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)

ECOLOGICAL GROUPS OF FUNGI, SAPROTROPHS

ECOLOGICAL GROUPS OF FUNGI

According to the way of obtaining nutrition, fungi can be divided into several ecological groups (on which the following chapters will be focused):

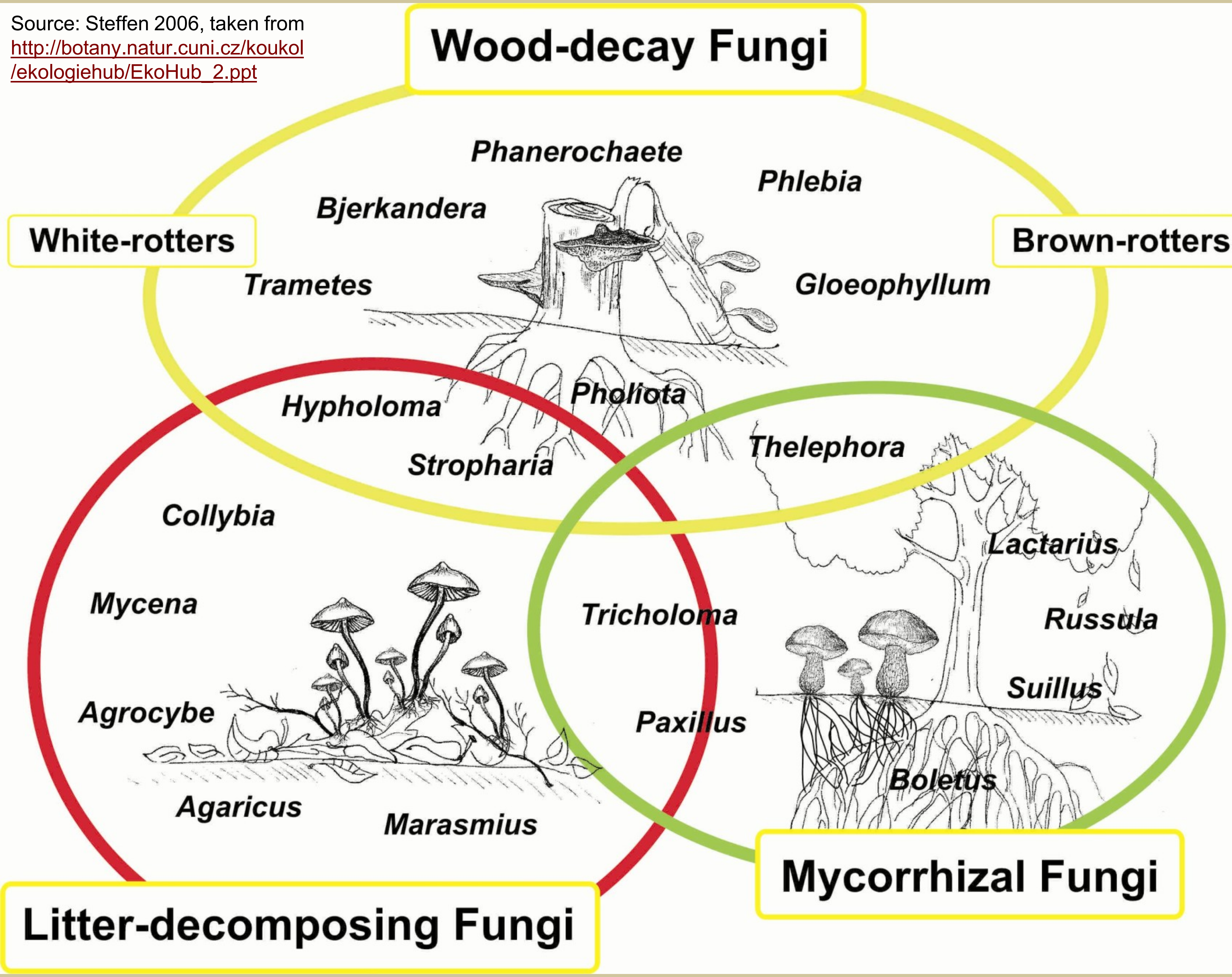
• **saprotrophs** obtain nutrients from decaying particles of organic origin, they have the necessary enzymatic equipment;

• **symbionts** (ideally a mutualistic symbiosis, i.e. mutually beneficial) obtain nutrients from the partner – vascular plants (mycorrhiza), algae or cyanobacteria (lichenism) or even an animal (e.g. *Septobasidiales*);

• **parasites** or **pathogens** – one-sided relationship, the fungus only takes and gives nothing for it; some authors use the term symbiosis in a broader sense as a long-term relationship between different organisms, i.e. including parasitism (there is not always a sharp line between parasitism and mutualistic symbiosis);

• a special case are „**predatory fungi**“.

Source: Steffen 2006, taken from
http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt



The **substrate** is more important than all external factors for many species – its changes can be fatal for lots of fungi, even if they are otherwise able to respond flexibly to changes in the environment. Connection to the substrate is different in different groups – some parasites or symbionts die with the death of their host/ partner (obligatory parasites, it is also common in mycorrhizal fungi), whereas other fungi can freely switch to saprotrophy (if parasitic species can become saprotrophs, we call them saproparasites).

Substrate requirements vary for different fungi – some of them simply need a carbon source to live (they occur non-specifically in soil, litter, wood, dead plant parts, …), others need a variety of specific organic substances and are found on functionally (e.g. plant roots) or taxonomically defined substrates. A strong connection to a particular species (genus, family) of the host is a typical feature of parasitic fungi (given by the gene-gene relation) – some fungal genera have over a thousand species, each connected to a different host, and some tree genera have hundreds of specific fungal species connected to their species.

We can mention interesting numbers of fungal species (saprotrophs, symbionts and parasites) known exclusively from some species (groups) of plants: *Pinus sylvestris* - 893 spp. (186 only on it); *Eucalyptus globosus* - 282 spp. (150 only on it); *Quercus suber* - 590 spp.; palms - 112 spp. per 1 palm species, other palm species share 75%; *Urtica dioica* - 92 spp. (17 on it only); *Oryza sativa* - 135 spp. (2 on it only); *Phragmites australis* - 77 spp.

Demands and physiological behaviour of fungi also often change during onto-genesis (both ontogenesis of the fungus and the potential partner or host – e.g. young fungal mycelia, entering a mycorrhizal relationship with young seedlings).

Zhou & Hyde (2001) proposed these categories for the relationship of fungi to substrate:

• specificity – the fungus obtains nutrients from living plants, but only from a limited species range, although it has other species available in the area; only for parasites, mycorrhizae and endophytes;

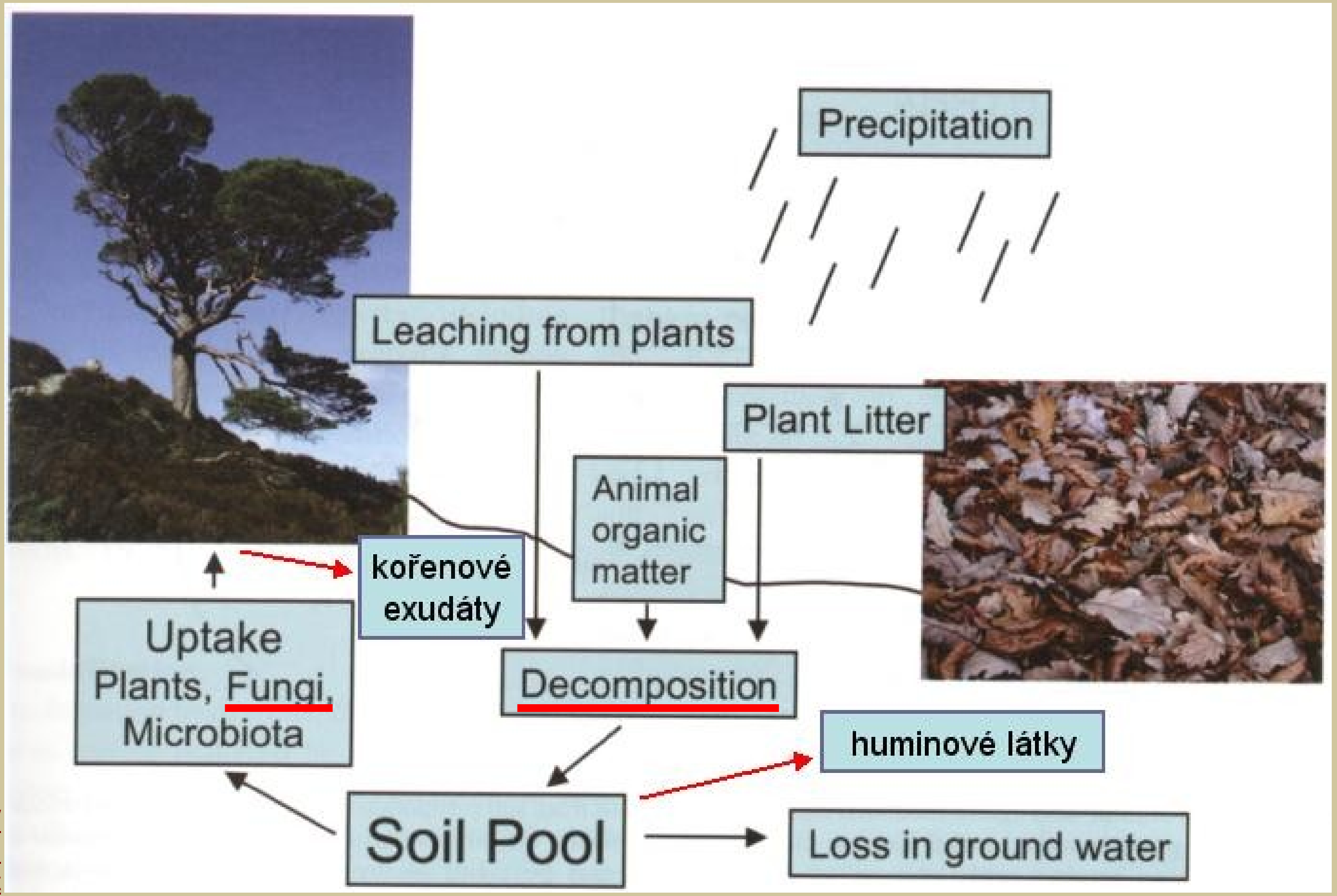
• exclusivity – occurrence of saprotrophic species only on one substrate;

• recurrence – the fungus occurs more frequently on a particular substrate (species), but may occur elsewhere; this applies to parasites, mycorrhizae and saprotrophs.

Thus, for example, if we often find one saprotrophic fungal species on one particular substrate, it may be a specific endophyte of the host plant, switching to saprotrophic nutrition after its death, or it may be a saprotroph with a high recurrence due to the substrate having the most suitable conditions (chemical composition, physical state), or do we not yet know all about its life cycle? :o)

SAPROTROPHIC FUNGI AND THEIR SUBSTRATES

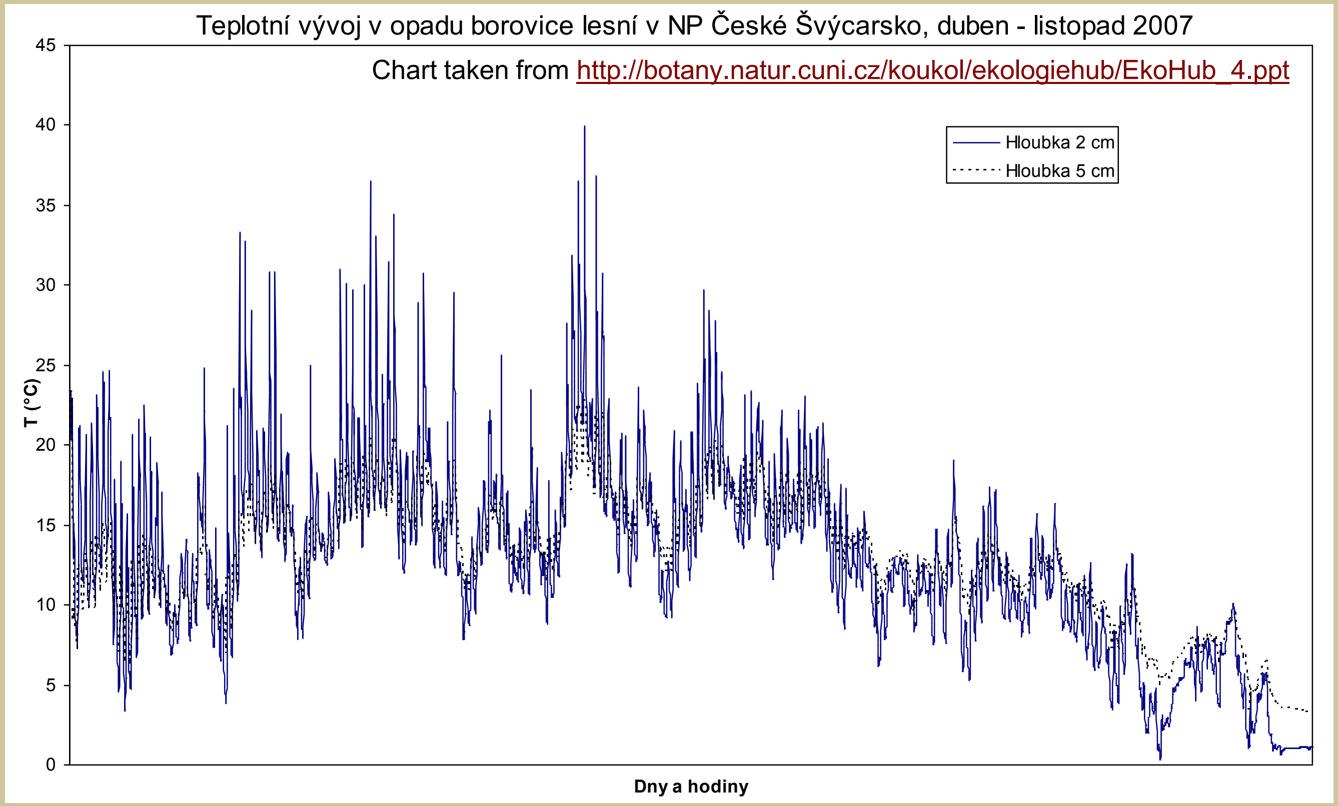
The basic group of saprotrophic fungi are **terrestrial fungi**, decomposing the layer of litter and detritus (aboveground – dead aboveground parts of plants – and underground – dead roots, whose mass may be equal to aboveground mass, for example in meadows), but also root exudates, excrements, animal remnants, ...



Scheme of processes in litter/detritus/soil (position of saprotrophic fungi in the ecosystem underlined in red).

Source: Gadd 2004, modified, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

While the soil in humus horizons is more homogeneous (individual components can no longer be distinguished) with a more stable microclimate and a larger proportion of inorganic material, the litter („overlying humus“ when taken broadly as part of the soil) is heterogeneous with easily distinguishable components representing diverse niches, exposed to weather conditions (regular drying, temperature changes).



Due to its heterogeneity, litter is often studied by mycoflorists (these are easily definable habitats for collection of fungi) and succession is monitored (samples can be dated relatively accurately together with the spectrum of colonising fungi); the mycobiota of soil horizons is much less explored.

The average amount of detritus in natural ecosystems is 50,000–100,000 kg/ha; coniferous litter 2,000–7,000 kg/ha, broadleaf litter 5,000–10,000 kg/ha. Leaves are decomposed to humus within 2–3 years, while needles (protected by a wax cuticle) within 8–10 years. (The data are valid in Central European conditions; in the tropics several months are enough, plant debris in the rainforest is completely processed during one year, whereas decomposition of sclerified plant tissues in arid areas takes several decades.) Availability of phosphorus in the environment is important – when sufficient, the plants form softer leaves, easily decomposable.

In addition to fungi, the detritus food chain includes bacteria, actinomycetes and detritophagous animals (earthworms, mites and springtails). The primary role of animals is mainly in mechanical disruption of detritus particles – transformed to rubble, their surface area is increased for the action of microbes, which also have more available nitrogen here. The disrupted substrate is also suitable for bacteria (higher humidity suits them too); however, involvement of fungi is the largest, specifically they play a major role in decomposition of wood and leaf litter (animal excrements are processed by other fungi than primary decomposers).

Soil micromycetes (*Penicillium*, *Trichoderma*, etc.) can boast the largest volume of decomposition, while *Basidiomycota* show the greatest intensity (esp. of lignin).

Processing of degraded substances can be expressed by a simple sequence: excretion of enzymes releasing partial components from the substrate => their absorption in solution. The decomposition activity of fungi is concentrated in the terminal cells of hyphae.

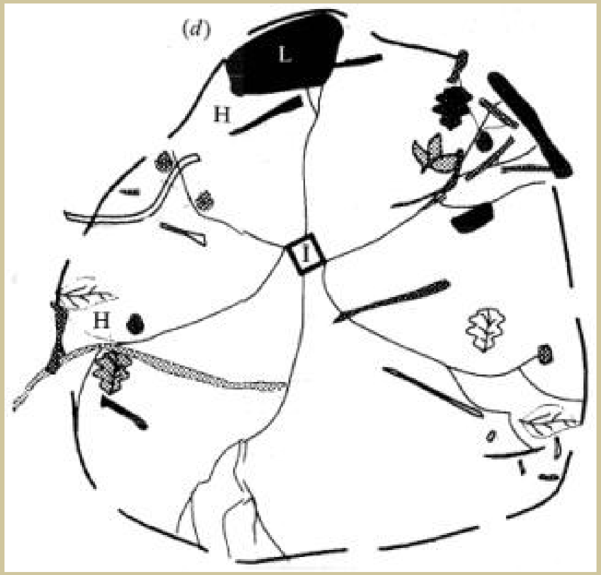
If the **nutrient sources** are **continuously distributed** at the site, the fungi have no problem with their gradual absorption. Different case is **discontinuous distribution** of resources (places where nutrients are available are referred to as „units“ or „patches“); it is either a locally limited substrate (tree trunk, fruit, droppings, ...) or numerous, but separate units (from the point of view of the fungus – for example, needles of a certain quality in the litter).

Species that grow through the litter and do not distinguish between its components, connect various components of the litter and colonise large areas, are referred to as **non-unit-restricted**. These are mainly *Basidiomycota* in litter, fungi living from root exudates (and possibly also ectomycorrhizal species), forming a diffuse uniformly growing mycelium (for example, species of the genera *Marasmius*, *Mycena*, *Collybia*, *Clitocybe*).

For **unit-restricted** species, specialised to discontinuous nutrient sources, two main ways to deal with the situation can be distinguished. Specialists for certain isolated habitats, which are not able to grow anywhere else (e.g. coprophilic species), do not invest much in the formation of mycelia and spread to the new habitat by spores.

The second type are **foragers**, especially *Basidiomycota* (mainly lignicolous) growing in heterogeneous litter with different quality of its components. These fungi form specific structures for growth and search for a new source – mycelial cords (e.g. *Phanerochaete velutina*) or rhizomorphs (*Armillaria gallica*), which grow over considerable distances (up to tens of meters) and colonise large areas („foraging“, „explorative growth“). When a suitable substrate is found, the morphology changes to a dense absorbing mycelium (increasing total surface of the hyphae), which colonises and „exploits“ the substrate („exploitative growth“); lysis of mycelial cords may also occur due to nitrogen recycling.

However, it is not just nitrogen; in general the translocation of nutrients is of great importance for foragers, which we can show on phosphorus: while the „connecting“ mycelial strands often remain phosphorus-free, the fungus translocates this element to growing parts of mycelia, colonised wood and other litter components (phosphorus can reach unexpected recipients such as bryophytes).



Top: *Phanerochaete velutina*, scheme of mycelial cords growth.
Source: Wells & Boddy 1995; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Bottom: *Armillaria* rhizomorphs.
http://botany.upol.cz/atlasy/system/nazvy/armillaria.html

Fungi are most abundant in the upper layer of the soil profile (several cm) – the substrate aeration is the most important factor, the aerobic fungi represented here necessarily need oxygen; therefore they are more damaged by too much water in the soil than by its deficit (there is a difference compared to bacteria).

An important factor for terrestrial saprotrophic fungi is the type and amount of **humus** in the soil. Detriticolous fungi live in the litter and overlying humus layers and participate in its transformation into fine humus, later contained in the humus soil horizon. The formation of humic substances in the soil is extremely important for the accumulation of carbon (they retain 60-80% of C from soil organic matter) and nitrogen, their stabilisation (up to decades), absorption of elements (phosphorus, metals) and prevention of their leaching.

Most fungal species (about 40%) form their mycelia in mull (typically in shady deciduous forests of lower elevations), less in humus of the moder or mor types (higher and colder regions). The smallest number of species grows in raw humus, which is formed by the accumulation of slow-decaying needles or wood decayed by lignicolous fungi (species causing brown rot /*see below*/) – subsequent decomposition of lignin and needles releases phenolic substances with fungicidal effects (mycorrhizal fungi are more sensitive to this than saprotrophic species; therefore they are rare in old-growth forests, riparian or ravine forests with a high layer of raw overlying humus).

A specific case is represented by mire fungi, adapted to peat substrate (it can be regarded as special form of humus) with a high water content in the environment.

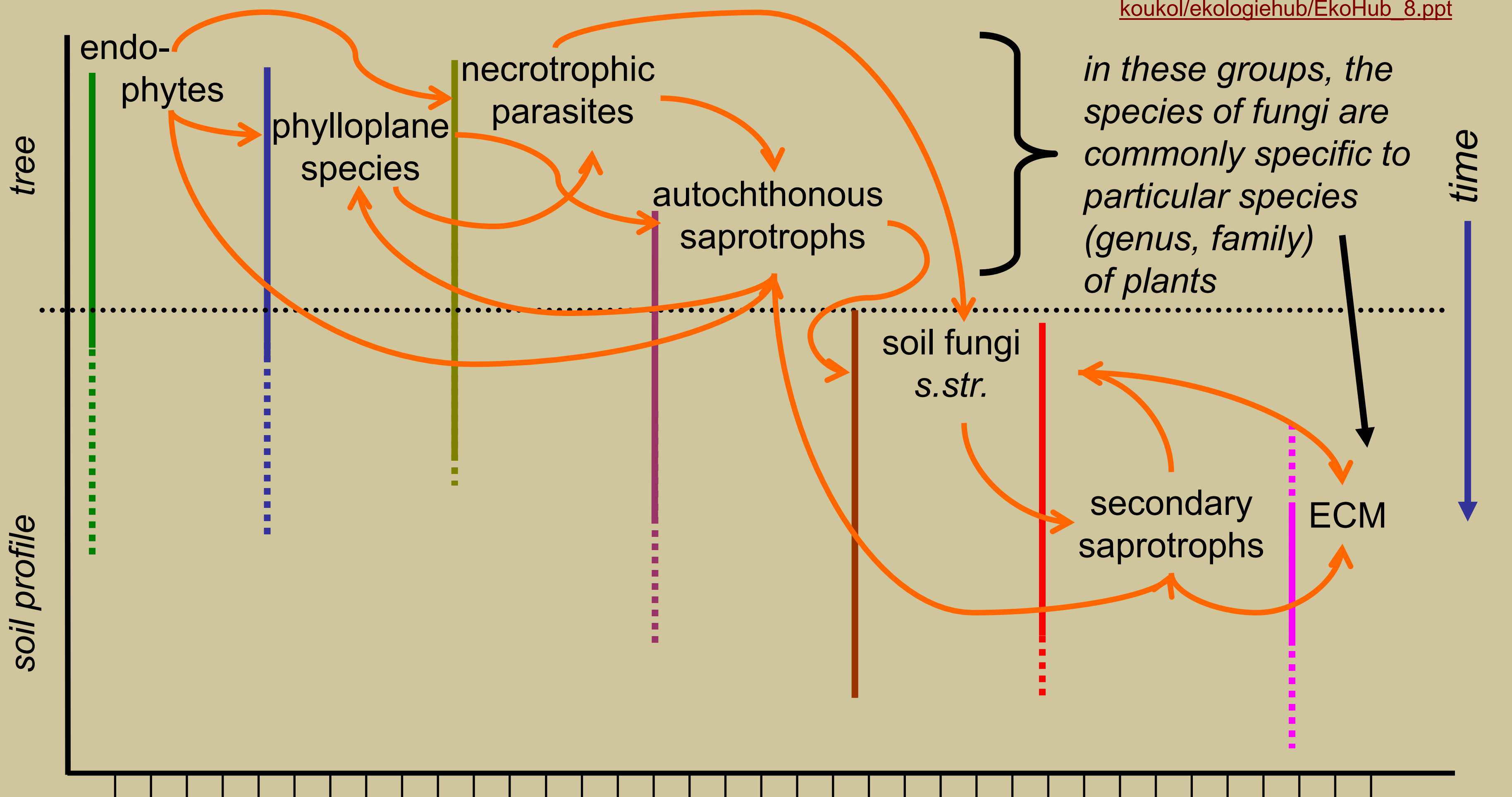
A **succession** takes place during the **detritus decomposition** – some species form a community of decomposers at the beginning and others at the end:
– fast-spreading species decomposing monosaccharides and disaccharides, or optionally starch, are the first to emerge;
– these are subsequently replaced by cellulolytic species; micromycetes, mainly in the anamorphic stage, have a decisive share in both groups;
– the final phase of succession is represented by ligninolytic fungi; they come after depletion of supplies of simpler nutrients, when fast-growing species (of the previous groups), at first competitively stronger, „leave the scene“ – in this time basidiomycetes, especially hymenomycetes, start to prevail. Some ascomycetes, degrading the components of cleaved lignin, follow the ligninolytic fungi.

Succession is an irreversible process; gradual change of the substrate quality associated with depletion of certain nutrients leads to its decomposition and extinction of the existing community, followed by emergence of a new one, whose representatives decompose the metabolites of their predecessors, or nutrients not yet used. According to the systematic groups, the succession (roughly) corresponds to the sequence *Peronosporomycota* + *Mucoromycota* => *Ascomycota* + *Deuteromycota* => *Basidiomycota*.

(Traditional study of succession in litter and detritus is based on collection and direct observation of fruitbodies, or cultivation in humid chambers or on agar media. Compared to results that can be obtained by next generation sequencing, fast-growing, sporulating and fructifying species are overestimated in this case.)

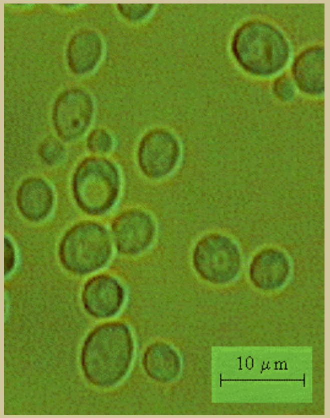
A sequence of ecological groups of fungi utilising nutrients from plant tissues. As can be seen, in addition to saprotrophs, also endophytic, parasitic and mycorrhizal fungi (ECM = ectomycorrhiza) are involved in various stages of succession.

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_8.ppt



Note to previous text: Detriticolous fungi *sensu stricto* decompose litter, plant remnants and raw overlying humus, but not humic substances in the soil like other saprotrophic fungi.

We can describe the decomposition process in detail on the example of leaves: Colonization really begins on the plant, when microscopic **phylloplane fungi** inhabit the phylloplane (habitat on the leaf surface). Filamentus species (of the genera *Alternaria*, *Cladosporium*, *Helminthosporium*, *Stemphylium*, *Aureobasidium*, *Epicoccum*) are represented here, but yeasts often dominate (*Sporobolomyces*, (*Rhodotorula*, *Tilletiopsis* etc., incl. dimorphic fungi); many of them are less tolerant to air pollution (especially SO_2 – a tolerant species is e.g. *Aureobasidium pullulans*, which in a polluted environment can predominate even over yeasts). Some species are specific colonisers of specific plants (*Ceuthospora pinastri*, *Lophodermium pinastri* and other species, see drawings at the following page).



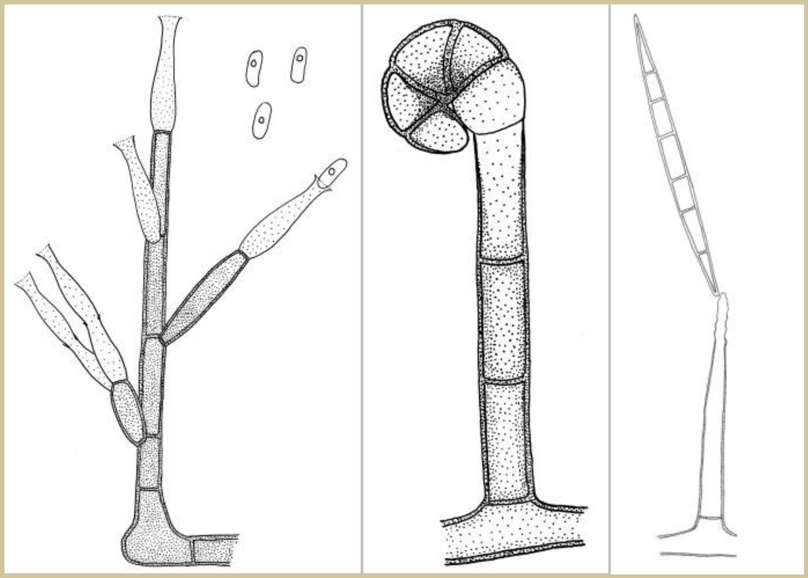
Top left: *Sporobolomyces roseus* (*Microbotryomycetes, Pucciniomycotina, Basidiomycota*)
http://genome.jgi-psf.org/Sporo1/Sporo1.home.html

Right: *Rhodotorula glutinis* (also *Microbotryomycetes*).
http://eso.vscht.cz/cache_data/1154/www.vscht.cz/kch/galerie/kvasinky.htm

Bottom: *Aureobasidium pullulans* (*Dothideomycetes, Pezizomycotina, Ascomycota*) – filamentous mycelium fragmenting into dark-walled arthroconidia.
http://www.pristineinspections.net/html/mold_types.html

From left:
Phaeostalagmus peregrinus, *Troposporella monospora* and *Pseudocercospora deightonii* (anamorphic *Pezizomycotina*), examples of species living specifically on pine needles.

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_8.ppt

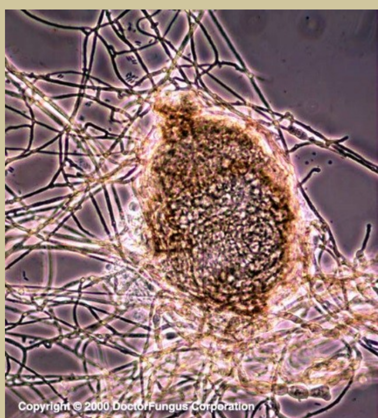


Phylloplane fungi colonise the surface of healthy green leaves or needles; they grow very slowly and draw nutrients only from precipitation, exudates of epidermal cells, cuticle or mycelia of other species; if the leaf is concurrently attacked by a parasite, phylloplane species can also utilise the dead cells. Peak of their activity occurs in the autumn, when the environment is more humid and the aging leaves release more nutrients; some species can also cause premature fall of leaves (needles).

After fall, these species become the first colonisers to initiate **leaf decay**; they represent the first succession stage with not very strong enzymatic equipment. Subsequently pure saprotrophic fungi (anamorphic *Phoma*, teleomorphic *Pleo-spora*) join them, hyphomycetes possessing antibiotics (*Aspergillus*, *Fusarium*, *Gliocladium*, *Penicillium*, *Trichoderma*) are replacing the previous ones, some parasitic fungi are more pronounced (by sporu-lation or fructification, such as powdery mildews or *Rhytisma*) – so-called „L“ layer (litter) appears on the soil surface.

Photo M. Sedlářová, *Uncinula necator*
http://botany.upol.cz/atlasy/system/nazvy/uncinula-necator.html

Bottom right: stroma with hystero-thecia of *Rhytisma acerinum*



Pycnidium of *Phoma*
http://www.doctorfungus.org/thefungi/phoma.htm

Photo inset: asci of *Pleospora herbarum*
http://www.biodiversity.ac.psiweb.com/pics/0000308_.htm

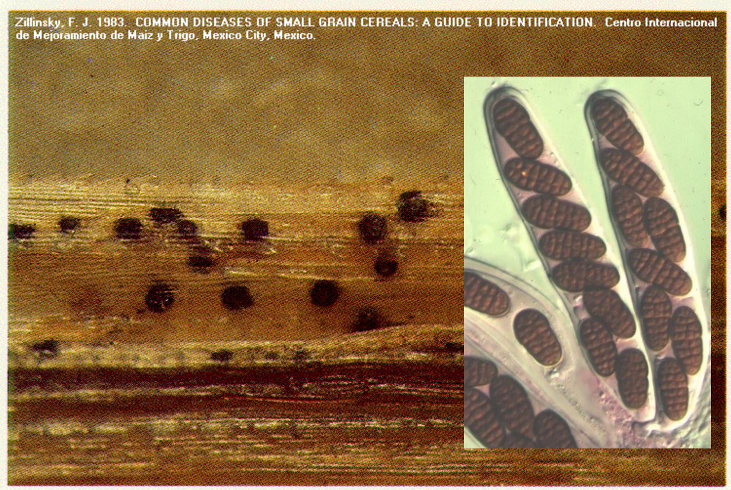
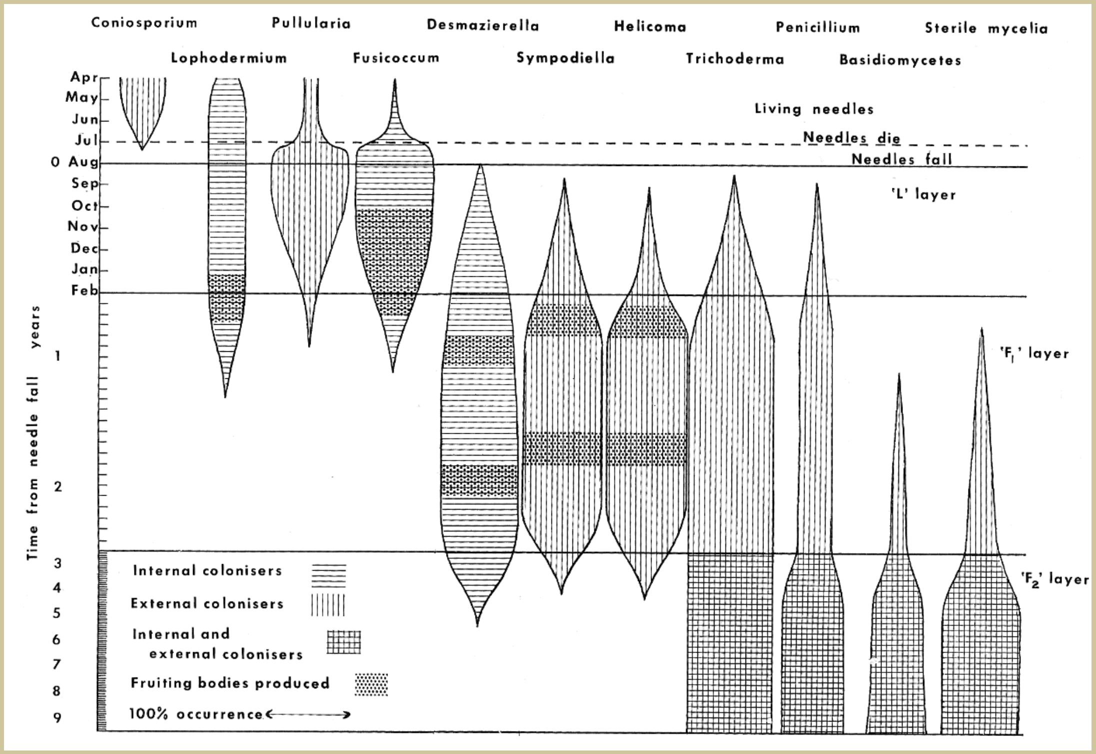


Figure 187. A colony of perithecia of *Pleospora* species in oats (50x).

Detritus particles (soil animals are involved in their fragmentation, see above) in the surface layer of the soil are then a nutrient substrate for lignocellulolytic *Basidiomycota* (*Pluteus*, *Lepiota*) => decomposed particles then get deeper into the soil (sink, water flush, animal activity), into the so-called fermentation („F") layer.



Kendrick & Burges 1962; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_1.ppt

Here, a wide range of basidiomycetes (*Marasmius*, *Mycena*, *Collybia*, *Clavaria*, etc.) are active and their mycelium is most clearly visible a few centimeters below the surface (even with the naked eye thanks to the association of hyphae into mycelial cords).

Activity of soil fungi also leads to decomposition of protein-phenolic complexes => protein release (with simultaneous detoxification of phenolic substances; the above-mentioned hyphomycetes, *Aspergillus* etc., are phenol-tolerant) leads to enrichment of soil with nutrients (nitrogen in organic form) usable for animals.

Decomposition of plant debris (60–75% of dry weight consists of leaves or needles, 10–20% bark, 10–15% twigs, 2–15% fruits) proceeds similarly to wood /*see later*/, the main decomposed components are cellulose (15–60%), hemicelluloses (10–20%) and lignin (5–30%; other components may be soluble hydrocarbons, tannins, proteins, lipids, pectins, storage polysaccharides, ...). It is not possible to strictly distinguish between litter and wood substrate – for example, a fallen trunk becomes part of litter after several seasons of litter accumulation around it (besides saprotrophic fungi, the community involved in decay includes also ecto-mycorrhizae, seedlings and so-called „nurse log" – utilisation of a dead trunk by young individuals); some litter decomposers are able to decompose branches that have lower water potential (becoming dry on the litter surface).

„Nurse log" – young trees draw nutrients from a fallen trunk.

http://www.phlumf.com/gallery/gorge/larch-mountain/image-003.jpg.php

Two types of plant debris decomposition can be distinguished:

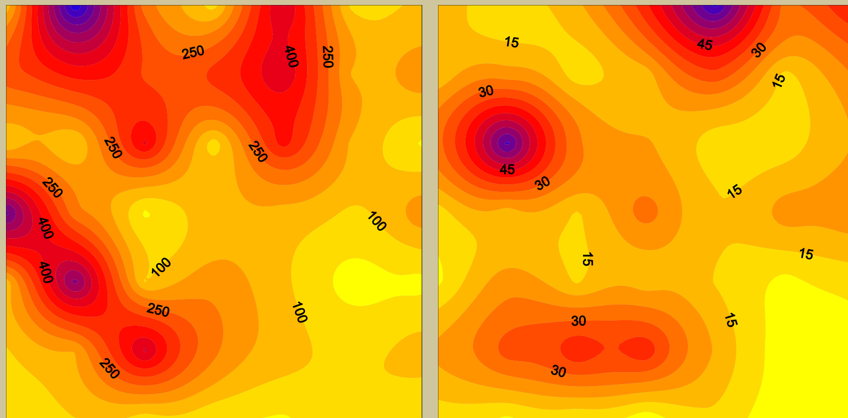
• Destructive decomposition (of cellulose only) produces dark raw humus rich in humic acids, long resistant to the decomposition by microbes (up to hundreds of years). It is caused e.g. by *Chaetomium*, while gilled fungi are rarely involved.

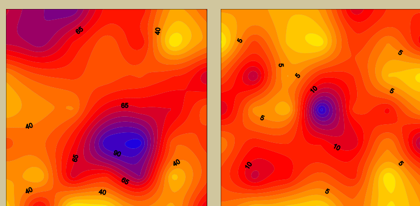
• Corrosive decomposition produces light brown humus rich in fulvic acids; it is made by fungi able to degrade proteins or lignin, thus returning a significant proportion of carbon, hydrogen and nitrogen to the nutrient cycle. (The litter also contains significant amount of lignin in needles or sclerified plant tissues, and some saprotrophic litter decomposers have enzymatic equipment similar to white rot fungi, which will be discussed later.)

Corrosive decomposition – „white rot“ of *Pinus sylv*. needles and leaf litter.

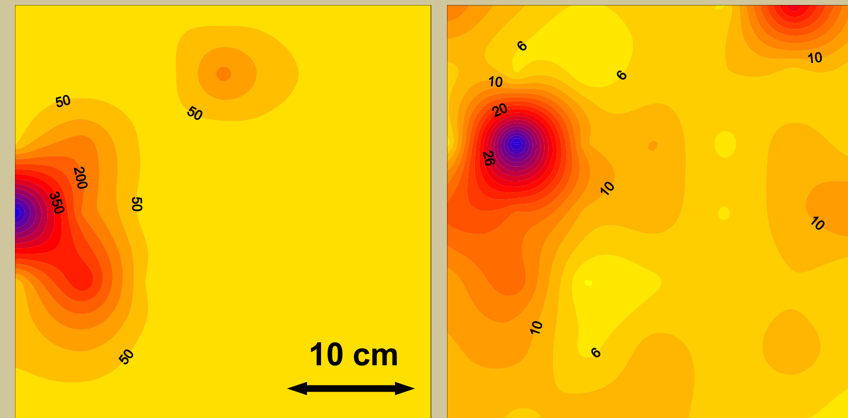
Source: Steffen 2006; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_1.ppt

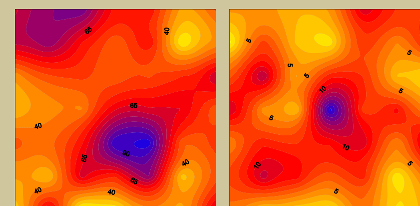
Many macromycetes of *Tricholomataceae* s.l. (*Clitocybe*, *Collybia*, *Laccaria*, *Lepista*, *Marasmius*) and others, usually not substrate-specific, are involved in it.



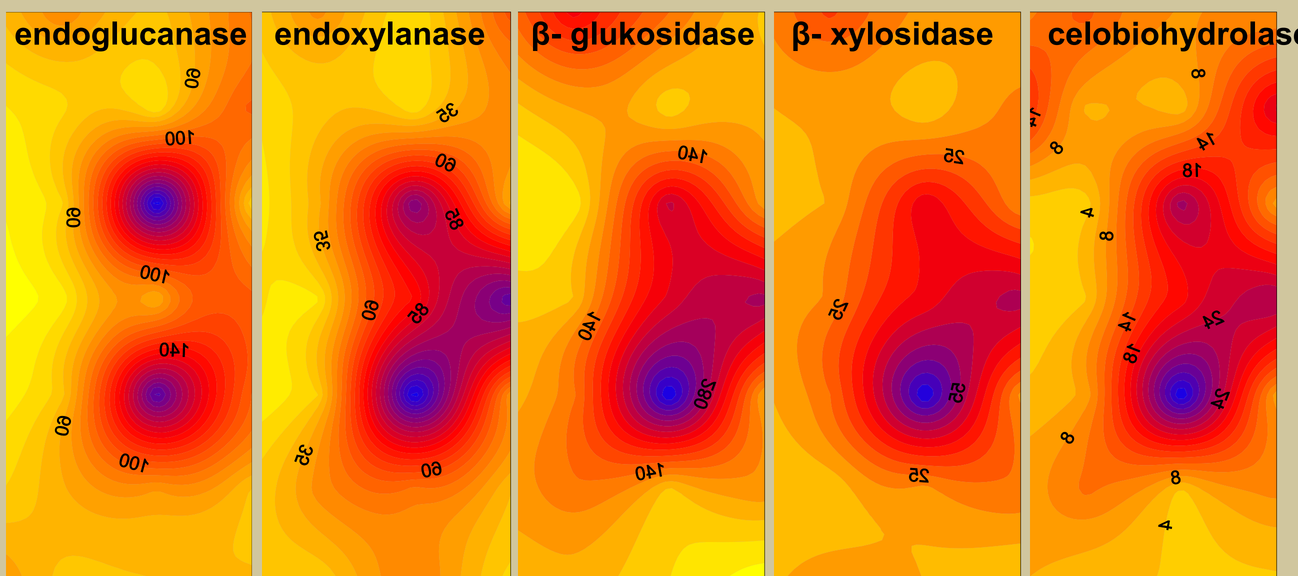


Left: laccase activity distribution in oak debris; right: detection of ergosterol = fungal biomass.





Left: Mn-peroxidase activity distribution here; right: detection of ergosterol = fungal biomass. (Large □ = „L“ horizon; small □ = „O“ horizon, Distribution of ligninolytic (originally humus) enzymes (see above) is not linear and does not exactly correspond to distribution of fungi.



<= Similar distribution of activity of polysaccharide cleaving enzymes.

Source of images: Baldrian 2007; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

When a large amount of plant biomass accumulates, it is decomposed on the principle of **composting**. Mostly aerobic processes take place here; initially microorganisms (endophytes, epiphytes, microbes from the air) decompose soluble substances => due to release of heat during the massive decomposition of organic matter inside the biomass (exothermic processes) there will be heating (up to 80 C) => thermotolerant bacteria and fungi appear, decomposing more complex substances including lignin and cellulose (supply of diaspores mostly by air, in the final phase of decomposition soil fungi are involved) => decrease in metabolic rate, temperature returns to normal => fungi with lower temperature tolerance, surviving on the surface, reinvade the inside of the compost and complete the decomposition.

This process needs optimal humidity – too high humidity induces anaerobic conditions, whereas drying prevents dissolution and access to nutrients.

Also access to oxygen is important (without it, bacteria prevail and silage is formed), enough biogenic elements (P, Ca) and especially nitrogen (it is needed for the production of enzymes; advanced fungi, capable of autolysis, transport and redistribution of nitrogen in the mycelium, have an advantage in this regard).

During the process there is a temporary increase in pH (up to 8–8.5) due to the release of ammonia, which then evaporates, or is used for formation of other organic substances.