Fomes Annosus—A Forest Pathogen[1]

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Summary

Fomes annosus (Fries) Cooke is a pathogenic fungus that decays roots and heartwood of living trees. The fungus is one of the most destructive of all the parasites encountered in coniferous plantations. Its distribution is widespread. Modern silvicultural practices have enhanced its spread and development.

The pathogen has a life cycle typical of most wood-inhabiting Hymenomycetes. Inoculation occurs when basidiospores of the fungus come in contact with freshly cut stump surfaces or other wounds. If environmental conditions are favourable, such as temperature and relative humidity, germination penetration and colonisation occurs and eventually the sexual stage, a perennial basidiocarp, develops on the stump or root surface. Basidiospores released from these fructifications are disseminated by wind and are eventually deposited by impaction or gravity. The disease cycle may be renewed by viable spores which alight on a suitable substrate, such as an exposed stump. Secondary disease cycles have not been studied in great detail but it has been shown that the conidial state, *Oedocephalum lineatum* Bakshi, is also capable of stump infection.

Disease losses occur as the fungus grows, via root contacts from colonised stumps to living trees, where it causes a root and butt decay. The merchantable volume of timber, therefore, is greatly reduced and the infected trees are liable to be wind-blown. An intensive research programme has been initiated to study the complexity and diversity of this ubiquitious pathogen. Chemical treatment of stumps has been the chief method of control used although biological control by stump inoculation with antagonistic micro-organisms has also been suggested. However, as with many diseases of forest trees, there is need for an economically feasible silvicultural control.

Name and Classification

Fomes annosus (Fries) Cooke is the fungus that causes a root and butt-rot of conifers throughout the temperate regions of the world.

1. This literature review was prepared in early 1973 while the author was a post graduate student at the University of Florida, U.S.A. Many of the references are of American origin but the general principles apply universally.
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It is a facultative parasite. In Europe, the disease is commonly called Conifer Heart Rot. Because of its ability to decay lignin material, it is classified as a white rot fungus. Other synonyms used are Annosus root rot, Fomes decay and Fomes heartrot.

Susceptible Plants

Probably all conifers and most dicotyledonous trees are in varying degree subject to infection (7). Koenigs (27) records that spruce, larch, cedar and hemlock are the most susceptible genera. Since 1960, in the U.S., the pathogen has been found associated with most species of pine, spruce, larch, fir, Douglas fir, hemlock, juniper, cedar, elm, ash, Rhododendron and mountain laurel (11, 12, 36). Moderately resistant pines are the red, Virginia and longleaf species. The most susceptible pines are shortleaf, loblolly and eastern white pine (34). In European forests both Norway spruce and European larch are highly suceptible species (7). Trees are predisposed to infection by drought, by insect defoliation, by thinning or by any other adverse climatic, edaphic or biotic factor (13). Though infection can occur on healthy vigorously growing trees, colonisation usually does not take place except when such trees are wounded during their dormant season. Antagonistic fungi such as *Trichoderma viride* and *Peniophora gigantea* can more readily colonise these trees and exclude *Fomes annosus* (8).

F. annosus more easily colonises suppressed and weakened trees. It has been suggested by several authors (9, 10, 29, 33) that these trees prove more susceptible because of their lower resin content. Large reserves of carbohydrates in the root are conducive to rapid colonisation by the fungus (34). Suppressed tree roots are rich in carbohydrate reserves and are more amenable to infection (30). A major site factor affecting susceptibility of trees to infection is the afforestation of arable soils. These sites are normally calcium enriched with a pH value greater than 5.0. It is agreed that such sites increase the susceptibility of trees to infection by *Fomes annosus* (5, 13, 17, 18, 20, 32, 48). In Western Ireland where most of the afforestation programme is concentrated in the acid oligotrophic peatlands, the incidence of *Fomes annosus* there is unknown. However, in the fertile valleys of the Southeast, *Fomes annosus* is the major forest pathogen and is responsible for most of the decay in susceptible conifers. In general, trees planted on sites of low organic matter where the soil is light and sandy are more likely to be infected (17, 18, 32). Resistance to infection increases in stands over 30 years old (32). The fact that so many different tree species are susceptible to attack by the fungus suggests that its physiological tolerance spectrum is very broad.

History and Geographical Distribution

Robert Hartig first described the pathogen in 1874 and later thoroughly investigated the disease in 1878 (22). Because it is now considered to be the cause of one of our most important diseases of conifers, research on the fungus and on the disease it causes has been increasing at a rapid rate during the past decade. In the U.S., *Fomes annosus* was first recognised as a potentially dangerous pathogen in 1954 when large areas of southern pine plantations in South Carolina and Georgia were attacked (35). Since then, numerous surveys have demonstrated how extensive and widespread the disease has become. Naturally regenerated forests are not adversely affected. It seems that the problem is man-made and a consequence of plantation-type forestry practice. The natural forest had its own inbuilt system of checks that counteracted the detrimental effects of potential pathogens such as *Fomes annosus*. However, economic practice dictated the planting of extensive areas of pure plantations. These forest monocultures, regularly thinned and mechanically harvested, provided ideal material for the spread and development of the formerly unimportant parasite.

Fomes annosus is worldwide in distribution but is more damaging and widespread in the temperate climatic zones with as yet only sporadic and minor occurrence in the subtropical and tropical climatic zones (7). On the American continent the pathogen is present throughout the softwood forests from Canada to the Gulf of Mexico and from Nova Scotia to the Pacific Coast (C.M.I. Map 271, ed. 2, 1968). The disease has reached epidemic proportions in sections of the South and is expected to increase in the Northwest as thinnings or other forms of selective cutting become more common in the second-growth stands.

Economic Importance

Financial data available about the economic impact of the pathogen are scarce and when available, are very subjective. In Sweden, for example, it is estimated that the annual loss due to stem decay in Norway spruce is $10m. In Denmark an investigation on the same species showed an annual reduction in profits of 32% and a reduction in capital value of 47%. In Germany it is estimated that a reduction in timber yield due to *Fomes annosus* amounts to 10–15% annually. In East Anglia, in England, losses due to the disease were calculated to be in the region of $3.50 per acre per annum. A pilot survey recently carried out in Ireland showed a loss of timber due to stem decay of 5%. It is conservatively estimated that the disease destroys a quarter million cubic metres of timber annually in the United States (1). Any true appraisal of the economic

importance of this disease is further complicated by the fact that *Fomes annosus* sometimes causes outright mortality, sometimes slows tree growth, and at other times acts as a heart rot leading to actual loss, of, or degrading of, merchantable volume. Suffice to say that the fungus causes very serious economic losses, some of which cannot even be quantified.

Symptoms

Foliar symptoms are not always evident although some species show thin and chlorotic crowns. In most conifers the earliest symptom of infection is a red or purple discolouration of the stem wood (4). The colour varies with the host. In the incipient stage, decayed wood is generally indicated by very small white pockets of rot. Minute black specks are visible as the decay progresses. The final state of the decayed wood varies from fibrous to slimy, according to the amount of moisture present. Resin flow may occur from the butt (4) and occasionally distress coning is obvious. Root decay is characterised by a yellow stringy rot. Trees with severe root rot are susceptible to windblow. Infection groups of trees or "*Fomes annosus* pockets" occur. These are dead trees where the pathogen has acted as a killing agent. Hodges (24) observed that tap roots and main vertical roots became infected more frequently than laterals. His observations indicate that tree species with long tap roots are more liable to be killed by *Fomes annosus* than to be subjected to stem decay. Other symptoms of the disease include reduction in growth increment and a degrade of wood quality.

Morphology, Taxonomy and Nomenclature of the Pathogen

The basidiocarp, sometimes called a carpophore or conk, is a perennial fructification. It is very irregular in shape. Often imbricate and confluent, it is sessile with a broad basal attachment and is at times resupinate. The upper surface is grey-brown to bay and it darkens with age. This surface is glabrescent and zonate and has a tuberculate rugose crust. The actively growing margin is white, thin and acute. The context is up to 1 cm thick, whitish and firm, corky to woody. The pore surface is white to yellowish and the irregular pores are circular to labyrinthoid. The basidiospores are ovoid to broadly ellipsoid. They are hyaline and thin-walled. Four basidiospores are borne on each short clavate basidium. Cystidia are absent. The hyphal system of *Fomes annosus* is dimitic, non-agglutinated with generative and skeletal hyphae. The former type are thin-walled, freely branching and simple septate whilst the latter are unbranched, are of unlimited growth are thick walled and have a narrow lumen. They are non-septate. Conidiophores produced in culture are

oedocephaloid and vertical. The conidia are unicellular, hyaline, ellipsoid to piriform and thick walled.

The pathogen is a Basidiomycete and is a member of the Polyporaceae. *Fomes annosus* is sometimes known as *Polyporus annosus* (Fr.) or as *Trametes radiciperda* (Hart.). Another synonym, *Fomitopsis annosus* (Fr.) Karst., is commonly used in Australia and New Zealand. The imperfect stage of the fungus is referred to as *Heterobasidion annosum* (Fr.) Bref. and as *Oedocephalum lineatum* Bakshi. (Fungi Imperfecti, Moniliales).

Proof of Pathogenicity

The ability of basidiospores to establish root disease fungi such as *Fomes annosus* or mycorrhizal fungi was shown to be possible (29, 37, 40). This was achieved by finding favourable substrates and using natural inoculation methods. Hüppel (25) reported in 1968 that he successfully inoculated both pine and spruce seedlings with conidia of *Fomes annosus* or *Heterobasidion annosum* and reproduced the disease syndrome. Thus the postulates demanded by Koch (in Garrett (19)) to complete a disease investigation were realised.

Life Cycle of the Pathogen

The life cycle of *Fomes annosus* is comparatively simple. It is generally accepted now that spores produced by the fungus are the primary source of inoculum for initial infection. Of the two spore types produced, basidiospores and conidia, the former are thought to be of much greater significance. It has been demonstrated that the inoculum potential of basidiospores is 60 times more effective than that of conidia (23). Conidial production is infrequently observed in nature (3). Basidiospores, however, are frequently and abundantly produced in the fructifications that are formed on the trunks of infected trees, normally at ground level (31).

These spores are very light and are quite effectively transported and disseminated by air movements. Viable spores have been found airborne 70 miles from the nearest possible source of production (38). Basidiospores can be leached through a sand column 40 cm. thick and still infect susceptible root tissue (24). In view of the vicissitudes these spores encounter in the soil and the thin nature of their cell wall, this evidence is remarkable. Jorgensen (26) showed that basidiospores isolated from soil were still viable after 2 months. Several investigations (42, 43, 44, 45, 46, 49) have attempted to correlate basidiospore release with season of the year, time of day and various other environmental parameters. Much of the evidence which has been presented is somewhat conflicting or inconclusive. It does appear, however, that basidiospores are produced in all

seasons and are released in largest numbers, in many areas, primarily in the spring and autumn.

Since *Fomes annosus* is not a vigorous microbial competitor (8, 37), the basidiospores are most efficient in initiating infection when they directly intercept interior root tissue or the heartwood of the lower stem of susceptible hosts. In coniferous plantations, stump surfaces of recently cut trees are excellent infection courts. Because these stump surfaces are also colonised by other microbes, several of which are more vigorous competitors than *Fomes annosus,* the length of susceptibility of these stumps is quite short. In the case of most species, susceptibility estimates have been less than 1 month. Cobb and Schmidt (10) have suggested that the susceptibility of eastern white pine stump surfaces may be only 1–3 days after felling. The significance of other wounds such as those resulting from pruning, extraction damage or animal feeding is generally thought to be less important than that of stump surfaces.

Following basidiospore germination on the stump, the haploid mycelium of the fungus grows through the heartwood into the root system. It grows at a variable rate which may approximate 20–40 centimetres per week (12, 21). Following anastomosis, the diploid mycelium grows between the bark and wood and eventually gives rise to the perennial basidiocarp. The mycelium grows down the colonised root causing death, disease and decay as it spreads. It transfers to live healthy roots of adjoining trees by root contact or grafting. It is incapable of growing freely in the forest soil (37). Viable conidia or basidiospores, however, may be leached to susceptible roots. These spores may be stimulated by the ninhydrin-positive root exudates of the rhizosphere and they then germinate, penetrate and colonise the suscept. The cycle is repeated.

Infection Biology and Physiology

The literature abounds with conflicting evidence about the interaction of the host/parasite relationship. Perhaps the greatest obstacle in evaluating the role of this pathogen or its suscept is the difficulty of experimentation under natural conditions. Most studies, therefore, have been and are made under artificial conditions of controlled laboratory experimentation, with emphasis on single reactions. It appears that in many cases, the experimental methods of the investigator have determined the outcome of the host/parasite relationship.

Rishbeth's work (37, 38, 39) has clarified many misconceptions about the infection biology of *Fomes annosus.* He also found that superficial growth of the pathogen was abundant on roots in alkaline soils but absent or feeble on more acid soils. Roots in the latter

soils were colonised by *Trichoderma viride* which was demonstrated to have a marked *in vitro* antibiotic effect on *Fomes annosus*. These observations and others formed the basis for studies on the biological control of the pathogen.

Physiologic specialisation of the fungus is unknown. No evidence for the existence of races nor for host-specific variation in decay ability has been found. Growth rates of 45 isolates from different parts of the world showed no significant difference (12). Optimum growth of the mycelium *in vitro* and on pine discs has been found to be as much as 6.8 mm/day at 24 °C (12, 21, 45, 47). Maximum infection by the fungus occurs when the mean monthly temperature is around 21 °C (14). Thermal inactivation period for conidia is 1½–2 hours at 45 °C (24). Basidiospores are inactivated at 40 °C for 2 hours (8, 41).

Infection of stump-tops occurs most frequently in the autumn. Spring is the second most vulnerable period. Where the climate in Summer is warmer, successful infection of most stumps by *Fomes annosus* does not occur because of the high stump-top temperatures (6, 8, 14, 15, 16, 41, 50). Once the pathogen is established it can survive for a relatively long period during the decomposition of woody material in the soil (28). Rishbeth found that *Fomes annosus* could survive in infected root systems for as long as 30 years (37).

Fomes annosus is classified as a white rot fungus; movement through the stump and in the roots involves decay of both lignin and cellulose. The mechanism of decay by the pathogen is thought to be via production of typical extracellular enzymes of the white rot group. Studies of the fungus *in vitro* by Bassett et al. (2) have revealed, however, the presence of fomannosin. This compound is a sesquiterpene which when applied artificially to host roots will produce symptoms similar to those in natural infections. Demonstration of this material in diseased tissue would support the suggestion that it is a fungal toxin.

Control of the Disease

Control measures are aimed at prevention rather than cure, as diseased stumps may remain as sources of infection for up to 30 years. Prompt treatment of thinned stumps by painting with a substance inhibitory to *Fomes annosus* has been the practice in most countries since 1950. The original stump protectant used was creosote but in field use this was variable in performance and liable to breakdown. Since then various chemicals such as sodium nitrite, urea, powdered borax, ammonium sulphamate and others have been used with greater success (38). The rationale behind this stump treatment policy was advanced by Rishbeth and his associates (28,

37, 38). They had shown that the still-living tissues of the stumps were strongly selective for the pathogen *Fomes annosus,* and for a small number of harmless saprophytes such as *Peniophora gigantea.* Rishbeth, therefore, sought for chemical treatments that would destroy this dangerous selectivity of the stump tissues for *Fomes annosus* and permit colonisation by harmless saprophytes instead. Any treatment that kills the living host tissues is likely to promote this result, but the most promising chemicals were found to be disodium octaborate, ammonium sulphamate and urea. All three treatments favoured colonisation of the stump surface by mould fungi in place of the Basidiomycetes colonising untreated stumps. Ammonium sulphamate and urea encouraged a particularly vigorous growth of moulds, partly perhaps through their nitrogen content.

Biological control of the pathogen by stump inoculation with spores of *Peniophora gigantea* has been successful with pine species (39). This saprophyte—the candle-wax fungus—is an indigenous species in Britain and Ireland. It is the most effective natural competitor of *Fomes annosus* in pine stump colonisation in East Anglian plantations (37, 38, 39). Rishbeth has perfected a technique for producing lyophilised suspensions of *P. gigantea* oidia. These suspensions are placed in water and the resultant liquid is then applied to the freshly cut pine stumps. Chemical treatment of stumps other than pine is still practiced in Britain and Ireland. Sodium nitrite is commonly used except in water-catchment areas where urea is substituted.

Silvicultural means of control include (a) the avoidance of thinning—especially in high hazard sites. Trees may be planted at wider spacings to avoid thinning and to reduce root contact. (b) If thinning is necessary it should be done at a time unfavourable to the fungus—i.e., in warm seasons when stump-top temperatures may inactive the pathogen (8, 14, 26, 41). (c) Stump removal has been resorted to in an effort to decrease the amount of inoculum available. This method, is occasionally used on high value amenity sites. (d) The use of mixed stands with a variety of species and the planting of resistant species such as some hardwoods are other control measures often employed. (e) Phytosanitary controls involve the avoidance of intercontinental and inter-regional spread by excluding shipments of logs and unseasoned wood containing incipient decay.

It is obvious from the above review that further studies on the biology of the fungus and the etiology of the disease are necessary. This is especially true of studies on factors affecting host predisposition, fungal antagonism and physiology. Such studies could lead to some form of control by imparting resistance to the host. This could be accomplished either by plant breeding or by culturally

modifying the environment the tree is growing in so as to take advantage of the pathogen's natural antagonists.

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