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Chronicles of *Fibroporia radiculosa* (= *Antrodia radiculosa*) TFFH 294

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Abstract

The brown-rot fungus, *Fibroporia radiculosa*, has been included in numerous research studies because many isolates of this fungus demonstrate an unusually high tolerance to copper. This fungus has undergone several recognized changes in taxonomic nomenclature, and through DNA technology, scientists have correctly identified isolates that had been misidentified microscopically. *Fibroporia radiculosa* is not uncommon. In fact, the isolation and prevalence of *Fibroporia radiculosa* has been documented by mycologists since the 1930s, but the mechanism of copper tolerance remains a mystery. Here, we look at the history of research involving *Fibroporia radiculosa* and trace the changes in taxonomic nomenclature.

Keywords: *Fibroporia radiculosa, Antrodia radiculosa,* TFFH 294, taxonomic nomenclature

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Cover Caption: *Fibroporia radiculosa* growing on treated wood in the Harrison Experimental Forest in Mississippi and growing on culture medium in the laboratory, Forest Products Laboratory.

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Contents

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History

The Forest Products Laboratory (FPL) has played an important role in evaluating field performance of wood preservatives since it was established in 1910. Field performance is determined by placing wood specimens that have been treated with preservative formulations in field plots that have a high decay hazard potential. Decay hazard potential is determined by a combination of temperature and humidity providing a long active growing season for decay fungi and termites. The Harrison National Experimental Forest (HEF) in Mississippi has a high decay hazard potential and has served as the primary research site for field performance tests since 1938. Field plots contain many treated stakes partially buried in the ground in a grid pattern. Each stake is periodically removed and individually inspected for signs of decay or termite damage. A standardized rating system is used to rate each stake until it fails from fungal decay or termite damage. For a particular preservative treatment, replicate stakes (up to 20) are installed to account for natural variability by microorganisms present in a particular field plot. The 02 Report (Comparison of Wood Preservatives in Stake Tests: 2011 Progress Report), summarizing the results from field stake plots is published approximately once each decade (Woodward and others 2011). Stake plot tests are considered to be realistic tests of treated wood in a realistic application. For example, Southern Pine posts treated with pentachlorophenol in oil, creosote, and copper naphthenate in oil that were installed in 1949 in the HEF were still performing well in 2005 and have a calculated life span exceeding 60 years (Freeman and others 2005).

Creosote and pentachlorophenol were once the main preservative treatments of wood until the 1950s, when copper formulations were introduced. While creosote and pentachlorophenol continue to be the preservative of choice for specific applications such as utility poles, cross-arms, railway sleepers, and marine pilings, copper-based formulations have been used to treat a majority of the wood used in the United States since the early 1970s (Lebow and others 2004; Lebow 2010), resulting in numerous field-plot tests in the HEF to evaluate those formulations.

The first documented incident of preservative tolerance by *Poria luteofibrata* Baxter (synonymous with *Poria radiculosa* Peck) was in 1952 in an official report written by George H. Hepting, Division of Forest Pathology in Ashville, North Carolina. *P. luteofibrata* was first described by Baxter from a Northern Florida collection in 1938 and later shown to exactly duplicate every detail of Peck's description of *P. radiculosa*. In the 1952 report, creosoted poles were prematurely failing at the ground line in the Piedmont region in as few as 7 years. Hepting had noted for some years "a fungus that produced yellow strands in and on the decayed wood was very consistently associated with these decayed poles." The fungus that caused 22% weight loss in creosote-treated wood blocks in laboratory tests was identified from a mature sporophore by Josiah Lowe as *P. radiculosa* in 1950. In 1946, when Lowe's manual on *Poria* was published, *P. radiculosa* was considered to be a rare species (Lowe 1946); by 1950 it was reported to be a widely distributed and fairly common species in the Eastern United States (Hepting 1952).

In 1965, a report by the U.S. Department of Agriculture identified 1,464 fungi isolated from decayed wood items to species (Duncan and Lombard 1965). Observations were compiled regarding associations with type of wood product, wood type (softwood or hardwood), decay types (brown-rot or white-rot), geographical location by region, and treatment type (if the product had been treated with a preservative). Of the 152 different species identified, *P. radiculosa* was one of the 10 most prevalent fungi, occurring 34 times on softwoods primarily in the southern United States. Twenty-four percent (8 of 34) of the specimens were isolated from poles treated with creosote, zinc chloride, copper naphthenate, and pentachlorophenol. Seventy-four percent (25 of 34) were isolated from experimental stakes treated with chromate zinc chloride, chromate copper zinc chloride, chromate zinc arsenate, copper chromate, copper naphthenate, creosote, fluor-chrome-dinitrophenol or zinc chloride in ground contact.

In 1971, stakes in a field plot in the HEF treated with copper chromate arsenic (CCA) and acid copper chromate (ACC) began to fail prematurely. Decay by a fungus with bright yellow mycelium and thick hyphal cords was noted on one ACC-treated stake that catastrophically failed within the first 12 months of exposure (unpublished field data, Lee Gjovik, Forest Products Technologist (retired), USDA Forest Service, Forest Products Laboratory, 11/12/1972). The failed stake was brought to the FPL for culturing. Three isolates were cultured from the thick yellow hyphal strands by Wallace Eslyn, Research Plant Pathologist at FPL, and microscopically identified using morphological and chemical characteristics by Francis Lombard, Mycologist at FPL. All three isolates, initially identified as *Meruliporia incrassata*, were given the designation of ME which stood for "Madison strain isolated by Eslyn." These isolates were presumed to be highly tolerant of copper and chromium but not arsenic. Subsequently, the isolate designations were changed to TFFH 294, TFFH 296, and TFFH 128. TFFH is an acronym for "The fungus from hell" because of its very high tolerance to wood-preserving chemicals. Major research results involving TFFH 294 will be discussed chronologically by topic with pertinent references after each section, followed by current and past nomenclature.

Historical References

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Bioremediation (1996 to 2006)

No published research could be located for these isolates until 1996 when Terry Highley and Barbara Illman published that *M. incrassata* TFFH 294 caused 40.2% weight loss in CCA-treated Southern Pine sapwood in a laboratory soil block test (Illman and Highley 1996; Illman and others 1996). These were the first in a series of reports on screening of fungal isolates for preservative tolerance that culminated in a patented method for bioremediation of CCA-treated waste wood (Illman and others 2000; 2002; 2005; Illman and Yang 2006; Yang and Illman 1999). In screening studies, TFFH 294 did not show tolerance to creosote or pentachlorophenol.

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Role of Oxalic Acid Production in Copper Tolerance (1999 to present)

Copper has been the major biocide used in the formulation of new preservatives to inhibit fungal decay; however, the ability of copper-tolerant decay fungi to circumvent copper toxicity has been a concern for decades. As long ago as 1931, Rabanus hypothesized that oxalate production in decay fungi may be linked to copper tolerance (Rabanus 1931). Copper oxalate crystal formation in decayed wood was documented in the literature (Murphy and Levy, 1983; Sutter and others, 1983). The presumption was that oxalic acid (OA) precipitates copper into copper oxalate crystals (insoluble form) and renders the copper ion inert. They also hypothesized that a number of diverse factors such as growth rate, pH, OA production, and decay capacity all contribute to copper tolerance. Subsequently, brown-rot wood decay fungi in the genus *Poria* (Pers. ex Gray), and other genera related to *Poria,* such as *Serpula* [(Pers.) Gray], *Antrodia* (D.C.: Fr.) Ryv., and *Wolfiporia* (Schw syn. *Poria cocos*), were shown to be copper tolerant (Davidson and Campbell 1954; Collet 1992; Leithoff and others 1995; Schmidt and Moreth 1996; Tsunoda and others 1997). Rodney DeGroot and Bessie Woodward studied copper tolerance in *Wolfiporia cocos* and concluded that *W. cocos* has the ability to immobilize copper by precipitating copper oxalate (DeGroot and Woodward 1999). This study was expanded by Carol Clausen and Frederick Green, who reported considerable intra-species copper tolerance variability in the *W. cocos* isolates that they evaluated. They also found no statistical relationship between the amount of oxalic acid production in liquid culture or wood and copper tolerance in that group of *W. cocos* isolates and OA production did not seem to be the sole controlling factor for copper tolerance in this study (Clausen and others 2000). Green and Clausen continued to evaluate the ubiquity of copper tolerance in other aggressive brown-rot isolates including TFFH (Green and Clausen 2001). They showed that there are varying degrees of copper tolerance in brown-rot isolates from seven genera representing some of the most aggressive brown-rot fungi including *Antrodia*, *Wolfiporia*, *Tyromyces*, *Postia*, *Serpula*, *Meruliporia*, and *Coniophora,* with species of *Gloeophyllum* being the only recognized copper-sensitive brown-rot fungi. Following the finding that high levels of oxalic acid (OA) were a dominant characteristic in copper-tolerant brown-rot basidiomycetes, the mechanism of copper tolerance became a topic of research interest.

Throughout their studies, Green and Clausen (2001, 2005), and Clausen and Green (2003) consistently linked high levels of OA production to copper tolerance in these genera. Exposure of copper-tolerant fungi to low concentrations of ammoniacal copper citrate accentuated OA production. Up to 17 times more OA was produced in ammoniacal copper citrate-treated wood than untreated wood by the test fungi from these genera with *Antrodia* repeatedly producing the most OA. At week 4, ammoniacal copper citrate stimulated 66% to 93% more OA production in treated wood than the untreated controls. Additionally, tolerance to copper was laboratory tested on wood treated with several different copper-based wood preservatives including those that are arsenic-free. TFFH 294 was included for comparison in two additional studies on the role of OA production. First, the role of OA production on tolerance of *Tyromyces palustris* TYP 6137 to the copper-free wood preservative, naphthaloylhydroxylamine (NHA) was evaluated (Arango and others 2006). Unlike *T. palustris*, TFFH 294 was not tolerant of NHA-supplemented malt agar and Arango and others concluded that NHA tolerance of *T. palustris* was not mediated by overproduction of OA. Second, the effect of calcium chloride on growth and decay of 12 strains of *Serpula lacrymans* was evaluated by Hastrup and others (2006). In this study, rate of decay was estimated in Southern Pine blocks treated with ammoniacal copper citrate followed by calcium chloride ($CaCl_2$). Decay by *S. lacrymans* was found to be significantly inhibited by treatment with $CaCl_2$ in the presence of copper, suggesting that $CaCl_2$ was functioning as an OA sink, leaving Cu ions in the solution to act as a fungicide. However, TFFH 294 and *Postia placenta* displayed notable wood decay despite $CaCl_2$ treatment.

Oxalic Acid References

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Genetic Analysis (2005 to 2011)

In 2005, Anne-Christine Hastrup, University of Copenhagen, conducted phylogenetic analyses on *S. lacrymans*, an economically important dry-rot fungus in Europe, and several North American fungi, including TFFH 294, which was then called *M. incrassata*. Following DNA extraction and polymerase chain reaction (PCR), the ribosomal DeoxyriboNucleic Acid–Internal Transcribed Spacer (rDNA-ITS) sequence was compared to known sequences deposited in GenBank. GenBank, the National Institutes of Health genetic sequence database, is a collection of all publicly available DNA sequences. Hastrup (2005) reported that TFFH 294 most closely aligned with *Antrodia vaillantii* and not *M. incrassata*. Simultaneously, Dan Lindner, Research Plant Pathologist, USDA Forest Service Northern Research Station, sequenced the isolate and based on the ITS sequence, TFFH 294 was placed in the *Antrodia* clade. Dr. Lindner felt the ITS sequence information in GenBank was not specific enough to confidently name the species in 2006 (personal communication to Clausen, 2006). In 2010, Juliet Tang, doctoral student at Mississippi State University, sequenced the genome of TFFH 294 (Tang and others 2010). She also amplified, cloned, and sequenced the rDNA–ITS region to confirm the identity of the isolate. This time, however, the GenBank database contained many more entries and the sequenced DNA aligned to two different *Fibroporia radiculosa* (=*Antrodia radiculosa*) voucher specimens (Tang, doctoral student, Mississippi State University, Starkville, Mississippi, personal communication to Clausen, 2010), thereby confirming that the fungus was, in fact *A. radiculosa.* That finding was not surprising since other *A. radiculosa* isolates are the most copper-tolerant brown-rot fungi and produce the highest amount of oxalic acid compared with other brown-rot fungi tested to date.

Genetics References

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Metal Tolerance (2009)

While evaluating nanometals as potential preservatives, Nami Kartal of Istanbul University and scientists at FPL confirmed that *A. radiculosa* TFFH 294 was also resistant to nanozinc, nanocopper, and a commercial combination of nanozinc and silver (Kartal and others 2009; Clausen and others 2009). Recall that in 1950, the original concern about *P. radiculosa* Peck was tolerance to creosote (22% weight loss). However, tolerance to creosote has not been reported for isolate TFFH 294. In addition to copper, zinc, and silver, TFFH 294 is known to be tolerant of chromium and arsenic present in CCA-treated wood (40.2% weight loss).

Metal Tolerance References

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Future Research: Mechanism of Copper Tolerance (2010 to Present)

The question that has remained unanswered is what mechanistic role, if any, does the accumulation of OA coupled with copper oxalate crystal formation play in copper tolerance of basidiomycetes? Understanding the biosynthesis of oxalic acid will lead to a better understanding of the copper-tolerance mechanism used by isolates of *F. radiculosa* to overcome copper-based wood preservatives. Munir and others (2001) investigated the role of OA biosynthesis in the copper-tolerant fungus, *Tyromyces palustris* (=*Fomitopsis palustris*), and linked it to both the tricarboxylic acid (TCA) and the glyoxylate (GLOX) pathways. Their work discovered that there are two major oxalate producing enzymes: glyoxylate dehydrogenase and oxaloacetase, with isocitrate lyase acting as a vital enzyme involved in the production of OA. To understand the mechanism of copper tolerance, production of key enzymes from the TCA and GLOX pathways by *F. radiculosa* TFFH 294 will be assayed from untreated and copper-treated wood in an attempt to establish the pathway involved in OA production for this organism (Jenkins and others 2012). Using functional and comparative genomics, Tang and others (2010, 2011) hope to identify novel genes that regulate wood decay under different environmental conditions. Gene expression levels will be compared for decay on untreated and copper-treated wood to determine if expression is enhanced by the presence of copper (Jenkins and others 2012). Finally, gene expression will be correlated to enzymes responsible for the oxalic acid production (Jenkins and others 2012). Unraveling the mechanism of copper tolerance through genetic expression and enzyme production will enable development of novel targeted biocides to circumvent preservative-tolerance in *Antrodia* and other brown-rot genera.

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Nomenclature (1921 to Present)

Whereas mycological taxonomic nomenclature remains a dynamic field, genetic analysis based on nuclear rDNA–ITS sequences support returning *Antrodia radiculosa* (Peck) to the name *Fibroporia radiculosa* (Peck), while separating *Antrodia* into a separate genus more closely related to other genera of brown-rot fungi such as *Fomitopsis* P. Karst., *Daedalea* Pers., *Gloeophyllum* P. Karst., and *Oligoporus* Bref (Bernicchia and others 2010). Below is the taxonomic history of the nomenclature for *Fibroporia radiculosa* described by Gilbertson and Ryvarden (1986) and documented in the Index Fungorum database (www.indexfungorum.org 2011). Index Fungorum, in partnership with CBS (Centraalbureau voor Schimmelcultures), CABI (Centre for Agriculture and Biosciences International) and Landcare Research, is the internationally recognized online database for fungal nomenclature. Based on current literature and entries in Index Fungorum, the current name for TFFH 294 is *F. radiculosa* (Peck), which is synonymous with *A. radiculosa* (Peck) Gilb. & Ryvarden and *P. radiculosa* (Peck) amongst others.

Current name:

Fibroporia radiculosa (Peck) Parmasto. Conspectus Systematis Corticiacearum (Tartu): 177.

Synonymy:

Antrodia radiculosa (Peck) Gilb. & Ryvarden. 1985. Mycotaxon 22(2): 363.

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