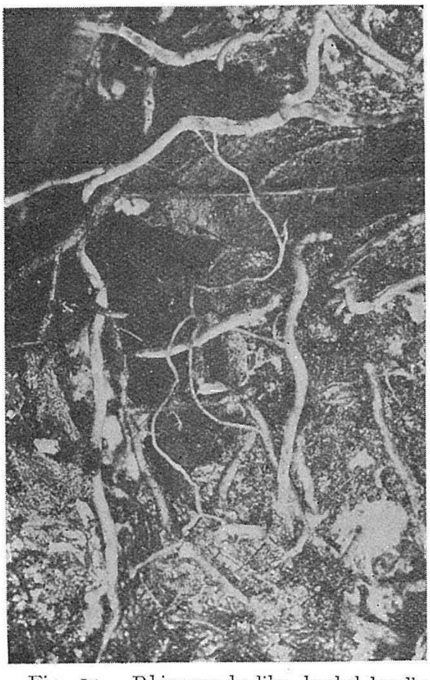


Fig. 14. Rhizomorpha-like hyphal bundle arisig from the surface of a mycorrhiza. ×3.5.

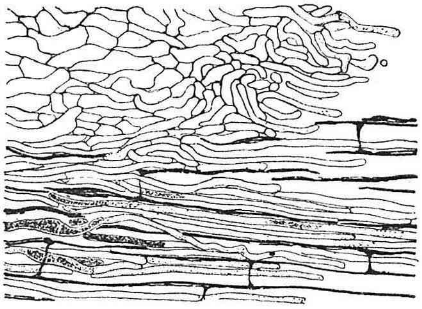


Fig. 16. A section of a hyphal bundle which is lying on a rotten leaf, showing proliferated filaments penetrating the dead tissue. ×260.

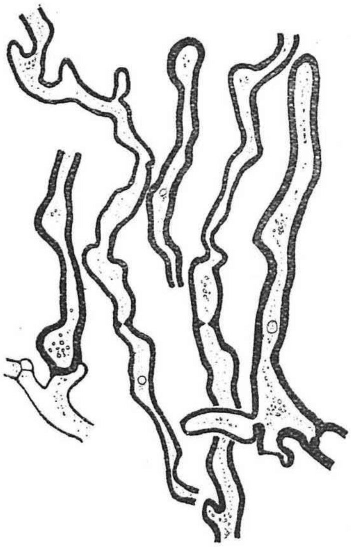


Fig. 17. Thick-walled filaments wich constitute the middle layer. ×320.

in Text–fig. 16. Moreover I observed occasionally that the filaments, given off from the surface of the bundle, interweave a loose network at the side of the mother bundle, including a considerable number of humus particles. In these respects, it may be concluded that these bundles serve not only for the further infection of the mycorrhizal fungus but also for obtaining food substances from the humus.

The bundle is composed of three different layers. The outer layer is composed of thin-walled thin filaments, 3.3—4 μ in diam., with clump-connections. The middle one is of thick-walled large filaments, 7.1 – 10.9 μ in thickness, and plasmodesmen is clearly seen between two cells of the filament through the minute hole in

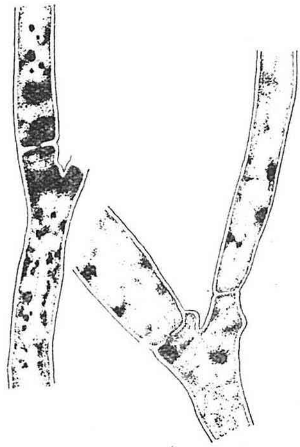


Fig. 18. The elements of the central pseudoparenchymatous tissue. × 320.

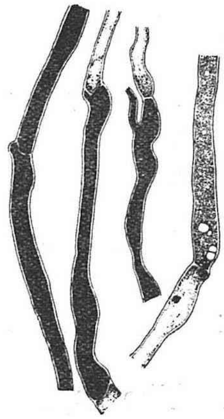


Fig. 19. Food storage hyphae. ×320.

the septum (Text-fig. 17). They bend very irregularly hooking with their processes into each other until they build up a strong texture.

The central portion of the bundle is pseudoparencymatous, composed of rather large filaments, 4.6—23 μ in thickness, provided with more plasmic contents than those of the outer layers (Text-fig. 18). Embedded in the tissue, there are particular filaments in small numbers. They are septated and filled up with substances colouring black with haematoxylin and red with fuchsin. They may be the food-storage hyphae described by DOUGLAS ('18) and MASUI ('26 a) (Text-fig. 19). When the sections

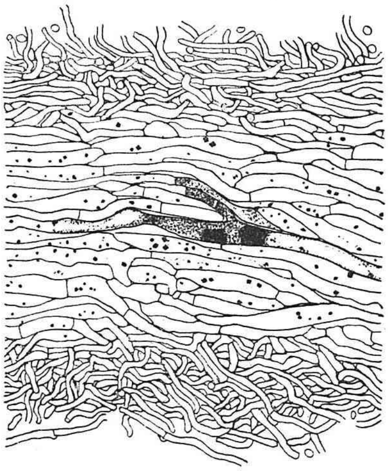


Fig. 20. A longitudinal section of the hyphal bundle, stained by ALTMANN'S method, showing numerous protein crystals dispersed in the filaments. ×253.

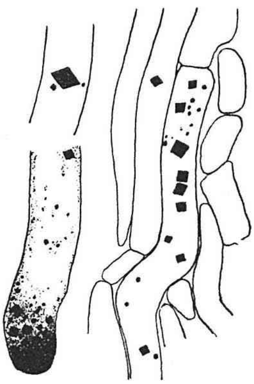


Fig. 21. Protein crystals in the hyphae. ×866.

are stained by ALTMANN'S acid fuchsin method, numerous protein crystals are demonstrated. They are minute cubes or octahedral bodies as shown in Text-fig. 21.

II. The mycorrhiza of Alnus firma S. et Z. var. Sieboldiana Winkel.

The plants are found, in this locality, in large numbers in open granitic sand on sharp hill slopes. Abundant roots given out from them densely interweave until the porous sand soil is cemented. A careful examination even with a pocket lens reveals usually numerous mycorrhizas among them, though MIMURA ('17) found no ectotrophic mycorrhizas on the same tree standing in the Forest Experiment Station, Meguro, Tokyo. After detailed observation, I could distinguish in the mycorrhizas three different types which I may denote as Forms A, B and C.

From A.

This form of mycorrhiza is white in colour and its surface is rather smooth, rarely giving off hyphal bundles (Text-fig. 22). The fungous mantle, 10—25 μ in thickness, is composed of binucleated hyphae, measuring 1.8—3.8 μ in thickness. The epidermal layer is formed of large, obliquely arranged cylindrical cells which contain a large mass of tannic substances, while those of normal roots are long in the axial direction. Inserted between the fungous mantle and the epidermal layer, there is a row of demolished root-cap cells. The HARTIG's network is found well-developed only between the epidermal cells. Hyphal nuclei are also clearly observable (Text-fig. 23).

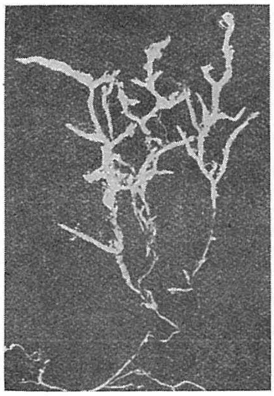


Fig. 22. Ectotrophic mycorrhiza Form A of *A. firma var. Sieboldiana.* ×ca 2.

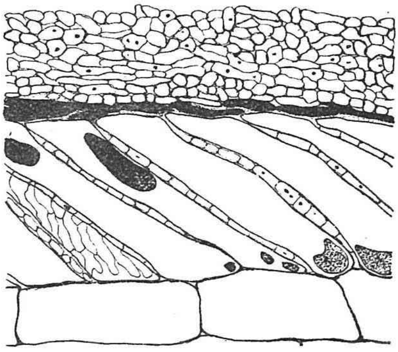


Fig. 23. A Longitudinal section of a mycorrhiza Form A. ×580.

Form B.

This form of mycorrhiza is yellow in colour, and its surface is rough, giving off numerous hyphal bundles (Text-fig. 24). The fungous mantle is composed of rather loosely associated filaments which are 2.2—3.5 μ in thickness. The nuclei in the hyphae of the mantle and the HARTIG'S network are unobservable in preparations stained with DELAFIELD'S haematoxylin, contrary to the case of Form A. In its other features, the mycorrhiza resembles the Form A (Text-fig. 25).

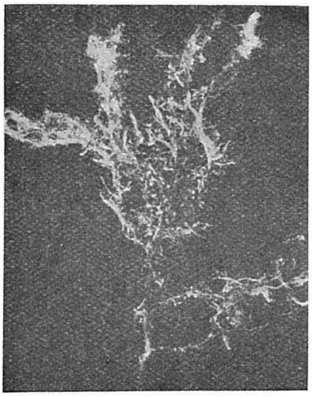


Fig. 24. Ectotrophic mycorrhiza Form B. ×2.

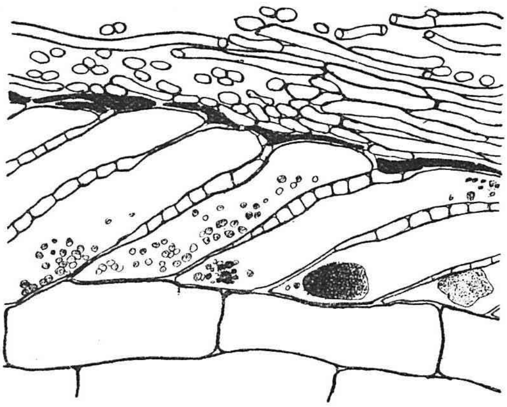


Fig. 25. Longitudinal section of a mycorrhiza Form B. ×704.

Form C.

This form of mycorrhiza is dark in colour provided with long

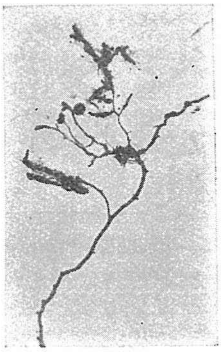


Fig. 26. Ectotrophic mycorrhiza Form C. ×2.

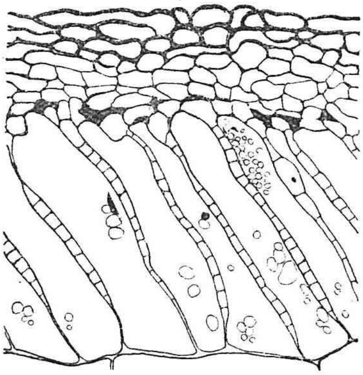


Fig. 27. Longitudinal section of a mycorrhiza Form C. ×608.

dark setae on its surface (Text-fig. 26). Occasionaly small dark sclerotia are found associated with the mycorrhizas.

The fungous mantle is divided into two layers. The outer layer is composed of thick-walled dark filaments, 4.6—7.8 μ in diam., while the inner layer is of thin-walled rather small cells measuring 1.8—6.0 μ in diameter. There is not only a well developed HARTIG's network between the epidermal cells, but occasionally hyphae that have entered them intracellulary (Text-fig. 27).

The overlapping of the different fungous mantles.

A notable fact about the mycorrhiza of *A. firma var. Sieboialdna*, is that there occur occasionally combinations of different mycorrhizas among these three forms. Text-fig. 28 shows examples of the white mycorrhiza attached on the black one, and inversely the latter on the former. Text-fig. 29 shows also the same relation between the yellow mycorrhiza and the black one. But I have not yet met with the case of combination between the white and the yellow ones.

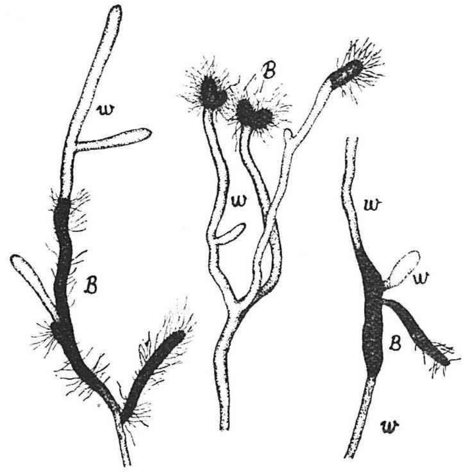


Fig. 28. Mycorrhizas Form A which have been partly overlapped by the mycorrhizal fungus which causes Form C on *A. firma var. Sieboldiana*. *W*, Form A; *B*, Form C. ×4·6.

In order to make clear the mycelial relation at the connecting point of these different mycorrhizas, microtomic sections of these specimens were prepared. In every case they showed that the dark mycelium had grown lapping densely over the white or the yellow mycorrhiza (Text-fig. 30). In other words, it is only the black one that can lap over the already formed mantle.

Such an overlapping of heterogenous mantles, I have reported previously in the case of mycorrhizas

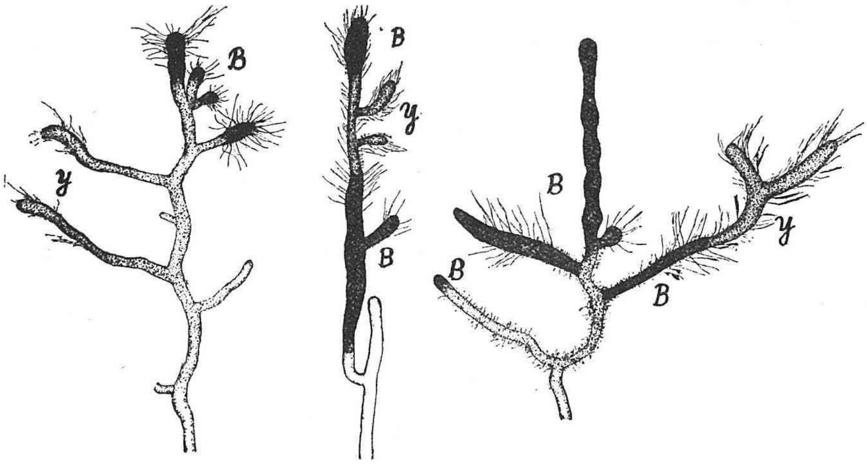


Fig. 29. Mycorrhizas Form B which have been partly overlapped by the mycorrhizal fungus which causes Form C on *A. firama var. Sieboldiana.* *Y*, Form B; *B* Form C. ×:.6

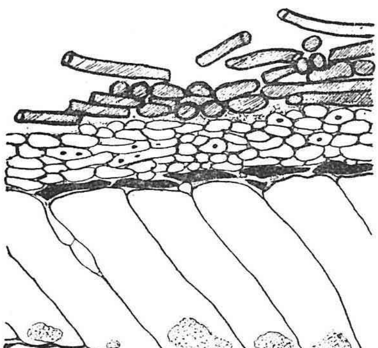


Fig. 30. A longitudinal section of the mycorrhiza Form A which has been overlapped by the fungous mantle of Form C. ×580.

Form C of *Abies firma* (MASUI '26, a, p. 74). In that case it is however confined to the same species of mycorrhizal fungus, whereas in *Alnus firma var. Sieboldiana* W. here, different kinds of fungi are concerned in the relationship. The formation of a mantle seems therefore to be a process of mycelial growth excited by some substances excreted from the surface directly from the root or indirectly through the mantle of the same or different species of fungi.

III. The mycorrhiza of A. firma S. et Z. var. multinervis Regel.

This variety grows in localities of the same environmental conditions as *A. firma var. Sieboldiana.* Roots which have been transformed into ectotrophic mycorrhizas are found in large numbers among their roots.

The mycorrhiza is yellowish in colour when young, becoming brown with age, and 0.24—0.4 mm. in diameter. A superficial examination with the microscope reveals a rather smooth surface and short filaments sparsely projecting out from it. Moreover long rhizomorpha-like hyphal bundles are found connected intimately with it. Microtomic section of the mycorrhiza shows a rather thick fungous mantle. It is made up of hyphae measuring 1.8—4.6 μ in diameter. The HARTIG's network is found well developed between the epidermal cells (Text-fig. 31).

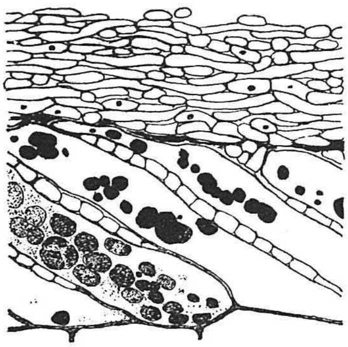


Fig. 31. Longitudinal section of a mycorrhiza of *A. firma var. multinervis.* ×. 650.

Conclusion.

The main contributions contained in the present paper may be summarized as follows:

1. *Cortinarius sp.* (a) causes a white mycorrhiza on the roots of *Alnus japonica* S. et Z. In this mycorrhiza, sometimes, the intercellular filaments enter into the cortical cells as if they were endotrophic filaments.

2. There is still another type of ectotrophic mycorrhiza on the roots of the same plant. The rhizomorpha-like hypal bundle, which is occasionally given off from the surface of this mycorrhiza, contains numerous protein crystals which are fully demonstrated with ALTMANN's staining.

3. There are three types of ectotrophic mycorrhizas, on the roots of *Alnus firma* S. et Z. *var. Sieboldiana* WINKEL, the white, the yellow and the dark one. The mycelium of the dark mycorrhiza grows sometimes lapping over the white or the yellow mycorrhiza.

4. *A. firma* S. et Z. *var. multinervis* R. has a yellowish ectotrophic mycorrhiza.

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

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Explanation of Plate XV.

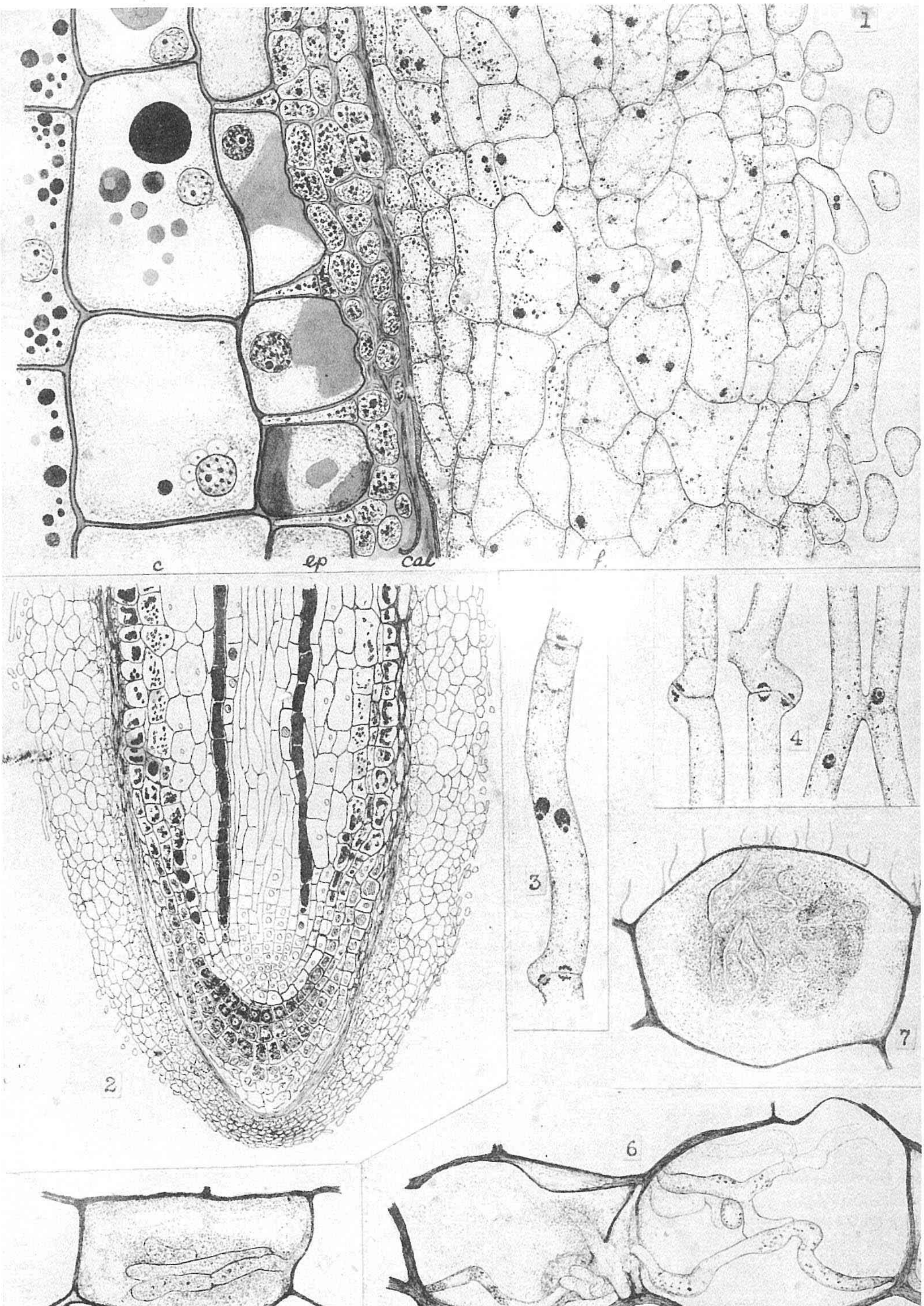
Fig. 1. Longitudinal section of mycorroiza Form A of *Alnus japonica* S. Z. *cal*, calyptral layers; *ep*, epidermis; *c*, cortex; *f*, fungous mantle. ×867.

Fig. 2. Longitudinal median section of an apex of this mycorrhiza. ×200.

Figs. 3 and 4. Filaments projected from this mycorrhiza. ×1300.

Figs. 5 and 6. Intracellular filaments of this mycorrhiza. ×1300.

Fig. 7. The sporangiole-like body found in the cortical cell of this mycorrhiza. ×1300.



MASUI phot.