Decomposition by polypores can take many forms. Let's take a closer look at wood decay where the real work of these fungi takes place.

WOOD DECAY:
The Action Behind the Polypores

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Polypores are fruiting bodies of wood decay fungi with pores. People find them in every forest but their role in ensuring healthy ecosystems is often overlooked. The fruiting bodies or sporophores, the only part of these decay fungi we see, can be exceedingly diverse. They range from thin annuals to huge perennials, earth tones to multi-colored and dull

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Figure 1. Two common brown rot fungi: *Laetiporus sulphureus*, chicken of the woods, occurs on oaks and other hardwoods (page 10) and *Fomitopsis pinicola*, the red belt fungus, usually found on conifers (left). Advanced stages of decay is brown in color and the residual wood often cracks and checks into cubical pieces (2 photos above). *Laetiporus* photo by Russell Kennedy.

to shiny. Some are edible and choice while others are like shoe leather or as hard as wood. These structures, however, are a small part of the fungus. The main body is mycelium that grows within trees or dead wood causing decomposition. Polypores are important to the environment because they are the key players that recycle carbon and other nutrients for reuse by the next generation of trees and other organisms. The actions of polypores can also be problematic. They can cause decay in living trees resulting in hazardous conditions and can degrade wooden structures resulting in billions of dollars in losses annually. If you have ever chopped off a few bracket fungi from trees you will have noticed differences in the underlying decayed wood. There are thousands of different species of polypores and these fungi cause many different patterns of degradation. The residual wood can be brown, white or yellowish. It may be soft or stringy with decay that is diffuse or found in distinct pockets. On your next fungal foray I encourage you to take a closer look at wood decay. The different types of rot are fascinating and worthy of attention.

As fungi colonize wood they utilize an array of different enzymatic and

Figure 2. Brown rot fungi are cellulose degraders; when the cellulose is degraded and depolymerized the wood loses its strength properties. Decayed wood is rich in lignin giving the rot its brown color (left photo). Although brown-rotted wood may appear intact, without cellulose the wood breaks into fragments easily. A scanning electron micrograph (right photo) shows the fragile cell walls of brown rot that have crumbled into minute pieces with just a slight touch.

Figure 3. Brown rot fungi usually cause a diffuse attack that is widely distributed in wood. However, some brown rot fungi that attack living cypress, cedar, and other trees with resistant heartwood produce brown rot that occurs in distinct pockets of various sizes. Pecky cypress and pecky cedar are examples.

non-enzymatic processes to degrade the main components of wood: lignin, cellulose and hemicellulose. These compounds are broken down outside the fungal hyphae. The wood sugars and other degraded substances produced are then utilized by the fungus. With so many different types of wood decay fungi, it is not surprising that they have evolved different mechanisms to decay wood. Many polypores have the ability to degrade all cell wall components while others produce different types of rot by selectively degrading one compound over another. The sequence and intensity of the degradative actions also affects the physical appearance of the decayed wood. These differences have been used to categorize the decay based on its appearance. The two main types caused by polypores are white and brown rots, but a lot of variation exists within each type of rot.

Brown rot fungi are cellulose degraders. They modify lignin that surrounds the cellulose microfibrills in the woody cell wall and break down the cellulose chains into sugars. During decomposition, the wood becomes darker as the fungus metabolizes cellulose leaving lignin behind. The high lignin content of the residual decayed wood is responsible for the brown color. This type of decay is very common in coniferous forests but also can be found in some hardwoods like oak, maple and birch. It is also the major type of decay that is found in wooden buildings and other structures. Cellulose is a polymer in the wood cell wall that gives wood its strength. When wood is attacked by brown rot fungi and the cellulose polymer is degraded, the wood loses its strength properties and is weakened. The breakdown of cellulose by brown rot fungi and subsequent loss of wood strength early in the decay process can lead to big problems. Hazardous conditions can result in landscape trees that are decayed by brown rot fungi. In buildings, brown rot results in structural failure. A common brown rot fungus found in living trees is *Laetiporus sulphureus* or chicken of the woods. Finding this on trees can be a delight for mushroom collectors interested in eating the golden brackets that resemble chicken when sautéed. If you look behind this polypore, you will find extensive brown rot. Over time it will lead to hazardous conditions and ultimately tree failure. As brown rot continues, it is only a matter of time before these trees fail. The fruiting of this fungus on living trees should be considered a sign of danger. The red belt fungus, *Fomitopsis pinicola*, is another brown rot fungus, but it is most commonly found in spruce, hemlock, pines and other conifers.

Advanced stages of brown rot have cracks and checks that fracture into a brown cubical rot when dry. At this stage, the decayed wood can be crumbled with just the slightest amount of pressure. When wet, brown rot is like a sponge and can absorb lots of moisture. In forest ecosystems, brown-rotted woody debris is an important component of forest soils. The decayed wood persists in the soil because it has a high lignin content that resists further attack. The decayed wood adds tilth and texture to soils and acts as a moisture and nutrient sink. Tree roots as well as mycorrhizal fungi colonize brown-rotted wood in soils. Brown rot fungi usually cause a diffuse attack in wood with degradation extending far beyond the hyphae that colonize the wood cells. However, some species of brown rot attack living trees that have resistant heartwood extractives such as cedar, juniper, and cypress producing a

Figure 4. *Inonotus obliquus* (upper left) the fungus that produces chaga and the tinder fungus, *Fomes fomentarius* (upper right) are white rot fungi. As decay progresses the wood becomes lighter in color and takes on a bleached appearance. These white rot fungi have the capacity to degrade all cell wall components including lignin, cellulose, and hemicellulose. As the fungus grows in the wood cells, degradation removes the entire cell wall causing an erosion. The decay is called a simultaneous white rot since all of the cell wall components get degraded simultaneously. A scanning electron micrograph (lower right) shows a cross section of birch wood with localized eroded areas where all cells are degraded resulting in voids next to cells that are less affected. SEM by Benjamin Held.

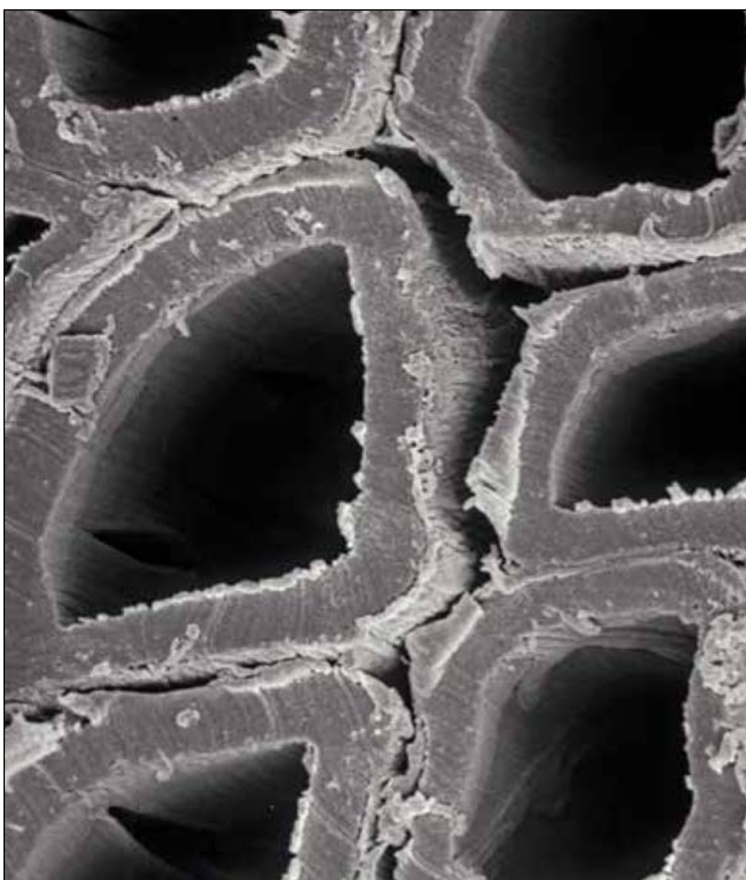

Figure 5. White pocket rot fungi are another type of white rot. Behind the fruiting bodies of fungi such as *Porodaedalea pini* (previously called *Phellinus pini*), a fungus that attacks conifers (upper left) selective degradation of lignin and hemicellulose occurs in the wood while cellulose is left relatively untouched. Spindle-shaped pockets of white cellulose occur in the wood (upper right and page 15 photo). A scanning electron micrograph of a cross section of delignified wood shows the cellulose rich parts of the walls remaining and the area between cells (the middle lamella where most of the lignin is concentrated) removed. It is an extraordinary ability to degrade lignin, one of the most recalcitrant natural substrates known, while not removing cellulose.

localized attack with the rot occurring only in pockets.

Another category of decay is **white rot**. These fungi are capable of degrading all woody cell wall components including lignin. Often referred to as simultaneous rot fungi, they modify and degrade lignin along with cellulose and hemicellulose. The degradative actions cause a bleaching of wood and the decayed wood turns white. The fungus that produces Chaga, *Inonotus obliquus*, the turkey tail fungus *Trametes versicolor*, and the tinder fungus, *Fomes fomentarius*, are a few examples of the many fungi that produce white rot. In the early stages of decay, the bleaching is referred to as spalted wood. We now know that there are many enzymes and non-enzymatic processes involved in white rot degradation

and different species produce varied forms of white rot. In addition to the simultaneous white rot fungi that remove lignin, cellulose and hemicellulose in about the same ratio, there are white-mottle rots, white-stringy rots, white-pocket rots and others that degrade cell wall components in different amounts.

An extraordinary group of white rot fungi are those that selectively degrade lignin but not cellulose. The white cellulose may be left in distinct pockets or there may be large zones where the lignin has been degraded. Different species of white-pocket rot fungi produce different sized pockets of delignified wood. Some fungi initiate pockets of rot in earlywood, the larger spring wood cells, or latewood which are the thick-walled cells produced later in the growing season. White pocket-rotters include *Porodaedalea pini* (*Phellinus pini*) which is common in conifers and *Inonotus dryophilus* in oak. There are also white rot fungi with the ability to change decay patterns within the same substrate producing a simultaneous type rot in one area and delignification in another. This results in a mottled pattern of decay consisting of different types of white rot. The selective degradation of lignin from wood while sparing the cellulose is a remarkable feat for a fungus, and it appears to have evolved a very long time ago. An extinct species of conifer, *Araucarioxylon*, was found with a white-pocket rot in 200-million-year-old fossil wood from the Triassic period. The mechanisms involved in selective white rots are being studied with interest because these fungi have great biotechnological potential including biological pulping of wood for paper production, biobleaching, bioethanol production (removal of lignin from perennial plants releasing cellulose for sugar production and fermentation) and biodegradation of other complex substances such as organopollutants. The degradation of lignin in

Figure 6. *Ganoderma applanatum*, the artists conk (top), produces a mottled white rot (bottom left). This decay is a mixture of simultaneous white rot and selective lignin degradation. Black spots in the decayed wood are manganese deposits which accumulate during delignification. The composition of the mottled decay can be differentiated using histological reagents that are applied directly to the surface of the decayed wood. Iodine-Potassium-Iodide / H_2SO_4 stains wood (middle photo at bottom) showing cellulose blue and lignified areas yellow. Another reagent used to identify lignin is phloroclucinol HCL. This stains lignin red while cellulose remains white (bottom right photo).

nature takes place slowly and the white delignified pockets or zones in wood may take months to several years to be produced. Identifying the mechanisms of lignin degradation and speeding up this process will undoubtedly be a major advancement for future industrial bioprocessing applications.

You may wonder why the cellulose is not used by these fungi during decay and also what keeps the residual cellulose from being degraded by other fungi? During the decay process, it appears that the white-pocket rot fungi and other delignifying fungi use hemicellulose as a carbon source while attacking lignin. The hemicellulose is spatially associated with lignin in

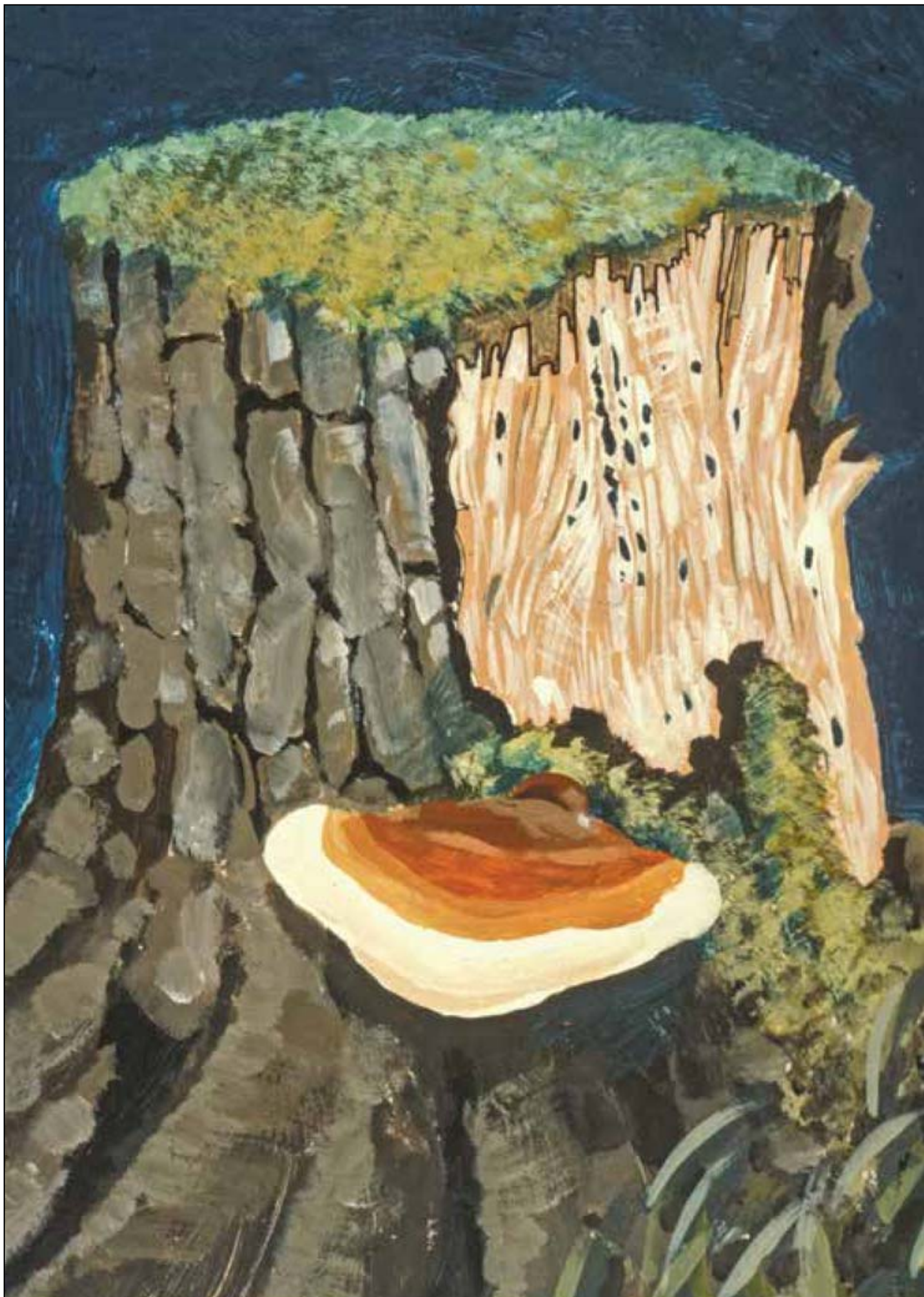

Figure 7. An illustration of *Ganoderma tsugae* on a spruce stump with a section of the wood cut away showing the underlying white mottled rot. A considerable amount of delignified cellulose remains in the decayed wood. This fungus produces black melanized zone lines or psuedosclerotial plates around the edges of the wood as a morphological and chemical barrier that prevents other fungi and insects from getting into the decayed wood. Black spots in decayed wood are manganese deposits. Drawn by Robert A. H. Bonawitz.

the cell wall and is degraded along with lignin. Production of cellulose degrading enzymes, however, are apparently inhibited or delayed and cellulose may remain in the decayed wood for decades. Black spots can often also be found in the delignified wood. These are manganese deposits. It seems strange to have manganese accumulating in decayed wood but this commonly occurs. It is likely due to changes in elemental gradients induced by manganese dependent enzymes, non-enzymatic processes, and pH changes in the decayed wood. These white rot fungi also have mechanisms to prevent other fungi from invading their niche and attacking the residual cellulose. Zone lines, or pseudosclerotial plates, are three dimensional barriers produced by white rot fungi consisting of fungal melanin that prevent other fungi and even insects from gaining entrance. These fungal structures are often produced around the outer edges of a substrate and function as a very effective barrier. Other antimicrobial substances are also likely being produced. Zone lines are produced by most white rot fungi, and often they can produce multiple black melanized lines in wood to defend the territory they occupy.

The size of the delignified areas found in decayed wood is governed by many factors including species causing the rot, substrate composition and the environment. The white mottle-rots cause decay that is a combination of simultaneous rotted and delignified wood. I use histological reagents and microscopy to identify changes in cell walls during decay and found these stains can also be used to help differentiate the mixture of decay types. When applied to wood, the location of cells with lignin, and those that are

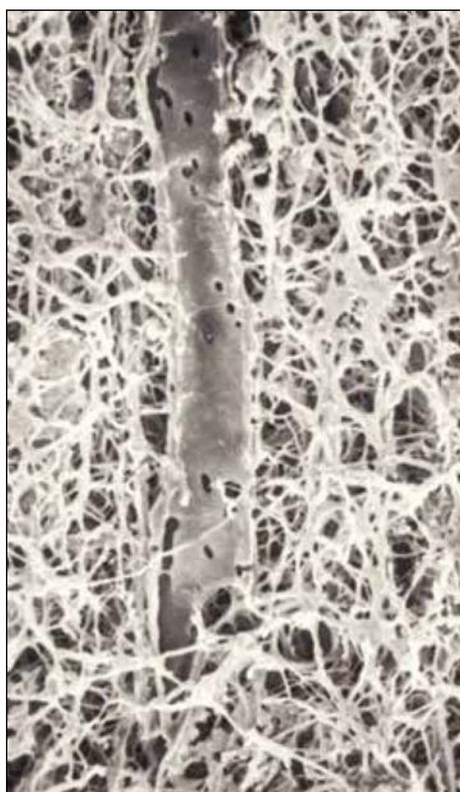

Figure 8. *Ischnoderma resinosum*, the benzoin bracket, (top of page) produces a decay that mimics white pocket rot; instead of pockets of delignified cells containing cellulose, this simultaneous white rotter has degraded voids in wood that fill with fungal mycelia (photo on left). A scanning electron micrograph shows one of the white zones (photo on right). The cell walls are degraded and voids are filled with remnants of the woody cell walls and masses of mycelium.

delignifed with only cellulose remaining are clearly seen. In areas with the simultaneous rot, the degradative actions remove all components of cell walls in localized areas causing voids to form. These voids can get filled with masses of fungal mycelium and appear white. The pockets of mycelium and white pockets consisting of cellulose can look somewhat similar but close inspection reveals the differences. Many species of white rot fungi cause mottle rots, and two that are frequently encountered are *Ganoderma applanatum* and *Ganoderma lucidum*, a species complex that includes *G. sessile*, *G. curtisii*, and many others. The mottled rot caused by *Ischnoderma resinosum*, the resinous polypore or benzoin bracket, is different since it can consist of degraded zones that fill with fungal hyphae giving the appearance of white pockets.

Heterobasidion is a fungal pathogen that attacks the roots of conifers causing root rot. Species of *Heterobasidion* usually cause a stringy white rot in roots and lower trunk of trees. A simultaneous attack of the wood leaves some cells degraded while others are less affected. The weakened wood can be easily ripped apart into a stringy

Figure 9. Some white rot fungi such as *Heterobasidion*, a serious root rot of conifers, produce decay that is stringy (top photo). The fungus causes a simultaneous attack on all cell wall components that leaves many eroded areas throughout the wood. The weakened wood shreds and separates into a stringy mass as it is pulled apart. Under certain conditions, some *Heterobasidion* species are more selective in their degradative attack causing delignification. This results in large amounts of white cellulose remaining in the decayed wood (middle photo). Although somewhat rare to find, extensive delignification can occur. In southern beech trees located in the coastal rainforests of Chile, a decay called "palo podrido" can be found (bottom photo). Entire logs can be delignified by some white rot fungi that selectively remove lignin and leave massive amounts of cellulose in the residual decay wood.

mass of degraded yellowish-white wood. Under certain conditions these same species can cause delignification and a mottled white rot. In the wet temperate forests of the Pacific Northwest, I have found *Heterobasidion* causing extensive delignification where large areas of wood have been selectively delignified. This phenomenon also takes place in the temperate rain forest of Chile. Entire downed trees filled with delignified wood have been reported. Historically, this wood has been called "*palo podrido*" and years ago farmers would split open these logs to allow cattle to feed on the large masses of cellulose. Without lignin, the decayed wood can be readily digested by ruminants.

Decomposition by polypores can take many forms. Next time you are out in the forest, check out the action behind the polypores. Take a closer look at wood decay where the real work of these fungi takes place.