Mycorrhiza

By- Dr Ekta Khare
Department of Microbiology,
Chhatrapati Shahu Ji Maharaj University, Kanpur

Mycorrhiza

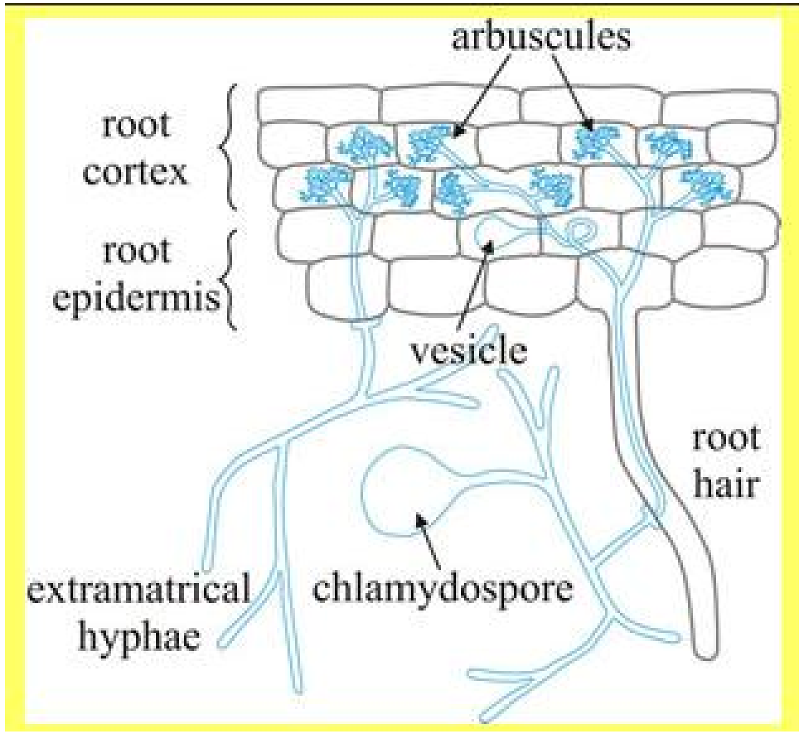
- According to Harley and Smith (1983), a mycorrhiza is defined as “an association between a fungus and a host plant in which destructive disintegration of the host does not occur and which is a prevalent and usual condition of the host plant in natural habitats and as such is very common and widespread.”
- *Myco*, of course, means “fungus,” and *rhiza* is “root,” so mycorrhiza literally means “fungus root.”
- A point about spelling - you’ll often see **mycorrhizae** as another older spelling of the plural of mycorrhiza.
- More than 90% of plants in nature have a mycorrhizal symbiont.
- The only groups of plants that regularly lack mycorrhizae are some crucifers, sedges, and some legumes.
- Through mycorrhization, the plant obtains phosphate and other minerals, such as zinc and copper, from the soil.
- The fungus obtains nutrients, such as sugars, from the plant root.
- Mycorrhizae help increase the surface area of the plant root system because hyphae, which are narrow, can spread beyond the nutrient depletion zone.
- Hyphae are long extensions of the fungus, which can grow into small soil pores that allow access to phosphorus otherwise unavailable to the plant.
- The beneficial effect on the plant is best observed in poor soils.
- The benefit to fungi is that they can obtain up to 20 percent of the total carbon accessed by plants.
- Mycorrhizae function as a physical barrier to pathogens.
- They also provides an induction of generalized host defense mechanisms, which sometimes involves the production of antibiotic compounds by the fungi.
- Fungi have also been found to have a protective role for plants rooted in soils with high metal concentrations, such as acidic and contaminated soils.

Mycorrhizal types

- Mycorrhizas were traditionally classified into the two types: ectotrophic and endotrophic, a classification based on the location of the fungal hyphae in relation to the root tissues of the plant; *ecto* means outside the root, *endo* means inside.
- This classification is now regarded as too simplistic, and there is now a nomenclature identifying seven mycorrhizal types; however we will telescope this into four major types with three additional subclasses as follows:
- **Endomycorrhizas**, in which the fungal structure is almost entirely within the host root, comprising three major and two minor groupings:
  - Arbuscular (AM) endomycorrhizas
  - Ericoid endomycorrhizas
    - Arbutoid endomycorrhizas , and
    - Monotropoid endomycorrhizas
  - Orchidaceous endomycorrhizas
- **Ectomycorrhizas**
  - Ectendomycorrhiza

Arbuscular (AM) endomycorrhizas

- Arbuscular (AM) endomycorrhizas are the most common type of mycorrhizal association, and were probably the first to evolve; the fungi are members of the **Glomeromycota**.
- In other textbooks you may find these fungi placed in the Order Glomales and Phylum Zygomycota but this is incorrect.
- The AM fungi are **obligate biotrophs**, and they are associated with roots of about 80% of plant species (that's equivalent to about two-thirds of all land plants, or around 90% of all vascular plants), including many crop plants.
- The AM association is endotrophic, and has previously been referred to as a vesicular-arbuscular mycorrhiza (VAM).
- This name has since been dropped in favour of AM, since members of the Family Gigasporaceae do not form vesicles.



… Arbuscular (AM) endomycorrhizas

- There is a wide-ranging fungal mycelium within the host root, and AM fungi explore the soil or other substrata with an extensive **extraradical mycelium**.
- Externally to the host the fungal hyphae produce the very large spores (often called chlamydospores).
- Formation of the mycorrhizal association is an infection process.
- Spores germinate near a plant root and the germinating hyphae penetrate the root in response to root exudates.
- Hyphae grow through the root tissues and in the root cortex hyphal branches form appressoria that penetrate the plant cells.
- The host plasmalemma invaginates and proliferates around the fungal intrusion. Repeated dichotomous branching of the fungal ‘hypha’ produces the **arbuscule** inside the cortical cell.
- Arbuscules have a lifespan of 4-15 days, after which they break down, and the plant cell returns to normal.
- The large surface area of the arbuscles is ideal for the fungus to receive carbohydrates from the plant and for the plant to obtain mineral nutrients that the hyphae have scavenged from the soil.
- AM fungi may also produce vesicles inter- or intracellularly within the roots.
- These are swollen spherical or oval structures containing lipids, which are thought to be used for storage.
- Since AM fungi are obligately biotrophic, attempts to grow them on their own in culture have so far failed.

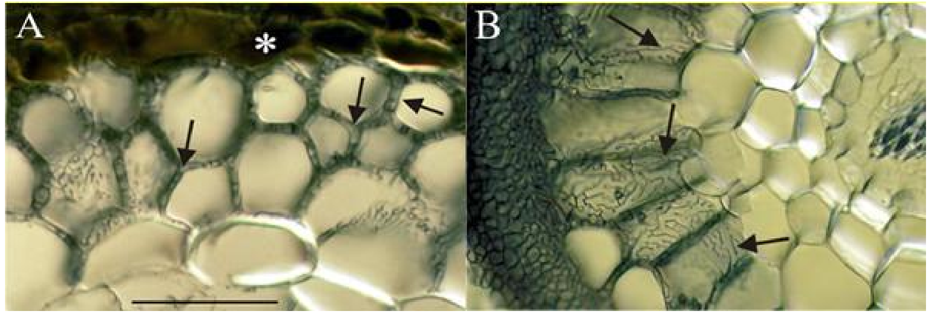
Ericoid endomycorrhizas

- **Ericoid endomycorrhizas** are mycorrhizas of *Erica* (heather), *Calluna* (ling) and *Vaccinium* (bilberry), that is, plants that endure moorlands and similar challenging environments.
- Fungi are members of the Ascomycota (an example is *Hymenoscyphus ericae*).
- The plant's rootlets are covered with a sparse network of hyphae; the fungus digests polypeptides saprotrophically and passes absorbed nitrogen to the plant host; in extremely harsh conditions the mycorrhiza may even provide the host with carbon sources (by metabolising polysaccharides and proteins for their carbon content).
- The ericoid fungal hyphae form a loose network over the hair root surface; the hyphae can also penetrate the epidermal cells, often at several points in each cell; and coiled hyphae fill the cell.
- Up to 80% of root volume can be fungal tissue and it is through these coils that nutrient exchange is thought to occur.
- Colonisation by ericoids is restricted to expanded epidermal cells (i.e. mature cells). Therefore the apical region of the hair root, behind the growing meristem, remains uncolonised until the cells differentiate and mature.
- The fungi involved in ericoid associations are facultative; that is, they can be free-living in soil, and can also be cultured *in vitro*. When grown on nutrient agar the fungi produce dark-coloured, slow growing, sterile mycelia.
- Two specialised subgroups may be separated out of the ericoid endomycorrhizal group:
  - **Arbutoid mycorrhizas** are, like those of Ericoid and Monotropoid mycorrhizas, found in the plant order Ericales. Like ericoid mycorrhizas, the family Ericaceae is represented, with arbutoid mycorrhizas b.eing formed in the genera *Arctostaphylos* and *Arbutus.*
  - It is however different from ericoid mycorrhiza and resembles ectomycorrhiza, both functionally and in terms of the fungi involved (basidiomycetes).
  - A major difference between the **arbutoid** and ectomycorrhizal association is that the hyphae of the former **do actually penetrate** the outer cortical cells, and fill them with coils, which the hyphae of ectomycorrhizas do not. The intracellular coils, along with the mantle sheath and Hartig net are the diagnostic features of arbutoid mycorrhizas.
  - **Monotropoid mycorrhizas:** Until fairly recently the mycorrhizal association formed by plants of the Montropaceae were classified as arbutoid. However, fundamental differences were noted and resulted in a new category of mycorrhiza being created.
  - Typical arbutoid mycorrhizas such as *Arbustus* and *Pyrola* show extensive intracellular penetration, with coils of hyphae filling large volumes in many cells. In contrast, fungi colonising achlorophylous plants in the Monotropaceae family (but now included within the Ericaceae), such as *Monotropa hypopitys* (in Europe) and *M. uniflora* (North America), never actually penetrate the plant cell walls.
  - The Monotropaceae are also unusual in that all 10 genera in the family are entirely achlorophyllous, hence are unable to photosynthesise and produce carbohydrates. Instead, they use their mycorrhizas not only to obtain minerals and nutrients, but also to tap the carbon supplies of nearby plants via their roots.
  - *Monotropa* species are most commonly found in coniferous forests. Fungi in forest soils form ectomycorrhizal associations with trees and also monotropoid associations with the *Monotropa* species.
  - Carbohydrates pass from conifer to *Monotropa* via their common mycorrhizal partner, in what is termed a source-sink relationship (demonstrated by supplying conifer trees with sucrose labeled with the radioactive isotope ^{14}C. *Monotropa* was subsequently shown to have absorbed the radiolabelled carbon).
  - *Monotropa* may supply a different source of carbon to the fungus, or nothing at all, and whether there is a net carbon gain by *Monotropa* over the course of a season is not yet known. Radiolabelled phosphorus (^{32}P) injected into *Monotropa* has been recovered in neighbouring trees and so this relationship may not be entirely one-sided.

Orchidaceous endomycorrhizas

- Orchidaceous endomycorrhizas are similar to ericoid mycorrhizas but their carbon nutrition even is more dedicated to supporting the host plant as the young orchid seedling is non-photosynthetic and depends on the fungus partner utilising complex carbon sources in the soil, and making carbohydrates available to the young orchid.
- All orchids are achlorophyllous in the early seedling stages, but usually chlorophyllous as adults, so in this case the seedling stage orchid can be interpreted as parasitising the fungus.
- A characteristic fungus example is the basidiomycete genus *Rhizoctonia* (although this is a complex genus which can be divided into several new genera).
- The infection of an orchid seed by fungi occurs after the embryo takes up water and swells, rupturing the seed coat.
- The embryo emerges and produces a few root hairs, which hyphae rapidly colonise.
- As hyphae penetrate a cell of the embryo, the plasma membrane of the orchid cell invaginates, and the hypha becomes surrounded by a thin layer of cytoplasm.
- An orchid embryo consists of only a few hundred cells and the fungi spread quickly from cell to cell.
- Within cells, hyphae form coils called pelotons, which greatly increase the interfacial surface area between orchid and fungus.
- Each intracellular peloton has a short life-span, lasting only a few days before it degenerates and is digested by the orchid cell.
- In fact hyphae in the orchid have short life-spans too; older hyphae develop large vacuoles and thick cell walls, and the cytoplasm degenerates.
- The hyphal cells eventually collapse and are consumed by the orchid cell.
- During this process, the plant cell remains functional and can be recolonised by any surviving hyphae, or by fungi invading from adjacent cells.
- Infection by mycorrhizal fungi does not necessarily result in the germination and growth of an orchid. Upon the association, three outcomes are possible:
    - a mycorrhizal interaction, as described above;
    - parasitic infection, in which the orchid cells are invaded and the embryo dies;
    - the orchid cells reject the fungal infection.
- A successful fungal infection results in the germination of an orchid seed. The fungus may be the sole source of nutrition during the first years of life. Most orchid species develop chlorophyll in their adult stage and become less dependent on the mycorrhiza. However, most still have mycorrhizal roots, and gain nitrogen and phosphorus from the fungus. Whether they still induce the fungi to transfer carbon to them is unknown.
- Around 200 species of orchids remain achlorophyllous throughout their lifetimes. Species such as *Galeola, Gastrodia, Corallorhiza, Rhizanthella* and many others continue to gain carbon from their mycorrhizal fungi. Even some chlorophyllous species, such as *Cephalanthera rubra* (Red Helleborine, one of the rarest orchids in Britain) spend several years underground before producing overground flowering scapes.

Ectomycorrhizas



- **Ectomycorrhizas** are the **most advanced symbiotic association** between higher plants and fungi, involving about 3% of seed plants including the majority of forest trees.
- In this association the plant root system is completely surrounded by a sheath of fungal tissue which can be more than 100 μm thick, though it is usually up to 50 μm thick.
- The hyphae penetrate between the outermost cell layers forming what is called the **Hartig net**.
- From this a network of hyphal elements (hyphae, strands and rhizomorphs) extends out to explore the soil domain and interface with the fungal tissue of the root.
- Ectomycorrhizal fungi are mainly Basidiomycota and include common woodland mushrooms, such as *Amanita* spp., *Boletus* spp. and *Tricholoma* spp.
- Ectomycorrhizas can be highly specific (for example *Boletus elegans* with larch) and non-specific (for example *Amanita muscaria* with 20 or more tree species).
- In the other specificity direction, 40 fungal species are capable of forming mycorrhizas with pine.
- Ectomycorrhizas can link together groups of trees, the submerged mycelium acting as what has been described as a 'wood-wide-web'.
- Ectomycorrhizal fungi depend on the plant host for carbon sources, most being uncompetitive as saprotrophs.
- With few exceptions (*Tricholoma fumosum* being one), the fungi are unable to utilise cellulose and lignin; but the fungus provides greatly enhanced mineral ion uptake for the plant and the fungus is able to capture nutrients, particularly phosphate and ammonium ions, which the root cannot access.
- Host plants grow poorly when they lack ectomycorrhizas.
- This ectomycorrhizal group is reasonably homogenous, but a subgroup, ectendomycorrhizas, has been appended.

Ectendomycorrhiza

- Ectendomycorrhiza is a purely descriptive name for mycorrhizal roots that exhibit characteristics of both ectomycorrhizas and endomycorrhizas.
- Ectendomycorrhizas are essentially restricted to the plant genera *Pinus* (pine), *Picea* (spruce) and, to a lesser extent, *Larix* (larch).
- Ectendomycorrhizas have the same characteristics as ectomycorrhizas but show extensive intracellular penetration of the fungal hyphae into living cells of the host root.

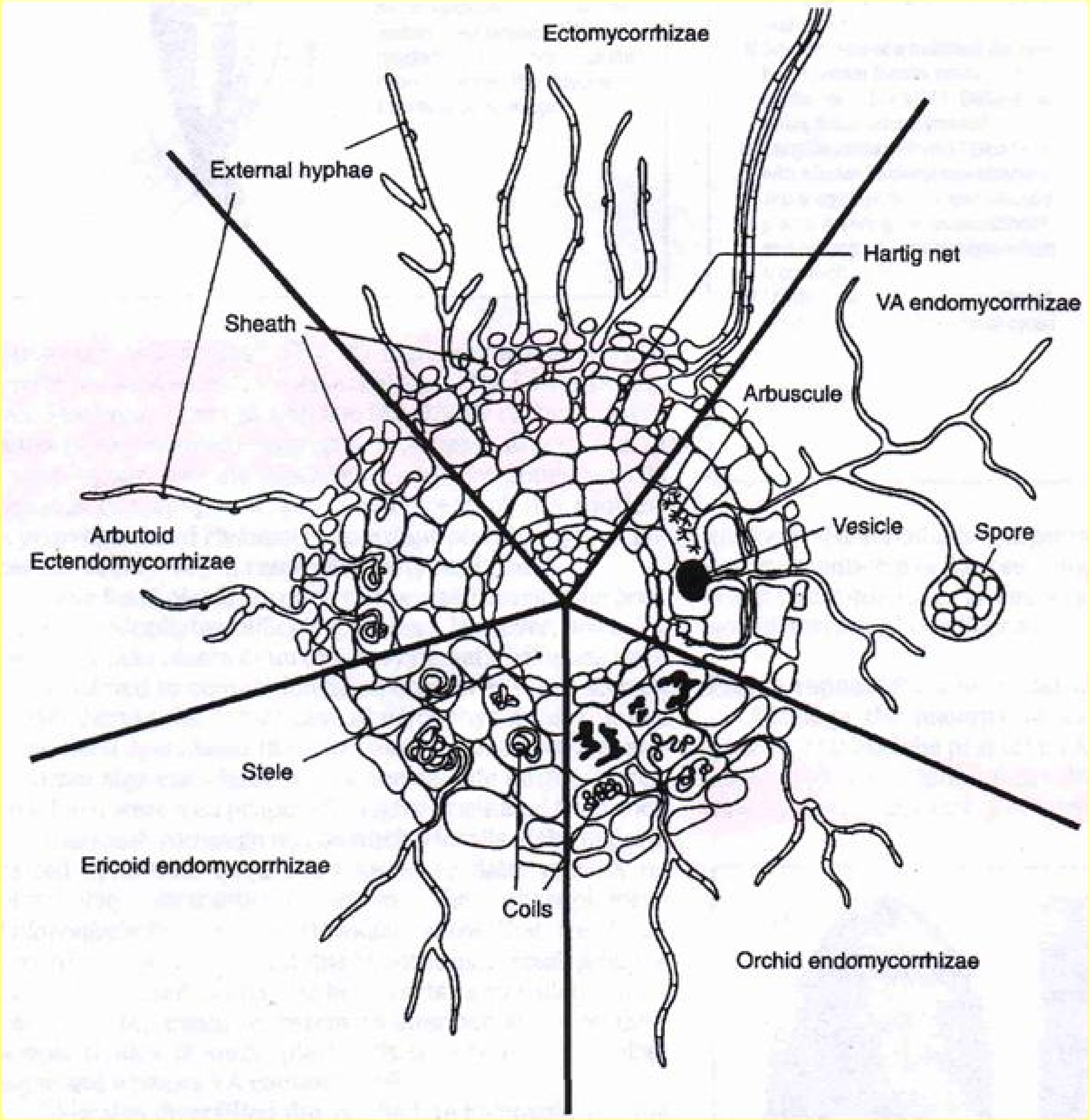


Fig. 1. The principle structural features of the five main types of mycorrhiza. From Selosse & Le Tacon (1998) with permission from Elsevier Science.

Table 1. Summary of the characteristics of the seven types of mycorrhiza.

Feature	Mycorrhizal type						
	Endomycorrhizas					Ectomycorrhizas	
	AM	Ericoid	Arbutoid	Mono-tropoid	Orchid	Ecto-	Ectendo-
Fungi septate	no	yes	yes	yes	yes	yes	yes
Fungi aseptate	yes	no	no	no	no	no	no
Intracellular colonisation	yes	yes	yes	yes	yes	no	yes
Fungal sheath	no	no	yes or no	yes	no	yes	yes or no
Hartig net	no	no	yes	yes	no	yes	yes
Vesicles	yes or no	no	no	no	no	no	no
Plant host chlorophyllous*	yes (? no)	yes	yes	no	no*	yes	yes
Fungal taxa	Glomero-mycota	Asco-mycota	Basidio-mycota	Basidio-mycota	Basidio-mycota	Basidio-mycota Asco-mycota	Basidio-Asco-(Glomero-mycota)
Plant taxa†	Bryo Pterido Gymno Angio	Ericales Bryo	Ericales	Monotrop-aceae	Orchid-aceae	Gymno Angio	Gymno Angio

*All orchids are achlorophyllous in the early seedling stages, but usually chlorophyllous as adults. Source: †Bryo = Bryophyta, Pterido = Pteridophyta, Gymno = Gymnospermae, Angio = Angiospermae. Table taken from Moore *et al.*, 2011 (URL).

The ecology and roles of mycorrhizas

- In many cases there is an exchange of nutrients between the two organisms, but in some mycorrhizal associations the benefits flow one way rather than both ways, as in the orchid example noted above. Where there is an exchange, the fungus receives some of the carbohydrates photosynthesized by the plant and the plant obtains various inorganic nutrients and trace elements which the mycelium has extracted from the soil.
- Photosynthesis provides a chlorophyll-containing plant its source of carbon. Other important nutrients, such as nitrogen, potassium and phosphorus (as well as various trace elements) come from the soil. Usually those other nutrients will be dispersed in the soil, so necessitating the exploration of a large volume of soil if the plant is to get the required amounts of those nutrients. In addition, the non-carbon elements will be present in the soil in various chemical compounds - some of which are readily soluble and easily absorbed by roots whereas others are insoluble (and therefore inaccessible to plant roots). If a plant were to use roots to explore a large volume of soil, it would require a considerable expenditure of energy by the plant. Making use of fungal hyphae saves this expenditure. Moreover, the very fine fungal hyphae can explore much finer cavities than roots and are also capable of exploiting compounds that are inaccessible to roots.
- Various mycorrhizal fungi also help protect the associated plants against pathogenic fungi, a number of soil microbes, heavy metals and toxic compounds. Experimental studies have shown that many photosynthesizing plants fail to develop into strong individuals, if deprived of their mycorrhizal partners. All in all, the plants get a fair return on the 10-30% of photosynthesized carbohydrates that pass through to the attached mycelia.

- Mycorrhizal associations can be fairly complex, with numerous mycelia (from more than one fungal species and of more than one type of mycorrhiza) simultaneously latching onto the roots of one plant. Conversely, a given mycelium may be attached to more than one plant, perhaps even to plants of different species. This latter plant-mycelium-plant connection allows the carbon produced by one plant to move through the attached mycelium to another plant. In this way, a seedling growing in heavy shade (and therefore unable to make much use of the sunlight) can benefit from the photosynthesizing activities of some other, better-placed plant. These intricate, multiway connections have led some people to refer to the underground roots-and-mycelia network as the "wood wide web"!

- In the world there are over 400 species of plants which lack chlorophyll. These achlorophyllous plants are found in many families and the majority rely on fungal associates for the carbohydrates which chlorophyllous plants would produce via photosynthesis. In some cases an entire plant family is achlorophyllous (such as the Monotropaceae in the northern hemisphere) while in others (such as the Orchidaceae) only certain genera lack chlorophyll.

- In Australia the orchids Gastrodia sesamoides (the Potato Orchid), Dipodium punctatum (the Spotted Hyacinth Orchid) and the two species of the genus Rhizanthella (Rhizanthella gardneri and Rhizanthella slateri) lack chlorophyll. The Rhizanthella species are unusual because they are underground orchids, whereas both Gastrodia and Dipodium produce above-ground flower spikes. The fungi involved in these associations are quite varied, both in terms of species and lifestyles. For example the species of Gastrodia (both in Australia and overseas) are associated with species of Armillaria (a genus of virulently parasitic fungi, which the orchids manage to keep under control). The Western Australian underground orchid Rhizanthella gardneri forms an orchid mycorrhiza with a fungus that also forms ectomycorrhizas with Melaleuca (one of the Australian native Tea Trees). Incidentally, this also shows that some fungi can form more than one type of mycorrhiza. The eastern Australian species, Rhizanthella slateri, pictured here, has been rarely seen. It was discovered in 1931 on Alum Mountain, in Bulahdelah on the New South Wales north coast, and these photos (taken in 2002) are also of specimens growing on Alum Mountain. The fungal associate of this species is unknown.

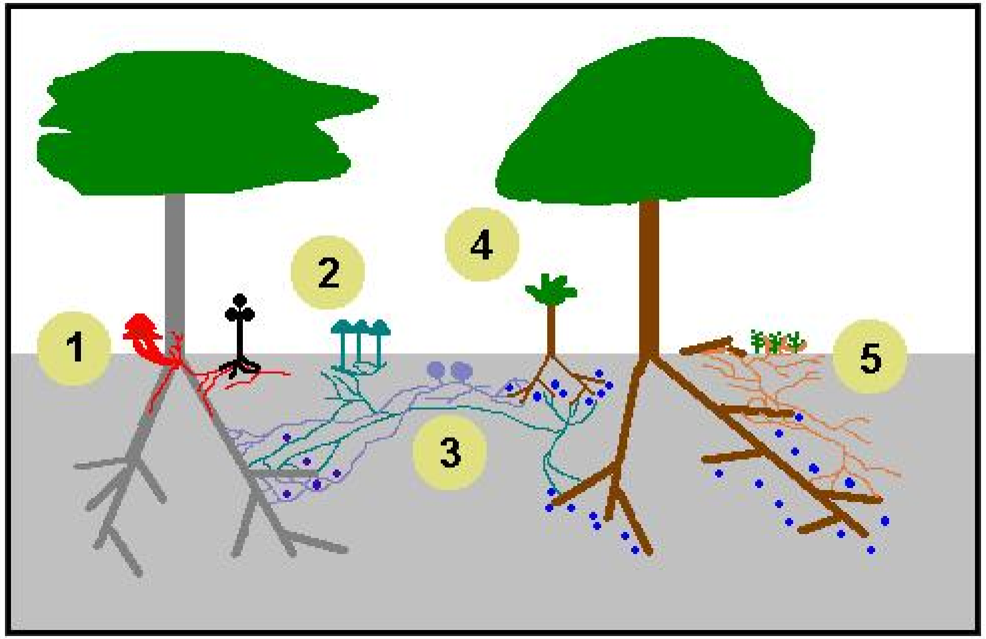
- All such orchids are directly parasitic on the associated fungi. The carbohydrates that end up in *Gastrodia* and at least the Western Australian *Rhizanthella* originated in other living plants, so you could also look at these orchids as being indirectly parasitic on other plants.
- Not all the achlorophyllous plants have fungal associates. Some attach directly to the roots of host plants and the best known are probably the Broomrapes, which constitute the genus *Orobanche*. Another example is the genus *Balanophora*

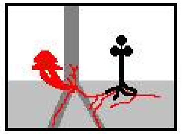
•. Both *Balanophora* and *Orobanche* are flowering plants, but are often mistaken for a fungi.

•The mycorrhizal associations formed by a particular plant need not be static. Over time, the fungi that are involved can change. Some may associate only with young plants, others come into the picture only when the plant is a few years old - while some may stick around and it is possible that, depending on conditions, there are some which come and go. A study of the ericoid mycorrhizas on several epacrid species in the south-west of Western Australia showed that the mycorrhizas were seasonal. The area has a Mediterranean climate with cool, wet winters but hot, dry summers. The mycorrhizas are formed on the very fine hair roots that grow out from the main roots. In summer many of the hair roots die but regrow, and become mycorrhizal, in the wet winter months. Similar studies around Sydney, not subject to a Mediterranean climate, didn’t show this die-regrow pattern and studies in the northern hemisphere also show year-round persistence of mycorrhizal roots in most species. In summary it seems that, except in very dry conditions, ericoid mycorrhizas are present and functioning all year round.

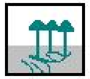
•Finally, the formation of the mycelium-root connection is not just a simple matter of fungus-meets-plant, fungus-hooks-onto-plant.

- There are soil bacteria, known as **mycorrhizal helper bacteria**, which promote the formation of mycorrhizas.

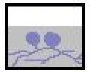




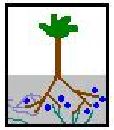
Well at **1** we have an achlorophyllous plant (in black) using a parasitic fungus (in red) as its source of carbon. Notice that the red hyphae have penetrated a tree and some red mushrooms have been formed at the base of the trunk.



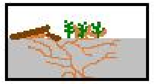
At **2** there are some mushrooms that have arisen from a mycorrhizal fungus. Note how the associated mycelium is linking several plants.



You can see the buried fruiting bodies of a mycorrhizal, truffle-like fungus at **3**. In this case the mycelium connects just two plants.



The young plant at **4** is growing in the shade of a mature plant, but it is connected to two mature plants by a couple of mycorrhizal mycelia. Notice the numerous dark blue Mycorrhizal Helper Bacteria.



The mycelium of yet another mycorrhizal fungus has formed corticioid fruiting bodies on fallen twigs and mosses at **5**.