MASARYK UNIVERSITY, FACULTY OF SCIENCE

DEPARTMENT OF BOTANY AND ZOOLOGY

FUNGAL ECOLOGY

(sometimes with special regard to macromycetes)

Fungi and their environment • Life strategies and interactions of fungi • Ecological groups of fungi, saprotrophs (terrestrial fungi, litter and plant debris, wood substrate, etc.) • Fungal symbioses (ectomycorrhiza, endomycorrhiza, endophytism, lichenism, bacteria, animal relationships) • Parasitism (parasites of animals and fungi, phytopathogenic fungi, types of parasitic relations) • Fungi in various habitats (coniferous forests, broadleaf forests, birch stands and non-forest habitats, fungal communities) • Fungal dispersal and distribution • Threat and protection of fungi

(the study material has not been corrected by native speaker)

Wood decomposition (decay) is performed by **lignicolous fungi** – mainly *Basidiomycota*, mostly non-gilled fungi (former order Aphyllophorales s. l.). The first in succession re saproparasites, already colonising living trees and then able to live in dead wood; they are followed by primary saprotrophs (they directly decompose wood mass, e.g. *Fomitopsis pinicola*) and secondary saprotrophs (they take nutrients from the matter decomposed by primary saprotrophs, e.g. *Pycnoporellus fulgens*).

Fomitopsis pinicola

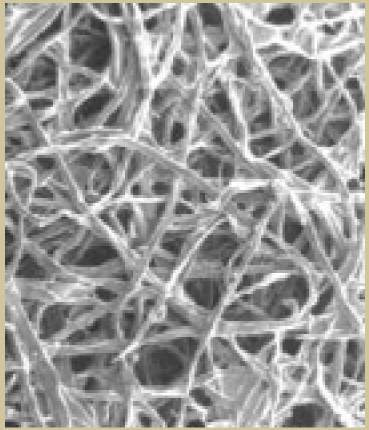
http://www.mykonet.ch/images/Porlinge/fomitopsis_pinicola_rotrandiger_baumschwamm300.jpg

Pycnoporellus fulgens

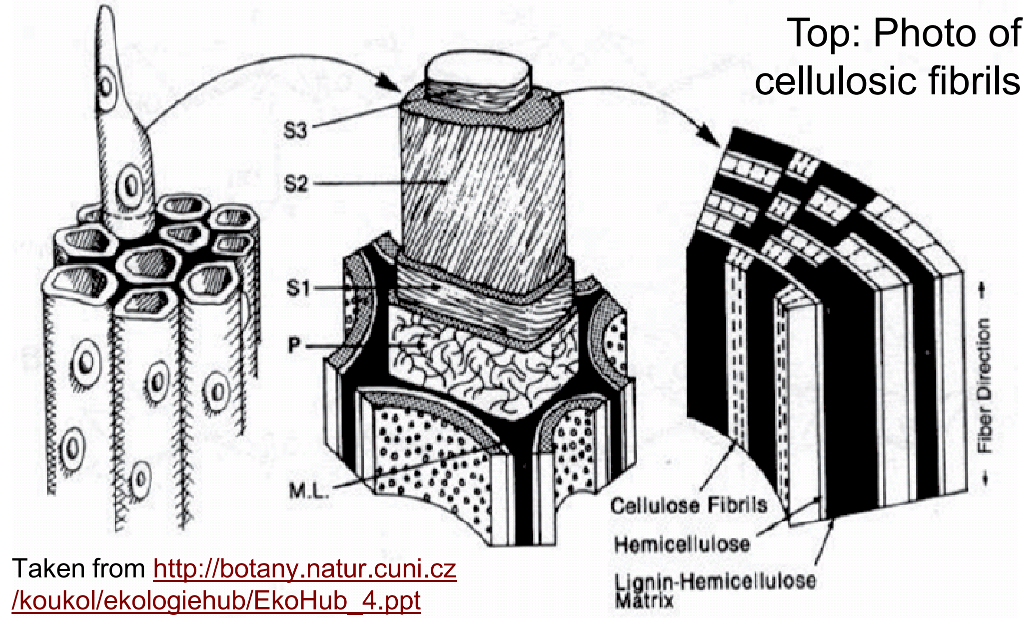
http://grzyby.strefa.pl/Pycnoporellus_fulgens.html

Specific conditions can prevail in wood – still standing trunks or branches on the trees are drying out (they have lower water potential than later, when they fall into litter) and inside the trunks there can be up to 20 times more CO_2 than O_2. The course of wood decomposition can be divided into three stages: substrate colonisation, decay process and incorporation of its products into the soil.

Wood substrate contains cellulose, hemicelluloses (mixed polymers with other carbohydrates - xylose, etc.) and lignocellulose (cellulose microfibrils coated with hemicelluloses and embedded in lignin) – it is a rich source of carbon, but poor in other basic nutrients (C/N ratio 300:1 up to 1000:1). Lignicolous fungi are adapted to this – the degradation of lignin may be important not so much for the nutrient recovery itself, but for release of covalently bound nitrogen (its deficiency inhibits proteosynthesis and hyphal growth => degradation of cellulose is alternated by ligninolysis => nitrogen and cellulose components are released, which are reused until storage substances are depleted around the hypha => further degradation of lignin and so on). Lignicolous fungi must also deal with presence of tannins, terpenes or flavonoids, which are toxic to fungi.



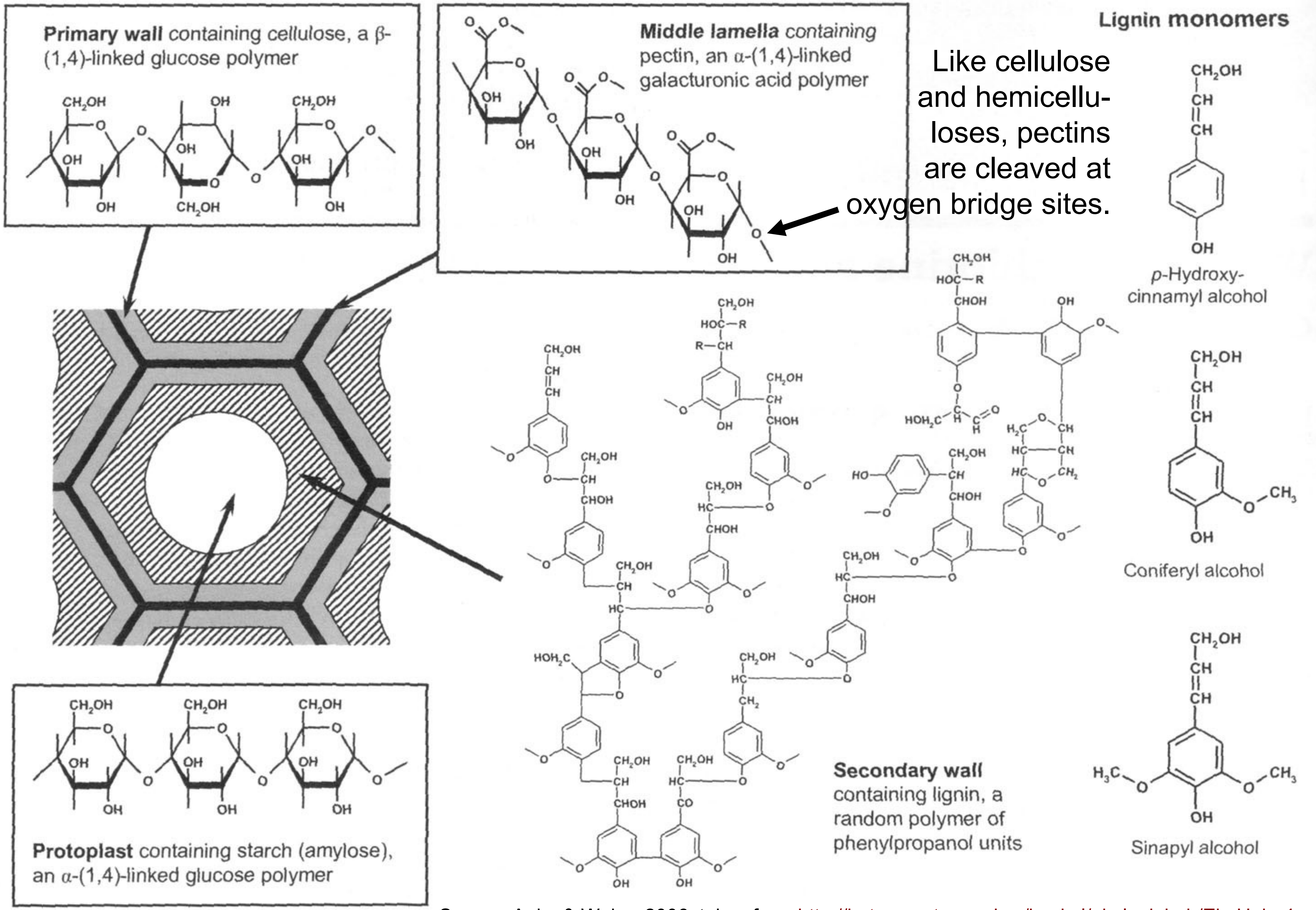
Top: Photo of cellulosic fibrils



Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Structure of wood and its components

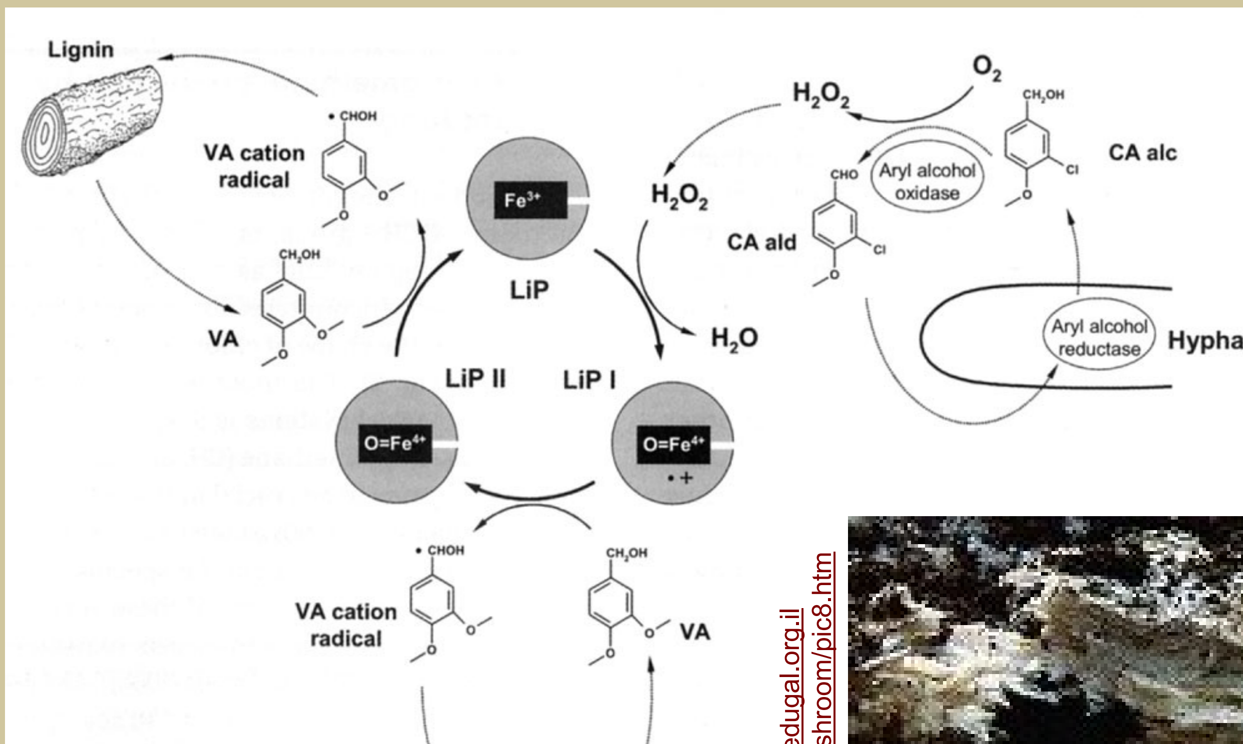
Figure 1.1: A schematic illustration of wood structure showing adjacent tracheids, each ca 30 μm in diameter (left), wood cell wall layers (middle): P - primary wall, S1 - S3 - secondary cell wall layers, M. L. - middle lamella, and lignocellulose complex of the secondary cell wall (right) (Kirk and Cullen, 1998).



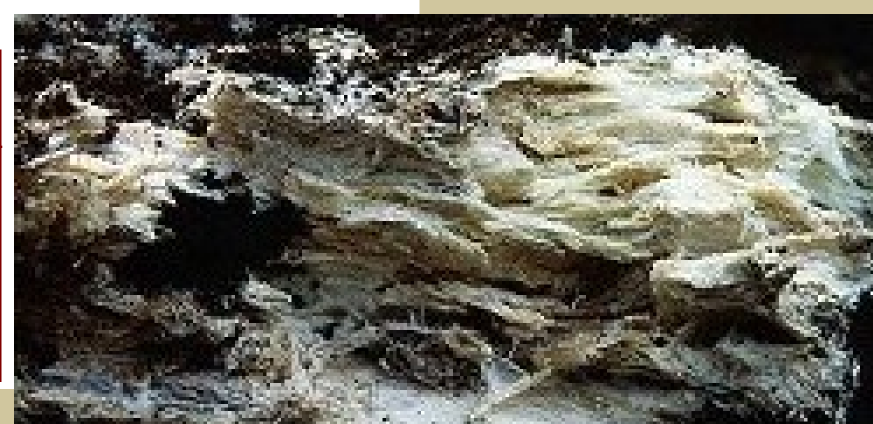
Like cellulose and hemicelluloses, pectins are cleaved at oxygen bridge sites.

Source: Anke & Weber 2006; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

The mechanisms of lignocellulose degradation are best studied on the model species *Phanerochaete chrysosporium* (see photo). **Lignin** has a strongly irregular structure that does not allow direct contact with the active sites of enzymes – the oxidation of lignin is therefore allowed by free radicals: veratryl alcohol produced by lignin peroxidase and Mn^{2+} produced by manganese peroxidase; these reactions require H_2O_2 as an electron donor. Furthermore, lignin fragments can be directly cleaved by laccase (interestingly: this enzyme is also secreted by plant roots) or the fragments (e.g. syringyl, guaiacyl, p-hydroxyphenyl) can become radicals capable of further cleavage of lignin. Other enzymes also participate in the degradation of ligno-cellulose – hydrolases (cellulases, cellobiases), cutinase, pectinase, amylase, lipase, ...

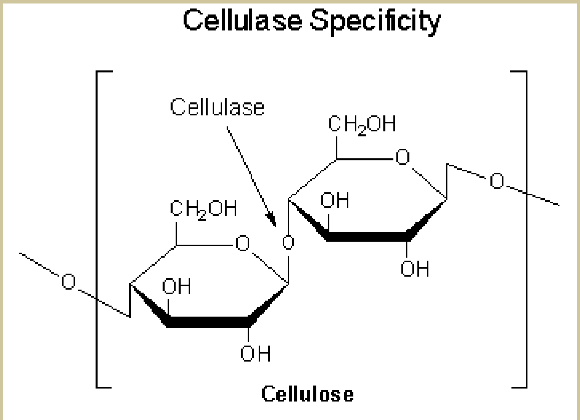


Source: Anke & Weber 2006; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt



http://www.edugal.org.il/chazav/mushroom/pic8.htm

Lignin, a three-dimensional polymer formed by alcohol units (three types of cinnamic acid alcohols – coumaryl alcohol, sinapyl alcohol and coniferyl alcohol, see scheme above) with admixture of nonstructural phenolic substances (vanilla, gallic, ferulic acid; flavonols, catechin, catechol, pyrogallol), terpenes, resins, etc., occurs not only in wood, but also in herbal parts of plant bodies; each plant family has a specific ratio of building blocks.



http://www.sigmaaldrich.com/life-science/metabolomics/enzyme-explorer/learning-center/lysing-enzymes.html

Cellulose consists of glucose units linked by a β-(1-4)-glycosidic bond; it may be in crystalline or amorphous form. Its breakdown involves endoglucanase, cellobiohydrolase (exocellulase) and β-glucosidase.

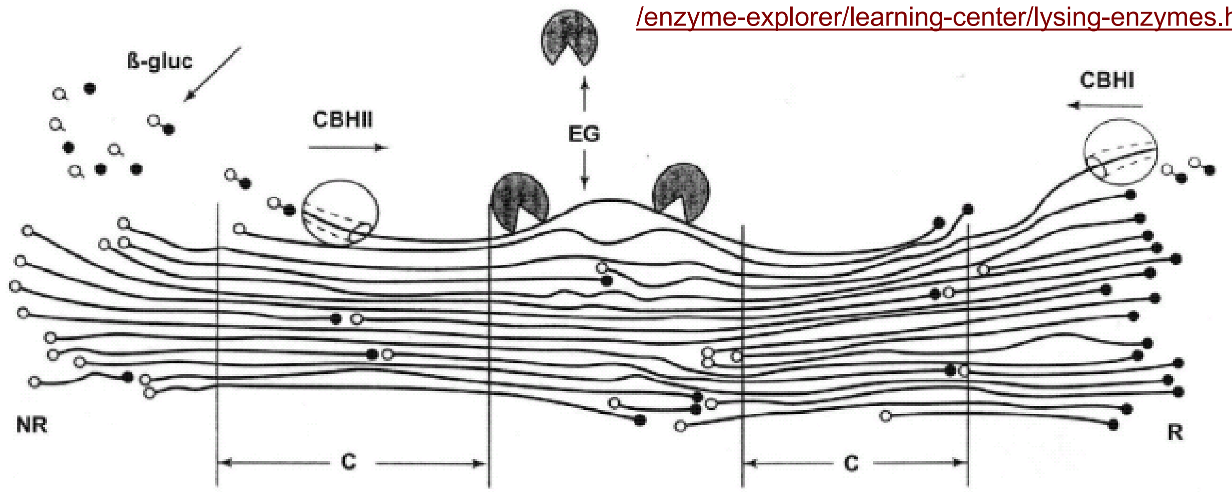


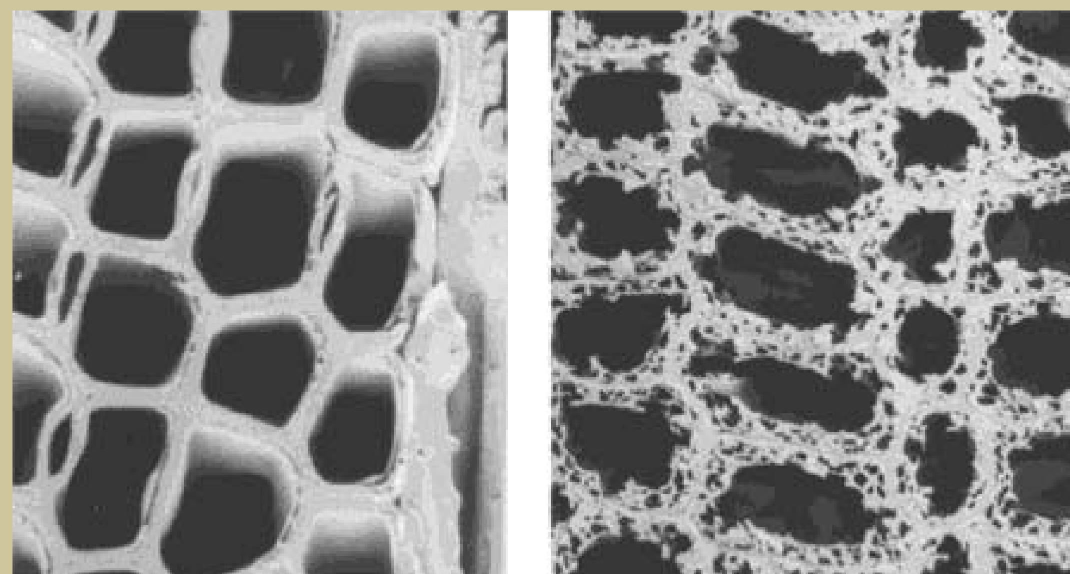
Figure 1.2: A schematic view of the cellulose structure and action of the cellulolytic enzymes: EG - endoglucanase, CBH - cellobiohydrolase, β-glucosidase in *Trichoderma reesei*. C defines the highly ordered crystalline region, R the reducing ends (filled circles), and NR the nonreducing ends (open circles) (Teeri, 1997).

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Lignicolous fungi are divided into two groups according to enzymatic equipment – the first causes soft and brown rot, the second white rot.

• The first fungi colonising wood, especially very moist wood, cause **soft rot** (SR) – in principle, it is a „steaming“ of wood at higher temperature and humidity, during which cellulose and hemicelluloses are degraded, while lignin is only slightly disturbed (side chains are split off); the wood breaks in a cube structure. *Deuteromycota* (*Acremonium, Phialophora, Cephalosporium, Doratomyces*, even aquatic *Tricladium*) are mainly involved here, also teleomorphic *Ascomycota* (*Chaetomium*), to a lesser extent *Basidiomycota* (*Mucidula mucida*).

http://forestpathology.coafes.umn.edu/microbes.htm; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt



SEM image of normal cedar wood (left) and cedar from the tomb of King Midas which was subject to soft rot deterioration. Filley et al. (2001).

http://palaeos.com/fungi/ascomycota/ascomycota.html

• Pectins, cellulose and hemicelluloses are degraded by fungi which have (similarly to the previous case) cellulase and cellobiase and cause destructive decomposition; the wood is coloured with released lignin (which is not degraded or only minimally), resulting in **brown rot** (BR; also the term red rot may be used).

Wood decreases in weight and volume, breaks and crumbles, often in cube structure. Brown rot is caused e.g. by *Gloeophyllum, Fomitopsis, Piptoporus, Postia, Laetiporus, Phaeolus* or *Conio-phoraceae*, total about 10% of lignicolous basidiomycetes.

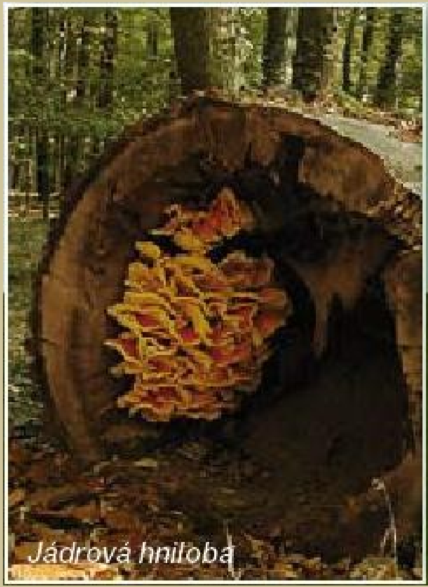
http://forestpathology.coafes.umn.edu/microbes.htm; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

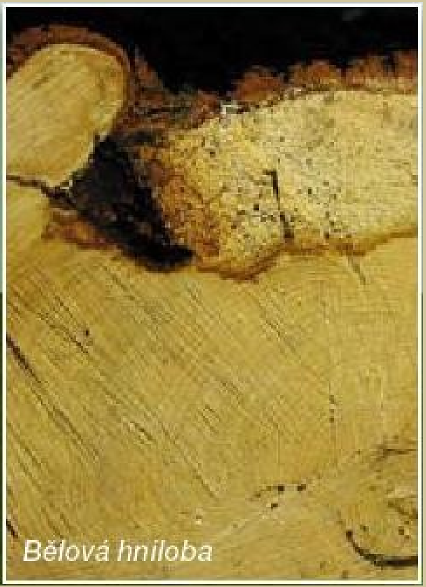
Top right: brown-red rot caused by *Laetiporus sulphureus*; bottom: brown rot caused by *Leucogyrophana mollusca*.

Photo A. Lepšová, http://botanika.bf.jcu.cz/mykologie/galerie/Basidio/Aphyllophorales/Laetiporussulphireushnil1.jpg
..../mykologie/galerie/Basidio/Aphyllophorales/Leucohygrophanamolluscahnil1.jpg

• In contrast, fungi which have the strongest enzymatic equipment, including polyphenol oxidases (ligninolytic enzymes; lignin is degraded together with cellulose or hemicellulose), cause corrosive decay. The wood tissue is completely decomposed, it does not disintegrate in a cube (holes can be formed in the spring wood of the annual ring => white pocket or honeycomb rot), the wood loses colour and **white rot** (WR) is formed. It is caused mainly by basidiomycetes (*Pleurotus, Phanerochaete, Stereum, Onnia, Phellinus, Ganoderma, Daedalea, Fomes, Trametes*, *Polyporus squam.*), and ascomycete *Xylariaceae* (*Xylaria, Hypoxylon, Ustulina, Daldinia*).

Left to right: white rot of *Fomes fomentarius,* white pocket rots of *Trichaptum abietinum* and *Phellinus nigrolimitatus*. Anna Lepšová,
http://botanika.bf.jcu.cz/mykologie/galerie/Basidio/Aphyllophorales/Fomfomentariushnil.jpg
http://botanika.bf.jcu.cz/mykologie/galerie/Basidio/Aphyllophorales/Trichaptumabietinumhnil.jpg
http://botanika.bf.jcu.cz/mykologie/galerie/Basidio/Aphyllophorales/Phellinusnigrolimitatushnil.jpg





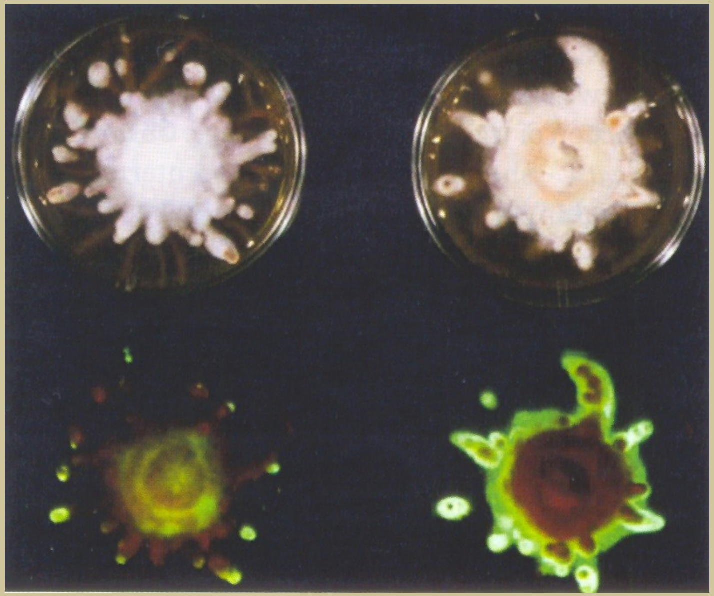
Sapwood rot (right) spreads from sap- to heartwood (i.e. towards trunk inside), while heartwood rot (left) begins in the centre and can lead to cavity formation.

http://www.biolib.cz/DOC/horak-proc-je-dulezite-mrtve-drevo.pdf

Even slower than in wood, bark decay takes many years; pyrenomycetes are mainly involved, mechanically tearing the bark by their stromata.

Source: Weitz 2004;
taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

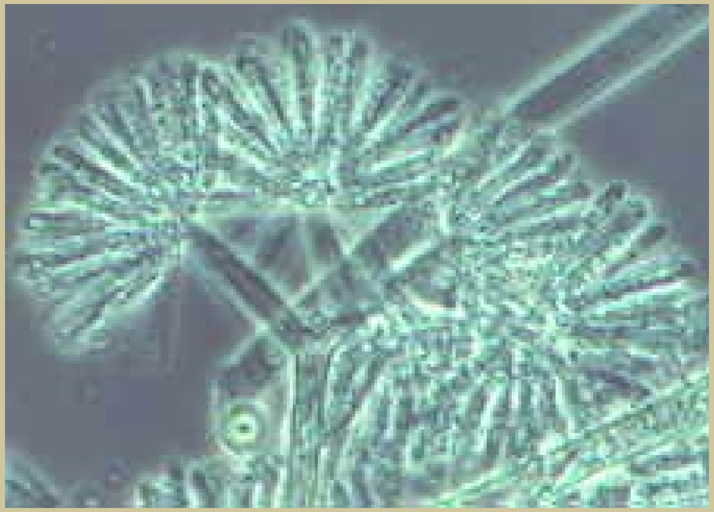
So far, the phenomenon of **bioluminescence** is only known in lignicolous basidiomycetes (*Panellus*, *Pleurotus*, *Armillaria*) – it occurs when oxygen reacts with luciferin with the participation of the enzyme luciferase.
It activates DNA repair and detoxification of radicals, which are formed, for example, during the lignin degradation. The possible ecological significance has not yet been clarified – there are hypotheses of attracting invertebrates (to spread spores) or, conversely, a warning for nocturnal fungicolous invertebrates.



Bioluminiscence of *Armillaria mellea* cultures in the dark (expozition 16 hours).

A special case is **coprophilic fungi**, growing mainly on the feces of herbivores. Excrement is a fairly ideal nutrient medium, at least initially sufficiently moist and with a neutral pH (coprophilic fungi, unlike others, prefer a pH higher than 6), which contains carbohydrates (oligosaccharides and structural polysaccharides), nitrogenous substances, minerals, vitamins, fatty acids, ...

The community composition on excrement is influenced by the animal species and its food (food selection and digestion), environmental humidity, contact with soil and surrounding vegetation, coprophilic insects, interactions with other microorganisms. With the changing composition of the substrate, a succession similar to that of soil saprophytes is applied here – first zygomycetes (*Mucor*, *Pilobolus*, *Piptocephalis* /this genus may rather contain parasites on coprofiles/) – fungi capable to quickly utilise simple sugars, „ending“ after their depletion), ...



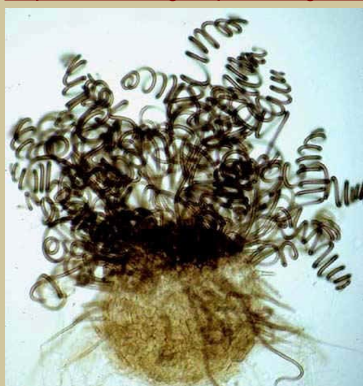
Left: *Piptocephalis* (*Zoopagales*), right: *Pilobolus* (*Mucorales*), photos of sporangia.

http://www.mycolog.com/chapter11a.htm; http://www.uoguelph.ca/~gbarron/MISCELLANEOUS/pilobolu.htm (George Barron)

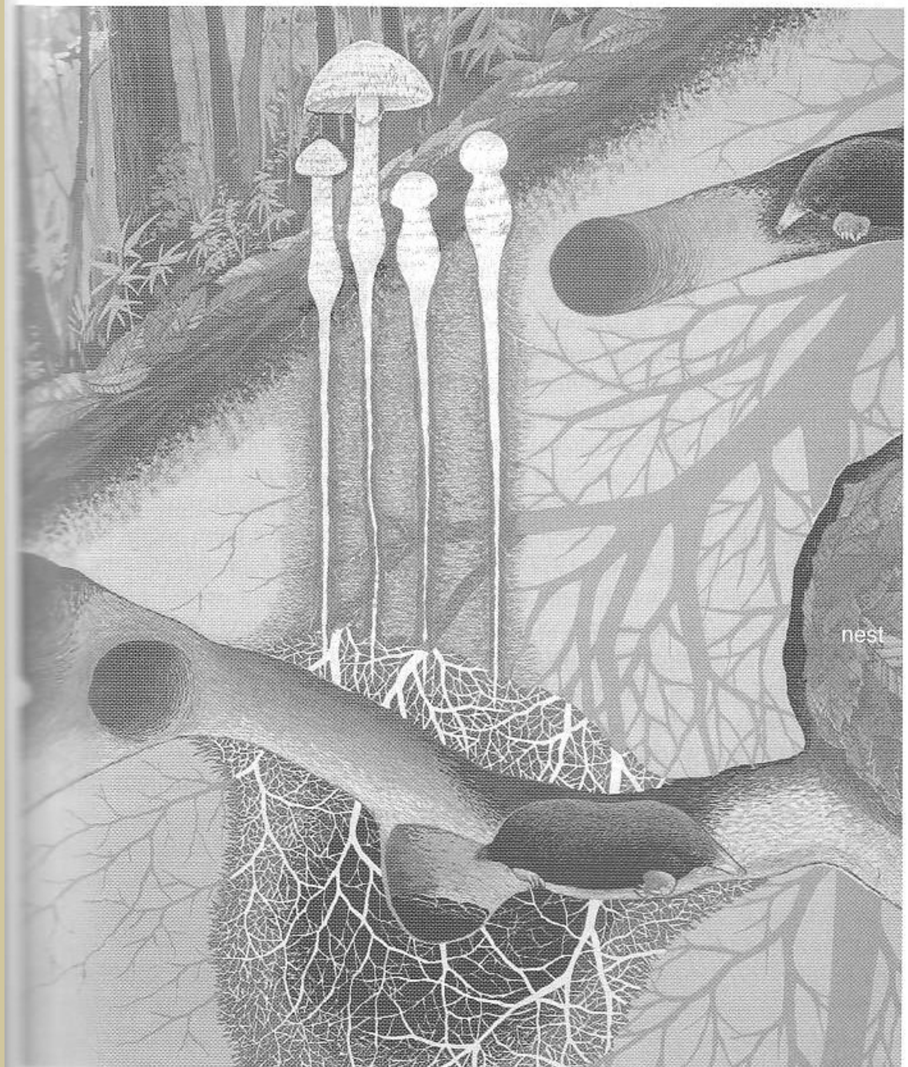
... followed by ascomycetes (*Ascobolus*, *Podospora*, *Sordaria*, *Chaetomium*) and basidiomycetes (first *Coprinus*, later *Bolbitius*, *Psathyrella*, *Panaeolus*, *Nidularia*).

Top left: *Chaetomium*, bottom left: *Sordaria* (both perithecia); centre: *Ascobolus* (bottom: apothecia, top: cross section of apoth.); bottom right: primordia of *Coprinus*, top right: *Panaeolus ovatus*.

http://www.mold-help.org/content/view/412/ .../chapter11a.htm
http://www.uoguelph.ca/~gbarron/MISCE2002/sordaria.htm ↓



Their mycelia probably develop continuously, but fructify gradually; later-stage fungi prevail over time due to stronger enzymatic equipment and often antibiotic action => suppression of earlier stages (hyphal interference, known in basidio-mycetes – for example, degeneration of *Pilobolus* cells and stopping the formation of sporangiophores was observed after contact with *Coprinus* mycelium).
For comparison: *Pilobolus* was noted on horse manure after 2 days, *Ascobolus* after 7 days and *Coprinus* after 2 weeks after defecation; the total decomposition of excrement takes about 2 months.



gure **9.78:** A semi-diagrammatic drawing illustrating *Hebeloma radicosum* growing with long, ender pseudorhizae from the latrine site of a mole. The mole's nest is at the far right. – By Taka-ma from Takayama & Sagara (1985), modified from the original colour-drawing.
les make latrine sites (besides scent marks). After they have deserted the latrines, the fungal celia and tree roots colonize there forming ectomycorrhizas, and clean away the excrement. I ose this association which involves moles, fungi, and plants as a new kind of symbiosis under e term habit-cleaning symbiosis. ... The habit-cleaning symbiosis might enable ... long-lasting ting ..." (Sagara 1999).

Pretty life of *Hebeloma radicosum* – in the soil it grows into mole latrines, draws nutrients from excrements and shares them with mycorrhizal partner.

Heinz Clémençon: Cytology and Plectology of the Hymenomycetes. Bibliotheca Mycologica, vol. 199. J. Cramer, Berlin-Stuttgart, 2004.

Coprophilic fungi tend to have dormant spores, the germination of which is stimulated by contact with certain enzymes as they pass through the digestive tract of the animals concerned. For better transfer to (or into) the animal, spores of some species have specialized structures (hooks, mucous membrane cover) or developed special mechanisms of spread (long-range firing; *more in the Fungal spread chapter*).

A similar group are **ammonia fungi**, growing on substrates rich in alkaline nitrogen sources (urea, feces, ...).
They belong to ascomycetes (*Amblyosporium botrytis, Ascobolus denudatus*) and basidiomycetes (*Hebeloma vinosophyllum, Tephrocybe tesquorum*).

Tephrocybe tesquorum
http://users.skynet.be/bs133881/champis/tephrocybe_tesquorum_(yd)_7873.htm

Keratinophilic fungi are group of specialists, colonising keratinised parts of dead animal bodies (horns, hooves, bird quills) – this group includes some *Chytridiomycota* and *Ascomycota*, typically keratinophilic are representatives of the order *Onygenales*). In addition to dead body parts, bird nests are a rich source of nutrients for these fungi.

Onygena equina

Photo Lairich Rig, http://www.geograph.org.uk/photo/920334

Compared to common soil fungi with a wider scope, specialized coprophilic and keratinophilic fungi have considerable substrate specificity. On the other hand, non-specialized zygomycete or imperfect saprotrophs, as well as some basidiomycetes, are also growing on excrements or animal remnants (e.g. *Marasmius oreades* is a soil saprotroph with an overlap to coprophilic nutrition). The spores of these fungi are spread directly through the air, they are usually not bound to specific way of transfer (such as the above-mentioned endozoochory).

Fungi of the mentioned groups and so-called "postputrefaction fungi" (colonising carcasses) often occur at places with a higher incidence of animals.

Anthracophilic fungi (also pyrophilic, carbonic or phoenicoid /according to Phoenix/) grow in habitats affected by fire (it can be a regular natural fire, a volcanic eruption or an artificial fire). Ash is a specific substrate with a high pH (pH rises even in the soil under the ash due to rain leaking) with a large amount of minerals, which are often insoluble in water. The substrate is sterilised by the fire => there is a lower competition of other saprotrophs, anthracophilic species are competitively promoted; in some species, higher temperature stimulates the germination of spores.
The environment, in which they live, usually creates optimal conditions for specialised fungi to grow, develop and form competitive relationships; however, when competitors are eliminated, their optimum may be different. An example is *Rhizina undulata*, a fungus associated with burnt places, not successful elsewhere in an undisturbed ecosystem; when the ecosystem is disturbed, e.g. by surface fire, it becomes a facultative parasite of spruce.

Rhizina undulata

Photo Jaroslav Malý, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=23274&next_img_type=gallery

Some anthracophilic species, which produce fruitbodies in burnt places, appear to be ectomycorrhizal (*Geopyxis carbonaria*); it is possible that fructification in this case is a reaction to the loss or weakening of the partner tree by fire.

Geopyxis carbonaria

Photo Tomáš Chaluš, http://www.nasehouby.cz/houby/taxon_list.php?taxon=genus&key=Geopyxis

In addition to the above-mentioned ones, there are a number of partial or „complementary“ groups of saprotrophic fungi specialised in certain substrates, such as dying mosses (muscicolous fungi), *Sphagnum* (sphagnicolous fungi), peat (turficolous fungi) , ...

Muscicolous *Arrhenia retiruga*

Photo Petr Bílek, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=145658

... dead parts of herbs (herbicolous fungi), grasses and sedges (graminicolous fungi), conifer cones (strobilicolous fungi), plant fruits (fructicolous fungi), exudates on/near the leaf surface (already mentioned phylloplane / phyllosphere fungi) or on/near the root surface (rhizoplane / rhizosphere fungi, or in the case of mycorrhizal roots there are mycorrhizosphere fungi).

Left: strobilicolous *Auriscalpium vulgare*
Photo Igor Kramár, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=138522

Right: fructicolous *Lanzia echinophila*
Photo Braňo Ivčič, http://www.fotonet.sk/?idi=4138

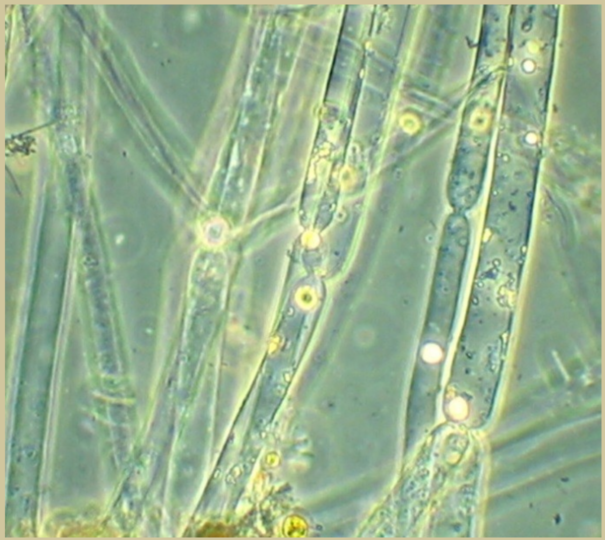
With the involvement of molecular methodology (analysis of environmental samples, in addition to the „classical“ approach of monitoring substrate affinity and succession based on observation of macromycete fruitbodies, or isolation of micromycetes), unexpected species (which deviate from the expected groups) are detected on various substrates – therefore the question arises, to what extent can the above-mentioned traditional categories still be applied?

REPRESENTATION OF SAPROTROPHS IN SYSTEMATIC GROUPS

• **Oomycetes** – mainly aquatic species (*Leptomitales*) are saprotrophic.

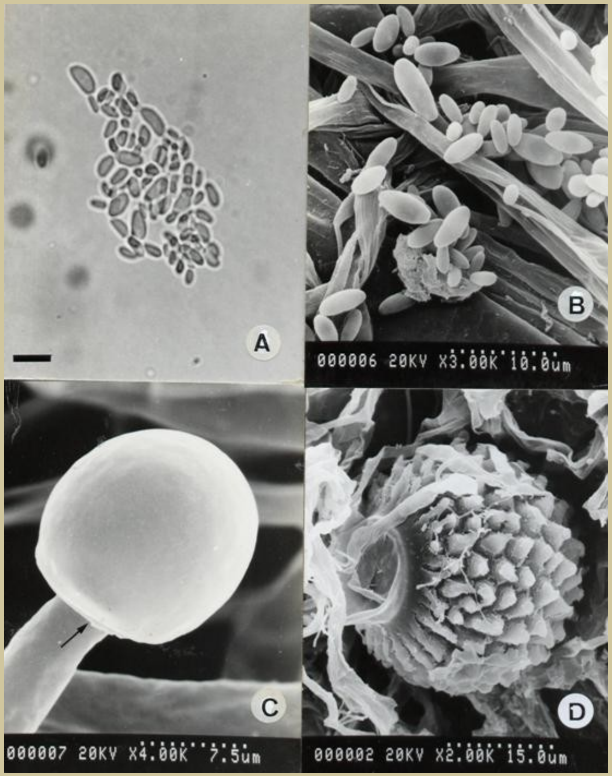
• **Chytridiomycetes** – saprotrophic fungi are celulolytic, or some keratinophilic (stripped snakeskin, crustacean exoskeleton).

• **Zygomycetes** – true saprophytes belong to *Mucorales*; they use proteases, lipases and amylases, few are cellulo- or chitinolytic.
Compared to other groups, they are not so abundant, but often play a pioneering role („R“ strategists, „sugar fungi“).
Some of them are secondary saprotrophs (e.g.*Mucor hiemalis* grows on decaying wood and utilises products of basidiomycete decomposition).



Leptomitus lacteus

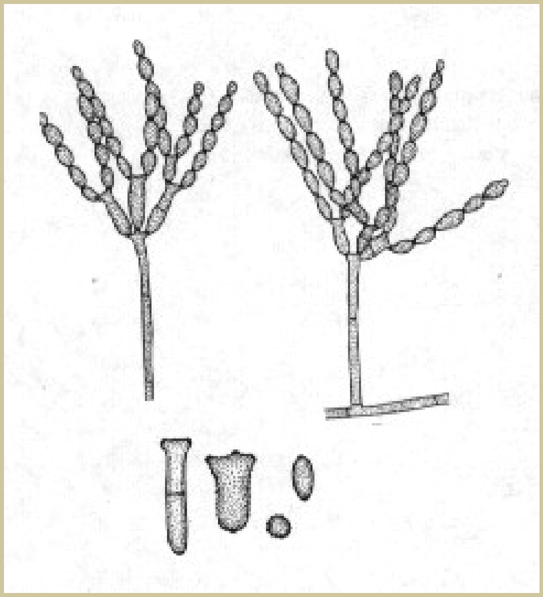
Photo Dirk Klos, http://protist.i.hosei.ac.jp/pdb/Galleries/Klos/Bavaria/Leptomitus_1.html



Mucor hiemalis

http://www.bcrc.firdi.org.tw/fungi/fungal_detail.jsp?id=FU200802070045

• **Ascomycetes and imperfect fungi** – the largest number of soil fungi (species of the genera *Aspergillus*, *Penicillium*, *Trichoderma*, *Fusarium*, etc.) are mainly cellulolytic (some of them degrade lignin, some keratin).
Many of them compete against other fungi by producing antibiotics; tolerance to antibiotics of other species is just as important.
Some ascomycetes also decompose wood – either they are normally soil fungi, which colonise e.g. twigs in the soil (only cellulose component, on the surface), or they are true lignicolous fungi, causing white rot (cellulo- and ligninolytic – e.g. *Helotiaceae*, *Bulgaria*, *Xylariaceae*).
Among all fungi, *Ascomycota* (resp. *Deuteromycota,* represented especially by anamorphs of sac fungi) have probably the highest tolerance to extreme environmental factors, such as temperature, drought, UV radiation (melanin in the spore walls of *Alternaria* or *Cladosporium*).



Left: *Bulgaria inquinans*, apothecia
http://houby.humlak.cz/popis.htlm/bulgaria_inquinans_popis.htm

Right: *Cladosporium herbarum*
http://ww5.stlouisco.com/doh/pollen_site/MoldInfo.html

• **Basidiomycetes** usually come in the final stages of succession, they are „C“ strategists with long-lasting mycelium. In particular, they are cellulo- and ligninolytic (brown or white rot, see above).

• A special form is represented by **yeasts**, which we encounter mainly on the surface of animal and plant bodies, where they can have enough nutrients from exudates rich in carbohydrates. The spherical shape is advantageous for survival – there is a risk of lack of water or, conversely, the need to balance the osmotic pressure during heavy rainfall (flushing of other substances => hypotonic environment), exposure to considerable lighting, etc. – together with yeasts, this environment is also used by bacteria (mostly spherical as well).

• **Slime moulds** feed phagotrophically, but in the plasmodial phase they are also able to absorb nutrients (using extracellular enzymes to break down macromolecules, such as cellulose or chitin), i.e. partially saprotrophic nutrition.

Trametes hirsuta (+ white rot)

Source: Anke & Weber 2006; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Plasmodium of *Fuligo* sp.

http://www.environment.gov.au/biodiversity/abrs/publications/fungi/fuligo-plasmodium.html