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J. George Harrar
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J. GEORGE HARRAR, RESEARCH INSTRUCTOR[1]
THE FIRESTONE FUND, UNIVERSITY OF MINNESOTA

INTRODUCTION

The economic importance of *Hevea brasiliensis* has served to focus the attention of those interested in latex production on the diseases that affect the plant. During the last thirty years increasingly intensive rubber cultivation has been practiced. A natural result has been a corresponding increase in the incidence of diseases of *Hevea.* Altho all parts of the plant are parasitized by one or more fungi, the pathogens causing root rots are most destructive and least amenable to treatment. Investigations have been made in various parts of the world in an attempt to determine the life habits of these organisms and to devise methods for their control. While the problem still is far from being solved, the bulk of the evidence points toward the conclusion that the most important organism concerned with root rot of *Hevea* is *Fomes lignosus* Klotzsch. A great many conflicting statements have been made concerning this organism, and it was in an effort to learn more about its cytology, physiology, and pathogenicity that the present work was undertaken.

HISTORY AND SYNONOMY

Much confusion has resulted from attempts of many mycologists to describe *Fomes lignosus* from material collected in various parts of the world, as material in all stages of development and in all states of preservation apparently has been used as a basis for taxonomic description. According to Van Overeem (26), the first published description was that of Swartz in 1806, who designated the organism as *Boletus microporus.* In 1821 Fries (5) changed the name to *Fomes microporus* (Swartz). In 1836-38 Klotzsch placed the fungus in the genus *Polyporus,* giving it the specific name *lignosus.* The generic term *Polyporus* was generally accepted until 1886, altho the specific name was changed several times by various workers. In 1888 Saccardo (19) combined the generic term offered by Fries with the specific name suggested by Cesati and published the name of the organism as *Fomes pusiolus* (Cesati). A succession of other names followed, the most important of

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[1] The investigation was made by the author during his tenure of the Firestone Fellowship, supported by the Firestone Plantations Company, Akron, Ohio.

This is abridged from a thesis presented to the Graduate Division of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The writer wishes to express his appreciation to Dr. E. C. Stakman for his advice and criticisms throughout the course of the investigations, to the Firestone Plantations Company for suggestions and materials, and to Dr. K. G. McIndoe, Dr. E. B. Babcock, and other members of the Firestone research staff for plant materials, cultures, and suggestions.

which were *Fomes semitostus* Petch and *Fomes lignosus* (Klotzsch) Bresadola. Finally, in 1924, Van Overeem (25) submitted the new combination, *Rigidoporus microporus* (Swartz) Van Overeem, using the original specific name given by Swartz and the generic name used by Murrill. In the same paper, Van Overeem published a list of 34 synonyms of the fungus with which he was dealing.

In an effort to settle the taxonomy of the white root rot fungus, Petch (16), Lloyd (7), and Van Overeem have all made exhaustive studies of herbarium and exsiccati material of various collections. Petch and Lloyd agreed that the fungus causing white root rot of rubber was not identical with *Fomes semitostus* Berk. Lloyd accepted the name *Fomes lignosus* Klotzsch as valid for the organism, while Petch concluded that the organism causing white root rot had never been correctly described and consequently was still an unnamed species. Van Overeem claimed that the fungus was identical with the cosmopolitan form *Polyporus zonalis* but that his new combination *Rigidoporus microporus* should be accepted on the basis of priority. A final decision has not yet been reached.

A survey of recent literature on rubber diseases makes it apparent that three distinct names are in common use, namely, *F. lignosus, F. semitostus,* and *R. microporus.* The name which appears most commonly in modern literature on rubber pathology is *Fomes lignosus* Klotzsch. Where either of the other two names is used, *F. lignosus* is usually given as a synonym. For the sake of clarity, this name will be used throughout this bulletin.

DISTRIBUTION AND HOST INDEX

Since the true identity of *Fomes lignosus* is still somewhat in question, it is difficult to give its geographical distribution accurately. In order to be as accurate as possible, the distribution of the fungus as given in this bulletin is limited to regions from which it has been reported on *Hevea brasiliensis* or *Ficus elastica.* If the statement of Van Overeem that *F. lignosus* is identical with *P. zonalis* is correct, the fungus is world-wide in distribution, as the latter has been found in almost every region where fleshy fungi exist. On the other hand, if *F. lignosus* is to be considered a distinct form, reports of its distribution must be limited by the distribution of its host plants.

Fomes lignosus was first reported on *Hevea brasiliensis* by Ridley (18) in 1904, the identification being made by Massee. Ridley found the fungus in Singapore and called it *Fomes semitostus.* The following year, Petch reported it from Ceylon. Since that time *Fomes lignosus* has been reported on *Hevea* from Malaya, Java, Sumatra, Borneo, West Africa, and South India. Unconfirmed reports from South America suggest that it may occur there and wherever *Hevea* is grown. The organism often has been reported also on other hosts from the West Indies and from South America. However, until its taxonomic position is finally fixed, most workers prefer to proceed on the assumption that *F. lignosus* is limited to the eastern hemisphere, where it is well known as a destructive root parasite of *Hevea* in all regions mentioned in the preceding list.

The host range of *Fomes lignosus* is perhaps not completely known, but it has been reported as parasitizing a wide range of plants throughout the tropics. The range should perhaps be modified to exclude reported hosts in regions where *F. lignosus* is confused with *Polyporus zonalis* or *F. semitostus*. There is some doubt as to whether the fungus actually is parasitic on some of the plants reported as hosts, as it is a facultative saprophyte and may have been only a secondary invader on some of the dead roots on which it was found. The following hosts have been reported by mycologists who are entirely familiar with the organism causing root rot of *Hevea* in rubber-growing areas: *Berrya ammonilla, Camphor, Cassava, Cocos* spp., *Coffea* spp., *Cola acuminata, Crotalaria* spp., *Derris dalbergioides, Elaeis guineensis, Eriodendron anfractuosum, Ficus elastica, Hevea brasiliensis, Leucaena glauca, Manihotis* spp., *Mimosa* spp., *Ochroma lagopus, Palaquium oblongifolium, Pogostemon* spp., *Tephrosia candida, Thea* spp., *Theobroma* spp., and *Uncaria gambier*. The countries or regions from which the organism has been reported are as follows: Ceylon, Malaya, New Guinea, Belgian Congo, Sierra Leone, Malang, Dutch East Indies, and the Gold Coast.

The above list comprises the plants on which *Fomes lignosus* has been shown to be parasitic but does not include the numerous plants on which it will grow saprophytically, altho it is apparent from many reports that the fungus can grow on various jungle stumps and on woody debris in the soil. Once the organism has been introduced into a particular region as a parasite of rubber, tea, coffee, cocoa, or some other host, it is able to live saprophytically on dead parts of numerous jungle plants. Thus inoculum increases in the soil, enabling the fungus rapidly to attack host plants which may be planted as economic crops. Fructifications are found on almost all the material on which the fungus will grow.

A rhizomorphic habit of growth makes it possible for the organism to spread through the soil by growing over any plant material present. Thus, the strands of *Fomes lignosus* are often found growing along the roots of living plants that are not hosts to the organism. Consequently certain plants have been erroneously described as being hosts when they were merely facilitating the spread of the organism.

For some time it was believed that the basidiospores of *Fomes lignosus* were sterile and therefore of no importance in its dissemination. Brooks (1) reported that the sporophores were apparently sterile, and, according to Napper (11), an official publication of the Department of Agriculture of the Federated Malay States contained the statement that they were consistently sterile. Petch (14) reasoned from circumstantial evidence, however, that the spores must play some part in dissemination. Napper obtained many viable spores from fruiting bodies, and it is now generally accepted that the spores can germinate. The fact that they are shed rapidly as soon as ripe may explain in part why sporophores often were found with few or no spores in the tubes. Nevertheless, the bulk of evidence indicates that local spread is largely by means of rhizomorphic strands and that this is the important method of spread of root diseases through a rubber plantation. Spores are important only when carried by wind or water to very favorable locations for germination and growth, effective dissemination thus being slower than that by growth of the rhizomorphic strands.

EXPERIMENTAL DATA

Cytological Studies

As the cytology of *Fomes lignosus* is imperfectly known, the writer attempted cytological studies in order to learn more about the life history of the organism. The difficulty of inducing the fungus to fruit in culture, however, was a serious handicap. Altho abortive sporophores have been produced, spores have never been found. Sporophores sent from Liberia had few spores, and none were viable. In addition, these sporophores were so badly infested with secondary molds that satisfactory isolations were impossible.

The vegetative mycelium of *Fomes lignosus* is made up of innumerable hyphae, varying from 1.8 μ to 6.2 μ in diameter. The hyphae are hyalin, with relatively homogeneous protoplasm in which granules and droplets are frequently present. In unstained material nuclei are invisible and even the septa are often difficult to distinguish. The presence of large and small hyphae seems to be not a matter of age but of the nature of the individual hyphae. Large hyphae with large clamp connections are often found parallel to small hyphae with correspondingly small clamps. Branch hyphae are often produced by the large hyphae but apparently never attain the size of the parent.

There is a marked tendency for the hyphae to unite into strands. True rhizomorphs are not formed in culture or in nature, altho the migrating vegetative strands function as rhizomorphs and are often so designated. From their early white color they gradually change to a brown or golden color. As might be expected, they are rather resistant to desiccation and remain viable long after mycelial cultures have been killed. In nature these strands penetrate healthy host roots and, after a period of establishment, proceed to parasitize the root system of the host. The distance to which the strands can grow has not been fully investigated. It has been thought that they might grow for considerable distances through the soil, but Petch (14) states that their maximum linear growth is limited to a few feet from the source of nutrients. In culture the tendency is toward a matted rather than a linear growth.

The longest strands thus far observed have been approximately one foot long, altho it is doubtless possible to obtain even longer ones by proper manipulation of materials. The strands seem to form most readily on solid matter and prefer to grow along such material, rather than directly through loose soil. On nutrient media strands do not form without special stimuli, but they may form when the mycelium reaches the sides and lid of the culture dish, altho they are usually small and rather atypical.

Clamp connections are formed profusely on the hyphae of *Fomes lignosus*. Clamps are readily found throughout the mycelium, on branches as well as primary hyphae, and are typical of those found in the group of Basidiomycetes in which the fungus is placed (Figs. 1 and 2). Commonly, one or two clamps are found at a septum. Often two clamps and two branches arise from one septum, and each branch in turn may have one or two clamps at the first septum from the parent hypha. This process may go on indefinitely, so that clamps become the most conspicuous structures of the mycelium, often forming in series along one side of a hypha (as many as seven in line). Sometimes a branch hypha may arise directly from a clamp, and clamps may be produced for which no septum can be demonstrated.

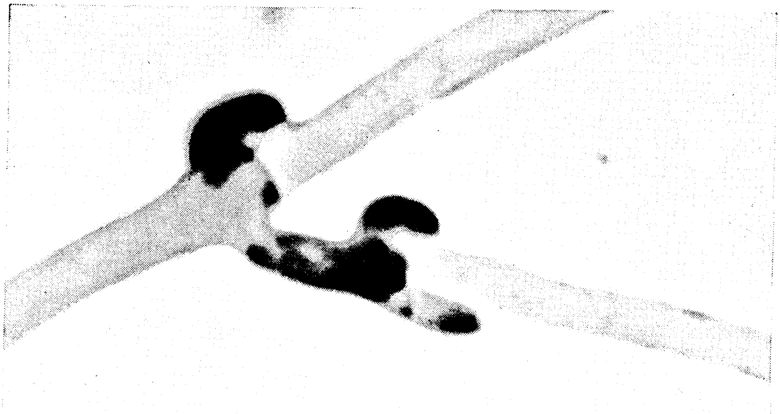

FIG. 1. PHOTOMICROGRAPH OF CLAMP FORMATION ON PRIMARY AND BRANCH HYPHAE OF F. LIGNOSUS (×2000)

A lateral branch has arisen at the level of a clamp and has in turn formed a clamp connection and secondary branch. Several nuclei are obscured by the presence of many deep-staining granules. (Stained with iron aceto-carmine).

From the foregoing statements it may be seen that there is no apparent system to clamp formation in *Fomes lignosus*. No correlation could be found between anastomosis and clamp formation, for clamps were as numerous where no anastomoses were found as where they were common. The function of so large a number of clamp connections has not been demonstrated, but it is thought that perhaps they may serve to pair conjugate nuclei in the multinucleate hyphae, particularly since the clamps were not always formed at a septum.

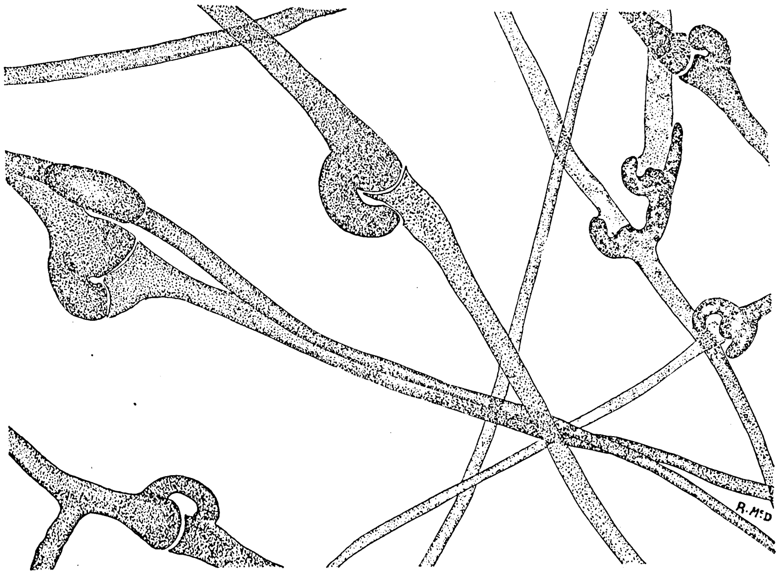

Fig. 2. Appearance of Clamp Connections of F. lignosus from a Young Culture of the Fungus

Clamps of different sizes are noted but no definite nuclei are visible.

The nuclear condition of *Fomes lignosus* was studied by staining cultures of the organism on glass slides. Iron-alum haematoxylin, iron aceto-carmine, and Feulgen's (8) nuclear stain were used. The nuclei of the fungus are usually so small that they are exceedingly difficult to demonstrate. Altho nuclei were demonstrated with each of the three stains, the results were not always entirely satisfactory. In many cells a pair of nuclei could be observed, in others none were seen, and in still others a number of bodies of various sizes could be seen, thus rendering nuclear counts impossible, altho at least several nuclei could be distinguished. Microscopic examinations of more than 50 stained preparations led to the conclusion that the hyphae of the cultures used in this work are in the binucleate or multinucleate condition. In binucleate hyphae the nuclei were found to occur in pairs near the middle of the cells, and in a few instances conjugate division was observed. In many cells the nuclei were inconspicuous, while in tip cells there was always a concentration of deep staining material which made the identification of nuclei difficult or impossible.

In stained material the clamp connections took a very heavy stain and thus often obscured the nuclei. When destained long enough to correct this condition, the nuclei also were destained. Improved technique resulted in preparations in which the clamps could be rather clearly observed. In many clamps no nuclei were present, while in others one or two were visible. The nuclei often were indistinct, but small masses of granular material were noted which took a deep stain. This material could not be shown to be nuclear in origin, however.

Apparently the nuclear condition in hyphae of *Fomes lignosus* is variable. The binucleate condition predominates, but the multinucleate condition is quite common, particularly in the large hyphae. There are two possible explanations for this situation, viz., the mycelium is normally multinucleate until after the clamp connections are formed, or the multinucleate condition is brought about by the anastomosis of two or more hyphae. The fact that the smaller hyphae seem to be binucleate while the large ones are usually multinucleate would be an indication that size is correlated with the nuclear condition of the hyphae. Clamping and subsequent branch production from the vicinity of a clamp or a clamp itself is apparently a means of returning to the smaller, binucleate type of hypha. Brunswick (2) found that in *Coprinus sterquilinus* the mycelium was multinucleate until conjugate nuclei and clamp connections appeared. He also found that in *C. narcoticus* and *C. stercorarius* the multinucleate condition persisted even after clamp formation. Kniep (6) later reported that *Stereum hirsutum* and *Coniophora cerebella* had multinucleate cells in the mycelium, with several clamps on each cell. This appears to be true for *F. lignosus* also.

The significance of the nuclear phenomena observed in *Fomes lignosus* is not well understood, due in part to the lack of success in attempts to bring about fructification. It is not known how the multinucleate hyphae arise, but, since the hyphae are at first small in very young cultures, with larger filaments appearing later, it is possible that anastomosis is one source of multinucleate hyphae. The large hyphae tend to aggregate into rhizomorphic strands, and eventually many of them lose their identity. The abortive fructifications are made up of smaller hyphae which are largely binucleate. The central mass of hyphae later becomes plectenchymatous but does not differentiate into a true sporophore.

Altho no true spore formation has been found in *Fomes lignosus* in culture, certain peculiar structures are sometimes seen. Frequently in old, somewhat desiccated cultures a number of chlamydospore-like structures are formed which appear to be fundaments of chlamydospores rather than true spores. Single spores were picked up and placed on nutrient media, but they never germinated. The spores themselves appeared to be immature, as they were pale yellow in color, with an intine and rather rudimentary extine. The protoplasm was clear and homogeneous and without inclusions. These chlamydospores have been found only occasionally and do not germinate readily, so that at present little can be said as to their nature and function.

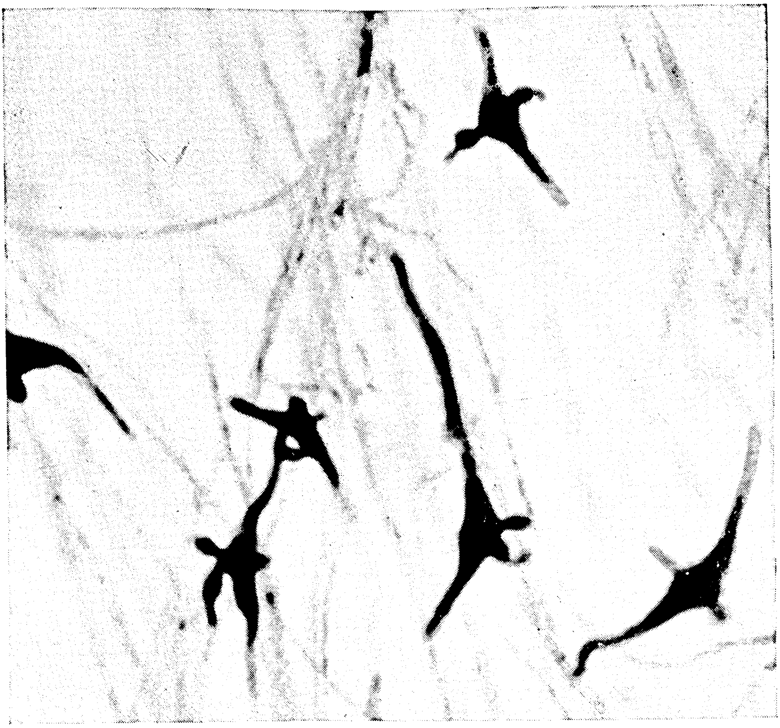

FIG. 3. A HIGHLY MAGNIFIED PHOTOMICROGRAPH OF THE CHARACTERISTIC MODIFIED HYPHAL TIPS OF FOMES LIGNOSUS (×2000)

Clamps may be seen just below the swollen portion of the tips, and some of the structures have been pinched off by the parent hypha. (Preparation stained with iron-alum haematoxylin.)

In the presence of antagonistic compounds, or when partially desiccated or staled, cultures of *Fomes lignosus* begin to form peculiar structures at the tips of the vegetative hyphae (Figs. 3 and 4). In place of the typical blunt, filamentous tips, long pointed tips with a subterminal swelling are formed. These structures always take a deep chromatic stain so that nuclei are difficult to demonstrate, altho it has occasionally been possible to distinguish a single nucleus in a cell. From the subterminal swelling two or more spore-like structures are produced in a whorl. Each of these bodies may bud terminally to produce a chain of pseudospores. The chain does not break up nor does it separate from the parent cell. Instead, the whole modified tip is pinched off the parent hypha. When one of these structures is placed upon nutrient agar the spore-like bodies germinate to produce a mycelium. From this it appears that these structures may probably function as sclerotia rather than spores and that they are composed of cells which are resistant to desiccation or other unfavorable conditions.

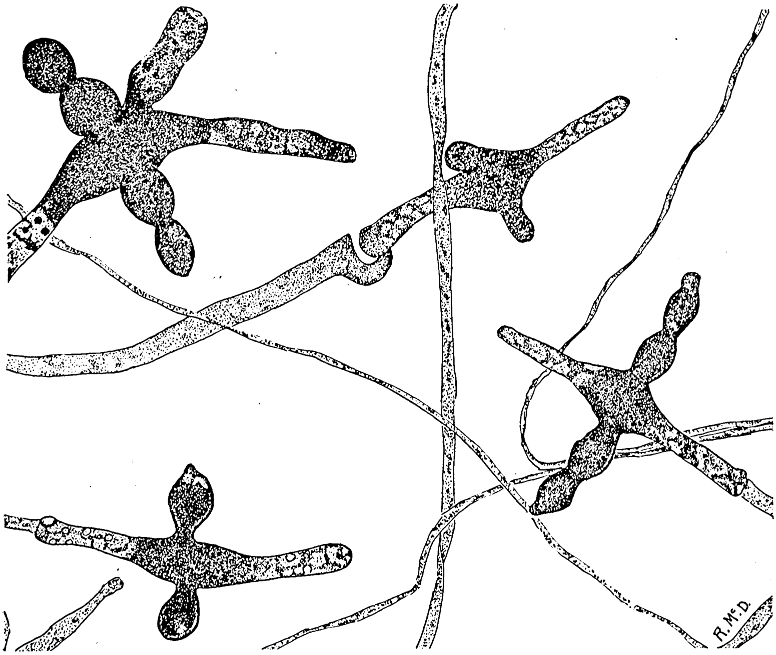

FIG. 4. DETAILED DRAWING OF STRUCTURES SIMILAR TO THOSE WHICH APPEAR IN FIG. 3

In one instance a clamp is shown, and the granular nature of the modified tips is brought out.

As far as the writer has been able to determine, the structures described were previously not known in the Polyporaceae. Additional work is being done in an effort to learn more of the nature and function of these structures. It has been found that they are commonly formed by the surface hyphae of older rhizomorphic strands. This suggests that they are commonly produced as a result of unfavorable conditions.

Culture Studies

The cultures of *Fomes lignosus* used in this work were tissue cultures from rotted *Hevea* roots. The isolations were made at the Firestone rubber plantations in Liberia and were brought to the University of Minnesota in 1934. The original cultures were kept in stock on malt extract agar and were the source of inoculum for the experiments described.

To determine the best medium for the growth of the fungus, the following nutrient media were tested: 3 per cent malt extract agar, prune extract agar, potato dextrose agar, corn-meal agar, Duggar's agar, Leonian's agar, Coons' nutrient agar, and Czapek's agar. In addition, the fungus was grown on blocks of 25 different woods, on pieces of *Hevea* stem and root, and in various soils.

Each of the above nutrient media was tested thoroly in comparison with the others to ascertain its suitability for the growth of *Fomes lignosus.* Both the rate and type of growth were taken into consideration. In the final analysis it was found that 3 per cent malt extract agar was the most satisfactory. This medium, which is known to be very satisfactory for the growth of most wood-rotting fungi, has been used in all subsequent experiments, either alone or in connection with other media. As a further check on the suitability of several media, they were tested under a range of temperature and pH conditions, and malt extract agar proved most satisfactory.

Temperature Relations

The large rubber estates do not follow standard practices. From 60 to as many as 200 trees are planted to an acre. Some estates are interplanted with one of several cover crops, while others may be clean cultivated, and still others are allowed to return partially to native vegetation. The effect of these different conditions on the incidence of white root rot is not well understood. Heavy cover crops shading the soil cause high humidity, with a lowering of soil temperature. Clean cultivation has an opposite effect. Tests were made of the reaction of the pathogen to various temperatures in order to evaluate the possible relationship between soil temperatures and incidence of white root rot.

In all temperature experiments, the fungus was grown on petri plates and placed in triplicate in a series of controlled temperature chambers in which temperature ranged from —3° C. to +40° C. The plates were examined daily, and periodic measurements were made of the growth of the fungus. The temperatures used in preliminary experiments were as follows: —3°, 2°, 5°, 10°, 15°, 20°, 27°, 32°, 36°, and 40° C. It was soon found that *Fomes lignosus* could not live at temperatures above 36° C. nor below 2° C. At temperatures above 36° the organism was rapidly killed, while at the lower limit death was slower (Fig. 5).

The optimum temperature for growth was found to be about 28° C. As the temperature rises or falls from this point, the rate of growth decreases rather rapidly. At 33° C. the growth ceases, and at points above 36° C. the organism is rapidly killed. At 40° C. death occurs within three days. The inhibition of growth at temperatures lower than 28° is less abrupt. The organism grows slowly at 20° C. and very slowly at 15° C. Growth usually ceases below this point, but there was a trace of growth in a few plates after 10 days at 10° C. At 5° C. no growth occurs, but the inoculum is not killed until a temperature of 2° C. is reached. At temperatures below 0° C. death is rapid, taking place within five days.

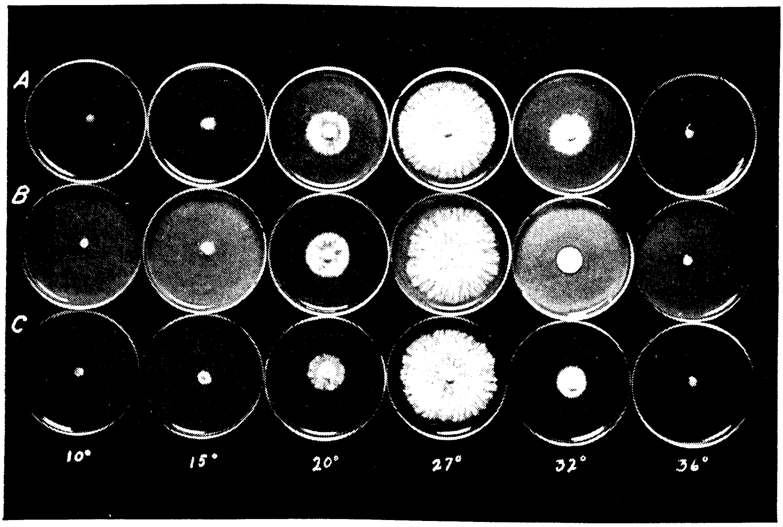

FIG. 5. THE GROWTH OF FOMES LIGNOSUS ON MALT AGAR (A), PRUNE AGAR (B), AND LEONIAN'S AGAR (C) AFTER 5 DAYS AT A pH OF 6.5 AND AT VARIOUS TEMPERATURES

At 10° and 36° C. the fungus does not grow. It is inhibited at 10° and slowly killed at 36° C. Growth sharply decreases as temperature rises or falls below the optimum, and type of growth varies at 20° and 32° C.

It is apparent that *Fomes lignosus* is rather tolerant to a wide range of temperatures. However, its optimum temperature is very sharply defined, and relatively narrow fluctuations reduce the rate of growth decidedly. Unfortunately, the optimum temperature coincides very well with soil temperature often prevailing under jungle cover. Modifications of the temperature to such a degree as to affect the growth of the fungus appear to be economically impractical. The ability of the fungus to progress through the soil by means of rhizomorphic strands is an added protection, as it is thus shielded from the action of direct sunlight. The hyphae of *F. lignosus* are killed rather rapidly when exposed to high temperatures.

In all the previous experiments the media used were adjusted to a pH of 6.5. This point was arbitrarily chosen as one at which the fungus might reasonably be expected to grow well. The interrelation of temperature and hydrogen-ion concentration was also investigated, as was the effect of light rays.

The Effect of Hydrogen-ion Concentration

It often has been postulated that the incidence of *Fomes lignosus* in the soil could be decreased by manipulation of the hydrogen-ion concentration of the soil solution. Steinmann (22) and Petch (13) both recommended the application of lime for this purpose. Bryce (3), however, published evidence to show that no control could be effected through the use of lime, and, altho lime is still used to some extent, most rubber pathologists recognize that it has only limited value. However, it is still held by many workers that there is a direct correlation between soil pH and the prevalence of white root rot.

Attempt was made to determine the hydrogen-ion relationship of *Fomes lignosus* in a series of controlled experiments. The fungus was grown on different media which had been adjusted to a range of pH values (Table 1). In preliminary experiments the organism was grown on 3 per cent malt agar plates which had been adjusted to pH values ranging from pH 3 to pH 10.5. Both the quinhydrone potentiometer and the colorimetric system were used to ascertain pH values. Triplicate plates of each pH value were inoculated with *F. lignosus* and placed in each of the temperature chambers from 10° C. to 36° C. When the fungus was grown at optimum temperatures on media adjusted to a range of pH values, it was found that the acid limit for growth is at pH 4 to 4.5 (Fig. 6), while no definite alkaline limit was reached. It was possible to adjust media to ±10.5 with a reasonable degree of accuracy, and at this point the fungus still grew slowly. Approximate values up to 11.5 were reached, and slight growth still appeared. According to Bryce (3), who used Fuller's scale in his calculations, the fungus is able to live and even grow slightly in a medium which has a pH of approximately 14. Bryce was of the opinion that the organism grew better under alkaline conditions than under the acid conditions favorable to most wood-rotting fungi. A series of experiments with different media have shown that the optimum pH for growth varies slightly with the medium used; consequently, it is impossible to assign a definite point as the optimum. The range is from pH 6 to pH 7.5.

During the course of the pH experiments, it was noted that there was always a distinct difference between the type of growth on acid and alkaline media. On the former the growth was heavy, white, cottony, spreading, and homogeneous; on alkaline media, on the other hand, the individual hyphae tended to aggregate into rhizomorph-like strands. Many of the hyphae in these strands seemed only to be in physical contact, while in other cases many anastomoses could be seen. These strands began to appear as soon as pH values greater than 7 were attained. It is impossible to say that strand production increases as the alkalinity rises, as the subsequent reduction in the rate of growth makes such a comparison impossible after values of pH 8.5 are reached. Beyond this point strands were still produced, but the growth was so reduced that they were less conspicuous.

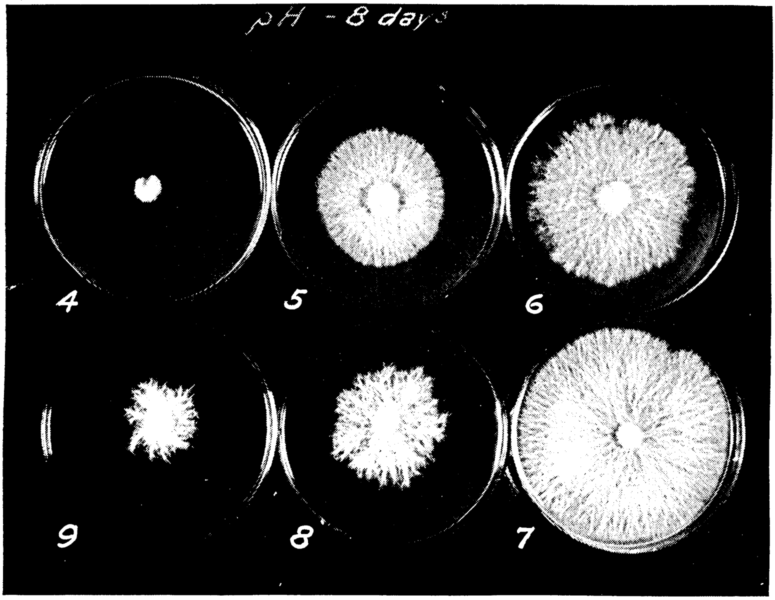

FIG. 6. THE INFLUENCE OF pH ON THE GROWTH OF FOMES LIGNOSUS.
On malt agar at 27° C., pH 7 is optimum for the fungus. Growth decreases as the pH varies from this point. At pH values below 4 the fungus is killed. As the medium becomes more alkaline, growth is slower and strands are produced.

Table 1. The Effect of Hydrogen-ion Concentration on Fomes lignosus on Different Media, as Measured by the Diameter of Colonies In Petri Dishes After Six Days

pH value	Diameter of colonies in centimeters on different media				
	Malt	Prune	Leonian's	Corn meal	Czapek
4 — 4.3	0.88	0.85	1.85	1.01	0.00
4.5— 5.2	4.00	4.77	5.84	3.68	3.16
5.7— 6.5	6.15	5.32	5.31	5.21	3.84
6.8— 7.5	6.85	6.15	5.44	6.56	5.12
7.9— 8.4	5.76	5.15	4.91	5.74	5.01
8.8— 9.4	4.75	2.85	2.61	4.66	4.11
9.6—10.5	3.41	2.65	0.37	2.40	1.79

From these experiments it will be seen that *Fomes lignosus* has an extremely wide range of pH tolerance, the greatest tolerance being on the alkaline side. The fact that the organism will grow in media ranging from pH 4 to more than pH 10 indicates that the normal changes in soil pH would have little detrimental effect on its growth, and the pH within the host plant would never reach a point at which the pathogen could not grow. It seems unlikely, therefore, that alteration of the pH of the soil, within practical limits, would result in appreciable reduction in the amount of root rot, altho the effect of pH on the formation of rhizomorphs may possibly be significant and will be discussed later.

The Effect of Light

The intensity of the light which reaches the soil of rubber plantations may vary considerably as a result of planting rates and the use of different covers. The effect of light rays on *Fomes lignosus* has not been reported previously, altho it has been noted that sporophores are produced more freely in the open than under shade. Napper (11) has suggested that fructification is largely dependent on the action of light rays. If basidiospores are important in the spread of white root rot, light would then be important. Therefore, experiments were made with the fungus under the following light conditions: total darkness, alternate light and dark, in red rays, in blue rays, in violet rays, in direct sunlight, in yellow rays, under laboratory conditions with daily applications of ultra-violet light, and on blocks of *Hevea* wood, with and without exposure to ultra-violet light. Except in the last experiment, all were made with the fungus growing in petri dishes on 3 per cent malt agar. In order to obtain the full effect of the light rays, the tops of the petri plates were replaced with cellophane. Checks with glass tops were included in a parallel series.

Light conditions had little effect on growth of *F. lignosus* on nutrient media. The cultures grown in ordinary daylight were little different from those grown in darkness or under the red, blue, or yellow rays. Minor differences, such as the amount of zonation and variation in the rate of growth, were noted, but such differences should be characterized as normal fluctuations rather than as responses to light. Red rays seemed to stimulate a more luxuriant vegetative growth, but here again the results were not consistent enough to be considered significant.

When cultures of the fungus were exposed to direct sunlight at rather high temperatures (80° F.) death was rather rapid, and, when the plates were simply exposed to the sunlight, rapid desiccation followed. When the cultures were kept in a humid atmosphere during exposure, death was slower but none the less certain. Depending on other environmental factors, cultures of *Fomes lignosus* are killed by the action of direct sunlight in from three hours to five days.

To test the effect of strong ultra-violet light on the organism, cultures in petri plates and on *Hevea* blocks were exposed to the light from an ultra-violet light apparatus, and a series of exposures were made to determine the amount of light which would be lethal. Small amounts of light were found to stimulate vegetative growth, while longer exposure resulted in the production of contorted mycelial masses which looked like abortive sporophores (Fig. 7). These were particularly apparent on the *Hevea* blocks. Excessive ultra-violet light rapidly killed the cultures exposed.

It was hoped that ultra-violet light might stimulate the production of sporophores, which have not yet been produced in culture. Stevens (23) stimulated fructification of various fungi by such methods, but the writer has been unable to find any data indicating that ultra-violet light stimulated fructification of a fungus which never fruits in culture. Thus normal fructification of *F. lignosus* has not been induced by the use of ultra-violet light. The apparently abortive sporophores previously mentioned were irregular in shape and varied from white to golden brown. When sectioned, they were found to be either a closely woven weft of hyphae or even a pseudoparenchymatous hyphal mass. In the latter forms there was an occasional tendency toward porosity, altho true pores were never formed. Instead, secondary and tertiary mycelial masses developed over the original structures.

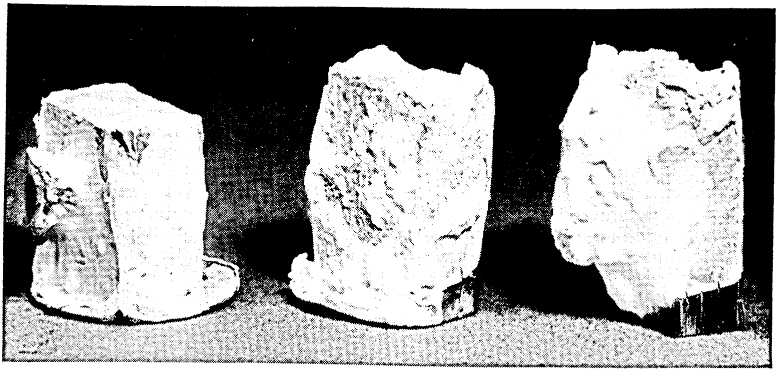

Fig. 7. The Effect of Ultra-Violet Light on the Growth of Fomes lignosus

The fungus is growing on three blocks of *Hevea brasiliensis* which were adjusted to 130 per cent moisture content, on an ovendry-weight basis. The inoculated blocks were exposed to the action of ultra-violet light for 5 minutes a day on 10 successive days. Some of the resultant structures appeared to be sporophore fundaments, but they did not develop beyond this point.

The results of the light experiments agree very well with field observations. *F. lignosus* is known to grow best below the surface of the soil; hence it should be relatively independent of light for vegetative growth. It is known that rhizomorphs may be killed by exposing them to the action of direct sunlight. Fructifications are produced only in the presence of light, and Napper (11) has shown that sporophores can be made to form at will on infected pieces of *Hevea* root by exposure to light. However, light rays alone are not a sufficient stimulus for production of sporophores in artificial media. Apparently *F. lignosus* is one of the many fungi which fruit prolifically in nature but which have not yet been induced to fructify under artificial conditions.

The Effect of Fertilizers on the Growth of Fomes lignosus

In many modern rubber estates fertilizers are applied at regular intervals. The effect of soil fertilization on the incidence of white root rot has not been studied experimentally, but field observations have been made. De Jong (4) reported that in most instances no significant effect was noted after the application of ordinary fertilizers or manures, but that a combination of nitrogen, phosphate, potash, and manganese sulfate tended to increase the incidence of the disease.

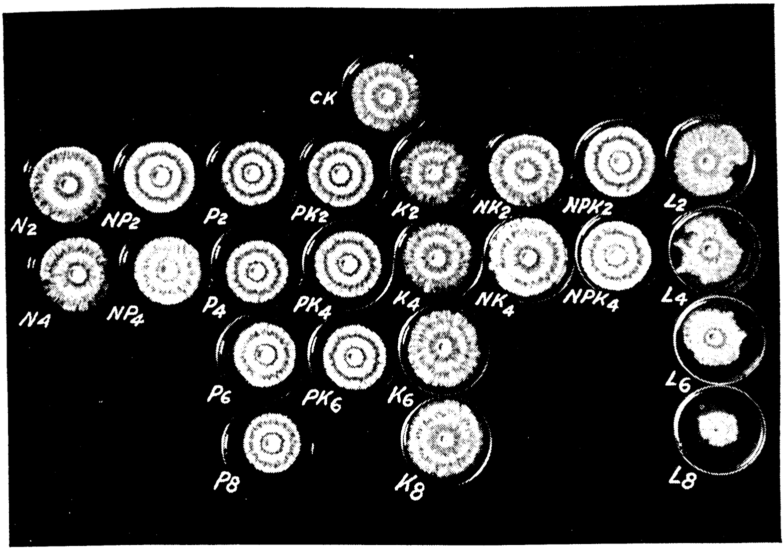

Fig. 8. The Effect of Commercial Fertilizers on the Growth of Fomes lignosus

Fertilizers were applied to malt agar plates at various rates and in several combinations. The compounds used were as follows: lime (L); ammonium nitrate (N); superphosphate (P); muriate of potash (K).

Figures refer to the number of hundreds of pounds per acre, except in the case of lime where they refer to the number of tons per acre.

Nitrogen and phosphorous are stimulatory, while potash is slightly antagonistic. Lime is at first stimulatory, but as the rate of application increases it becomes antagonistic.

The action of fertilizers on *Fomes lignosus* was studied in soil and in nutrient media in an attempt to determine whether or not they may have a significant effect on the fungus causing white root rot. The following four common fertilizers were used: lime, superphosphate, muriate of potash, and ammonium sulfate. The fertilizers were added to plates of malt agar and to six-inch pots of soil inoculated with the organism. As in previous experiments, the soil experiments were negative; but both quantitative and qualitative differences were obtained on nutrient media. From Figure 8 it may be seen that ordinary fertilization practices will have only a slight effect on the growth of *F. lignosus*. Some slight increase in the rate of growth might be expected with heavy application of nitrogen and phosphorous fertilizers, and potash fertilizers would have such slight antagonistic action as to be negligible in control. Lime would have little effect unless used in greater quantities than would be practical. It appears then that fertilizers would have no appreciable effect on the incidence of root rot except as the general health of the plants might be affected.

Toxicity Studies

Commercial fungicides have been used extensively in treating wounds of *Hevea* trees. Pruning wounds and tapping wounds are excellent avenues of entrance for pathogens and must be treated to prevent infection. Brunolinum Plantarium is widely used as a fungicide and has proved of great value. Semesan dust has also been used advantageously. It is quite probable that fungicidal dusts may be of value in the control of *Fomes lignosus,* as they are particularly adapted for use in soil. So little work has been done along this line that the effectiveness of such treatment is not known. In order to determine the most effective fungicides for use in the control of white root rot, the following were tested: Ceresan, New Improved Ceresan, Corona, Cuprocide, Germisan, Merko, Semesan, Semesan Jr., New Improved Semesan Jr., Trioxo, Trockenbeize, and Uspulun.

Triplicate plates of 3 per cent malt agar at pH 6.5 were prepared and adjusted to a 1 to 10,000 (0.01 per cent) concentration of each fungicide. The plates were then inoculated with *Fomes lignosus* and incubated at 28° C. The diameter of colonies of the fungus in the various plates, at the end of four days, is recorded in Table 2. Except in the case of Ceresan, New Improved Ceresan, and New Improved Semesan Jr., a definite graduated toxicity can be noted. These three compounds proved to be highly toxic and killed the inoculum within 24 hours at a 0.01 per cent concentration. The other ten dusts were eliminated from subsequent tests. Tests at greater dilutions with the same three compounds and with Semesan resulted in the selection of New Improved Ceresan as the most effective dust. This dust is lethal in concentrations of 0.001 per cent and inhibitory at concentrations of 0.0005 per cent. Ceresan is less effective, while New Improved Semesan Jr. is effective only in dilutions of 1 to 20,000 (0.005 per cent) (Table 3).

From the foregoing results, it is apparent that *Fomes lignosus* is extremely sensitive to the organic mercury dusts. Sulfur, formaldehyde, and copper dusts are much less effective. The action of the mercury compounds, observed microscopically, was manifested by a rapid granulation and precipitation of the protoplasm of the fungus hyphae. After death, the cells rapidly shrink and become brown. The high dilutions possible with these dusts make them especially worthy of trial in the control of *F. lignosus.*

Table 2. The Effect of 0.01 Per Cent Concentration of Several Commercial Fungicidal Dusts on Fomes lignosus, as Measured by the Diameter of Colonies After Four Days on 3 Per Cent Malt Agar Plates at 25° C.

Fungicides	Diameter of colonies in centimeters after 4 days
1. New Improved Ceresan	0.00 killed
2. Ceresan	0.00 do
3. New Improved Semesan Jr.	0.00 do
4. Uspulun	.36
5. Semesan	.41
6. Bayer	.45
7. Germisan	.50
8. Trockenbeize	.80
9. Semesan Jr.	1.95
10. Cuprocide	2.97
11. Trioxo	3.10
12. Corona	3.21
13. Merko	3.26
14. Check, no treatment	3.31

Similar tests were made with Brunolinum Plantarium, a commercial creosote oil which is made in England and widely used on rubber estates as a disinfectant of wounds and tapping panels. It was found to be lethal to *Fomes lignosus* in dilutions of 1 to 1,250 (0.08 per cent) and inhibitory in dilutions of 1 to 2,500 (0.04 per cent). Brunolinum Plantarium is less effective than organic mercury dusts, but it has the advantage of greater lasting qualities and greater ease of application. It is possible, however, that the organic mercury dusts may prove useful as soil disinfectants for special purposes.

Table 3. The Effect of Different Concentrations of the Four Most Effective Organic Mercury Fungicides on Fomes lignosus, as Measured by the Diameter of Colonies After Six Days on Malt Agar at 28° C., Adjusted to pH 6.5

Fungicide	Concentration of fungicide, in per cent, and growth in centimeters			
	.002	.001	.0005	.00025
Semesan	4.14	7.34	8.41	8.52
New Improved Semesan Jr.	2.24	3.75	4.92	6.46
Ceresan	.66	3.00	4.13	5.91
New Improved Ceresan	0.00	0.00	.45	3.25
Check	8.48			

Antibiosis and Metabiosis

While the use of toxic compounds may sometime be important for use in the control of white root rot, the value of possible biologic controls should be considered also. A knowledge of the effect of the several root-rotting fungi upon each other, as well as that of other soil microorganisms upon these fungi, may lead to the formulation of important control measures. With this in mind, a number of microorganisms were studied in relation to their effect on *Fomes lignosus.*

In the literature on rubber pathology there are a number of scattered observations on apparent interrelationships between *Fomes lignosus* and other microorganisms. Small (21) published evidence to show that *F. lignosus* was a very weak parasite and attacked *Hevea brasiliensis* only after the trees were partially destroyed by *Rhizoctonia bataticola,* but most pathologists do not agree. Murray (9) (10) reported that altho he found *R. bataticola* on some diseased rubber trees, *F. lignosus* was strongly parasitic and was able to kill rubber trees without the presence of other microorganisms. Weir (24), Napper (12), and Sharples (20) have also adduced evidence that *F. lignosus* is a strong parasite. This point is still in question, with strong advocates on both sides. De Jong (4) reported that the reason *F. lignosus* sometimes causes a wet and sometimes a dry rot is that secondary bacteria are responsible for the appearance of the wet rot.

Most rubber pathologists are inclined to consider root rot of *Hevea brasiliensis* as a "complex". Petch (15) stated that in many instances it was impossible to tell which fungus was causing the rot until sporophores were produced. In addition to *Fomes lignosus, F. noxius, F. pseudoferreus, Poria hypobrunnea, Ustulina zonata,* and *Sphaerostilbe repens* are all known to cause root rot of rubber. Petch (17), in Ceylon in 1922, found that the distribution of root diseases in a carefully surveyed district was as follows: 43 per cent *Fomes lignosus,* 41 per cent *Fomes lamaoensis,*[2] 11 per cent *Ustulina zonata,* and 3 per cent *Poria hypobrunnea.* While these figures may not apply to any large area, they suggest that several organisms may produce similar effects in a given region. The possible interaction of the root-rotting fungi on rubber has not been investigated thoroly, and, while plans for work along this line are being made, it is impossible to say at the present time that there is a metabiotic relationship within this group of organisms.

From cultures, soil, and pieces of diseased *Hevea* root received from the Firestone rubber plantations in Liberia, a number of organisms were isolated. Thirty fungi and 16 bacteria were obtained in pure culture from this material. In an effort to determine possible metabiotic or antibiotic relationships between any of these organisms and *Fomes lignosus,* several were grown in culture with it. Plates of malt extract agar and six-inch pots containing *Ficus elastica* plants in soil enriched with corn meal were used for the culture media. Flasks of enriched soil were also used in order that the growth of the organism might be under constant observation.

From the limited number of organisms studied, no organism was

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[2] Now usually attributed to *F. noxius.*

found which was particularly antibiotic to *F. lignosus*. However, since it was impossible to obtain a representative number of the soil- and root-rotting organisms found in rubber estates, final conclusions are not justified. The fact that *F. lignosus* has been reported both as a strong and as a weak parasite suggests that other organisms may play a part in its activities. Weir (24) claimed that *F. lignosus* was strongly parasitic and could kill a good-sized rubber tree within six months. De Jong (4), on the other hand, stated that the fungus was a rather weak parasite and did not readily attack unless the trees were predisposed to the disease. Napper's observation that the fungus could not readily grow in material already infested with other fungi may afford a partial explanation of the two conflicting ideas. Small, in his work with *Rhizoctonia* on *Hevea,* attempts to show that *F. lignosus* is secondary and a weak parasite. Evidently, therefore, the pathogenicity is variable because of environmental factors, including biotic relations, or the organism comprises different races. The writer has not had opportunity to investigate the latter possibility, altho it is very likely that there are different races.

All the experiments previously described were paralleled with similar experiments, using soil as the medium instead of nutrient agar. Under conditions obtainable in the laboratory and greenhouse the results were unsatisfactory. In the preliminary experiments the several soils were inoculated with *Fomes lignosus* and placed at temperatures ranging from 0° C. to 36° C. In every case, at favorable temperatures, the inoculum grew for a few days and then disappeared. Manipulations of the soil pH had no effect, as the fungus died as soon as the nutrients in the agar substrate of the inoculum were used up.

It is well known that *Fomes lignosus* migrates through the soil by means of rhizomorphic strands, which frequently emanate from organic material on which the fungus is growing. An attempt was made to duplicate such conditions by burying blocks of rubber wood in soil in which *F. lignosus* was present. It was thought that the fungus might begin to form the typical strands when the blocks were decayed. However, it was found that the fungus did not readily form strands under the conditions of the experiment. The blocks were buried at depths ranging from one inch to ten inches, and a few weak strands were observed growing from the blocks buried at depths to four inches. The strands were small, short, and weak, were not produced abundantly, and died rather rapidly. The fungus in the blocks died more slowly, as it was possible to reisolate it from the blocks after several weeks of burial in the soil. Neither the presence of living hosts, *Hevea* blocks, nor *Hevea* sawdust was sufficient to stimulate rhizomorph production.

Altho in these experiments the fungus did not grow readily in untreated soils, it grew readily when nutrient materials were incorporated into the soil. When potting soil was screened and enriched with 10 per cent corn meal, especially luxuriant growth occurred. The first growth is always over the surface of the enriched soil. Later the hyphae spread throughout the medium. If a layer of fresh sterilized dry soil is then placed on top of the enriched soil in which the fungus is growing, rhizomorphic strands will eventually be formed and will grow through this upper soil layer. However, so far no tendency towards fructification has been noted (Fig. 9).

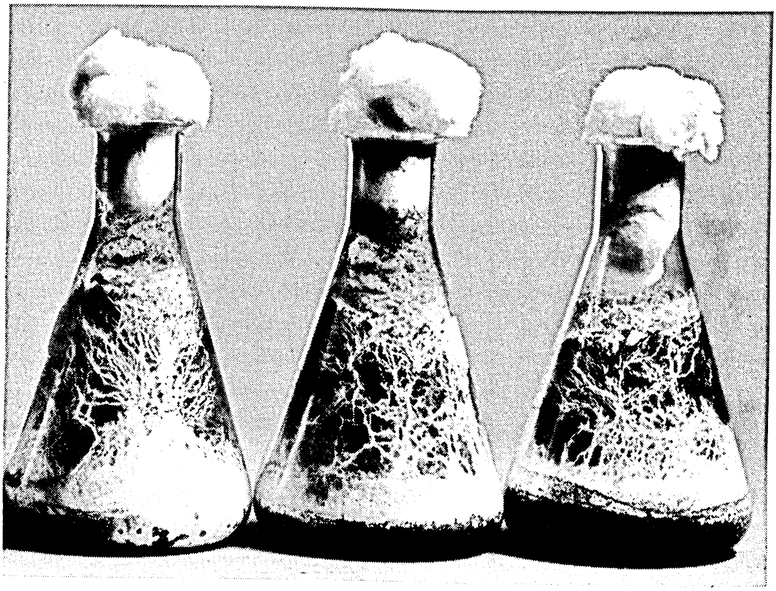

FIG. 9. RHIZOMORPH FORMATION IN FOMES LIGNOSUS

The fungus was grown for 10 days in sterile soil enriched with 10 per cent corn meal, and a layer of sterile soil was then added. The typical netted appearance of the anastomosed rhizomorphic strands, which grew through the soil, is very apparent.

Pathogenicity

Altho *Fomes lignosus* has been generally considered to be a strong parasite, a number of workers have seriously questioned the evidence upon which this theory is based. Frequently, the presence of the fungus in a killed *Hevea* tree has been considered sufficient evidence of its pathogenicity. When introduced into a host plant, a strong parasite is usually able to establish itself quickly and destroy the plant. There still is some doubt regarding the susceptibility of *Hevea brasiliensis* when artificially inoculated with *F. lignosus*. Proponents of the strong parasite theory claim that this is due to the fact that the fungus is not a wound parasite but only attacks healthy tissues under optimum conditions for growth of the parasite.

A number of experiments have been made in an effort to obtain data as to the pathogenicity of *Fomes lignosus*. Since the fungus has a wide host range, it was thought it should be possible to cause infection on *Ficus elastica* grown in the greenhouse. Well-grown plants, as well as young vegetatively propagated plants, were available for inoculation. Four methods were used in an attempt to obtain infection: (1) The plants were inoculated directly through wounds; (2) the fungus, on agar, was placed in the soil around the roots; (3) blocks of rubber wood infested with the fungus were buried in the soil in which the plants were growing; (4) the plants were planted in potting soil which had been enriched with 5 per cent corn meal, and the soil was then inoculated with *F. lignosus*.

The results of the foregoing experiments have been negative thus far. When the inoculum was placed in the soil, small strands of the fungus often formed on the roots of the host plant, but they were weak and small and always died without causing infection. Direct inoculation had no noticeable effect on the *Ficus* plants. According to the evidence obtained by Petch (13), Napper (11), and Sharples (20), *Fomes lignosus* infects host plants by direct penetration of young host roots by rhizomorphic strands that grow through the soil, reach the roots of the host, then grow along them and eventually send infection tubes into living roots. After a period of growth and ramification, the fungus becomes established as a parasite in the host plant.

Altho all pathogenicity experiments have been negative, it is not assumed that this is proof that the fungus is not parasitic.[3] The experiments were limited by many factors and cannot be used as a basis of specific conclusions. Parasitism would seem to be a process which is dependent upon optimum conditions for the parasite, predisposition of the host, and large amounts of inoculum which can support the fungus for a considerable period.

In the writer's opinion there is a strong possibility that the question of the parasitism of *Fomes lignosus* might best be answered through the study of the different strains of the fungus. It is extremely likely that many such strains exist and that they may differ in pathogenicity. The writer has had only two strains available, but they were distinctly different in many respects. A study of a large number of strains from various localities is very necessary to an understanding of the pathogenicity of the organism.

DISCUSSION

The importance of root-rot fungi in rubber production is generally appreciated, but basic research has been inadequate, due partly to the nature of the problem. Perhaps the principal reason, however, is that much of the pioneer work has been done by field mycologists without the time or facilities for supplementary experiments. Thanks to these early workers, field conditions have been very well described and many

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[3] In continuing the experiments started by the writer, Mr. E. W. Hanson showed that the Liberian strain of the fungus is strongly pathogenic.

control measures carefully evaluated. On the other hand, little is known of the physiology and cytology of the organisms involved and, in the case of *Fomes lignosus,* even its taxonomic position is in question. The present work represents an attempt to obtain more exact information as to the behavior of *F. lignosus* under different conditions in order to evaluate present practices and suggest new ones.

A fungus which has a wide host range and at the same time is able to live on a large variety of dead, woody materials is necessarily a rather successful competitive organism. When, in addition, it is extremely tolerant to fluctuating temperatures and pH concentrations, the problem becomes still more complicated. In view of the fact that the attack is made below the ground level and the first apparent symptom may be the blowing over of the tree, the treatment of individual trees is difficult. The problem is clearly a soil problem, with two main avenues of attack: (1) The production of resistant lines; (2) soil practices to lessen the incidence of the organism in the soil. The experimental data contained in this bulletin are intended to suggest the possibility of controlling *Fomes lignosus* by various methods, some of which are in use at present and others which have not been attempted.

The possibility of controlling *Fomes lignosus* by temperature modifications is generally conceded to be doubtful. However, it is still maintained by some workers that at least partial control can be obtained in this manner. The usual method has been to interplant with cover crops or secondary commercial crops. The latter practice has been largely abandoned, as many such crops are also susceptible to white root rot. While cover crops may be beneficial in conserving soil moisture and preventing erosion, they also aid the fungus by raising the humidity and by screening out direct sunlight. As seen from temperature experiments, the reduction of soil temperatures due to cover crops would seem to be of little value in controlling *F. lignosus.* If, as suggested by Napper (12), cover crops form a root barrier which retards the spread of the fungus through the soil, this is probably the only way in which cover crops reduce the incidence of the disease. Theoretically, the practice of clean cultivation should be more effective in controlling root rot by reducing the amount of inoculum in the soil. In addition, soil temperatures are higher under clean cultivation but probably are not raised sufficiently to control the fungus.

Closely allied to the question of temperature is that of the effect of light. Sporophores are produced in the light, while rhizomorphs form below the surface of the soil. Napper (12) has shown that the fungus will not fructify in the dark, but it has not been shown that light is the primary stimulus to fructification. However, in the writer's experience, the only tendency towards fructification was a result of the stimulus of ultra-violet light. Direct sunlight has been found to inhibit or even kill the fungus, and for this reason it is suggested that the roots of diseased trees be partially exposed to the action of direct sunlight to destroy the surface strands of the fungus.

The hydrogen-ion concentration of the soil has long been thought to have a direct effect on the growth of root-rotting fungi. Both acid and alkaline conditions have been postulated as being stimulatory to them. Various attempts have been made to control the disease by manipulation of soil pH. The writer has been able to show that such attempts are futile, as *Fomes lignosus* will grow luxuriantly at a rather wide pH range. In brief, the fungus is at least as tolerant of hydrogen-ion fluctuation as the host plant. Such a condition automatically limits the possibility of any effective control by changes of the soil pH.

The effect on the pathogen of commercial fertilizers, such as lime, potash, phosphates, and nitrates, when applied at prevailing rates, was negligible. A slight stimulatory effect on the fungus by nitrates and phosphates is so insignificant as to be over-balanced by the beneficial effect of the fertilizer on plant growth.

A number of fungicides have been tested, and several proved very effective. Semesan and copper sulfate have been used to some extent, but the use of chemical fungicides has not yet attained its proper place in rubber pathology. Several organic mercury dusts were shown to be much superior to any compounds in use at the present time. New Improved Ceresan is by far the most effective, as shown by soil and culture studies. Indications are that chemical control may be of value in the control of diseases of rubber.

The pathogenicity of *Fomes lignosus* is said by most rubber pathologists to be well defined, but Small (21) and some others have seriously questioned this view. Some evidence has been presented to show that it is only a secondary invader and can not act independently. The writer has been unable to obtain infection of host plants with his strains of *F. lignosus* in a large number of experiments. While the results obtained under artificial conditions can not be considered conclusive, they serve to show the need for further research on this phase of the problem. (However, see footnote on p. 23.)

A number of organisms are concerned in the root-rot complex of *Hevea brasiliensis*. The interaction of these organisms is not known, altho two or more may often be found in one host plant. *Fomes lignosus* has been reported as being unable to attack woody material already infested by other fungi. In an attempt to obtain information as to possible anti- or metabiotic relationships between it and other fungi, *F. lignosus* was grown in combination with a number of fungi and bacteria. No distinct metabiotic relationships were observed.

Extensive cytologic and genetic studies of the organism should be made as a basis for understanding its apparently variable pathogenicity. It is entirely possible that there are many parasitic races. If this is true, it would explain the conflicting results obtained by investigators in different regions. It is possible, of course, that the soil conditions and other environmental conditions differ so much in different countries as to account for the diverse results and conclusions regarding the pathogenicity of the organism. However, the writer knows of no extensive experiments to determine the existence of parasitic races. The possibility of the existence of such races was strengthened when it was found that basidiospores are produced and that they germinate normally under appropriate conditions. The possibility of the hybridization between haploid mycelia derived from different basidiospores should be investigated, particularly since it has been shown that in some of the Basidiomycetes haploid lines differ in many characters, including pathogenicity. The writer has not had opportunity to study this phase of the problem, but in view of the conflicting opinions regarding the degrees of pathogenicity of the organism, it certainly deserves extensive investigation. In fact, it is doubtful whether the chaotic situation with respect to pathogenicity of the organism can be clarified properly until such investigations have been made. The fact that different mycologists have described different types of fruiting bodies also suggests the probability of different varieties or races, altho here again the effect of environment and host plants on the morphological characters of the fruiting bodies must not be overlooked. All things considered, however, it is quite apparent that study of the cytology and genetics of the organism is of great importance in the practical solution of the root-rot problem. If there are different parasitic races, it is entirely possible that the pathogenicity of the organism may differ greatly in different regions, and the conclusions applicable to one region may not be applicable to another.

SUMMARY

1. *Fomes lignosus* is a tropical fungus causing root rot of rubber. It is a facultative parasite with a wide host range and is widely distributed throughout the eastern tropics.

2. The taxonomy of *F. lignosus* has long been in question. Thirty-four synonyms have been used, some of which are disputed. The fungus has also been designated as an unnamed species, because its identity has been confused with West Indian forms.

3. *F. lignosus* produces large and small hyphae. Anastomoses are common and clamp connections are very numerous. The cells may be either binucleate or multinucleate, the former predominating. No sporophores were formed, but imperfect chlamydospore-like structures were formed. Hyphal tip cells often produced spore-like structures which behaved as sclerotia. Rhizomorphic strands were formed under a number of conditions.

4. The fungus has a temperature range from 2° C. to 36°C., with an optimum range from 27° C. to 30° C.

5. *F. lignosus* will grow at pH values from 4 to 10+. The optimum range is from pH 6 to pH 7.5. Strand formation is induced by alkaline media.

6. The pathogen grows equally well in daylight or darkness. Growth in the presence of blue, red, or yellow rays only is not significantly

different. Direct sunlight at optimum temperatures is lethal. Ultraviolet in small quantities results in the production of distorted growth and what appear to be abortive sporophores.

7. Ordinary fertilizer practices were found to have no significant direct effect on the development of the organism in the soil.

8. Many organic mercury dusts are extremely toxic to *F. lignosus*. New Improved Ceresan was found to be effective when diluted at the rate of 1 to 200,000.

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