Fungal Degradation of Wood

Subjects: Materials Science, Coatings & Films Contributor: Jeff Morrell

Wood durability researchers have long described fungal decay of timber using the starkly simple terms of white, brown and soft rot, along with the less destructive mold and stain fungi. These terms have taken on an almost iconic meaning but are only based upon the outward appearance of the damaged timber. Long-term deterioration studies, as well as the emerging genetic tools, are showing the fallacy of simplifying the decay process into such broad groups.

Keywords: Fungal Degradation of Wood, Wood durability, coating

1. Introduction

Wood is among the most durable cellulosic materials, but it can be degraded by a number of biotic and abiotic agents. These agents often act simultaneously making it difficult to completely separate causal agents. This review will concentrate on the role of fungi in degradation but will also discuss other agents as they relate to the overall process. Our discussion will focus on those fungi capable of degrading the primary cell wall polymers of cellulose, hemicellulose and lignin, but will also touch on the many mold and stain fungi that not only cause aesthetic concerns and disfigure coatings but can digest the stored compounds in the parenchyma cells and the pit membranes while promoting more limited damage to the structural elements of wood.

Wood poses a major challenge to organisms seeking to extract the energy from its polymeric structure. While the stored compounds in parenchyma cells are digestible by many organisms, accessing the more complex polymers is a key challenge. The chemistry and arrangement of the cellulose and lignin polymers in the wood cell wall sharply reduces the number of agents capable of causing damage. Many fungi are cellulolytic but are unable to unlock the chemistry of the lignin polymer that both enrobes and is interspersed with the cellulosic components of the lignocellulosic matrix. Only those fungi that have developed strategies to surmount the recalcitrance of lignin are able to fully extract the embodied energy of the lignocellulose cell wall.

2. Biotic Deterioration—Wood Decay and Requirements for Fungal Attack

Wood decay is largely caused by fungi that fall into categories depending on the appearance of the degraded wood which is, in turn, related to polymeric materials that are degraded. Brown rot decay is an informal name for the most common type of decay occurring in timber products. Fungi that cause brown rot depolymerize cellulose and hemicellulose (holocellulose) for digestion, while lignin is also depolymerized and modified before being rapidly repolymerized. The general categories of white rot fungi and soft rot fungi are the other major types of decay, and these are covered later in this review, as these fungal decays can be quite important in certain environments. Fungi are Eukaryotic organisms that are in the same Domain in the Tree of Life as plants and animals ^[1]. Species within other Domains in the tree of life comprising the Bacteria and Archaea can also live in wood. Some species of Bacteria have been shown to cause limited wood deterioration over long periods of time (several centuries), resulting in mechanical property loss in wood. Because of their minor importance in deterioration of structures, these microorganisms will not be considered further in this chapter, although we recognize that they are almost always present and have been suggested to play supporting roles in the degradation process including pre-conditioning of wood, and extractives detoxification. Bacteria are also active in long-term degradation of submerged wooden foundation piling, which typically occurs over many centuries ^[2]. Insects and some types of marine boring animals also can cause significant biodeterioration of wood under some circumstances, but deterioration by these animals is reviewed elsewhere ^[3].

For all fungi, spores (microscopic seeds) or other small fragments of the fungi must be produced and be transported either in the air, water or on other organisms (such as insects) to other pieces of wood where a new fungal colonization can initiate. Several requirements must be met for colonization to occur. In addition to the wood substrate itself, these include:

2.1. Water and Air

Typically, wood must be at or near the point where the wood cell wall is saturated with "bound" water, known as the fiber saturation point (FSP) for the fungal spores or fragments to germinate and initiate new fungal colonies. There is considerable debate about the minimum moisture level required for fungi to colonize and decay wood exposed out of soil contact ^[4]; however, because the filamentous strands of fungi (hyphae-see Fungal Physiology/Anatomy below) are required to be surrounded by a watery extracellular polysaccharide matrix (ECM) when wood is being attacked, some level of free moisture in the wood cell lumen is required to support fungal growth. In most cases, fungal decay can begin at approximately 30% moisture content (oven dry basis), reaching an optimum between 40 and 80%, then declining with increasing moisture levels above 100% as cell lumens begin filling with water and oxygen becomes limiting. Water is often the most important limiting factor in decay, and some paradigm-shifting current literature ^[5] focuses on the critical moisture content that allows fungal metabolites responsible for depolymerization of the wood polymers to diffuse within the wood cell wall. However, fungi require liquid water to initiate the secretion of metabolites required for decay, even in the absence of wood or other suitable substrates. Because the biosynthesis of these metabolites is a prerequisite for their diffusion within the cell wall, it is important for wood to first attain a moisture content where fungi can synthesize metabolites as well as one that supports robust ECM production surrounding and attaching the fungal cells to the wood cell wall to allow compounds to diffuse between fungus and the wood cell wall. In this regard, appropriate moisture conditions for fungal activity are required even before diffusional aspects of metabolites within the wood can be considered, and inhibition of fungal ECM production represents a fruitful area for future research in controlling fungal growth.

Wood in contact with the ground is frequently above the FSP and, in addition to having a fully saturated cell wall, contains liquid water in the lumens of the fibers. For fungal growth to occur in wood, the moisture content of wood must also not be too high to preclude adequate oxygen levels. Although fungi do not require as much oxygen as humans, they are aerobic organisms and wood decay fungi typically will not grow on wood that is completely saturated or submerged. Oxygen is rarely limiting for fungal attack, although complete saturation of logs by "ponding" (submersion in natural or artificial bodies of water) has been used to limit decay for periods of several months prior to processing in mills. In some cases, logs that sank during freshwater storage have been retrieved decades and sometimes even centuries later and processed with little deterioration noted. Many of these logs remain on the bottom of fresh water bodies and are in pristine condition because of the lack of oxygen, and also because relatively cold temperatures limited anaerobic bacterial deterioration.

2.2. Temperature

Temperature is critical for most physiologic reactions. Fungi may continue to grow as temperatures decline to levels near freezing ^[6], but reaction rates involved in both fungal metabolism and in the chemistry/biochemistry of wood depolymerization decline, and the decay process ultimately stops at freezing temperatures. Metabolic reactions increase with increasing temperature with most fungi having growth optima between 24 and 32 °C ^[3]. This is well within the temperature range inside most inhabited structures but specialized fungi can grow well outside this range. As a result, temperature is generally not a limiting factor in decay. For most decay fungi, fungal metabolism becomes more constrained as temperatures exceed 39–40 °C; however, some thermophilic fungi survive and have been observed to be active at temperatures exceeding 50 °C in specialized environments such as pulp chip piles ^{[Z][8]}. Exposure to temperatures about 56 °C results in permanent denaturing of proteins and DNA, effectively killing most non-thermophilic organisms.

2.3. Other Essential Components for Fungal Growth and Decay Potential

As noted above, a primary requirement for decay is a nutrient source which is typically the timber itself. This wood or surrounding supporting materials/soils must also contain various micronutrients and microelements, including nitrogen, that are essential to fungal growth and the decay process. There are vast volumes written about the relationships between decay and wood properties, e.g., [9]. Relatively few fungi have evolved the ability to degrade and utilize the three primary cell wall polymers, and the mechanisms by which they accomplish this task will be the subject of the remainder of this paper.

3. Future Needs and Opportunities

There is a critical need for an expanded understanding of how fungi attack and exploit current wood coatings to enable development of strategies to prevent premature damage to both the coating and the substrates they are intended to protect. Integrated technologies are needed to reduce fungal attack and enhance coating performance against physical and environmental factors. For example, enhanced UV protection coupled with better matching of long-term coating elasticity with expansion/contraction characteristics of the wood will limit the development of coating defects that fungi are

known to exploit. Enhanced abrasion resistance and improved ability to shed environmental residues deposited on the coating will limit the ability of fungi to grow on and into the coating. Enhanced water repellency helps coatings shed water and reduces the time that a surface remains wet enough to permit fungal growth.

Biocides such as 3-iodo-2propynyl butyl carbamate and chlorothalonil have long been a component in many coating systems both for protecting the system against microbial attack prior to application as well as limiting fungal discoloration afterwards. While biocides ranging from tin and copper compounds to thiabendazoles are effective, they are not compatible with all polymeric systems. Novel approaches such as non-biocidal treatments that discourage attack by preventing fungal attachment to surfaces and preventing the development of biofilms have shown promise in the laboratory ^[10], but utilization of these coatings will likely remain limited to medical applications. While agricultural applications for this type of technology are proposed, it remains to be seen if cost-effective products can be developed that meet consumer needs for long-lasting surface protection under extreme UV exposures.

At present, a majority of coatings research remains proprietary, making it difficult to accurately assess the state of the science. However, market observations suggest that better coatings systems are still needed, and that fungal and UV resistance of coating systems has not dramatically improved in many consumer-available coatings in the past 20 years. The lack of long-lasting UV and moisture resistant coatings leads to premature replacement of functional structures, especially decking and this, in turn sharply reduces the normally positive life cycle attributes of timber. Developing a better understanding the mechanisms underlying fungal degradation of substrates, and the mechanisms involved in new biocidal and non-biocidal coating treatments will be essential for creating integrated coatings systems capable of limiting fungal attack while providing long term protection against environmental factors.

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