CORTINARIUS AS A MYCORHIZA-PRODUCING FUNGUS¹

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(WITH ONE FIGURE)

THE study of the mycorrhiza problems has received a new impetus during the last six years by the appearance of extensive papers by MACDOUGAL (1), STAHL (2), TUBEUF (3), HILTNER (4), and MÜLLER (5). Considerable evidence has been adduced showing that in the case of the endotrophic mycorrhiza the organisms concerned act as purveyors of nitrogen to the symbiont or host with whose roots they are connected (6-7); furthermore, the organisms in some of these cases have been quite exhaustively studied (8-9). On the other hand, the fungi which cause the ectotrophic mycorrhiza have not been investigated except in a very few cases.

It is a noticeable fact as one looks over the literature, that the larger part of the work hitherto attempted has been done on a basis of several unknown quantities. One of these is the identity of the fungus which causes the ectotrophic mycorrhiza. The earlier writers speak of the fungus as if it were a single species or genus. It was thought for quite a time that the ectotrophic mycorrhiza of European trees was due in all cases to the tubers or truffles. WORONIN (10), in 1885, showed that this cannot be true for Finland, where the tubers are not found, but where nevertheless the mycorrhiza are abundant. KAMIENSKI (11) also found no truffles in the regions where he studied the mycorrhiza of *Monotropa*. REES (12) was at first inclined to think that *Elaphomyces* was the cause of the mycorrhiza of almost all the trees he examined; later, he himself found mycelium of mycorrhiza which differed in structure from that of *Elaphomyces*.

The fungi whose fruiting forms have been definitely reported as belonging to mycorrhizal mycelium are comparatively few. MACDOUGAL (1) gives a list of mycorrhizal fungi whose identity has been reported. The list is as follows: *Fusisporium*, *Eurotium*, *Pythium*, *Nectria*, *Celtidia*, *Elaphomyces*, *Geaster*, *Boletus*, *Tricholoma*, *Lactarius*, and *Cortinarius*. Of the non-mycelioid forms

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which are known, *Phytomyxa leguminosarum* and Frankia are of course the most prominent. It will be seen that the list is remarkably small, especially if we remember that only one or two species is referred to in each case. As we are only concerned with ectotrophic forms, the first four can be omitted in the discussion, and if we consider the evidence on which the symbiotic connection of the remainder is based, we find the actual list even smaller.

In the case of the Boleti, WORONIN (10), after declaring the tubers out of the question, says: "Vielleicht gehört die hiesige Mycorhiza einem anderen, ebenfalls unterirdischen Pilze an, dies will ich nicht bestreiten, bin aber vielmehr geneigt anzunehmen, dass die oben angeführten Boleten mit der Mycorhizen zusammenhängen." It seems that WORONIN himself was not very certain of the connection. *Elaphomyces* was very exhaustively studied by REES (11), who showed that it is undoubtedly connected with the pines in localities where the truffle occurs. Two species of Geaster, *G. fimbriatus* and *G. joricatus*, were shown by NOACK (13) to be attached to the roots of the spruce and pine.

When we come to a consideration of the agarics our knowledge is meager indeed. Only one investigator, NOACK (13), in 1889, has concerned himself with them. He found that five species of this group were apparently mycorhiza-producers on the forest trees of the locality where he made his observations. Two were *Tricholomas*; one a *Lactarius*; and three were *Cortinari*. He merely makes the bare statement that they are connected with the rootlets by their mycelial strands, which he could easily make out. It is very probable that his observations are correct.

It seems to be appreciated that we need some investigation to determine what fungus we are dealing with, so that problems which have to do with the physiological side of mycorhiza may be undertaken more intelligently; for it is just as likely that knowledge concerning the fungus and its life history may lead to an understanding of the relation of the two organisms as a knowledge of the tree would. It seemed worth while, therefore, to report the identity of any such mycorrhizal fungi whenever the evidence seemed sufficient to make it acceptable.

OBSERVATIONS ON *Cortinarius rubipes*, sp. nov.²

In a previous paper (14) I pointed out that the members of the genus *Cortinarius* were so constantly found in limited areas, and some species in such close proximity to certain trees, that it seemed likely that there was some connection. This last summer an effort was made to find out to what extent this might be true. The season was wet during the early summer, and although one finds few *Cortinarii* as a rule before August, several did occur, and one of

FIG. 1.—*Cortinarius rubipes*, sp. nov.—Left hand sporophores show the mass of rootlets and humus with strands of mycelium projecting above; right hand individual shows the roots with the short mycorrhizal branches and the mycelial strands which are attached to the base of the stipe.—Photographed by the writer.

these proved to be favorable for my purpose. It not only showed beautifully its connection with the tree roots, but turned out to be an undescribed species of *Cortinarius*.

It was found July 4, 1905, on the south slope of a small ravine along the Huron River, near Ann Arbor, in a layer of humus and forest leaves. This species, as is indeed true of some other fleshy fungi, is characterized by its brick-red mycelial strands and stem. By removing the surface soil it was possible to see the brick-red strands intertwining with the rootlets apparently in all directions.

² For description in full, see 8th Report Mich. Acad. Sci. 1906.

But it was soon found that the reddish network extended along definite paths. Beginning with a tiny rootlet, the fungus was followed to a rather large root, apparently growing from a hickory. On examination, however, it was found that the mycorrhiza-bearing root passed the hickory, and that all the roots of the hickory examined were devoid of a colored mycorrhizal fungus. On the other hand, the root in question was now easily traced to a clump of red oaks, of second year growth, which were distant at least 54^{dm} from the starting point. Besides the hickory, the roots of a *Crataegus* which crossed the oak roots were likewise devoid of the fungus in question.

The red strands were attached only to the small rootlets, and where the roots extended below the black soil into the yellow subsoil the mycorrhiza gradually disappeared, facts which were known to FRANK, STAHL, and others. The leaf mold along with the remains of last year's leaves forms a thin covering beneath which the young buttons of the fungus are started.

About twenty paces down the slope, another troop of the same species of *Cortinarius* was found. These came up only 30^{cm} away from a fine young sugar maple and close to one of its main roots. Expecting that they were probably attached to the roots of an oak a short distance away, I dug down carefully and found to my surprise that the strands which were very luxuriant here were attached to the rootlets of the sugar maple; even the small roots growing directly from the base of the trunk were thickly beset by the strands. The sporophores were loosened and the attachment of the strands followed from the stipe to the rootlets and thence to the tree. Several days later on visiting the same hill, two more sporophores were found on the north slope of the hill, again with the characteristic strands, and connected with a red oak.

I had to leave Ann Arbor at this time, and not until I came back in September did I have any further opportunity to make observations. On October 30 the slope was dug over for a considerable area around the original habitat of the *Cortinarius* in question. The roots of the same maple were found to be hung with the reddish strands in all directions, just as luxuriant apparently as in the early summer. Here, also, other roots crossing or intertwining with the maple roots—with one exception—were not affected by the fungus.

An ash, basswood, and white oak were examined, but no trace of the fungus found. About 27^{dm} from the sugar maple, it was found that some of the strands were apparently attached to a different root. Following this up to a clump of red oaks about 54^{dm} away, I was again surprised to find that the oak roots in this case were not connected with the fungus at all, but that the root which was followed—which did not have the appearance of an oak root—belonged to a large *Celastrus scandens* which wound around one of the oaks. It was clear that we had another symbiont connected with the fungus.

DISCUSSION

It may be well here to call attention to the following points which have been brought out: (a) that *Cortinarius rubipes* (for so we will call it) is connected with three forest symbionts belonging to different families; (b) that it is apparently selective in the sense that the specific character of the symbiont does not necessarily attract it; (c) that one of the symbionts is a maple.

NOACK (12), who has been the only investigator of the agarics as producers of mycorrhiza, thinks he has connected *Tricholoma terreum* with both beech and fir, and *Lactarius piperatus* with beech and oak. My own observations seem to show that it is undoubtedly a fact that one fungus may be attached to trees of very different families. In the case of *Celastrus scandens* no fruit bodies were seen, but there can hardly be a doubt that it was the mycelium of the same species.

It is rather unexpected to find that the same tree species when exposed to the fungus does not always become associated with it. It is evident that the mycorrhizal fungus may attach itself to very different hosts, dependent for its initial attachment on certain environmental factors.

The maples of Europe are reported as seldom forming mycorrhiza (2). The roots of the sugar maple mentioned above were carefully examined with a lens, and also under the microscope, and mycorrhiza seemed to be everywhere abundant on the smaller rootlets. How generally they occur on our maples is not known, as hardly any work has been done in this line in our country.

With regard to the kind of mycorrhiza involved, there is of course

no uncertainty. Some of the strands and the connected rootlets were fixed and imbedded, and sections were made to determine the more intimate relations of the two organs. When stained rather deeply by fuchsin and gentian-violet the connection could be easily made out. It is clearly a true ectotrophic mycorrhiza. There is a close-lying layer of parallel hyphae which surrounds the rootlet, and, in all but the youngest rootlets, branches of this layer penetrate the root and form a close intercellular tissue exactly as figured by FRANK (13). The cells of the root at this time seem to contain little protoplasm and occasionally hyphal threads are seen to cross the cells of the cortical layer farther in. In the youngest roots no intercellular tissue appears to be present.

It would seem that there must be some close physiological relation; FRANK indeed thought he had demonstrated it. At the present time, however, nothing definite is agreed upon. To attempt in some measure to solve this question, experiments are now under way with the mycelium of the above-mentioned mushroom. One fact may have some bearing on the problem; the species of the genus *Cortinarius* develop relatively slowly. The writer has never been able to bring buttons into the house and develop them there, as is possible with *Amanitas* and *Volvaria*. For some reason they seem to have lost the vigor necessary to this end. It may be that the explanation of this is found in that a part of their food supply is cut off, and that the tree really supplies some of the necessities for the full development of the sporophore.

Let it not be supposed that all *Cortinari*i are mycorrhiza-formers, at least normally. *Cortinarius armillatus*, for example, although very partial to *Tsuga canadensis*, is usually found among rotten logs or leaf-mold near this tree, and is probably a saprophyte; on the other hand, it has been found growing out of a cleft at the base of one of these hemlock trees. It seems quite likely, however, that a good many *Cortinari*i are in symbiotic connection in the manner of the one described in this paper. During several seasons' observations, I have found *C. squammulosus*, *C. bolaris*, and *C. cinnabarinus* again and again in places which would indicate some relation to one kind of tree. *C. cinnabarinus* seems to prefer the oak, the other two the beech. NOACK (12) has shown the connection of *Cortinari*us *callisteus*

with the beech, *C. caerulescens* with the beech, and *C. fulmineus* with the oak. Others will no doubt be added to the list as soon as observers enter this interesting field.

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LITERATURE CITED.

1. MACDOUGAL, D. T., Symbiotic saprophytism. *Annals of Botany* **13**:1. 1899.
2. STAHL, E., Der Sinn der Mycorrhizenbildung. *Jahrb. Wiss. Bot.* **34**:539. 1900.
3. TUBEUF, K., Beiträge zur Mycorrhizafrage. *Naturwiss. Zeitsch. Land. Forstwirts.* **1**:Feb. 1903.
4. HILTNER, L., Beiträge der Mycorrhizafrage. *Idem* **1**:Jan. 1903.
5. MÜLLER, P. E., Über das Verhältniss der Bergkiefer zur Fichte in den Jutländischen Heideculturen. *Idem* **1**:Aug. & Oct. 1903.
6. HELLRIEGEL H. & WILFARTH H., Untersuchungen über die Stickstoffernährung. *Ber. Deutsch. Bot. Gesells.* **7**:138 and footnote. 1889.
7. NOBBE & HILTNER, Die endotrophe Mycorrhiza von Podocarpus und ihre physiologische Bedeutung. *Landwirts. Versuchsst.* **51**. 1899.
8. ATKINSON, G. F., Contribution to the biology of the organism causing leguminous tubercles. *Bot. Gaz.* **18**:157, 226, 257. 1893; and literature quoted.
9. SHIBATA, K., Cytologische Studien über die Endotrophen Mycorrhizen. *Jahrb. Wiss. Bot.* **37**:643. 1902.
10. WORONIN, M., Über die Pilzwurzel von B. Frank. *Ber. Deutsch. Bot. Gesells.* **3**:205. 1885.
11. REES, M., Über Elaphomyces und sonstige Wurzelpilze. *Ber. Deutsch. Bot. Gesells.* **3**:294. 1885.
——— Über den Parasitismus von *Elaphomyces granulatus*. *Bot. Zeit.* **38**:729. 1880.
12. NOACK, Über Mycorrhizenbildende Pilze. *Bot. Zeit.* **47**:389. 1889.
13. FRANK, B., *Ber. Deutsch. Bot. Gesells.* **3**:*pl.* 10.
14. KAUFFMAN, C. H., *Bull. Torr. Bot. Club* **32**:301. 1905.