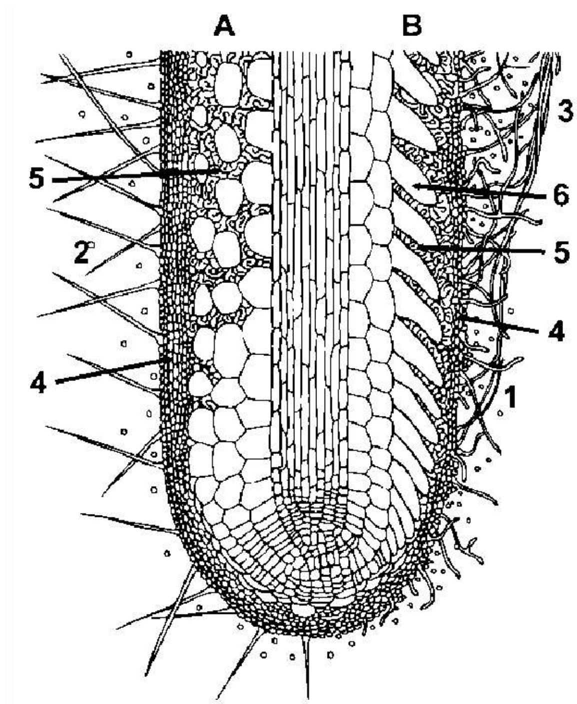
MYCORRHIZAE

Most land plants live in mutualistic symbiosis with fungi in their roots: this structural, functional unit is called mycorrhiza. Mycorrhizae are "dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing organs (roots, rhizomes or thalli) of most terrestrial plants and many aquatics and epiphytes". Different types of mycorrhizae can be distinguished according to the plant and fungal partners and structural characteristics. Important distinctions are whether the hyphae colonizing the plant grow intracellularly (**endomycorrhizae**) or only intercellularly in the plant tissue (**ectomycorrhizae**) or both (**ectendomycorrhizae**). The most common types are **arbuscular mycorrhizae** (AM) and ectomycorrhizae (ECM).

ECM are formed with fungi belonging to Asco- and Basidiomycota or a few zygomycetes, many of which produce macroscopic sporocarps. ECM plants are mostly woody plants, trees and shrubs. ECM have three main functional-anatomical parts: (i) special intraradical hyphal structures termed the **Hartig-net** formed in the intercellular spaces, (ii) the fungal mantle covering the root surface and (iii) the hyphal structures emanating from the mantle surface (e.g. cystidia, hyphae, rhizomorphs).



Main anatomical features of ectomycorrhizae (ECM). A: Cortical and **B**: Epidermal Hartig-net. 1: extraradical hyphae; 2: cystidia; 3: rhizomoph; 4: hyphal-mantle; 5: Hartig-net; 6: root epidermal cells; 7: cortical cells.

Two types of Hartig-net are distinguished. The cortical Hartig-net surrounds some layers of cortical cells and occurs in most gymnosperm and many angiosperm ECM plants. The epidermal Hartig-net surrounds radially elongated epidermal cells and occurs in most angiosperm ECM plant. As discussed above, two main types are distinguished based on the anatomy of the hyphal mantle. The hyphal organization can be detected in **plectenchymatic mantles**, whereas the cellular organization is characteristic of **pseudoparenchymatic mantles**. The main function of emanating hyphae is nutrient uptake from the soil. The hyphae can form **rhizomophs,** some can have differentiated anatomy, i.e. they have central hyphae with a big lumen and partially or completely disappeared septa which features make the nutrient transport more effective.

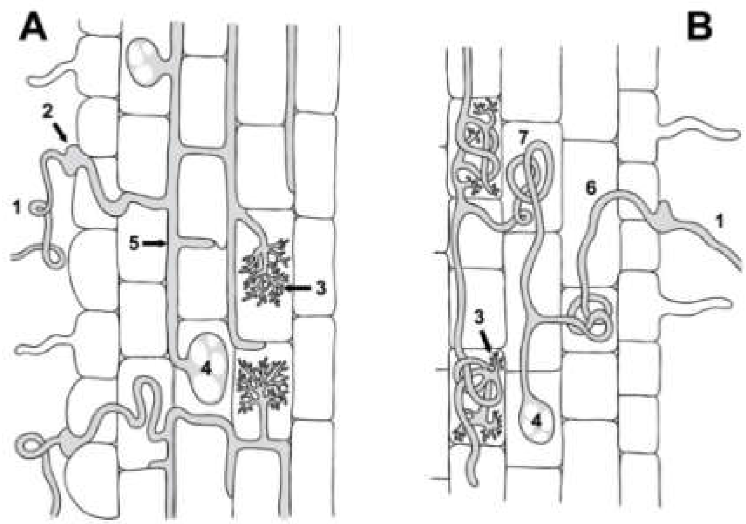
The most prevalent mycorrhiza type is the **arbuscular mycorrhiza (AM).** There are AM forming plants in all main terrestrial plant groups, on the other hand, all AM fungi exclusively belong to the phylum Glomeromycota. These fungi are obligate biotrophic endocellular symbionts. Their name refers to the special, multi-branched intracellular structure, the arbusculum resembling a small tree. Because of the high density of fine branches on the arbuscules, the surface of the plant cell membrane is multiplied, owing to a special membrane (**periarbuscular membrane, PAM**) that surrouns the arbuscules and contains special transporters and aquaporins etc. Arbuscules are ephemeral structures, they function for a couple of days,collapse and new arbuscules arise.

Prior to the colonization of the roots, the plant and fungal partners stimulate each other and their mutual recognition plays a crucial role in the success of the establishment of the interaction. The roots excrete strigolactons which stimulate the growth and branching of AMF hyphae and also the germination of AMF chlamydospores. The fungi produce "myc-factors" (**lipo chito_oligosaccharides)** which initiate processes necessary for the successful colonization in the plants.

The hyphae run on the surface of the roots and develop a swollen structure (**appressorium** or hyphopodium) from which a hypha grows into the root. The plant cells undergo a complete reorganization when the AMF hypha enters and grows through the cell, this special organization is called the pre-penetration apparatus (PPA). The endoplasmic reticulum (ER) forms a tube like structure which assigns the direction of the hyphal growth. The plant cell nucleus also moves to the penetration site and migrates in front of the growing hyphae through the cell. The intracellular growth of the hyphae needs continuous membrane development, so there is an intensive production of vesicules fusing into the plant cell membrane surrounding the hyphae. This process is controlled by the exocytosis regulation.

The arbuscules, albeit different, show several similarities with the intracellular haustoria of endocellular biotrophic pathogens. The AMF could also develop structures named vesicles in the roots, mainly in the intercellular spaces. The main function of these vesicles is storage. Their appearance could be seasonal and some AMF species do not form vesicles at all. Two main types of AM anatomy can be distinguished, of course, with several intermediate forms as well.

In the Arum-type the fungal hyphae grow intercellularly and well-developed arbuscules are formed on branches entering the neighboring cells. In the Paris-type the hyphae grow intracellularly, develop hyphal coils in some cortical cells and smaller arbuscules develop on these coils. Both the fungal and the plant partner influence the type developed



Two main types of root colonization in arbuscular mycorrhizae (AM). A: Arum-type **B**: Paris-type. 1: extraradical hyphae; 2: appressorium/hyphopodium; 3: arbusculum; 4: vesiculum; 5: intercellular hyphae; 6: intracellular hyphae; 7: hyphal coils.

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- ## Endophytic fungi

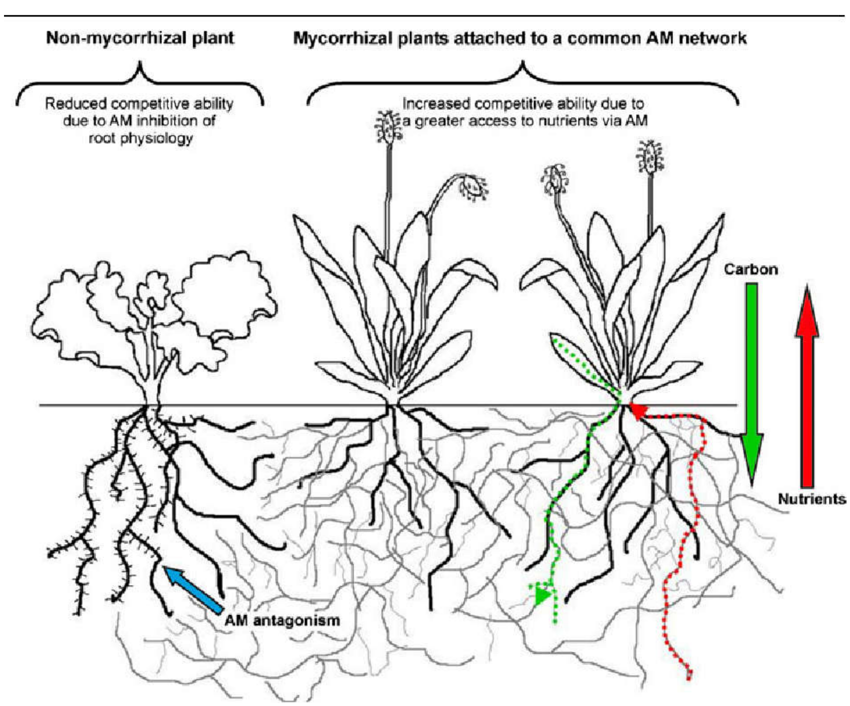
Endophytic fungi spend at least one phase of their life cycle colonizing plant tissues inter- or intracellularly causing no symptoms of tissue damage. This definition is not a phylogenetic term, endophytic fungi can thus be found in several fungal groups. The best known endophytes (C-endophytes) belong to the family Clavicipitaceae (ergot family, Pezizomycotina, Ascomycota) and colonize aboveground tissues of grasses. The rare intercalar growing of hyphae was found in these endophytes. Fungal endophytes can be grouped according to several aspects, e.g. plant tissues colonized, systemic, non-systemic spread in plant. A form-group of root-colonizing endophytic fungi is the so called dark septate endophytes (DSE) that belong to a few orders of the phylum Ascomycota. DSE fungi are septate and generally have melanized hyphae that colonize the cortical cells and intercellular regions of roots and form a densely septated intracellular structure called microsclerotia. Although C-endophytes have been intensively studied, our general knowledge on the function and diversity of endophytes is limited especially if compared to some types of mycorrhizae.

What are Common Mycorrhizal Networks?

Almost all plants have symbiotic mycorrhizal relationships with fungi, which are beneficial to both the plant and the fungi. The word mycorrhizae, derived from Greek that means fungus-root, describes how the fungi colonises the roots of plants. Plants transfer carbon they fix from the atmosphere during photosynthesis to the symbiotic fungi, in exchange for nutrients and water. The fungal hyphae also add to belowground carbon storage by exuding carbon-containing compounds into the soil. In return, the fungi has access to a far larger pool of other nutrients, such as nitrogen, due to the vast surface area of hyphal mycelium, which far exceeds the surface area and therefore nutrient availability of the trees roots. By trading these resources, both organisms benefit and this increases their chances of surviving. A common mycorrhizal network (CMN) describes a situation when the fungal network links plants together belowground. These networks, which plants use for communicating the presence of pests and diseases and to release chemicals that provide plants with a competitive advantage over other non-mycorrhizal plants and referred to often as the Wood Wide Web.

Why are they important?

Forest ecosystems represent one of the greatest stores of terrestrial carbon on the planet. Within this, Common Mycorrhizal Networks play an important role in regulating the storage and release of this carbon. Understanding the mechanics of these processes can help us to better understand biogeochemical pathways, enable us to manage forests to promote greater carbon storage and understand how forest ecosystems will respond to a changing climate. In addition, the CMNs mediate overstorey-understorey competition and competition amongst and between forest tree species. Underground signals carried through common mycelial networks can also warn neighbouring plants of imminent attack from pest and diseases as well as unfavourable condition such as drought and as such are essential members of forest ecosystem communities.



Hypothesis

Common mycorrhizal networks connecting trees of the same species will transfer less recently photosynthesised carbon than those of differing species

Why is it important to have this knowledge?

Climate change is probably the most significant problem faced by humanity in the 21st century. Atmospheric carbon dioxide has increased by 31% since the Industrial revolution rising from 280 ppm in 1900 to 400 ppm at the present day. Soil is the largest terrestrial pool of carbon dioxide although we know very little about the complex belowground carbon cycle. We know that plants fix atmospheric carbon dioxide in the soil and exchange this resource with mycorrhizal fungal symbionts. Mycorrhizal fungi are a significant component of soil microbial biomass and therefore carbon storage within soil. Small changes in soil carbon storage could therefore have a large effect on atmospheric carbon concentrations. Specifically my study will be investigating temperate forest soils and temperate forests globally are currently the only forest biome, which is increasing in size annually. If we can understand how best to plant and manage forests to increase the belowground carbon storage then we may mitigate some of the increases in atmospheric carbon dioxide. Results from this investigation will start to quantify the differences in belowground carbon transfer of trees in monoculture and mixed species forests.

Mycorrhizal Type	Fungal Taxa	Plant Taxa	Intracellular Coloniza-tion	Fungal Sheath	Vesicle
Arbuscular	Glomeromycota	Bryophyta Pteridophyta Gymnosperms Angiosperms	Present	Absent	Present or Absent
Ecto	Basidiomycota Ascomycota Zygomycota	Gymnosperms Angiosperms	Absent	Present	Absent
Ectendo	Basidiomycota Ascomycota	Gymnosperms Angiosperms	Present	Present or Absent	Absent
Arbutoid	Basidiomycota	Ericales	Present	Present or Absent	Absent
Monotro-poid	Basidiomycota	Monotropoideae	Present	Present	Absent
Ericoid	Ascomycota	Ericales Gymnosperms	Present	Absent	Absent
Orchi-daceous	Basidiomycota	Orchids	Present	Absent	Absent

Major categories of mycorrhizae and their attributes.