

## **Ecological Functions of Ectomycorrhizal Fungi**

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### **Abstract**

Ectomycorrhizae are considered as an integral component of the biology and ecology of soil that has a significant impact on the growth and absorption of nutrients and protection against diseases. ECM fungi are considered as an integral part of plant physiology and play a key role in plant adaptation to specific environmental conditions. This fungus gains carbon and other essential organic substances from the tree and in return helps the trees take up water, mineral salts and metabolites. It also fights off parasites, predators such as nematodes and soil pathogens. Most of the forest trees are highly dependent on their fungal partners especially in areas of poor soil. This association is supposed to be valuable for alleviating nutritional status for both plant and fungi hence is ecologically an important association. The present paper is an attempt to review the ecological functions of ectomycorrhizae.

**Keywords:** Ectomycorrhizae, nutrient cycling, soil microorganisms, forest ecosystems

### **Introduction**

The roots of terrestrial plants are colonized by mycorrhizae forming symbiotic fungi (Marschner and Timonen, 2005). However taxa belonging to families such as Brassicaceae, Caryophyllaceae, Cyperaceae and Juncaceae are largely non mycorrhizal (Peat and Filter, 1993). Mycorrhizae can be categorized into seven main groups according to their morphology and on the basis of the fungal and the plant taxa forming the symbiosis (Brundrett, 2004). Of these ectomycorrhizae (ECM) are considered an ecological guild distinguished by their stable biotrophic association with the roots of woody plants and the production of macroscopic sporocarps (Luoma *et al.*, 1991). Ectomycorrhizae (ECM) is an association of fungus and feeder roots (root tips) in which the fungus grows predominantly intercellularly in cortical region penetrating the epidermis by secreting proteolytic enzymes and develops extensively outside the root forming a network of hyphae called as mantle which is of variable thickness and color. There is an intercellular infection forming a network of fungal mycelium around the cortical cells called Hartig net (Sandeep *et al.*, 2015).

Worldwide an estimated 5400 species of fungi form ectomycorrhizal associations with the most dominant woody plant families like Betulaceae, Fagaceae, Pinaceae, Myrtaceae (Molina *et al.*, 1992). These fungi account for 25% or more of the root mass of forests, thus representing a major below ground structural component of forest ecosystems (Pande *et al.*, 2004). Present paper is an attempt to review the major ecological functions of these Ectomycorrhizal fungi.

### **Nutrient cycling**

Mycorrhizal fungi are major components of nutrient cycling in most of vegetation types. The cycling of nutrients is complex and involves numerous organisms performing processes such as the decomposition of organic and

complex inorganic compounds, the release and assimilation of inorganic minerals and the transport and transfer of these nutrients to host plants. ECM fungi play a primary role within this cycle, supplying nutrients to the host plant outside the depletion zone or mobilizing otherwise inaccessible complex/organic nutrient forms. There is evidence from studies along a north-south transect through Europe (Taylor *et al.*, 2000) that both the proteolytic capabilities and the biodiversity of ECM fungal communities are greater in raw humus soils of northern boreal forests, where nitrification is undetectable, than in more southerly locations where mineral N enrichment occurs, either as a result of natural or anthropogenic inputs.

ECM fungi are known to assimilate nutrients from a range of different sources. Plant litter is a rich source of organic nutrients for which a number of soil organisms, including ECM fungi compete. Within boreal and managed plantation systems, ECM fungi are particularly relevant in the decomposition and release of nutrients from the litter layer. A study by Dames *et al.*, (1998) in South Africa demonstrated the over-accumulation of litter in high altitude *Pinus patula* stands. Furthermore, the results indicate a build-up of immobilized nutrients of N and P and the major cations K, Ca and Mg. It was concluded that litter accumulation was not a result of increased litter production, but rather attributed to low levels of decomposition by organisms such as ECM fungi. Litter/organic decomposition rely heavily on rhizosphere microbial activity and this process is compromised when soil conditions, such as pH, are not optimal for microbial growth.

Decomposition of organic material by saprotrophic microorganisms creates a pool of mineral nutrients that can also be assimilated by ECM fungi. Rock weathering properties of ECM fungi provide direct access to nutrients, providing the ECM plants with a nutritional advantage. ECM host plants have a competitive advantage in terms of nutrient assimilation, as ECM fungi are able to by-pass the traditional nutrient cycle, absorbing nutrients directly from the litter layer without first having to be degraded by saprotrophic organisms (Van Breeman *et al.*, 2000).

Organic matter present in the rhizosphere is derived from plant litter. Both saprotrophic and ECM fungi are able to decompose the organically bound nutrients. Saprotrophic fungi release mineral nutrients into the nutrient pool and mineral nutrients ECM fungi assimilate these nutrients. Nutrient transfer occurs between the two groups of fungi and exudates of soil borne organisms and dead organic matter are the source of organic nutrients. Uncolonized plant roots are able to take up nutrients independently from the pool but are dependent on ECM to gain access to nutrients outside depletion zones.

### **ECM interaction with soil micro-organisms**

Mycorrhizae are thought to potentially have both positive and negative effects on other soil micro-organisms. The ectomycorrhizal mutualism involves interactions with soil microbes as well as with plants. It has been observed that certain bacteria associate with ectomycorrhizae and directly encourage the establishment of mycorrhizal associations. Bacteria known to assist mycorrhizal development are given the general descriptor "mycorrhizal helper bacterium" (Chen *et al.*, 2003; Frey-Klett *et al.*, 1999; Duponnois and Plenchette, 2003). These and other bacteria often associate with the sporocarp (fruiting body) tissue as well as the hyphae (Danell *et al.*, 1993). In a study of the bacterial flora of the ectomycorrhizal fungus *Suillus grevillei* sporocarps, the presence of twenty-seven distinct culturable bacteria species were revealed, the most prevalent genera being *Pseudomonas*, *Bacillus* and *Streptomyces*. Further dual-culture experimentation involving the bacteria isolates and *S. grevillei* showed that the *Pseudomonas* isolates tended to be "helper bacterium." The *Bacillus* strains tend to have little or no effect on the fungus, although some studies have shown them to promote plant growth independently of any interactions with mycorrhizae (Chanway *et al.*, 1996), while *Streptomyces* tended to inhibit the fungus (Luppi-Mosca *et al.*, 1996). Similar observations have been made in a study where bacteria were incorporated in an ectomycorrhizal fungi *Tuber borchii* (Sbrana *et al.*, 2002). Danell *et al.* (1993) suggests that bacterial presence within sporocarps may be incidental and although this was not addressed in the Luppi-Mosca *et al.* (1996) study it would be a logical

explanation for the presence of inhibitory microbes. According to some workers (Hildebrandt *et al.*, 2002; Chen *et al.*, 2003; Parks and Schmitt, 1997) other forms of mycorrhizal symbiosis are affected by various bacteria-mycobiont interactions. Garbaye (1994) suggested that mycorrhizal helper bacteria stimulate ECM fungal germination and enhance ECM formation. Mycorrhizal helper bacteria are also thought to enhance the breakdown of organic nutrients by secreting digestive acids and oxalates, breaking down organic N and C in the soil (Garbaye, 1994). Bacteria have also been identified as possible components of mineral rock weathering associated with ECM (Van Breeman *et al.*, 2000). Saprotrophic and ECM fungi compete for organic nutrient resources in the litter layer. Gadgil and Gadgil (1975) highlighted the importance of the existence of both mycorrhizal and saprotrophic fungi in forest biomes. They demonstrated that there was a decrease in litter decomposition when both trophic groups were present and suggested that this was due to competitive antagonism. Leake *et al.*, (2001), showed antagonistic interaction in microcosms between *Phanerochaete velutina* and *Suillus bovinus* and correlated the interaction with a reduced carbon pulse from the plant to the growing region of the mycelium. This implies a resultant dysfunctional ECM association where normal nutrient exchange is not occurring (Cairney and Meharg, 2002). Lindahl *et al.*, (2001) showed competitive sequestration of phosphorus between a saprotroph, *Hypholoma fasciculare* and an ECM fungus, *Suillus variegatus* and concluded that the potential for either fungus to out-compete depended on the carbon source available to either competitor. ECM fungi are also strong competitors with soil-borne root parasites. The antagonistic modes are both mechanical and biochemical. In the mechanical mode, ECM fungi compete for colonization space in the root and create physical barriers, such as the mantle (Marx, 1973). The biochemical mode involves antifungal compounds released by ECM fungi, as found by Kope *et al.* (1991) in *Pisolithus arrhizus* that suppress pathogenic growth and sporulation. Sen (2001) showed an inhibitory effect of *Suillus bovinus* in association with *Pinus sylvestris* against colonization of pathogenic uninucleate *Rhizoctonia* species. The same inhibitory effects were not observed when the plant host was inoculated with *Paxillus involutus* and *Wilcoxina mikolae*, indicating differences between species in protecting host plants from pathogenic infection. Sen (2001) also found associated *Bacillus* species with *S. bovinus*, suggesting a combined effort of both bacteria and ECM fungi to protect the plant host. The MHB effect has been reported for *Pseudomonas* spp., *Bacillus* spp., *Burkholderia* sp. and *Collimona* species (Garbaye and Duponnois, 1992; Aspray *et al.*, 2006 a, b; Izumi *et al.* 2006; Barbieri *et al.*, 2007; Frey-Klett *et al.*, 2007; Offre *et al.*, 2006). A new mycorrhizal helper bacterium, *Ralstonia* sp., promoting the ectomycorrhizal symbiosis between *Pinus thunbergii* and *Suillus granulatus*, was reported by Kataoka and Futai (2008). *Ralstonia* sp. enhanced hyphal growth of *Suillus granulatus* without cell contact between the mycorrhizal fungus and bacteria, probably because it secreted diffusible substances. This confirms earlier report of Duponnois and Plenchette (2003), who also found no significant correlation between the effect of *Pseudomonas monteilii* strain HR13 on fungal growth under in vitro conditions and mycorrhiza formation presumably due to involvement of different mechanisms in the two processes (Duponnois and Plenchette 2003; Bending *et al.* 2002).

Alternatively, Olsson *et al.*, (1996) found inhibitory effects on bacterial activity in the presence of ECM fungi such as *Paxillus involutus*, *Laccaria bicolor*, *Thelephora terrestris*, *Laccaria proxima*, *Suillus variegatus* and *Hebeloma crustuliniforme*. Bacterial activity was recorded by measuring the incorporation of thymidine. Reduced uptake is probably a result of fungal antibiotic production and competition for limited nutrient resources (Cairney and Meharg, 2002). Contrasting these results, Olsson and Wallander (1998) demonstrated stimulatory effects of *Suillus variegatus* on bacterial activity with amended soil containing biotite nutrient additions. The resultant stimulation/inhibition of bacterial activity as a direct consequence of the nutrient content of the soil supports the argument for potential competition for resources. Olsson and Wallander (1998) also noted effects of ECM fungi on the community structure of the bacteria in close proximity to the host plant roots. To identify the bacteria found associated with ECM fungi, Bowen and Theodorou (1979) isolates from roots of *Pinus radiata* were cultured.

These included three *Pseudomonas*-type and four *Bacillus* species. The study found a reduction of ECM colonization of between 42-100% in the presence of these bacteria.

### **Role of ECM in forest ecosystems**

Forest ecosystems are functionally and structurally highly organized systems of biotic and abiotic components, linked into a sensitive dynamic equilibrium (Kraigher, 1999). Being the most common type of mycorrhizae, ectomycorrhizal fungi (EMC) have the most important associations with forest trees (Horton *et al.*, 1999; Agarwal and Sah, 2009). They are facultative biotrophs belonging to division of Dikaryomycota, Basidiomycetes and some to Ascomycetes. They are usually found in temperate forests (where soils are used as storage compartments) and sub-temperate forests, but also in boreal, and sub-tropical forests, where Myrtaceae, as well as tropical forest trees can be found (Molina *et al.*, 1992; Wang and Qiu, 2006; He *et al.*, 2009). The abundance of ECM species belonging to Basidiomycetes, namely Hymenomycetes include *Boletus*, *Corinarius*, *Suillus*, *Russula*, *Gomphredries*, *Hebelema*, *Tricholoma*, *Laccaria*, and *Lactarius* and species of Gasteromycetes, e.g. *Rhizopogen*, *Scleroderma*, *Alpara*, and *Pisolithus* all form ectomycorrhizae makes ECM very important in forest ecosystems (Agarwal and Sah, 2009). ECM occurs in the trees like *Pinus*, *Picea*, *Abies*, *Populus*, *Salix*, *Fagas*, *Betula*, *Quercus* and in southern hemisphere trees such as *Eucalyptus*, *Northofagus*, and *Shorea robusta* of the Dipterocarpaceae family in the monsoon forests of Southeast Asia forming obligatory mycorrhizae (Moore, 2011). Some of them are active in cool or moist areas while others are active in warm or dry locations, and some thrive on coarse woody debris while others prefer humus or other substrate components (Trappe, 1977). These nonspecific characteristics also make ECM globally significant to forest ecosystems. The establishment and performance of outplanted seedlings has often been reported to depend on ectomycorrhizal (ECM) fungi (Perry *et al.* 1987; Kropp and Langlois, 1990; Stenström *et al.*, 1990; Pera *et al.* 1999; Baum *et al.*, 2002; Dunabeitia *et al.*, 2004), which may enhance uptake of water and nutrients (Smith and Read 1997) and lengthen the life and increase the growth of roots (Chilvers and Gust, 1982; Wilcox 1996) by protecting them against drought, pathogens, and heavy metal pollution (Chakravarty and Unestam, 1985; Colpaert and Vanassche, 1992; Morin *et al.*, 1999; Van Tichelen *et al.*, 2001; Ortega *et al.*, 2004). The seedlings used in afforestation are often cultivated as bare root seedlings in forest nurseries and reportedly are only colonized by ECM fungi to a lesser extent (Dunabeitia *et al.*, 2004; Menkis *et al.*, 2005). Consequently, failure in afforestation has been hypothesized to be caused by the absence of mycorrhizas (Bjorkman, 1970; Mikola, 1970; Marx, 1980).

The role of mycorrhizas in forest restoration has attracted lot of attention in past (Gaur and Adholeya, 2004; Hidelbrandt *et al.*, 2007). There are at least two mechanisms by which the mycorrhizas in plant roots promote forest restoration. First, as suggested by Galli *et al.* (1994), mycorrhizal colonization in roots plays a role in protecting the plant roots from various stresses, and the second, mycorrhizal colonization of roots increases root surface area for nutrient absorption. In fact, the extraradical mycelia of ECM fungi exploit the greater soil volume and can reach micropore areas and absorb nutrients that may otherwise be inaccessible to plants both physically and chemically (Perez-Moreno and Read, 2000).

Early research on the utility of mycorrhizae in reforestation of mined sites established that prior inoculation of pines with ectomycorrhizal fungi improved seedling growth and establishment (Marx, 1977; Marx *et al.*, 1977, Marx *et al.*, 1982). Ectomycorrhizal colonization of root systems is an important factor in determining seedling vigour, and consequently quality (Smith and Read, 1997). Apart from nutritional benefits to their hosts, some mycorrhizal fungi can enable seedlings to withstand high soil temperatures (Marx and Bryan, 1971) and increase resistance to drought (Parke *et al.*, 1983). Of practical importance to nursery management, some mycorrhizal fungi can protect roots against certain pathogens (Sinclair *et al.*, 1982; Sampagni *et al.*, 1985; Stenström *et al.*, 1997) and consequently can improve growth of the seedlings (Smith and Read, 1997). Menkis *et al.*, (2005) investigated

the effect of artificial inoculation on survival and growth of *P. sylvestris* and *P. abies* seedlings. The study showed importance of tree species in picking up the mycorrhizal species as the seedlings of pine and spruce were in most cases colonized by the different fungi. Thus, success of mycorrhizal inoculation in the field largely depends on the fungus, host tree, and ecological conditions of the soil which to a great extent regulate mycorrhizal colonization at a given site (McAfee and Fortin, 1986).

### Food for animals

Mycophagy serves to maintain populations of ECM fungi and provides nourishment to small mammals (Malajczuk *et al.*, 1987). Sporocarps are good source of water, protein, carbohydrates and minerals (Johnson, 1994; Claridge *et al.*, 1999). The tripartite relationship between truffles and vertebrates like squirrels and many ground dwelling marsupials and the host tree are well known (Dell, 2002). In this manner ECM also participate in the food chain.

### Conclusions

Ectomycorrhizae is a symbiosis between soil fungi and the rootlets of major forest trees and encompasses a wide range of ecological situations. They significantly contribute to a number of ecosystem processes and functions especially nutrient cycling and helps the host trees in survival especially in stress conditions. They also interact with the other soil microorganisms especially the helper bacteria associated with them. The Ectomycorrhizal associations also have proved to be beneficial in forest ecosystems especially in forest regeneration processes.

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