



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)

SYMBIOTIC RELATIONSHIPS OF FUNGI

The relationship between different organisms is generally referred to as symbiosis – if it is mutually beneficial, it is called mutualistic; if one organism benefits at the expense of another, we are talking about parasitism (this concept dates back to de Bary in the 19th century).

For simplicity, the term „symbiosis“ further refers to mutualistic symbiosis.

The basic mutualistic types of symbiosis in fungi are mycorrhiza and lichenism; somewhat complicated are symbiotic relationships with animals.

MYKORRHIZAL RELATIONSHIPS

Mycorrhiza represents the relationship between fungus and plant, i.e.

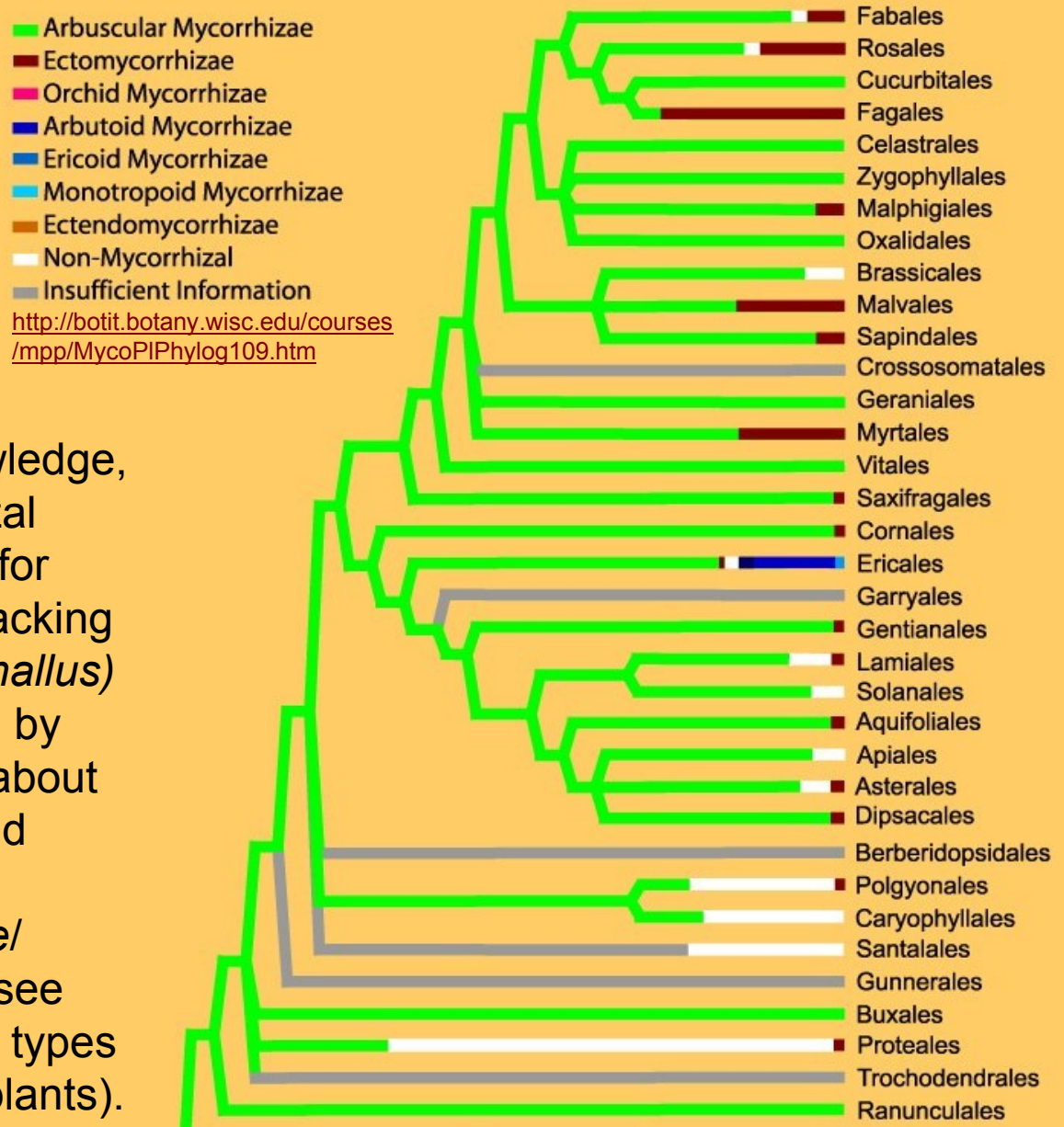
mycobiont and **phytobiont** (not to be confused with similar-sounding terms photobiont and phycobiont in lichenism!).

At the beginning, it is useful to clarify the basic concepts:

- **mycorrhiza** – functional symbiosis of the fungus with the plant (sensu lato); morphologically, this is also the place where exchange of nutrients takes place;
- **mycorrhizal** – term denoting fungi capable of forming mutualistic symbioses with plants;
- **mycotrophic** – term for plants capable of forming a functional mutualistic connection with the mycelium; mycotrophy can be quantified (more or less);
- not to be confused: mycophagous (= fungivorous) are organisms that eat fungi.

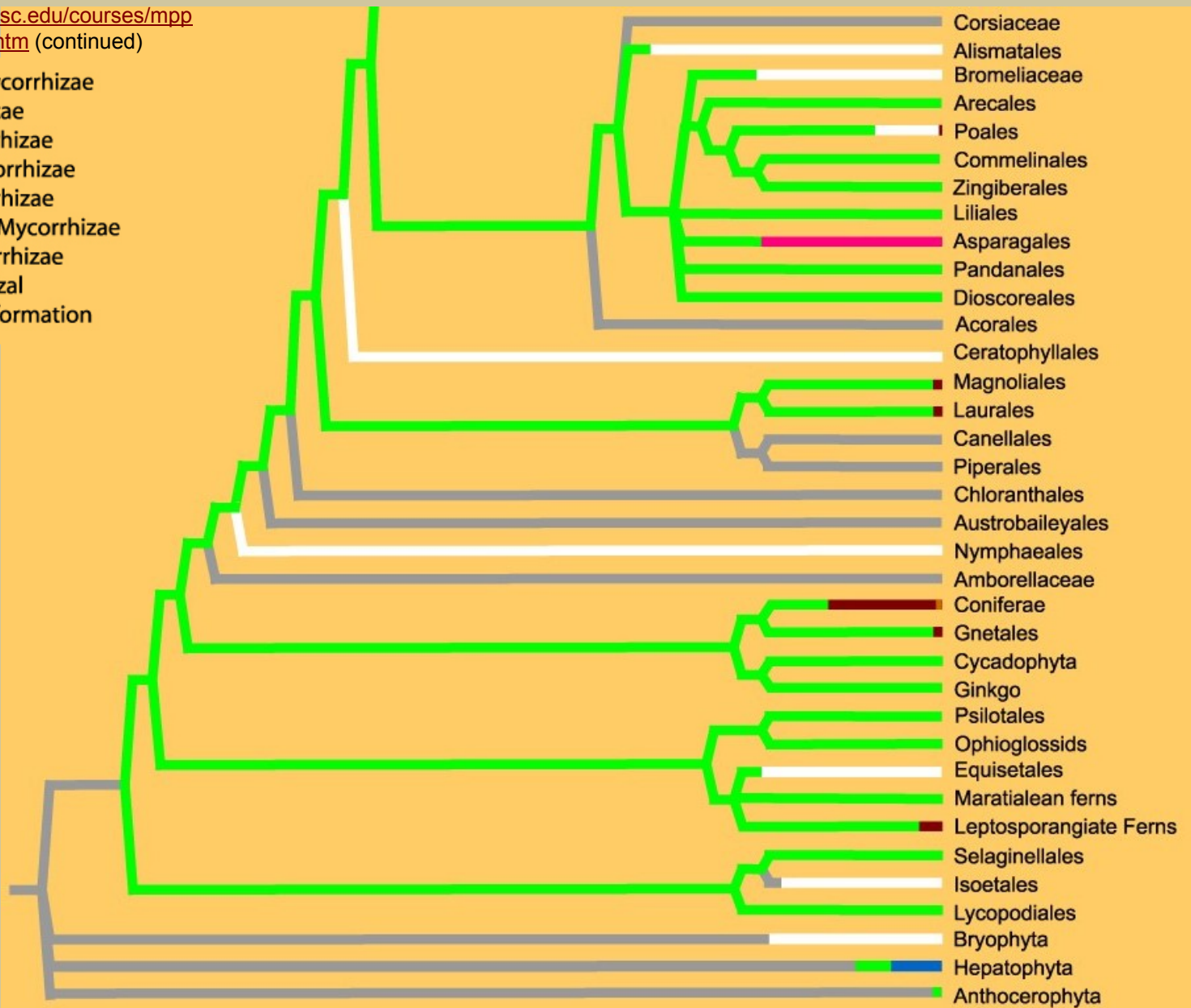
Note: see good study material about mycorrhizae [here](#) (PDF), with links to other „mycorrhizal websites“ at the end (recommended!).

According to current knowledge, most plants are mycorrhizal (not only vascular plants, for example the chlorophyll-lacking liverwort *Aneura (Cryptothallus) mirabilis* is also nourished by mycorrhiza), except only about 5% of species (aquatic and wetland plants, and some ruderal /e.g. *Brassicaceae*/ – in the diagram you can see representation of different types of mycorrhizae in higher plants).



<http://botit.botany.wisc.edu/courses/mpp/MycoPIPhylog109.htm> (continued)

- Arbuscular Mycorrhizae
- Ectomycorrhizae
- Orchid Mycorrhizae
- Arbutoid Mycorrhizae
- Ericoid Mycorrhizae
- Monotropoid Mycorrhizae
- Ectendomycorrhizae
- Non-Mycorrhizal
- Insufficient Information



For completeness, let us mention that fungi are of course not the only symbionts of plant roots – „root-nodule bacteria" (*Rhizobium*) or actinomycetes (*Frankia*) forming tumor-like galls on the roots, so-called actinorrhizae, are well-known; „cooperation" of these organisms is also possible, e.g. when the bacteria improve the plant's nutrition with nitrogen and mycorrhizal *Glomus* with phosphorus.

For the first time, a mycorrhizal relationship was established in the Ordovician or Silurian (see also *Origin of fungi in General mycology*), when plants left the water and rhizomes with rhizoids served only to anchor in the soil and potentially pump water; a significant limiting factor for plants was the availability of phosphorus. The original mycobionts were probably parasites who themselves suffered from a lack of phosphorus => they began to draw phosphorus from the surrounding soil and part of the phosphorus was subsequently transferred to the plant.

- **Benefits of the plant:** energy sources and organic nutrients (primarily carbohydrates, or carbon compounds in general, also some vitamins) – the fungus has a stable supply of nutrients in the soil, which is (with the exception of organic residues in the surface layer) essentially oligotrophic environment (significant competitive advantage compared to saprotrophic species).

The plant can give the fungus up to 30% of its production of assimilates, but it is still advantageous over the „cost" of creating a comparable root area. Also exudates (or exsudates) of the roots can favourably affect growth of the fungus; plants appear to be able to recognise „their" mycorrhizal fungi and produce substances that support formation and growth of their hyphae .

• **Benefits of the fungus:** supply of water and minerals (especially if it replaces root hairs) => more nutrients for the plant => higher rate of photosynthesis => higher production of carbon compounds, which in turn helps the fungus.

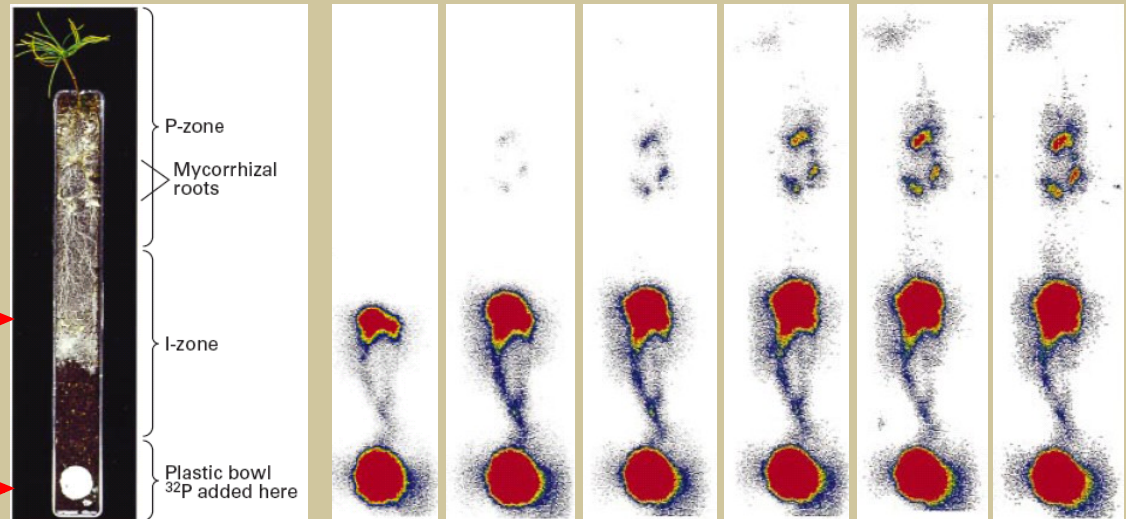
The most significant benefit of the fungus is the supply of phosphorus (phosphates degraded by phosphatase => it releases phosphorus from insoluble compounds and transfers it to the plant) and nitrogen (similarly proteinases, degrading proteins and amino acids => NH_4^+) => faster growth or development of seedlings of plants colonised by fungi. Endomycorrhizal fungi in particular help to improve phosphorus nutrition, while other types mainly supply nitrogen; this benefit is more pronounced in P or N poor soils than in rich soils. (Already in the 1920s, Melin experimentally proved that the connection with mycorrhizal fungus improves pine nutrition with nitrogen, which the fungus provides in exchange for assimilates and is then incorporated into the proteins of the tree..)

Significant nutrient translocation on the example of phosphorus transferred between saprotrophic *Hypholoma fasciculare*, mycorrhizal *Suillus variegatus* and seedling of *Pinus sylvestris*.

Suillus variegatus →

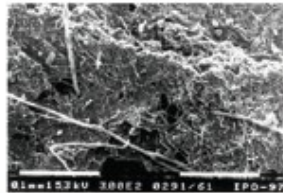
Source: Lindahl et al. 1999;
taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

→ *Hypholoma fasciculare*





Extraradical mycelium provides increased surface area for nutrient uptake, bridges nutrient depletion zones.



Ectomycorrhizal fungal hyphae colonising microsites in a rock surface

Jongmans et al. 1997. Nature 389:682-685

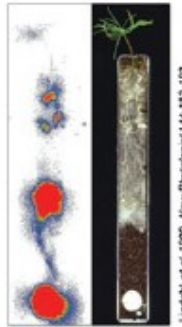


Solubilisation of tri-calcium phosphate by ectomycorrhizal fungus and associated bacteria

organic acids, siderophores and other chelating agents

Mobilisation of N & P from organic polymers from microbial biomass, micro- & meso-fauna and plant litter intervention in microbial mobilisation-immobilisation cycles

degradative enzymes, antibiotics & other chemically antagonistic compounds



Electronic autoradiography showing transfer of P from saprotrophic mycelium to a pine plant via an ectomycorrhizal fungus

Ludshilf et al. 1996. New Phytologist 144: 183-193

Penetration of microsites

mineral nutrients

weathering & solubilisation of minerals

organic nutrients

Synergistic, competitive or antagonistic interactions associative N fixation exudation of organic compounds at hyphal tips

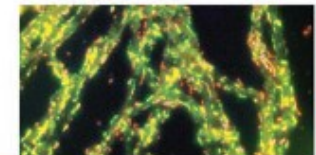
Possible effects of mycorrhizal symbiosis

interactions with other organisms

mediation of stress

carbon cycling

effects on plant communities



Vital (green) & non-vital (red) bacteria associated with the mycelium of an ectomycorrhizal fungus

Increased drought tolerance capture and restricted leaching of base cations in acidified soils chelation of toxic heavy metals and aluminium

Ca²⁺

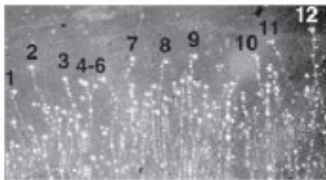
Flow of current assimilate drives soil respiration selective exploitation of soil heterogeneity effects on stability of soil aggregates (glomalin production)

carbon turnover and supply to soil aggregates and microbial populations

organic acids, siderophores and other chelating agents

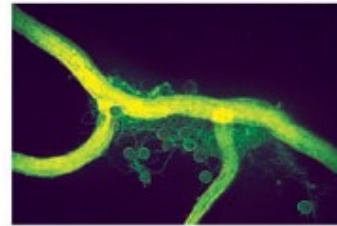
Mg²⁺

K²⁺



Exudation of liquid drops at hyphal tips of *Suillus bovinus*. The droplets are rich in oxalic acid

Source: Finlay 2008; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_8.ppt



© USDA-ARS

The AM mycorrhizal glycoprotein glomalin, covering AM spores and hyphae, is revealed by a green dye tagged to an antibody against glomalin.

Effects on floristic diversity & productivity carbon transfer to myco-heterotrophic plants



© Jim Stess @ USDA-NRCS PLANTS Database

The network of hyphae can reach far from the root (up to 10 cm for endomycorrhizal fungi, even more for ectomycorrhizal fungi) and the fungus can draw substances from the whole space – this is especially important in dry soils, where substances cannot diffuse through soil water and the fungal transfer thus replaces missing connection between the nutrient source and the root.

In addition to improving water intake (thus increasing drought tolerance) and nutrient transport, mycorrhizal fungi can also increase tolerance to heavy metals (mentioned at ectomycorrhiza and ericoid mycorrhiza, but arbuscular types apply similarly), resistance to certain pathogens or protection against root parasites (hyphal mantle of ectomycorrhizal species).

Dependence on mycorrhizal nutrition may vary from plant to plant – the growth of some species is strictly dependent on nutrient supply from the mycorrhizal partner, while other species may only be occasionally (facultatively) mycorrhizal in association with the fungus; similarly, different fungi are obligately (species of the genera *Amanita*, *Boletus*) or facultatively mycorrhizal (*Laccaria*, *Xerocomus*). Conversely, in the case of non-mycorrhizal plants, accidental colonisation by the fungus can decrease their growth rate or even lead to death of the seedlings (the fungus „steals“ their assimilates) .

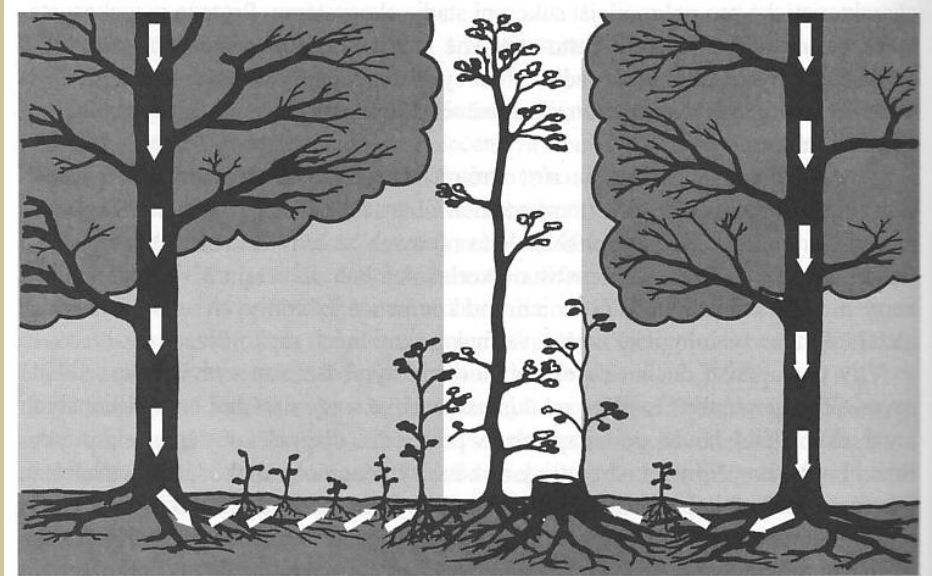
Auxins – growth hormones produced by the fungi – stimulate the flow of monosaccharides from leaves to roots (where they are absorbed by the fungus). Fungal tissue on the surface mechanically protects the root and can also have an antibiotic effect.

Mycelium usually connects more plant individuals => a complex root-mycelium-root system is created, enabling the transport of water and organic and inorganic compounds and their even distribution throughout the system (e.g. carbon transfer from „donor“ to „recipient“ plant helps the seedlings to grow in a shaded place, and the same applies for non-green plants /e.g. *Monotropa*, see below/).

In close vicinity of the roots (0.5-5 mm, a layer called rhizosphere) we can see so-called **rhizosphere**

effect – there are clearly more fungi compared to the surrounding soil (up to 10 times more, especially mycorrhizal, thus we can call it mycorrhizosphere), bacteria (very different amount – up to 100 times more, but may be fewer if the fungi deplete the available carbon from the roots and their exudates) and actinomycetes, which together with the roots affect soil moisture, aeration or pH.

It is also an area rich in nutrients – both from the exudates of living roots and from dead parts of the root system. Although rhizospheric fungi consume organic carbon, they actively decompose organic matter, ...



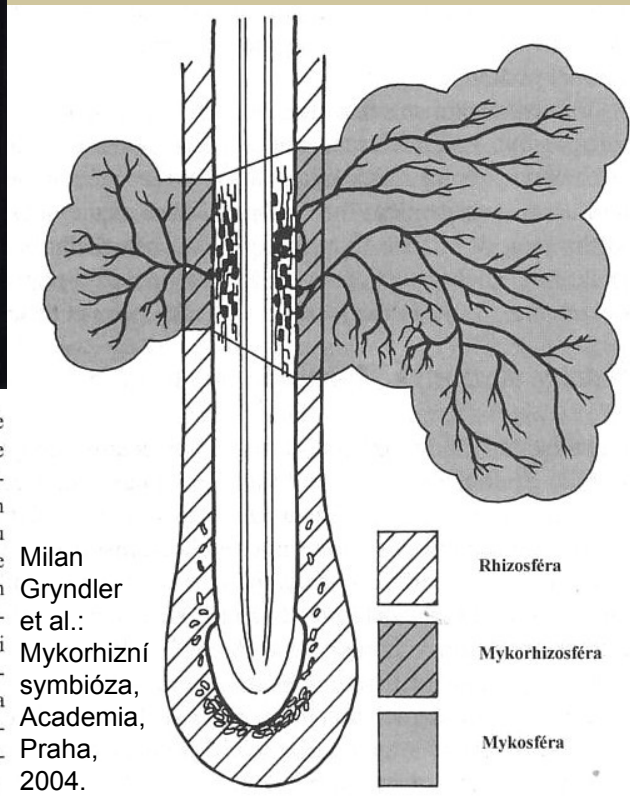
Obr. 55 Efekt chůvy (nurse effect). Pod stromovými porosty zastiňujícími povrch půdy žije i přes nedostatek světla značné množství semenáčků, jejichž kořeny jsou prostřednictvím mycelia myko-rhizních hub propojeny s kořeny vzrostlých stromů. Tím mají semenáčky možnost pro svou výživu částečně využívat energii bohaté látky získané myko-rhizními houbami od vzrostlých hostitelů, a přečkat tak období zástiny. Tok energie je na obrázku schematicky znázorněn šipkami. Po prosvětlení porostu padnutím stromu jsou takto udržované semenáčky připraveny odstartovat rychlý růst a zacetit vzniklý prostor. Milan Gryndler et al.: Myko-rhizní symbióza, Academia, Praha, 2004.



Visualization of the rhizosphere of roots of different species

Obr. 57 Prostor v půdě, který je pod přímým vlivem kořene, se nazývá rhizosféra. Obsahuje velmi mnoho bakterií. Je-li kořen kolonizován mykorhizní houbou (tj. jde-li o mykorhizu), pak se prostor pod jeho přímým vlivem nazývá mykorhizosféra. Mykorhizosféra má podobné vlastnosti jako rhizosféra, liší se od ní poněkud složením společenstva mikroorganismů. Prostor, do něhož zasahuje mycelium mykorhizní houby, se nazývá mykosféra.

Milan Gryndler et al.: Mykorhizní symbióza, Academia, Praha, 2004.



for plants far from the root (within reach of the hyphae).

Root exudates act as growth stimulants of fungi (which until then may survive in the soil, optionally as saprotrophs), which then disrupt the root cell walls using their extracellular enzymes. In this way, also populations of microorganisms can be stimulated to grow, which can then antagonise

... releasing nutrients

possible plant pathogens and thus provide the plants with a similar protection as the mycorrhizal fungus itself.

Conversely, in the case known as mycostasis, the fungi are present in the soil, but in the form of spores that do not germinate – the reason may be competition for deficient nutrients in very poor soils or production of inhibitory substances by plant roots or other organisms.

Mycorrhizal fungi are mainly „**C**“ **strategists** (they live long, they reproduce slowly), for which nutrient-rich substrate is not suitable (especially higher nitrogen content – over-fertilization can lead to suppression of these fungi and consequently weaken plant protection against other organisms). Habitats with less humus content in the soil, especially with a thin (or even missing) layer of raw overlying humus, are ideal for their occurrence.

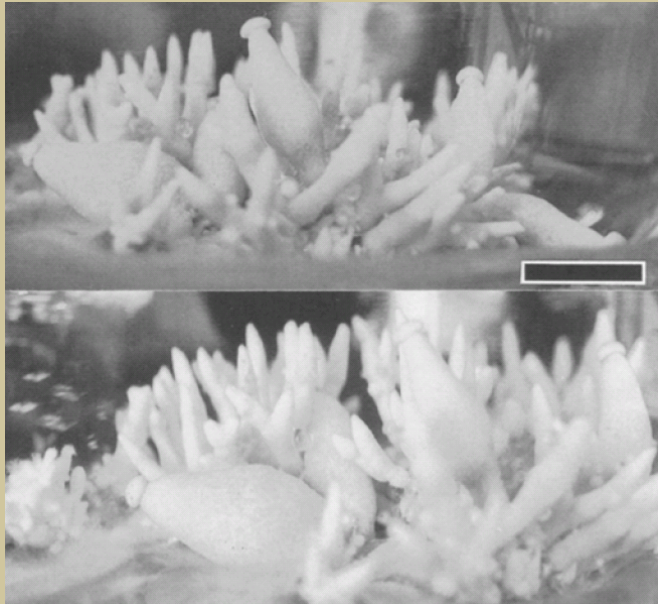
As in the case of saprotrophic fungi, **competition** can be observed between different species of mycorrhizal symbionts (both in terms of direct colonisation of roots and filling the space between them) => if more competitive species occupy the space and „do not let“ other fungi there, change of the species spectrum may occur only with a change of conditions in the rhizosphere (due to impact of external factors or ontogenetic development of the plant partner).

Even in communities of mycorrhizal species, a certain **succession** takes place – some species colonising the roots of young trees, others forming a mycorrhiza with mature trees and another species with old trees; due to the lifespan of trees, the time of change of these successive stages is significantly longer than in the case of succession of saprotrophs (especially terrestrial, but also lignicolous).

Although they often fructify in places affected by small local disturbances (road edges, ditch walls, terrain irregularities with exposed soil), in general, mycorrhizal fungi are quite **prone to disturbance**. Here is the main problem in the case of large-scale deforestation (or removal of vegetation cover in general) => communities of mycorrhizal fungi disappear, which are then missing for plants when trying to replant – the implementation of a simple recipe „to plant the plants together with mycorrhizal partners“ is difficult and expensive in practice.

„R“ strategists include some endomycorrhizal fungi involved in crop cultures – sudden harvest is a strong disturbance for which the fungi are „prepared“ by the formation of reproductive particles (up to thousands per millilitre of soil) => they maintain viability for months (in the extreme up to several years; some species of the genera *Acaulospora* and *Glomus* have endogenous dormancy) and „wait“ for suitable moisture and contact with the plant partner – it may happen that some spores germinate in moisture, but without the plant the fungus dies; however, a certain percentage of them is usually successful.

Related to the above is the fact that non-mycorrhizal plants are mainly among the ruderal species (R-strategists), often occupying disturbed habitats, where the conditions for long-term maintenance of mycorrhizal fungi are not suitable.



Boletus reticulatus forms only primordia on agar medium.

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

The **cultivability** of mycorrhizal fungi is **difficult** – many of them do not grow without mycorrhiza or grow more slowly, or do not form fruitbodies; mild parasitism may be considered, in any case nutrition of the fungus is dependent on the plant.

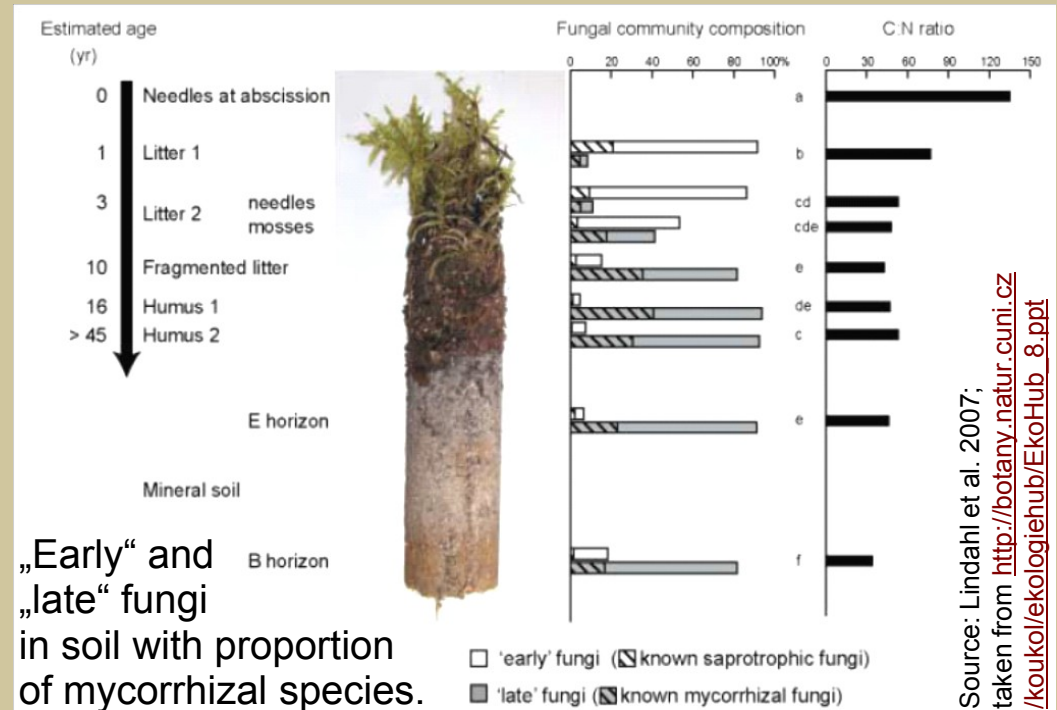
Facultatively mycorrhizal fungi are also capable of saprotrophic life (*Tricholoma saponaceum*, *Paxillus involutus*, *Xerocomus subtomentosus*, probably also *Imleria badia*; *Armillaria* species can live mycorrhizally, saprotrophically and parasitically), while obligately mycorrhizal fungi do not survive end of the symbiosis; this is generally true for endomycorrhizal species (cultivable only in „culture“ with the host plant,

i.e. in a pot or on agar with tissue culture of modified roots), but also for most ectomycorrhizal fungi (species of the genera *Russula*, *Suillus* or *Leccinum*). The reason is limited enzymatic equipment of these fungi, they do not produce cellulases or polyphenol oxidases (enzymes needed to degrade lignin).

While importance and function of hard-to-cultivate species are still underestimated, the easy isolation of other species led to erroneous conclusions about mycorrhizal association a hundred years ago (Möller /1908/ isolated *Mucor ramannianus* and Peklo /1913/ *Penicillium* and *Cladosporium* species from the roots of *Pinus sylvestris*).

Current research of mycorrhizal relations involves various forms of study (from classical to modern):

- fruitbody collection is good for mycofloristics and estimates of fungal diversity, but shows only a fraction of true diversity; some species fructify in cycles, it may not be clear to which tree species the fruiting fungi belong (it is still not known how far from the tree the fruitbody can grow);
- morphology of the root tips (Agerer's atlas, compiled since the 1980s) is given by a combination of fungal and plant species – for some combinations the morphology is well recognisable, but often the type is described e.g. as "piceirhiza bicolorata";
- DNA isolation from the tips showed that one tree forms mycorrhiza simultaneously with several species of fungi, that there is succession according to the tree age, but occasionally a saprotroph or parasite is isolated;
- DNA isolation from mineral soil horizons – mycorrhizal fungi occur even deeper in the soil, so it is possible to detect representatives of groups which do not form fruitbodies.



Source: Lindahl et al. 2007;
 taken from http://botany.natur.cuni.cz/koukol/ekologiejhub/EkoHub_8.ppt

ECTOMYKORRHIZA

Mycorrhizic contact takes place between the root and the mycelium – the basic types of mycorrhizae are distinguished according to whether the mycobiont penetrates the plant cells or not.

- | | |
|---|---------------------------------|
| 1. Mantle present. | |
| 2. Without a Hartig net and without intracellular hyphae: | Perimycorrhiza |
| 2* With a Hartig net. | |
| 3. Without intracellular hyphae: | Ectomycorrhiza |
| 3* With intracellular hyphae: | Ectendomycorrhiza |
| 4. Intracellular hyphae not forming knots, bursting open: monotropoid ectendomycorrhiza | |
| 4* Intracellular hyphae forming knots, not bursting open: | arbutoid ectendomycorrhiza |
| 1* Mantle absent. | |
| 5. Without a Hartig net; intracellular hyphae present: | Endomycorrhiza |
| 6. Intracellular hyphae are completely digested. Orchids: | Orchid-endomycorrhiza |
| 6* Hyphae are not digested. Ericales: | ericoid endomycorrhiza |
| 6** With large vesicles and hyphal knots: "VAM" = vesicular-arbuscular mycorrhiza | |
| 5* With a Hartig net: | «Aberrant Forms» |
| 7. Intracellular hyphae absent: | «mantle-less ectomycorrhiza» |
| 7* Intracellular hyphae present: | «mantle-less ectendomycorrhiza» |

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

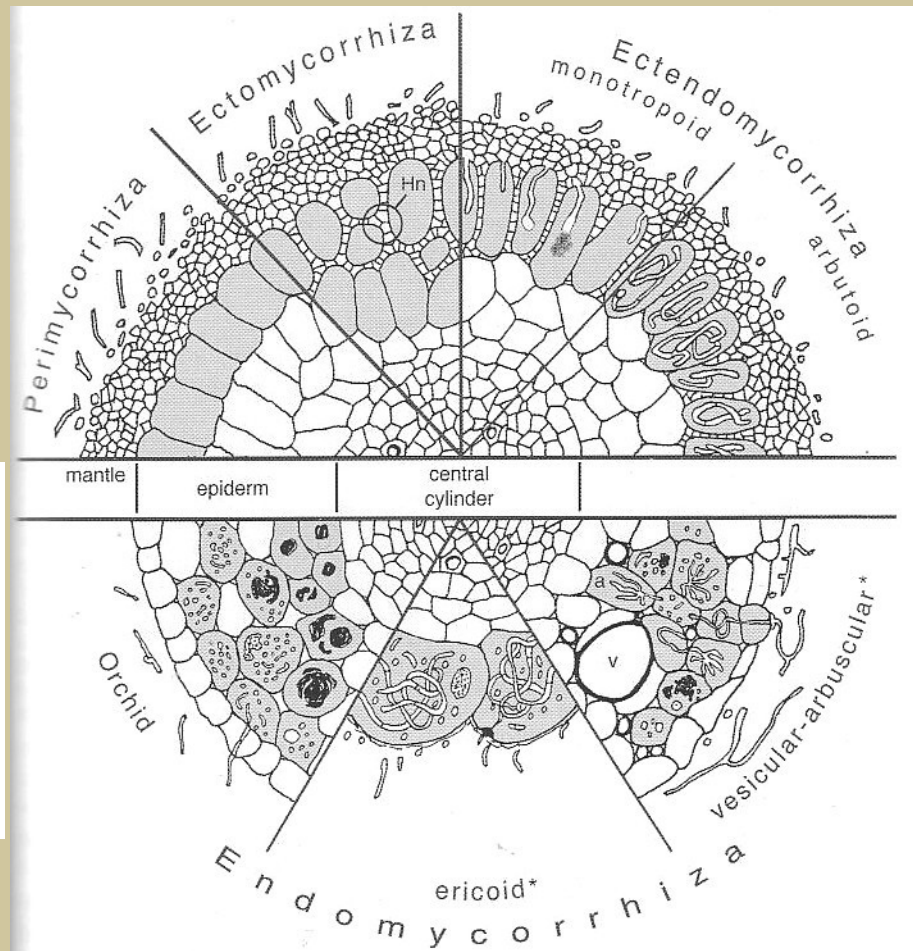
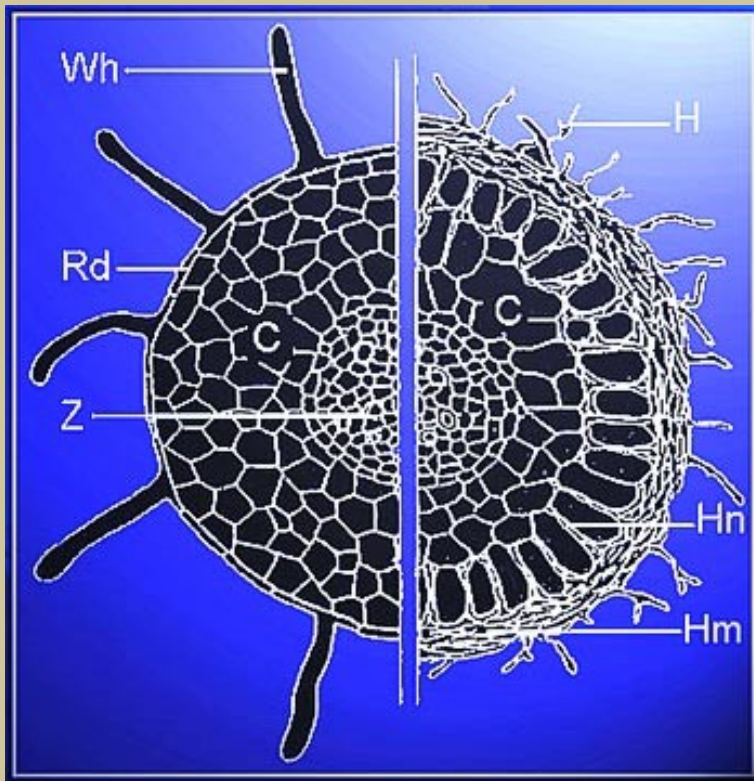


Figure 11.22: Diagrammatic comparison of mycorrhizal types; «aberrant forms» not shown. The physiologically active "exchange cells" are highlighted in grey. a: hyphal arbuscule; Hn: Hartig net; v: fungal vesicle. * not discussed in this book. – Based on Strullu 1985, strongly modified.

If the fungus does not enter the plant cells, it is an **ectotrophic mycorrhiza**.

Ectomycorrhiza is also visible macroscopically – pseudoparenchymal fungal tissue forms a **mantle** on the root surface, which replaces the root hairs (there can be both, near the soil surface the roots are covered with fungal mantle and deeper they are without the fungus, but with root hairs – however, often 100% of the root system possess mycorrhiza and the fungus is then fully responsible for transport of water and nutrients); the greatest activity of fungi is at the root tip.



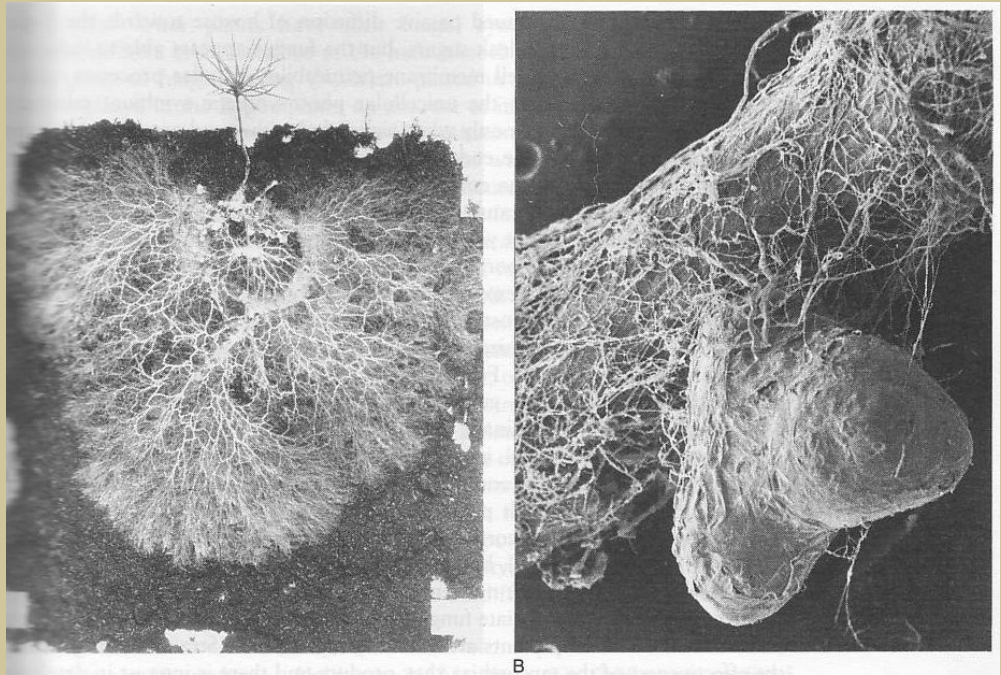
Top: root with mantle of *Boletus edulis*; bottom: with *Cenococcum geophilum*.

Photo Anna Lepšová,
[http://
 botanika.bf.jcu.cz/
 mykologie/galerie
 /mycorrhiza
 /Boletusedulis.jpg](http://botanika.bf.jcu.cz/mykologie/galerie/mycorrhiza/Boletusedulis.jpg)



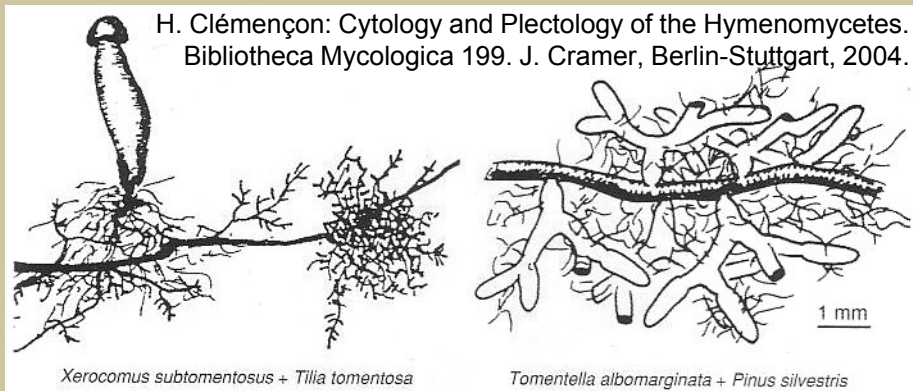
Comparison of cross sections: root with ectomycorrhiza (H - mycelial hyphae, Hm - mantle, Hn - Hartig net) and root without mycorrhiza, with root hair (Wh).

The fungus can also form a huge mycelial system (extraradical mycelium) distinctly exceeding root system of the symbiont (on average it makes up about 40% of dry weight of the roots), while the plant forms shortened, obtuse and sometimes dichotomously branched roots.



M. J. Carlile et S. C. Watkinson: The Fungi. Academic Press, London, 1994.

Suillus bovinus ectomycorrhiza on a pine seedling. Right: SEM photo of the hyphae covering the root surface and growing through the slimy cover of the lateral root bases.



H. Cléménçon: Cytology and Plectology of the Hymenomycetes. Bibliotheca Mycologica 199. J. Cramer, Berlin-Stuttgart, 2004.

Xerocomus subtomentosus + *Tilia tomentosa* *Tomentella albomarginata* + *Pinus silvestris*

Figure 11.24: Examples of ectomycorrhizae. **Left:** The horizontal root axis of *Tilia tomentosa* produces numerous secondary roots with mycorrhizae. A basidiome attached to the system allowed the identification of the fungus. From Ceruti & Bussetti 1962. **Right:** The root axis of *Pinus silvestris* bears several dichotomously branched, brightly coloured mycorrhizae with numerous emanating hyphae. From Agerer 1996.



Mycorrhizal roots of *Picea abies*

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

Some ectomycorrhizal fungi increase the tree tolerance to acid rains (in an acid environment, metal elements are released into the soil, from a certain amount toxic to the plants – the fungi to some extent prevent their intake to the roots). In general, mycorrhiza allows higher adaptability of trees and shrubs to extreme conditions => this fact is used in the artificial mycorrhization of seedlings planted in mountain areas, on reclaimed spoil tips or at another places.

Mycorrhization of roots can be realised in two ways:

- by the existing mycelium, which grows outside the mantle and colonises another part of the growing root or another root to which it grows through the soil. The root tip usually „grows ahead“ and the growing hypha is „chasing“ it; alternatively, ectomycorrhiza may grow in cyclic „jumps“: after a period of dormancy (when the apical meristem of the root is isolated from the hyphae by the metacutis layer) it grows – if it is slow, the mantle grows parallel to the root, while in the case of rapid growth the root tip penetrates it and the tip „grows ahead“ (in addition to hyphae from the elongated mantle, it can then be colonised by other hyphae from the rhizosphere).

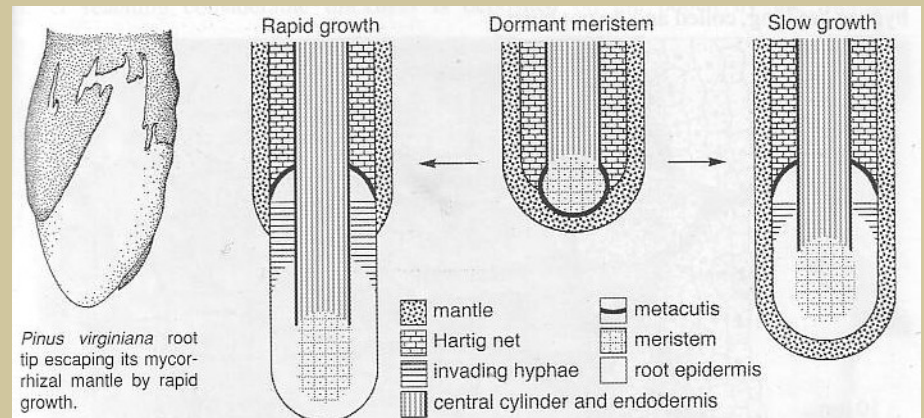
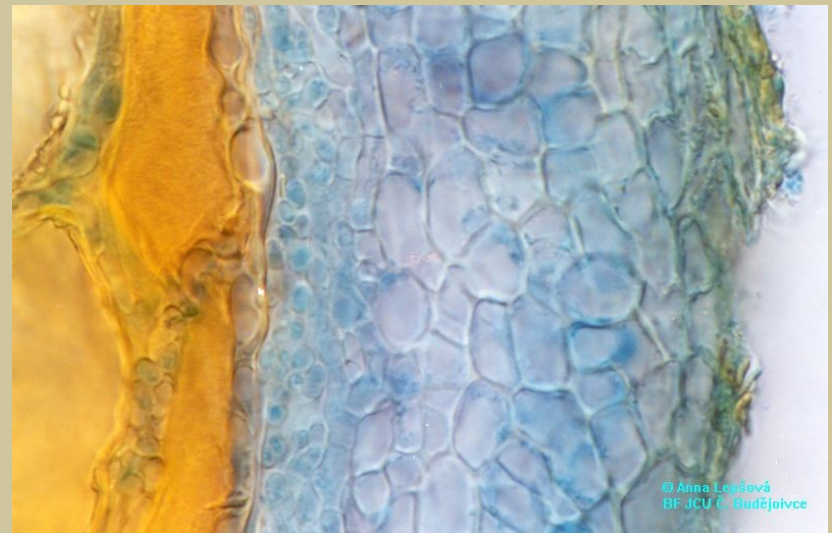


Figure 11.27: Accelerated root meristem activity leads from dormancy to rapid growth with the root apex escaping the mycorrhizal mantle; low meristem activity induces slow growth in approximate equilibrium with the growth of the mycorrhizal mantle. During dormancy, the meristem is protected from invading hyphae by the metacutis; during growth, the metacutis exposes the meristem. – Drawing from Kelley 1950; diagrams based on Kottke & Oberwinkler 1986. Clémentçon 2004

- is done by new hyphae germinating from spores (usually mutual recognition of symbiotic partners is needed, e.g. spores of many basidiomycetes germinate only near the roots of „their“ tree species); spore germination in the rhizosphere is usually stimulated by the growth of roots (their exudates) or other mycelia (they do not germinate in artificial medium, even if they have enough nutrients) => it enables the exchange of genetic material, the germinating hypha often quickly fuses with existing mycelium.

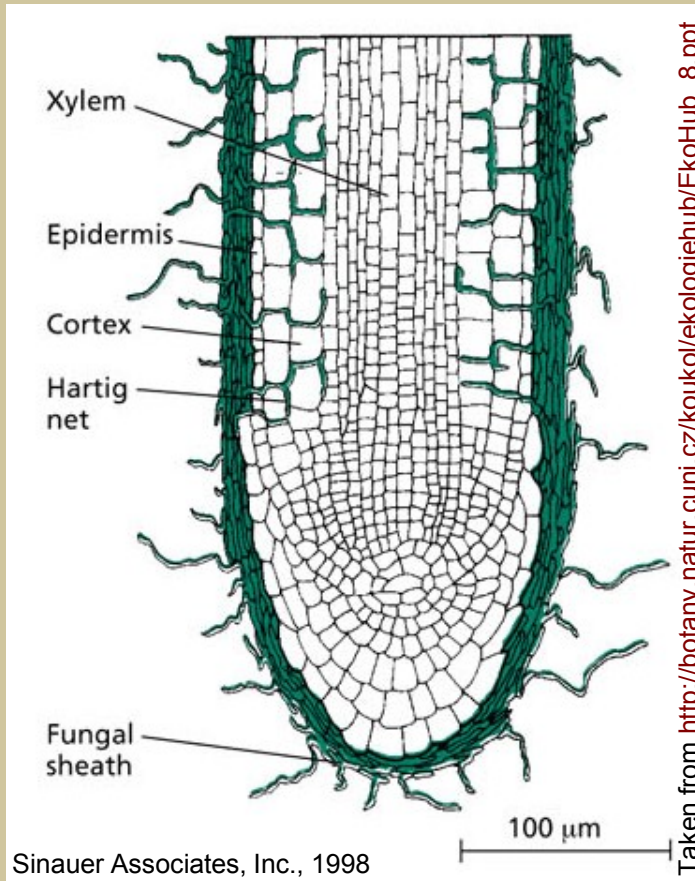
The colonization rate depends on the fungus, the plant and the environmental conditions (increased root growth is usually seasonally related with appropriate temperature and humidity). Roots with developing ectomycorrhiza grow slowly and seem to "get broader" (impression caused by formation of the mantle).

In the mantle, there are different hyphae of the outer and inner layers – while the outer hyphae are thick-walled and loose, the inner hyphae are thin-walled and tightly crowded at the root surface (a pseudoparenchym-like tissue is formed). The impermeable hyphal mantle isolates the root from the soil and nutrient transfer thus takes place exclusively through the extraradical mycelium.



Mycorrhiza of *Russula ochroleuca*: cross-section of the mantle with clearly smaller cells in the inner layer, adjacent to the root surface (left side of the photo).

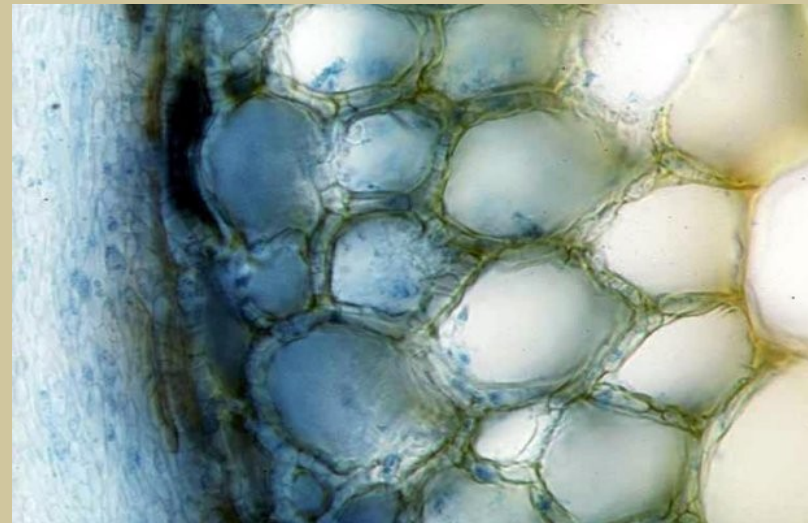
Photo Anna Lepšová, <http://botanika.bf.jcu.cz>



Sinauer Associates, Inc., 1998

Hyphae growing on the root surface surround the cells of the primary bark and penetrate into the intercellular space => here richer branching, shorter cells, without clamps => around individual plant cells they form the so-called **Hartig net**

<http://www.bio.mie-u.ac.jp/junkan/busshitsu/lab2/hartig.jpg>



(in some species invagination appears => enlargement of the contact surface)
 => the hyphae supply the plant with water and nutrients, strong metabolic activity can be observed in their cells (a lot of mitochondria and endoplasmic reticulum)
 => over time they vacuolate and acquire a storage function (as the root becomes older, cell walls of the outer layer of rhizodermis are suberised).

The ectomycorrhizal connection lasts several months to three years, then there is a gradual degradation of the mantle from the distal end (and from the outer cells inwards, other soil fungi decompose it) ...

Right:
the final stage of a mycorrhizal connection with crumbling tissue of the mantle.

H. Cléménçon: Cytology and Plectology of the Hymenomycetes. Bibliotheca Mycologica 199. J. Cramer, Berlin-Stuttgart, 2004.

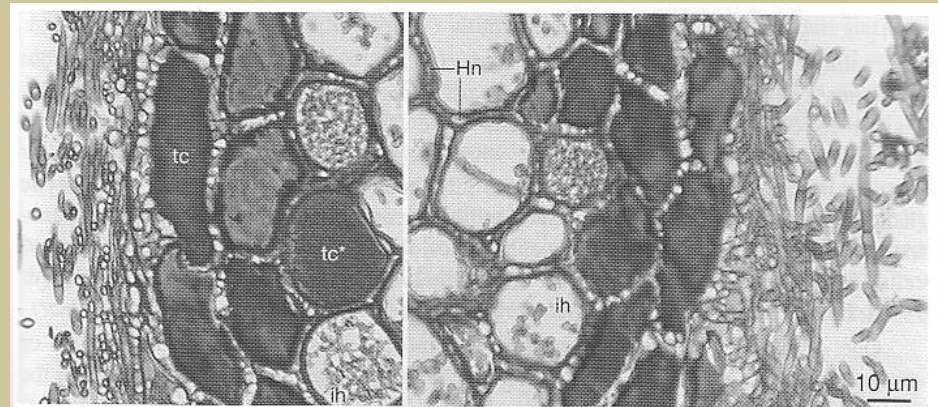


Figure 11.25: Cross sections through an old ectomycorrhiza of *Boletus pinophilus* + *Pinus silvestris*. The thin mantle is woven from cylindrical hyphae and devoid of any plectological structure. Subjacent are 2-3 layers of "tannin cells" with compact or finely granular content (tc and tc*). The large cells of the root epiderm are dead and contain internal hyphae (ih) possibly belonging to a different fungus. The Hartig net (Hn) is clearly visible around both, the "tannin cells" and the cells of the epiderm. – Preparation J. Zbären, University of Berne, Switzerland. Original photographs.

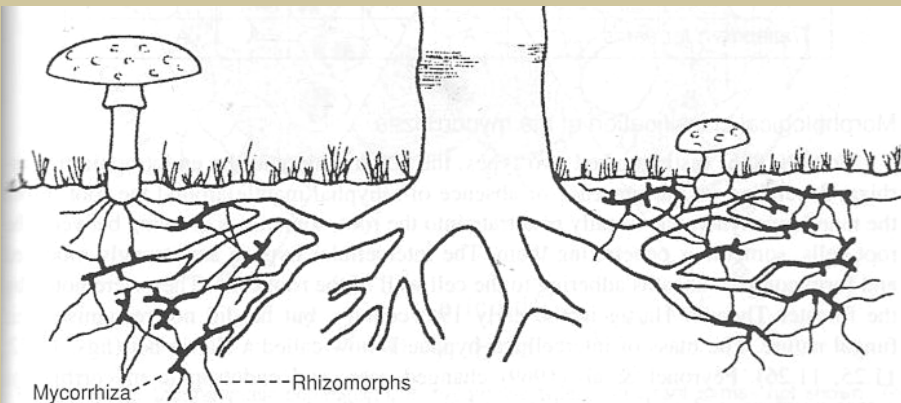


Figure 11.21: Diagram showing sheathing mycorrhizal associations of an agaric with tree roots. Mantles drawn thick black. From Jackson & Mason 1984.

... and then regeneration – the roots are branching and newly growing roots can be mycorrhized again, the hyphae grow through the soil to new roots (it is an extremely dynamic system, new connections are constantly emerging and others are disappearing).

Ectomycorrhizal fungi are characterised by active intake of organic substances using their enzymatic equipment („side effect“ is soil mineralisation) => organic compounds of nitrogen and phosphorus are transferred by hyphae to the roots (thus compounds can be transferred between roots, similarly to in endomycorrhiza). The ability to intake various substances is also affected by environmental factors (e.g. in acidic soils, nitrogen is more available as NH_4^+ , while at neutral pH more in the form of nitrates, and fungi adapt to it).

The second function of ectomycorrhiza is storage – the mantle tissue and external hyphae act as a reservoir of nutrients, which can be „mobilised“ if needed, and provided to the plant or used for further growth of the fungus or the root. (In general, there is a certain plasticity in the functions of ectomycorrhiza – the relationship works as needed.)

Exudates of the fungal cells probably contain hydrophobins, which „stick“ adjacent hyphae to each other and on the other hand repel water – the mantle (in detail its inner layer) thus represents a continuous envelope, which is a barrier to the movement of solutions and thus acts as a „filter“ of substances transfer (it is realised only through the way which the fungus „allows“, and the fungal cell takes what it needs directly from the solutions).

The fungus takes about 30% of assimilates from the symbiont (it converts simple saccharides into trehalose, mannitol and glycogen) => this uptake stimulates an increase of photosynthesis in the plant, which, however, can only be effective above a certain level of illumination; if there is not enough light and the possibility of photosynthesis falls below the compensation point (when the plant is still able to compensate for energy losses associated with „feeding“ the fungus), „impoverishment“ of the plant by the fungus slows down its growth => thus it gives the fungus less nutrients => it results in limitation of root colonisation.

The transfer of organic nutrients (especially carbon sources, carbohydrates) in the fungal thallus are also affected by the season. When establishing a mycorrhizal association, they are immediately used for hyphal growth and structure formation, while the most massive transfer to hyphae at the soil surface can be observed in autumn, which is related to their use for the formation of fruitbodies.

In some cases, the nutrients are transferred between plants through the hyphae – this fact allows to survive not only non-green plants (ectendomycorrhizal species, some orchids), but also, for example, shaded seedlings, which would have no chance to survive (would not succeed in competition for light) without „help“ from adult trees („nurse effect“, described in the introductory text to mycorrhizae). Such „help“ can also be provided by plants of different species (so-called "mycorrhizal socialism" :o).

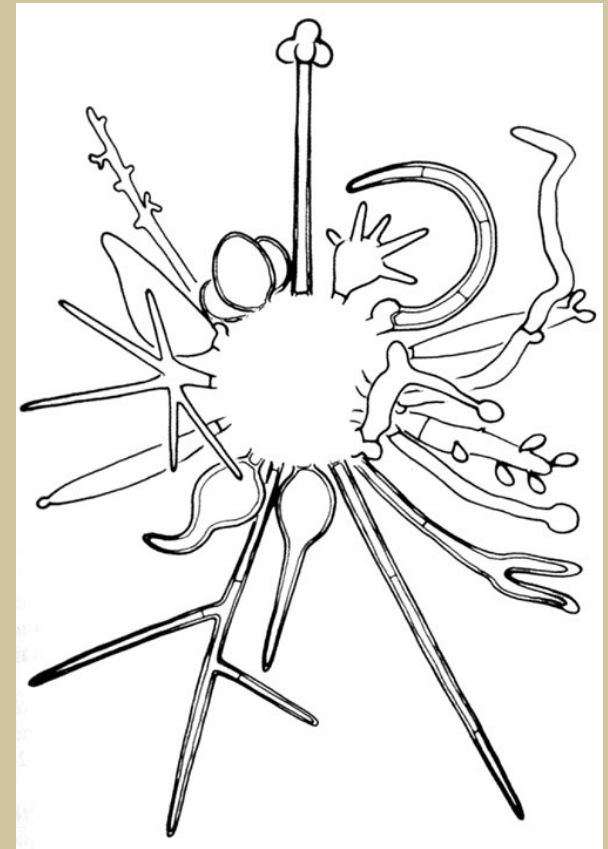
The ability to draw nutrients in various forms (even in mineral form, but especially in organic form in the litter and surface layer of soil) and at the same time the supply of energy and assimilates from the plant makes these fungi competitively strong (they successfully compete against saprotrophic fungi and bacteria); on the other hand, a „supply outage“ in the case of decrease in photosynthetic activity or death of the symbiote can be fatal for many species.

In some ectomycorrhizal species, the ability to degrade more complex organic compounds has also been demonstrated. They carry genes for various peroxidases (lithium peroxidase, manganese peroxidase) and laccase; their production, decomposition of humic acids and plant debris were confirmed in vitro. However, questions remain: Is this sufficient evidence that ectomycorrhizal fungi are also involved in the breakdown of compounds such as lignin in nature? In this case, how can they succeed in competition against saprotrophic fungi? A partial answer to the second question may be their ability to defend against the inhibitory effect of allelopathic compounds present in the debris or arising from its decomposition.

Anyway, this finding indicates the possibility that ectomycorrhizal fungi (and plants) utilise organic matter from the soil; from an evolutionary point of view, it shows the possible evolution of ectomycorrhizal fungi from saprotrophic ones, and in some species there is also a trend towards a saprotrophic lifestyle again (Hibbett et al., Nature, 2000).

Due to the fact that the hyphal mantle in the soil is exposed to soil invertebrates and due to high concentration of nitrogen and phosphorus it is an attractive delicacy, specialised cells have developed on the surface to protect against fungivorous organisms.

It can be either mechanical protection, provided by thick-walled needle-shaped cells, or chemical protection – cystidia filled with repellent compounds are formed on the hyphae. This way is found especially in the family *Russulaceae*, where these cells contain inactive stearylvelutinal, which after pouring from a damaged hyphae is transformed into the terpenoid isovelleral, which acts on invertebrates as a repellent. In addition to mycorrhizal tissues, cystidia with repellent compounds can also be found in the hymenium and on surface of the fruitbody primordia; in milkcaps the repellents are also present in latex. Other fungi may contain other compounds, such as calcium oxalate crystals (*Piloderma fallax*, *Atheliaceae*).



Different types of surface cells with a protective function.

In the northern hemisphere, ectomycorrhiza is abundant in boreal and temperate trees and shrubs – especially of the families *Pinaceae*, *Betulaceae*, *Fagaceae*, less frequently e.g. *Cupressaceae*, *Taxaceae*, *Salicaceae*, *Oleaceae*, *Ulmaceae*, *Juglandaceae*, *Platanaceae* (other trees are mainly endomycorrhizal – *Tiliaceae*, *Aceraceae*, *Corylaceae*, etc.). In the tropics, on the other hand, only a few tree species are ectomycorrhizal, contrary to wide range of trees, shrubs and herbs in the southern hemisphere – the cause of these differences remains a question.

Overall, ectomycorrhiza is less common among plants, only in about 3–5% of species. On the contrary, it is quite widespread among fungi, occurring in several

thousand species (estimation approx. 5,500 based mainly on morphological determination techniques – including the hidden diversity according to DNA it is 7–10 thousand species); most of them are known as hymenomycetes (mainly in the orders *Russulales*, *Boletales*, *Agaricales*, *Thelephorales*), but so far the importance of fungi of the order *Sebacinales* (capable of forming practically all types of mycorrhiza, see below) is probably completely underestimated.



13 Typické ektomykorhizy vytvořené ektomykorhizní houbou *Lactarius piperatus* (ryzec pepný) u borovice *Pinus sylvestris*.



In addition to *Basidiomycota* (95%), ectomycorrhizal fungi can also be found in the divisions *Ascomycota* (4.8%, e.g. all hypogeous, truffles and *Elaphomyces*) and *Mucoromycota* (*Endogone*, sometimes referred to as endomycorrhizal – this is a mistake based on the earlier classification of endomycorrhizal fungi /today's division *Glomeromycota*/ in the order *Endogonales*). Also in the case of ectomycorrhizal fungi, succession may occur – for example, at first the root is colonised by ascomycete, and then the hyphae of basidiomycete overgrow it (or they may coexist). Cases of species specificity are rare (mostly fungi associated with larch), usually one tree species can form mycorrhiza with more species of fungi (up to dozens of species, documented in representatives of *Pinaceae* + *Boletales*, especially various species of *Gomphidius*, *Chroogomphus* and *Suillus* with pine) and conversely, ectomycorrhizal fungi can connect more plants in the community (different species and different age stages, see above at transfer of nutrients).

At this point, it should be added that not all mycorrhizal connections, that can be synthesised in laboratory conditions, are realised in nature (e.g. *Suillus grevillei* can form connections not only with larch, but does not grow with other trees in nature); it is probably a matter of competition.

Interesting fact: Some ferns normally form endomycorrhiza, but they are able to „accept“ ectomycorrhizal fungi of dominant trees in pine or beech forests. Similarly, some tree species of the genera *Salix*, *Prunus* and *Acacia* form arbuscular mycorrhiza in addition to ectomycorrhiza.

A specific type is called **perimycorrhiza** – the mantle is formed around the root, but hyphae do not penetrate the cells or form a Hartig net. Sometimes this may also be a temporary stage in the development of an ecto- or ectendomycorrhizal relationship, when the hyphae wrap the growing tip of the root but have not yet penetrated the intercellular spaces.

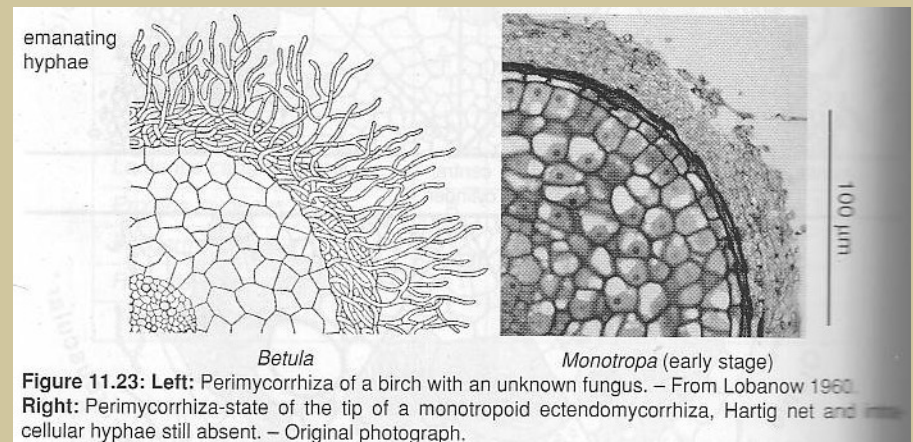


Figure 11.23: Left: Perimycorrhiza of a birch with an unknown fungus. – From Lobanow 1960. Right: Perimycorrhiza-state of the tip of a monotropoid ectendomycorrhiza, Hartig net and cellular hyphae still absent. – Original photograph.

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

Ectendomycorrhiza contains the derived types – from outside it appears as ectomycorrhiza (hyphal mantle and network of extraradical mycelium), but hyphae also penetrate into cells; Hartig net and mantle may or may not be formed (morphology depends on the host plant).

Fungal symbionts are ascomycetes of the genera *Phialocephala*, *Wilcoxina*, *Helvella*, *Sphaerosporella*, and basidiomycetes of the genus *Sebacina*.

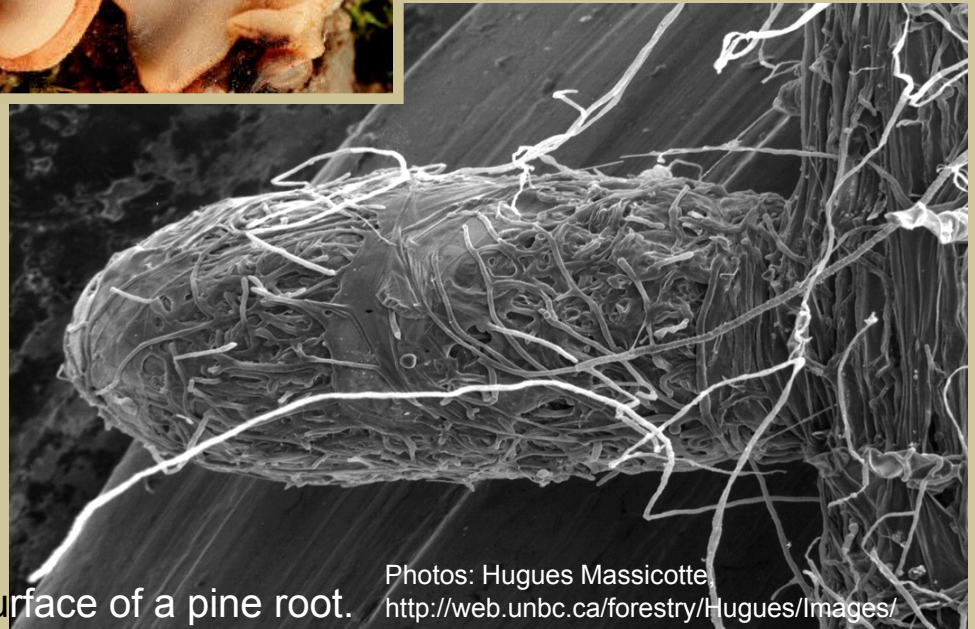
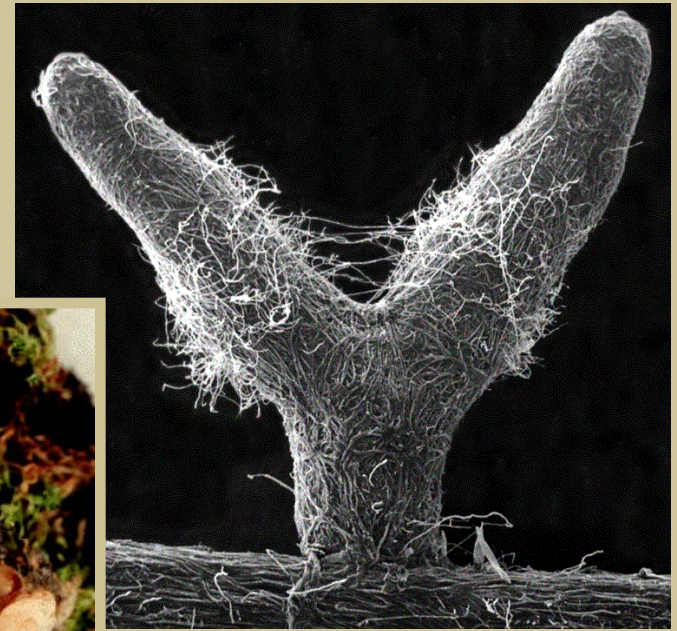
This type is formed temporarily in conifer seedlings (*Pinus*, *Larix*, relatively rarely, for example after fires; these fungi are probably not very competitive).

Top: branching of a pine root colonised by hyphae of *Wilcoxina* sp.

Bottom: hyphae forming a mantle on the surface of a pine root.



Wilcoxina sp.



Photos: Hugues Massicotte
<http://web.unbc.ca/forestry/Hugues/Images/>

On the contrary, the following types known in plants of the order *Ericales* are stable ectendomycorrhizal forms.

- **Arbutoid mycorrhiza** is formed by *Pyrolaceae* and some *Ericaceae* (*Arbutus*, *Arctostaphylos*, *Vaccinium*)

with various basidiomycete species (probably those that form ectomycorrhiza with surrounding trees). /The traditional families *Pyrolaceae* and *Monotropaceae* are mentioned here, but recent molecular systems also include their representatives in the family *Ericaceae*./

The colonised roots are shorter, forked, a hyphal mantle (thick outer „sheath“) and Hartig net are developed, and at the same time the fungus penetrates the rhizodermal cells (outer part of the bark) and forms a coils of hyphae in them; increased number of mitochondria, ER and ribosomes is a sign of massive metabolite exchange.

Mycorrhiza of *Lactarius deliciosus* with *Arbutus menziesii* – external view and cross-section of the root with external „sheath“ and coils of hyphae filling the surface cells.

<http://www.mycolog.com/chapter17.htm>

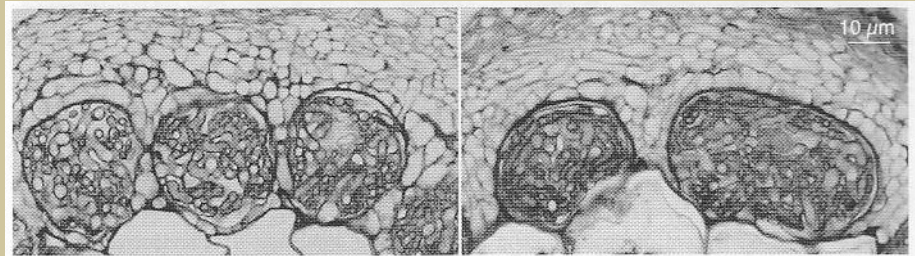
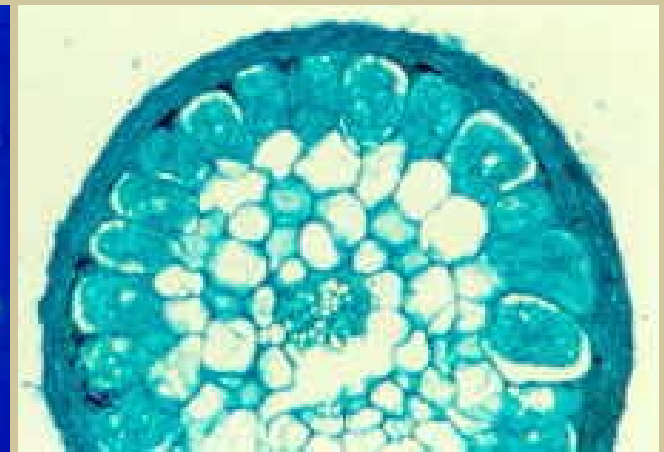


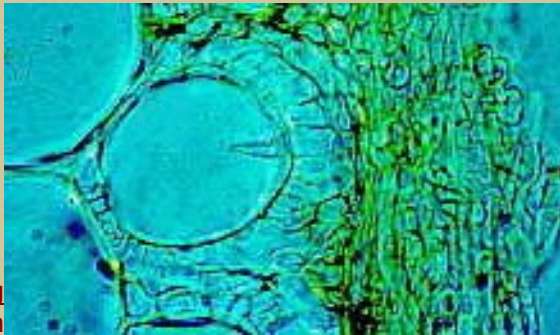
Figure 11.29: Arbutoid ectendomycorrhiza of *Arctostaphylos unva-ursi* with an unknown Basidiomycete. – Original photographs. Cléménçon: Cytology and Plectology ..., 2004.



• **Monotropoid mycorrhiza** has developed in non-green plants of the family *Monotropaceae*, which have lost chlorophyll and are thus completely dependent on their fungal partner for carbon gain (*Monotropa hypopitys* is associated probably with some *Xerocomus* s. l.; its root system is colonised by the fungus). During active phase of the mycorrhiza, the mantle is formed and Hartig net is developed only in the outer layer of rhizodermal cells; haustoria (hypha forming a „spike“) penetrate the cells, through which the fungus gives the non-green plant the nutrients needed for its growth (in fact it is not penetration, but only invagination of membranes => enlargement of the exchange surface).

Cléménçon: Cytology and Plectology of the Hymenomycetes, 2004.

Left detail:
penetration
of the hypha
in the cell of
*Monotropa
uniflora*.



<http://www.mycology.com/chapter17.htm>

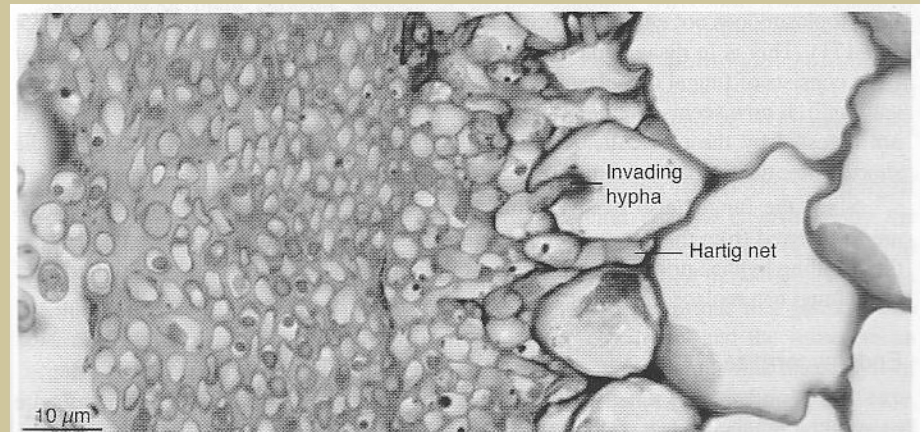
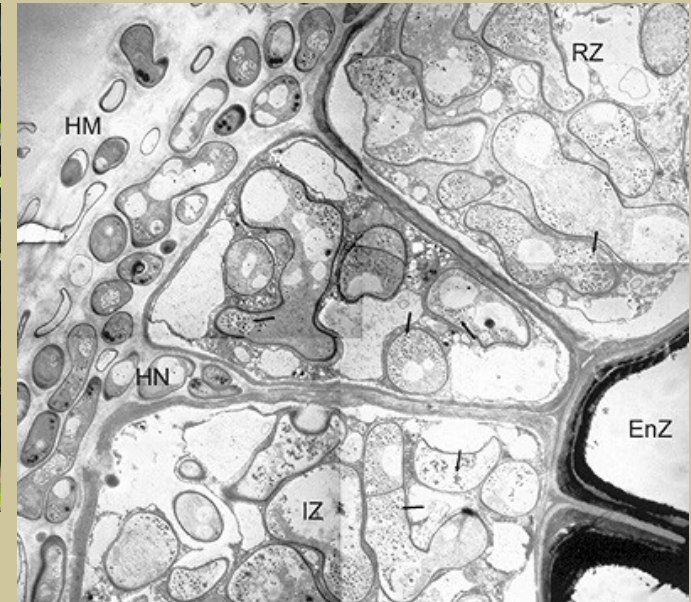


Figure 11.30: Monotropoid ectendomycorrhiza of *Monotropa hypopitys*. The thick outer layer of the mantle is an ixoplect of nearly parallel hyphae. The Hartig net is only a single root cell layer deep; and the root cell near the centre of the illustration shows an invading hypha. – Original photograph of a cross section stained with safranin O.

Similarly to arbutoid ones, monotropoid mycorrhizal fungi (also *Basidiomycota*) are usually able to form ectomycorrhiza with other plants at the same time. *Monotropa* actually parasitises another plant through a fungus – the direction of the assimilates flow may be spruce => *Xerocomus* => *Monotropa*.

• **Cavendishoid mycorrhiza** was discovered at the beginning of the 21st century. It was first observed in *Cavendishia nobilis* (Setaro et al. 2005) and is probably limited to the Andean group of members of the family *Ericaceae*. Fungal symbionts are species of the order *Sebacinales* and the class *Leotiomyces* (sometimes together in one cell!); hyphal mantle on the root surface and intracellular inflated cells are formed.

Right photo:
Setaro, S., Oberwinkler, F. & Kottke, I. (2006), Anatomy and ultrastructure of mycorrhizal associations of neotropical Ericaceae. *Mycological Progress* 5: 243–254



Left: *Cavendishia nobilis*; right: detail of mycorrhiza of *Psammisia guianensis* with fungus of *Sebacinales* (HM – hyphal mantle, HN – intercellular penetrating hyphae, IZ – intracellular cells, RZ – cells of outer layer of the root cortex, EnZ – endodermal cells). http://www.mycorrhiza-research.de/Pages/01_04Erica.html

Distinguishing of ecto-, ectendo- and endomycorrhiza is practical, but it does not correspond to evolutionary steps. Arbutoid, monotropoid and cavendishoid types (sometimes also collectively included among ericoid types) are theoretically more closely related to ericoid mycorrhiza (*sensu stricto*); likely they are more closely related to each other than to ectomycorrhiza (*s. str.*) or arbuscular mycorrhiza.