DC-1

SEM-2

Paper: Mycology and Phytopathology

Lesson: Mycorrhizal Associations in Plant

Lesson Developer: Dr. Bhoopander Giri

Dr. Bhawna Saxena

College/Dept: Swami Shraddhanand College/ Department of Botany

University of Delhi

Table of Contents

Chapter: Mycorrhizal associations in plants

Introduction

The term mycorrhiza, meaning fungi to the root, was used for the first time in the year 1885 by A. B. Frank who described 'Mykorrhizen' on the basis of experiments conducted with trees of temperate forests and pines. Mycorrhizal fungi are widely distributed in natural and agricultural environments and are known to colonizemore than 80% of land plants, including liverworts, ferns, many gymnosperms and most angiosperms. However, plants from the families Brassicaceae, Chenopodiaceae and Proteaceae rarely, if ever, have mycorrhizal association.

They are one of the most ancient associations having a long evolutionary history. The fossil records and phylogenetic analysis suggest that more than 450 million years ago certain early Devonian period plants have established an intimate association with filamentous fungi now known as mycorrhizal fungi. It is believed that translocation of plants from water to land would not have been possible without this association.

Definition of Mycorrhizas
Mycorrhizas are symbiotic associations essential for one or both partners, between a fungus (specialized for life in soils and plants) and a root (or other substrate-contacting organ) of a living plant, that is primarily responsible for nutrient transfer. Mycorrhizas occur in a specialized plant organ where intimate contact results from synchronized plant-fungus development.
Source: http://mycorrhizas.info/

Types of Mycorrhizal Fungi

Mycorrhizal fungi have been classified on the basis of the extent of plant root penetration, production of external mantle or sheath and inter and intracellular structures they form inside the plant root. Till date, so far seven different types of mycorrhizal fungi have been recognized such as Endomycorrhiza, Ectomycorrhiza, Ectendomycorrhiza, Arbutoid mycorrhiza, Ericoid mycorrhiza, Monotropoid mycorrhiza and Orchidoid mycorrhiza. Amongst them, two major types of mycorrhizal fungi that are important for plant growth and development are: Endomycorrhiza or Arbuscular mycorrhiza and Ectomycorrhiza. These two types are differentiated by the fact that ectomycorrhizal fungi typically form a thick sheath, or mantle, of mycelium around roots, and some of the mycelium penetrates between cortical cells. The hyphae do not penetrate individual cells within the root cortex, but instead surrounded by a network of hyphae called the **Hartig's net**. The hyphae of endomycorrhizal fungi grow within the root itself and extending outward from the root into surrounding soil. The hyphae enter the root through either the epidermis or root hairs, penetrate the cell wall and invaginate the cell membrane. The hyphae grow between and into root cortical cells, where they from dichotomously branched treelike structure – arbuscules, and form oval structures - vesicles within the cortical cells. Endomycorrhizal fungi develop mainly microscopic spores in the soil whereas ectomycorrhizal fungi develop aboveground fruit bodies (mushrooms) in the vicinity of trees.

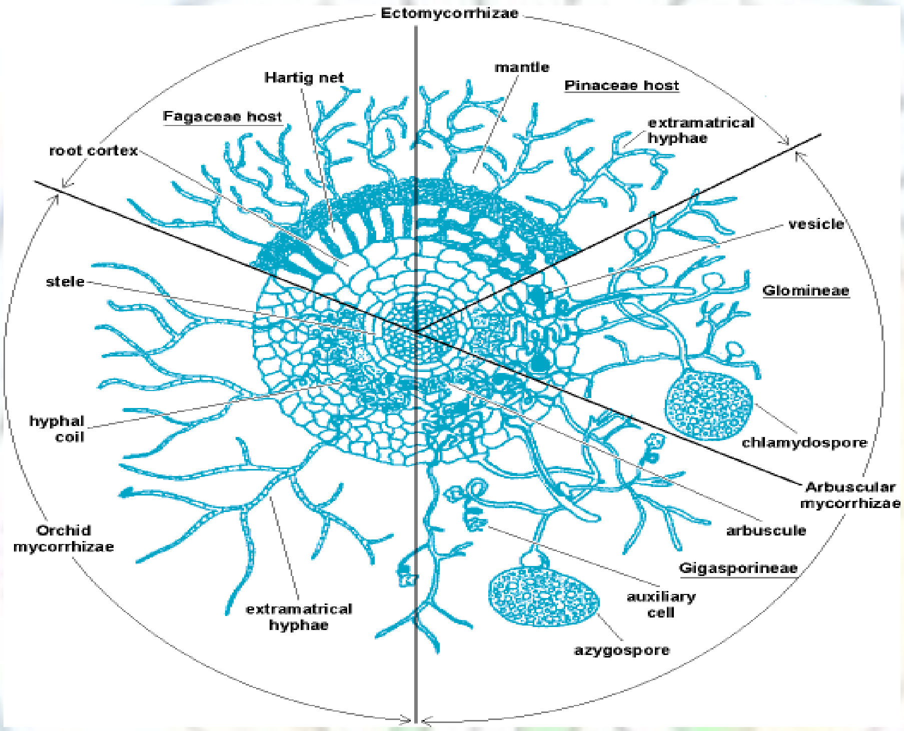


Figure: Different kinds of mycorrhizal associations

Source:http://www.accessscience.com/loadBinary.aspx?filename=YB010700FG0010.gif

Table: Types of mycorrhizal associations (Source: http://mycorrhizas.info/)

No.	Category	Definition	Hosts	Fungi
1	**Arbuscular mycorrhizas,** AM	Associations formed by Glomeromycotan fungi in plants that usually have arbuscules and often have vesicles (earlier known as vesicular-arbuscular	Plants	Glomeromycota

		mycorrhizas, VAM).		
1.1	**Linear AM**	Associations that spread predominantly by longitudinal intercellular hyphae in roots (formerly known as Arum series AM).	Plants	As above
1.2	**Coiling AM**	Associations that spread predominantly by intracellular hyphal coils within roots (formerly known as Paris series AM).	Plants	As above
1.2.1	**Beaded AM**	Coiling AM in roots, where interrupted root growth results in short segments divided by constrictions.	Woody plants	As above
1.2.2	**Inner cortex AM**	Coiling AM with arbuscules in one layer of cells of the root inner cortex.	Plants	As above
1.2.3	**Exploitative AM**	Coiling AM of myco-heterotrophic plants, usually without arbuscules.	Achlorophyllous plants	As above
2	**Ecto-mycorrhiza(ECM)**	Associations with a hyphal mantle enclosing short lateral roots and a Hartig net of labyrinthine hyphae that penetrate between root cells.	hosts	Higher fungi (asco-, basidio- and zygo-mycetes)
2.1	**Cortical**	Hartig net hyphae penetrate between multiple cortex cell layers of short roots	Most are gymnosperm trees	As above
2.2	**Epidermal**	Hartig net fungal hyphae are confined to epidermal cells of short roots	Angiosperms (most are trees)	As above
2.2.1	**Transfer cell**	Epidermal Hartig net with transfer cells (plant cells with wall	*Pisonia* (Nyctaginaceae).	*Tomentella* spp. in *Pisonia*

		ingrowths)		
2.2.2	**Monotropoid**	Exploitative epidermal ECM of myco-heterotrophic plants in the Ericaceae where individual hyphae penetrate epidermal cells.	Ericaceae (Monotropa, Pterospora, Sarcodes)	Basidiomycetes
2.2.3	**Arbutoid**	ECM of autotrophic plants in in the Ericaceae where multiple hyphae penetrate epidermal Hartig net cells.	Ericaceae (part only)	Basidiomycetes
3	**Orchid**	Associations where coils of hyphae (pelotons) penetrate within cells in the plant family Orchidaceae.	hosts	Most are basidiomycetes in *Rhizoctonia* alliance .
3.1	**Orchid Root**	Associations within a root cortex.	Orchidaceae	As above
3.2	**Orchid Stem**	Associations within a stem or rhizome.	Orchidaceae	As above
3.3	**Exploitative Orchids**	Associations of myco-heterotrophic orchids.	Orchidaceae (fully or partially achlorophyllous)	Orchid, ectomycorrhizal, or saprophytic fungi
4	**Ericoid**	Coils of hyphae within very thin roots (hair roots) of the Ericaceae.	Ericaceae (most genera)	Most are Ascomycetes
5	**Sub- epidermal**	Hyphae in cavities under epidermal cells, only known from an Australian monocot genus.	*Thysanotus* spp. (Laxmaniaceae)	Unknown

Endomycorrhiza or Arbuscular Mycorrhiza

Arbuscular mycorrhiza (AM) represent a symbiosis between terrestrial plant roots and fungi of phylum Glomeromycota. The symbiosis derive its name from the Latin word *arbusculum* (=little tree) specifying typical tuft-like structures formed by fine dichotomously branched fungal hyphae, and the Greek word for fungus roots. They are obligate symbionts with no confirmed sexual stage, although the hyphae of genetically distinct strains can anastomose and exchange genetic material. Spores are multinucleate, containing thousands of nuclei and heterokaryotic. In the syncytial mycelia of these fungi, nuclei are constantly translocated by rapid cytoplasmic streaming. The lack of a uninucleate cell stage in the life cycle of AM fungi along with above peculiar traits have contributed to the difficulties in standard molecular approaches such as genetic transformation, mutant generation and characterization, as well as large scale transcriptomic and genomic analysis.

The hyphae of arbuscular mycorrhiza (AM) enter into the plant cells, producing structures that are either balloon like - the **vesicles** or dichotomously branched invaginations –the **arbuscules**.

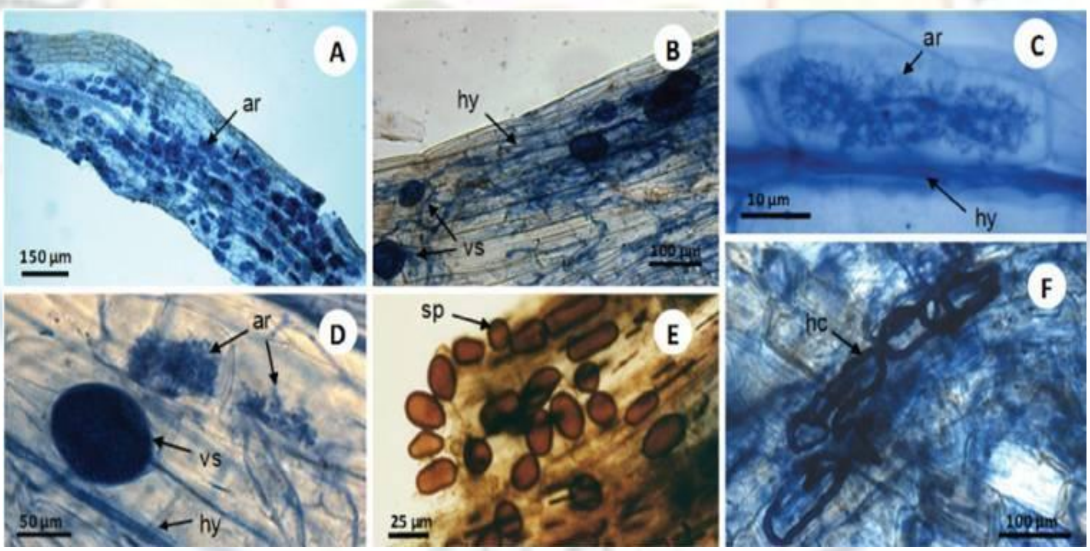


Figure: Arbuscular mycorrhizal fungi in the roots of weeds (A) Arbuscule (ar) in *Amaranthus retroflexus;* (B) Vesicle (vs) and hyphae (hy) in *Sinapsis arvense;* (C) *Leonurus sibiricus*; (D) *Leonitis neptaefolia*; (E) Spore (sp) in *Paniculum maximum*; (F) Hyphal coils (hc) in *Sorghum arundaceum.*

Source:http://www.scielo.br/scielo.php?pid=S1807-86212013000100006&script=sci_arttext (CC)

AM hyphae do not in fact penetrate the protoplast, but invaginate the cell membrane. The structure of the arbuscules greatly increases the contact surface area between the hypha and the cell cytoplasm to facilitate the transfer of nutrients between them.AM fungi have two types of mycelium systems: external and internal mycelium. External mycelium grows and spreads inside the soil, and is able to ease into the tiny pores of the soil where plant roots are normally out of reach. Internal mycelium grows in between and inside the parenchymatous cells of the host plant roots. Internal mycelia create many branches known as arbuscules within the plant root cells.

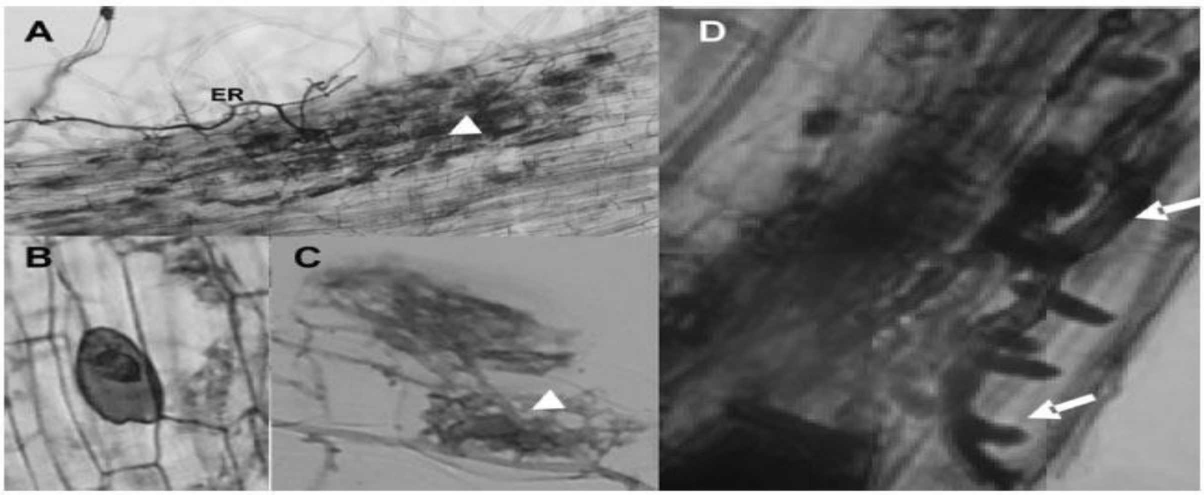


Figure 1. Functional mycorrhizal structures in roots of the plant host *Solanum lycopersicum* (Tomato). Fungal colonization was both inter- and intracellular and only involved the cortical cells of the roots. A, Root of *S. lycopersicum* showing extraradical hyphae (ER), arbuscules (Arrowhead). B, Detail of a vesicle and arbuscule (C) of *Glomus intraradices in S. lycopersicum roots*. (D) Hyphae of *Glomus intraradices* showing a typical hyphopodium (Arrows) or appressorium, at later stage, in the epidermal root cells.

Source:http://www.scielo.br/scielo.php?pid=S1677-04202011000100010&script=sci_arttext (CC)

The arbuscules are considered to be the site of nutrients exchange between fungus and plant. They are formed only by fungi in the division Glomeromycota. The hyphae of AM fungi produce the glycoprotein- **glomalin**, which may be one of the major stores of carbon in the soil. AM fungi have (possibly) been asexual for many millions of years and, unusually, individuals can contain many genetically different nuclei-a phenomenon called**heterokaryosis**.

Systematic Position of Arbuscular Mycorrhizal Fungi

Gerdemann and Trappe placed AM fungi in four different genera, *Glomus, Sclerocystis, Gigaspora*, *Acaulospora*andEndogonales. Later,a new order, Glomales was established by Morton and Benny in the phylum Zygomycota, which comprises six genera, as tabularized below. Thereafter, the classification of AM fungi was repeatedly refined by several taxonomists and emphasis was given on the structure of spores/sporocarps and their wall for the taxonomy of Glomales. Later,it was suggested that AM fungi are distinct from other zygomycotaen, as they do not seem to develop characteristic zygospores.

Till the early nineties, AM fungi were considered the members of Zygomycota. Recent studies based on nuclear-encoded rRNA gene markers supported that these fungal symbionts form a monophyletic group of true fungi, the phylum Glomeromycota, which comprises about 200 described morphospecies. Glomeromycotan fungi produce spores of different size ranging from 40-800 µm with layered walls containing numerous nuclei. The mode of spore formation has been important to circumscribe genera and families. Their spores may produce singly or in clusters (sporocarps). Molecular studies have described no genetic recombination or either very low level; therefore it was assumed that spores are formed asexually. The members of this group also lack formation of septa.

Molecular studies based on rDNA phylogenies revealed that AM fungi are the sister group of Asco- and Basidiomycota and not monophyletic with any part of the Zygomycota. Recently, Schüβler and co-workershave raised the order Glomales to the rank of a phylum Glomeromycota. They also corrected the grammatically incorrect order Glomales to 'Glomerales' and several new orders were established. An evolutionary systematic position of AM fungi classification is depicted in the table given below. Molecular studies conducted by researchers have shown much higher glomeromycotan diversity at phylum and genus level than expected through microscopic examinations and observations of spore morphology. It is speculated that some of the morphological characters that were used previously could have evolved multiple times independently.

The phylum Glomeromycota is currently divided into four orders namely, Diversisporales, Glomerales, Archaesporales and Paraglomerales (see table). However, Oehl et al 2011 and Gota et al 2012 have erected one more order the Gigasporales. They have described four families, Diversisporaceae, Acaulosporaceae, Sacculosporaceae, Pacisporaceae and Gigasporaceae within the order Diversisporales and five families, Scutellosporaceae, Gigasporaceae, Intraomatosporaceae, Dentiscutataceae and Racocetraceae within the order

Gigasporales. Glomerales describes two families, the Enthrophosporaceae and Glomeraceae. The order Archaeosporales describes three families, the Ambisporaceae, Geosiphonaceae and Archaeosporaceae. The fifth order Paraglomerales includes only one family, Paraglomeraceae like consensus classification of the Glomeromycota.

Table : Systematic position of arbuscular mycorrhizal fungi

Classification according to Goto et al. (2012), Ohel et al. (2011)	**Consensus Classification of the Glomeromycota and its comparison with the classification given by Goto et al. (2012), Ohel et al. (2011)**	**Classification according to Schubler et al (2001), Redecker et al (2000), Schwarzott et al (2001), Walker and Schubler et al 2004**	**Classification according to Gerdemann and Trappe (1974), Benjamin (1979), Warcup (1990)**	**Classification according to Morton and Benny (1990)**
Phylum: Glomeromycota	Phylum: Glomeromycota	Phylum: Glomeromycota	Phylum: Zygomycota	Phylum: Zygomycota
Order: Diversisporales Family: Diversisporaceae Genus: *Tricispora, Otospora, Diversispora, Redeckera* Family: Acaulosporaceae Genus: *Kukiospora, Aculospora* Family: Sacculosporaceae Genus: *Sacculospora* Family: Pacisporaceae Genus: *Pacispora* Order: Gigasporales Family: Scutellosporaceae Genus: Orbispora, Scutellospora Family: Gigasporaceae Genus: Gigaspora Family: Intraomatosporaceae Genus: Intraomatospora, Paradontisculata Family: Dentiscutataceae Genus: Dentiscutata, Quetunica, Fuscutata Family: Racocetraceae Genus: Cetraspora, Recocetra Order: Glomerales Family: Enthrophosporaceae Genus: *Viscospora, Claroideoglomus,*	Order: Diversisporales Family: Diversisporaceae Genus: *Tricispora, Otospora, Diversispora, Corymbiglomus, Redeckera* Family: Acaulosporaceae Genus: Acaulospora Family: Sacculosporaaceae Genus: Sacculospora Family: Pacisporaceae Genus: *Pacispora* Family: Gigasporaceae Genus: *Scuteliospora, Gigospora, Intramatospora, Paradentiscutala* Order: Glomerales Family: Claoideoglomeraceae Genus: *Claroideoglomus* Family: Glomeraceae Genus: *Glomus* Genus: *Funneliformis*	Order: Diversisporales Family: Acaulosporaceae Genus: *Acaulospora* Family: Diversisporaceae Genus: Diversispora Family: Gigasporaceae Genus: *Gigaspora* Order: Glomerales Family: Glomaceae Genus: *Glomus* (with two distinct clades) Order: Archaesporales Family: Archaesporaceae Genus: *Archaespora* Family: Geosiphonaceae Genus: *Geosiphon* Order:	Order: Endogonales Family: Endogonaceae Genera: *Endogone* *Sclerogone* *Glomus* *Sclerocystis* *Acaulospora* *Entrophosphora* *Gigaspora*	Order: Endogonales Family: Endogonaceae Genera: *Endogone* *Sclerogone* Order: Glomales Sub-order: Glomineae Family: Glomaceae Genera: *Glomus, Sclerocystis* Family: Acaulosporaceae Genera: *Acaulospora* *Entrophosphora*

Entrophospora, Albahypha Family:Glomeraceae Genus: Simiglomus, Funnaliformis,Septoglomus, Glomus Order: Archaeosporales Family: Ambisporaceae Genus: Ambispora Family: Geosiphonaceae Genus: *Geosiphon* Family: Archaeosporaceae Genus*: Intraspora, Archaeospora* Order: Paraglomerales Family: Paraglomeraceae Genus*: Paraglomus*	Genus*: Septoglomus* Genus: *Rhizophagus* Genus*: Sclerocystis* Order: Archaeosporales Family: Ambisporaceae Genus: *Ambispora* Family: Geoosiphoneceae Genus*: Geosiphon* Family: Archaeosporaceae Genus: *Archaespora* Order: Paraglomerales Family: Paraglomeraceae Genus*: Paraglomus*	Paraglomerales Family: Paraglomeraceae Genus: *Paraglomus*		

Development of Arbuscular Mycorrhizal Association in Plant Root

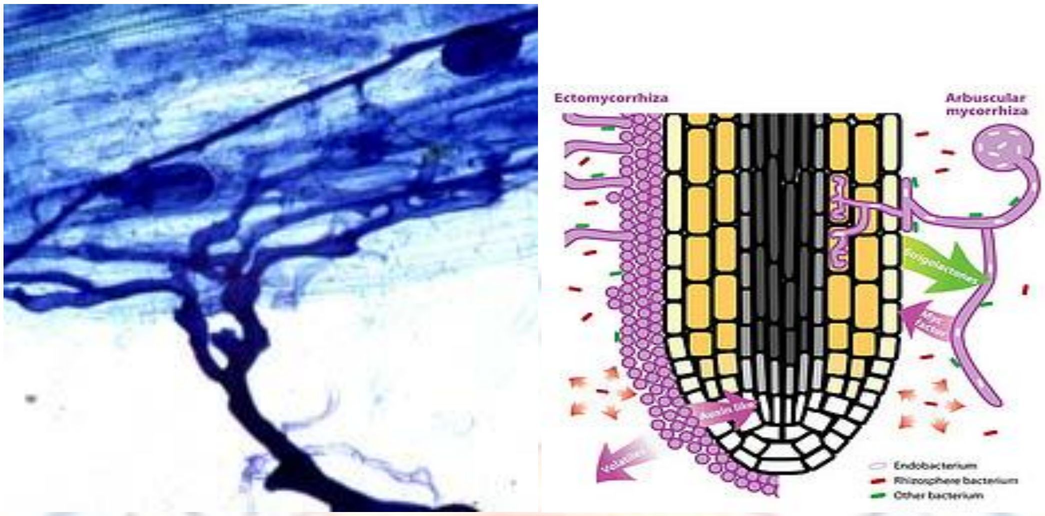
AM symbiosis development takes place in three distinct phases:

1. Asymbiotic phase

This phase includes the germination of AM fungal spores in soil and production of little amount of mycelium. The germinating spores produce diffusible factors Myc factors- the fungal signaling molecules, which induce symbiosis specific responses in the host root which are perceived by plant roots leading to the transcriptional activation of specific genes even in absence of direct physical contact. The germinated AM fungal spores respond to host plant root exudates by switching to an active pre-symbiotic growth phase, which leads to intense hyphal ramification in the vicinity of root. The active molecules, which cause intense hyphal branching, are strigolactones.

2. Pre-symbiotic phase

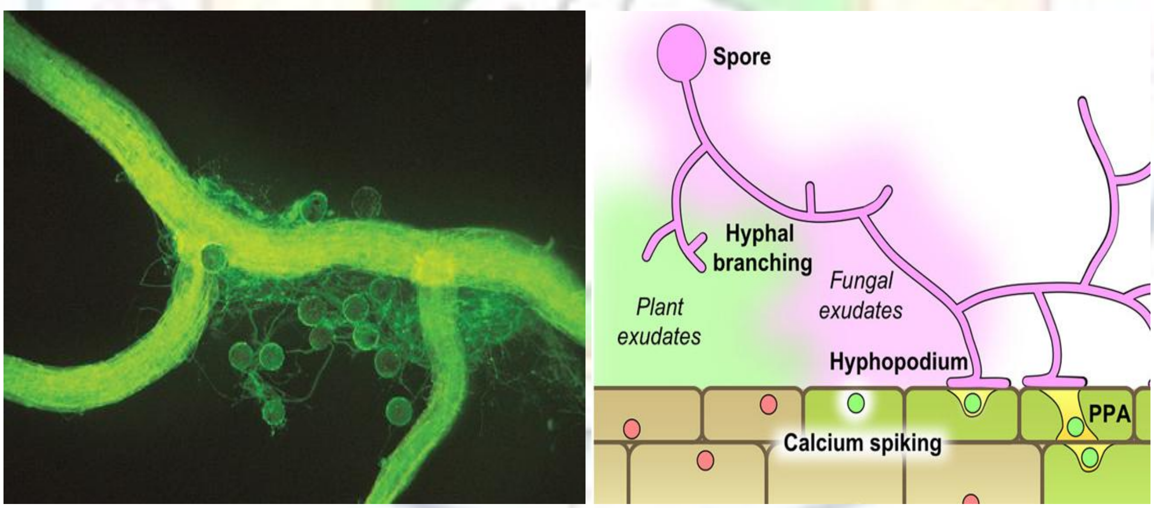
During this phase, the aseptate and coenocytic hyphae develops from the germinating hyphae. Presymbiotic mycelium perceives the presence of host plant by the root exudates. Strigolactones present in the root exudates induce hyphal branching and unusual mitochondrial activity in the fungus. After perceiving the plant signal, AM fungi releases the bioactive molecules with molecular weight less than 3kDa and partially lipophilic.



(a) (b)

Figure: a) Penetration of Epidermal Cells by AM Fungal Hyphae and its Proliferation in Root Cortical Cells; b)Root epidermal cells penetrated by germinating AM fungal spore and production of diffusible factors to establish AM symbiosis

Source:www.soilhealth.segs.uwa.edu.au/components/fungi,http://farm3.static.flickr.com/2544/4133805666_405b54b92d_m_d.jpg



(a) (b)

Figure: (a) Fungal spore coming in contact with root; (b) Spore germinate and fungal mycelium coming in contact with root cells forming appressorium/hyphopodium and PPA.

Source: http://cnx.org/content/m44632/latest/Figure_24_03_04ab.jpg(CC)

3. Symbiotic Phase

This phase includes the formation of appressorium/hyphopodium, organization of prepenetration apparatus, epidermal opening to facilitate penetration of hyphae and formation of arbuscules. The formation of appressoria takes place on the root epidermal cells. After that fungal growth stops for 4-6 h, before new tip growth is initiated to develop the penetration hypha. Penetration of AM fungi through the outermost root tissues of host plant is the critical step during establishment of AM fungi. An assembly of a transient intracellular structure with a novel cytoskeletal organization develops in epidermal cells before infection, which is called as prepenetration apparatus (PPA). PPA is considered as a key cellular factor in AM infection based on following facts;

1) transcellular nuclear migration during PPA assembly always initiates from a position directly below the appressorium.

2) successful hyphal infection always follows transcellular path laid down by PPA.

PPAapparatus plays a very important role in the synthesis of membrane matrix interface that surrounds and isolates the infection hypha from cell cytoplasm when it penetrates the cell lumen.The penetration is characterized by localized production of wall-degrading hydrolytic enzymes by the fungus and by the exertion of hydrostatic pressure by the hyphal tip. During hyphal penetration, the plant actively mediates at least two steps allowing the fungus to penetrate the rhizodermis;

1) anticlinal cell walls of two adjacent epidermal cells separate from each other in the vicinity of fungal hyphae allowing the intercellular passage of the hyphae.

2) fungal hyphae are then allowed to pass intracellularly through an exodermal cell and an adjacent cell from the outermost cortical layer. Thereafter, dichotomously branched tree shaped structures – the **arbuscules** are formed in the cortical cell, separated from the cytoplasm with the help of peri-arbuscular membrane (PAM), which formed by the invagination of plasma membrane and surrounds the arbuscules all over. This leads to increase in the surface area of plasma membrane. A type of apoplastic interface is formed between the plant and fungus by PAM.

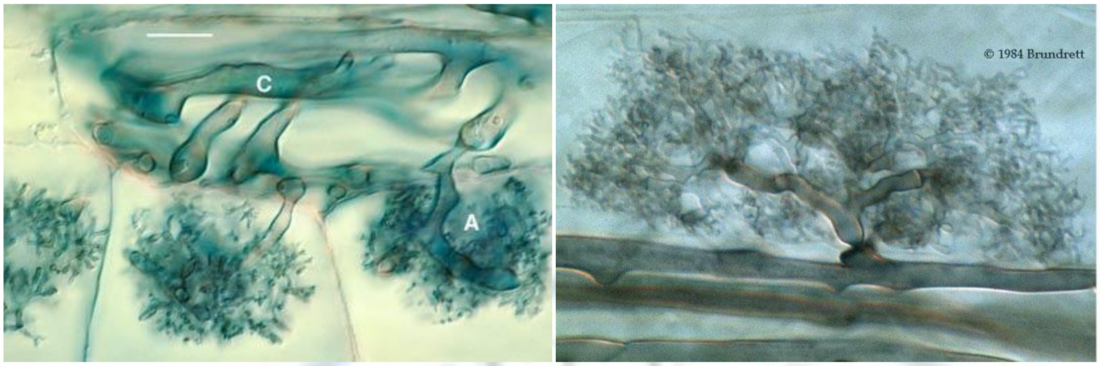


Figure: Development of dicotomously branched arbuscules in the Root Cortical Cells. Source: http://mycorrhizas.info/vam/asarumarb.jpg, http://biology.kenyon.edu/fennessy/SrexMarx/arbgood.jpg

Figure: Different types of AM fungal spores

Source:http://www.omicsonline.org/2161-0517/images/2161-0517-2-116-g006.gif

Benefits of Arbuscular Mycorrhizal Association

1. Absorption of nutrients

Arbuscular mycorrhizal fungi exhibit higher metabolic rate and diffused distribution in the upper soil layers and play a significant role in the uptake and accumulation of minerals from soil and their translocation to the host plant. In fact they serve as a very efficient extension of host root system. They absorbboth macro- (P, N, K and Ca) and micro- (Zn, Cu and Mn) nutrients from soil and translocate them to host. The mineral nutrients like P, Zn, Cu which do not readily diffuse through soil due to their poor diffusion become unavailable to host plant. The extraradical hyphae of AM fungi tend to proliferate several centimeters beyond the nutrient depletion zone, increasing the absorbing surface of host root.AM fungal hyphae extend into the soil penetrating the zone of nutrient depletion and enhance the effective uptake of immobile nutrients therefore, manage the deficiency of such elements in host plant.

Phosphorus (P) is a vital soil nutrient for normal functioning of plant. The deficiency of P in soil may stop normal growth and development of plant. AM symbiosis alters P nutrition of host plant improving growth of host under the conditions of nutrient stress/ deficiency. In nature, P occurs in different forms. Phosphate is the major form of phosphorus available for the uptake by plants. Plants absorb it in the form of trivalent phosphate ions. However, it is readily insoluble in soil solution, therefore, is not readily moving by mass flow. AM fungal hyphae explore more soil volume beyond the root and root hairs zone absorbing additional P, and transport it to the host plant. Further, AM fungi enhance the absorption of mineralized P by degrading and decomposing organic waste matters. Although, micronutrients are required by plants in small quantities but are very important for plant growth and functions, as they are the parts of various enzymes, pigments and other bio-molecules essential for plant life. However, due to rapid development of zone of nutrient depletion around actively growing plant roots, uptakeof micronutrients such as Zn, Cu, Mn, Co from soil solutionby plant is usually limited.However, AM fungi not only expand out of the depletion zone, but also help in the mobilization of soil nutrients and facilitate the host for ready uptake of these nutrients.

2. Protection against pathogens

Plants colonized with AM fungi exhibit increased tolerance against certain root born diseases. Several reports indicate positive effects of AM fungi on root born fungal diseases like wilt and root rot, and stem and leaf born diseases. The severity of nematode infection found to be reduced in the plants colonized with AM fungi. The effects of mycorrhizal fungi on root pathogenic bacteria-*Pseudomonas syringae* and tomato showed significant reduction in damage when plants are exposed to mycorrhizal colonization.Antagonistic interactions between a few AM fungi and microorganisms invading rhizosphere are summarized below.

AM fungi	***Rhizosphere Microorganisms***

Glomus intraradices	*Fusarium oxysporium, Pratylenchus vulnus*
Glomus macrocarpum	*Fusarium sp.*
Glomus mosseae	*Phytophthora nicotianae var. parasitica, Azotobacter chrocococcum*
Glomus intraradices	*Ordium lini*
Glomus fasciculatum	*Pythium ultimum, Phytophthora fragariae, Aphanomyces euteiches*
Glomus sp.	*Verticillium albo-atrium*
Glomus fistulosum	*Meloidogyne hapla*
Glomus sp.	*Rhizoctonia solani*
Glomus etunicatum	*P. fragariae, Rhodopholus similis*
Gigaspora margarita	*Pratylenchus vulnus*
G. manihotis	*Meloidogyne incognita*

Websites for additional information on:
Glomus spp.
http://www.zor.zut.edu.pl/Glomeromycota/Life%20cycle,%20significance%20and%20properties%20of%20AM.html
Gigaspora spp.
http://www.zor.zut.edu.pl/Glomeromycota/Development%20of%20Gigaspora.html

3. Protection against abiotic stress

I. Salinity stress

Due to the effects of high concentrations of salts on availability, uptake, transport or physiological inactivation of a given nutrient, plants are deprived of essential mineral nutrients under saline conditions. AM fungi mitigate adverse effects of salinity stress and improve salt tolerance of host plants by enhancingselective uptake of nutrients and prevention of nutritional disorder, accumulation of osmo-regulators, control of reactive oxygen species and enhanced activities of antioxidant enzymes and molecules, photosynthetic efficiency and structural adaptations.AM fungi prevent ionic imbalancein host plants in saline soils. AM hypha readily extends the fungalcolony and upon perception of signals from the nutrient ions, it produces branchedabsorbing structures or spores, which absorb the nutrients and translocatethem to host. Therefore, under saline conditions mycorrhizal plant can potentiallyaccess nutrients from a larger area than the non-mycorrhizal controls thus, offers huge benefit to host plants byimproving the uptake of essential nutrients. The strategies by which AM fungi benefits plant under saline soilare tabularized below.

Table: Strategies by which AM fungi leading to salt stress tolerance in plants

Strategies	Leads to
Antioxidant production	Protection of plant from oxidative damage
Increased Mg^{2+}/Na^{+} ratio	Maintenance of chlorophyll and thereby improves photosynthesis
High K^{+}/Na^{+} ratio	Improvement in ionic balance
Accumulation of Osmolyte	Reduction of osmotic potential of plant
Increase transpiration rate due to improved Stomatal conductance	Increase in water use efficiency

II. Drought stress

Arbuscular mycorrhizal fungi have the ability to alter plant water status under drought stress. The improved drought tolerance in mycorrhizal plants may be the result from enhanced P nutrition, changes in root hydraulic conductance, soil water relations, increased soil aggregate stability, greater soil available water, and improved stomatal conductance and plant water potential components. Mycorrhiza mediated changes in plant water relations under drought stress conditions may involve complex interactions among multiple mechanisms. However, the primary impact of this symbiosis changes in stomatal conductance and transpiration. Under drought stress, mycorrhizal and nonmycorrhizal plants differentially regulate the expression of several stress related genes in root tissue. Among these,aquaporin genes have been described well under drought stress in mycorrhizal plants. Aquaporins are membrane intrinsic proteins which facilitate water uptake in plant root, following an osmotic gradient.

Moreover, other important mechanisms which are involved in adaptation to drought stress are the induction of genes encoding important component of endoplasmic reticulum –the luminal binding protein. The extrametrical mycelium changes chemical and physical properties of soil, affecting the plant response to drought. Therefore, AM fungal hyphae not only influencing plant response to drought conditions by colonizing root tissue but also by altering the soil properties in which the plant is growing. The colonization of soil by fungal hyphae may influence host behavior and also increase the efficacy of root water absorption in water deficient soil. AM fungi help in managing soil structure – soil aggregate stability which is a crucial soil property and important for sustainable crop production. They release a glycol protein- **Glomalin**, which is long lived in soil and help in managing soil aggregate stability. Because soil aggregate regulates soil water flow, thus, it seems that AM fungal colonization improves the water relations of plants. Improved soil structure has a positive impact on the moisture retention propertiesof soil.Therefore, colonization of soil by AM fungi could change soil retention properties. Glomalin could influence soil carbon storage indirectly by stabilizing soil aggregates, which substantiate the role of mycorrhizal inmaintaining more stable soil aggregates and consequently higher soil moisture.Some of the benefits of AM fungi to plant under droughtstress are tabularized below.

Benefits	**Strategies**
Improved tolerance	• Improved nutrient uptake • Increased chlorophyll concentration • Increased photosynthesis • Increased biomass
Altered water relation	• Stomatal conductance • Transpiration • Water absorption • Improved hydraulic conductivity
Increased in Oxidative stress	• Increased Antioxidant production • Decreased lipid peroxidation • Less membrane damage • Less leakage of ions
Increase in Nitrogen fixation	• Improved nodulation

	• Prevention of nodule senescence
High shoot/root ratio	

III. Heavy Metal

Heavy metals have been found naturally in a variety of habitats including agro-ecosystems, where these elements constitute a potential hazard for soil and plants. However, some of the heavy metals are serving as essential plant micronutrients such as copper, zinc, iron and manganese are required for normal functioning and improved plant growth. On the other hand some of the heavy metals have no known biological functions such as mercury, lead and cadmium but had been reported in plant tissue. Excessive levels of these elements in soil are generally affected normal functioning and growth of plant, therefore, has been considered a serious matter of concern. High concentrations of heavy metals in plant tissues influence the structures of enzymes, consequently affecting the structure of proteins andcell membrane, and also the permeability and functions of plants membranes. Besides, higher accumulation of heavy metals induces oxidative stress, which on the other hand affects plant growth and development.

AM fungi have significantlyalters the uptake and concentration of heavy metals in plant tissues. The role of mycorrhizal fungi in enhancing plant tolerance to heavy metal stress is however, very much dependent on their species, plant genotype and type of the element of the soil. A study conducted on zinc-mycorrhizal fungi interaction where it was reported that zinc is absorbed and crystallized in mycorrhizal hyphae and cortical cells of mycorrhizal roots. However, in spite of increasing knowledge in mycorrhiza-heavy metal interaction little is known about whether there is a synergism between plant and fungal heavy metal tolerance. This area of research needs further attention to prove the role of AM symbiosis under heavy metal stress.

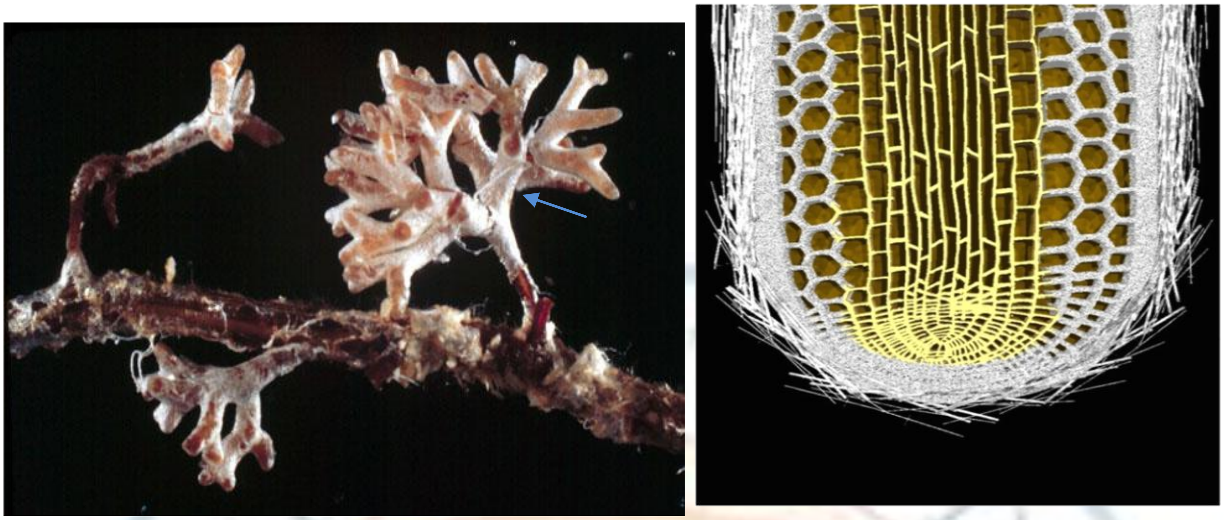
Some of the mechanisms by which AM fungi benefits plant under heavy metal stress are tabularized below

Benefits	**Mechanisms**
Improved tolerance	• Increased biomass • Dilution effect • Less conductance of heavy metals • Improved nutrient status

Increased sequestration • Absorption of heavy metal on fungal hyphae • Binding of heavy metal to fungal cell wall • Sequestration of heavy metal to Glomalin
Transfer of Heavy metal to vacuole • Activation of metal transporters • Increased activity of ABC transporters
Decreased Heavy metal availability • Change in soil pH

Ectomycorrhiza

Ectomycorrhiza (EcM) is the symbiotic association typically formed between the roots of conifers and broadleaved woody plants such as birch, dipterocarp, eucalyptus, oak, pineand fungi belonging to the phylum Ascomycota, Basidiomycota, and Zygomycota. Thousands of ectomycorrhizal fungal species exist, hosted in over 200 genera. In this association, the fungal hyphae form a sheath like covering or mantle on the root surface, increasing the surface area of the roots, with hyphae forming the branching network in the intercellular surface between the epidermis and cortex, known as **Hartig's net**. This association helps in the nutrient and water uptake of host, and in return, obtains carbohydrate from the host plant.



(a) **(b)**

Figure: (a) Short roots coated with white hyphal mat represented shown with an arrow; (b) Digrammatic representation of EcM colonization in plant root

Source: http://upload.wikimedia.org/wikipedia/commons/9/9d/Ectomycorrhizae_001.jpg

Source: http://www.scivit.de/blog/wp-content/uploads/2010/08/quer.jpg

EcM consists of a hyphal sheath, covering the root tip and a Hartig net of hyphae surrounding the plant cells within the root cortex. Outside the root, the fungal mycelium forms an extensive network within the soil and leaf litter. Often the fungal hyphae grow into the root system of adjacent plant and create a new mycorrhizal association, thereby, linking the different plants through a common mycorrhizal network, as has been shown in the figure given below. This mycorrhizal network helps in the movement of nutrients between different plants, and thereby, promotes ecosystem succession.

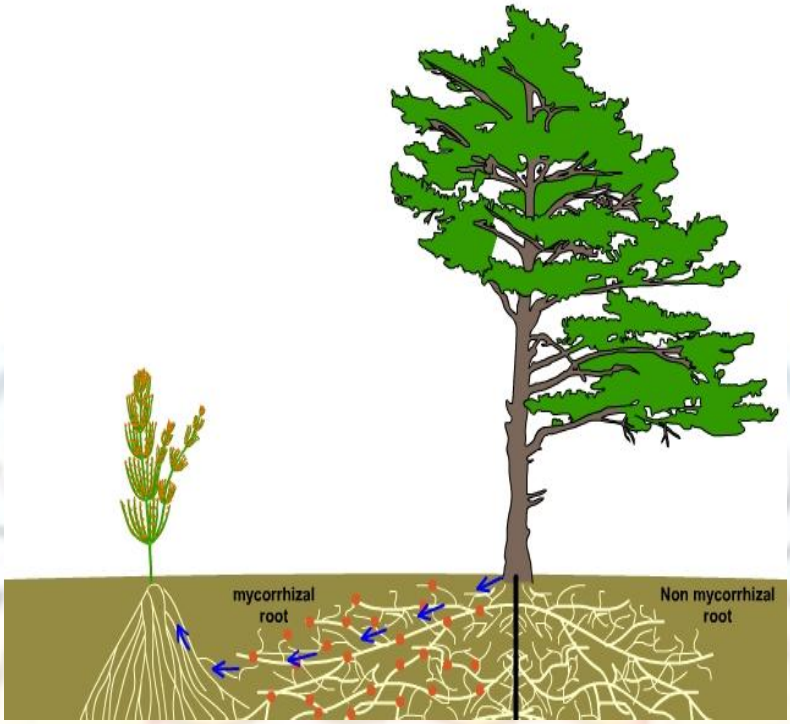


Figure: Establishment of ectomycorrhizal network linking other plant

Source:

Comparing Ectomycorrhiza with Arbuscular Mycorrhiza

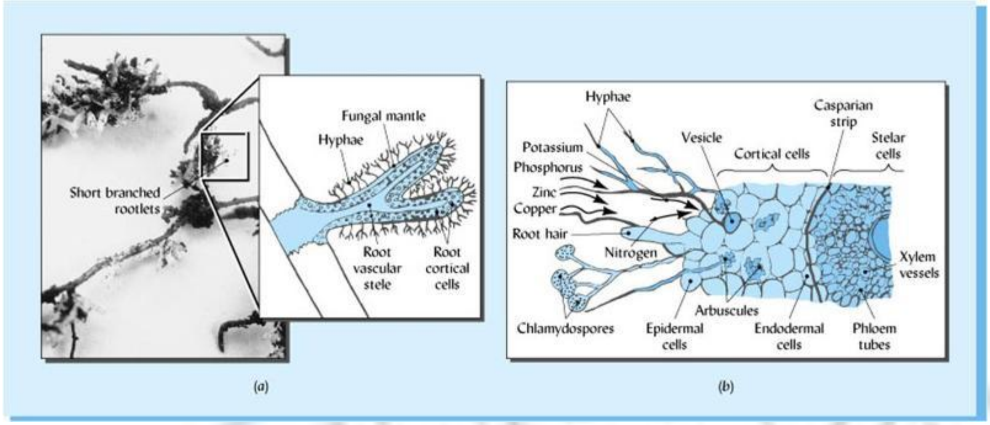


Diagram of ectomycorrhiza and arbuscular mycorrhiza (AM) associations with plant roots. (a) The ectomycorrhiza association produces short branched rootlets that are covered with a fungal mantle, the hyphae of which extend out into the soil and between the plant cells but do not penetrate the cells. (b) In contrast, the AM fungi penetrate not only between cells but into certain cells as well. Within these cells, the fungi form structures known as arbuscules and vesicles. The former transfer nutrients to the plant, and the latter store these nutrients. In both types of association, the host plant provides sugars and other food for the fungi and receives in return essential mineral nutrients that the fungi absorb from the soil.

Source:http://faculty.yc.edu/ycfaculty/ags105/week10/soil_organisms/soil_organisms4.html

The ectomycorrhizal fungal structure associated with root can be distinguished into three parts:

1) Mantle or hyphal sheath

2)Hartig's net

3)Extraradicular hyphae and rhizomorph

1) **Mantle**: Mantle form a interphase between the root and the soil. It is sheath like covering on the outer surface of root, leading to root bifurcation and clustering. Sometimes, they are referred as **pseudoparenchymatous**, as they resemble the parenchymatous tissue of the plant. The active mycorrhizal zone appears several millimeters behind the root tip. In older roots it persists even after the association becomes inactive, and functions as storage structure and propagule. The size, colour and branching pattern of ectomycorrhizal root may vary with the host-fungus interaction.

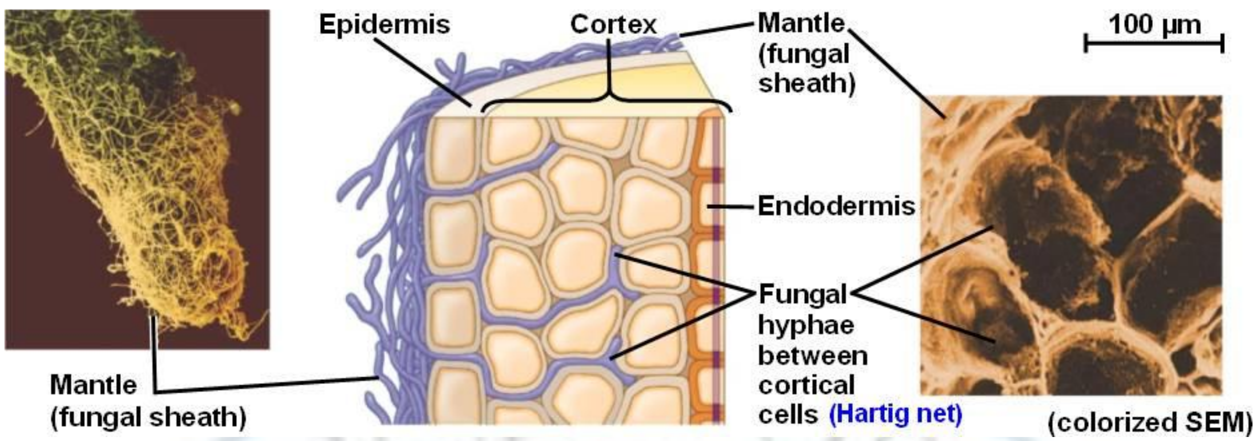


Figure: Colonization of Ectomycorrhiza in plant root

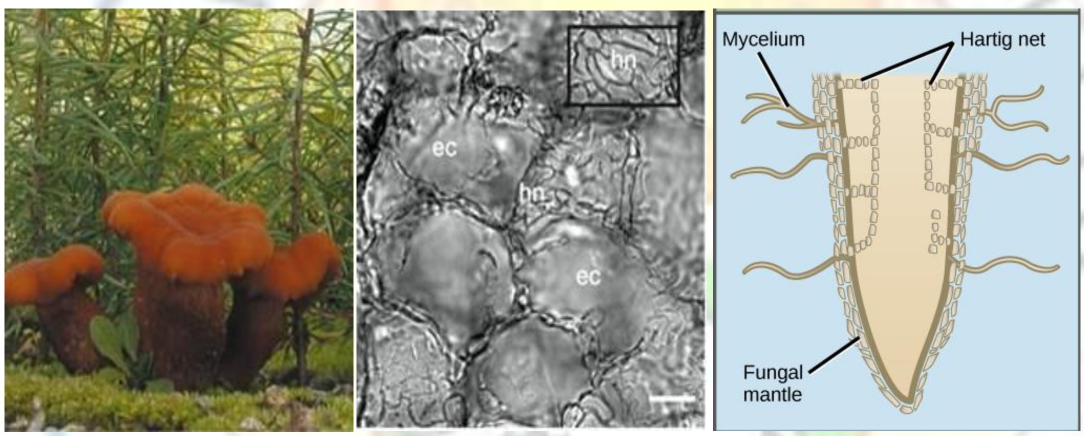
Source:http://upload.wikimedia.org/wikipedia/commons/6/69/Ectomycorrhiza_illustration.jpg

Development: At the time of development of fungal–root association, the fungal hyphae come in contact with the lateral roots, and interact with root hairs, root cap and root epidermal cells. This interaction changes the morphology of fungal hyphae, consequently, altering its diameter and branch repeatedly to form a mat like covering on the surface of root hairs. As the root is covered by mucilaginous polysaccharide, eventually the whole sheath becomes embedded. Hyphae forming the mantle layer may be loosely arranged or compact. Texture of mantle may also vary. It may be smooth, warty, cottony or spiny.

Function: A bi-directional movement of nutrients occurs through the mantle. The fungus absorb glucose from the host cell and convert it into glycogen, mannitol or trehalose, which are either get stored temporary or longer duration in the mantle. The heavy metals present in the soil bind to the polyphosphate deposits present in the mantle, thereby preventing their uptake by the roots. Compact arrangement of hyphae in the mantle also vanishesoff the harmful bacteria from the root surface. There are also certain reports in the literature indicating the association of some useful bacteria with the mantle surface, helping in the N_2 fixation by the plant.

2.Hartig's net: It is a net like structure formed by the growth of fungal hyphae in the cells of plant root. It is named after the forest biologist Robert Hartig. The Hartig net is formed in 2-4 days after the root contact of fungus. In some plant species it develops in the epidermal cells while in others in the cortical cells. The Hartig net is a plexus of fungal hyphae between epidermal and cortical cells. Thefurther development of Hartig net is blocked by the formation of suberized walls of the underlying cells. In *Dyras,* further growth of hartig net is blocked by the formation of Phi (Φ) shaped thickenings of lignin known as Phi-thickenings.

Development: At the time of development of Hartig net the hyphae from the inner layer of mantle, penetrate mechanically, and intrude the middle lamella present between the epidermal and cortical cells. Sometime the process is enhanced by the release of certain hydrolytic enzymes by fungus, which solubilizes the middle lamella. The tubular fungal hyphae are then replaced by multidigitate mode of growth. The complex branching pattern thus formed by the hyphae of the fungus is known as **labyrinthine**, shown in the figure below, which increases the surface area of the fungus, in contact with the root cell for nutrient exchange. The cytoplasm of these hyphae is generally rich in mitochondria for enhanced metabolic activity.



(a)(b) **(c)**

Figure:(a) Fruiting bodies of *L. bicolor* colonizing seedlings of Douglas fir; **(b)**sections of ectomycorrhizae with rectangles show the finger-like, labyrinthine hyphal system (ec: epidermal cell; hn: hartig net); **(c)** Digrammatic representation of Mantle and Hartig's net.

Source:**a,b**http://www.nature.com/nature/journal/v452/n7183/full/nature06556.html ;

Function: Hartig net provides a large surface area for the interchange of nutrients between host and the fungi. Most of the sugar is absorbed through hartig net by the fungus and mineral nutrients and water is passed to the host root. It may also serve as a store house of carbohydarates, lipids, phenolics and polyphosphates.

3) Extraradicle hyphae and rhizomorph: Extraradicular hyphae arise from the outer layer of mantle growing in the soil. They may either grow singly or aggregate together to form a structure known as rhizomorphmeaning "root form". In rhizomorph, extraradicular hyphae develop interconnections with each other. They show tubular structure, with empty core, suggesting its role in the movement of air, water and nutrient to the plant. The peripheral hyphae are thick walled and pigmented, thereby, providing structural support to the rhizomorph. Rhizomorph may vary considerably in their form, colour and internal structure. Some rhizomorph have calcium oxalate ornamentation on their surface, which may vary in size and shape, helping in the identification of fungal specie involved in the association.

Development: The development of extraradicular hyphae has been poorly documented. Extraradicular hyphae arising from the mantle, become thick walled and pigmented, which undergo aggregation and develop interconnection resulting in the formation of rhizomorph.

Function: Extraradicular hyphae are considered as the organ of exploration for the plant. They grow beyond the depletion zone and facilitate the plant to absorb mineral nutrients when nutrients in the surrounding environment get exhausted. Extraradicular hyphae aggregate and form rhizomorph. These rhizomorph serve as a connection enabling the movement of nutrients to the plant system.

Development of Ectomycorrhizal Association in Plant Root

Formation of the symbiotic association between fungi (mycobiont) and plant (phycobiont) is affected by the presence of nutrients like nitrogen and phosphorus, and level of aeration in the soil. High levels of nitrogen and phosphorus, and poor aeration in the soil are known to inhibit the mycobiont development in the soil. Management practice like reducing nitrogen level, and introducing water stress, are generally followed to accelerate the growth of fungal mycelia. The development of EcM symbiosis can be differentiated into following stages:

1. Pre-infection Stage

This is the first stage involved in the development of mycorrhizal infection in root cells. This step is triggered by certain secondary metabolites produced by the plant.These metabolites are not essential in the growth and development of plant but direct the growth of fungal hyphae towards the plant root.

2. Fungal Colonization Stage

Fungal hyphae upon coming in contact with the root, grow inwards to the epidermal cell, and eventually form a mantle layer. As the outer surface of root is covered with mucilage polysaccharide, the whole sheath becomes embedded in it. The remnants of epidermal cells, root hairs and phenolic compounds become incorporated at the interface of the fungal sheath and root surface.

Depending upon the type of symbiont partners involved, either a direct contact between the root epidermal cells and fungal partner may establish or a layer may develop between the two.Once the inner layer of mantle is fully established, the hyphae start penetrating the epidermal cells. EcM,like other symbiotic fungi, also breakdown the wall polymers locally by secreting certain hydrolytic enzymes like cellulase and pectinase. Some plants respond to this, by producing certain pathogenesis-related protein like chitinase and peroxidase; which could inhibit the development of Hartig net. However, these hallmarks of resistance seem to be of short duration, soon the fungus colonizes the root cell and the symbiotic association between the two gets established. Certain EcM are also known to produce certain proteins-the **ectomycorrhizins**, which favor the development of fungal hyphae inside the plant cell.

3. Symbiois Stage

As the hartig net is established in the intercellular region, the exchange of nutrients begins between the two partners. The tip of the hyphae forming the hartig net, accumulate mitochondria and endoplasmic reticulum in large number, suggesting that the transfer of nutrients is localized to this part. The hyphae arising from the mantle are long and grow several centimeters in the soil. They transport water and nutrients to the plant. Besides providing nutritional benefits the mantle layer may exclude nematodes from the root. They also have known to provide tolerance against heavy metal, organic xenobiotics and high salt concentration.

Benefits of Ectomycorrhizal Association

1. Absorption of nutrients

Root proliferation in plants is relatively slow. EcM enhances the plant growth, through improvement in nutrients uptake. The mycorrhizal association increases the surface area of the plant roots, due to which its access to soil resources is increased. Extraradical mycelium also plays a direct role in nutrients mobilization by secreting enzymes, absorption and transport of elite nutrients. They secrete significant quantities of chitinase, phosphatase and protease, which help to dissolve hard to capture nutrients such as organic phosphorus, nitrogen and iron. Most of the EcM are known to secrete acid phosphatase in the mycosphere, which hydrolyse the organic phosphate into orthophosphate.Some ectomycorrhizal fungi produce tuberculate structures, and colonize nitrogen fixing bacteria in these structures, thereby making the nitrogen available for plant growth.

EcM Fungi	**Host Plant**	**Nutrient**	**Reference**
Laccaria laccata	*Picea mariana*	Nitrogen	Abuzinadah and Read, 1986
Paxullus muelleri	*Eucalyptus globulus*	Phosphorus	Burgess et al.,1993
Paxillus involutus	*Pinus sylvestris*	Phosphorus	Colpaert et al.,1999
Scleroderma variegates	*Pinus sylvestris*	Phosphorus	Wallender, 2000
Hebeloma syrejnse	*Salix* hybrid	Nitrogen, Phosphorus	Tibbette and Sanders, 2002
Piloderma sp.	*Picea abies*	Nitrogen, Phosphorus, Pottassium, Calcium	Mahmood et al., 2003

2. Phytoremediation

Phytoremediation include all kind of biological, physical and chemical processes carried out by plants, resulting in the remediation of soil contaminated with pollutants such as heavy metals, salts and organic compounds etc. Compared to conventional techniques, phytoremediation is cheaper and generate useful products such as wood and pulp. Fast growing plants with deep root system and high transpiration rate are generally preferred for this purpose. They are known to produce certain root exudates which enhance the growth of microbial community, and establish the favorableenvironment by altering pH and osmotic potential that stimulate the degradation of toxic compounds. Majority of such trees live in symbiotic association with ectomycorrhizal fungi. *Populus* has been extensively studied for its role in phytoremediation. It forms symbiotic association with more than 60 different ectomycorrhizal fungal species. Ectomycorrhizal symbiosisbetween*Populus*and*Paxillus involutus*have shown two fold increases in cadmium uptake from the soil. Moreover, EcM increases the plant tolerance to heavy metals, and limits its transfer to the shoot. They form a sheath like covering and act as a filter, thereby restricting their movement to root cortex. They also cause their intracellular precipitation and transfer them to the vacuole.

Nevertheless, ectomycorrhizal fungi and their extraradical mycelium increase the surface area for the establishment of microbial communities. Their synergestic, competitive and antagonistic effect, shifts the soil microflora towards those communities capable of degrading the soil pollutants. While some of the saprophytic actinomycetes are capable of degrading the biopolymers, and also known to degrade certain pollutants in the soil like pesticides, hydrocarbon. They are also known to produce certain lignocellulytic enzymes, which enable them to metabolize compounds having structural similarities to lignin and are organic pollutants in nature. *Phanerochaete chrysosporium* produce lignin peroxidase, which enable them to degrade DDT present in the soil.

3. Resistance to biotic stress

Some ectomycorrhizal fungi produce certain compounds, which inhibit the growth of numerous soil borne pathogens. Compact arrangement of hyphae in fungal mantle creates an obstruction to the nematodes attempting to penetrate the root. As they cover the root meristem, they also protect against the pathogenic fungi and bacteria.Studies have shown that the EcM fungi *Boletus* and bacteria like *Bacillus* sp., *Suillus grevillei*, *S. luteus*, *Chromogomphus rutilus* and *Xerochomus* sp. by producing certain non-volatile substances inhibit the development of *Fusarium* sp. *Rhizoctonia solani, Pythium* sp. and *Agrobacterium tumefaciens*. There are many reports on the parasitism of plant root by pathogenic microbes, but optical microscopic studies of EcM showed that their hyphae may adhere on the hyphae of pathogen forming finger like projections leading to parasitism of the disease causing pathogen. Some of the plant pathogens to which EcM show resistance are tabulated below:

Plant	Pathogen/ Disease
Pinus sp.	*Rhizoctonia*
Pinus tabulaeformis	Damping off
Dauglas fir	Bacterial disease of root
Picea sp.	*Fusarium roseum, Pythium* sp. and *Rhizoctonia solani*

4. Resistance to abiotic stress

There are a number of abiotic factors, which affect the plant performance or physiology. First line of defense for the adverse environment conditions is found in plant roots. In the rhizosphere,roots develop a number of positive interactions with different microbes, which help plantto resist the various forms of abiotic stress. Studies have shown that the ectomycorrhizal fungi provide resistant to drought stress in the seedlings of Spruce plant. The EcM association enhances the absorbing area of root surface and improves the soil root contact. Beside, the fungal hyphae can penetrate the soil pore more easily than the root hair, thereby, increasing the access to deep water system.

Another abiotic stress faced by many plants growing in the saline soil.However, EcM symbiosiswith poplar species has been found to improved salt tolerance in salt stress soils. The fungus by changing the concentration of nutrients and phyto-hormones, and ratios of fatty acids, alter the leaf physiology leading to prevent chlorosis and leaf shedding.EcM fungus*Scleroderma bermudense* was able to alleviate salt stressin *Coccoloba uvifera*(seagrape). In the seagrape tissue, there was a decrease in both Na and Cl, but an increase in K and P, implying this trend might represent a mechanism to explain the observed tolerance. Another study in*Boletus edulis* has shown the production of 22 different proteins leading to abiotic stress tolerance.Studies on Gray Poplar (*Populus* X *canescens*) showed that salt-exposed EcM roots showed stronger accumulation of myoinositol, abscisic acid, and salicylic acid and higher K^+-to-Na^+ ratio than stressed nonEcM roots.

Summary

Mycorrhizae are one of the most ancient associations between plant root and filamentous fungi. The fossil record suggests that mycorrhizal association would have been established more than 450 MYA. They are ubiquitous soil fungi distributed in a wide range of habitats. They colonize more than 80 % of land plants, including virtually all plant species of economic importance. So far, seven different types of mycorrhizal fungi have been recognized colonizing bryophytes, pteridophytes, gymnosperms and angiosperms. Amongst them, the most common are endomycorrhizal and ectomycorrhizal fungi. Recently, endomycorrhizal fungi have been placed in a separate phylum- Glomeromycota. These fungi penetrate epidermal cells, reach the root cortex where the develop finger like projection-the arbuscules. They may also develop balloon like structures-the vesicles. The presence of arbuscules and vesicles provide a large surface for nutrient exchange between the host and the invadeing fungus. Ectomycorrhizal fungi belong to the phylum Ascomycota, Basidiomycota and Zygomycota, colonizing largely temperate trees and shrubs, such as pines and beech. They develop a sheathlike covering- the mantle, which helps in bi-directional movement of nutrients and an intercellular network called as Hartig’s net in the intercellular or apoplastic space of rootcortex, which helps in interchange of nutrients between host and the fungi. In addition to improved plant nutrient uptake, mycorrhizal fungi play significant role in alleviation of salt, drought and heavy metal stresses,phytoremediation and protection against diseases.

Glossary

Phytoremediation: Removal or detoxification of unwanted chemicals present in the environment through the use of plants.

Mycelium(a): A branching network of hyphae.

Mycobiont: The fungal component of a symbiotic association.

Arbuscules: Finely branched organ produced by endomycorrhizal fungi inside host root cells involved in the exchange phosphorus and photosynthates.

Ectomycorrhiza: Mycorrhiza in which a dikaryomycotan mycelium ramifies through the soil, forms a mantle around individual rootlets, and grows between cells of the root cortex, forming a Hartig net. Many forest trees, esp. *Pinaceae*, *Fagaceae*, have ectomycorrhizal associations with agarics or boletes.

Endomycorrhiza: Symbiotic association of fungi with green plants; hyphae gathering nutrients from the soil, esp. phosphorus, are continuous with others that grow between and within root cells and produce ARBUSCULES; also called vesicular-arbuscular mycorrhizae.

Hartig's Net: Intercellular hyphal network formed by an ectomycorrhizal fungus in the surface layers of a root.

Hypha (pl. = HYPHAE): The tubular structure found in almost all fungi, its wall chitinous in eumycotan fungi, cellulosic in oomycetes.

Mantle: A compact layer of hyphae enclosing short feeder roots of ectomycorrhizal plants; connected to the Hartig net on the inside, and to the extramatrical hyphae on the outside; acts as a sink for nutrients.

Exercises

1) What are Mycorrhizal Fungi?
2) How do mycorrhizal fungi increase nutrient uptake?
3) Classify the different types of mycorrhizal fungi on the bases of their interaction with the plant roots.
4) Suggest the possible applications of Ectomycorrhiza in controlling biotic stress in plants.
5) Write short note on:
    i. Hartig's Net
    ii. Mycorrhizal association and abiotic stress tolerance in plants
    iii. Phytoremidiation
    iv. Taxonomic position of Endomycorrhiza
    v. Rhizomorph
    vi. Stages involved in the development of mycorrhizal association in plants
6) Does soil already contain mycorrhizal fungi?
7) Define the following:
    i. Labyrinthine
    ii. Phi thickenings
    iii. Extraradicular hyphae
    iv. Mycorrhizal Network
    v. Arbuscules
8) Differentiate between
    I. Ectomycorrhiza and endomycorrhiza
    II. Mycorrhizal root and Nonmycorrhizal root

References/ Bibliography/ Further Reading

1) Hopkins WG and Huner NPA 2009. Introduction to plant physiology (4th edition). John Wiley and Sons, Inc.
2) Taiz L and Zeiger E 2010. Plant physiology (5th edition). Sinauer Associates Inc., Publishers, USA.
3) Smith S E and Read D J. (2008) Mycorrhizal Symbiosis (third Ed.), Academic Press, London.
4) Smith S.E. and. D.J. Read. 1997. Mycorrhizal Symbiosis (second Ed.). Academic Press, San Diego and London.

5) Whipps, J.M. 2000. Microbial Interactions in the Rhizosphere. J. Exp. Botany. V. 52: 487-511.
6) Mukerji KG 1996. Concepts in Mycorrhizal Research. Kluwer Academic Publishers, The Netherlands.
7) Zhang, R.Q. *et*. *al*. 2010. Forest Pathology (on-line) Nov 2013.
8) Bonfante P and Genre A. 2008. Plants and arbuscular mycorrhizal fungi: an evolutionary-developmentalperspective. *Trends Plant Sci.* 13:492–98
9) Pirozynski KA and Malloch DW 1975. The origin of land plants: a matter of mycotropism. *Biosystems*6:153–64.
10) Goto BT, da Silva GA, de Assis DM, Silva DKA, Souza RG, Ferreira ACA, Jobim K, Melo CMA, Viera HEE, Maia LC, Oehl F (2012a) Intraornatospora (Gigasporales), a new family with two new genera and two new species. Mycotaxon 119:117–132
11) Oehl F, Sieverding E, Palenzuela J, Ineichen K, da Silva GA (2011f) Advances in Glomeromycota taxonomy and classification. IMA Fungus 2:191–199.

Web Links

http://link.springer.com/article/10.1007%2Fs00572-013-0486-y/fulltext.html

http://mycorrhizalsymbiotics.com/plantlist

http://www.mcqbiology.com/2012/12/mcq-on-mycorrhiza.html#.UpmBUNIW3K4

http://mycorrhizas.info/

http://www.soilhealth.see.uwa.edu.au/components/fungi

http://web.utk.edu/~htoler/448_assignments/ystudymyc/ystudymyc_introduction.htm

http://www.zor.zut.edu.pl/Glomeromycota/Life%20cycle,%20significance%20and%20properties%20of%20AM.html

http://www.tolweb.org/Glomeromycota