OCCURRENCE OF ROOT-ROTTING BASIDIOMYCETES

IN FOREST SOILS

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by

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PREFACE

The term "root-rotting fungi" as used in this paper refers to decay fungi which enter through roots. With this definition the assumption can be made that root-rotting fungi were in the soil near the root or on the root just prior to entry. It is possible that there is a build-up of the amount of the parasite, or that there is a change in its form just prior to entry. In an attempt to find what information was available on this aspect of this group of fungi a search of the literature was made.

The presence of root-rotting fungi is obvious when the rot they cause is found in roots. However, this is the resulting damage of these organisms, and the process by which it is accomplished is of importance if a more complete understanding of root-rots is to be attained.

In attempting to study one or more of the root-rots in trees it would be well to know if possible what form or forms of the causal organisms to look for, and in what part of the soil profile they are likely to occur. It is hoped that some of this information found by other workers will be revealed by this literature review.

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INTRODUCTION

Numerous reports have been published on the damage caused by individual root-rotting fungi, and on the behavior of these fungi under laboratory conditions. However, information on their occurrence in forest soils and whether or not they occur there commonly is almost lacking. This research has been mostly incidental to appraisal of damage and to laboratory cultural studies.

Some of the information obtained by research on soil fungi in general provides knowledge of the root-rotting fungi. However, the findings of Rishbeth (1950) studying *Fomes annosus* (Fr.) Cke., and Leach (1939) studying *Armillaria mellea* (Vahl.) Quel. show the root-rotting fungi to have many characteristics differing from the non-root-rotting fungi of the soil.

Garrett (1950) has set up a general classification of soil fungi. He groups specialized root parasites and mycorrhizal fungi together in a class of root-inhabiting fungi. The remainder of the root-infecting fungi, together with the obligate saprophytes he designates as soil-inhabiting fungi. The specialized root parasites are mostly Basidiomycetes, although a few belonging to such genera as *Xylaria*, *Phytophthora*, *Phymatotrichum*, and *Verticillium* are not. Basidiomycetes that are parasitic on roots are the group of fungi considered in this paper.

THE FUNGI CONCERNED

Species

According to the literature reviewed, the species of Basidiomycetes listed in Tables 1 and 2 cause root-rots in trees. Those in Table 1 are definitely known to enter trees through the underground portions. That is, they have been isolated from roots when the decay column caused by them did not extend above the ground line. These fungi may, therefore, exist in the soil on or near roots, and are the ones of greatest interest here. The fungi in Table 2 are not definitely known to enter trees through roots. However, most of these are presumed to be root-rotting fungi because the heart-rot caused by them has been found at ground level and the fungi do not appear to have entered through above-ground parts of the tree. Further investigation will probably prove at least some of these enter through roots.

Two members of the group considered here, *Polyporus circinatus* Fr. and *Armillaria mellea* (Vahl.) Quel., form mycorrhizae (Gosselin, 1944, and Hamada, 1939, respectively).

Abundance

Some of the root-rotting fungi are world-wide in distribution but they are probably all restricted locally to conditions which favor them. Although the conditions may not be exacting they include a build-up of mycelium in suitable substrates such as wood. Otherwise they would be found more commonly in the forest occupying roots of suppressed trees. *Armillaria mellea* is the only one reported widely in such trees. Garrett (1950) states a local distribution in the soil is a well established characteristic of root-inhabiting fungi and this results from their poor competitive saprophytic ability. He says that apart from living host roots, root-inhabiting fungi are distributed through the soil in dead infected host tissue in which

TABLE 1

The Basidiomycetes that are definitely known to enter trees through the roots.

FUNGUS	REFERENCE
Armillaria mellea (Vahl ex Fr.) Quél.	Thomas, 1934
Clitocybe tabescens (Scop.) Bres.	Rhoads, 1948
Coniophora puteana (Schum. ex Fr.) Karst.	Whitney, 1953
Corticium galactinum (Fr.) Burt	Cooley and Davidson, 1940
Flammula connissans Fr. sensu Ricken	Denyer and Riley, 1953
Fomes annosus (Fr.) Cke.	Rishbeth, 1950
Fomes applanatus (Pers.) Wallr.	Bier et al., 1946
Fomes lignosus Klotzsch.	Dejong, 1933
Ganoderma oregonense Murr.	Bier et al., 1946
Ganoderma pseudoferreum Wakef. van Overeem and Steinman	Bobilioff, 1929
Lentinus Kauffmanii A. H. Smith	Bier et al., 1946
Odontia bicolor (Fr.) Bres	Whitney, unpub. manus.
Peniophora gigantea (Fr.) Massee	Whitney, unpub. manus.
Pholiota adiposa Fr.	Nordin, 1954
Pholiota spectabilis Fr.	Nordin, 1954
Polyporus Berkeleyi Fr.	Bier et al., 1946
Polyporus borealis Fr.	Bier et al., 1946
Polyporus circinatus Fr.	Gosselin, 1944
Polyporus circinatus var. dualis Pk.	Denyer and Riley, 1953
Polyporus dryadeus Fr.	Long, 1913
Polyporus guttulatus Pk.	Bier et al., 1946
Polyporus montanus (Quél.) Ferry	Bier et al., 1946
Polyporus schweinitzii Fr.	Bier et al., 1946
Polyporus sulphureus (Bull.) Fr. var. Overholtsii var. nov.	Rosen, 1927
Poria albipellucida Baxter	Bier et al., 1946
Poria asiatica (Pilát) Overh.	Bier et al., 1946
Poria colorea Overh. and Englerth	Bier et al., 1946
Poria subacida (Pk.) Sacc.	Boyce, 1948
Poria weirii Murr.	Buckland et al., 1954
Sparassis radicata Weir	Weir, 1917

TABLE 2

The Basidiomycetes causing butt rot that are not definitely known to enter trees through roots.

FUNGUS	REFERENCE
Fomes pinicola (Sw.) Cooke	Denyer and Riley, 1954
Ganoderma applanatum (Pers.) Pat.	Denyer and Riley, 1954
Merulius himantioides Fr.	Denyer and Riley, 1953
Polyporus balsameus Pk.	Hubert, 1929
Polyporus immitis Pk.	Denyer and Riley, 1954
Polyporus sulphureus Bull. ex Fr.	Denyer and Riley, 1954
Poria tsugina (Murr.) Sacc. and Trobt	Denyer and Riley, 1954
Stereum chailletii Pers.	Denyer and Riley, 1954
Stereum sanguinolentum Alb. and Schw. ex Fr.	Hubert, 1935
Stereum sulcatum Burt	Denyer and Riley, 1953
Trechispora brinkmanni	Denyer and Riley, 1953

the fungi persist as resting spores and sclerotia.

It is very difficult to ascertain presence or absence of these fungi by plating them from the soil. The saprophytic fungi there grow so much faster on artificial media that they cover the mycelial fragments of Basidiomycetes before the latter begin growth. As for producing abundant mycelium in the soil in any one place, this is unlikely, for even where fruiting is abundant, little, if any, mycelium of the root-rotting fungi is reported to be found in the soil.

LOCATION

Soil

Waksman (1952) states the various groups of micro-organisms are largely concentrated in the surface layer of the soil, usually the A1 horizon in forest soils. He also found addition of cellulose-rich material to the soil increases the abundance of cellulose-decomposing fungi. This includes the root-rotting fungi.? Little is known of the distribution of mycelium of root-rotting fungi away from the tree. Harley (1952) states the presence of mycorrhizal fungi is detectable with certainty either by presence of their fruit bodies or by presence of mycorrhizal roots. Most of the root-rotting fungi have not been recognized as mycorrhiza-formers, and their presence must be determined by presence of their fruit bodies of by the decay they cause as verified by culture.

Rishbeth (1950) was not able to grow *Fomes annosus* on unsterilized soil in the laboratory, though the mycelium in pure culture advanced profusely through sterilized soil. When he grew *F. annosus* either in soil or on roots with *Trichoderma veride* Fr., a soil saprophyte, he found *F. annosus* was completely inhibited. It appears that *F. annosus* cannot exist as free mycelium in competition with soil-inhabiting fungi such as *T. veride*. To exist in the forest, F. annosus must have woody material in which to grow.

Other root-rotting Basidiomycetes also have this requirement, and are thus found in woody debris of the forest floor. White to buff-colored mycelium of Corticium galactinum was found in the duff at the ground line under white pines in northeastern United States as described by Marshall (1948). Dealing with certain Basidiomycetes that are not known to be root-rotting fungi, Warcup (1951) found mycelium inhabiting the litter zone rather than the mineral layers of the soil. According to Harley (1952) beech roots made contact with mycorrhiza-forming Basidiomycetes that were colonizing decayed wood deep in the soil below the humus layers. Weir (1923) states that several root-rotting fungi are present in litter and surface layers of soil. It is noteworthy how few investigators have reported the occurrence of root-rotting fungi in the surface layers of soil. Weir found also that fruiting bodies of Armillaria mellea, Fomes annosus, Polyporus schweinitzii, Poria subacida, and Poria weirii were greatly reduced for a number of years on areas where slash was broadcast burned.

These findings indicate Basidiomycetes generally may be confined to woody material rather than any particular layer in the soil. There may be exceptions to this generality. A. mellea, for example, has been found at depths of four feet by Leach (1939), apparently not in the presence of woody material. In this instance the fungus may have been present as rhizomorphs and could have been attached to a woody substrate some distance away.

Root Surfaces

Many root-rotting fungi may be located on the surface of living roots prior to or even after entry. Garrett (1951) thinks root-inhabiting fungi make a successful attack on living roots by first covering a large area of roots with mycelium than attacking with a number of simultaneous infections at different places. The zone of "enhanced microbiological activity" in soil includes the root surfaces and the immediately surrounding area known as the rhizosphere (Hiltner, 1904). Root-parasites probably take part in this "enhanced microbiological activity". Mycelium of Fomes annosus, still connected with that on an infected root, has been observed (Rishbeth, 1951b) growing along the bark of sound roots prior to entering. Leach (1939) states infection of tea plantations with Armillaria mellea is largely by contact of infected tea roots with sound ones. This fungus spreads in tea, mainly by advancing along moribund or very recently dead roots. Mycelium of Ganoderma pseudoferreum passes from the lateral roots of diseased trees to the tips of those of adjacent individuals (Bobilioff, 1929, and Zboray, 1931). Mycorrhizal fungi also apparently grow luxuriantly on living root surfaces (Bjorkman, 1942, and Harley, 1952).

Stumps

The largest volume of mycelium or potential inoculum of root-rotting fungi is probably located in stumps. Original infection by Fomes annosus in old field plantations is by stumps, left after thinning, becoming infected from air-born spores (Rishbeth, 1950). Many root-rotting fungi such as Fomes lignosus (Dejong, 1933), Armillaria mellea (Thomas, 1934), Corticium galactinum (Cooley, 1948), and Poria weirii (Baxter, 1953) remain for years in stumps of trees which became infected while living. This or some other mycelium-impregnated food-base is essential for future infection (Garrett, 1951).

FORM

Mycelium

Many of the root-rotting fungi occur as mycelium on living roots, and some, usually to a very limited extent, as mycelium free in the soil. Corticium galactinum is reported abundant on living apple roots by Cooley and

Davidson (1940). Long (1913) has found irregular white patches of mycelium of Polyporus dryadeus on roots of oak. This fungus, by impregnation of soil and litter with its hyphae, causes compact bricklike soil masses around its sporophores. Tufts of mycelium of Poria weirii are found on the outer surface of the bark of diseased roots and on the soil immediately surrounding them (Mounce, Bier and Nobles, 1940). Ganoderma pseudoferreum can persist free in the soil for some months without any apparent source of nutriment from roots (Gadd, 1929). Rosen (1928) reports a conspicuous characteristic of Polyporus sulphureus var. Overholtsii is its habit of living in and permeating the soil for distances of a foot or more around rotted roots. This does not seem to be characteristic of root-rotting fungi, however. On only one occasion did Rishbeth (1950) find Fomes annosus free in the soil. Berk (1948) was unable to prove Polyporus schweinitzii remained in the soil saprophytically during a period of cultivation though it was found on the tree roots both before and soon after the area was under cultivation.

Rhizomorphs

Armillaria mellea occurs extensively in the form of rhizomorphs in forest soils. Leach (1939) considers A. mellea probably moves more by rhizomorphs than by dead root material, but he found rhizomorphs only sparsely in soils in Africa. Harrar (1937) reports rhizomorphs of Fomes lignosus occurring in soil, and Dejong (1933) produced them profusely by inoculation in roots of rubber trees. The hard, blackish, stromalike structures, known as xylostromata, formed by Corticium galactinum on the bark of infected roots (Rhoads, 1948) have been confused with rhizomorphs. They are completely different, however, consisting of longitudinal outgrowths of mycelial felts between the bark and wood. Basidiomycetes other than the two root-rotting fungi mentioned above produce rhizomorphs. A species of Lycoperdon has stout rhizomorphs according to Warcup (1951).

Spores

Some of the fungi causing disintegration of living roots actually enter trees by means of spore infections through above-ground wounds, and the mycelium then spreads into the roots. This is apparently the case with Polyporus balsameus (Hubert, 1929), Poria weirii (Baxter, 1953), and Stereum sanguinolentum (Hubert, 1935). It is unlikely these fungi (with the exception of P. weirii) are present below ground for any extent of time after the host tree they occupy dies. Spores spread Fomes annesus and Armillaria mellea to uninfected stumps and thus start infection centers in new locations. According to the literature reviewed, spores probably play a very small part in underground spread of root-rotting fungi.

Sclerotia

It is apparently common for certain species of soil fungi not belonging to the Basidiomycetes to form sclerotia in soil. However, only one root-rotting fungus is reported as forming sclerotium-like structures. Weir (1917) reports Sparassis radicata develops perennial sclerotial bodies consisting of hyphae and soil cemented together. These extend from a root to the surface of the ground where a fruit body may be formed each year.

INFLUENCE OF SOIL PROPERTIES

As would be expected, the type and characteristics of the soil influence the occurrence and the form of soil micro-organisms. Soil properties may not be as important in this respect, except in an indirect way, as are competing micro-organisms and presence of a suitable substrate supplied by higher vegetation, particularly trees.

Moisture

Moisture seems to be an important factor for influencing presence of root-rotting fungi (Feher and Besenyei, 1933a, and Thomas, 1934). Waksman (1952) states Basidiomycetes develop better at a low moisture content of the substrate than do other groups of soil fungi. With pot cultures of pines, Rishbeth (1951b) found after 18 months those heavily watered had much less root damage by Fomes annosus than those subject to rainfall only (21 inches per year). Weir (1923) states some root-rotting fungi fruit and apparently thrive best where there is a large amount of slash and minor vegetation. He says the reason for this is that the moisture and shade conditions caused by slash and minor vegetation are favorable for these fungi. Abundant rainfall is necessary for formation of mycorrhizae (Boyce, 1948).

Acidity

The pH of the soil greatly influences the presence or absence and aggressiveness of root-rotting fungi. Rishbeth (1951a) found growth of Fomes annosus to be much more abundant and vigorous on roots of trees in alkaline soils than in acid soils. He states that F. annosus alone is tolerant to both acid and alkaline soils, but certain fungi such as Trichoderma veride that are very antagonistic to F. annosus are favored by acid soils. Polyporus schweinitzii was very parasitic in pot cultures with nutrient solutions at a pH of 6.0 to 7.0 (York, Wean and Childs, 1936); and Gadd (1929) found Ganoderma pseudoferreum grows most rapidly between pH 6.24 and 6.46. Bjorkman (1924) says within broad limits pH in soils does not exert noteworthy influence on formation of mycorrhizae. Apparently the effect of pH on a number of interacting factors is more important for occurrence of root-rotting fungi than the effect of pH on these fungi themselves.

Structure and Texture

Root-rotting Basidiomycetes have been found decaying roots in heavy and light textured soils and in soils of varying structure. Cooley (1948) found Corticium galactinum first killing plantation trees on a clay ridge where the soil was poorer, while Dejong (1933) found Fomes lignosus particularly favored by quartz-sand soils. Hatch (1937) found trees on substrates with high colloidal content having more mycorrhizal roots than those on sands, while Rhoads (1948) has found Clitocybe root-rot most frequent on the lighter, well-drained, sandy soils. These statements prove that root-rotting Basidiomycetes are not confined to one type of soil. If soil structure or texture do affect the occurrence of these fungi, the influence is probably indirect.

Nutrients

Very little is known of the effect of soil nutrients on root-rotting fungi; however, the following observations by investigators have been made. It is generally accepted that calcium seems to be essential to the majority of Basidiomycetes (Harley, 1948). Hamada (1940) found rhizomorph-production of Armillaria mellea increases with rise in dextrose concentration and decreases with rise in nitrogen concentration. Therefore, the C/N ratio in substrates is probably important for occurrence and growth of rhizomorphs. Leach (1939) states A. mellea cannot enter roots depleted of carbohydrates. Similarly, Bjorkman (1942) found production of mycorrhizae in spruce roots was correlated directly with carbohydrate excesses in roots. Since the amount of carbohydrates is dependent upon assimilable nitrogen and phosphorus, the quantity of mycorrhizae is affected by these two elements. Infection by Fomes lignosus is increased with combined application of nitrogen, phosphorus, potassium, and manganese sulphate (Dejong, 1933). Gosselin (1944) found a relationship between soil nutrients and presence of rot caused by Polyporus circinatus, however, this may have little or nothing to do with presence or absence of the fungus.

INFLUENCE OF FUNGI ON THE SOIL

Probably the greatest influence root-rotting fungi have on forest soils is the formation of humus by breakdown of woody material. York, Wean, and Childs (1937) and Wean (1937) found nearly 21% more calcium in the upper four inches of soil where Polyporus schweinitzii occurs than where it does not occur. This fungus appears to render calcium less available to the trees. Of the soil micro-organisms, Swaby (1949) found fungi exert the greatest binding effect on the soil.

Mycorrhizae, are not reported as having any direct influence on soil properties. Routien and Dawson (1943), however, state mycorrhizae increase the average rate of aerobic carbon-dioxide production by nearly two to four times the amount produced on non-mycorrhizal roots. They suggest that mycorrhizae increase the salt absorbing capacity of the roots, which, though not an influence on the soil, makes more nutrients available to the plant. Gosselin (1944) too, states that plants with mycorrhizae generally absorb more nitrogen, potassium and phosphorus from soil than those without mycorrhizae.

SUMMARY

1. The literature surveyed contains very little direct information on occurrence of root-rotting Basidiomycetes and their soil relationships.
2. Basidiomycetes causing root-rot in trees are few. Those found in the literature are listed.
3. The root-rotting fungi considered here belong to a group of Basidiomycetes which live mostly in woody substrates in the upper layers of the soil.
4. Rhizomorphs are produced by only two of the root-rotting fungi considered here.
5. Many new infections take place by mycelium moving from an infected woody substrate to a sound root with which it is in contact.
6. Antagonistic fungi such as <u>Trichoderma</u> <u>veride</u> suppress growth of <u>Fomes</u> <u>annosus</u> in acid forest soils.
7. Root-rotting fungi exist as free mycelium in the soil only to a very limited extent around infected roots or fruit bodies.
8. The effect of soil properties on the presence of root-rotting fungi is largely indirect.
9. <u>Polyporus</u> <u>circinatus</u> and <u>Armillaria</u> <u>mellea</u> are apparently the only root-rotting Basidiomycetes of those considered which have been reported authentically forming mycorrhizae.

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