21st Century Guidebook to Fungi, Second Edition of the online version, by David Moore, Geoffrey D. Robson and Anthony P. J. Trinci

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Chapter 10: Fungi in ecosystems

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Chapter 10: Fungi in ecosystems

Fungi make crucial contributions to all ecosystems because of their abilities as decomposers. One of the most important Kingdom-specific characteristic of fungi is that they obtain their nutrients by external digestion of substrates. In the real world, though there is some digestion and chemical modification of ***inorganic*** substrates (see Chapter 1, CLICK HERE to view a reminder), the bulk of the substrates that fungi recycle are the remains of animals and, most particularly, plants. In this Chapter we give an account of the ways in which fungal hyphae obtain, absorb, metabolise, reprocess and redistribute nutrients.

In doing this, fungi obviously contribute to recycling and mineralisation of nutrients and in what follows we will describe the enzyme systems that enable this activity. Our description is relatively brief, and more details can be found in the premier text on fungal physiology (Jennings, 2008). For clarity we have to describe separately the enzyme systems involved, and in an order that we have chosen for descriptive purposes. This introduction is intended to convey the impression that for most fungi in most circumstances the initial nutritional step is the excretion of enzymes able to convert polymers to the simple sugars, amino acids, carboxylic acids, purines, pyrimidines, etc., that the cell can absorb. Also, in most circumstances most fungal mycelia will be carrying out all of these biochemical changes simultaneously.

In this Chapter we will see how fungi contribute to ecosystems. How they breakdown the polysaccharides cellulose, hemicellulose, pectins, chitin, starch and glycogen. Their (unique) ability to degrade lignin, and the ways they digest protein, lipids, esters, phosphates and sulfates.

The flow of nutrients is dealt with in terms of transport and translocation; and in the final two Sections we deal briefly, but comprehensively, with the main pathways of primary (intermediary) metabolism as well as secondary metabolites, including commercial products like statins and strobilurins.

10.1 Contributions of fungi to ecosystems

Wood, that is, plant secondary cell wall, is the most widespread substrate on the planet. Except for lignin (see below), the bulk of plant cell biomass consists of the polysaccharides cellulose, hemicelluloses, and pectins in varying proportions depending on the type of cell and its age. Even though wall components predominate, the cytoplasm of dead cells contributes lipids, proteins and organic phosphates to the remains; however, wood itself is relatively poor in nitrogen and phosphorus. Plant biomass does not consist of neatly isolated packets of polysaccharide, protein and lignin; these three (and other materials) are intimately mixed together, so that it is better to think of the degradation of lignocellulosic and/or lignoprotein complexes.

A typical **agricultural residue**, like cereal straw or sugar cane bagasse, contains 30-40% cellulose, 20-30% hemicellulose and 15-35% lignin. Organisms that contribute to recycling may differ widely in their ability to degrade components of this mixture. On this sort of basis wood-decay fungi have been separated into white-rot, brown-rot and soft-rot species. The white-rot fungi (about 2 000 species, mostly Basidiomycota) can metabolise lignin, on the other hand, brown-rot fungi (about 200 species of Basidiomycota) degrade the cellulose and hemicellulose components without much effect on the lignin. Soft-rot species (mostly soil-inhabiting Ascomycota) have rather intermediate capabilities, being able to degrade cellulose and hemicellulose rapidly, but lignin only slowly. These differences in behaviour are a reflection of the different enzymes produced by these organisms and serve to emphasise that the organisms must digest complexes of potential nutrient sources and assemble panels of different enzymes to do so.

Bacteria and fungi are responsible for cellulose digestion in nature, but the ability to degrade lignin is restricted to fungi; specifically, Basidiomycota and a few Ascomycota. Lignin is a highly branched phenylpropanoid polymer (see Section 10.7, below), and the ability to degrade a polyphenolic means that as well as contributing to nutrient recycling fungi can also help to compensate for damage done to the environment by industrial operations; a process called **bioremediation** with fungi. Many wastes are hazardous because they contain tannins and phenolics, which are toxic to plants and animals, and this applies to **agricultural wastes**, such as residues from extraction of oils such as cotton, rape, olive, and palm oils, fruit processing residues, like citrus wastes, as well as wastes contaminated with pesticides.

Indeed, the agricultural industry produces vast quantities of wastes: on average, world agriculture currently loses 40% of its primary production to pests and diseases, and then throws away more than 70% of what's left because the crop always represents so little of what is grown. Remember, the 'crop' may only be the seeds of the plant that is grown, or even only a portion of the seed, like its oil content. It is typical for 80 to 90% of the total biomass of agricultural production to be discarded as waste. Whether this waste is ploughed-in, composted or otherwise left to rot, it is up to the fungi in the environment to recycle the bulk of these wastes.

There are three major fungal nutritional modes: probably the majority are ***saprotrophs*** for which the substrates are dead organic materials not killed by the fungus itself. ***Necrotrophs*** invade living tissues which they kill and then utilise, whereas ***biotrophs*** exploit host cells which remain alive. In the latter case one might expect that though local digestion of host tissue may be necessary for penetration or establishment of the pathogen, only simple nutrients would be removed from the host because of the damage which would be inflicted on the host by large-scale digestion of polymeric cell constituents. Biotrophs may be host-specific, but saprotrophs and necrotrophs generally have a very large range of habitats open to them, and in the majority of these polymeric sources of nutrients predominate.

This predominance of polymers as sources of nutrients is obviously true for such materials as herbaceous **plant litter**, wood and herbivore dung. As we have just mentioned, immediate plant litter, though rich in carbon, is poor in nitrogen and phosphorus. Digested litter (a euphemism for herbivore dung) is relatively enriched in nitrogen, nucleic acids, vitamins, growth factors and minerals, since in passage through the intestine it accumulates the remains of bacteria, protozoa and other microorganisms. The composition of animal tissue varies enormously according to the particular organ system considered, but in nature most animal remains will be eaten by animal scavengers too rapidly for any microbes to be able to compete, so the microorganisms will be left with the parts, 'skin, gristle and bone', that other organisms cannot reach.

Nitrogen in the soil is mostly in the form of organic compounds; the proportion of nitrogen occurring as ammonium and nitrate (the nitrogen sources commonly added to synthetic agar cultivation media) or nitrite rarely exceed 2% of soil nitrogen, although some clay soils do trap more ammonium. Inorganic nitrogen compounds only predominate in agricultural soils which are repeatedly treated with chemical fertilisers. Nitrite is not usually detectable and nitrate content is usually very low in natural soils because these salts are so readily leached out by rain, so in most cases exchangeable-ammonium on clay particles and the organic nitrogen provide saprotrophs with their nitrogen. In most surface soils, 20-50% of total nitrogen occurs in proteinaceous form and 5 to 10% as combined and complexed amino sugars. Amino sugars also contribute to the carbohydrate component of the soil, which represents 5 to 16% of total organic matter. Here, again, though, most soil carbohydrate is polymeric; simple sugars make up less than 1% of soil carbohydrate but cellulose can account for up to 14% and chitin is also well represented in view of the amino sugar content. About 50-70% of total phosphorus in soil is organic, mostly as phosphate esters related to or derived from compounds like nucleic acids, inositol phosphates and phospholipids.

Inorganic forms of **sulfur** may accumulate in some soils (e.g. as calcium and magnesium sulfates in arid regions; calcium sulfate co-crystallised with calcium carbonate in calcareous soils) there is little inorganic sulfur in the surface horizons of soils in humid regions. Organic sulfur occurs in the form of methionine and cystine (and derivatives), and sulfate esters, including sulfated polysaccharides and lipids.

Extracellular enzymes are produced within the cell but act outside it. Consequently, they must be secreted across the plasmalemma. The processes involved in protein translocation across membranes are very similar in all eukaryotes. Polypeptides destined for secretion are identified by short amino terminal transient 'signal' sequences which consist of uninterrupted stretches of at least six hydrophobic amino acid residues. The signal sequence is in the first part of the polypeptide to be synthesised on the ribosome and, as its hydrophobicity confers an affinity for the lipid environment of a membrane bilayer, the signal sequence 'targets' the ribosome producing it onto the endoplasmic reticulum membrane (CLICK HERE to view a reminder).

Some of the extracellular enzymes which are produced are soluble and are freely dispersed in fluid films surrounding the hyphae, but others are fixed in space by being bound to the hyphal wall, extracellular matrix or to the substrate itself. This natural **immobilisation of enzymes** is advantageous to the producing fungus because it localises substrate degradation to the immediate vicinity of the hypha, so ensuring that the organism producing the enzyme has advantage in the competition with surrounding organisms for the soluble nutrients produced by the enzyme activity. In this way the fungus can exert a degree of control over its immediate environment.