Chapter 2
Mobilization of Micronutrients by Mycorrhizal Fungi

Priyanku Teotia, Manoj Kumar, Ram Prasad, Vivek Kumar, Narendra Tuteja, and Ajit Varma

Abstract Mycorrhizal fungus constitutes heterogeneous fungal taxa embracing an array of plant species. This group is found allied with the roots of beyond 90% of the plant species in this world. There is a range of mycorrhizal associations, among which arbuscular and ectotrophic mycorrhizal interactions are of high biological and economic significance. This chapter gives details about habitation, host range, and structural components of these mycorrhizal groups, along with a meticulous discussion on the mineral absorption, mechanisms involved in different absorption pathways. In addition to enhancement of mineral nutrient uptake by plants in soil, several mycorrhizal fungi execute an important task in mobilizing mineral nutrients from inaccessible organic substrate, mineral particles, and rock surfaces. Mycorrhizal fungi adopt various methods to achieve the purpose effectively, like greater area of absorption for the roots of plant, liberation of biochemical compounds, and consortium with different microbes. Furthermore, mycorrhizal fungi also provide an imperative C sink in soil other than mobilizing nutrients, consequently playing an important role in the cycling of these mineral elements. The role of every partner in a mycorrhizal association is to be exposed by the application of molecular and genetic tools, coupled with high-throughput sequencing and advanced microscopy. The signaling pathways between plants and fungi have recently been elucidated, and recognition of a range of novel nutrient transporters has unveiled a number of cellular processes which are fundamental to the mycorrhizal symbiosis. Various transporters, particularly proton-coupled phosphate transporters, have been documented on both the fungal and plant membranes which contribute to transmission of phosphate from fungi to plants. Even though much work has been formerly done on several aspects, such as symbioses, the extent to which these are functionally essential in agriculture remains uncertain. It is a vital need to spotlight on the questions, whose answers will offer novel perspectives on mycorrhizal utility.

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2.1 Introduction

Even the modest things are vital to the world particularly in relation to getting plants established. Under natural environmental condition, plants remain in close association with soil microorganisms called mycorrhizal fungi. The mycorrhizal fungi inhabit plant roots and extend the root system into the adjoining soil. Unexpected quantities of mycorrhizal filaments are found available in healthy soil. An extremely small section of soil associated with dynamically growing plants may be full of numerous fungal filaments. The affiliation is favorable for the reason that the plants have the benefit of improved uptake of water and mineral nutrient, resistance against diseases, greater survival, and enhanced growth.

The term "mycorrhiza" was coined by the German scientist, A. B. Frank, about a century ago. Factually, word "Mycorrhiza" stands for fungus root; however, it is a symbiotic association existing among a group of soil fungi and the roots of higher plant (Habte 2000). This is a mutualistic organization that depicts the bidirectional interaction and exchange of resources across the mycorrhizal interface. In this association, the mycorrhizal fungus provides the host plant with mineral nutrients, like phosphate and nitrogen, and amplifies the abiotic stress tolerance against conditions of drought, salinity, and heavy metal and biotic stress resistance from various root pathogens, and in return, the host plant transports about 4–20% of its photosynthetic product, i.e., carbon compound to the mycorrhizal fungus (Wright et al. 1998). Records of fossil study indicate that mycorrhizal association commenced about 400–450 million years back, and these mycorrhizal interactions played a significant role in colonization of land by the plants (Smith and Read 2008). Even though mycorrhiza came to light nearly 100 years back, their significance in enhancing plant productivity did not get appropriate credit until past 50 years, until molecular biology got highly developed and gave an insight into the mode of action of mycorrhizal fungi. Presently, numerous scientists around the globe are engaged in study of the mycorrhizal interactions, and any research on plant productivity can hardly be considered as complete, without inclusion of mycorrhizal associations (Habte 2000). About 90% of the identified land plant species formulate mycorrhizal relationship with the ubiquitous fungi in soil (Bonfante and Genre 2010). In dissimilarity with the reciprocal beneficial mycorrhizal association, several mycoheterotrophic plants, nearly 400 species from diverse plant families of bryophytes, pteridophytes, and angiosperms, rely on mycorrhizal fungi to fulfill their carbon need. Such plants lose their photosynthetic efficacy and become parasitic on mycorrhizal fungi coupled with adjacent autotrophic plant (Bücking et al. 2012).

In the following chapter, the main prominence is given to mutually beneficial ectotrophic and arbuscular mycorrhizal associations, since they have great ecological and economic implications (Marschner and Dell 1994). In environmentally sustainable agriculture, arbuscular mycorrhizal fungi can be regarded as "biofertilizer and bioprotector" owing to their capability to colonize and facilitate ample variety of food and cash crops. In contrast, ectomycorrhizal fungi colonize a smaller number of plant species and operate as symbiotic cohort of trees and shrubs; these play a foremost role in the forest ecosystem (Finlay 2008) and could be a fundamental element in phytoremediation as well as revegetation purposes (Bücking 2011; Giri et al. 2005).

2.2 Occurrence and Host Specificity of Mycorrhizal Fungi

AM fungi in general belong to six genera from the class azygosporous zygomycetes. While ectomycorrhizal fungi largely belong to the class basidiomycetes, a few belong to the class zygosporic zygomycetes and ascomycetes. AM are remarkably proficient in mobilizing the inorganic phosphorus (P) and thus prevail well in temperate and arid climates where P is frequently a limiting factor. The AM associations subsist in a large variety of tropical and temperate tree species, as they are not much specific in forming association with the host plant species (Bücking et al. 2002). These associations are known to rarely exist in members of the plants belonging to families Amaranthaceae, Pinaceae, Betulaceae, Brassicaceae, Chenopodiaceae, Cyperaceae, Juncaceae, Proteaceae, and Polygonaceae. As compared to AM, ectomycorrhizal fungi are more efficient in captivating N, and these are more frequent in boreal zone as well as in the temperate zone with high humidity, as the occurrence of low temperature with high humidity promotes the accretion of organic matter, reduced pH, and less N availability (Kilpeläinena et al. 2016). Ectomycorrhizal fungi interact with reasonably lesser section of all plant species, probably just about 3%; however, this 3% embodies almost all of trees of the temperate and boreal forests (especially the plant species of family Fagaceae and Pinaceae); therefore, it can be said that the majority of the forests (in terms of land area) on the surface of earth are dependent on ectomycorrhizal fungi (Habte 2000; Smith and Read 2008; Bonfante and Genre 2010).

2.3 Variation in Structure Among Mycorrhizal Fungi

Mycorrhizal fungi form a variety of associations with the plants; among these, endomycorrhizal association of the arbuscular (AM) type and ectomycorrhizal (ECM) associations have a greater economic and ecological importance. Arbuscular mycorrhizal (AM) and ECM associations differ in their structural aspects as well as the plant and fungal species these embrace (Fig. 2.1 and Table 2.1).

In the ECM, the fungal hyphae infringe the cortex section in the root of the host plant but do not penetrate the cortical cells. The ECM forms hyphal network around cortical cells of the root; this hyphal network is known as the “Hartig Net.” In addition to Hartig net, the ECM also forms a thick layer of hyphal mat on the surface of roots, known as sheath or mantle; this sheath covers feeder roots. Thus,

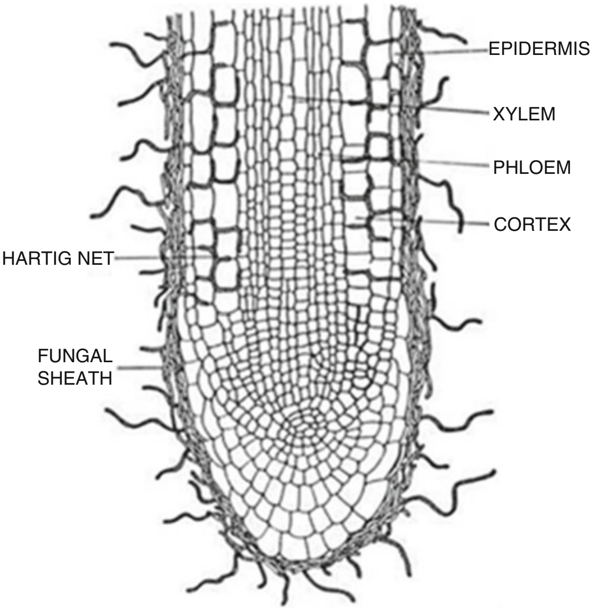

Fig. 2.1 Ectomycorrhizal fungi showing its structure in an infecting root (Source: http://www.biologydiscussion.com/plants/absorption-of-mineral/absorption-of-mineral-salts-by-higher-plant-with-diagram/22764)

Table 2.1 Comparison between AM and ECM associations (Modified after Bücking et al. 2012)

Features	AM fungi association	Ectomycorrhizal fungi association
Transport of nutrients to plant	Specifically important for phosphorus transport, also contribute to nitrogen transport	Specifically important for nitrogen Transport but also have significant Contribution in P transport
Occurrence of fungi	Mainly in warm and dry climates where phosphorus availability is low	Climates with low temperature and high humidity, where nitrogen availability is low
Plant host range	Associates with a very wide range of hosts	Associates with comparatively lower portion of plant species
Type of fungal nutrition	Obligate biotrophophic fungi	Facultative saprotrophytic fungi
Structural elements in fungi	Arbuscules, ERM, and vesicles in some types	Mantle, Hartig net, and ERM
Fungal mode of penetration in host plant	Both inter- and extracellular penetration	Only intercellular penetration
Pathway of nutrient uptake	Both plant and mycorrhizal pathway	Mainly mycorrhizal pathway

they are also known as “sheathing mycorrhiza.” Infectivity of the host plants by ectomycorrhizal fungi generally leads to modification in the feeder roots that can be observed by naked eyes (Genre 2010). The feeder roots inhabited by fungi are thicker, show more branching, and are differently colored as compared to uncolonized roots. Usually, the ectomycorrhizas initiate in between the fine roots and dikaryotic mycelia, which are formed by the union of two different monokaryotic hyphae that germinate from spores. The distinctive fungal sheath or mantle which is composed of aggregated hyphae appends to the surface of roots. This mycelium is correlated to the extramatrical hyphae to facilitate exploration of the substrate; moreover, these are accountable for mineral nutrition mobilization and uptake of water in the symbiotic tissues (Fig. 2.2). “Hartig Net” in the inner zone of the mantle forms an interface where exchange of metabolites takes place. The root cells bounded by fungal hyphae are living; the fungal hyphae are apoplastic but can colonize the epidermal cells as in angiosperms or cortical cell as in gymnosperms (Barker et al. 1998).

In AM or in the fungi, hyphae enter into the cortical cells of the roots and either may produce balloon-like, membrane-bound organelles of diverse shapes, outside or inside the cortical cells, called vesicles, or may constitute finely divided dichotomously branched hyphal invaginations called arbuscules. These structures are supposed to be the site for the exchange of materials among the host plant and fungi. Vesicles, on the other hand, have twin function, they commonly act as storage structure, and lately after they are aged, they function as reproductive structures. The characteristic features of the VA mycorrhizas are vesicles and arbuscules together with large spores. Vesicles are mostly invisible in these types of mycorrhizal associations; therefore, several scientists recommend the use of the term AM, more favorable over the designation vesicular–arbuscular (VA) mycorrhiza. Both AM fungi and ECM fungi expand their hyphae from the root into soil (extraradical hyphae), which are responsible for mobilization of nutrients from soil into the roots (Fig. 2.2).

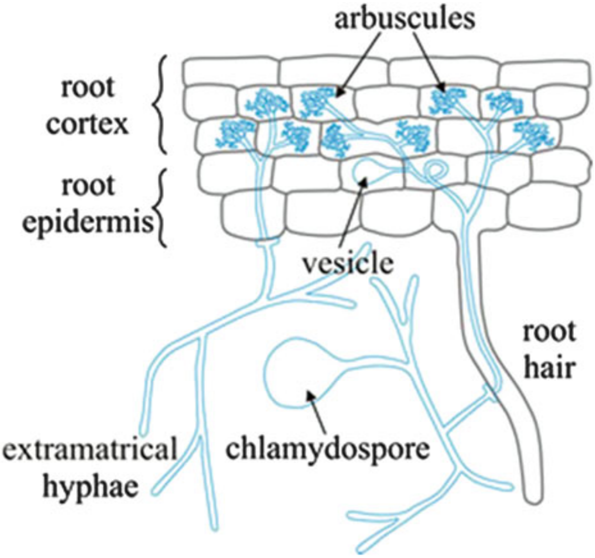

Fig. 2.2 AM fungi showing its structures in infecting root (Adopted from: © http://www.davidmoore.org.uk/assets/mostly_mycology/diane_howarth/am.htm)

2.4 Nutrient Uptake Pathways in Mycorrhizal Roots

There are two pathways *via* which the plants take up nutrients from the soil (Smith et al. 2011). The intake could be either by "plant pathway" that comprises of unmediated uptake of the nutrients by the epidermal cells of the root hairs from the soil or the nutrient uptake by plants can take place through the "mycorrhizal pathway," which consists of nutrient uptake by the extraradical mycelium of its fungal associate which further transfers the nutrients to "Hartig net" in the ECM association, or else to the intraradical mycelium in the AM association, and ultimately to the plant from the interfacial apoplast (Harrison et al. 2002). The nutrient uptake from the soil by means of plant pathway, on the other hand, is consistently constrained by the reduced mobility of nutrients in the soil (Bücking and Kafle 2015). AM and ECM roots diverge in their structural aspects, and this dissimilarity has correlation with their slightly diverse method of nutrient uptake in the AM and ECM plants (Fig. 2.3 and Table 2.2).

The AM roots do not create the fungal sheath and therefore can apparently exploit both the pathways for uptake of nutrient from soil (Bücking et al. 2012). The AM symbionts show a collective mode of the nutrient uptake, which has also been suggested previously (Bücking and Kafle 2015). This led to the supposition that the nutrient uptake through the mycorrhizal pathway can be evaded while availability of nutrient in the soil is excess. Moreover, the plants associated with mycorrhiza do not always show a affirmative growth response. However, such notion has become contentious now (Smith and Read 1997; Smith et al. 2009, 2011), and it has been established that the mycorrhizal pathway can direct the entire P uptake as well as that the factual role of mycorrhizal pathway toward complete P uptake can be "veiled" (Smith et al. 2003; Nagy et al. 2009). The transporters in plants, which are concerned with P uptake by means of plant pathway, are downregulated in reaction to AM symbiosis (Harley and Smith 1983; Chiou et al. 2001; Grunwald et al. 2009); at the same time, mycorrhizal transporters that are particularly involved in the P uptake from mycorrhizal interface are upregulated (Xu et al. 2007; Paszkowski et al. 2002). The total amount of P uptake by common investment of the pathways also depends on plant and the fungal species. Zhang et al. (2015) confirmed that *Rhizophagus irregularis* was more proficient in P absorption as compared to *Acaulospora longula* and *Gigaspora margarita* in *Lotus japonicus*. Grunwald et al. (2009) have established that the *Glomus intraradices* species has the utmost capability to repress the expression of P transporters in plants within the plant pathway; at the same time, *G. mosseae* showed the slightest outcome. This evidence also supports the concept that the positive input of mycorrhizal pathway to the nutrient accessibility is reliant on the effectiveness with which the AM associates interact along with exchange of nutrient across the mycorrhizal interface (Bücking et al. 2012). The suppression of the plant pathway by AM fungi can result in growth reductions in mycorrhizal plants, once the mycorrhizal pathway is unable to reimburse the reduced uptake by the plant pathway (Smith and Smith 2011). The assumption is that the AM fungus can induce the downregulation of the transporters

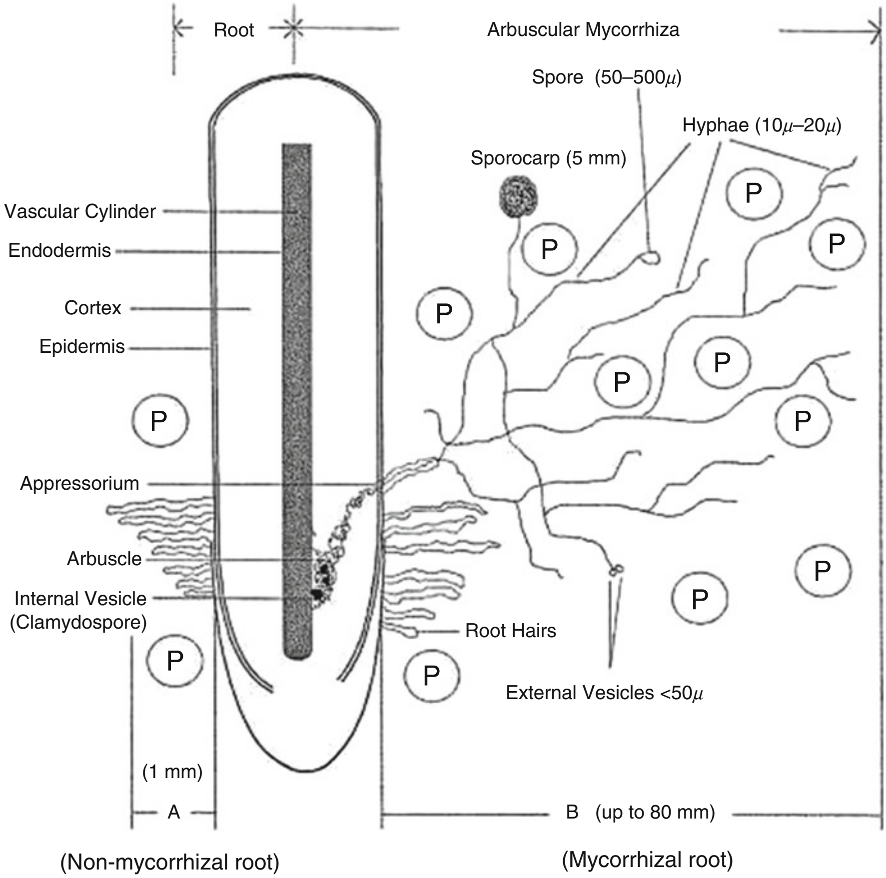

Fig. 2.3 Nutrient uptake pathways in non-mycorrhizal and mycorrhizal roots (Adapted from: Available from: http://dx.doi.org/10.5772/52570)

Table 2.2 Transportation of various nutrients by AM fungi and ectomycorrhizal fungi

Nutrient transported	AM fungi	Ectomycorrhizal fungi
P	+	+
NH_4^+	+	+
Co	+	+
NO_3	–	+
K	+	+
Ca	+	–
SO_4^+	+	–
Cu	+	–
Zn	+	–
Fe	+	+
Mn	+	+
Mg	+	+

of plant pathway to augment its C accessibility. The higher reliance on mycorrhizal pathway for the nutrient acquirement has shown to stimulate the C circulation to root system of the plant (Nielsen et al. 1998; Postma and Lynch 2011).

Of the tree species associated with ectomycorrhiza, most parts of their root surface consist of the region that is nonfunctional in nutrient uptake and the regions that are actively responsible for nutrient acquisition like non-mycorrhizal white or the ECM roots that stand for merely 2 or 16% of the entire root length, correspondingly (Taylor and Peterson 2002). In this condition, the role of the fungal mantle or the sheath that surrounds the root tips is mainly essential (Taylor and Peterson 2005). In a situation, when the fungal layer restricts the infusion of nutrient ions through it, the root tissue lying beneath the fungal mantle would be separated from the nutrient solution in the soil, and such roots will be exclusively reliant upon mycorrhizal pathway for the nutrient acquirement. The ECM fungal species and its structural and functional properties of the mantle are responsible for determining whether the fungal sheath would present an apoplastic barrier or not. Taylor and Peterson (2005) carried out research in relation to the evaluation of permeability of the *Pinus banksiana*/*Hebeloma cylindrosporum* fungal mantle to the berberine and the radioactive sulfate ions. They established that the fungal mantle was absolutely impervious to the tracer dye. Above an exposure period of 24 h to sulfate ions, the fungal mantle still demonstrated to be impermeable. Such outcomes revealed that plant can exceedingly depend on the fungal partner for the supply of mineral nutrients, because there is modest amount of plant tissue which has the ability of nutrient absorption from exterior of fungal mantle. Some other fungi have been shown to release hydrophobins during ECM development (Coelho et al. 2010). Hydrophobin is a diminutive hydrophobic protein that is accountable for clasping of the fungal hyphae to a surface; moreover, it may add to the impermeability of water in the fungal sheath (Unestam 1991; Unestam and Sun 1995). Therefore, only 2% of root surface of the pines is non-mycorrhizal, as well as ERM of the ECM fungus can signify nearly 99% of the nutrient-exchange interface along the length of the roots in pine (Rousseau et al. 1992), ECM-associated tree species like pine are thought to be greatly dependent on their fungal cohort (Ouahmane et al. 2009; Brundrett 2002), and it may be established that the mycorrhizal pathway plays a more significant role for nutrient acquisition in the ECM root systems as compared to the AM root systems (Bücking et al. 2012).

2.5 Possible Mechanisms of Nutrient Acquisition by Mycorrhizal Fungi

Mycorrhizal fungi are capable of absorbing and transporting almost all the 15 essential macro- and micronutrients vital for growth of the plant. Mycorrhizal fungi ooze out strong chemical compounds into the soil that mobilize firm or rock-bound nutrients such as phosphorous, iron, and other “tightly arrested” mineral nutrients in the soil. The entire process of dissolution and transportation of nutrients is of great importance in providing nutrition to the plant, and this requires the consideration of high levels of fertility by the non-mycorrhizal plants for maintaining their health. Mycorrhizal fungi create an elaborate web of hyphae that confines and absorbs nutrients restoring the nutritional assets in soils. In the non-mycorrhizal situation, much of this fertility is exhausted or mislaid from the soil system. Mycorrhizal interactions may directly influence the growth of the host plant through the improvement in nutritional attainment by the fungal associate or obliquely by altering the transpiration rates and constitution of the rhizospheric microflora (Marschner and Dell 1994), mobilization of nutrient from the organic substrates (Finlay 2008), by improving the fertilizer use efficacy (Jeff et al. 2005), or by advantageous alliance with other soil microbes (Finlay 2008).

The two key steps in nutrient absorption from the soil and release of the nutrients through mycorrhizal association involve:

(1) Mobilization and acquisition by the fungal mycelia
(2) Transportation of absorbed nutrients across the fungal–root interface

2.5.1 Mobilization and Absorption of Nutrients

In addition to the hyphae that are in the direct touch with the surface of the root, every mycorrhizal fungi also builds up extramatrical mycelium that extends from surface of infected root into the adjacent soil. Both the fungi, arbuscular mycorrhizal (AM) and ECM, manufacture huge quantity of the extramatrical mycelium. Among these, arbuscular mycorrhizal mycelium extends up to many centimeters from the surface of the infected root while ECM mycelium most likely spreads up to some meters (Goltapeh et al. 2008). In both cases, the mycelium stretches adequately afar from the nutrient depletion zone for inaccessible and bound mineral nutrients around each root; moreover, it also exhibits an intricate structure that provides it with an efficient nutrient gathering network (Schachtman et al. 1998; Bücking and Heyser 2001; Goltapeh et al. 2008). One of the components of mycorrhiza is the extramatrical mycelium that competently exhumes bulk soil for sparse nutrients plus transports obtained nutrients to the fungal–root interface where nutrients are transferred to the host plant (Bücking and Kafle 2015). Many ectomycorrhizal fungi spread extramatrical mycelium in the form of a dispersed mat of the individual hyphae forming intricate linear multi-hyphal arrangement recognized as rhizomorphs. The hyphae that are at the center of rhizomorphs are devoid of cell wall and measure about 35 μm in diameter; these play an important role in the transport of photosynthetic assimilates and inorganic mineral nutrients (Table 2.2). Conversely, diffused hyphae in the disperse mat that grow in front of the arbuscular mycorrhizas that measure nearly diameter 1–5 μm in diameter make available a widespread surface area for the absorption of nutrient from the soil. At the same time, hyphae with larger diameter of up to 10 μm are liable for an exceptional translocatory infrastructure for efficient transfer of solutes from the bulk soil from the rhizospheric soil to the surface of root (Ravnskov and Jakobsen 1995). Other than increasing uptake of mineral nutrients by the plant, which are previously there in soil, numerous mycorrhizal fungi could perhaps perform a major function in mobilization of the mineral nutrients from the organic substrate (Hodge and Fitter 2010), mineral element, or else cover rock surfaces (Finlay and Rosling 2006).

Several mycorrhizal fungi can possibly perform an important task in the mobilization of nutrients, for example, nitrogen and phosphorus from the structural or any other polymers that are, however, inaccessible to the plant roots. Withdrawal of nutrients like N and P by means of mycorrhizal fungi from a variety of organic substrates like saprotrophic mycelia (Lindahl et al. 1999), dead and decaying nematodes (Perez-Moreno and Read 2001b), pollen grains (Perez-Moreno and Read 2001a; Finlay 2008), and *Collembola* (Klironomos and Hart 2001) has been verified by many researchers. The association of mycorrhizal fungus in the microbe-based mobilization and immobilization cycle leads to mobilization of the N and the P from plant litter, microfaunal, mesofaunal, and microbe base, permitting the unique plant commune to flourish alongside the altitudinal or the latitudinal ascent (Smith et al. 2003, 2009).

The ectomycorrhizal fungi that inhabit boreal forest ecosystems are the appropriate example of events like mobilization and transportation of nutrients. In such ecosystems, N and P are present in the organic form that is not easily available for utilization by the autotrophs. In these forests, the foremost plant species are significantly dependent on the mycorrhizal symbionts to gratify their nutritional requirements. Ectomycorrhizal symbiont has the capability to immediately act on the structural polymers that might be a cause for nutrient unavailability and in the mobilization of N as well as P from organic polymers (Read and Perez-Moreno 2003). Lindahl et al. (2007) observed that the saprotrophic microbes and fungi produce a harmonized assembly of debris-degrading enzymes that are essential for early phase of decomposition process; in addition, the N mobilized by such saprotrophic fungi is reserved in their mycelia. With the fall of C:N ratio in the decomposed organic matter, the saprotrophs contemplate to be less vigorous with respect to mycorrhizal species that directly receive the host assimilates (Hodge et al. 2000). The occurrence of ectomycorrhizal fungi in the finely degraded litter along with humus presents signal that the mycorrhizal hyphae play a substantial role in the mobilization of N from well-degraded organic waste in the boreal forest soils. Moreover, the unsteady carbon librated in the soil *via* roots and allied mycorrhizal fungi could play a crucial role to mobilize N. The production of extracellular enzymes such as proteinases and peptidases by ectomycorrhizal fungi enables them to competently hydrolyze the organic nitrogen resource to liberate amino acids; these can be taken up by fungi. Also, the secretion of extracellular phosphomonoesterase and phosphodiesterase enzymes by Ectomycorrhizal fungi enables to mobilize mineral nutrients in the soil. The enzyme phosphodiesterase is capable of mobilizing phosphorus, which is confiscated inside nucleic acids. Several ectomycorrhizal fungi also produce enzymes which are hydrolytic in action; these fall within the family of cellulase, hemicellulase, or lignase. The enzymes support the entry of hyphae into the dead and decaying organic matter in the soil and get in touch with the mineral nutrients seized within. In this way, the ectomycorrhizal fungi condense the typical mineral nutrient cycles, releasing nutrients seized within the organic matter of the soil. There are reports that suggest that the Ectomycorrhizal fungi are capable of siderophores production, which bind and form complexes with iron and oxalate that amplify potassium uptake by the symbiont. Production of reducing agents by the ectomycorrhizal fungi magnifies the acquisition of ions from then stable oxides like MnO_2, consequently serving in enhanced plant nutrition (Lindahl et al. 2001, 2007).

The strict biotrophic character of AM fungi suggests that such fungi are unable to utilize organic nitrogen sources (Bücking and Kafle 2015); nevertheless, a number of studies reveal that the hyphae of AM fungi develop on the organic matter and relocate nitrogen to its host plant (Leigh et al. 2009; Hodge and Fitter 2010), which results in elevated plant nitrogen content in the mycorrhizal plants (Thirkell et al. 2015). Reynolds et al. (2005) established that there is no confirmation about the promotion of plant N acquisition by AM fungi and the better growth of old field perennial trees under low N supply situation; however, AM fungi could be associated with the decomposing organic material in several ecosystems. While Hodge et al. (2001) verified the improved decomposition and N mobilization from dead and decaying grass foliage in the existence of AM fungi, Leigh et al. (2009) established that AM fungi did not exhibit saprophytic competence and the fungus captures N from organic matter almost certainly as the product of decomposition. Though AM fungus speeds up the N absorptions from organic substance (Atul-Nayyar et al. 2009) and manipulates the C exchange within the soil microbe population during the decomposition process (Herman et al. 2012), advanced research is still required to discriminate between direct competence of AM fungi to mobilize organic material along with their probable, indirect consequence on putrefaction and nutrient uptake by plant, which occurs by stimulation by decomposers and followed by uptake of the decomposed products by the mycorrhizal fungus (Li et al. 2006; Finlay 2008).

In addition to the organic matter, mycorrhizal fungi are also accountable for dynamically mobilizing nutrients from the mineral particles and the rock surfaces by means of weathering; this may occur either by mycorrhizal fungi alone or in alliance with other microbes like bacteria or any other fungi (Wallander et al. 1997; Landeweert et al. 2001; Finlay and Rosling 2006; Finlay 2008). The role of arbuscular mycorrhizal (AM) fungi in mineral/rock weathering is contradictory; moreover, there are barely few verifications that suggest improved consumption of comparatively insoluble type of inorganic phosphorus like rock phosphate by the AM fungi. Such effects may perhaps depend on synergistic association among AM fungi and the P solubilizing microbial community. Wallander (2006) confirmed the vital contribution of mycorrhizal fungi in mineral weathering of forest soils. Reports suggest that Ectomycorrhizal fungi produce certain low-molecular-weight (LMW) organic acids, which are utilized in weathering of the minerals rocks

(Ahonen-Jonnarth et al. 2000). Breemen et al. (2000) reported that several open tubular apertures of about 3–10 μm in size were existing in the weatherable minerals in every podzol surface soil and the shallow granitic rock under European coniferous forests, and they suggested that these pores were created by complexing LMW organic acids, which leach out in association with mycorrhizal fungi. The hyphae of ectomycorrhizal fungi penetrate and, perhaps, generate microsites that are otherwise far from the contact of the plant roots and inaccessible from the bulk soil solution. The mobilized and dissolved nutrients can be further carried to roots of the host plant, shunning soil solution with the frequently toxic concentrations of the $A1^{3+}$ ions from the acid rain (Clark 1997), and also avoiding antagonism for uptake of nutrient with other microorganisms.

2.5.2 Movement of Carbon and Nutrients Across the Fungus–Root Interface

Whatsoever the form of mycorrhizal fungi is or the approach they take up for mobilization of the nutrients, these ultimately reach at the fungal–root interface within symplasm of fungus. The transfer of nutrients to the host plant engrosses the efflux of mineral ions through plasma membrane of fungus followed by the inclusion from apoplasm interface across the plasma membrane of the cells of host root (Cairney and Burke 1996). Escape of the nutrient substances across the interface is lowered by complex fungal arrangements.

It has been suggested that the local physiochemical conditions are directed by the series of events occurring in either of the symbionts in an association. This includes accumulation of impermeable extracellular resources between mycelium within the mantle in several ectomycorrhiza and on the tip of the hyphal ingress into root cells in the arbuscular mycorrhiza. Ectomycorrhizas produce an explicit apoplasmic compartment, which averts surfeit of the nutrients from interface apoplasm. The carbon required for growth and metabolism of the mycorrhizal fungi is largely acquired as photoassimilate from the roots of the host plant (Smith and Read 2008; Bonfante and Genre 2010). In distinction to ericoid mycorrhizal fungi and phytopathogenic fungi, arbuscular mycorrhizal (AM) and ectomycorrhizal fungi (ECM) are unable to utilize sucrose as a source of carbon, and therefore they seize on simple sugars like glucose and fructose, from mycorrhizal interface. The fungal genome contains invertase gene, which is associated with its mode of nutrition, and in divergence to various plant-allied fungi, like pathogenic fungi and endophytic fungi, there does not exist any proposal that confirms the presence of invertase genes in AM or ECM fungi (Parrent et al. 2009; Bonfante and Genre 2010; Wahl et al. 2010) or else holding invertase activity (Salzer and Hager 1996). As a result, mycorrhizal fungus depends on host cell for its invertase activity, specifically in the region of interfacial apoplast, in favor of sucrose hydrolysis. This hydrolysis of sucrose makes simple sugars such as hexoses, glucose, or fructose, available for fungal utilization. Further, the reports suggest that the glucose is mostly engrossed by the hyphae of "Hartig net" while fructose is largely taken up by the hyphae present in the inner layers of mantle (Nehls et al. 2002). Numerous carriers have been recognized that are present uniformly on plant and the fungal membranes, which are mainly responsible for transporting nutrients from the fungal to plant cell. In perspective of the ECM relationship, the transporter AmAMT2 of *Amanita muscaria* has high affinity for NH4+ ions. This importer is induced in extraradical mycelium, while it is downregulated in fungal sheath and "Hartig net" (Willmann et al. 2007, Martin and Nehls 2009). The good expression of AmAMT2 transporter in ERM implies a high competence of ERM for uptake of NH4+ ions. On the other hand, the reduced level of expression in "Hartig net" specifies that NH4+ ions serve as imminent nitrogen source, which is transported by mycorrhizal fungus to the roots of host plant. The reduced level of expression of the NH4+ importer in "Hartig net" reduces the reabsorption of the NH4+ in the fungual hyphae from interfacial apoplastic zone along with rise of the total NH4+ transport to the host. The existence of upregulated high-affinity NH4+ importers of plant in ECM roots also supports the transport of NH4+ across the ECM interface (Selle et al. 2005; Couturier et al. 2007). A study conducted on the rice and *Medicago truncatula* by Wang and Qiu (2006) suggested that the transporter enzymes in plasma membrane, proton-ATPases (H+-ATPase), are specifically upregulated in arbuscule enclosing cells, and these are requisite for the improved proton pumping action in the membrane vesicles of AM colonized roots (Harrison et al. 2002). Any alteration in the regulation and function of H+-ATPase decreases the arbuscule size and diminutive uptake of nutrients by the host plant via mycorrhizal symbiosis. Overexpression of the gene regulating H+-ATPase Os-HA1 improved the phosphate uptake and the plasma membrane efficacy, indicating that the H+-ATPase performs a significant role stimulating peri-arbuscular membrane, so as to facilitate the nutrient exchange in plant cells having arbuscule. A high-affinity phosphate (P) transporter, Pt4, is entirely manifested in the mycorrhizal roots; besides, it is concerned with the getting hold of the P delivered *via* the fungus (Xu et al. 2007). Another transporter, AMT2;2, is a high-affinity ammonium transporter, which is positioned in peri-arbuscular membrane (Guether et al. 2009). Furthermore, the occurrence of mycorrhizal induced sulfate transporters in the AM roots proposes that the sulfate too is transferred across the mycorrhizal interface from AM fungus to host plant (Casieri et al. 2012; Allen and Shachar-Hill 2009; Helber et al. 2011).

2.6 Conclusions

A greater fraction of the higher plants are found to be allied with the Mycorrhizal fungi. These symbiotic interactions differ extensively in their structures as well as functions. Of the numerous kinds of mycorrhizal fungi, Arbuscular mycorrhizal (AM) and ECM fungi play an important role in nature. Both the categories of mycorrhizal fungi not merely assist in uptake of the major plant nutrients such as P and N but also help in captivating other micronutrients like Fe, Cu, Zn, etc. Mycorrhizal fungi implement various means to achieve the task effectively: measuring the greater absorbing surface area of the plants, releasing biochemical compounds along with alliance with other microbes in its ambience. Other than mobilizing the mineral nutrients, mycorrhizal fungi also provide significant C sink in soil; hence, these have a critical impact on cycling of the elements within soil. Consequently, mycorrhiza is established as a significant association for nutrient management in the ecosystem.

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