



The effect of *Fomes igniarius* on *Populus tremuloides* in the Gallatin National Forest of Montana
by Marvin F Kelly

A THESIS submitted to the Graduate Committee in partial fulfillment of the requirements for the
degree of Master Science in Botany

Montana State University

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Stages of decay are defined. Isolation and growth characteristics of the fungus in pure cultures are outlined. It is shown that the fungus is found throughout the entire Gallatin National Forest and is causing the heaviest damage in the more moist areas of the stand.

Evidence is presented showing that *Populus tremuloides* is increasing in the Gallatin National Forest of Montana.

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IN THE GALLATIN NATIONAL FOREST OF MONTANA

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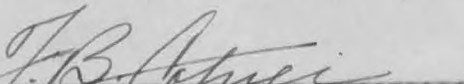
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Chairman, Examining Committee


Chairman, Graduate Committee

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CONTENTS

	Page
Contents	2
Abstract	3
Introduction	4
The Host	5
Nomenclature of the Fungus	6
History of the Disease	8
Sources of Material	10
Gross Anatomy of <u>Fomes igniarius</u>	12
Stages of Decay	13
Hosts	16
Histological Studies	17
Cultural Characteristics	21
Production of Methyl Salicylate Odor in Culture --	22
Spore Production	23
General Discussion	25
Summary	33
Conclusion	33
Literature Cited	34
Description of Plates	36 - 37
Plates	38 - 46

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ABSTRACT

A survey was made of the Gallatin National Forest of Montana showing the distribution of Fomes igniarius (L.) Fries. on Populus tremuloides Michx. This survey also included the distribution of Populus tremuloides in this forest. Special reference is made to the possible predisposing factors of infection, ecological distribution of the fungus, and the severity of attacks. Effect of game as causing wounds in the host which may provide possible points of entrance of the fungus were carefully considered.

Stages of decay are defined. Isolation and growth characteristics of the fungus in pure cultures are outlined. It is shown that the fungus is found throughout the entire Gallatin National Forest and is causing the heaviest damage in the more moist areas of the stand.

Evidence is presented showing that Populus tremuloides is increasing in the Gallatin National Forest of Montana.

INTRODUCTION

The primary objective of this study was to determine the distribution of Fomes igniarius (L.) Fries., on Populus tremuloides Michx. in the Gallatin National Forest of Montana. Special reference is made to the ecological aspect of the stands of Populus tremuloides, their distribution and severity of infection.

Aspen, or poplar (Populus tremuloides Michx.), because of its wide distribution, can be considered one of the most important tree species. Although hardwoods originally occupied a large portion of the land, a comparatively small part was in aspen. Due to the demand for hardwood the aspen has been constantly increasing. In Minnesota it is estimated that 50 per cent of the total forest area of the northern half of the state, or 10,000,000 acres is now in aspen. Aspen will therefore be a very important tree in any attempt at systematic management of forest lands.

Unfortunately, there is a prejudice against the use of aspen wood, even for purposes for which it is well suited. This prejudice is largely due to its susceptibility to "white heart-rot" or "false-tinder", resulting, as a rule, in large losses, especially in older trees. This heart-rot is caused by the mycelia of Fomes igniarius (L.) Fries.

It is important, therefore, that silvicultural practices and methods of management for these stands be worked out which will reduce the losses from decay to a minimum.

THE HOST

Populus tremuloides, Michx. or aspen is the best known and most extensively distributed species of populus, being common from the Atlantic to the Pacific Oceans, and from Canada to Mexico. (Pl. I). The tree is conspicuously whitish, smooth, straight trunked, and has small trembling leaves which distinguish it from its associates. The tree may grow from 60 to 80 feet high, and from 14 to 20 inches in diameter; more commonly from 30 to 40 feet high, and 8 to 12 inches through. Populus tremuloides is used for lumber, box shock, slack cooperage, excelsior, paper pulp and railroad ties, besides cord wood and other small uses such as local mining timbers. According to Winslow (1941) it is also used for shipping war cargoes, especially bombs because less lumber, less weight, and less space are required, and it absorbs shock and is cheaper than other containers.

When this wood is treated with a preservative it serves very well as railroad ties. The resiliency of the wood makes it absorb shock easily. When healthy the wood also has a pleasing color for boxes, long fibers and little resin which makes it valuable for paper pulp and excelsior. Rapid growth of this species makes it very valuable for these purposes, reducing the amount of investment and yielding a bigger return in a shorter time.

Ecologically Populus tremuloides is usually regarded as temporary, but frequent fires tend to make it more nearly permanent. In its conquest of better soils the aspen has been materially assisted through unwise and unregulated cutting, and through the injudicious use of fire.

Obviously then, whether or not the acreage now in aspen will increase or decrease in the future depends largely on the protection from fire which these areas receive, and upon the silvicultural methods employed to convert aspen stands to those of more valuable species.

In certain regions, and on limited areas this conversion is taking place naturally, but future fires and unwise cutting methods too easily undo nature's efforts in this direction.

NOMENCLATURE OF THE FUNGUS

Fomes igniarius (L.) Fries., is a perennial Polyporaceous Basidiomycete which was named by Linnaeus and later renamed and reclassified by Fries. The forms vary considerably depending on the host. The typical form as described by Overholts (1915) is the one to which the author has reference. Lloyd (1905) said, "The fact that there are two very definite plants referred to by different botanists is not generally appreciated. The old tubes of Fomes igniarius have a deposit (lime, I presume) which shows plainly in a section. This point has never been mentioned, to my knowledge, in books." Lloyd (1919) says further that no commoner fungus grows, yet every writer had his own idea for a name, no two of them were alike. Thus they wrote "Linnaeus" after Fomes igniarius although it is doubtful if anyone knew what he designated, Linnaeus probably did not know himself. Not much can be told from his vague description. According to Lloyd (1909), "Voilà un bon spécimen, et c'est bien la même plante que celle qui fut connue de Fries comme igniarius. Je crois que la plupart des mycologues français sont dans l'erreur en ce qui concerne la plante qu'ils appellent igniarius."

Overholts (1915) describes the distinction between Pomes igniarius and Pomes igniarius var nigricans. He further states that forms intergrade into the variety to such an extent that illustrations are hard to refer.

According to Verrall (1936) after careful macroscopic and microscopic examination of many specimens, and from cultural characteristics, it seems that three groups are represented, viz: those from Betula, those from Poplar, and those from other tree species. There are, however, such intergradations of characters that many specimens cannot readily be classified as to the host on which they grew.

Kauffman(1929) states that, "in the large group of fungi, the Agaricaceae, we rarely find types of any consequence in connection with the classic works of Persoon, Fries, Quellet, and others before them." Figures without adequate description occur in abundance.

Unfortunately one can obtain very little accurate knowledge of certain structures from these illustrations. All one can get is a general conception. Here the future demands consideration. Are we to pass on to other generations the unending task of passing judgement on pictures until they crumble into dust? Eminent students of the Agarics have attack the thankless job of trying to put such species on a more clear cut footing. They have tediously compared the illustrations and descriptions of the old masters like Fries, Persoon, and Quellet. They have sought for and found specimens in the fields and forest today, and have then passed judgement on their identity. Common sense, it seems to me, bids us to accept their judgement.

Due to the complexity of taxonomic characters, and many views as presented by various authors, it seems proper to simplify the nomenclature, following Kauffman's (1926) paper as presented to the International Congress of Plant Science. Therefore in this study the author will use the name as started by Linnaeus, reclassified by Fries following the typical description as given by Overholts (1915).

HISTORY OF THE DISEASE

Fomes ignarius produces a discoloration of the wood and the sporophores (fruiting bodies) vary according to the host. The size and shape vary from eight inches wide and four inches thick to very small bodies. It was these fruiting bodies that first attracted attention of the mycologists in Europe. In general, the distribution of the disease may be given as follows: In North America it occurs in Alaska, Baxter and Wadsworth (1939); in various parts of Canada, Buller (1931); and in the following places according to Schrenk and Spaulding (1909); In South America it has been collected in Surinam, Brazil, Argentina, and Patagonia. It is prevalent throughout Europe from England to Russia, and from Scandinavia and Finland to Italy and Spain. In Asia it is known from Siberia, Japan, the Philippines, and India. It also occurs in Tasmania, Australia, Java, New Zealand, Admiralty Islands, Sierra Leone, and South Africa.

It is to be noted that these localities embrace the four quarters of the world. Because of the lack of knowledge of the mycological flora of many countries, no statement can be made as to the occurrence of this fungus in them.

Where this fungus occurs extensively almost the entire stand of Populus tremuloides is frequently found so badly damaged by the white heart-rot as to be practically worthless. In certain areas of deciduous forest in the Adirondacks in the State of New York, as pointed out by Schrenk and Spaulding (1909), where the timber was comparatively a mature stand, actual counts showed that from 90 to 95 per cent of the otherwise merchantable trees of beech were rendered valueless from the attack of this fungus. Schrenk and Spaulding (1909) have also shown that the same is true to a certain degree in the regions where the aspen is grown extensively for pulp wood. In the New England States, Colorado, and New Mexico it is almost impossible to find healthy groves of aspen which have attained any age, because of the extreme destruction brought about by the white heart-rot. In the mature beech stands of Texas and Louisiana, where the trees are 150 years old or more, a very large percentage are wholly decayed in the interior by this fungus. The same is true of many of the tracts of the Appalachian deciduous forests. It may be stated that the amount of damage caused by the white-rot is very great; and its wide distribution, together with the almost universal susceptibility of deciduous trees thereto, make it the worst enemy of these species, especially during the period when they are approaching maturity.

According to Schmitz and Jackson (1927) the fungus is common throughout the entire range of Populus tremuloides and everywhere causes heavy losses. It is sometimes associated with Fomes applanatus Fries., but the author did not find this fungus where the material used for this study was collected.

Vorrall (1937), working in Minnesota, found Fomes igniarius common throughout the state and the sporophores varied according to the host on which it was growing.

It has been pointed out by Schrenk and Spaulding (1909) that New England, as well as Colorado and New Mexico, has no appreciable aged healthy stands of aspen. In Minnesota the aspen is one of the commonest trees.

Lightfoot (1777) made the following statement in relation to Fomes igniarius, "An excellent touchwood is made from this fungus by first paring off the outer rind, then boiling the remainder in lye, and afterwards drying and pounding with a hammer, or else pounding and boiling it up with salt-peter. The same fungus beaten into soft square pieces is well known to surgeons by the name of Agaric, and has been much celebrated for stopping the bleeding of arteries."

The fungus is parasitic and will attack the living tissue or sapwood, continuing its activity after the host is dead. It is not uncommon to find fruiting bodies on old dead stumps. For this reason old stumps and boles of the trees are possible sources of infection.

SOURCES OF MATERIAL

Fruiting bodies used in this study were first collected by the writer in the fall of 1939 from Buffalo Horn Creek, the exact location being Township 8 South, Range 4 East, North West $\frac{1}{4}$ of Section 25. (Pl. II, 1.) It was observed at the time of collection that the infected area was near the north west boundary of the Yellowstone Park, and that game concentrated in this creek bottom. Many of the aspen trees had been peeled by the larger

game animals while polishing their antlers. It is not uncommon to find trees with the entire phloem region completely destroyed and the xylem region exposed due to the polishing of antlers. Several of the trees which exhibited this condition had large sporophores. Game animals also eat the young trees. The trees which were examined were mostly confined to the creek bottom, and varied in diameter from six to twelve inches.

Several sporophores were taken to the laboratory for examination. Some were placed in the refrigerator for further study. Portions of several infected trees were also taken. Fragments of the infected wood were placed on Blakeslie's Agar¹ and produced small mycelia. This agar did not give good results as only a sparse growth of mycelium was formed. Fungus grown on this agar did exhibit, however, the clamp connections characteristic of the mycelium of Basidiomycetes.

In the summer of 1940 several field trips were taken to various sections of Gallatin National Forest and specimens were collected. Hebgen Lake, which is on the south end of the forest is bordered in many places by aspen. Here the infection was found to be heavy.

Aspen trees at Cusel Falls on the south fork of the West Fork of the Gallatin River were also found to be infected. Aspen trees in several small drainages in this area showed early signs of infection by increment borings. Nearly all of the tree infection observed was confined to within 100 yards of the creek bottoms.

¹ Blakeslie's Agar

agar agar	2%	20 gm)
Peptone (Witte)	1%	1 gm) 1 liter
Dextrose	2%	20 gm) H ₂ O
Dry Malt Extract (E. & A.)		20 gm) 939 c.c.

Increment borings show that small trees of aspen are infected, but have not produced sporophores. According to Schrenk and Spaulding (1909) the point of entrance is usually indicated some years later by the location of the oldest sporophores.

Aspen trees in Haw Gulch on the north boundary of the forest were found to be infected and producing sporophores. Here the disease had caused several trees to become so badly damaged that many were blown over. Again increment borings showed that small trees without fruiting bodies had already been infected.

GROSS ANATOMY OF FOMES IGNIARIUS

Considerable variations in the general appearance of fruiting bodies of Fomes igniarius have long been recognized, as is shown by the common recognition of the variety nigricans Fries., which has been considered by some as a distinct species.

Overholts (1915) gives the following differences between the typical Fomes igniarius and the variety nigricans.

F. igniarius: "Pileus convex or ungulate, 3-10 x 5-20 x 2-10 c.m., grayish black or black, rarely rimose with age; . . . the older layers conspicuously white-stuffed or incrustated, . . . setae present though sometimes rare." (Pl. III, figs. 2-3-4.)

Var. nigricans: "Pileus plane to convex, 3-10 x 3-15 x 2-7 c.m., black, sometimes shining black, the surface often cracking in both directions but not becoming roughly rimose, . . . tubes decidedly white incrustated; . . . the setae often abundant."

It usually is possible to recognize at a glance fruiting bodies from aspen (*P. tremuloides*). They are usually smaller than those from other hosts and the pore surface often is at a greater angle from the horizontal. (Pl. III, figs. 1-2.) The line of the tube layers does not curve upward at the margin so strongly as in *Fomes applanatus*. The top surface checks, but is seldom rimose, probably chiefly because the fruiting bodies seldom live long enough on aspen to attain large size. However, fruiting bodies with a rimose top are occasionally found on large aspen trees. The coloring of all specimens is fairly constant, the tube layer being argus brown except for the white incrustations or stuffings; the margin, sudan brown the first season and weathering through various grays to black; the pore surface, buff yellow at first, then becoming argus brown at maturity. (Pl. III, figs. 2-3-4.)

STAGES OF DECAY

In the earliest stages of decay the wood of *Populus tremuloides* appears to be hard and firm, the only evidence of attack, if any, being a slight to marked color change from the normal. This is known as the incipient or invasion stage. In some cases there is no indication of incipient decay. Such a hidden stage can be detected only by a microscopical or cultural diagnosis. This stage of decay is dangerous since it is easily overlooked. It is also mistaken for color markings. When the wood is used in this stage its durability and strength are greatly reduced, not to mention secondary decays which will inevitably follow. Boyce (1938) states that the fungus has not been found decaying timber in storage yards or in service.

The intermediate stage includes all degrees of coloration from straw to chocolate brown, but the wood is apparently still hard and firm. The final

stage includes all soft, punky wood irrespective of color. The wood is changed in appearance and structure and the tissues have been completely modified. The strength of the wood has been so reduced that it can be crumbled between the fingers or easily broken. The destruction may even go so far that the heartwood breaks down completely, leaving a large hollow space in the tree with only a relatively thin layer of sapwood to serve as support.

The disease of deciduous trees caused by the false-tinder fungus (Fomes igniarius) has been called the "white heart-rot". It is usually confined to the heartwood of the tree, including the trunk and larger branches, but it may also affect the sapwood. As a result of the action of the false-tinder fungus the heartwood is changed into a whitish, soft substance, which differs little in the different species of hosts. (Pl. IX, b.)

A tree attacked by the fungus shows no particular change in its general external appearance during the early stages of the disease; in fact, it is practically impossible to recognize a diseased tree until the fruiting bodies of the fungus form on the outside of the trunk. During the surveys made in the Gallatin National Forest only trees which were bearing sporophores were considered infected, but numerous increment borings were made to determine whether the disease was already in the tree. There was evidence of discoloration in nearly every tree, regardless of the age. During the later stages of the disease infected trees can be recognized by the presence of the fruiting bodies of the fungus, of which there may be from one to ten on a single tree, at or near wounds, branch stubs, or knot holes. (Pl. VIII, fig. 1.) When these fruiting bodies appear it may be taken for granted that the disease has progressed within the trunk in both directions for several feet from the point of infection.

The disease may infect trees at any time. In the final stages of the disease it brings about a complete destruction of the heartwood of the tree, so that it becomes weakened and liable to be broken off by windstorms, thus terminating the existence of the affected tree. Diseased trees may sometimes be recognized by the sound emitted when the trunk is pounded on the outside. While healthy trees give a vibrant sound, trees in the later stages of the disease give a more or less deadened sound. This is especially true where, owing to the destruction of the decayed wood by insects, holes have been formed. As a general rule, however, the only safe way to recognize a diseased tree is by the presence of the conk or fruiting bodies on the outside of the trunk.

When cut in two, the trunk of a tree affected with the white heart-rot presents an appearance as shown in Plate IX which represents both the early and late stage of the disease. It will be noticed that the center of the tree has been transformed into a white mass having an irregular outline. (Pl. IX, b.) This mass is definitely limited on the outside by one or more narrow black layers. (Pl. IX, c.) In some instances the wood is discolored outside of these black layers. One of the most characteristic features of the decay of the trunk is that the decayed wood is confined to one large central mass, differing in this respect from the pocket-like destruction brought about by several other wood-destroying fungi such as Fomes applanatus and Fomes fraxinophilus (L.) Gill.

Trees attacked by this fungus rarely become hollow, for after the wood has become thoroughly decayed by the fungus it remains in the interior as a whitish mass.

HOSTS

The white heart-rot fungus is probably one of the most widely distributed forms of wood-destroying fungi; it occurs on more different species of broadleaf trees than any other similar fungus. Among its hosts are to be found the most important timber trees of the deciduous forests of North America. Hubert (1931) points out that this disease is prevalent on broad leaf species and possibly one of the most common and also one of the most destructive fungi. As far as known to date, according to Schrenk and Spaulding, the fungus has been found on the following host species: beech (Fagus atropurpurea (Marsh.) Sudworth), aspen (Populus tremuloides Michx.), Bals of Gilead (P. balsamifera L.), red maple (Acer rubrum L.), silver maple (A. saccharinum L.), striped maple (A. pennsylvanicum L.), yellow birch (Betula lutea Michx.), butternut (Juglans cinerea L.), black walnut (Juglans nigra L.), oaks (Quercus spp.), apple (Pyrus malus L.), beech (Betula papyrifera Marsh.), ironwood (Ostrya virginiana K. Koch.), and hickory (Carya cordiformis K. Koch.).

In this country certain species are almost universally affected with the white heart-rot, irrespective of the region where they are found. An excellent example is the aspen. This tree has the widest range of any species of forest tree in North America and is subject to the disease. (Pl. I.)

Schrenk and Spaulding (1919) have pointed out that in New York and New England the beech has been found to be the most common host of this fungus. Wherever any considerable amount of beech timber is found, white heart-rot is prevalent. In some sections as many as 90 to 95 per cent of the beech trees of merchantable size have been found affected with this disease. Both

the butternut and the black walnut are frequently affected. The oaks are quite generally affected, but more especially those belonging to the black oak group.

A marked difference in susceptibility is occasionally found in certain species of the same genus. Buller (1909) has reported that the aspen is more seriously affected in western Canada than is the Balsam of Gilead (Populus balsamifera). Among the maples it has been found that the striped maple is quite generally attacked in those localities where the disease is present in the same vicinity upon others of its host species. According to Schrenk and Spaulding (1909) the silver maple seems to be nearly as susceptible as the striped maple, while the red maple and sugar maple are rather rarely affected. The yellow birch is even less frequently attacked than are the red or sugar maples.

HISTOLOGICAL STUDIES

Sections 20 microns in thickness, were cut from radial, tangential, and longitudinal surfaces from blocks which formed a continuous series extending from the central portion of the rotted area outward through the final, intermediate and incipient stages of decay into the sound wood. All blocks were asperated in 20% glycerine. Several of the blocks were asperated in a solution of 1 gram of chromic acid, 1.5 grams of acetic acid and 150 c.c. of water. This solution killed the mycelium and prevented any distortion. It is quite satisfactory for work of this nature.

Various methods of staining these sections were used:

(1) Asperating

Infected blocks (3/8 inch cubes) were boiled in water for 1/2 hour or more and soaked in glycerine alcohol (50 parts glycerine and 50 parts of 70% alcohol) for four hours.

(2)

- A. Excess water was drained from the sections, which were then flooded with Bismark brown (2% solution in 70% alcohol) for one or two minutes, according to density, thickness, and stage of decay.
- B. Excess stain was drained and the sections were washed with distilled water.
- C. Sections were flooded from 2 to 5 minutes with a solution of methyl violet made by mixing 4 parts of a saturated aqueous solution of methyl violet with 12 parts of distilled water.
- D. Excess stain was drained and the sections were washed in distilled water.
- E. Sections were mounted in water and examined for depth of staining. If violet color was faint C. and D. were repeated using full strength stain from 1/2 to 1 minute. If counterstain was faint A. was repeated.
- F. Sections were dehydrated in alcohol series, 5-10-20-30-50-70-90-100%
- G. Zylol was added to the sections, and they were mounted in balsam.

This stain was tried, but it did not give as good results as Erythrosin (1% solution in 95% alcohol) cleared in clove oil and mounted in balsam.

Sections 20 microns in thickness were stained in 1% aqueous safranine solution, washed with water and counterstained with anilin blue and Pyric acid (12-15 parts). This stain gave the best results when the mycelia were grown on agar (25 grams of agar, 20 grams of malt extract and 1000 c.c. of water.) All of these mycelia were killed in a solution of 1 gram of chromic acid, 1.5 c.c. acetic acid and 150 c.c. of water.

Mycelia were evident in all three stages of the decayed wood, but it was interesting to notice the marked difference in the size of the hyphae. The incipient stage produced hyphae which were varying in size. The smallest hypha observed being 1 micron in diameter. This stage of decay produces many mycelia, but only small hyphae are found. The hyphae branch and re-branch profusely. Numerous punctures were observed in the radial walls of the wood elements. This would indicate that the fungus produces cellulase and lignase which dissolve the cell wall, composed mostly of cellulose and lignin. Schmitz (1921) demonstrated the presence of the following enzymes: esterase, maltase, lactase, sucrase, raffinase, diastase, amylase, cellulase, hemicellulase, glucosidase, urease, rennet and catalase in Fomes igniarius.

Brom thymol blue was tried as a stain, but did not prove satisfactory.

Inward from the incipient stage the mycelium become more abundant, and the hyphae are larger in diameter. Tyloses are started in this stage and continues into the final stage of decay. In the vicinity of the black zone (Pl. IX, c.) the mycelium commonly ran horizontally in the medullary rays and vertical in the wood fibers. The difference in the size of the filaments may

be due to nutrition or growth habit. When grown on agar from spores the mycelium is composed of small hyphae at first, and do not exhibit clamp connections or septations, but in about two weeks the conditions are reversed.

Buller, (1931) in his study of Coprinus lagopus was able to follow the change of haploid hyphae. He found that as the hyphae branched in a wide angle manner it was evident from the disposition of the clamp connections on its branches that it was undergoing diploidisation from its older to its younger parts. This he proved by watching a single hypha. No clamp connections were present on the youngest branches, but each of the three older branches bore a single clamp connection. After watching the hypha in a Petri dish continuously for four hours and ten minutes he was able to observe the change. The hyphae grew along the surface of the agar and therefore did not dry up when exposed to the air. He observed that the young hyphae did not produce clamp connections, but as the hyphae grew older, and spread out the clamp connections became apparent.

In observing Peziza igniarius the young hyphae exhibited these same properties, but the age at which diploidisation took place was not determined. It was noticed, however, that young hyphae did not have septations, but after considerable branching and rebranching the clamp connections and septations were evident.

The presence of a mycelium disturbs the normal physiology of a tree, bringing about a weakened framework, increasing the mortality of crop-producing wood, and causing increased susceptibility to winter injury.

It is no doubt possible that tyloses in decayed or partially decayed aspen wood may influence penetration of wood preservatives. If tyloses

increases the resistance to preservatives, wood intended for treatment should be carefully chosen. This is especially true of railroad ties, or any aspen wood which is to be treated with a penetrating preservative.

There is also indications that the lack of water conduction in wood having such an abundance of tyloses has a direct contributory bearing on the physiological disturbances within the tree. Movement of liquids is curtailed.

In the final stage of decay the wood turns from light brown to black. During the change in color the hypha become more numerous and also larger.

CULTURAL CHARACTERISTICS

When grown on agar the fungus will be white at first, but will turn brown in about two weeks. (Pl. IV.) This is the color it will remain, and mycelium become leathery. Concentric growth rings are easily detected, being white at first and turning brown with age. Plate V shows mycelium of Fomes igniarius on Populus tremuloides after seventy-two days. The wood was carefully selected from a tree that showed no outward signs of infection, autoclaved for one and one-half hours and then inoculated with hyphae in a sterile culture room. During the period of seventy-two days 20 c.c. of distilled water was added by a sterile pipette. It will be noticed that the mycelia are covering the entire block, and that the color is mostly white, but is turning brown.

Plate VI shows the mycelium of Fomes igniarius on Populus balsamifera which was treated the same way. It is clearly evident that the fungus does not cover the entire block, but the color change is nearly the same.

This would indicate that Populus tremuloides is a better host to the fungus, and produces a heavier growth of mycelium.

Plate VII shows a block of Populus tremuloides which was autoclaved for one and one-half hours, inoculated with the mycelia of Fomes igniarius and left standing at room moisture and temperature for sixteen months and seven days. No water was added during this time, but the mycelium is still growing on the block of wood. This indicates that the mycelium can grow for a long period of time without a great deal of water. The brown color is evident, although not outstanding. Invasion lines of infection are not clear. Cotton was clamped around the top of the jar in order to allow for the exchange of gas and moisture. No contamination is evident.

When grown on agar the mycelium turns brown and after removing it from the agar it has a spongy texture. As they get older they have a tendency to dry and shrivel up, but still retain the same brown color, characteristic of the younger mycelium.

PRODUCTION OF METHYL SALICYLATE ODOR IN CULTURE

Fomes igniarius produces a methyl salicylate (wintergreen) odor when grown on agar. This odor is especially strong. Fritz (1925) using cultures of Fomes igniarius from Fagus americana, Sweet; Ulmus americana, Chapm.; Betula lutea, Michx.; Betula alba, L.; Acer saccharum, March.; Ostrya virginiana, K. Koch.; Populus grandidentata, Michx.; and Populus tremuloides, Michx. found that all produced a wintergreen odor on Czapek's synthetic agar, but she does not mention it on malt agar, which she also used. When cultures are grown in 150 c.c. flasks the odor will remain for a long time,

as compared to a short time when grown in a petri dish. Evaporation is less from the 150 c.c. flask, and no doubt should account for the longer presence of the odor.

SPORE PRODUCTION

Spores are produced at various times and will vary according to the elevation and location. Buller (1909) found that Fomes igniarius produced spores over a period of two months (July, August and the first of September) in Manitoba. The pilei which he observed were projecting from the trunks of Populus tremuloides in the woods along the Red River at Winnipeg. He placed microscope slides on platforms just below the pilei for the purpose of catching the spores immediately after their discharge. These slides were first put out on April 15, 1921. The hymenial tubes of the 1920 tube layer were open, but neither at that time nor subsequently did they discharge any spores. Possibly the tubes produced in one year are active for several years.

Buller (1931) further states that, "On May 27, the center of the fruit bodies showed a dark brown coating of the new hyphae which were to produce a new tube layer. By June 21 signs of the production of pore openings in the new growth were evident, but up to that time no spores had been discharged. Slides were not examined again until July 17, and at this time spores were being discharged in great numbers. Thus the exact date at which the (hymenon) of spore discharge began in 1921 was unfortunately not determined, but it must have been between June 21 and July 17. Probably it was about July 1."

"Spore discharge continued until the beginning of September. During the first of September only a few spores were liberated. The two fruit bodies observed therefore, had a spore discharge period in 1921 of about two months duration. It was observed that the spore discharge would vary, being heavier some days than other. Fewer spores were liberated on cooler or rainy periods."

Tests indicate that about the same number of spores are discharged during the twelve hour period (9:00 a.m. to 8:30 p.m.) as during the twelve hour night period (8:30 p.m. to 8:30 a.m.). Evidently here as other Polyporaceae and the Hymenomycetes generally, the production and liberation of spores from mature fruit bodies is not affected by light.

Buller (1931) also found that a rough count of the spores of this fungus deposited on a slide during a 24 hour period, August 2-3, 1921, gave a total of about 83,000 spores per square m.m. (about 100 spores per 1,200 square micron of slide in an average deposit, the deposit being one or two layers deep and practically covering portions of the slide). The medium sized fruit body which produced the spores from which this count was made was about 32 square c.m. in area. With favorable conditions for spore discharge, therefore, it probably liberated about 260,000,000 spores in 24 hours. There are about 1,800 hymenial tubes per square centimeter of each tube-layer. Each tube, therefore, may liberate about 4,600 spores per day.

From Buller's (1909) investigation it is evident that Fomes igniarius produces a new tube layer the first part of the summer, that spores are discharged for about two month duration, and a quiescent period follows in the autumn, winter and spring.

Verall (1934) working in Minnesota, found that the period of spore discharge was limited to two weeks (August 6-21) in 1932.

GENERAL DISCUSSION

Table I shows the number of trees which were bearing sporophores. (Pl. II, e.) This includes only the trees that produced fruiting bodies in the entire gulch within the boundary of the Gallatin National Forest. There were 346 trees growing on the south exposure of the West Divide in the Bridger District and 27 trees growing on the north exposure of the West Divide. This makes a total of 373 trees within the forest on the west side of the Bridger Mountains. Of the total number of trees, 18 were producing sporophores or .04 per cent. There were no doubt many more of these trees infected, but as yet were not producing fruiting bodies. From the table you will observe that one tree had 10 sporophores, and this tree was six inches in diameter. Evidently once a tree starts to produce fruiting bodies it can infect itself or surrounding trees because the size of these bodies varied greatly. Four of the eighteen trees which were producing fruiting bodies had been infected in the lenticels. Table I shows that .22 per cent of the infections had taken place in the lenticels, and the remainder were in old branch scars. Natural pruning of the trees makes each branch scar a possible source of infection. All of the trees in this canyon were within 100 yards of the creek bottom, and varied in diameter from one to fourteen inches.

TABLE I

Date Collected	Area	No. of Trees	No. of Sporophore Branches	Lenticels
May 3, 1941	Potter Gulch	1	6	6
"	"	1	1	1
"	"	1	1	1
"	"	1	2	2
"	"	1	2	2
"	"	1	4	4
"	"	1	3	3
"	"	1	1	1
"	"	1	1	1
"	"	1	2	2
"	"	1	10	10
"	"	1	2	2
"	"	1	2	2
"	"	1	5	5
"	"	1	1	1
"	"	1	1	1
"	"	1	1	1
Totals		18	47	42

Plate VIII, Figure 1 shows a sporophore where the young branch was produced. Infection no doubt took place at this point. This shows that infection can take place where branches are, and that the tree is not able to properly heal itself against possible places of invasion. From the number of spores which are liberated per sporophore it is evident that the fungus can infect many trees even if only a small percentage find a suitable host.

TABLE II

Date Collected	Area	No. of Trees	No. of Sporophore	Branches Lenticels
May 20, 1941	Pass Creek	1	8	8
"		1	7	7
"		1	1	1
"		1	3	3
"		1	1	1
Totals		5	20	20

Table II shows the number of trees bearing sporophores in Pass Creek. (Pl. II, c.) Again this includes only the trees within the National Forest. Of the 357 trees found in this creek bottom only 5 were producing sporophores or .01 per cent. All of the fruiting bodies were found on old branch scars. The infected trees produced on an average of 4 fruiting bodies per tree. One tree in this group had eight sporophores, but was eight inches in diameter as compared to Table I in which one tree six inches in diameter had 16. These trees were also confined to within 100 yards of the creek bottom, and varied from 1 to 16 inches in diameter. This canyon is on the west side of the Bridger Mountains and well toward the north end of the district. The infected trees were confined to within one hundred yards of the divide between Pass Creek on the west of the Bridger Mountains and the South Fork of Sixteen Mile Creek on the east. The elevation here would indicate that the wind has ample opportunity to disseminate the spores to the surrounding areas.

The amount of destruction caused by this fungus in the North American forests is beyond computation, because of both the wide occurrence of the

fungus and the large number of host species upon which it grows. The loss caused thereby differs considerably with the locality and the host species. The greatest losses are brought about in more or less definitely limited localities. There are districts which are badly affected with this disease, and others which are comparatively free from it. This fact may indicate that it should be possible to effectively prevent the destructive action of this fungus if we can ascertain the reasons for the freedom from this disease in certain areas.

Trees found on areas which are well watered or relatively close to a creek bottom are found to produce more sporophores. This may mean that a correlation exists between water and infection of the tree. Trees growing on areas a greater distance from creek bottoms and higher on the ridges are not found to be so badly infected. In view of the fact that Populus tremuloides does not produce a heavy pitch they do not have the advantages that other trees have to combat possible points of entrance. It is shown in Tables I and II that trees growing in a moist habitat are more heavily infected than trees growing in drier areas.

It is evident from Tables I and II that the majority of sporophores are found on branch scars. (Pl. IX.) From a theoretical point of view, every branch scar is a possible source of infection. It is, however, in most cases impossible to determine the exact mode of entry of the fungus. This is particularly true when the more advanced stages of decay are concerned, and when almost every branch scar is producing a fruiting body of Fomes ignarius. On older trees from one to ten fruiting bodies of this fungus on a single tree are not at all uncommon.

Field observations show that fire scars, branch scars, and wounds are possible sources of infection. Schmitz and Jackson (1927) found that fire scars were very important points of entrance of the fungus. They seldom found a tree of any age with fire scars that did not show the final stage of decay. Lenticels are also possible sources of infection as shown in Tables I and II.

Where game concentrate for the winter months such as along creek bottoms throughout the Yellowstone National Park, it was found that very young trees were infected with the fungus. This is caused, no doubt, by the fact that deer, moose, and elk browse on this tree. Then to further increase the possibility of infection they polish their antlers on the tree in the spring of the year and remove the bark, thus exposing it to infection. This is especially noticeable at Buffalo Horn Creek, where some of the first material was collected for this study in 1939. The trees at the game farm at Gardiner are also infected by the fungus. On the north end of the Bridger Mountains no game had concentrated, yet the trees were bearing sporophores in large numbers. This would indicate that the game is only an added source to possibilities of infection. From the increment borings that were taken it appears that infection takes place from a very early date and continues until the host is partially disentrigated. This means that no age class is evaded, all are subject to the fungus. Old trees with mature sporophores of Fomes ignarius are no doubt possible sources of infection to the younger trees. The old stumps are also found to bear fruiting bodies which means they can infect the young trees.

As aspen reproduce largely by means of suckers, the possibility of infection through the mother root needs consideration. After an aspen tree has been cut, the stump decays very rapidly and as heart-rot extends into the stump this possibility has been considered. Aspen may sprout from the stump, but this method of reproduction is comparatively unimportant as indicated by the work of Baker (1925). During their course of work in Minnesota Schmitz and Jackson (1927) found that in thirty stumps the decay did not extend into the root system. They also found there was no evidence to indicate that the decay caused by Fomes igniarius extends any appreciable distance out in the root system, or that the suckers are infected through the parent root of the old mother stump.

From the surveys made by the author in 1939, 1940 and 1941 it is apparent that Fomes igniarius is found throughout the entire Gallatin National Forest. (Pl. II.) From Hebgen Lake (Pl. II, j.) on the south end of the forest to Haw Gulch (Pl. II, a.) on the north fruiting sporophores were found, which is definite evidence that the fungus has covered the entire forest. The severity of infection is confined to the creek bottoms, and it is here that the trees (P. tremuloides) reach their best growth. Once the fungus gains entrance to the tree it will continue to reinfect the same tree and those which surround it. This is quite evident as shown by the size of the fruiting bodies. (Pl. III.) Small sporophores and large ones are commonly found on the same tree. It is quite possible that some size variation is due to nutrition, but marked differences are present. Is it possible for the same infection to have produced this large variety of fruiting bodies? No, because the fungus goes into the heart wood and then travels up and down in the tree. It does not come to the surface, except at the

point of entry, until the sapwood has been nearly destroyed. The fungus continues its activity after the host is dead, and thus is able to infect the surrounding area. Sporophores or fruiting bodies are not produced for several years after infection takes place. Their size indicates they occur where infection took place. The fungus destroys the center of the tree and produces a discoloration marked by concentric rings which vary in color from black to brown. It is nearly impossible to observe the infection in the incipient stage because no outward signs are present. Increment borings will show that the tree has been attacked, and that no age class is free from infection. It is apparent, however, that the older trees produce more sporophores and consequently produce less valuable wood. The fungus has broken down more of the heartwood.

Populus tremuloides is used for mine timbers, lumber, fence posts and numerous small uses in the State of Montana, as has been shown by the author earlier in this paper. Its aesthetic value is very hard to determine, but is extremely great as it is the most characteristic tree in this state. Its value to wild life is also hard to determine, but it is evident that game animals eat the young trees during the winter and spring months. Experimental plots on the game area in Yellowstone National Park have shown that elk eat the tree from the very small stage up to the time they are two or three inches in diameter. As yet it has not been determined if the tree is a necessary part of their diet. Eating of these trees may be due to lack of other food.

Ecologically the tree (P. tremuloides) is increasing in acreage each year and is further being assisted by unwise cutting and the injudicious use

of fire. This is especially true in the Gallatin National Forest of Montana. The author has observed that P. tremuloides is increasing in acreage throughout the forest. It is gaining most in moist areas. At the present time there are few extensive areas of aspen in the forest. Most of these large stands are confined to the moist sections. They disseminate their seed in May and June and quickly germinate in soil made fertile by fire. The seedlings grow rapidly in exposed sites. There are very few drainages at the present time on the entire Gallatin National Forest which do not have some stands of P. tremuloides in them. This means that with favorable conditions the tree can increase its acreage rapidly. It should eventually play an important part in watershed, aesthetic, lumbering and game management in this state. Unfortunately its use is little recognized and there is prejudice against the wood at the present time. If it is placed on a short rotation of 50 years it can be grown with some success. To prevent the trees from becoming infected will require care in that all wounds will need to be protected or painted with some disinfectant. This will prevent the fungus from attacking the tree.

SUMMARY

A study was made of the various stands of Populus tremuloides in the Gallatin National Forest of Montana showing the distribution of Fomes ignarius. The importance and progressive development of the heart-rot of Populus tremuloides caused by Fomes ignarius was studied with special reference to the possible factors predisposing its infection. Consideration was given to the possible effect of the browsing and other activities of game animals as contributory to infection by this fungus. The parasite was isolated and grown in pure cultures, and the characteristics of these cultures recorded.

The ecology of the host, Populus tremuloides, was also stressed.

CONCLUSION

1. The distribution of F. ignarius extends throughout the entire Gallatin National Forest of Montana.
2. The fungus is found most abundantly in the more moist parts of the stands of P. tremuloides.
3. Pure cultures of the fungus were found to be more prolific on P. tremuloides than on P. balsamifera.
4. On P. tremuloides the vegetative mycelium is able to grow under reduced moisture conditions.
5. The fungus hyphae in pure cultures are white at first and turn brown with age. This is true when the fungus is grown on sterile blocks of wood as in 3 above, and also when grown on nutrient agar.
6. The acreage of aspen is increasing in the Gallatin National Forest of Montana.

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DESCRIPTION OF PLATES

Plate I. This map shows the distribution of Populus tremuloides in the United States, and you will notice that it crosses the entire continent, being confined mostly to the hardwood area and the Pacific Coast region. The Great Plains area is only sparsely covered with this tree.

Plate II. This map shows the areas within the Gallatin National Forest that were infected and producing sporophores. From Hebgen Lake on the South of the forest to Haw Gulch on the North infected areas have been found.

Plate III. Figure 1 shows a sporophore of Fomes applanatus on beech, and figures 2, 3, and 4 show sporophores of Fomes igniarius. It will be noted on figure 3 that the sporophore has grown around a branch. A lichen is also present.

Plate IV. This was the concentric growth rings of the mycelium on agar. This culture is two weeks old. The white areas are the youngest and gradually turn brown with age.

Plate V. This was mycelium growing on Populus tremuloides for 72 days. The white mycelium are the youngest and the brown mycelium are the oldest. The entire block of wood is fully covered with the mycelium. Before the block of Populus tremuloides was inoculated with the mycelium it was autoclaved for one and one-half hours and allowed to cool. During the 72 day period 20 c.c. of distilled water were added by a sterile pipette.

Plate VI. This shows the mycelium growing on Populus balsamifera which was treated in exactly the same manner as Plate V. It is evident that fungus does not grow as well on this species. More wood can be seen and a smaller growth of the fungus.

Plate VII. This shows the growth of the fungus on a block of Populus tremuloides at the age of sixteen months and seven days. It was treated in the same manner as Plates V and VI except no water was added. The fungus is still growing on the wood, and from this it is evident that little moisture is required for the growth of the fungus. Cotton was placed over the top of the jar in order to allow for the exchange of moisture, temperature and gases.

Plate VIII. Figure 2 shows an old sporophore which has accumulated lime and gives it a whitish color. It will eventually become black in color. Figure 3 shows a young sporophore which is argus brown in color and very active. Figure 4 shows a sporophore which has both the argus brown color and the light color due to age.

Plate IX. On the left of this plate is the sporophore (a.) which apparently started its growth at an old branch scar and has then gone to the center of the tree. Dark colored lines (b.) show the invasion stage and that the sap wood (d.) is relatively free from any infection. The center of the tree has been turned to a whitish punky mass (c.). It is evident from this picture that the sporophore is produced on the outside of the tree and is connected directly to the heartwood. The fungus has extended its infection both up and down in the center of the tree.

Plate I



POPULUS TREMULOIDES MICHAUX

MAP 69

ASPEN

(Distribution of aspen is shown as one species, although dendrologists separate *Populus tremuloides* Michaux from *Populus tremuloides aurea* (Tidestrom) Donnell, the latter extending westward from Saskatchewan to the valley of the Yukon River and southward in the western part of the United States and Mexico.)

Plate II

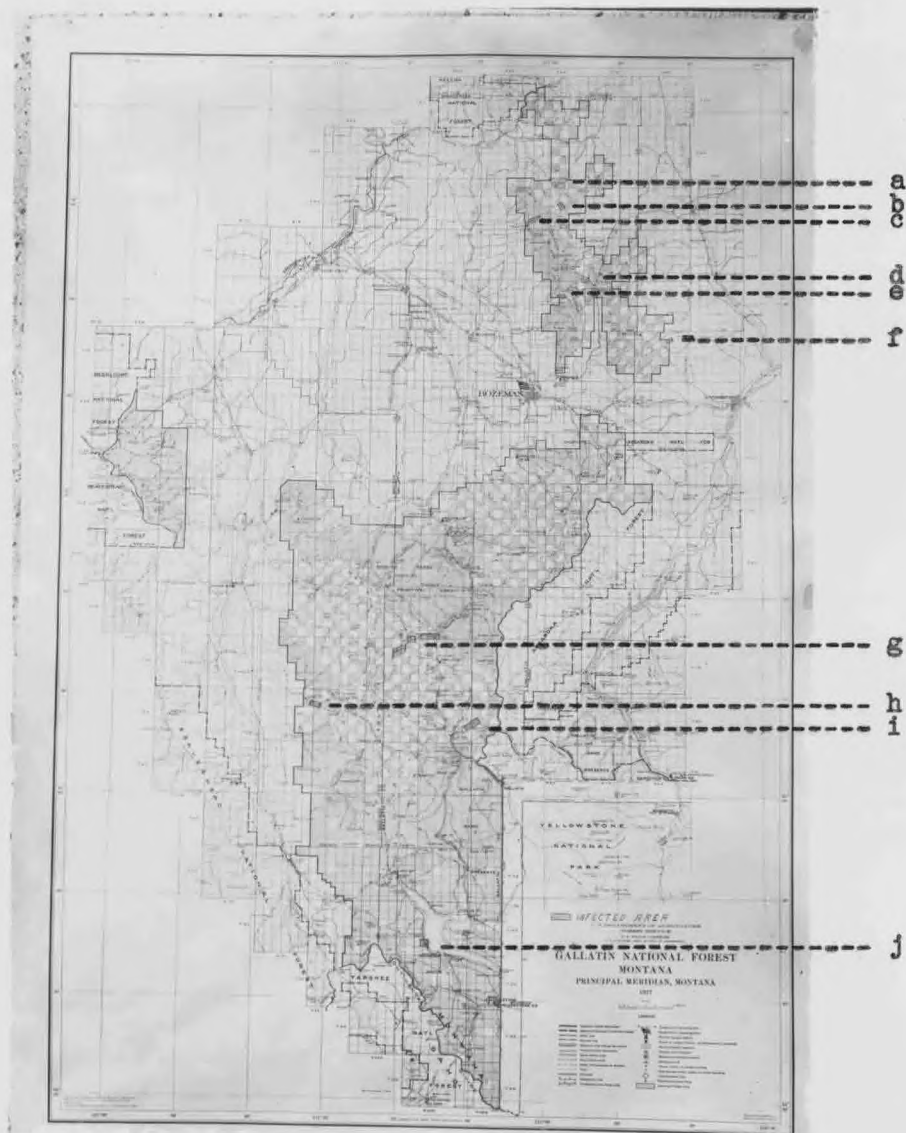


Plate III



Fig. 1.--F. applanatus Fries. on Beech.

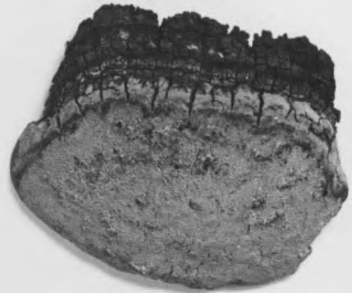


Fig. 2.--F. igniarius Fries.
on Aspen.



Fig. 3.--F. igniarius Fries. on Aspen.



Fig. 4.--F. igniarius Fries.
on Aspen.

Plate IV





Plate VI



Plate VII



Plate VIII



Fig. 1.



Fig. 2.--Oldest sporophores



Fig. 3.--Youngest sporophores



Fig. 4.

Plate IX



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The effect of Fomes
igniarius on Populus
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