Mycorrhizal fungi and their association with plants

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Introduction

Over 90% of all plant species are associated with mycorrhizal fungi. The term mycorrhiza literally means "fungus-root", indicating that these soil fungi form an intimate symbiotic association with plants. They derive energy from photosynthetically produced plant sugars and in return plants gain access to nutrients (Smith and Read, 2008).

Mycorrhizal fungi live within and around the roots of plants and extend fungal threads, called hyphae, into the soil environment where they search for nutrients far beyond the host plants own rooting zone. It is estimated that for every 1 mm of root there is over a meter of an associated hyphal network in the soil, which explores the soil environment for nutrients and water (Lindalh et al 1999; Finlay 2008). Benefits attributed to this symbiotic interaction are promotion of nutrient uptake and plant growth, increased tolerance to stress such as drought, salinity and disease, enhanced microbial activity and improved soil structure (Smith and Read, 2008).

Mycorrhizal types

Mycorrhizal interactions are broadly divided into types based on the fungi and host plant species involved as well as the fungal structures formed in and/or around roots. In South Africa exotic trees such as pines are ectomycorrhizal while the majority of our indigenous plants, trees and crop plants have endomycorrhizal associations (Hawley and Dames, 2004; Hawley et al., 2008; Chartier FitzGerald et al., 2020).

Ectomycorhizal associations are distinguishable by the presence of fungal hyphae which are wrapped around the root forming a mantle. Individual roots or clusters of roots may be covered and appear variously coloured and sometimes fluffy (Fig 1). The fungi penetrate the roots and grow between the cortical root cells forming a 'Hartig' net. Fungal hyphae, single or aggregated, also extend into the soil environment to forage for nutrients. Some of the fungi involved in this association produce mushrooms e.g. ceps (*Boletus edulis*) and pine rings (*Lactarius delicious*), but not all mushrooms are mycorrhizal and conversely not all mycorrhizal fungi produce mushrooms (Hawley et al., 2008, Chartier FitzGerald et al., 2020).

Ericoid mycorrhizal fungi are endomycorrhizal associating with plants belonging to the Ericales, these include the indigenous *Erica*'s which contribute to our fynbos vegetation and blueberries. These fungi produce tightly woven hyphae within the hair root cells of the plants (Fig 1). Hyphae extend from the roots into the soil and are well known for secreting an array of enzymes which assists with nutrient access and ability of plants to grow in nutrient poor, acidic soils (Bizabani and Dames, 2015; Bizabani et al., 2016).

The majority of crop plants are associated with arbuscular mycorrhizal fungi (endomycorrhizal). Hyphae penetrate into the plant roots and grow between cortical cells, entering these cells forming finely branched arbuscules. At no time will the integrity of the root cell be compromised as the protective plant cell membrane will always remain intact, the surface area of the membrane will increase to fully engulf the arbuscular structure. Vesicles may also be formed which store excess carbon in the form of lipids (Fig 1). The fungi involved in this symbiosis are obligate biotrophs and cannot grow if not associated with a host plant (Smith and Read, 2008).

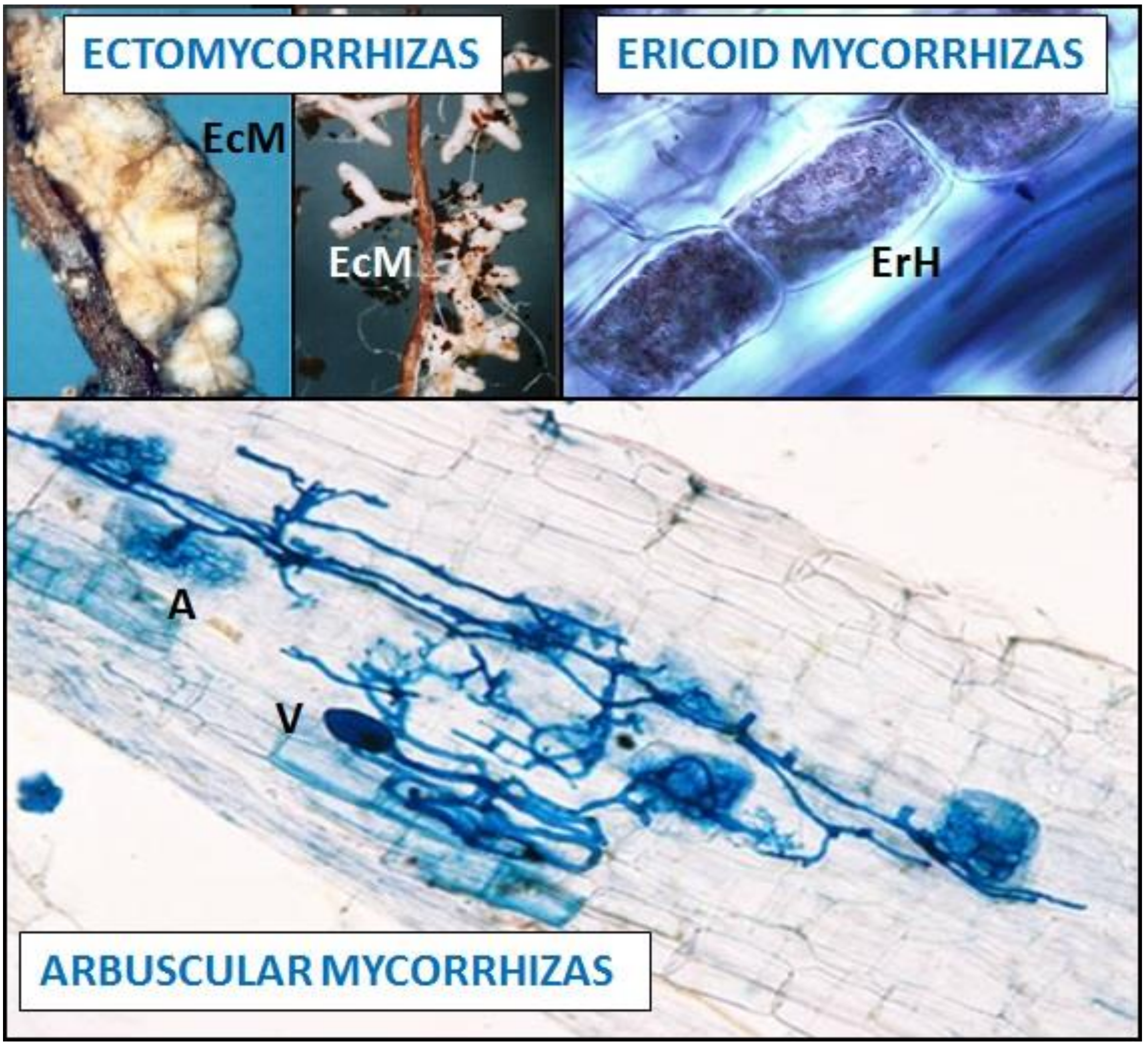

Figure 1: Mycorrhizal types: EcM – ectomycorrhizal mantle surrounding root tips; ErH – ericoid mycorrhizal hyphae within a hair root cell; A – arbuscule, V – vesicle of arbuscular mycorrhizas.

Nutrient uptake

Fungi are absorptive microorganisms. The exploitative mycorrhizal hyphal network extends into the soil, crossing depletion zones, in search of nutrient resources. Enzymes and other organic molecules are released aiding in dissolution of complexed nutrient sources and the smaller subunits are absorbed into the hyphae where they can be transported to the host plant roots thus allowing mycorrhizal plants to acquire nutrients at a distance. The uptake of P has been the primary focus of many research studies reported in the literature although mycorrhizal fungi contribute to the uptake of N as well as other macro and micronutrients (Smith and Read, 2008).

A root colonised with AM fungi has two pathways with which to access nutrients. Taking P as an example there is the direct pathway through epidermal cells and root hairs absorbing P from the soil solution adjacent to the roots and the mycorrhizal pathway in which P is absorbed by the fungal threads, being rapidly transported to the fungal/plant interface and subsequently absorbed by the plant cortical cells (Smith et al 2004) across the apoplastic space.

The balance between these two pathways is likely to depend on the carbon demand of developing and maintaining the symbiosis and any compensatory changes in root growth. It has generally been accepted that uptake from the soil decreases as the concentration of P in solution decreases. The ability of AM fungal hyphae to exploit the soil environment beyond this depletion zone was thought to be the main advantage of mycorrhizal colonisation. The result of this enhanced uptake is the mycorrhizal effect and is visually manifested in the “big plant- little plant” syndrome (Smith and Read, 2008). Non-responsiveness was assumed to indicate that the mycorrhizal pathway was not functioning. Research over the past 15 years has repeatedly shown that the mycorrhizal pathway can become the dominant uptake pathway even in “unresponsive plants” accounting for the majority if not exclusive uptake of P (Smith et al, 2003). Unravelling the complexities of the mechanisms involved is the focus of many plant physiologists, ecologists and molecular biologist.

AM fungal life cycle

AM fungal spores are concentrated in the top 20-30 cm of the soil and are filled with stored carbon in the form of lipids. Spores will germinate when conditions are moist. In order to produce a germ tube requires energy gained from these stored reserves. This is the asymbiotic phase which does not require a host plant, however if no host plant is available spore germination will cease. Several attempts at germination may occur depleting the energy reserves. If a host plant is detected through signal molecules in root exudates the germ tube hypha will continue to elongate and branch growing and fanning out in the direction of the host plant roots during this pre-symbiotic phase. On contact with the roots, fungal hyphae will penetrate the root and develop into the typically observed intraradical and extraradical mycorrhizal structures which effectively support the symbiosis during the symbiotic phase. The extraradical hyphal exploit the soil for nutrients, colonise new plant roots and produce spores which will complete the life cycle (Smith and Read, 2008).

Agricultural practices

The presence of spores in soil, their ability to colonise roots and effective mycorrhizal symbiosis are undoubtedly affected by agricultural practices. Tillage can mix spores deeper into the soil profile, out of the reach of germinating seeds, and disrupts the mycorrhizal network that develops in the soil. Fallow lands and presences of non-host plants (e.g.

canola) can reduce viable spore numbers due to several failed germination attempts. Excessive use of inorganic P fertiliser alters root exudate composition affecting signalling and recognition between AM fungi and the host plant. Several agrochemicals negatively affect spore germination and colonisation (Smith and Read, 2008).

Mycorrhizal associated bacteria

Mycorrhizal fungi do not reside in isolation they are associated with many soil microorganisms some finding shelter on or within mycorrhizal structures, others free living in the mycorrhizosphere. Bacteria for example contribute to nutrient acquisition producing acids and enzymes that can degrade complex polymers such as cellulose and starch, many produce phytohormones, Fe-chelators and antimicrobial compounds that promote root development and pathogen protection (Dames, 2014). These bacteria not only exhibit plant growth promotion properties but may also facilitate mycorrhizal spore germination and colonisation acting as Mycorrhizal Helper Bacteria (Dames and Ridsdale, 2012; Dames, 2014).

Legumes are associated with symbiotic nitrogen fixing rhizobia which convert atmospheric N_2 into ammonium within root nodules as well as AM fungi forming a tripartite symbiotic interaction. Nitrogen fixation is a highly energetic process requiring 16-24 ATP (energy) molecules to convert 1 molecular of N_2. The mycorrhizal uptake pathway assists in the acquisition of P to facilitate this process. The P concentration inside root nodules is approximately 3 times higher than in other root parts (da Silva et al, 2017).

Sustaining mycorrhizal fungi

Sustaining mycorrhizal populations in soils requires viable mycorrhizal propagules and compatible host plants and awareness that some agricultural practices and agrochemicals may negatively impact the development of mycorrhizal associations. The adoption of integrated soil management practices which enhances and sustains mycorrhizal fungal diversity is the key to ensuring that maximum benefit is derived from this symbiotic association.

References

Bizabani, C., Fontela, S., Dames, J.F. (2015) *Lachum* and *Cadophora* fungal interactions with *Vaccinium corynbosum* (2015). Microbiological Research. 181:68-74

Bizabani, C., Dames, J.F. (2016). Ericoid fungal inoculation of Blueberry under commercial production in South Africa. Scientia Horticulturae 209:173-177.

Chartier FitzGerald, V., Hawley, G., Dames, J.F. (2020). Screening of ectomycorrhizal and other associated fungi in South African forest nurseries. Southern Forests, https://doi.org/10.2989/20702620.2020.1759301 (in press).

Dames, J.F., Ridsdale, C.J. (2012). What we know about arbuscular mycorrhizal fungi and associated soil bacteria. *African Journal of Biotechnology* 11: 13753-13760*.*

Dames, J.F. (2014). Biological control: PGPR and arbuscular mycorrhizal fungi working together. Miransari M (editor). Use of Microbes for the Alleviation of Soil Stresses. Volume 2: Alleviation of Soil Stress by PGPR and Mycorrhizal Fungi. Springer, New York. ISBN 978-1-4939-0720-5 Chapter 3.

Da Silva, J.S., de Carvalhol, T.S., dos Santos, J.V., de Almeida Ribierol, P.R., de Souza Moreira, F.M.(2017). Formononetin stimulates mycorrhizal fungal colonization on the surface of active root nodules in soybean. Symbiosis 71: 27-34.

Finlay R.D. (2008). Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. Journal of Experimental Botany 95:1115-1126.

Hawley, G.L., Dames, J.F. (2004). Mycorrhizal status of indigenous tree species in a forest biome of Eastern Cape, South Africa. *South African Journal of Science* 100: 633-637.

Hawley, G.L., Taylor, A.F.S., Dames, J.F. (2008). Ectomycorrhizal fungi in association with *Pinus* in South Africa. *South African Journal of Science* 104: 273- 283.

Lindahl, B, Stenlid, J., Olsson, S., Finlay R.D., (1999). Translocation of ^{32}P between interacting mycelia of a wood-decomposing fungus and ectomycorrhizal fungi in microcosm systems. New Phytologist 144: 183-193.

Smith, S.E., Smith F.A., Jackobsen, I. (2003). Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiology 133:16-20.

Smith, S.E., Read, D.J. (2008). Mycorrhizal symbiosis, 3rd edition. Academic Press. San Diego and London.

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