WHITE ROOT ROT OF RASPBERRIES

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Summary

The disease known as white root rot affects raspberries, and to a less extent loganberries, in Victoria. The causal organism is a white, sterile fungus that has not been identified. The disease is favoured by dry soil conditions and high soil temperatures. It spreads externally to the host by means of undifferentiated rhizomorphs, and requires a food base for the establishment of infection. The spread of rhizomorphs through the soil is hindered by high soil moisture content and consequent poor aeration of the soil.

The known natural host range of the fungus includes the raspberry, loganberry, and plum, but some other rosaceous plants have been infected artificially. It has not been recorded on any native plants. It is spread from one plantation to another by planting infected canes, and is spread within a plantation by root contact and movement of infected root and cane material during cultivation.

I. Introduction

The disease referred to by Victorian raspberry growers as white root rot has been known in that State for almost 50 years, and was first described in 1897 (McAlpin). No other references to the disease have been published though it was the subject of an unpublished paper by Miss Halsey, who studied the disease at the University of Melbourne.

Commercial raspberry growing in Victoria is now practically confined to a relatively small area east of the Dandenong Ranges, and the disease is present throughout the district. In some plantations it has spread rapidly, and a few have been practically wiped out in three or four years, but usually it spreads slowly and only a few bushes are killed each year.

The disease has recently (January 1950) been recorded from one plantation in the Molesworth district of Tasmania, but a survey of raspberry plantations in that State did not reveal any other cases. No similar trouble has been reported outside Australia.

The investigations described here were conducted during the years 1941 to 1947.

II. Symptoms of the Disease

The disease is characterized by rotting of the roots and cane bases below ground level. The affected regions are covered with a dense mycelial mat, which is predominantly white in colour, though portions become cream-coloured

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and very compact and smooth in texture. Conspicuous, white rhizomorphs develop on the surface of the affected areas. The fungus does not attack the plant above ground level.

The first symptom on the above-ground portions of the plant is usually a yellowing of the foliage, accompanied by premature autumn tints. Shortly after the development of these symptoms, the affected portion of the bush wilts rapidly and dies. Sometimes, however, wilting and death may occur without any preliminary symptoms. When young plants are attacked, the whole bush dies simultaneously, but old bushes die gradually, a few canes at a time.

III. The Causal Organism

(*a*) *Isolation and Proof of Pathogenicity*

A white fungus, which remained sterile in culture, was isolated consistently by planting out pieces of infected roots on potato dextrose agar (P.D.A.), the pieces being surface-sterilized with 1 in 1,000 mercuric chloride and then washed with sterile water.

Many infection experiments, which will be described in detail later in this paper, have been conducted and typical symptoms of the disease produced by inoculation with a soil culture of the organism. The same fungus has been re-isolated from the inoculated plants, thus proving that it is the cause of the disease.

(*b*) *Morphology of the Fungus*

In culture on P.D.A. the fungus produces a white mycelium, which grows fairly rapidly, producing a colony 8 cm. in diameter in 10 days at 25°C. The advancing edge of a young colony is even with a silken sheen, while the central portions are white and appressed. As the colony ages the edges develop a brownish tint, and portions of the central area become compressed into a flat, felty layer with a cream coloration.

The surface of this compressed layer bears highly branched structures consisting of hyphae about 0.5 to 1 μ in diameter. The structures are variable in size and range from 10×15 μ to 30×50 μ. They are one of the most characteristic features of the fungus and are illustrated in Figure 1. They do not stain readily, but several hours in Harris's haemotoxylin is effective.

The hyphae of the fungus are of two types. Young colonies consist entirely of septated hyphae, 2.5 to 5.2 μ (average 3.8 μ) in diameter. Older colonies consist of the same type of hyphae, mixed with very fine hyphae, 0.4 to 1 μ in diameter. These fine hyphae predominate in the compressed portions that develop as colonies age.

The fungus produces white, undifferentiated rhizomorphs on its natural host, in soil culture, and occasionally on agar media. They are 0.5 to 1 mm. in diameter and similar in type to those produced by *Fomes lignosus* and classified by Garrett (1944) as type 5.

No fruiting stage of the fungus has been found either in the field or on artificial media. For that reason the fungus has not been identified. Material was forwarded to the Commonwealth Mycological Institute, but they were unable to identify it.

McAlpin (1897) stated that *Hypholoma fasciculare* (Huds.) was the cause of the disease, but cultures made from sporophores of that fungus bore no close resemblance to the causal organism of white root rot.

Though the general appearance of cultures of the white root rot fungus resembles those of a Basidiomycete, no clamp connections have been found, so that it has not been proved to belong to that group.

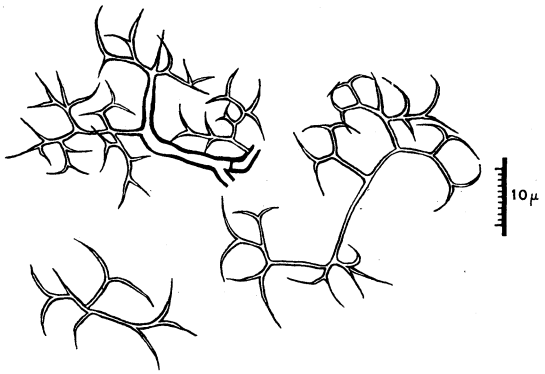

Fig. 1.—Freehand drawing of highly branched structures of the white root rot fungus.

(c) *Physiology of the Fungus*

(i) *Growth on Culture Media.*—The fungus grows readily on potato dextrose agar, malt agar, or raspberry cane extract agar. The media rapidly become brittle and numerous octahedral crystals develop. It grows very sparsely on synthetic media such as Czapek's solution, unless thiamin is added. In a typical experiment Czapek's solution (formula as given by Riker and Riker 1936) was prepared and thiamin added to half the solution at a concentration of 20 μg./l. Fifty ml. of the solutions were distributed into 250 ml. erlenmeyer flasks and six of each solution were inoculated. The fungus grew rapidly on the flasks with thiamin, but scarcely any growth occurred on those without thiamin, even with prolonged incubation.

(ii) *Temperature.*—To determine the optimum temperature for the growth of the fungus P.D.A. plates were inoculated at the centre with a piece of culture about 1 mm. in diameter. Six plates were incubated at each of the temperatures shown in Table 1 for five days, when the diameters of the colonies were measured. These results indicate that the optimum temperature for the growth of the fungus is about 27°C.

IV. Effect of the Fungus on the Plants

Infection by the fungus is confined to the underground portions of the plant. However, extensive growth of the fungus may be present on the main root without causing death, and death does not usually occur until a large proportion of the fibrous roots have been destroyed.

Sections of fibrous roots, main roots, and of canes at ground level, 1, 3, and 6 in. above ground level were cut and stained by Haidenhain's haemotoxylin. The sections showed that attack commences on the outside of the root, and then grows into the inner tissues, causing general rotting of all tissues. There was no evidence that the fungus spread internally in the vascular tissue, and it was not detected in the above-ground portions of the plant.

Table 1

EFFECT OF TEMPERATURE ON GROWTH OF THE WHITE ROOT ROT FUNGUS

Temperature	19°C.	21°C.	23°C.	25°C.	27°C.	29°C.
Mean colony diameter	3.7 cm.	4.3 cm.	5.2 cm.	5.6 cm.	6.6 cm.	6.1 cm.

V. Factors Influencing Infection

(*a*) *Method of Inoculation*

Early infection experiments with pure cultures of the fungus grown on sterile soil to which dextrose and peptone were added were only occasionally successful, while inoculations with naturally infected root material were successful. It was then found that pure cultures produced infection if a piece of raspberry cane was added to the culture, and therefore experiments were undertaken to determine whether the fungus requires a "food base" to establish infection.

(i) *Pot Experiments.*—Lloyd George raspberry canes were planted in virgin red mountain soil in glazed porcelain crocks. Of these, 24 were inoculated with cultures on 500 g. of sieved soil plus 1 g. dextrose and 0.1 g. peptone, 24 with similar cultures to which a piece of sterile raspberry cane had been added when the medium was prepared, 24 with soil cultures to which sterile raspberry canes had been added one week before inoculating the plants, and a further 24 were left uninoculated as controls. A mulch of grass clippings was added to half of each group to determine the possible effect of organic matter on infection.

To avoid the effect of position, each series of 12 pots was divided into three groups of four pots, and the groups randomized. The first experiment was conducted in 1945-46 and inoculations made on January 5. It was repeated the following season and inoculated on November 27.

The plants were observed throughout their growing period and a record was kept of all deaths from white root rot. On May 29, 1946, and on April 10, 1947, all surviving plants were pulled up, and examined for evidence of infection.

In both seasons no uninoculated plants, or plants inoculated with a soil culture without the addition of raspberry cane material, became infected with white root rot, but infections occurred when the inoculations contained a piece of raspberry cane. The progressive development of infection is shown in Table 2.

TABLE 2

EFFECT OF METHOD OF INOCULATION ON INFECTION WITH WHITE ROOT ROT

Method	Added Material	Deaths from White Root Rot			Infections Noted at Conclusion	Total Infection in 12 Plants
		Jan.	Feb.	Mar.		
1945-46						
Soil culture (Method *A*)	No addition	0	0	0	0	0
	Grass clippings	0	0	0	0	0
Raspberry cane added when soil culture prepared (Method *B*)	No addition	0	1	1	1	3
	Grass clippings	0	0	1	4	5
Raspberry cane added to soil culture one week prior to inoculation (Method *C*)	No addition	0	2	1	2	5
	Grass clippings	0	0	1	4	5
1946-47						
Method *A*	No addition	0	0	0	0	0
	Grass clippings	0	0	0	0	0
Method *B*	No addition	3	1	0	2	6
	Grass clippings	1	0	0	1	2
Method *C*	No addition	1	1	0	5	7
	Grass clippings	0	1	0	3	4

The most important result was to demonstrate that, under the conditions of these experiments, infection could not be established without the presence of a "food base." There are several examples in the literature of other root disease fungi behaving in the same way, and this literature has been discussed by Garrett (1944). Bliss (1941) found that *Armillaria mellea* was unable to establish infection unless the rhizomorphs were in contact with a food base, and results of Petch (1921, 1928) and of Tunstall (1930), as quoted by Garrett (1944), showed that *Fomes lignosus* and *F. noxious* behave similarly.

The stage at which the food base material was added to the culture did not appear to affect the infectivity of the inoculum. Although the addition of

organic matter did not prevent infection, it appeared to delay the death of infected plants. It was noted that the addition of grass clippings markedly increased the root development of the plants. Infected plants do not die until a considerable proportion of the fibrous roots have been destroyed, so that any factor that increased root development could be expected to delay death.

As no infection developed on plants inoculated with a soil culture of the organism, and receiving a dressing of grass clippings, it is apparent that grass clippings will not replace raspberry cane material as "food base." A further experiment was conducted to determine whether the "food base" could be replaced with a simple carbohydrate, with or without addition of vitamins. A single Lloyd George raspberry was planted in red mountain soil in each of 36 porcelain crocks. Sucrose at the rate of 5 cwt. per acre was added to 12 crocks, and sucrose at 10 cwt. per acre plus ground yeast at ½ cwt. per acre to a further 12 pots. These crocks were inoculated with a soil culture of the organism, and the 12 untreated pots with a soil culture containing raspberry cane material. No plants became infected in the first two treatments, while six of the plants inoculated with raspberry cane material developed white root rot. Therefore, sucrose, with or without vitamins, cannot replace the natural "food base."

(ii) *Field Experiments.*—To determine whether similar results would be obtained under field conditions, an experimental plot of Lloyd George raspberries was planted in virgin soil in August 1945. The method of inoculation already described and the effect of organic matter were tested when the plants were established. There were three replicates, each consisting of two rows of 12 plants of each method of inoculation and of uninoculated raspberries. A guard row of uninoculated raspberries was left between the paired rows of inoculated plants. Tick beans were sown in one row of each pair in May 1946, and were hoed in as a source of organic matter in October.

The inoculations were made on December 4, using cultures prepared in the manner described previously. A hole was dug with a trowel within four inches of a root near the crown of the plant and the culture added and covered with an inch of soil.

The experiment was kept under observation until the author left Victoria in April 1947. Up to that time no plants died, but examination of the roots near the sites of inoculation showed that infection had become established on a number of plants that had received inoculations containing raspberry cane material.

On May 20, 1948, the experiment was examined by Mr. C. R. Millikan, Senior Plant Pathologist of the Victorian Department of Agriculture, who recorded the number of plants that had died of white root rot and kindly supplied the figures shown in Table 3.

The results were examined statistically by Mr. G. A. McIntyre, Division of Mathematical Statistics, C.S.I.R.O., who reported that the addition of organic matter had no significant effect on the results, treatment 3 differed from treatment 4 ($P < 0.001$) and treatments 1 and 2 differed from treatments 3 and 4.

The main conclusions of the pot experiments were therefore confirmed in the field. In the field, however, the addition of a food base was more effective if the fungus was well established on it before inoculation of the plants.

TABLE 3
DEATHS FROM WHITE ROOT ROT IN GROUPS OF 12

Method of Inoculation	No Addition			Organic Matter		
1. Uninoculated	0	0	0	0	0	0
2. Soil culture	0	0	0	0	0	0
3. Raspberry cane added when soil culture prepared	12	12	11	11	12	12
4. Raspberry cane added to soil culture one week prior to inoculation	9	8	9	12	8	9

(*b*) *Influence of Soil Moisture Content*

(i) *On Infection of Growing Plants.*—Field observations suggested that the disease was more severe in dry, exposed situations. An experiment was therefore conducted to determine the effect of soil moisture on infection with the white root rot fungus.

Waxed canisters 12 in. in diameter and 15 in. deep were filled with a weighed amount of red mountain soil of known moisture content. Lloyd George raspberry canes were planted in August 1945 and one month later were inoculated by the addition of a culture of the white root rot fungus on sterile soil mixed with raspberry cane material. They were then divided into three groups of 16. They were watered twice weekly to constant weight, so that if uniformly wet the soil of one set would have been at 50 per cent. of the water-holding capacity, another at 70 per cent., and the third at 90 per cent. of the water-holding capacity. The water-holding capacity of the soil was determined by the method described by Riker and Riker (1936). Hendrickson and Veihmeyer (1941) have pointed out that soil does not become uniformly moist when water is applied to the surface. Therefore the three series are better described as dry, medium wet, and wet soil series.

The pots were sheltered by a canopy of a transparent fabric to keep rain from wetting the soil. The 16 canisters in each series were divided into four groups and randomized to overcome chance effects due to position. The dates when plants died of white root rot were recorded and in May 1946 the remaining plants were pulled up and examined.

All the plants in the dry soil series died from the disease, the first death occurring on December 4 and the last on February 13. One plant in the

medium wet series died on February 5, but no plants in the wet series died of white root rot, though three plants died through waterlogging when they were accidentally overwatered by exposure to rain.

When the surviving plants were examined it was found that three plants in the medium wet series and one plant in the wet series showed infection of the tap root only, but the fibrous roots were uninfected. These results demonstrate that infection is inhibited if the soil is kept close to saturation with water, but develops readily if the soil is kept relatively dry. They also suggest that the disease only kills the plants when general root infection, involving the fibrous roots, develops.

(ii) *Effect of Soil Moisture on Growth of the Fungus in Soil Culture.*—The results of the experiment just described suggested that the soil moisture content may influence the growth of the fungus through the soil. Therefore a laboratory experiment was conducted to determine if that was correct.

Cylindrical glass jars 8.5 cm. wide and 11 cm. deep were filled with a weighed amount of red mountain soil of known moisture content. Water was then added to bring the moisture content of five jars to 30, 50, 70, and 90 per cent. of water-holding capacity. The soil was then stirred thoroughly. The jars were inoculated by inserting a piece of raspberry cane, on which the fungus had been well established, in a vertical position in the centre of each jar. Two clean glass slides were then pushed vertically into the soil on opposite sides of each jar.

TABLE 4
EFFECT OF SOIL MOISTURE CONTENT ON GROWTH OF THE WHITE ROOT ROT FUNGUS IN SOIL

Percentage of Water-holding Capacity	Time Taken for Rhizomorphs to Travel 4 cm. (days)	Depth of Penetration into Soil (cm.)
30	24	4
50	36	4
70	49	1
90	*	0.5

* In one of the five replicates rhizomorphs travelled 4 cm. in 45 days, but in the others no rhizomorphs travelled that distance during the period of the experiment.

The jars were incubated at 25°C. and the weight restored by spraying with water twice weekly. They were observed daily and the time taken for rhizomorphs to reach the sides of the jars was noted. After eight weeks the slides were removed, loosely adhering soil particles rinsed off, and stained with dilute carbol-erythrosin. They were examined microscopically, and the depth of penetration of the fungus measured. The slide burial method employed was based on that of Rossi-Cholodny as described by Blair (1945).

The results are shown in Table 4, the figures being the mean of five replicates. The experiment showed that rhizomorphs of the white root rot fungus travel more rapidly through dry soil and penetrate more deeply than in moist soil. This at least partly explains the greater development of the disease in dry soil. It seems probable that high moisture content reduces soil aeration, and the fungus is inhibited through carbon dioxide accumulation and lack of oxygen.

Some support for this suggestion was obtained when cultures of the fungus, placed in an incubator in which an orange storage experiment was in progress, failed to grow. Analysis of the air in the incubator showed that it contained 12 per cent. CO_2. Cultures made at the same time, and placed in another incubator, grew normally. Cultures of *Penicillium italicum* and *P. digitatum*, which were in the incubator containing 12 per cent. CO_2, grew normally.

Very few raspberry plantations in Victoria are irrigated, and there was no opportunity of testing the effect of irrigation at regular intervals on the incidence of the disease. The few irrigated plantations observed were practically free from the disease. It is not troublesome in sheltered, low-lying situations where the soil remains moist throughout the summer, and the most serious outbreaks of the disease were noted in exposed, dry situations. The only Tasmanian record occurred in soil that frequently became very dry during the summer months.

(*c*) *Effect of Soil Temperature*

As shown in Section III (*c*) (ii), the raspberry white root rot fungus has a high optimum temperature. To determine whether infection of raspberries would develop more rapidly at high rather than low temperatures, unsterilized red mountain soil was placed in metal canisters and inoculated with cultures of the white root rot fungus grown on sterile soil plus raspberry cane material.

Raspberry canes of the Lloyd George variety were placed in the canisters on August 14, 1946. The canisters were then placed in temperature tanks of the Wisconsin type and eight canisters were held at 28°C. and eight at 18°C.

On October 26, five plants at 28°C. showed signs of wilting, but all the plants at 18°C. appeared healthy. On November 30, seven of the eight plants at 28°C. and one plant at 18°C. died of white root rot. The experiment was continued for several weeks, but no further deaths occurred and examination of the roots did not reveal any further infections.

The disease is, therefore, favoured by high temperatures.

(*d*) *Effect of Lime*

A small-scale pot experiment was conducted in which red mountain soil of pH 5.6 was placed in porcelain crocks. Slaked lime was added to 12 pots at the rate of 1 ton per acre and to 12 pots at the rate of 4 tons per acre, while no lime was added to a further 12 pots. The pots were inoculated with the white root rot fungus, and Lloyd George raspberries planted.

Two plants in each series developed white root rot and died. Although the amount of infection was not high in this experiment, the results suggest that alteration of soil pH by addition of lime does not have a marked influence on the disease.

VI. Method of Spread in the Field

The white root rot fungus has not been detected on native plants, and is apparently introduced into new plantations on virgin soil entirely by planting canes obtained from infected raspberries.

In 1945 an experimental plantation of 1½ acres of Lloyd George was laid down under the author's supervision on virgin soil in the Silvan district. All the canes were examined carefully before planting, and any that showed the presence of the white root rot fungus were discarded. No fungicidal treatment was applied to the remaining canes, as it was considered unlikely that surface contamination with the mycelium of the fungus would produce infection. The plot was examined frequently and only one plant of a total of 2,000 canes developed the disease.

The disease may also be introduced by replanting on soil that has recently carried infected raspberries, and still contains infected root material. If white root rot becomes established in a plantation, subsequent spread takes place more rapidly along the rows than across from one row to the next.

Detailed examination of the spread of infection from one plant to its neighbour has shown that it usually takes place by root contact. As raspberries have an extensive root system, roots of neighbouring plants intermesh, and contact between infected and healthy roots occurs. Rhizomorphs of the fungus then pass from the diseased to the healthy root. No evidence was obtained that rhizomorphs can spread more than four inches from the food base. Most raspberry growers practise deep ploughing between the rows, thus preventing lateral spread of roots near the soil surface. This reduces the infection across rows since the fungus requires good soil aeration and would be less likely to spread along deep roots spreading across from row to row, than along surface roots between plants in the one row.

New foci of infection become established by carrying pieces of infected root and cane base material along the rows during cultivation. If this material lodges near raspberry roots, rhizomorphs developing from it produce infection. Subsequent spread to adjacent plants then takes place in the manner already described.

VII. Host Range

Under natural conditions this disease is a serious trouble only on raspberries, but it also affects loganberries. However, the disease does not kill infected loganberries rapidly, and no serious losses have been noted. One case of a root and crown rot due to a fungus morphologically identical to the white root rot fungus was observed on plums on cherry plum (?) stocks at Wandin, Vic. The plums had been planted immediately after a severely infected patch of raspberries had been removed. When observed the plums were 12 years old and three trees showed infection. The disease has not been seen on any other host in the field.

To determine whether any other rosaceous plants could become infected with the disease by inoculation, six plants of apples, pears, peaches, apricots,

blackberries, cherries, plums, *Rosa multiflora, Rosa noya,* and the native raspberry (*Rubus parvifolius*) were planted in earthenware pots. They were inoculated with a culture of the white root rot fungus grown on sterile soil plus raspberry cane material on November 18. No plants died and on the following April 10 the plants were pulled up and examined.

Infection was present on four plants of *Rosa multiflora,* one plant of *Rosa noya,* five apples, three pears, and three cherries. However, the infection had been arrested in all cases and plants of those species appeared to be naturally resistant to infection. Plums, peaches, apricots, and the native raspberry were entirely free from infection. All the blackberries were infected with the disease though the plants were not killed. However, natural infection of blackberries has not been observed in the field.

VIII. Discussion

Apart from one record in Tasmania, white root rot of raspberries has not been reported outside Victoria, and it seems probable that few raspberry-growing districts would provide the conditions that favour the development of the disease. The necessary factors are low soil moisture content and high soil temperature. The Victorian summer is hot and dry, and as few raspberry growers are able to irrigate, suitable conditions are present. It appears significant that the only case reported in Tasmania was in an exceptionally dry situation, and it was absent from more favoured portions of the same property.

Pot experiments showed that the disease is inhibited in soil of high moisture content, and at least part of this effect is probably due to reduced soil aeration. A similar explanation of the effect of high soil moisture content on certain other soil-borne diseases has been offered by other workers, e.g. Hull and Wilson (1947) in their work on factors influencing infection with *Helicobasidium purpureum.* In laboratory experiments it was found that high soil moisture content reduced the depth of penetration and rate of laterial spread of rhizomorphs. In investigations on the behaviour of *Rhizoctonia solani* in soil Blair (1943) found that it grew most rapidly through soil of the lowest moisture content tested and that its growth was accelerated by aeration of the soil.

Infection with raspberry white root rot can only be established if the fungus is growing on a food base, and inoculations with cultures on soil were completely ineffective. This has an important bearing on the control of the disease as there is little chance of spreading the disease through a plantation, except by distribution of pieces of infected root material during cultivation. If the plantation is inspected and all infected plants removed as completely as possible before cultivation, the disease will not spread, except to neighbouring plants. Soil sterilization should not be necessary because the movement of soil that contains the fungus not attached to root or cane material will not spread the disease. The spread of the disease by root contact to neighbouring plants can be avoided by completely removing an apparently healthy plant on either side of the infected one.

IX. Acknowledgments

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Mr. G. A. McIntyre, of the Division of Mathematical Statistics, C.S.I.R.O., kindly made the statistical analyses of the data.

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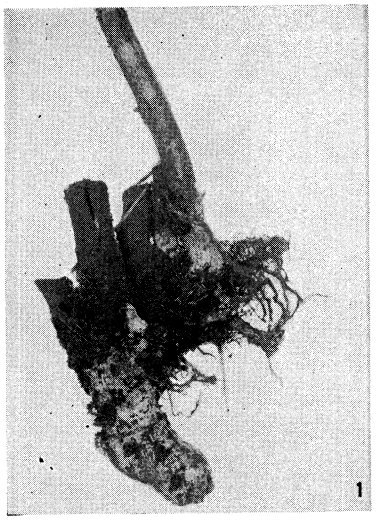

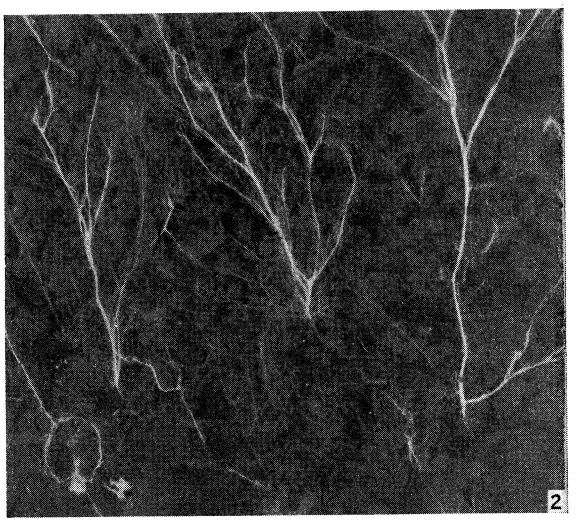

Fig. 1.—Raspberry root infected with white root rot.
Fig. 2.—Rhizomorphs of the white root rot fungus growing in soil culture.
Fig. 3.—Culture of the white root rot fungus on potato dextrose agar.