NOTES AND FIGURES ON FUNGI
for the SOIL BIOLOGY COURSE
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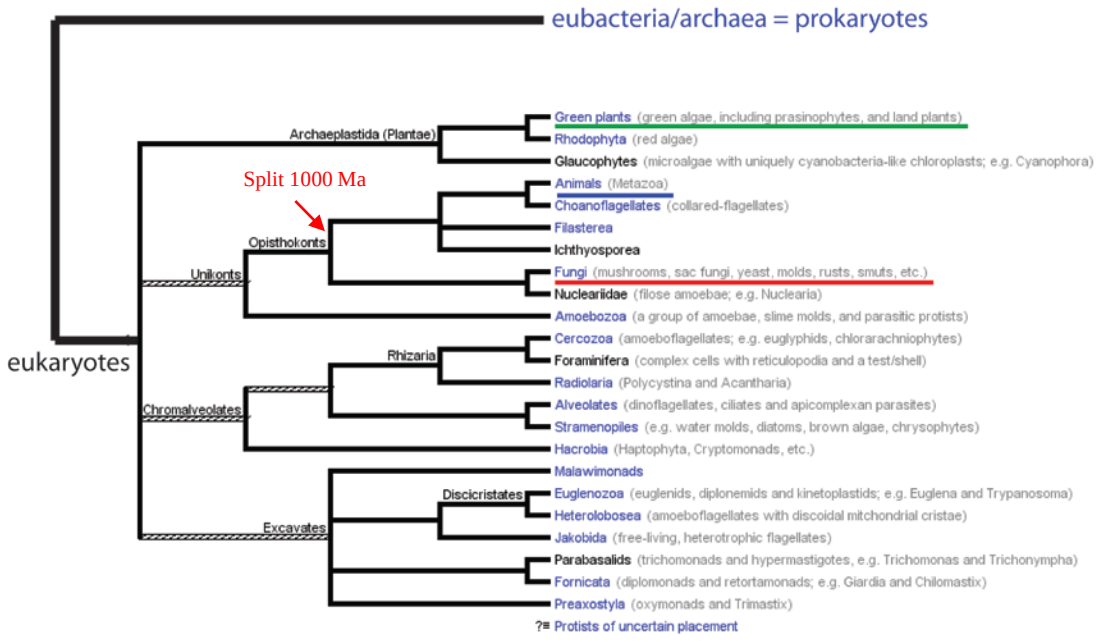
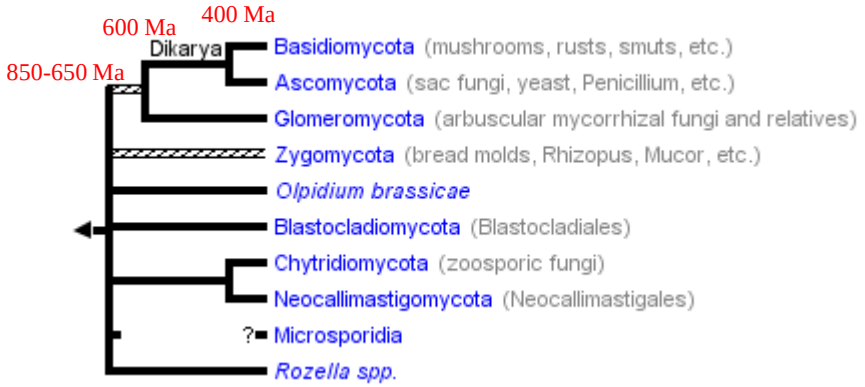
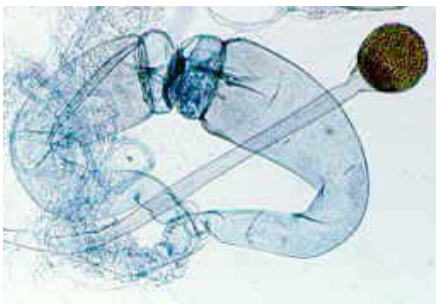
Phylogenetic and ecologic groups of fungi

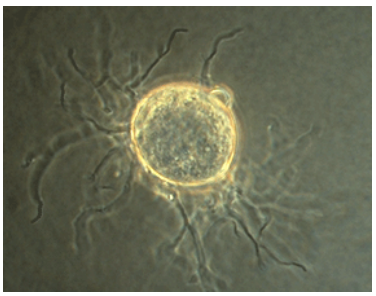




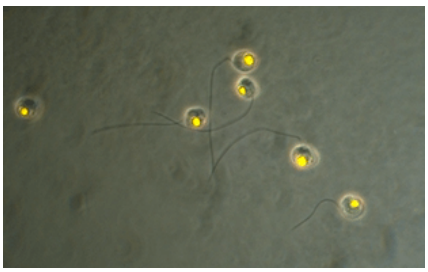
Fungi are eukaryotic organism whose closest relatives in the evolutionary tree are the animals. They are distinguished from other eukaryotes by their lack of chlorophyll and their chitin containing cell walls. Also, fungal cells are usually organised in hyphae (with the exception of yeast fungi). The fungal kingdom consists of three major groups: Glomeromycota, Ascomycota and Basidiomycota and several smaller groups, such as the Mucoromycetes (Zygomycota) and Chytridiomycota. (Ma = million years ago)



Mucoromycete



A chytridiomycete with a sporangium and short hyphae

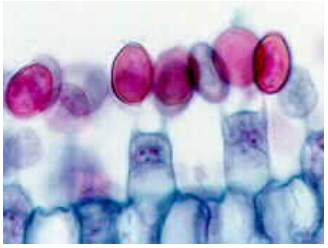


Swimming chytridomycete spores with flagellae

Ascomycete structures: fruitbody of a morel (top left), fruit body - apothecium (left), small fruitbody (perithecium) with sexual spores (black) formed in spore sacks - asci (middle) and asexual spores = conidia on conidiophores (right).

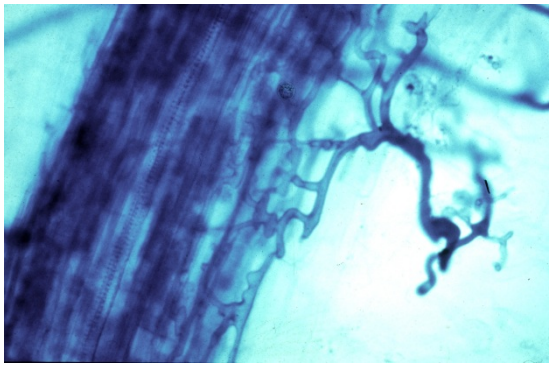
Ascomycetes have haploid mycelium - each cell has a single nucleus with a single genome. Mating (with a spore from another individual) takes place in association with fruit body formation. Meiosis take place in the asci (se above). Asexual reproduction with conidia is common.

Various kinds of **Basidiomycete** fruit bodies: Two ectomycorrhizal (left and middle) and one wood decomposer (right).

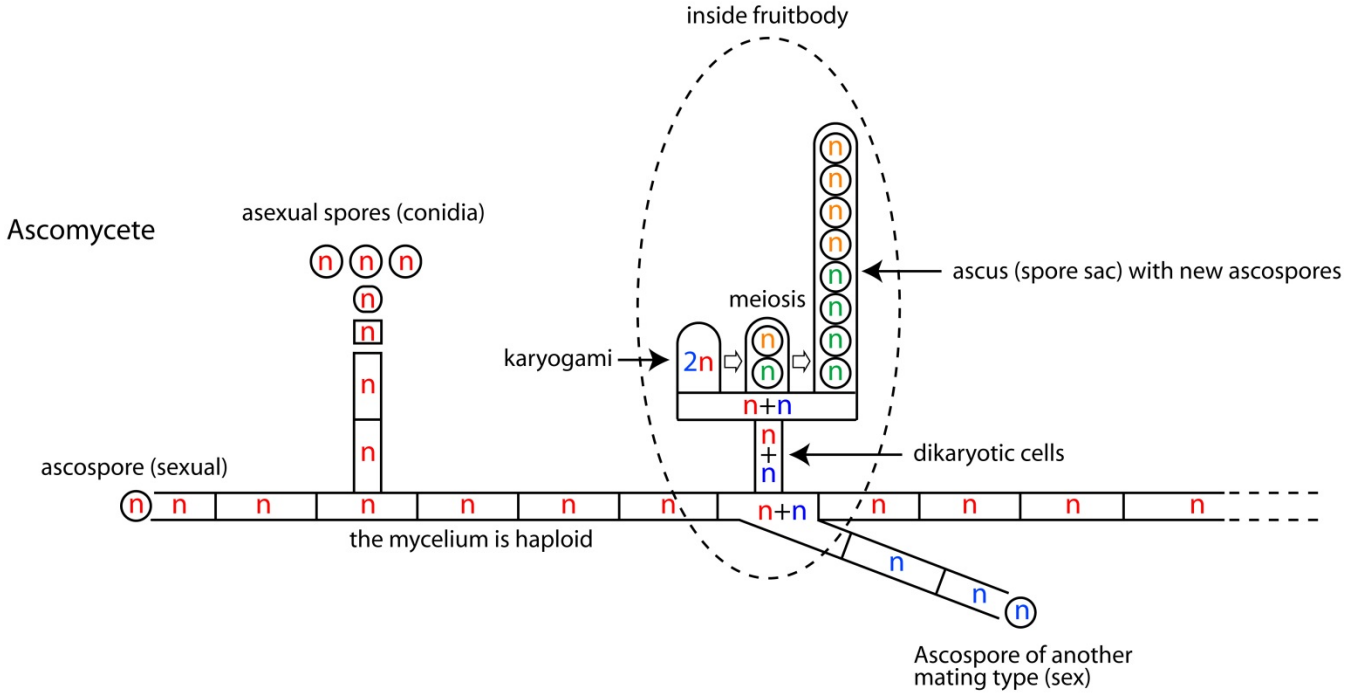


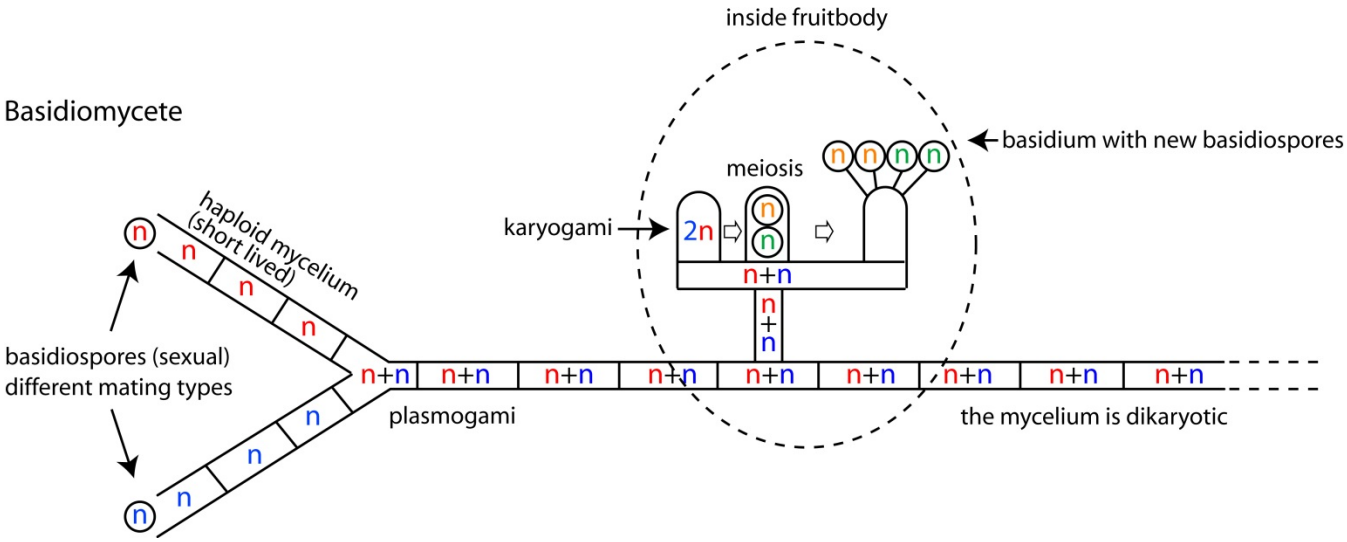
Sexual spores formed on basidia. Basidia are produced in the fruit bodies (eg. on gills or in pores under the cap of mushrooms).

Basidiomycetes have dikaryotic mycelium – each cell has two nuclei (one from each parent), each with a different genome. Mating takes place between small haploid mycelia that fuse to form a dikaryotic mycelium, which is the principal growth form. The dikaryotic mycelium may form fruitbodies without fertilization. Meiosis take place in the basidia (see left).



Hyphae of a **Glomeromycete** inside a plant root. Glomeromycetes are obligate mycorrhizal biotrophs. They form *arbuscular mycorrhiza*. They have coenocytic mycelia - the hyphae are not divided into cells, and many nuclei move around in the mycelium. Asexual spores contain a large number of nuclei with many different genotypes. It is uncertain if glomeromycetes have sexual reproduction.





Ascomycetes have haploid mycelia. After fertilization by a spore or mycelium of another individual with different mating type, a fruitbody is formed. Plasmogami (cytoplasm fusion) takes place in the fruitbodies and only a few cells in are dikaryotic. Karyogami and meiosis takes place in a ascus (pl. asci), where haploid ascospores are formed. Asexual reproduction with conidia is also common in ascomycetes.

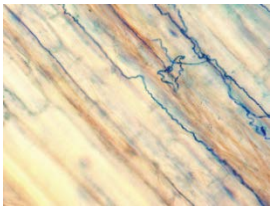
Basidiomycetes have dikaryotic mycelia. Basidiospores germinate into a short-lived haploid mycelium. When the haploid mycelium meets a haploid mycelium of another mating type, plasmogami takes place and a dikaryotic mycelium (with two nuclei in each cell - one from each parent). The dikaryotic mycelium may form fruitbodies *without further fertilization*. Karyogami and meiosis takes place in a basidium (pl. basidia), where haploid basidiospores are formed.

Grime's triangle

S strategists
tolerant to abiotic stress (e.g. drought)
or biotic stress (e.g. plant defence responses inside living hosts)
slow growing
not competitive
specialised (live where other fungi cannot live)

C strategists
competitive
large and long lived
efficient resource mobilisation
(high enzymatic capacity)
live on common resources
live in stable environments
low production of (mainly sexual) spores

R strategists
not competitive
fast growing, small and short lived
depend on high quality resources (simple sugars)
live on rare resources with patchy distribution
live in fluctuating, disturbed environments
high production of (mainly asexual) spores

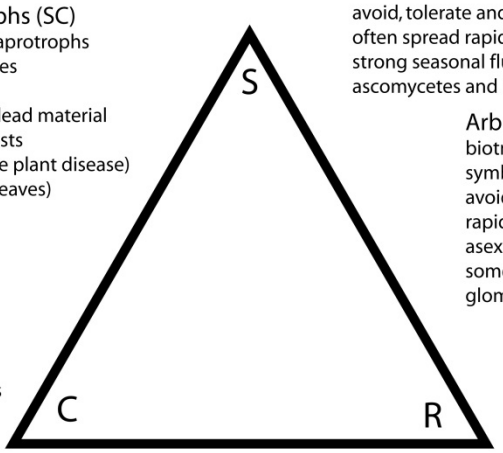


Plant Endophytes (S)
biotrophs
colonise living plant tissues
avoid plant defenses
grow slowly
live on simple sugars
ascomycetes

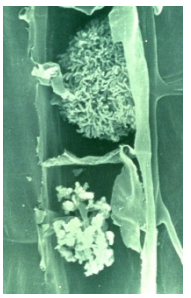
Lichen forming fungi (S)
biotrophs
symbiosis with algae and/or cyanobacteria
tolerand to drought
live exposed to sun light
ascomycetes

Plant pathogens (SR)
necrotrophs
create their substrate by killing host tissues
avoid, tolerate and/or subdue plant defences
often spread rapidly with asexual spores
strong seasonal fluctuations
ascomycetes and basidiomycetes (rusts and smuts)

Endophytic saprotrophs (SC)
biotrophs/necrotrophs/saprotrophs
colonise living plant tissues
avoid plant defenses
grow rapidly in recently dead material
are replaced by C strategists
may be pathogenic (cause plant disease)
ascomycetes (herbs and leaves)
basidiomycetes (wood)



Arbuscular mycorrhizal fungi (SR ?)
biotrophs
symbiosis with roots of most plants
avoid plant defences
rapid growth, short lived mycelia
asexual reproduction
sometimes high spore production
glomeromycetes



Ectomycorrhizal fungi (C ?)
biotrophs
symbiosis with roots of some trees
may form large mycelia
may produce hydrolytic and oxidative enzymes
may mobilise nutrients from humus
mainly basidiomycetes

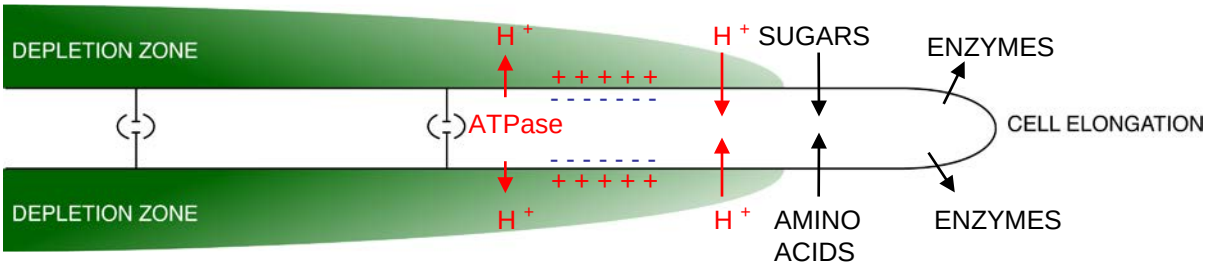
Yeast fungi (RS)
saprotrophs
uni-cellular
often live in liquids
multiply rapidly (asexually by budding)
form sexual resting spores
may tolerate anaerobic conditions
may tolerate osmotic stress
often ascomycetes

Lignocellulose degraders (C)
saprotrophs
may form large mycelia
produce hydrolytic and oxidative enzymes
(cellulases and peroxidases)
degrade wood and recalcitrant litter
(needles and some leaves)
mainly basidiomycetes

Cellulose degraders (RC)
saprotrophs
produce hydrolytic enzymes (cellulases)
degrade litter of herbs, leaves and grasses
strong seasonal fluctuations
mainly ascomycetes

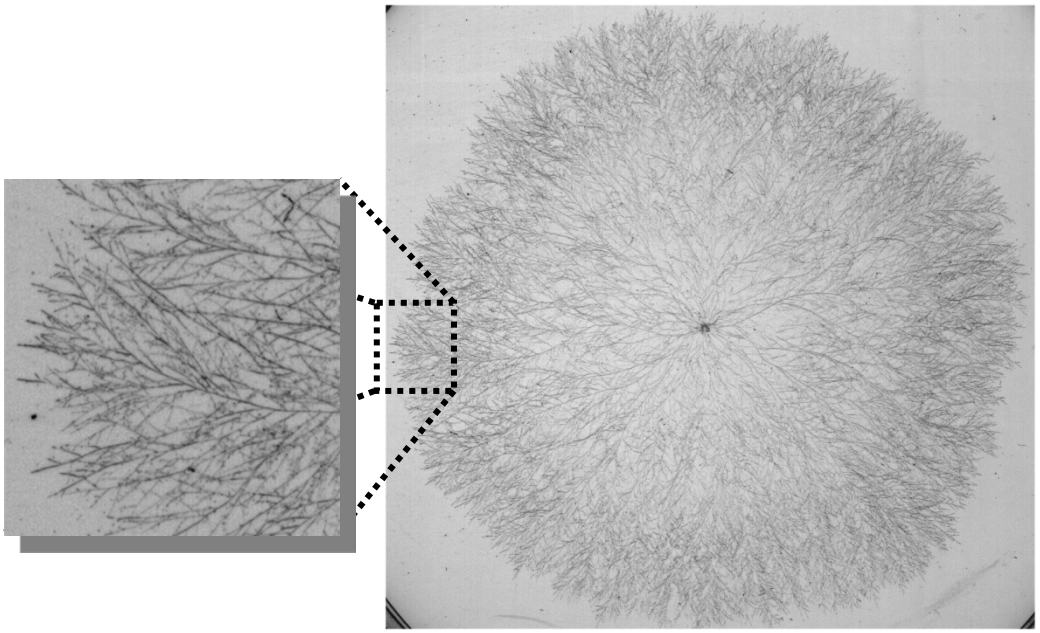
Mould fungi (R)
saprotrophs
grow fast on simple substrates (sugars)
short lived
live on fruits and freshly fallen litter
spread rapidly with asexual spores (conidia)
mainly ascomycetes and mucoromycetes

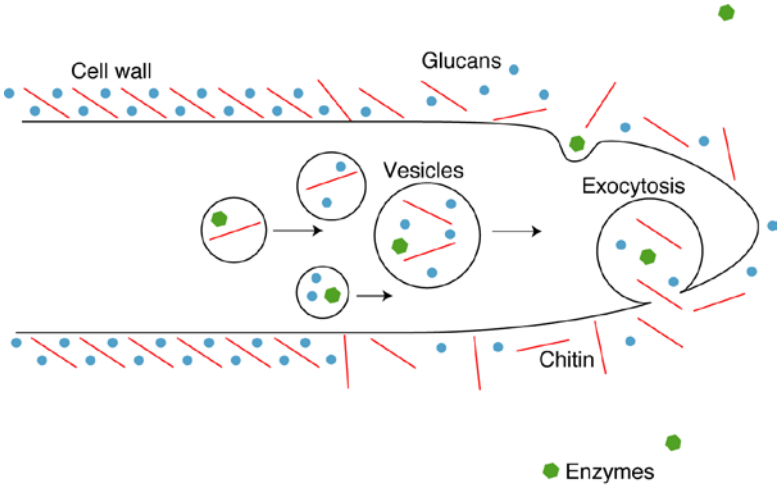
Fungal physiology

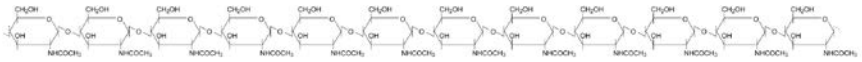


Fungal cells are organised in 1-10 µm thick hyphae. By growing at the hyphal tip, fungi push themselves out of the depletion zone that develop when resources are taken up from the environment. The tip of a hypha extends into fresh substrate. At the tip, enzymes are excreted that facilitate degradation of large molecules in the surrounding into assimilable compounds. Some distance behind the hyphal tip, ATP dependent (energy demanding) proton pumps transport H+ out of the hyphae creating a electric potential across the cell membrane. At the tip, sugars, amino acids and other compounds are taken up into the hyphae. This uptake is driven by a simultaneous uptake of H+ (symport transport) and is thus indirectly powered by the ATPase pumps and the electric potential across the cell membrane that they create.

The hyphae are organised into a mycelium.

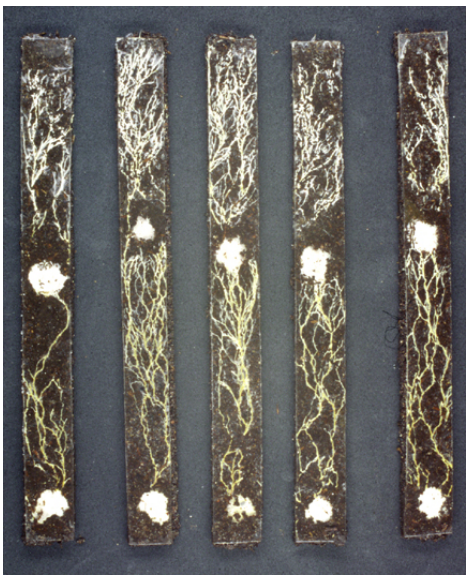


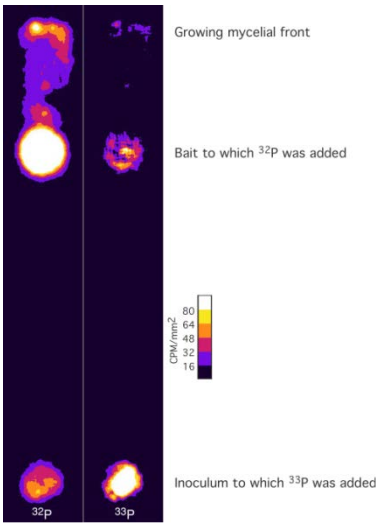




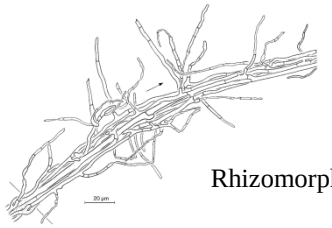
chitin

The hyphae are surrounded by a cell wall built up from polysaccharides - chitin and glucans. Chitin fibrils, which make the cell wall tough and rigid, are bound together by glucans, which act as a glue and bind the chitin fibrils together (similar to cellulose and hemicellulose in plants). Cell wall precursors are transported in vesicles to the hyphal tips. At the tip, the vesicles fuse with the plasma membrane and deposit the cell wall precursors at the cell surface. This process is called exocytosis and is also used to release extracellular enzymes. At the tip the newly formed cell wall is soft, as the chitin and glucans have not yet cross-linked into a tough matrix. By taking up water, the hyphae build up pressure in the cell (turgor). The only place where the cell may expand is at the soft tip. Therefore, hyphae almost always grow at the tip only. When hyphal branches are formed behind the tip, the cell wall has to be loosened up by enzymes (chitinases).



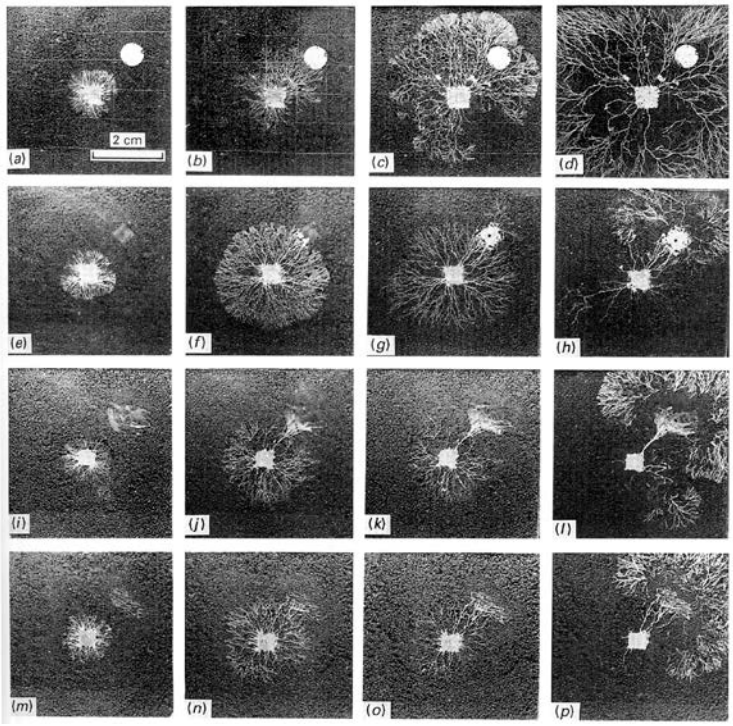


Lindahl *et al.* 1999 *New Phytologist* **150**, 189-194.



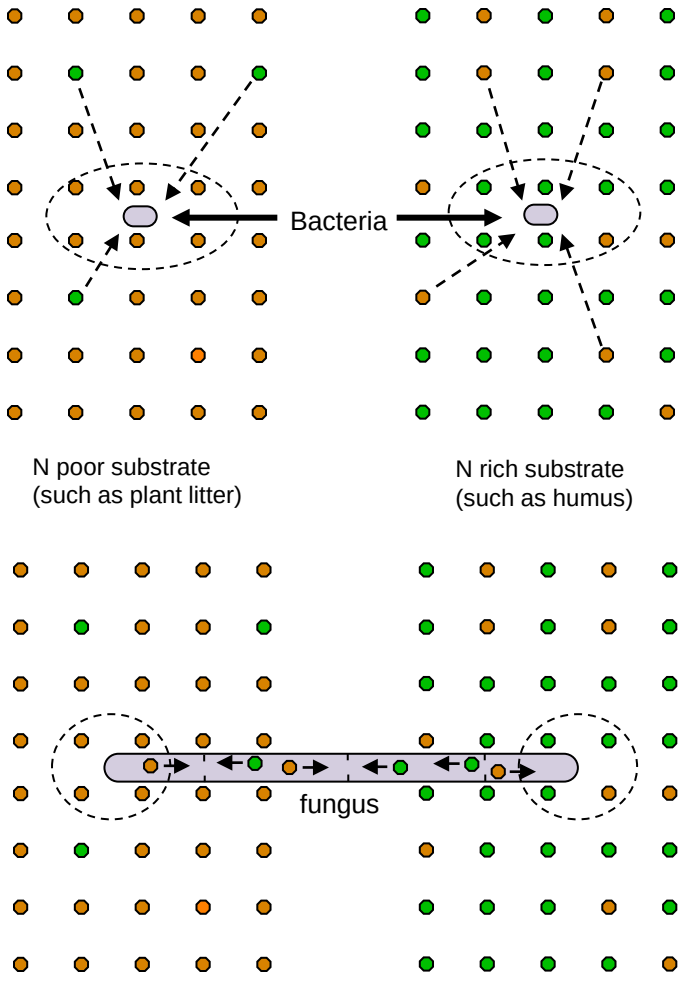
Rhizomorph

The left photo shows experimental systems with a thin layer of soil and two wood blocks connected by a fungal mycelium. The fungal hyphae are aggregated into thick, visible bundles called rhizomorphs (these are common among basidiomycetes). Two different radioactive isotopes of phosphorus were added to the wood blocks. After one month, the distribution of radioactivity was studied using in a radioactivity scanner (right picture). The picture shows the distribution of ^{32}P and ^{33}P in a single system. ^{32}P that was added to the upper wood block had been transported trough the fungal mycelium to the lower wood block (and to the hyphal tips at the top of the figure). At the same time, ^{33}P that was added to the lower wood block had been transported to the upper wood block. Phosphorus is, thus, transported bi-directionally throughout the fungal mycelium. This phenomenon has been observed also for amino acids.

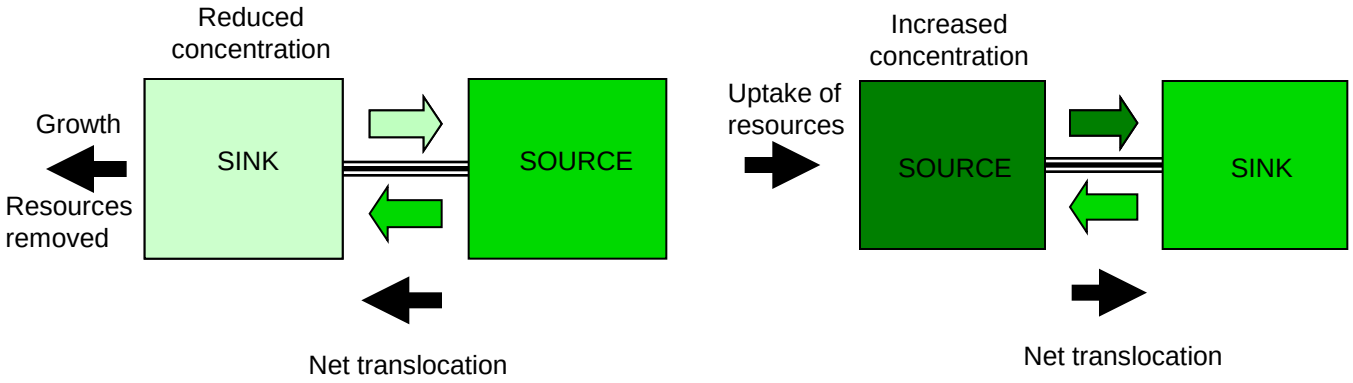


The photos show time series (left to right) of mycelia of a wood decomposing fungus that grows out into soil from a wood block. When the fungus finds another wood block (a bait) (second row) or leave or needle litter (third and fourth rows), all resources are allocated to colonisation of the new substrates. The rest of the mycelium dies. When the new substrate is colonised the fungus continues to explore the soil (the first row is a control experiment with a plastic bait). This experiment demonstrates that a fungal mycelium is not a colony of cells that happens to be physically connected, but an integrated unit with communication between the different parts. If resources are added to one part of the mycelium, all other parts are affected.

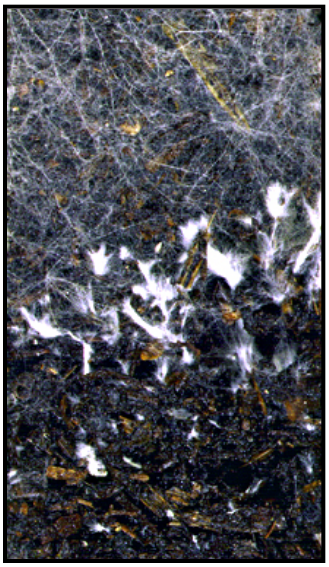
Dowson et al. 1989 *New Phytologist* **111**, 501-509.

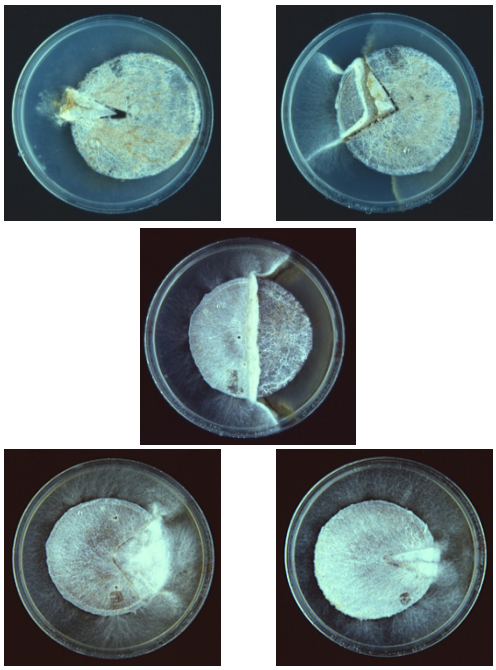


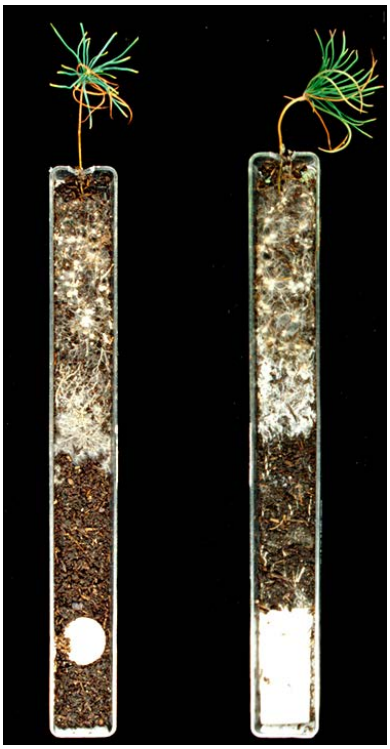
Unicellular microorganisms (yeasts or bacteria) depend on resources in there immediate surroundings. In substrate with low carbon availability (such as humus) they become C-limited, whereas in N-poor substrates, they become N-limited. Fungi with hyphae, on the other hand, may connect substrates of different qualities and transport resources between them. Thereby, fungi may reduce local resource limitations and exploit substrates more efficiently.



Resources are translocated in fungal mycelia according to source-sink relationships. Substances circulate in fungal mycelia and net-translocation depends on concentrations of mobile resources in the cell. When a part of a mycelium grow rapidly, resources are incorporated into non-mobile structures (cell walls, cell membranes, nuclei etc.) and the concentrations of mobile resources decline. Growing mycelium, thus, become a sink for resources. When a mycelium take up nutrients, the concentrations of mobile resources increase, and the mycelium become a source for resources. In reality, growth and uptake occur simultaneously, but at different rates in different parts of a mycelium. Source-sink relationships may differ for different resources; a source of C may be a sink for N (think of the mycelium colonising a mycorrhizal root).



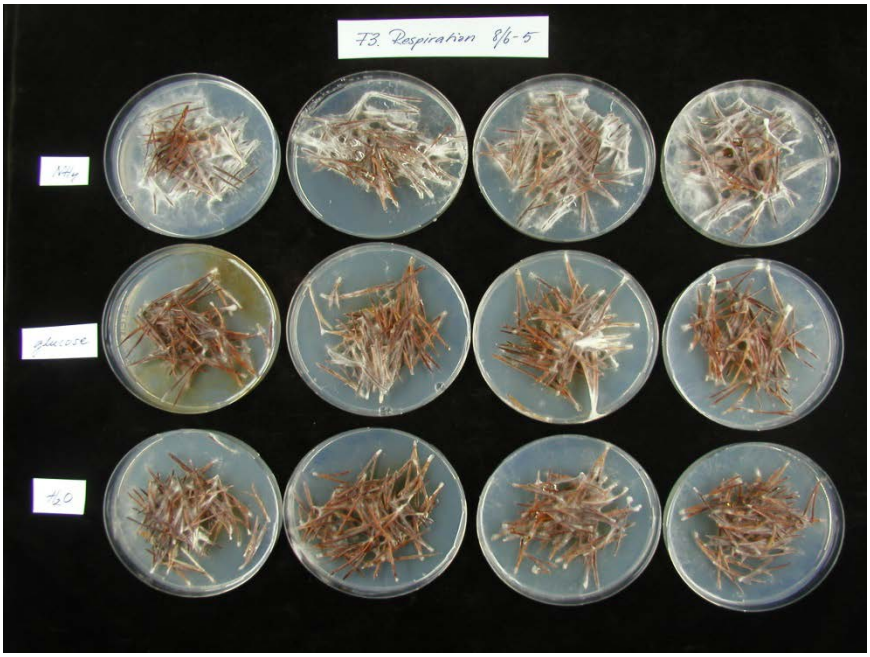




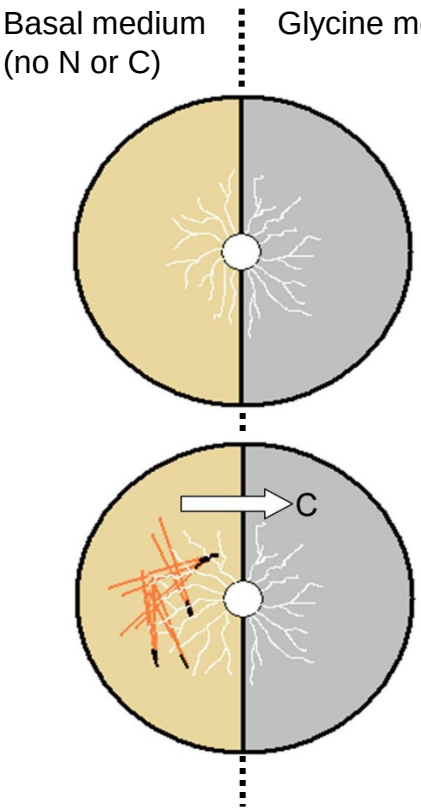
Antagonistic interactions between fungal mycelia. Fungi often compete through interference competition. This means that they attack the mycelium of the opponent, competing for space or territory, instead of competing directly for the resources (exploitation competition). The outcome of mycelial interactions depend on the amount of resources available to the fungi.

Holmer & Stenlid, 1993 *FEMS Microbiology Ecology* **12** 169-176.
Lindahl et al., 2001 *FEMS Microbiology Ecology* **38** 43-52.

Decomposition



Fungal colonisation of degrading pine needles is limited by low N-availability. Additions of NH_4 increase mycelial growth.
Boberg *et al., Soil Biology & Biochemistry 40: 995-999.*



NH_4 concentrations in the agar after 90 days:

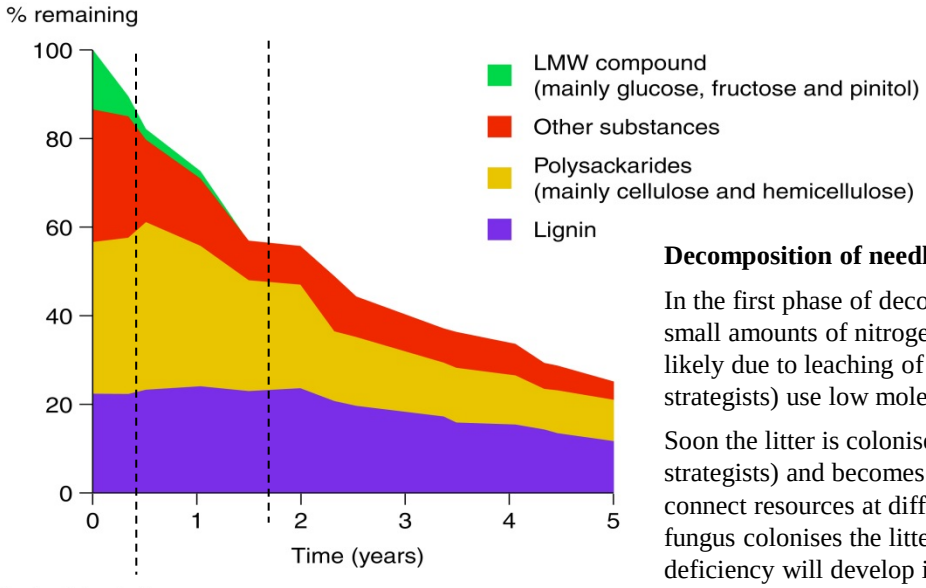
Mycena epipterygia: 2724 µg NH_4 l^{-1}

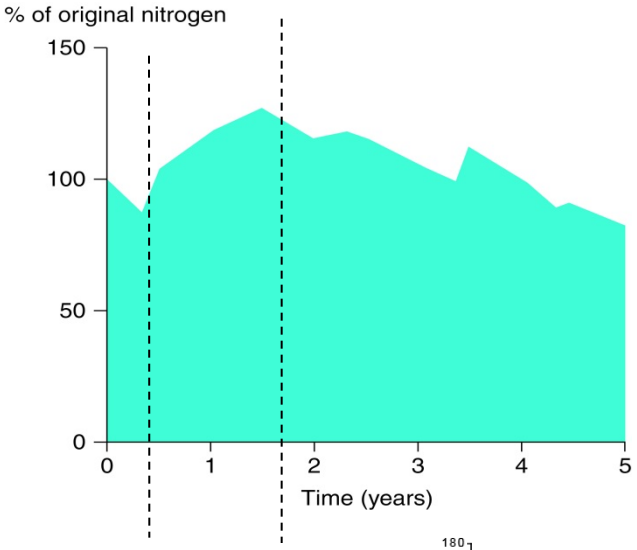
Marasmius androsaceus: 1164 µg NH_4 l^{-1}

Mycena epipterygia: 14 µg NH_4 l^{-1}

Marasmius androsaceus: 178 µg NH_4 l^{-1}

By translocating carbon from the needles, litter decomposers may grow in low C:N ratio substrates without significant ammonium release (mineralization). Many fungi may be able to translocate C from external sources, in order to avoid mineralisation and losses of N, when utilising low C:N resources. External C sources may be fresh needles, wood or mycorrhizal roots (compare fig. on page 8). Boberg *et al., Functional Ecology 24: 454-459.*





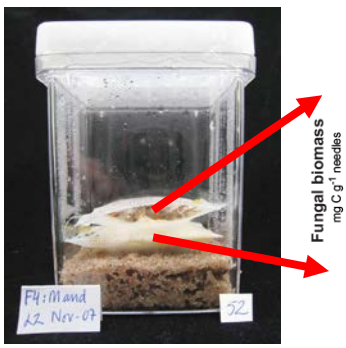
Decomposition of needles in a mor soil:

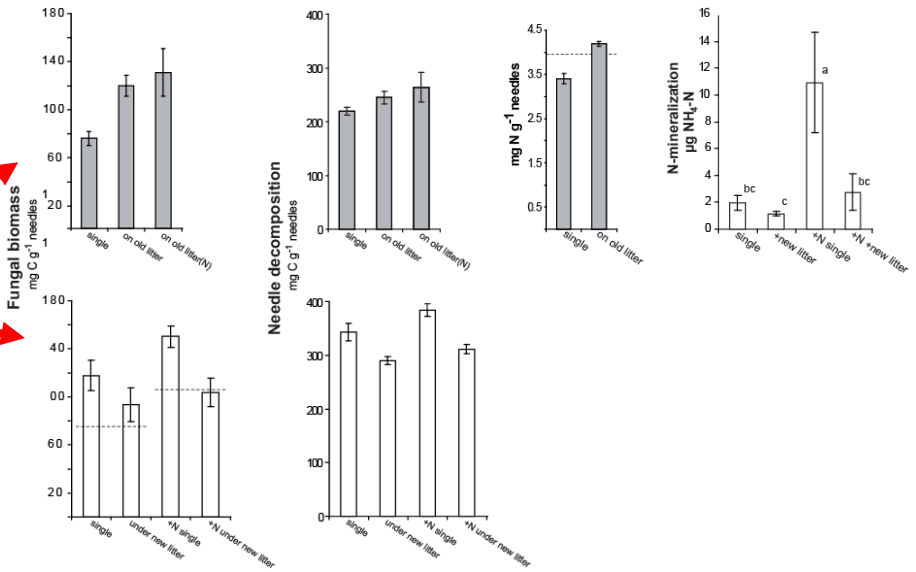
In the first phase of decomposition (the mould fungi phase), small amounts of nitrogen is lost from the decaying litter, most likely due to leaching of soluble compounds. Mould fungi (R strategists) use low molecular weight (LMW) compounds.

Soon the litter is colonised by lignocellulose decomposers (C strategists) and becomes incorporated in large mycelia that connect resources at different stages of decomposition. As the fungus colonises the litter and degrades cellulose, nitrogen deficiency will develop in the growing mycelium, which will become a sink for N. Therefore, net translocation of nitrogen from more degraded litter to mycelium colonising less degraded litter will take place.

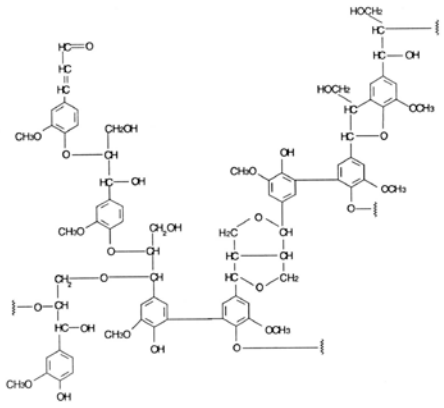
After about two years, when much of the cellulose is used up, the mycelial growth in the litter decreases and the import of nitrogen into the needles stops. In the late phase of decomposition (lignin degradation) the needles become a source for N. Note that, after five years of decomposition, when only 25% of the initial weight remains, the amounts of nitrogen in the needles are similar to the amounts in the fresh needle. There is little net loss of nitrogen. This could partly be explained by the incorporation of nitrogen into recalcitrant humus compounds (humification).

Berg *et al.*, 1982 *Canadian Journal of Botany* 60 1310-1319.





A mesh bag with recently dropped needles was placed on top of a bag with pre-degraded needles and colonised by a fungus. Fungal biomass and needle decomposition was reallocated to the fresh needles, which have more cellulose left. There was a net transport of N from the mycelium in the degraded needles (source) to the mycelium in the fresh needles (sink). The access to fresh needles reduced N mineralization.



Phenolic compounds, such as lignin and humus, are degraded by **oxidative enzymes**:

Lignin peroxidases
- uses H_2O_2 as a co-substrate
-interacts directly with lignin

Manganese peroxidase
- uses H_2O_2 as a co-substrate
- oxidizes Mn^{2+} to Mn^{3+}
- Mn^{3+} interacts with lignin

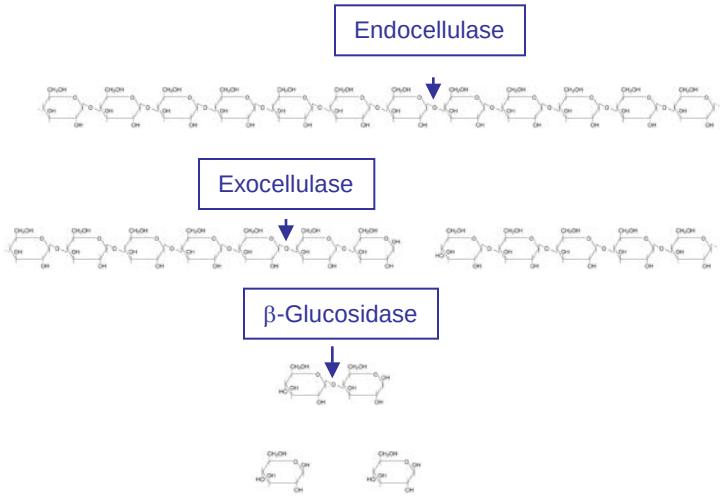
or through non-enzymatic oxidation:
Fenton reaction
$Fe^{2+} + H_2O_2 \Rightarrow Fe^{3+} + .OH + OH^-$

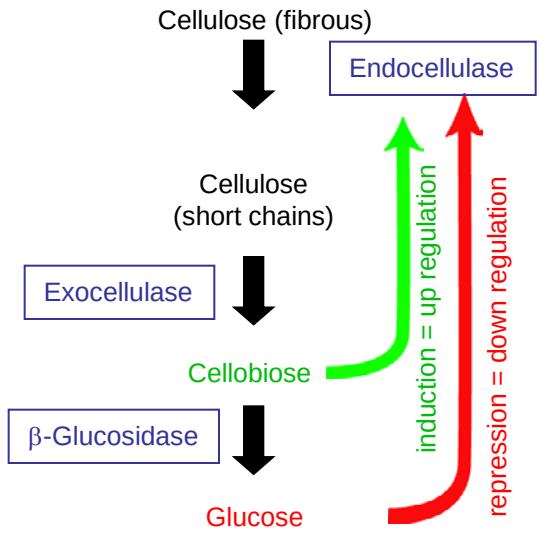
White-rotted wood, degraded by hydrolytic cellulases and peroxidase enzymes. Both lignin and cellulose is degraded. Only brittle, bleached wood fibers remain.

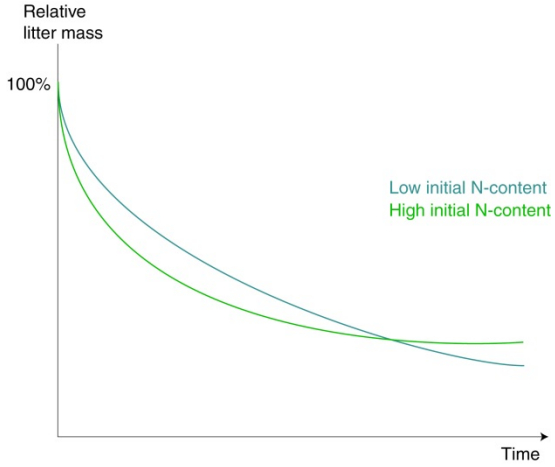
Brown-rotted wood, degraded through non-enzymatic cellulose degradation and lignin modification (Fenton reaction). Cellulose is degraded, but the partly degraded lignin remains, forming a cubic structure.

Regulation of cellulose decomposition

Endocellulase and exocellulase are always produced at a very low (constitutive) level. When cellulose is present close to a hyphal tip, small amounts of cellobiose will be taken up by the hyphae. This is a signal that induce a higher production of all three enzymes. High levels of glucose inside the hyphae means that the fungus is not using all the glucose it is taking up. This is a signal to stop the production of cellulose degrading enzymes.

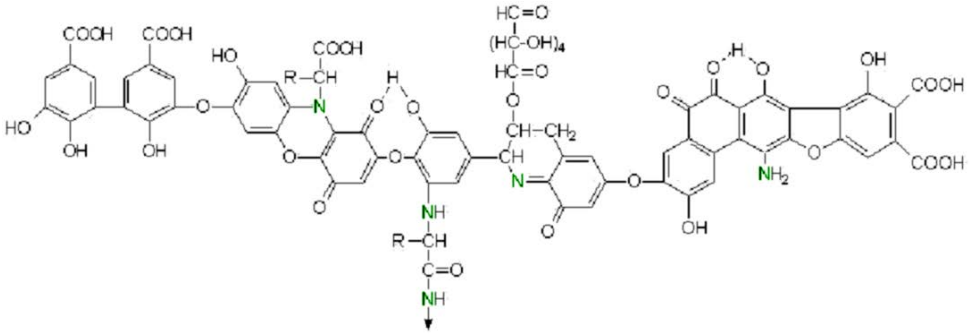




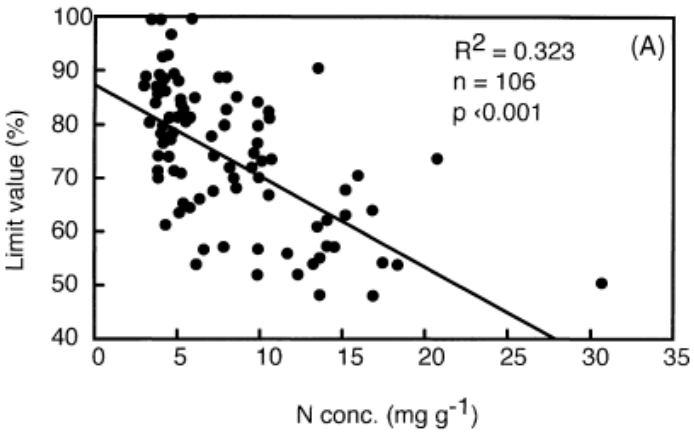


Effects of N on decomposition of lignin-rich litter:

Nitrogen rich litter degrade quickly in the beginning, but slowly at later decomposition stages. Nitrogen poor litter degrade slowly in the beginning, but decomposition goes on for a longer time. In early decomposition stages, fungal colonisation and decomposition is N-limited. A possible explanation of the negative N-effects on later decomposition stages is that the fungi degrade late-stage, cellulose depleted litter primarily to obtain N, which is translocated to support mycelial colonisation of fresh litter. In litter with high N-availability, they don't need to do this, and therefore late-stage decomposition is down-regulated.



Lignin is a complex molecule with many phenolic rings which makes it very resistant to degradation. Lignin decomposition is performed by oxidation. Lignin peroxidase acts directly on the lignin molecules. The enzyme is oxidised (an electron is removed from the active site of the enzyme) by hydrogen peroxidase (H_2O_2) that is also released by the fungus. The enzyme then in turn oxidises covalent bonds in the lignin structure, which then breaks apart. Manganese peroxidase is also oxidised by hydrogen peroxide. The enzyme in turn oxidises Mn2+ to Mn3+. Mn3+ is a very reactive atom that can penetrate into the lignin and degrade it through oxidation. The decomposition products of lignin are also very reactive. Possibly many different LMW compounds (sugars, amino acids, ammonium etc…..) may be incorporated into the degrading lignin superstructure. The end product is what we call **humus** and is quite rich in nitrogen (lignin contains no nitrogen to begin with). Most researchers agree that lignin decomposition consumes more energy than it yields. Some claim that the decomposition products are not even taken up, but that lignin may be degraded all the way to CO_2 outside the hyphae. The lignin, however, coats the cellulose fibres and the fungi may need to remove it to gain access to all cellulose. The fungi may also produce lignin degrading enzyme to mobilise nitrogen from partly or fully humified lignin. This new theory is supported by the fact that, in many fungi, the lignin degrading enzymes are produced only when the fungi are nitrogen starved. Currently there are several parallel models of the chemical nature of humus and humification.

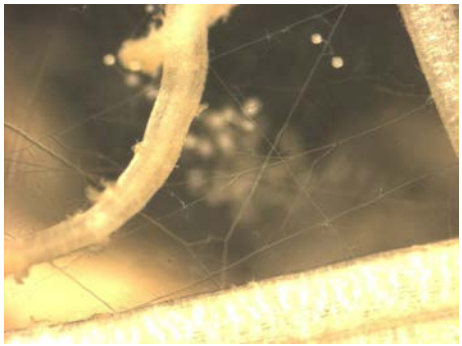


The limit value of decomposition reflects the fraction of the litter which is never degraded and accumulates in the soil as humus or SOM (100% = no humus accumulation, 50%= half of the litter left as humus). Since oxidation of late stage litter and humus is repressed by N, humus accumulation is higher under litter with a high N-content.

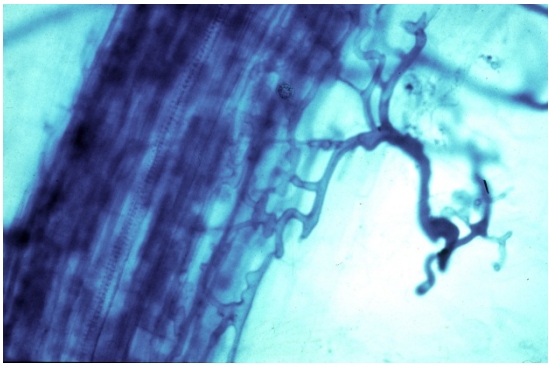
Berg *et al.*, 1996 *Canadian Journal of Botany* 74 659-672.

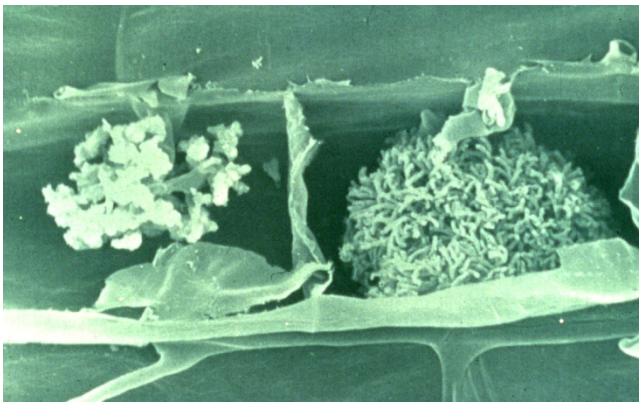
Mycorrhizal symbiosis and nutrient cycling in forest ecosystem

Arbuscular mycorrhizal symbiosis take place between fungi in the phylum Glomeromycota and most land plants, including herbs, grasses and most broadleaf trees. This symbiosis is as old as land plants (ca 450 Ma).
Fungal hyphae grow out from the plant roots and colonises the soil with an extraradical mycelium.

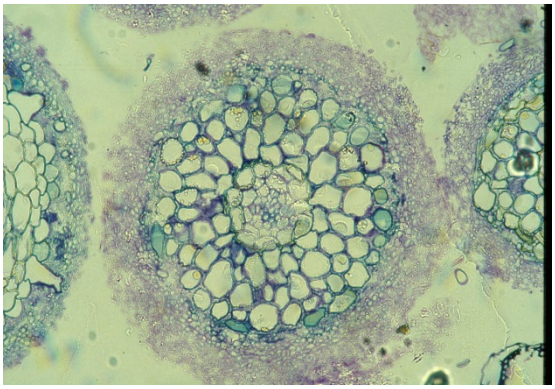


The fungal hyphae grow into the plant root and into the root cells, where the fungus forms arbuscules (arbos=tree). In the arbuscules the fungus take up glucose provided by the plant, and the plant receives nitrogen and phosphorus from the fungus.

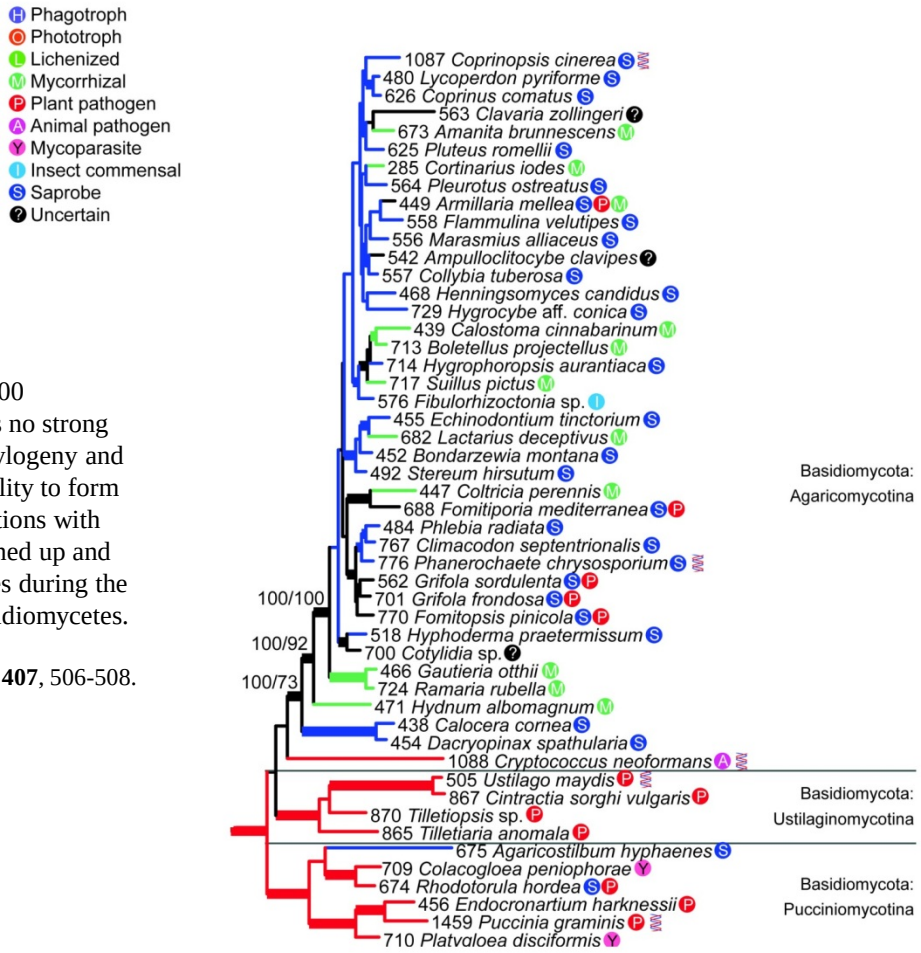




Ectomycorrhizal symbiosis take place between Basidiomycetes (and some Ascomycetes) and forest trees, primarily on mor soils. Trees that only form ectomycorrhiza are e.g. Pine, Spruce, Fir and Birch. Aspen, Willow (Salix), Beech, Oak, Eucalypt and many other trees may form both ectomycorrhiza and arbuscular mycorrhiza.
Ectomycorrhizal symbiosis evolved ca 100 Ma ago, and is thus much younger than arbuscular mycorrhizal symbiosis. The high enzymatic capacity of basidiomycetes makes ectomycorrhizal symbionts more efficient than Glomeromycetes on humic mor soils.



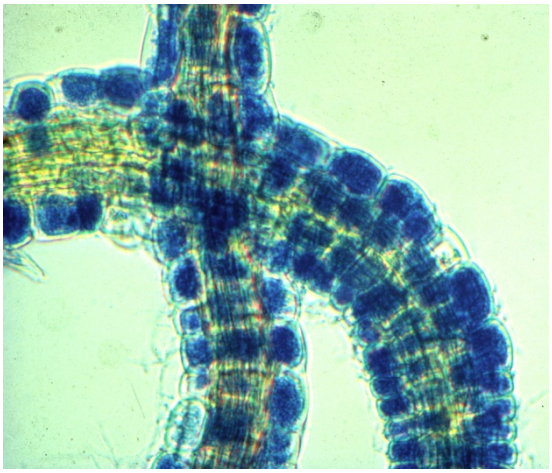
Ectomycorrhizal root tips. The fungus encloses the root tip in a mantle of hyphae. Hyphae also grow between the root cells, forming a Hartig's net. No intracellular penetration.

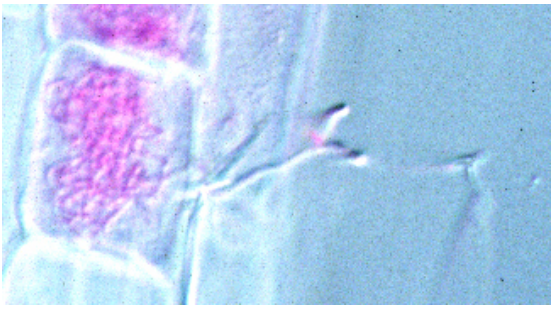


A phylogenetic tree of 200 basidiomycetes. There is no strong relationship between phylogeny and trophic strategy. The ability to form ectomycorrhizal associations with plants seems to have turned up and disappeared several times during the evolution of today's basidiomycetes.

Hibbett *et al.*, 2000 *Nature* **407**, 506-508.

Plants within the *Ericaceae* form a special type of mycorrhizal symbiosis together with certain Ascomycetes - **Ericoid mycorrhiza.**
The ericoid mycorrhizal fungi form hyphal coils inside the host root cells (fungus = blue or red in the images).

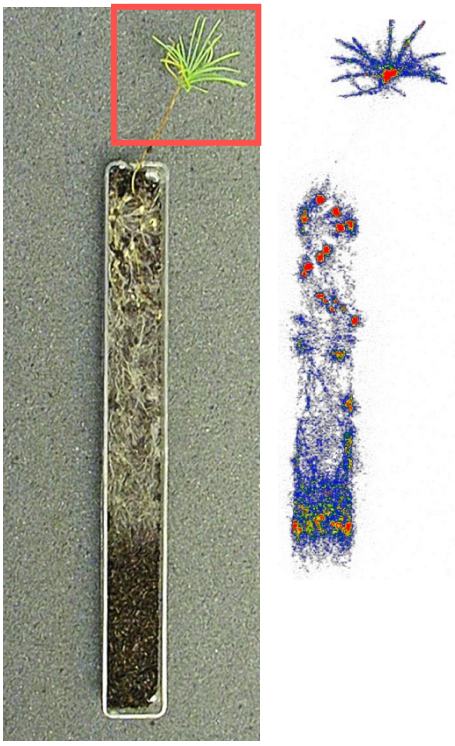


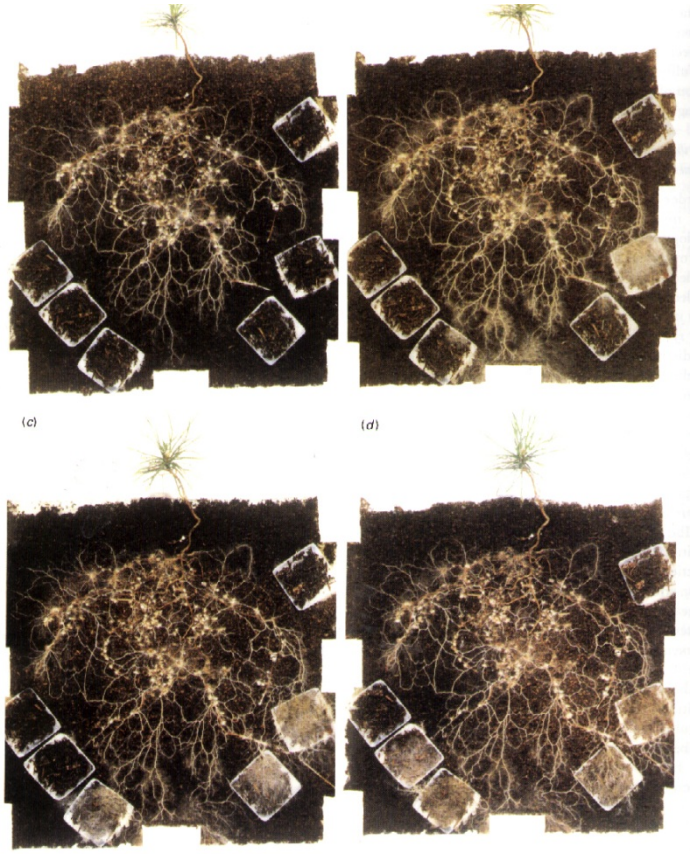


Ectomycorrhizal fungi may form very extensive extraradical mycelia that efficiently exploit the soil for nutrients.

By enclosing the plant shoot in a air-tight box, and filling the box with radioactive CO_2, the photosynthetic products may be traced, using a radioactivity scanner. On the image to the right (1d after labelling), radioactive carbohydrates have been produced in the shoot and transported to the roots. The ectomycorrhizal root tips are strong sinks for plant-derived carbon. Strong radioactive labelling of the mycorrhizal extra-radical mycelium indicate that the mycelium is provided with carbon directly from the photosynthesis.

Radioactive $^{14}CO_2$



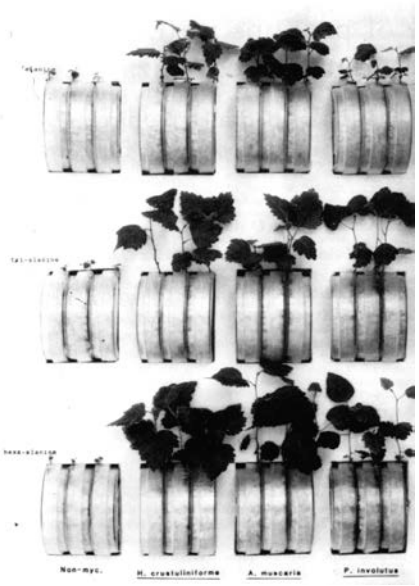


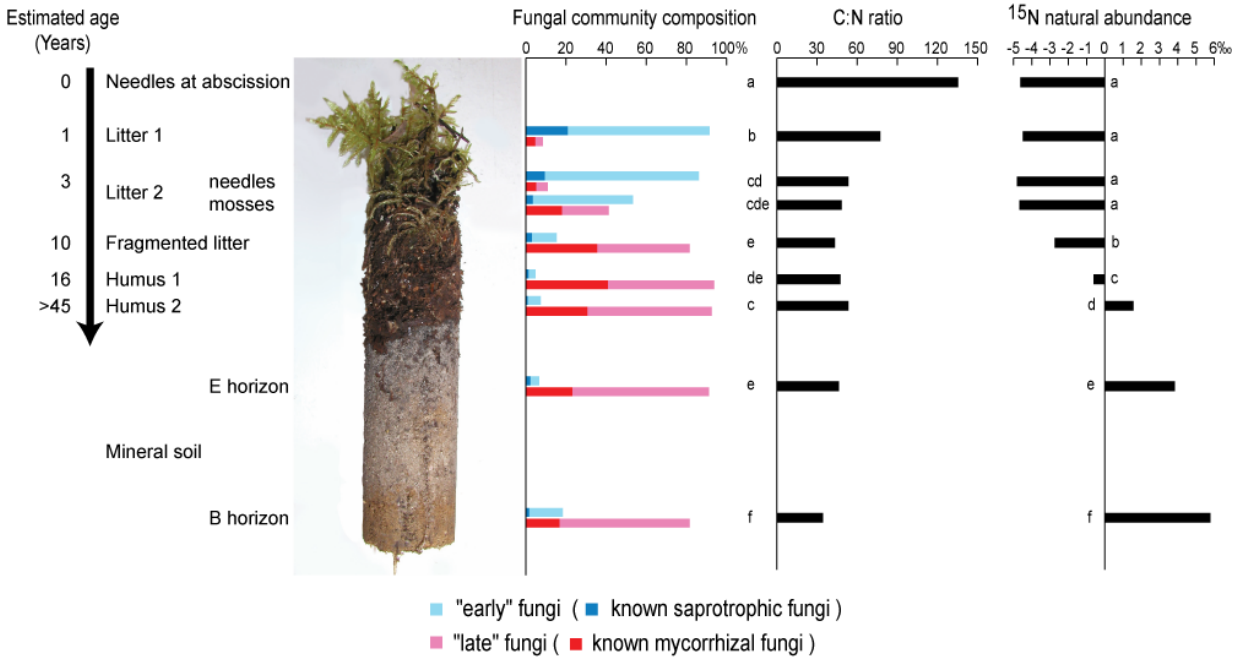
Time series (above) of a micro-cosm with a ectomycorrhizal pine seedling. The extraradical mycelium colonises small trays filled with litter material. The fungus produces dense mycelium in response to the nutrient rich litter. These mycelial patches are associated with increased enzymatic activities of proteases and oxidizing enzymes. At the end of the experiment, the litter is depleted in N and P compared with the uncolonised litter. This experiment suggest that ectomycorrhizal fungi may utilise nutrients directly from organic matter.

Bending & Read, 1995 *New Phytologist* **130,** 401-417.

In the experiment to the right, birch seedlings are grown in a sterilised substrate with organic compounds - amino acids or small peptides (proteins), as the only source of nitrogen. Without mycorrhizal fungi, the seedlings cannot take up nitrogen and grow, but with mycorrhizal fungi present, the seedlings may use the organic nitrogen without prior mineralisation.

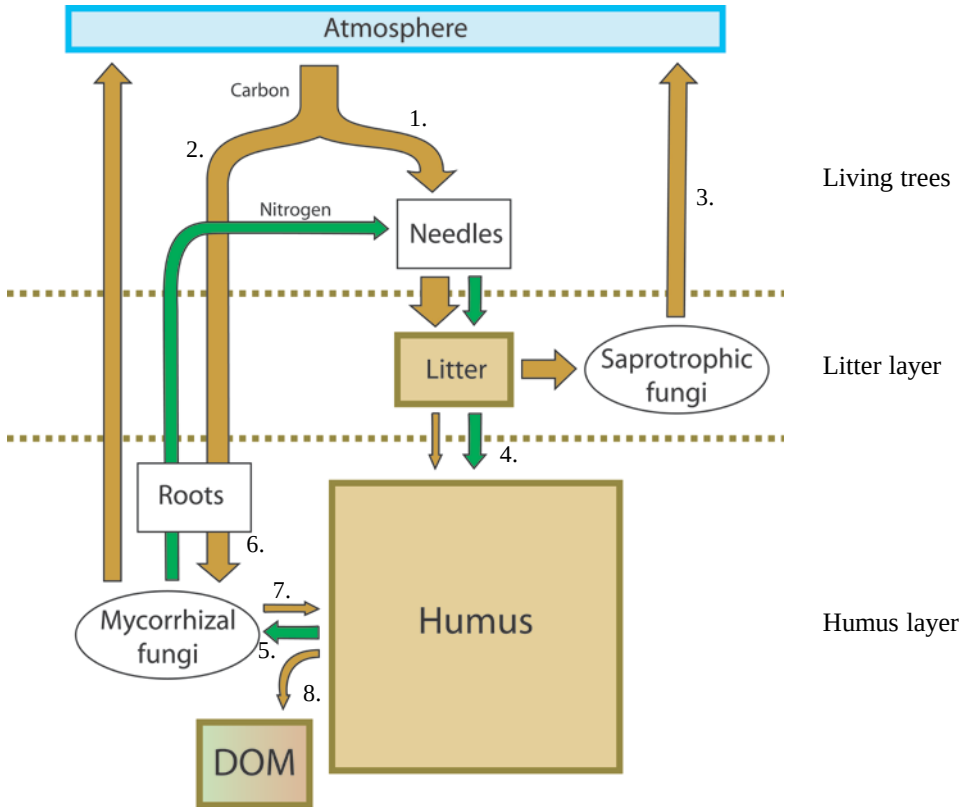
Abuzinadah & Read 1989 *New Phytologist* **112**, 55-60.





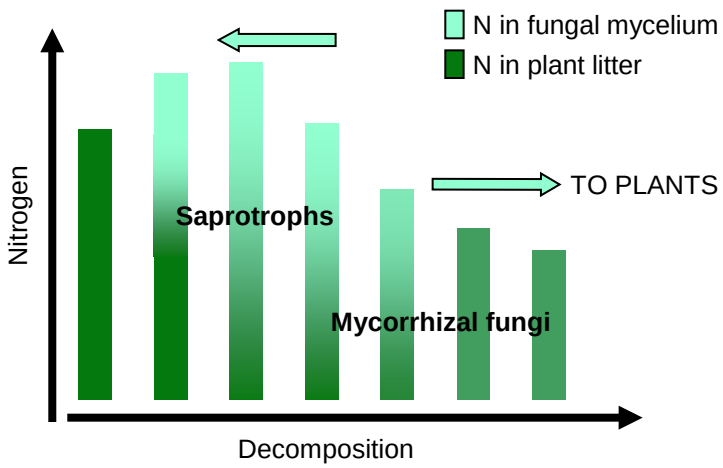
In this podzol soil under a pine forest, saprotrophic fungi colonise litter under early stages of decomposision. In more decomposed litter and humus, ecto- and ericoid mycorrhizal fungi dominate the fungal community. During the saprotrophic phase of decomposition, C:N ratio decreases with time (and depth), as cellulose is degraded and carbon is lost due to saprotrophic respiration, whereas nitrogen is retained in fungal mycelium within the litter. During the mycorrhizal phase, C:N ratio increases slightly, indicating that N is mobilised from the organic matter and translocated to the plant host, whereas new C from plant host photosynthesis is added to the humus. The enrichment in ^{15}N with time during later decomposition stages, confirm the separation of saprotrophic and biotrophic decomposition. During the transfer of N from mycorrhizal fungi to their host plants, ^{14}N is preferred, leaving the extraradical mycelium enriched in the heavier isotope ^{15}N.

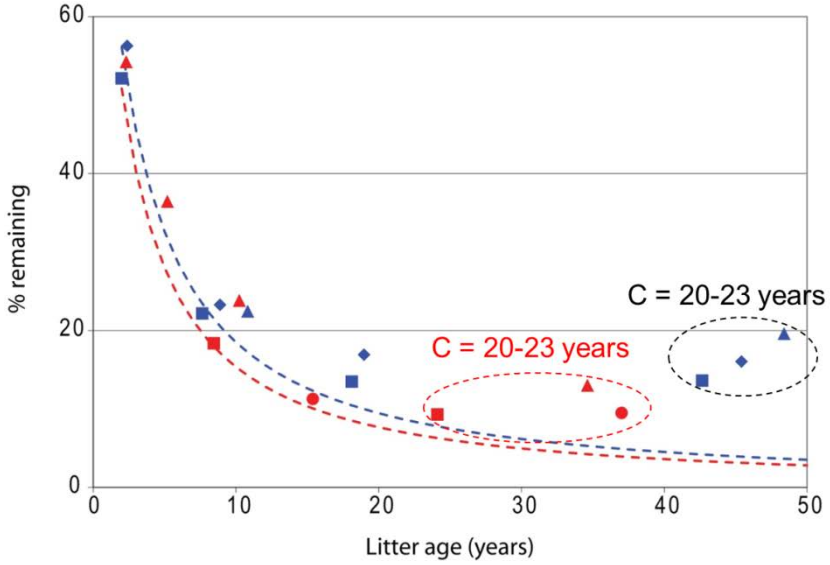
Lindahl et al 2007, *New Phytologist* **173**, 611-620.



A model of C and N cycling in a coniferous forest soil. Photosynthesised C is allocated to needles (1) or to the plant roots (2). The needle litter is degraded by saprotrophic fungi that return most of the needle C to the atmosphere (3) but leave the N incorporated into complex humus compounds (4). N is <u>not mineralised</u>, due to N limitation of decomposer fungi. N is then mobilised by mycorrhizal fungi from older organic matter (5). The mycorrhizal fungi are provided with C via the plant roots (6). The N cycle is, thus, driven by recently photosynthesised C via the mycorrhizal roots rather than by litter C. This contrasts to the situation in mull soils, where N often is mineralised during saprotrophic decomposition.

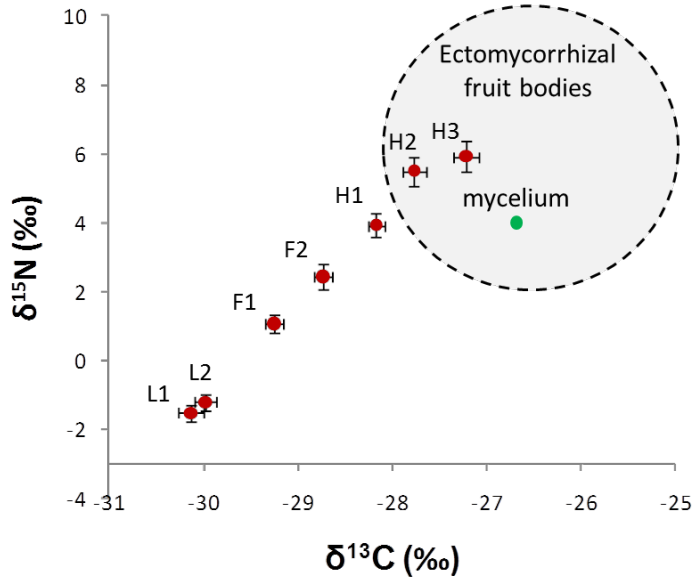
N-limited saprotrophs maintain N in their mycelium, by translocating N from older litter to fresh litter components. Mycorrhizal fungi translocate N to their host plants. This causes competition for litter N between saprotrophs and mycorrhizal fungi. The saprotrophs may compete successfully in relatively fresh litter, which is rich in cellulose, but are outcompeted in older organic matter, which is depleted in cellulose. Here, fungi need an external carbon source, such as living roots (remember that humus degradation is a co-metabolic process. The accumulation of humus depend on the relationships between litter production (1), saprotrophic decomposition (3), mycorrhizal mycelial growth (7) and mycorrhizal degradation of humus to dissolved organic matter (8).

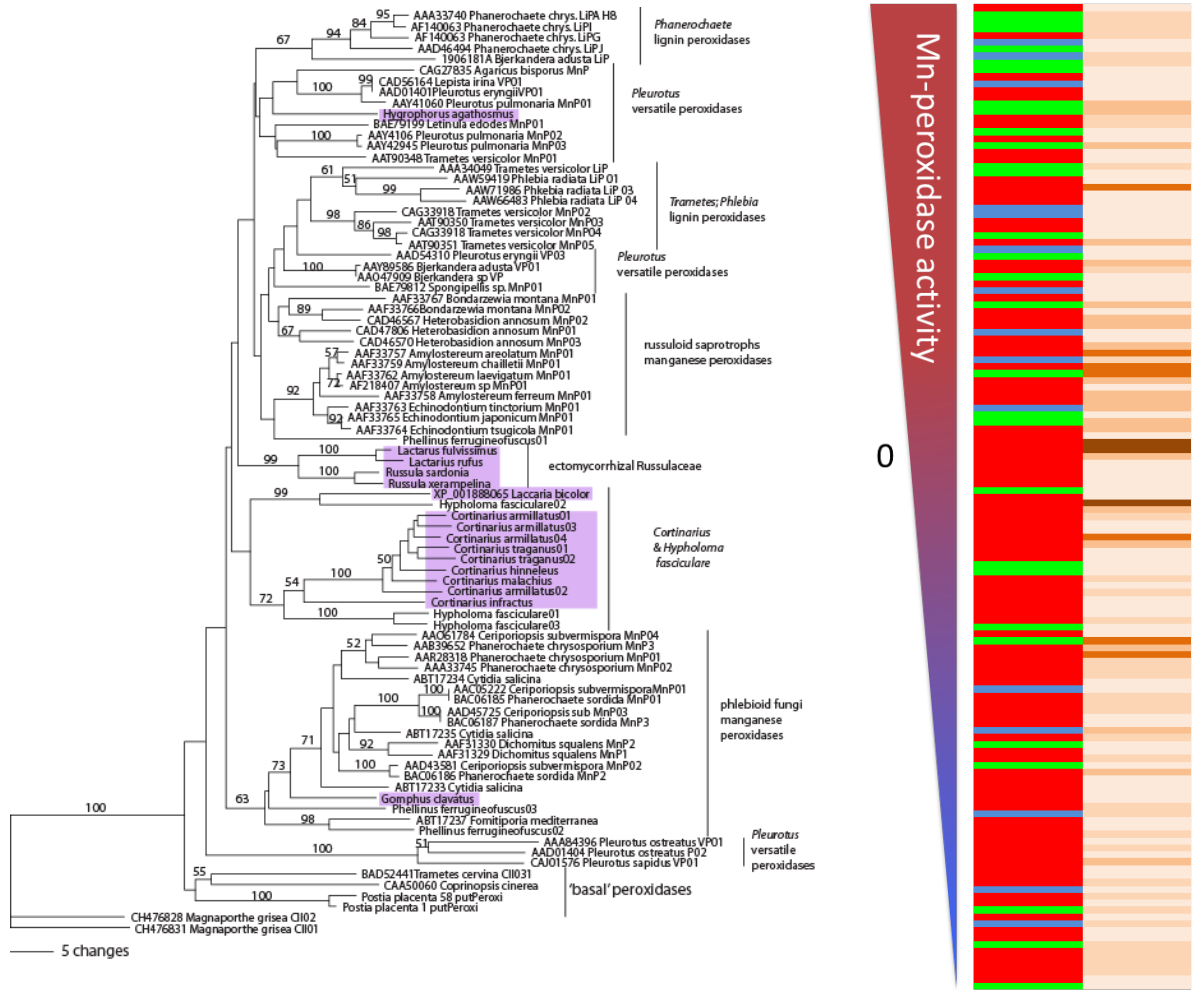




Mycorrhizal mycelium may also contribute to the *formation* of humus (7 in the box model).

In a field experiment, the age of organic matter (humus) was determined by ^{14}C analysis. Humus cores were segmented in vertical horizons, and the amounts of organic matter in different horizons were analysed with respect to mass and C age. When the data was compared to a theoretical model of decomposition of above ground plant litter (dotted lines), it was clear that there is too much C deeper in the profile, and that this C is younger than it should be (compare the predicted litter age (x axis) with the measured C age). The conclusion is that a major fraction of the C enters humus via roots, presumably as mycorrhizal mycelium. As the litter (L1,2 below) turns into humus (H1,2,3), the concentrations of the rare isotopes ^{13}C and ^{15}N approaches those found in mycorrhizal mycelium. Thus it seems as humus is largely built up from mycorrhizal mycelium added below ground.





Clade	Cluster size	Species
		Aureobasidium pullulans
		Cortinarius paragaudis
		Cortinarius testaceofolius
		Cortinarius diasemospermus
		Penicillium canescens
		Fomitopsis pinicola
		Cortinarius semisanguineus
		Resinicium bicolor
		Cortinarius obtusus
		Cortinarius acutus
		BL89_Saccharomycetales
		BL88_Agaricomycotina
		Candida
		Mollisia
		Suillus variegatus
		Tricholoma fucatum
		Davidiella tassiana
		Rhytismatales (Cudonia)
		Piloderma olivaceum
		Verticillium
		Cortinarius armillatus
		Dothidiomycetes (Venturiaceae)
		Coniozyma leucospermi
		Cortinarius obtusus
		Cortinarius biformis

An active role of ectomycorrhizal fungi in humus degradation/dissolution (8 in the box model) would require that these fungi have the necessary oxidative enzymes. Upper left: When mycorrhizal fungi were screened for the presence of Mn-peroxidase genes these were found in several groups, particularly in the genus *Cortinarius*. Previously, only white-rot wood-decayers were known to produce Mn-peroxidases. The figure shows a phylogenetic tree of Mn-peroxidase sequences in basidiomycetes with newly discovered ectomycorrhizal genes in purple. Upper right: In samples of forest humus, Mn-peroxidase activity was correlated against the fungal community composition, as analysed by DNA sequencing. Ectomycorrhizal species (green lines) were positively correlated with Mn-peroxidase activity. Lower left: Close up of top species in upper right figure. In particular, *Cortinarius* species were strongly correlated, *i.e.* only samples containing *Cortinarius* DNA had high Mn-peroxidase activity .

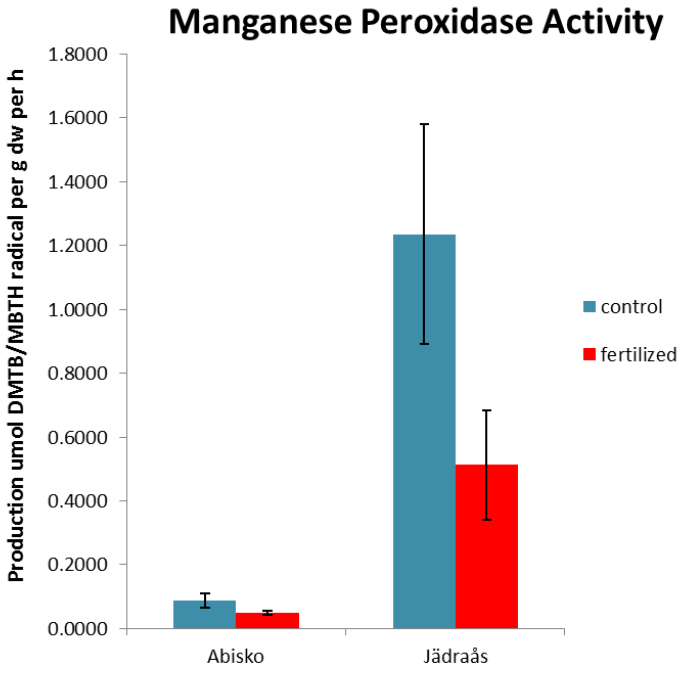
Bödeker *et al*. 2009 ISME Journal

Cortinarius paragaudis

Cortinarius semisanguineus

Cortinarius diasemospermus

Cortinarius obtusus



Mn-peroxidase activity decreased to half, only 2 days after N fertilization of humus. As it seems, ectomycorrhizal *Cortinarius* species produce humus degrading enzymes to obtain N from organic matter, but only when mineral N is not available.