Role of Mycorrhizal Fungi in Ecosystems

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INTRODUCTION

Most land plants form associations with mycorrhizal fungi. Mycorrhizas are mutualistic associations between fungi and plant roots. They are described as symbiotic because the fungus receives photosynthetically derived carbon compounds and the plant has increased access to mineral nutrients and sometimes water. The two most common associations are the arbuscular endomycorrhizas (AM) formed by Zygomycete fungi, and the ectomycorrhizas (ECM) formed by Basidiomycetes, Ascomycetes, and a few Zygomycetes. Other mycorrhizal associations include the orchid, ericoid, arbutoid, monotropoid and ectendo- mycorrhizas (Brundrett et al., 1996).

Mycorrhizal associations predominate in most natural terrestrial ecosystems (Brundrett, 1991). Whereas the AM fungi are widespread geographically and have a very extensive host range, the ECM fungi are more restricted, forming associations predominantly with genera of important woody plants. Nevertheless, ECM fungi are dominant components of the ground-dwelling macro-fungi in ecosystems where members of the following plant families abound: Betulaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Pinaceae, Ulmaceae, Salicaceae. ECM fungi are common in tropical forests of Asia but are uncommon in many forests in Africa and South America. In Asia, the number of host species tends to increase with altitude and at higher latitudes.

BENEFITS TO PLANTS

Supply of inorganic mineral nutrients

Many thousands of experiments have shown that mycorrhizal fungi can overcome nutrient limitation to plant growth by enhancing nutrient acquisition, especially phosphorus (Marschner and Dell, 1994; Clark and Zeto, 2000). Most studies have investigated P, but mycorrhizas have been implicated in the uptake of most essential nutrients. A notable exception is the element boron which is often the main micronutrient limiting growth in SE Asia (Dell and Malajczuk, 1994).

The main mechanisms for an increase in inorganic nutrient uptake in mycorrhizal plants are:

- The large surface area for nutrient acquisition provided by the fungal hyphae external to the root compared to uninfected roots. A high proportion of ECMs are located in soil pores (Babel, 1987) from where hyphae radiate out into soil particles. The aerobic environment of such pores facilitates nutrient transfer from the fungal sheath to the root (Harley et al., 1953). As the fungal mycelium grows through soil, it scavenges for mineral nutrients and is able to make contact with uninfected roots, sometimes of different host species. The ratio of length of hyphae to root length has been measured in the range 300 to over 8,000 (Read and Boyd, 1986; Jones et al., 1990). Expressed per unit of soil volume, values of 16 to 2,000 m hyphae/cm^3 have been measured in plantations and forests (Read and Boyd, 1986; Pampolina et al., 2001).

- The small hyphal diameters compared to roots which allows penetration into some crystalline minerals, aggregates and organic matter, with smaller pores than could be exploited by roots alone.
- The secretion of enzymes capable of solubilising otherwise unavailable forms of phosphate (Joner and Johansen, 2000).

Nutrient uptake sites in AM hyphae are discussed by Bago (2000).

There is good evidence that some inorganic and organic nutrients may pass via the mycelia network from one host plant to another, but the significance of this has not been adequately quantified in the field.

Supply of organic mineral nutrients

Although many mycorrhizal fungi can access inorganic forms of N (Chalot and Brun, 1998) and P (Koide and Kabir, 2000), the relative importance of these modes of nutrition have yet to be quantified in the field. Some litter-inhabiting ECM fungi produce proteases and distribute soluble amino compounds through hyphal networks into the root (Read et al., 1989). Recently, *Glomus* has been shown to transport the amino acids glycine and glutamine into wheat (Hawkins et al., 2000).

Water

Ectomycorrhizal tree seedlings can often resist drought better than non-mycorrhizal seedlings (Bowen, 1973). Several studies indicate that *Rhizopogon* can help plants to tolerate and recover from water deficits and this can aid seedling establishment. Plants colonised by AM fungi may have increased tolerance to drought. In flax (*Linum usitatissimum*), AM mycorrhizal plants had lowered sensitivity to stress, higher assimilation combined with lower increase of transpiration, and enhanced root conductance (Vonreichenbach and Schonbeck, 1995). Unlike for AMs, large mycelial strands of ECM fungi may increase water flow by bridging the gap between the soil and the root (Lamhamedi et al., 1992).

Antagonism of parasitic organisms

There are many claims that mycorrhizal plants are more resistant to disease from pathogenic fungi and bacteria than nonmycorrhizal plants. In particular, mycorrhizal fungi can provide some protection against root invading primary pathogens (Schonbeck, 1979; Duchesne et al., 1989). Some examples for woody species include [host/pathogen/ mycorrhizal fungus(i)]: *Castanea/Phytophthora/Laccaria, Hebeloma, Paxillus* (Brazanti et al., 1999); *Picea/ Cylindrocladium/Paxillus* (Morin et al., 1999); *Pinus/Fusarium/ Paxillus* (Chakravarty et al., 1991; Farquhar and Peterson, 1991); *Pinus/Phytophthora/ Pisolithus* (Marx, 1973; Barham et al., 1974); and *Pseudotsuga/Fusarium/Laccaria* (Sylvia and Sinclair, 1983). However, rarely is complete protection provided. Unlike in pines where the fine roots near the soil surface are usually all ensheathed by ECM fungi, the feeder root system of many broadleaf trees contains a mixture of nonmycorrhizal and mycorrhizal short roots. Whilst the mechanisms of disease suppression remain unclear, it has been surmised that the fungal mantle in ECMs provides a physical barrier to pathogen ingress. Other proposed mechanisms include the production of antibiotic or antifungal compounds by mycorrhizal fungi, and the activation of plant defence genes.

Further, mycorrhizal plants may be less impacted by pathogenic nematodes than nonmycorrhizal plants (Smith, 1987; Pinochet et al., 1996), probably because they are better able to maintain a water and nutrient absorbing surface in infected soil. However, further work is needed as Ryan et al., (2000) showed that AM inoculation of potato plants stimulated production of the potato cyst nematode-selective hatching chemical.

Amelioration of adverse soil conditions

An increasing number of studies indicate the importance of mycorrhizal fungi for the survival of plants in places with problem soils or regions with extreme climate. The topic has been reviewed (Haselwandter and Bowen, 1996). Often, growth stimulation through the supply of essential nutrients dilutes the potential impact of damaging ions in the shoot.

i. Heavy metals

The capacity of plants to colonise soils containing high levels of heavy metals (such as Zn, Cu, Mn, Ni, Cr) is enhanced by their colonisation by mycorrhizal fungi (Galli et al., 1994; Hartley et al., 1997; Leyval et al., 1997). Possible mechanisms by which mycorrhizas deal with excess metals include the immobilisation of metals in the fungal hyphae or in root tissue (Hildebrandt et al., 1999). Thus, mycorrhizal plants often show less toxicity symptoms in the shoot.

ii. Unfavourable pH

ECM plants in alkaline soils may be advantaged by the capacity of fungal hyphae to access limiting nutrients such as P and Zn. Some ECM fungi produce oxalic acid which dissolves sparingly soluble calcium phosphates (Lapeyrie et al., 1991). Iron uptake may be enhanced by the release of siderophores (Marschner, 1995).

iii. Salinity

AM fungi can protect some non-halophytic plants against yield losses in moderately saline soils. Possible mechanisms include the stimulation of root growth (Ruiz-Lozano and Azcon, 2000), improved plant nutrition (Al-Karaki, 2000) and increased synthesis of plant polyols (Juniper and Abbott 1993) in mycorrhizal plants. The incidence of mycorrhizal halophytes is generally quite low (Brundrett, 1991). Little information is available for ECM associations (Dixon et al., 1993).

ROLES IN ECOSYSTEMS

The ecology of mycorrhizal fungi is not well documented (Abbott and Gazey, 1994; Francis and Read, 1995). Hence, in the discussion that follows, conclusions are mostly drawn from short-term studies with a small range of partnerships, often under experimental conditions. In nature, the situation is far more complex as a single tree may have fungal partners which can vary in time and space. The study by Moyersoen et al., (1998), on the co-occurrence of AM and ECM fungi in rainforest in Cameroon, provides a good example of a field study exploring possible functional roles of mycorrhizal fungi. More studies of this type are needed to elucidate the dynamics of mycorrhizal fungi in ecosystems and the impact of disturbance.

Carbon transport

The fungal/plant interface provides a conduit for the movement of carbon from the plant to the fungus, and for movement between plants linked by mycelia (Francis and Read, 1984; Simard et al., 1997; Wu et al., 2001). The nature of the interface and its mode of regulation are still being elucidated (Hall and Williams, 2000). It is generally believed that mycorrhizal plants direct more of their photosynthates into the soil than nonmycorrhizal plants. This extra carbon accumulates in patches and at the edge of hyphal mats (Finlay and Read, 1986), and boosts the energy supply to the detrital food web, benefiting saprohytic microbes and other soil organisms (Barea, 2000). Because the chemical (Dieffenbach and Matzner, 2000) and physical environment around mycorrhizas (the mycorrhizosphere) differs from nonmycorrhizas, presumably it provides microhabitats for soil biota that are not present in the rhizospere of nonmycorrhizal roots.

Mycorrhizal fungi are estimated to consume from 15 to 50% of net primary production (Fogel and Hunt, 1979; Vogt et al., 1982).

Nutrient cycling and nutrient conservation

Fungi are crucial components of ecosystems as they transport, store, release and cycle nutrients. A good example of the potential of mycorrhizal fungi to capture and deliver nutrients to their host comes from studies using inoculated eucalypts in field trials in sub-tropical China. Generally, trees in this region grow well below their potential. The main constraint to productivity appears to be low soil fertility (Dell and Malajczuk, 1994; Xu and Dell, 1998). Most of the land available for plantation forestry have been degraded over recent centuries with extensive loss of the A horizon caused by population pressure, inadequate management and over-harvesting (Xu, 1996). Topsoil crusting is common, contributing to enhanced erosion, reduced soil water storage, compaction and poor root development (Xu et al., 2000). Low soil organic matter (SOM) content (<2%) also restrains productivity. As most soils for plantation eucalypts in southern China have lost their Ao layer, we need urgently to consider how to recover microbial biodiversity as there is no doubt that this will be important for improving long-term soil fertility. The capacity of some ECM fungi to promote both early growth and survival of eucalypts is very important for commercial plantations on these disturbed and difficult sites. Significant effects of ECM fungal inoculation on growth of plantation eucalypts were obtained at two sites in southern China (Xu et al., 2001). Effects were isolate dependent with some isolates stimulating tree growth and some isolates depressing tree growth. Similar results were obtained in a trial in the Philippines where two isolates increased survival while one isolate decreased survival of *Eucalyptus urophylla* (Aggangan et al., 1999). The improvement in growth could be attributed to the acquisition of P as other essential mineral nutrients were supplied at establishment. Generally, inoculation only increased stand volume under P-limiting soil conditions.

In forests, litter is an important nutrient reservoir. ECM fungi can mobilise P, N and other nutrients from litter to tree roots (Attiwill and Adams, 1993; Perez-Moreno and Read, 2000). Fogel (1980) estimated that ECMs account for 43% of the annual turnover of N in a *Pseudotsuga menziesii* forest in Oregon. Litter type can affect the diversity and function of ECMs (Conn and Dighton, 2000). Buscot et al., (2000) propose that the high diversity of fungal partners that a tree may have allows optimal foraging and mobilisation of various N and P forms from organic soil layers.

Soil structure

It is obvious from the examination of ECM mycelial mats, that mycorrhizal fungi have a big impact on soil structure. Yet, there is scant information in the literature regarding soils in tropical ecosystems. In agricultural soils, AM fungi increase the formation of soil aggregates (Bethlenfalvay et al., 1999).

Food for animals

Long-distance dispersal of spores from ECM fungi with hypogeal (truffle-like) sporocarps depends largely on mammal mycophagy (Kotter and Farentinos; Claridge and May, 1994). Mycophagy is widespread and has been demonstrated in Europe, Australasia and North America. Mycophagy serves to maintain populations of ECM fungi and provides nourishment to small mammals (Malajczuk et al., 1987). Sporocarps are good sources of water, protein, carbohydrates and minerals (Johnson, 1994; Claridge et al., 1999). The tripartite relationship between truffles/truffle-like fungi, vertebrates such as squirrels and many ground-dwelling marsupials, and the host trees, are well known. Less well known is the role that mycorrhizal fungi play as a food source for invertebrates and the role of invertebrates in dispersal of ECM and AM fungal spores.

VALUE TO PEOPLE

In many upland forest regions of SE Asia, sporocarps of fungi, mostly basidiomycetes, have traditionally been collected for local consumption and trade (Dell et al., 2000). Many of these fungi, especially members of the Amanitaceae, Boletaceae, Russulaceae, and Tricholomataceae, form ectomycorrhizal associations with trees in the families Dipterocarpaceae, Fagaceae and Pinaceae and are important for maintaining ecosystem function. The highest diversity of edible fungi is collected from mixed forests in China and the lowest diversity from areas of tropical pine and dipterocarps. In general, traded fresh sporocarps are 2 to 20 times more valuable, by weight, than local seasonal fruits and vegetables. International trade in a small number of species is having a major impact on the quality and sustainability of the mushroom harvest from some collecting sites.

Forest fungi are also valued for medicine, for their aethetics, as bio-indicators of environmental quality and for bio-remediation.

LAND MANAGEMENT EFFECTS ON MYCORRHIZAL FUNGI

Any form of land management that involves tillage, timber harvesting, vegetation clearing, or other forms of disturbance can affect mycorrhizal populations. Severe soil disturbance, such as fallowing agricultural soils (Thomson, 1987), crop rotation with a non-host species (Gravito and Miller, 1998) or topsoil stripping and storage during mining (Jasper et al., 1987; Gardner and Malajczuk, 1988; Bellgard, 1993), markedly reduces populations of mycorrhizal fungi. Unlike AM fungi, ECM fungi may be able to quickly invade disturbed soils (Jasper, 1994). This is often the case for what have been termed “early colonising” genera such as *Laccaria, Pisolithus, Rhizopogon*, *Scleroderma* and *Thelephora*. Recolonisation mostly results from spore dispersal by wind and animal vectors from sporocarps in adjacent vegetation.

The mycelial network appears to be an important component of the inoculum potential of an undisturbed soil (Evans and Miller, 1990). Even minor soil disturbance can impact on the function of mycorrhizas. Severing mycelium reduces the extent of inter-root and inter-plant connections, thus reducing access to existing and new food bases (Read and Birch, 1988). The mycelial mats of ECM fungi, mentioned earlier, are vulnerable because they are easily disrupted by raking litter during the collection of leaves for fuel or the collection of edible fungi.

Studies in a number of ecosystems (Reeves et al., 1979; Janos, 1980; Allen et al., 1987; Siqueira et al., 1988) show that in climax communities, normally dominated by species heavily colonised by mycorrhizal fungi, disturbance leads to a successional sequence in which re-colonisation is initiated by plant species which are non-mycorrhizal or little infected (Read and Birch, 1988). Gap-preferring species thus may have lower rates of mycorrhizal infection than species preferring undisturbed microsites (Onipchenko and Zobel, 2000). However, Brundrett et al., (1995) found that for parts of tropical Australia, the activity of mycorrhizal fungi was higher in patches of early-successional vegetation than in undisturbed habitats. In a study in deciduous tropical forest in Mexico, Allen (1998) concluded that regrowth of vegetation in small gaps was not limited by mycorrhizal fungi, since they were still abundant after treefalls. However, recovery in pastures could be affected by low fungal diversity and dominance of grasses. Jasper et al., (1991) found that disturbance of forest and heathland soils decreased colonisation of test plants (clover) compared to disturbance of clover soil. They proposed that a larger number of propagules in the pasture soil may have allowed the pasture soil to maintain infectivity after disturbance. There is a suggestion that ecosystems with a high proportion of grasses and high numbers of AM spores may also be be more tolerant of disturbance (Visser et al., 1984).

The abandonment of agricultural land in the Italian Alps resulted in succession from nonmycorrhizal ruderal annuals to AM-colonised perennials and an increase in floristic richness (Barbi and Siniscalo, 2000). Over time, ECM hosts will increasingly dominate if old-field succession is allowed to continue.

Use of fertilisers can affect mycorrhizal fungal populations (Baum and Makeschin, 2000; Pampolina et al., 2001). Increasing soil fertility, especially P and N, can suppress mycorrhiza formation and/or mycorrhizal diversity but the effects are often host and fungal dependent. For example, the number of epigeous basidiocarps in an 11-year-old *Pinus taeda* stand in north California was reduced to 17 % following the addition of 25 kg P ha^{-1} (Menge et al., 1977). In *Betula pendula*, the addition of 20 kg P ha^{-1} at 3 and 9 weeks after outplanting reduced ectomycorrhizal root colonization (Newton and Pigott, 1991). By contrast, Fransson et al., (2000) applied repeated balanced additions of nutrients to 36-year-old *Picea abies* and could find no measurable effect on morphotype richness (>60 ECM morphotypes) or total number of root tips. However, *Cenococcum* was more common in fertilised plots than in the controls. Soil P content is often negatively correlated with % root colonisation (Maldonado et al., 2000).

MANAGING MYCORRHIZAL FUNGI

Most emphasis on the management of mycorrhizal fungi has focussed on disturbed habitats such as occur in agriculture and forestry, or in semi-controlled environments such as in nurseries or in production horticulture. Few studies have investigated the ecology of mycorrhizal fungal populations in natural systems. We know relatively little about how perturbations such as fire, flood, drought, volcanism affect the diversity, function and genetic composition of mycorrhizal fungal populations. Our knowledge is depauperate concerning seasonal changes in mycorrhizal populations and fungal succession. However, it is clear from the earlier part of this paper that mycorrhizal fungi are an integral part of ecosystems (Klironomos et al., 2000) and provide physical links between the primary producers, the comsumers and the decomposers.

Clearly we need to understand a lot more of the biology and ecology of the mycorrhizal fungi in their natural habitats. In the meantime, we can undertake the following:

- maintain populations of host plants and variety of habitats for each species of host.
- increase activity of target organisms in disturbed habitats by adjusting soil management strategies, and where necessary, introducing indigenous organisms.
- document fungal diversity in all areas but initially direct resources to threatened habitats.
- reduce disturbance to a level that maintains fungal fruiting.
- harvest non-wood forest products sustainably.

FUTURE RESEARCH IN THAILAND

Unlike for the temperate latitudes, where large numbers of taxonomic and ecological studies have been made on mycorrhizal fungi, there is only a meagre knowledge of the mycorrhizal fungi associated with many tropical and subtropical ecosystems. A great deal of taxonomic effort is required, for example, in SE Asia to adequately describe and delineate the fungal biota and allow ecological studies to proceed on specific organisms. This is particularly the case for Northern Thailand where the vegetation changes markedly with topography. There, montane ECM fungal elements occur within short distances in elevation from lowland species associated with either evergreen or deciduous Dipterocarps. Researchers working on AM and ECM fungi should ensure that representative specimens of taxa referred to in their studies are lodged in curated national or regional fungal herbaria. Over time this will allow definitive names to be applied and facilitate linkages between the different studies.

Furthermore, many fundamental aspects of fungal ecology require intensive study, such as: seasonal dynamics of fungi, fungal succession, nutrient turn-over, host range, and fungal resilience/sensitivity to disturbance, to name a few. Such studies are not facile, as populations must be studied below-ground. It is becoming evident that neither the diversity nor the abundance of sporocarps above-ground can be used to assess below-ground ECM fungal diversity or abundance (van der Heijden et al., 1999). Furthermore, in eucalypt forests in Australia, there is probably a greater diversity of ECM fungi that fruit below-ground than above-ground (Bougher, 1995). These truffle-like fungi, and many fungi that produce sporocarps infrequently, or have insignificant fruit bodies, have been little studied in SE Asia.

Research being undertaken by PhD students at Chiang Mai University on edible ECM forest fungi and on AM fungi associated with *Macaranga denticulata* in Swidden fields of Karen farmers in Mae Hong Son Province, hopefully will be extended by other researchers in the region in the future. In addition to the types of mycorrhizal fungi covered in this review, the orchid mycorrhizal fungi also need further attention (Purshotam-Kaushik, 1998) as issues of orchid conservation and cultivation become more pressing.

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