History of *Heterobasidion annosum* in Western United States[1]

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Abstract: H. annosum was first discovered as a root pathogen of pine in western United States by E. P. Meinecke in 1909. Other early researchers reported it as a root and butt decay of nonresinous conifers in the west. Olson demonstrated its pathogenicity to western conifers and Wagener and Cave described its occurrence and role in the eastside pine forests. In the last 20 years pathologists have become more aware of H. annosum's role as a root pathogen of true fir. The adverse effects of annosus root disease in the Institute of Forest Genetics and Yosemite National Park have helped to call attention to this disease.

A history of Heterobasidion annosum is a history of Fomes annosus until 1968, when the fungal root pathogen's name was changed (Pegler and Waterston 1968). The reader must keep in mind that F. annosus (which is used in this paper as in the original literature) currently is H. annosum. One of the first finds of F. annosus in western United States was made in Monterey, California by E. P. Meinecke in 1909, about 80 years ago. In an unpublished office report, Meinecke described the disease as he observed it on Monterey pine. In his field notes he first described the pathogen as a Trametes sp. but later concluded that it was F. annosus, which was very well known in Europe where he (Meinecke) had studied. In light of the great impact this root disease has on our forest recreation areas today, it is interesting that he found this disease in a grove of Monterey pine which had been converted into a park and in which considerable tree mortality had occurred. In his manual, Forest Tree Diseases Common to California and Nevada, (Meinecke 1914), he states "This fungus (Fomes annosus--pronounced fomeez) is one of the most dangerous forest fungi in Europe and is also destructive in the eastern United States. Although at the present, apparently somewhat rare in California it may prove to be more prevalent." His prediction has proven to be correct.

The history of F. annosus in the western United States is closely related to the evolution of forestry during its developmental stages in the west, and how forestry influenced the interest and research in forest pathology. During the early stages when old-growth forests were being harvested, foresters and lumbermen were not concerned about scattered and occasional tree mortality, but rather were concerned about decays in old growth trees and how much decay was likely to be present in various species and stand types. This information was the basis for estimation of the volumes and values of old-growth timber stands and which stands should be entered first. This was an interesting period of research in the western United States. It was largely a period of descriptive research; large old-growth trees were dissected and their external and internal features were examined to determine the amount and position of decay in the tree and the resulting amount of cull, the causes of the decay (the species of wood rotting fungi), the infection courts or methods of fungal entrance into the tree, and the external indicators of decay in the standing tree. This information was used to develop statistical tables to indicate the probable amount of cull based on the tree species, its age, location, and external features. Forest pathologists spent whole summers out in the forest conducting these old-growth dissections. Willis Wagener, a young researcher in this period, described this research several decades later to the next generation of forest pathologists (personal communication).

> "We would leave San Francisco by train in May for Quincy, a small logging town at the juncture of the northern Sierra Nevada and the southern Cascade Mountains. From here we would travel by horseback to the study area and set up a long term summer camp. We worked a six-day week, dissecting and describing old-growth trees and the decay and cull they contained. Sundays were set aside as a rest day, when we went over our field notes and corrected any errors they contained. In September, some 5 to 6 months later, we returned to San Francisco via horseback and train. The winters were spent analyzing our data, writing office reports and preparing for the next field season."

It was these kinds of research efforts from 1900 to 1940 by notable forest pathologists, such as Boyce(1932), Weir and Hubert(1919), and Englerth(1942), that first described F. annosus as a fungus causing a root and butt rot in conifers in the western United States. Even in these reports, except for western hemlock, the incidence

[1]Presented at the Symposium on Research and Management of Annosus Root Disease in Western North America, April 18-21, 1989, Monterey, Calif.

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of F. annosus in nonresinous conifers was reported to be rather low. This is somewhat surprising in light of the high incidence of F. annosus found in both old-growth and second-growth true fir today. Years later, toward the end of his career, Wagener wrote an office memo to another western pathologist, "My first work was in 1917 as a member of Meinecke's field crew working on the dissection studies in virgin white fir on the Sierra N.F. Working with Meinecke and Boyce, I had an unusual opportunity to become acquainted with some of the misconceptions and difficulties which helped to shape the conclusions of that period. In those days no one thought of confirming the identity of decays through culturing. --no guides, such as Miss Nobles were available. Practically all the decay in true fir found originating from fire wounds was put down in the field notes as 'atypical E.t.', although I was to learn in later years that probably none of it was E.t." (E.t. is an abbreviation for Echinodontium tinctorium, a wood rooting fungus.) I imagine that most present day forest pathologists would suspect that a good deal of the atypical butt decay behind those fire scars was in fact caused by F. annosus.

After World War II we were still concerned about decay and cull in old-growth stands, and these research efforts continued and were reported by Wright and Isaac(1956), Kimmey(1964), and Kimmey and Bynum(1961) in the United States and Buckland and others(1944) in British Columbia. During this period there were more reports of F. annosus causing a frequent root and butt rot of fir and hemlock and of its role as an invader of fire scars and logging wounds.

It is interesting, but not surprising, that during this period F. annosus was not recognized to be an important cause of tree mortality in these nonresinous old-growth conifers. Wagener and Cave(1946) refer to the saprophytic life style of F. annosus in fir and hemlock.

In 1934, some 2 decades after Meinecke found F. annosus in Monterey, K.A. Salman, a forest entomologist, reported some unusual mortality of Jeffrey pine in Lassen County to E. Wright, forest pathologist with the Bureau of Plant Industry in San Francisco. Salman, who was studying bark beetle-caused tree mortality in the eastside pine type, had found some tree mortality which was not caused by bark beetles and in which the roots appeared to be dying. Wright visited these trees with Salman that year and made some root isolations from three diseased trees, measuring from 14 to 16 inches in diameter. He consistently isolated a single fungus, which later proved to be F. annosus, from these trees. He started some pathogenicity testing with this isolate, but was forced to discontinue those tests when he was transferred out of the state.

Later, in 1937, the problem was brought to the attention of Willis Wagener, who interested a young plant pathology student, Alver Olson, in the problem. Olson spent 3 years studying this disease in the greenhouse and in the field. In his paper on this disease Olson(1941) states, "The disease thus far has been found only at Lasco. The pine regions of California have been extensively inspected by Wagener and Salman, who state that they have not seen the disease elsewhere." Olson, in his first visit to Lasco in May of 1937, made the following observations. The area in which the mortality was occurring had been logged from 7 to 18 years earlier, and the soils were well drained soils of volcanic origin. The disease was found on the roots of only Jeffrey and ponderosa pines. The dead and diseased trees varied from 5 to 17 years old, and occurred in localized centers that were always observed to be in the vicinity of an old stump. The distance from the dead tree to the stump varied from touching to 19 ft. Diseased trees may be found on one or more sides of the stump, or they may completely surround it. Trees closest to the stump were usually affected first. Both ponderosa and Jeffrey pine stumps were involved. In later observations, Olson found that the tree mortality most commonly occurred during the onset of warm weather in early May and late June. Affected trees often exhibited yellowish-white pitch exudates on the surface of diseased roots. These diseased roots were always found to be in contact with an old dead root of the neighboring stump or with a diseased root from an adjacent diseased tree. In most cases these roots were in simple contact, but on occasion the contact involved a more intimate overgrowth of one root over its neighbor's root. Small lesions were found on the infected root where it came in contact with the initially infected root. Although only one root was infected initially, the entire root system was invaded by the time the tree died. This is an accurate description of this disease in pine as it is described today, some 50 years later.

Olson(1941) isolated species of Cunninghamella, Penicillium, and Pythium from the diseased roots. He recognized Pythium as the only known pathogen among the fungi he had isolated and made a series of pathogenicity tests using isolates of this fungus obtained from the roots of diseased pines. He was unable to reproduce the disease or to recover the Pythium from the inoculated roots and came to the conclusion that Pythium was not the cause of the disease. He returned to Lasco in the summer and fall of 1938 and made numerous isolations from widely scattered infection centers. Cunninghamella was the only fungus consistently isolated from over 100 diseased trees. He isolated this fungus from cambial regions, the xylem, and the advancing margins of the pitch infiltrations of affected roots. He remembered Wright's similar experience of consistently isolating one fungus, and sent an isolate of Cunninghamella to him. Wright responded that this was indeed the same fungus that he had isolated.

In 1939, Olson made several attempts to inoculate 1-year-old pine seedlings with Cunninghamella in the greenhouse, but for one

reason or another was unsuccessful in reproducing the disease. In May of 1939 Olson(1941), using artificially infested root pieces of Jeffrey and ponderosa pine, inoculated Jeffrey pines in the field by placing these root pieces adjacent to live roots of naturally established trees. In November of that year he examined the inoculations and found that all 10 of the inoculated Jeffrey pines had typical symptoms and he was able to re-isolate the fungus from these inoculated roots. In February 1940, Olson(1941) inoculated the tap roots of 2.5-year-old Jeffrey pine seedlings in the greenhouse with wheat grains infested with Cunninghamella, and this time was able to reproduce the disease. Olson(1941) wrote, "The production of the typical symptoms of pitch infiltration, and the recovery of Cunninghamell from the inoculated roots establishes this fungus as the organism causing the root disease" and "These experiments prove that the disease can be spread by root contact." Olson included other conifers (white fir, sugar pine, and incense cedar) in the inoculation trials but was unable to infect them with his isolates.

Still, neither Olson nor his major professors were aware that this pathogen, Cunninghamella, which Olson was working with, was F. annosus, and Olson, having seen only the asexual fruiting stages of this fungus, was under the impression that he had discovered a new root pathogen and disease. Thus, he described a new species of Cunninghamella and named it C. meineckella, unaware that he was mistakenly renaming the fungus after the person who first discovered this same fungus in its perfect stage in California some 32 years earlier. It was both ironic that the fungus should be mistakenly named after the person who had first found and correctly identified it years earlier and sad that Olson is now better remembered for his taxonomic mistake, than for his valuable contributions to forest pathology. Olson came so close to uncovering the role of the cut stump as the primary infection site that initiates the infection center, that one cannot help but wonder what might have happened if he had not gotten discouraged by his taxonomic mistake and had continued his research on this disease. Olson became a professional photographer and opened a store in Burney, not far from Lasco, where he had done his forest pathology work.

In May 1941, just a month after Olson's paper (1941) on annosus root disease was accepted for publication in Phytopathology, an unpublished office report was written by Donald De Leon, entomologist for the Department of Entomology and Plant Quarantine, describing a root fungus which appeared to be contributing to the dying of many pines marked for treatment in a bark beetle control program on Laguna Mountain in the Cleveland National Forest. These dying trees showed no evidence of bark beetle attack, but they did have a fungus mycelium which appeared to be killing the cambium under the bark at the root collar. Willis Wagener and De Leon made a joint examination and found that F. annosus and Armillaria mellea were active in these stands and were responsible for much of the Jeffrey pine mortality (Wagener and Cave 1946). It is interesting that 38 years later Wood and others(1979), in a Region 5 Forest Pest Management Evaluation reported that F. annosus was responsible for 48 percent of the high level of pine mortality on Laguna Mountain.

Wagener and Cave(1946) made some interesting comments in their paper which give an indication of the level of knowledge at that time. In this paper they state:

> "Prior to these discoveries (Olson's and De Leon's) fruit bodies of this fungus had been collected at a number of places in California, but almost entirely in connection with heart rot or from decayed stumps where the fungus had presumably developed as a saprophyte after the trees had been cut."... "In Europe, as already noted, the fungus has long been known for its desructiveness [sic], especially in pure coniferous plantations, but in North America, where it is widespread as a saprophyte on dead wood or as a butt rot of older conifers, it has been regarded as seldom attacking live parts of trees."... "Recent evidence indicates that in white fir (Abies concolor [Good. and Glen.] Hoppes) and in red fir (A. magnifica A. Murr) in California the fungus is also much more prevalent than previously supposed, producing a butt and root rot in these species but apparently seldom killing them through the killing of the bark and cambium at the base and roots as in pine. Englerth has found that it causes a prevalent butt rot of western hemlock (Tsuga heterophylla [Raf.] Sarg.) in western Oregon and Washington."

From these comments it appears that the western forest pathologists in the 1940's were as yet unaware of the role of the cut stump in becoming infected and starting an infection center in pines, although they noted the frequent association of this disease with stumps. They were aware of the frequent association of this fungus with true firs and hemlock, but appeared to be unaware of its pathogenicity to true firs. The forest pathologists had by then identified many areas in the eastside pine type forest as areas in which the disease was present, particularly the Lassen country and the mountains of southern California. They noted that the disease occurred more frequently on the light, friable, and sandy soils and less frequently on the heavier soils. They found that the soils harboring F. annosus were less acidic than most western forest soils, with pH's from 5.7 to 6.7. More research on these soil characteristics may prove useful in rating the hazard of sites for annosus root disease in the future. Wagener and Caves's paper also extends the pine host range to include sugar and Coulter pines.

Wagner and Cave (1946) state, "Killing of the bark and cambium of attacked trees by the fungus ordinarily extends little above the ground

level... The balance of the trunk is usually invaded by bark- and wood-boring beetles before fading of the foliage occurs and thereafter the tree appears superficially no different from one killed primarily by bark beetles. This is one of the main reasons why the importance of this disease went unrecognized for so long in our western pine stands and why killing by this disease in the past was commonly charged to bark beetles." This important relationship between root diseases and bark beetles was re-emphasized and expanded by Cobb and others (1974) and Ferrell and Smith (1976).

Wagener and Cave (1946) further describe some symptoms they found helpful in diagnosing this disease, which to my knowledge are no longer used by present-day pathologists in diagnosing this disease. They are:

1. The bark at the root collar of infected and recently killed trees separates easily from the wood.
2. The separate surfaces of the infected inner bark of the root and root crown are usually a characteristic light brown to russet with finely penciled white streaks. This pattern of coloration is quite distinct for the disease in pine and it is readily recognized once one has become familiar with it.
3. A thin weft of whitish mycelium is also usually visible between the wood and bark of infected roots and root crown.
4. Thin partial felts of whitish to light buff mycelium are also found between the bark scales of infected roots.
5. The red turpentine beetle avoids making galleries in bark areas invaded by F. annosus.

It might be well to investigate the reliability of using these symptoms to diagnose annosus root disease in the future. I have found them to be reliable indicators of annosus root disease. Repeated culturing of specimens with these signs and symptoms will allow investigators to develop confidence in using this system to diagnose for F. annosus.

Lastly, Wagener and Cave (1946) state, "The common means of establishment of new centers in pine stands, and the reasons for apparent greater virulence of this fungus in California as compared to other parts of the United States are not yet known." and "A full appraisal of the status of the fungus as a killing agent in western pine stands has not yet been made. It is expected to increase in importance in the future."

Most of the forest pathology research on F. annosus between the mid 1940's and the 1950's was in reference to this fungus as a root and butt rot in nonresinous conifers. Englerth and Isaac (1944) reported that in the Pacific Northwest F. annosus commonly enters western hemlock through logging wounds. An article by Rhoads and Wright (1946) states that F. annosus is more commonly a wound pathogen than a root parasite of western hemlock in western Oregon and Washington. In a Forest Pest Leaflet Kimmey and Bynum (1965) summarize the 1950's work done with red and white firs. They state that white rots cause about four-fifths of the decay loss in true fir and that F. annosus was the second most important cause of white rot. In this period, Wright and Issac (1956) also found this fungus to be the most important and frequent decay fungus in hemlock and true firs in Oregon and Washington and reported that wounds on these infected trees were a common infection court of this fungus. It is unclear whether these forest pathologists were aware of the pathogenic effects of this fungus further down in the roots of these nonresinous conifers.

In the mid-1950's an important research finding by Rhishbeth (1950,1951) in East Anglia revealed that the initial entry of F. annosus into pine stands usually was through a freshly cut pine stump. These stumps were infected by spores of F. annosus which germinated and produced hyphae that colonized the stump and its root system. And then, as observed by Olson (1941) and other western forest pathologists, the fungus spread to adjacent living conifers via root contacts. This vital piece of information enabled the forest pathologist to completely describe the disease cycle and to explain heretofore puzzling observations.

In the 1960's there was an increased interest and awareness of F. annosus in western United States and western Canada. Some interesting observations were made and some important research information was obtained during this period. Several factors were responsible for this increased awareness. More forest pathologists had been employed in the west at this time. Some of these scientists had obtained their academic training in the east and in Europe where there was greater recognition of F. annosus as a forest problem. In the 1950's, in response to the post-World War II housing boom, logging in the western National Forests had greatly increased, thus increasing the opportunity for stump infection, which characteristically started to appear in the affected stands in the 1960's, about 10 years after logging (Bega and Smith 1966). Interest in the health and productivity of second-growth forests greatly increased as the supply of available old-growth forests decreased. Certain specific occurrences of F. annosus, such as its appearance in the Institute of Forest Genetics (Bega 1962) and in Yosemite National Park (Parmeter and others 1978), brought this disease to the attention of both foresters and forest pathologists. The predecessor of what has become Forest Pest Management was formed in the Regional Offices of the Forest Service around the country, and it was staffed with trained forest pathologists, who recognized the importance of F. annosus and brought it to the attention of both the forest manager and their fellow forest pathologists. There were also old-timers like Willis Wagener who had maintained an interest in this disease and who were willing and able to impart their experience and knowledge to the new generation of forest pathologists.

Bega (1962) reported the effects of annosus root disease in the arboretum of the Institute of Forest Genetics at Placerville, California. This report was noteworthy because it publicized the susceptibility of a large number of pine species, including numerous western pines, which were attacked and killed by this fungus. The attack by F. annosus was extended (1951 to 1962) and tree mortality was extremely high. Because this was a planted stand, it may have represented what could be expected in future plantations with frequent stand entries and high levels of management activities. Bega concluded his report with the statement "... as virgin timber diminishes with cutting in western United States, and plantation forestry becomes more prevalent, the importance of Fomes annosus will increase rather than decrease." Because of the high value of this collection of pines, new and radical attempts were made to control the disease. The infected trees were identified, the infested area delimited, the borders of the infection centers were trenched and all roots removed, and the infested areas inside the trenches fumigated with methyl bromide and tarped. Periodically, the boundaries (the original boundary trenches were filled back in after the roots had been removed) of the infested area were fumigated with carbon bisulfide to keep tree roots from growing across this root-free area and into the fumigated areas. A few years later the fumigated areas were replanted with pines. This control effort was partially successful. It did successfully eradicate the pathogen from the fumigated areas, but because accurate identification of the limits of the infection centers was not possible, some infested areas external to the boundaries remained unidentified and were not fumigated. The pathogen continued to spread from these areas radially outward into the plantation.

In 1967 Miller and Bega in an office memorandum reported their finding of F. annosus in fallen trees near recreation facilities in Yosemite National Park. Later, as a direct result of tree failures in the winter storms in 1969 and 1971, which resulted in two deaths and extensive property damage, the Park Service requested a joint Forest Service-University of California evaluation of the tree failures in developed sites in Yosemite Valley. Again root disease, caused by F. annosus, was found to be the major factor in predisposing the fallen trees to failure. In 1971, Felix, working with Parmeter (Parmeter and others 1978), identified 67 F. annosus infection centers in which over 1,100 trees had died within the developed recreation areas of the valley. The intensity of infection and the frequency of tree failure resulting in deaths and property damage in Yosemite vividly demonstrated the potential impacts of this root disease in the many recreation sites in California. Partially as a result of these experiences, the Forest Service now requires all freshly cut conifer stumps in forest recreation areas to be treated with borax to prevent stump invasion by F. annosus.

Up to this time western forest pathologists had been concerned about F. annosus as causing a root disease in pine and recognized the fungus as causing a butt and root decay in true firs and hemlock (Wallis and Reynolds 1970). Nelson (1963) reported on his investigations on the causes of progressive crown decline leading to death in subalpine fir. He noted that branch flagging was, in some cases but not always, associated with branch cankers; that flagged firs commonly occurred in groups with one to several dead trees toward the center of the group, and trees in various stages of flagging at the outer margins of the groups. He examined the roots of trees in various stages of crown decline and found a direct correlation between the amount of branch flagging and the percentage of rotten (nonfunctional) roots. F. annosus was the fungus most commonly isolated from the decayed roots. These were among the first research results that suggested F. annosus was also the cause of a slower, less dramatic death of true firs and not just the cause of a butt rot.

In the early 1970's, as many of the true firs (which had been released in the earlier pine high-grading harvests of the mixed conifer and eastside pine types) were approaching commercial size, an unexplained crown decline and tree death of pole-sized and larger white fir was observed. Investigations by several forest pathologists have yielded evidence that annosus root disease is a major factor causing this-crown decline and eventual death of the tree. Results of surveys by Parmeter and others (personal communication) show that annosus root disease is so common in true fir that it approaches being an epidemic and that it may become more of a problem in true fir forest management than it will be in pine forest management. Surveys by Forest Service, Forest Pest Management forest pathologists in California and southern Oregon show that F. annosus is a major cause of true fir mortality that until recently went unrecognized.

In the 1970's, pathologists in the west began to see the need for control of annosus root disease in the eastside-pine-type forests and in forest recreation areas. By now the work of Driver (1963) and associates in southern United States had shown that stump infection could be prevented rather cheaply and effectively with a light dusting of the freshly cut stump surface with dry powdered borax. Graham (1971) tested the effectiveness of borax in the west and found that it prevented infection of ponderosa and Jeffrey pine stumps in California. Because of an increased awareness of annosus root disease in true fir and the presence of this species in a large number of recreation areas, we saw the need to test the effectiveness of borax in preventing infection of the surface of freshly cut true fir stumps. Smith (1970) showed that borax also effectively blocks stump infection of true firs. Still, however, there is concern that F. annosus may enter true fir trees and stumps via their roots and that stump surface treatment with borax

may not be completely successful in keeping this fungus out of true fir stands.

The history of H. annosum as prepared for this symposium is really the recorded history of the knowledge we had at various periods in the past of this fungus and the disease it causes. This is not to be confused with the real occurrence and role that H. annosum has played in past western forests. We can only guess and estimate what that might have been. We will never know more about the past than that which is written and this we must view with some question. Even our own recollections of past experiences and thoughts are clouded by our currently held views. This being the case, the readers of this history of H. annosum are obligated to take the parts of this history and their own experiences and formulate their own views of the true role of H. annosum in our past western forests.

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