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Fungi at work 4: Recycling leaves and wood

David Moore: World of Fungi www.davidmoore.org.uk/index.htm

Ever wondered what happens to all the leaves that fall from the trees, the branches that fall to the ground in storms, or what happens to the wood when a tree dies? Somehow there's never a build-up of all this organic matter; but what happens to it? Where does it go?

Well, it's broken down and recycled. Many small organisms such as bacteria, insects, worms and many types of fungi break down the plant material. The resultant humus enriches the soil; it's nutrient rich and can be used by plants for their growth.

The components that provide strength to plant cell walls are the polymers: cellulose and lignin. Fungi are the only organisms capable of breaking down both cellulose and lignin.

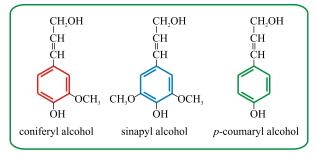
Cellulose is a polymer of glucose that forms incredibly strong fibres. Brown rot fungi break down cellulose. They are called 'brown rot' fungi because, following cellulose decomposition, the lignin remains intact, so the wood keeps its brown colour. The enzymes released by brown rot fungi break the cellulose chains into single molecules of glucose sugar that can be reused by the fungus.

Lignin is the second most abundant natural polymer on Earth after cellulose. Fungi that break down lignin are called 'white rot' fungi because the wood becomes lighter in colour as the lignin content decreases. White rot fungi degrade lignin by producing oxidising enzymes that are released from their hyphae - they 'burn' the wood in an enzymecontrolled way. Lignin contains phenols and the white rot fungi are the only organisms that can deal with them.

The principal function of lignin in the plant is to protect the cell wall by providing resistance to microbial degradation. It does this by having an unusual polymer structure. Most polymers in living cells (polysaccharides, proteins, lipids) are made by condensation reactions joining the monomers together (and expelling a molecule of water in the process). This structure allows the polymer to be cleaved by enzymes called hydrolases that catalyse the hydrolysis of the chemical bonds, effectively reinserting the water molecules and breaking the bonds holding the polymer together.

Lignins are very different. They are made from three 'phenylpropanoid alcohols', which are joined together using ether linkages and carbon-carbon bonding (Fig. 1). Above all, note the word 'phenyl'; it means that every one of the monomers brings a benzene ring into the polymer's structure. Of course, the monomer is also an alcohol, which contributes a few hydroxyl groups that can take part in cross links to other polymers (polysaccharides and proteins).

Now, step back and look at this chemical structure from the point of view of a microbe trying to extract some nutrition from it. How many foods do you know that are full of benzene rings? How would you metabolise a benzene ring? In your kitchen, benzene rings, especially phenols, are more likely to be found in disinfectants than foods, and that's the key to the *function* of lignin. Any microorganism that succeeds in degrading a lignin molecule only produces anti-microbial disinfectants. This is what makes lignin so resistant to microbial attack.



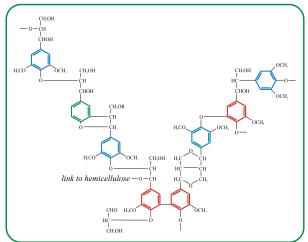


Fig. 1. Structure of lignin. The top panel shows the three phenylpropanoid alcohols used to construct the lignin polymer. These are also called monolignols. They are colour coded to indicate how they probably contribute to the lignin polymer illustrated below. The proportions of these three alcohols differ between the lignins of angiosperms and gymnosperms, and between lignins of different plant species. The bottom panel shows a schematic formula of the polymer structure of angiosperm lignin. Note the way the three phenylpropanoid alcohols are used in the structure. Note also the predominance of ether linkages, the carbon-carbon bonds, and the presence of a few hydroxyls that allow cross links to other polymers.

Image © David Moore.

Other microbes couldn't break down lignin, but the fungi eventually found a way. In the course of their evolution, a range of enzymes arose that use oxidative processes to break the carbon-carbon and ether bonds that join subunits together in lignin. As you might expect, several enzymes are involved; there are three broad classes. First are **oxidases** that generate hydrogen peroxide. Then there are **peroxidases** and **laccases** that use the hydrogen peroxide for oxidative lignin breakdown. They involve four chemical reactions:

- · cleavage of ether bonds between monomers;
- · oxidative cleavage of the propane side chains;
- · demethylation (mainly done by the laccases);
- benzene ring cleavage to ketoadipic acid which is fed into the tricarboxylic acid cycle as a fatty acid.

Although an ability to digest simple, synthetic lignins has been reported for a few bacteria, only certain types of fungi a few ascomycetes and several basidiomycetes - have evolved to be capable of degrading the more-complex, natural lignins. These fungi found a way to open the benzene rings of all those phenols and use them to make ATP and, as a result, have important roles in the recycling of nutrients in the natural world.

Without these fungi, old plant material would not decay, and the soil nutrients would be locked into an ever-accumulating mass of undegradable biomass. Without fungal wood decay, the world would fill up with dead timber.

This is just what happened in the vast swamp forests of the Carboniferous geological time period. During the late Palaeozoic era, the Carboniferous period lasted from about 360 to 300 million years ago, and its swamps produced the major coal seams around the world.

Technically, all fungi are chemo-organoheterotrophs, meaning that they derive their carbon, energy and electrons (with which they do further chemical work) from a wide variety of organic sources.

There are several intriguing side issues to fungal degradation of timber that you might like to think about.

Decay of timber in buildings

Not all timber is in forests, and fungal spores are all around us. A wood-degrading organism growing in the timbers of your house roof is only doing what comes naturally to it, but it is certainly a damaging pest as far as you are concerned. The dry rot fungus, *Serpula lacrymans*, is by far the most serious cause of decay of building timbers in the UK and northern Europe (Fig. 2), yet the species has only been found in the wild in the Himalayas, where it is typically found in forest conifers.



Fig. 2. The dry rot fungus, *Serpula lacrymans*, growing in the wall panelling (A) and roof beams (B) of an infested basement.

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When trees from these Himalayan forests were harvested for constructing buildings, the dry rot fungus migrated indoors, adapting to thrive in man-made environments. Then the international trade in timber gave it the wide distribution in buildings in the temperate zones that it enjoys today. All kinds of timber are liable to attack; any wood will decay unless kept dry. So, the mantra for healthy constructional timber is this: *keep it dry and well-ventilated*.

Not all wood deterioration results in destruction of the timber. The sap-stain fungi discolour wood without lessening the strength of the timber. Some staining of this sort causes pleasing colour patterns of dark winding lines and streaks (called zone lines) that can be highly decorative.

Agriculture and gardening by insects

Several insects have established mutualisms with wood decay fungi that are so close that they are called gardening insects. 'Parasol' or leaf-cutting ants in Central and South America actively inoculate their nests with a fungus (*Leucocoprinus gongylophorus*). They then cultivate the fungus by providing it with pieces of leaves (Fig. 3), pruning the hyphae and removing intruder fungi. As a reward, the fungus produces special hyphal branches containing nutrients for the ants.



Fig. 3. A leaf-cutter ant worker transporting its cut leaf to the nest. The large size of the leaf fragments they carry is the origin of their alternative common descriptive name: 'parasol ants'.

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In Africa and Asia, some species in the termite subfamily Macrotermitinae also maintain a 'garden' of fungi belonging to the genus *Termitomyces*. Nourished by digestion of dead plant material brought back to the nest by the worker termites, the fungus provides more digestible food for the termites. Woodboring beetles (Ambrosia, Bark and Pine beetles) are other examples of an association between insects and fungi. Adult female beetles burrow into the trunks of living trees and lay eggs on the tunnel wall, inoculating the wood with fungal material carried from a previous nest. The fungal mycelia grow in the wood and provide food for the larvae when the eggs hatch.

Wood decay fungi in forests release greenhouse gases

Photosynthetic carbon capture by trees is widely thought to be possibly our most effective strategy to limit the rise of CO₂ concentrations in the atmosphere, with several ambitious targets to promote tree planting on a global scale 'to save the atmosphere'. Unfortunately, forests don't only contain trees that can store gigatonnes of carbon in the wood they make; forests also contain wood-decaying fungi that digest dead wood and release greenhouse gases in the process, especially CO₂ but even including chlorinated hydrocarbons. On a global scale, decomposition of seasonally-shed leaves, petals, ripe fruit and dead wood releases billions of tons of CO₂ into the atmosphere **each year**; a similar amount, in fact, to the annual CO₂ emissions from burning fossil fuels!