

Wood Decay Fungi

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Advanced article

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Wood decay fungi are any species of fungi that utilise the structural components of wood as a source of nutrients. They comprise a very diverse group and have a worldwide distribution normally wherever trees are found. Wood decay fungi are vital to ecosystem functioning as they facilitate the decomposition of woody materials into soil. Wood decay fungi are also major contributors to damage to wood in service in both residential and industrial applications, leading to estimated \$1B in losses annually. Wood decay fungi have also been exploited for use in industrial processes ranging from product development to waste breakdown. This article focuses on the taxonomic and physiological diversity of wood decay fungi and their importance both on economic and environmental scales.

Introduction

In the broadest sense, wood decay fungi are those fungi specially adapted to break down woody tissue in the environment. They represent a diverse assemblage of lineages of mostly terrestrial microorganisms (see also: [Microorganisms](#)) that contribute to soil biogenesis and nutrient cycling. Without these fungi, soil carbon cycling could not take place (Watkinson *et al.*, 2006). Wood decay fungi are also critical to macro and micronutrient cycling (see also: [Fungi: Ecological Importance and Impact on Humans](#)), which regulates soil fertility (Boddy and Watkinson, 1995). In this regard, the importance of this group of microorganisms cannot be overstated as they facilitate the

flow of dissolved nutrients into the soil matrix where they are then translocated to plants. In the built environment, decay fungi present a constant threat to wood that is occasionally damp. They are typically the reason that wood needs to be treated with preservatives, particularly in severe exposures such as ground contact or when subject to splashing soil moisture (Lebow and Wacker, 2011). Decay of wood in service results in losses of \$1B annually (Clausen, 2010). In the same sense that fungi represent a biologically diverse group, they also represent an equally diverse source of potential industrial applications. Wood decay fungal systems have been extensively exploited for their capabilities to break down wood, wood byproducts and even industrial pollutants (see also: [Biodegradation of Organic Pollutants](#)) of man-made origin, which will be detailed later in this article.

Taxonomic Status

Many sources cite Theophrastus (371–288 BC), the Greek scholar from Lesbos, as the first classifier of fungi (Hort, 1916) followed by Pliny the Elder (29–79 AD) (Kern, 1943). Both considered fungi to be plants, a widely held convention until the twentieth century. More recent phylogenetic analysis indicates that fungi are more closely related to animals (Baldauf and Palmer, 1993). Currently, the two phyla that contain most if not all of the wood degrading fungi are the Ascomycota (see also: [Ascomycota](#)) and the Basidiomycota (see also: [Basidiomycota](#)), which are now grouped together as the subkingdom Dikarya. This group is named owing to the characteristic formation of dikaryons, a nuclear mostly condition unique to these fungi and involves cells pairing off without fusion (Hibbett *et al.*, 2007). The Ascomycota (see also: [Ascomycota](#)), also referred to as sac fungi, are currently divided into three subphyla and the majority of wood degrading fungi belong within the subphylum Pezizomycotina. This subphylum is incredibly diverse and contains a wide range of fungal opportunists. Some examples of the ascomycetous genera of fungi of importance in the decay process of wood are *Helotia* spp., *Coniothyrium* spp., *Chaetomium* spp., *Nectria* spp. and many others. A more complete overview of the Pezizomycotina can be found in Spatafora *et al.* (2006). Ascomycetous

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fungi that degrade wood almost all produce soft rot in woody substrates, which will be explained later. The sister group to the Ascomycota is the Basidiomycota (Hibbett *et al.*, 2007), which are organised similarly to the Ascomycota into subphyla: the ustilagomycotina (mostly smut fungi), pucciniomycotina (mostly rust fungi) and finally the agaricomycotina, which contains all of the basidiomycetous fungi that attack wood. Similar to the pezizomycotina in the Ascomycetes, the agaricomycotina contains a wide range of fungal strategies involved in the breakdown of woody biomass. An important order within the Agaricales is the order Polyporales, which contains the majority of the wood rot fungi, usually classified as either white or brown rot, which will be discussed later. The taxonomic status of the Polyporales has been the topic of often intense mycological debate for the last 75 years and has undergone numerous revisions based on evidence presented in morphological (Ryvarden, 1991; Stalpers, 1978; Gilbertson and Ryvarden, 1986, 1987), cultural (Nobles, 1958) and early genetic analyses (Hibbett *et al.*, 2007; Hibbett, 2006; Garcia-Sandoval *et al.*, 2011; Hibbett and Donoghue, 2001; Martin *et al.*, 2011; Ortiz-Santana *et al.*, 2013). Phylogenetic analysis is slowly resolving many of the long-debated groups in this order (Binder *et al.*, 2013).

Evolutionary History of Wood Decay Fungi

The basal groups of fungi have been well resolved but it is unclear exactly when fungi diverged from a common ancestor that existed as an aquatic flagellate eukaryote (Stajich *et al.*, 2009). Much debate is still ongoing about the divergence times within the basal groups of fungi and estimates range between 500 million and 1.5 billion years ago. The divergence of the order Agaricales, which contains almost all of the wood decay fungi, has been determined by molecular clock analyses to have occurred 290–295 MYA during the late carboniferous and developed simultaneously with the evolution of the lignified plant cell wall. It has been hypothesised that the development of genes encoding class II peroxidases (POD genes) coincides with the development of the lignified plant cell wall (i.e. wood) (Eastwood *et al.*, 2011). Another important development in the evolution of the decay fungi is the reduction of the enzymatic machinery controlling wood decay during the shift from white rot to brown rot, which is thought to have been owing to several independent reductions in POD genes, the first being in the Dacrymycetes (350 MYA), the Gloeophyllales (250 MYA), the Boletales (~150 MYA) and lastly the Polyporales (~100 MYA) (Floudas *et al.*, 2012). The peroxidase system, no longer utilised by many fungi represented in these groups, was gradually replaced with the chelator mediator Fenton (CMF) mode of decay now commonly associated with brown rot, but many representatives in these groups may have contained vestigial traces of the POD genes.

Wood Structure

Wood is a three-dimensional polymer made up of three main structural components: (1) cellulose-linear repeating units of

β -1,4-linked glucose units that give structural rigidity and form microfibrils, (2) highly branched networks of sugars called hemicelluloses that form a cross-linked network between cellulose microfibrils and (3) hydrophobic phenolic compounds called lignin, which serves as a binder to consolidate and harden the wood. These three components make up the primary structure of wood which makes up the wood cell walls. Secondly, this matrix is laid down in multiple layers, each of which has slightly unique characteristics. Gymnosperms (see also: **Gymnosperms**) (softwoods) and angiosperms (see also: **Angiosperms**) (hardwoods) have somewhat different specialised wood cellular structures. A generalised structural diagram of a softwood wood cell showing the different layers of the cell wall is shown in **Figure 1**. Softwoods typically have tracheids that are oriented apically in the tree to maximise solute conduction. Hardwoods have vessels and fibres that perform similar function but differ slightly in chemical and cellular composition.

Fungi typically colonise wood through direct hyphal contact via soil or by the germination of spores in cracks or on the wood surface. A generalised wood decay life cycle is shown in **Figure 2**. Decay fungi can also be vectored into wood by insects (Jacobsen *et al.*, 2017) and vertebrates (Jusino *et al.*, 2015). Fungi typically colonise larger spaces (more available oxygen) in wood first and then proceed to digest the wood extracellularly via the processes described in the section titled 'Nutrient Assimilation Modes Among Wood Decay Fungi'. Some fungi produce bore holes that facilitate faster movement of hyphae through cell walls (Worrall *et al.*, 1997).

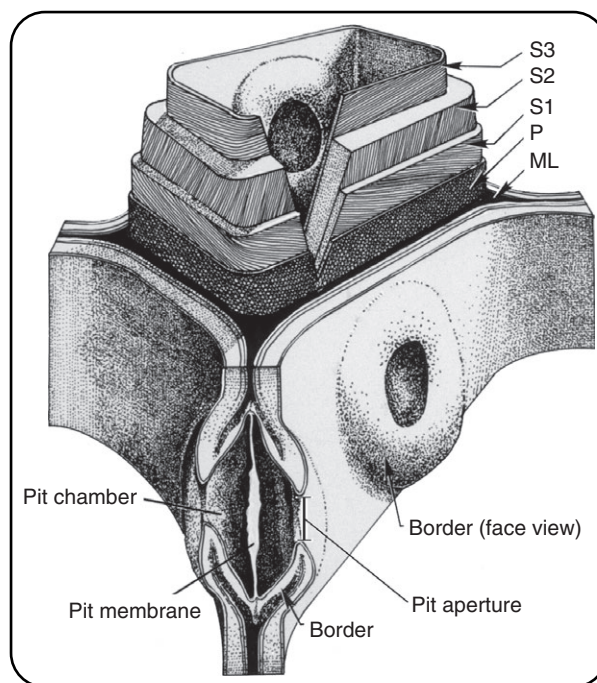


Figure 1 Diagram of the wood cell wall. U.S. Department of Agriculture.

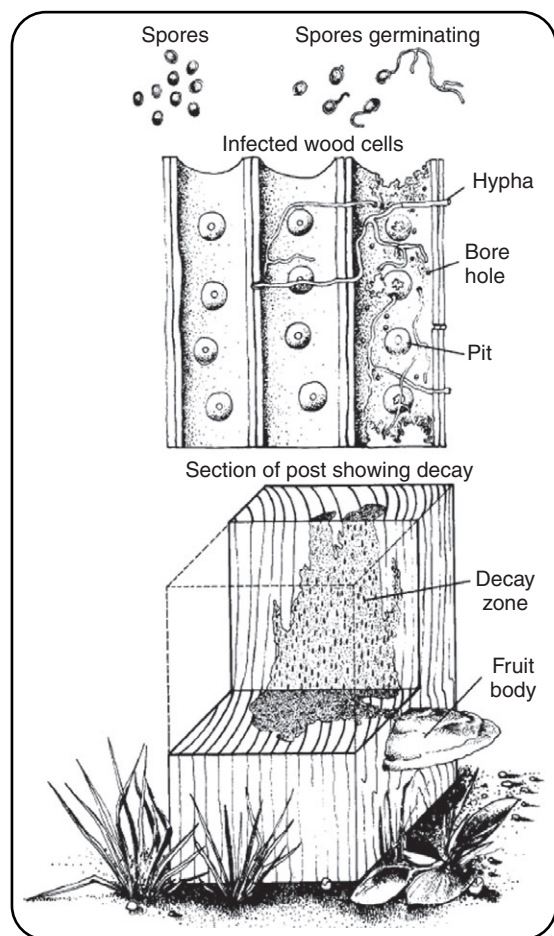


Figure 2 Generalised infection stages of wood decay fungi. U.S. Department of Agriculture.

Ecological Importance of Wood Decay Fungi

Wood decay fungi are almost exclusively involved in the breakdown of either living, stressed, dying or dead trees or other plant matter. The stage at which these fungi colonise and exploit their host dictates their life history strategies. If wood decay fungi are classified based on their order of arrival in decaying wood, they can be viewed as either primary or secondary colonisers. Primary colonisers are those which colonise and exploit the wood early in the decay process. Secondary colonisers follow and utilise any remaining substrate, usually sugars and other residual polysaccharides (Käärik, 1975).

Insects are often associated with various decay fungi and have been found to be important vectors. The importance of fungi in boreal forest ecosystems has been an issue of much debate and efforts are ongoing to preserve and improve the biodiversity of wood decay fungi in the boreal forest while reducing the impact of detrimental anthropogenic influences such as improper forest harvesting and forest fire (Stenlid *et al.*, 2008).

Nutrient Assimilation Modes among Wood Decay Fungi

Wood decay fungi are traditionally separated into three broad categories based on their varying nutritional assimilation modes: (1) brown rot fungi (**Figure 3b**), (2) white rot fungi (**Figure 3c**) and (3) soft rot fungi (**Figure 3d**). Recent research (Riley *et al.*, 2014) has suggested overlapping or alternative modes of assimilation, which have been coined as (4) grey rot, and those developments and their implications are also discussed briefly. Early literature suggested that brown rot fungi specialise on conifers (softwoods) while white rots specialise on angiosperms (hardwoods), but many exceptions to this convention have been discovered. It has also been hypothesised that the evolution of brown rot led to the displacement of white rot fungi from coniferous substrates as the mechanism was as such more efficient (Eastwood, 2014). Below is a summary of the nutritional modes of decay fungi with characteristic damage presented in **Figure 3(a–d)**; for comparative purposes only, **Figure 3a** illustrates mold growth on the surface of southern pine lumber, as molds do not typically cause structural damage they are not discussed in the context of this article. A more detailed description of the microscopy associated with these mechanisms can be found in Schwarze (2007).

1. *Brown rot fungi.* Most brown rot fungi also belong to the phylum Basidiomycota. Brown rot typically involves the nonenzymatic breakdown of cellulose and hemicelluloses via Fenton-mediated processes and can significantly remove these components from the wood matrix, leading to severe losses in strength and resulting in a brown cubical cracked appearance owing to the presence of residual lignin residues (**Figure 4**). As mentioned previously, brown rot represents an evolutionary adaptation where these fungi have a reduced enzymatic arsenal and rely more heavily on nonenzymatic modes of wood decomposition. The rapid depolymerisation of cellulose and hemicelluloses is thought to be due to the production of hydrogen peroxide (H_2O_2) generated via Fenton-mediated reduction of Fe in the wood cell wall and surrounding soil. There are certain genera within the brown rots (ex. *Antrodia*, *Serpula*, *Fibroporia*) which form thick walled mycelia called rhizomorphs that can translocate moisture and are commonly referred to as “dry rots” in the built environment. Alternatively, there are also white rot fungi that form rhizomorphs as well, but they are not as frequently encountered in construction.
2. *White rot fungi.* Most white rot fungi belong to the phylum Basidiomycota, with some outliers found in the Ascomycota. A characteristic sign of white rot fungi is a bleached and stringy wood appearance that results from widespread delignification of the wood, leaving behind some of the cellulosic components (**Figure 3c**). White rots may be further classified into either selective or simultaneous delignifiers based on timing at which the lignin component degrades.
3. *Soft rot fungi.* Soft rot fungi are found primarily in Phylum Ascomycota. Soft rot fungi secrete an enzyme called cellulase directly from their hyphae which causes localised

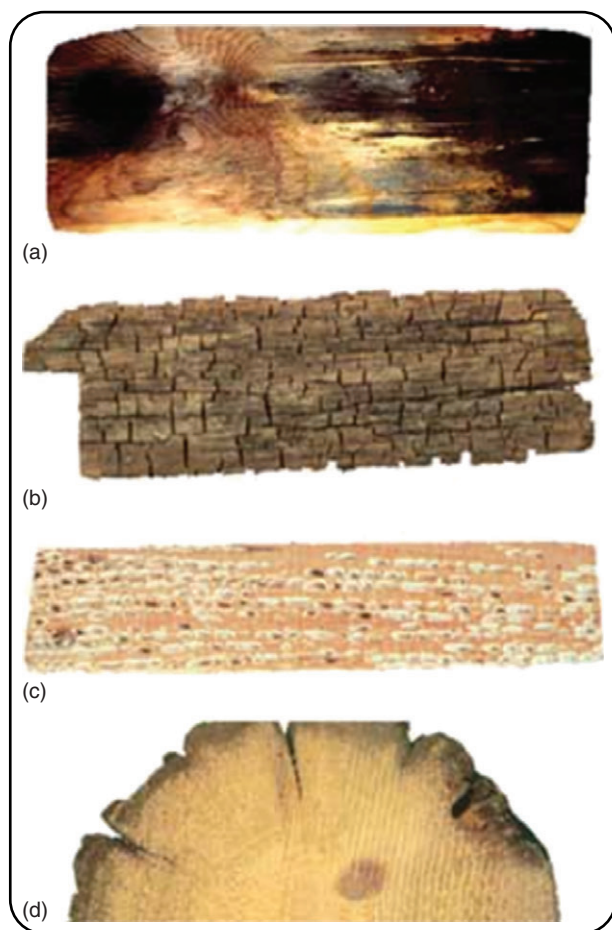


Figure 3 Photographic examples of four most common types of wood decay (a) discoloration by mild fungi, which does little to impact the structural components, (b) brown rotted pine depicting brown cubical cracking owing to the removal of cellulose and residual lignin remaining, (c) white rotted maple depicting white, stringy bleached residual cellulosic material owing to the removal of the lignin matrix and partial removal of cellulose and hemicellulose and (d) a section of soft rotted pine utility pole.

damage to the wood cell wall. Wood cellular damage from soft rot is structurally similar to brown rot in that cellulose and hemicelluloses are primarily affected. The unique characteristic that sets apart soft rot is the formation of cavities within the S2 layer of the wood cell wall. Soft rot can be further distinguished by the formation of T or L branches within the S3 layer, which follows the orientation of the cellulose microfibrils. This process requires externally supplied nitrogen in order to produce needed enzymes, so soft rot typically occurs in areas of high moisture and high available nitrogen. Whereas white and brown rot typically occur in a defined range of 40–80% wood moisture content, soft rot fungi typically occur in the wetter extremes of this range.

4. *Grey rot fungi*. Recent analysis of genomic data has led to the characterisation of some decay fungi as grey rots (Riley *et al.*, 2014). Grey rot refers to fungi that exhibit



Figure 4 Fruiting body of *Schizophyllum commune* on decaying wood. *S. commune* has been determined to be a grey rot, possessing capabilities found in both traditional brown and white rot modes of decay. Courtesy of Bernard Spragg, Christchurch, NZ.

modes of decay that fall outside of the normal convention of white and brown rot decay fungi. Correlation analysis of enzymes and secondary metabolites of a diverse group of decay fungi previously classified as either white or brown indicates a subset that exhibits intermediate decay strategies and possesses enzymes that target both lignin and cellulose. *Schizophyllum commune* (see **Figure 4**), *Jaapia agrillacea* and *Botryobasidium botryosum* all exhibit this intermediate mode of decay and have led to questioning of the classical description of brown and white rot. It is presumed that as more large scale genomic studies are performed, more examples of grey rot will be discovered.

Enzymatic Systems of Wood Decay Fungi

1. *Carbohydrate-active enzymes*. Often abbreviated as CAZYmes are those that degrade, modify or create glycosidic bonds and are implicated in the breakdown of cellulose, hemicelluloses or pectin. They include glycoside hydrolases (GHs), glycosyltransferases (GTs), polysaccharide lyases (PLs), carbohydrate esterases (CEs) and auxiliary activity enzymes (AAs) (Davies *et al.*, 2005).
2. *Lignin-degrading enzymes*. Lignin is one of the most abundant natural substances in nature and is composed mainly of cross-linked hydroxycinnamyl alcohols. The enzymes involved in lignin breakdown are peroxidases (lignin peroxidase (LiP), manganese peroxidase (MnP) and versatile peroxidase (VP)) and laccase. These enzymes are present in most of the white rot fungi and many of the 'grey rot' fungi discussed earlier. Lignin-degrading enzymes have been used extensively to break down recalcitrant compounds such as dyes, industrial pollutants and other persistent chlorinated hydrocarbons (Kirk and Lynch, 1987).

Nonenzymatic Systems of Wood Decay

Nonenzymatic decay is utilised by the brown rot fungi. As mentioned previously, brown rot fungi are thought to have adapted their decay strategies to employ low molecular weight hydroxyl radicals that enable them to more effectively penetrate the wood cell wall and facilitate efficient breakdown on the cellulose matrix. They have reverted to this mode from the ancestral enzymatic breakdown strategies. This paired down metabolic system enables them to rapidly depolymerise woody biomass. It has been hypothesised that brown rot fungi generate free radicals from iron atoms located on exposed ends of hemicelluloses. However, the nonenzymatic description is not entirely accurate in this case as enzymes such as glyoxal oxidase and others are required to facilitate the generation of the peroxide radicals. The process of chelation is also an important consideration in brown rot. Many brown rot fungi produce oxalic acid or oxalate, which can complex with elements in the surrounding environment to sequester excess cations in the decay environment (Dutton and Evans, 1996). An in-depth review of the current view of mechanisms of brown rot can be found in Arantes and Goodell (2014).

Economic Importance of Wood Decay Fungi

Wood decay fungi represent a bountiful source of industrial products. The obvious example is the use of wood decay fungi to break down and convert wood into its base sugars, which has been studied in great detail (Martinez *et al.*, 2009; Hatakka and Hammel, 2011). However, the ability of decay fungi, particularly white rot fungi, to break down highly recalcitrant compounds, owing to their enzymatic machinery originally adapted to break down lignin, makes them very useful for the breakdown of industrial cyclic pollutants (Asgher *et al.*, 2008). White rot fungi have been shown to effectively break down textile effluents containing synthetic dyes, explosive residues and polymers (Hamman, 2004). White rots characterised as selective delignifiers have been used as pretreatments for solid state fermentation (Keller *et al.*, 2003), bioincising to decrease wood density and lignin content before secondary processing for pulping (Millati *et al.*, 2011).

Glossary

Basal groups Groupages occurring nearer to the base of a phylogenetic tree, which represent the ancestral origins of a group of organisms.

Bio-incising Pretreatment process for wood that includes intermediate exposure to decay fungi that improves permeability of the wood.

Dikaryon Nuclear feature unique to fungi where two nuclei of two cells pair off without fusion.

Phylogenetics Study of the evolutionary history and relationships among individuals or groups of organisms based on heritable traits, also referred to as cladistics.

Sister group Phylogenetic term that denotes the closest relative of another given unit on an evolutionary tree.

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