

Understanding mycorrhizal fungi

Rod Rush

Agricultural Consultant
17 Catherine Street, Armidale NSW 2350
(02) 6772 3125
rodrush@bigpond.net.au

Abstract

Mycorrhizal fungi form symbiotic associations with the young fine roots of many plant species. Arbuscular mycorrhizal (AM) fungi form associations with 70% of flowering plants as well as many ferns and conifers and constitute an estimated 70% of the microbial biomass in most undisturbed soils. They can only survive in the presence of a live host. Mycorrhizae supply their hosts with mineral nutrients (notably phosphorus) in exchange for energy compounds. Arbuscular mycorrhiza (AM) dramatically increase the volume of soil from which plants are able to draw nutrients. AM associations at a particular root site only last for 5 to 6 days but are continually reforming closer to the root tip as the roots elongate. In healthy ecosystems the large amount of infective mycorrhizal propagules (hyphae, spores etc) quickly recolonise plant roots when relationships are disturbed. However, there are many land management practices that can severely deplete and sometimes extinguish mycorrhizal populations. These include over grazing; changing plant community composition to less mycorrhizal plant species such as annuals; ground disturbance such as ploughing and laser levelling; and removal of host plants e.g. fallow practices. This paper focuses on a discussion of these management practices and their consequences for ecosystem health and farm productivity.

Introduction

Mycorrhiza is a term used to describe a symbiotic relationship between plants and fungi.

Mycorrhizal fungi maybe classified into two distinct types based on their interaction with the host. That is:

- Ectomycorrhizal fungi enter the roots where the hyphae pass between root cells. There is often a mass of fungal filaments on the surface of the finest roots and this can often be seen with the naked eye.
- Endomycorrhizal fungi enter the root cells. This is a very diverse group and includes the group known as the arbuscular mycorrhizal (AM) or vesicular arbuscular mycorrhizal (VAM) fungi. This last group is so dominant in the plant kingdom that much of the discussion that follows is related to them. Only about 150 species of these fungi are known, yet they are capable of forming mycorrhizal associations with 70% of Angiosperms as well as many ferns and conifers.

Mycorrhizal fungi infect a layer of cells called the cortex, found only on relatively young roots, and at the same time pass into the soil, forming a bridge to the plant. They all provide soil nutrients to the plant and draw energy compounds from the host (St John, 2005). In agricultural field soils up to 50 metres of AM hyphae per gram of soil have been observed and hyphae can extend more than 9 cm beyond the roots (Nasim, 2005).

Many plants are very dependent on mycorrhizal symbiosis and make little growth without it unless heavily fertilized. Such plants are said to be mycotrophic. Perennial grasses are often strongly mycotrophic. Most weedy plants are either non-mycotrophic (i.e. annual grasses and weedy composites) or non hosts (e.g. the brassicas and mustards, spinach, buckwheat) (St John 2005).

Mycorrhizal fungi constitute the dominant microorganisms in most undisturbed soils – estimated at about 70% of microbial biomass (St John, 2005).

The best known mycorrhizal effect is that mycorrhizal plants take up more soil phosphorus and grow faster than corresponding non-mycorrhizal control plants.

In addition to phosphorus the hyphae also transport other resources to the host such as ammonium, calcium, sulphur, potassium, zinc, copper and water (Nasim, 2005).

In soil solution the concentration of phosphorus is very low and is transported to roots mainly via diffusion. However, the diffusion coefficient of P is very low and consequently P is easily depleted from the root zone. A mycorrhizal association can greatly increase a plant's access to P sources in the soil. (Nasim, 2005).

By extending beyond the depletion zone for phosphorus around the root, the external mycelium improves phosphorus absorption. Calculations have shown that a root associated with mycorrhizal fungi can transport phosphorus at a rate more than four times higher than that of a root not associated with mycorrhiza (Nasim, 2005)

The Qld DPI reports that they have shown that a lack of VAM colonisation can greatly reduce the ability of highly dependent crops to take up P and/or zinc even when fertilized at high rates. Without mycorrhiza the potential yield loss for linseed is > 90%; for sunflower, mungbean, pigeon pea, maize and chickpea is 60 to 80%; for sudan, sorghum and soybean is 40 to 60%; for wheat, barley and triticale is 10 to 30%; for panicum and canary is 0 to 10%; and for canola and lupins it is 0%.

Rodale Farm trials in the U.S. have shown yield increases of up to 50% with potatoes when grown with mycorrhizal fungi. Other crops shown to respond dramatically to mycorrhizal colonisation include citrus, onion and strawberry.

Jones et al (2004) reviewed plant and mycorrhizal regulation of rhizodeposition. They concluded that the exact signals by which roots stimulate AM hyphal growth from spores or root fragments and enhance root colonisation is currently unknown. A wide range of compounds has been proposed to be involved including flavenoids, volatiles (most notably elevated CO₂ concentrations), and unidentified water soluble or hydrophobic compounds. Once roots are colonized by AMF, plants appear to be able to regulate further colonisation through the exudates released. While the turnover of external AM hyphae is of the order of 5 to 6 days runner AM hyphae may persist for up to 30 days.

Many native plants fail if they are unable to become mycorrhizal soon after germination (St John, 2005).

Colonisation and influence on species composition of plant communities

Seedlings become mycorrhizal very quickly if the soil is full of mycorrhizal hyphae, but more slowly if the soil contains only dormant reproductive spores. The living mycelial network favours the diverse native species that must become mycorrhizal quickly. Soil with little inoculum selects against most natives and favours the plant species that do not need to become mycorrhizal early in life. These plants are better known as weeds (St John, 2005).

Mummey *et al* (2005) looked at whether adjacent plant roots of one species exert a strong influence on the subset of the AM community colonizing roots of a different species. They found that the subset of the AM community colonizing the roots of a common grass species *Dactylis glomerata* was strongly controlled by neighbouring roots of a different plant species, *Centaurea maculosa*, an invasive forb. Their results indicate that with the presence of *C. maculosa*, AM communities of *D. glomerata* shift to reflect community composition associated with *C. maculosa* roots. An additional dimension to this study is that *C. maculosa* is an aggressive invasive plant in parts of the USA. Viewed in this light, these results suggest that pervasive influences of this plant on AM communities, specifically in roots of its competitors, may represent a mechanism contributing to its invasive success.

As the instrument of rapid root colonisation, the mycorrhizal network virtually determines the plant species composition of the community (St John, 2005).

As more and more plants become mycorrhizal, the fungus links one root system to the next. This is possible because the fungus can colonize almost any plant species. Experiments have shown movement of soil nutrients and even photosynthate between plants of different species (St John, 2005).

Wilson and Hartnett (1998) grew 36 grass and 59 forb species common to tallgrass prairie ecosystems with and without AM fungi inoculation. Among the grasses, they reported that fungal inoculation increased the average dry mass of perennial C4 species by 85%. However, fungal inoculation had no significant effect on dry mass production of perennial C3 species or in any annual grass species, regardless of photosynthetic physiology. With respect to the forbs, over 80% of the perennial species exhibited significant increases in dry mass with fungal inoculation, while only 15% of the annual species displayed enhanced growth with inoculation.

Mycorrhizal fungi are in general more specific to soil type than to host type. Soil pH is the biggest selective factor, but soil texture and organic matter may also influence the suitability of the soil for particular fungi. There are fungi that tolerate cool spring temperatures and others that remain dormant until the soil warms up (St John, 2005).

Endophyte infected tall fescue inhibits many soil organisms, including pathogenic fungi, parasitic nematodes and beneficial mycorrhizal fungi (USDA, 2001)

If an area has no vegetation or is occupied by weeds of, say, the mustard family you may assume that inoculation is mandatory. If it is occupied by weedy annual grasses and composites, or exotic perennials known to be highly invasive there may be some inoculum but the site would probably benefit from inoculation (St John, 2005).

High concentrations of Na, Cl, B, Cd, Zn, and Mn have been shown to interfere with colonisation. Extreme pH values can affect colonisation and soils in a more acidic range may have toxic levels of aluminium ions. Very raw compost materials can sometimes be inhibitory, although mature compost and most humic materials can be neutral or even stimulatory to fungal growth (St John, 2005).

In a soil with an established mycorrhizal network, the active kind of propagule is fungal mycelium. Most new seedlings in healthy native vegetation are colonized in this way. Most species of AM fungi form resting spores, either in the soil or in the root. Spores are more resistant to environmental stress than other propagules, but do not produce mycorrhiza as quickly as live mycelium or fragments of mycorrhizal roots (St John 2005).

When growing from root to root the fungi spread between 0.5 and 1 metre per year. Soil animals may move it somewhat faster. Most often the roots grow to the inoculum rather than the reverse, so the real requirement is to be sure that there is some inoculum close enough to each new seedling that its roots can find the fungi quickly. Mycorrhizal fungi generally have no effect on the germination stage (St John, 2005).

Other beneficial soil biology

Research by the USDA has shown that beneficial soil bacteria are more abundant in soils permeated by mycorrhizal fungi, and pathogenic organisms less abundant.

Bhowmilk and Singh (2004) demonstrated that plant growth promoting rhizobacteria considerably enhanced mycorrhizal colonisation compared to yeast with *Azospirillum* sp. being the most efficient. They not only stimulated AM development but also accelerated the root growth.

Influence on soil structure

Fungal hyphae, and the bacteria they encourage, are the primary agents that bind soil particles into soil aggregates. The ones that produce the best result are those that produce a glycoprotein called glomalin. Soil structure allows water and air to infiltrate the soil and keeps soil particles from washing or blowing away. Soil structure is usually poorly developed on conventionally farmed or badly disturbed sites, and very well developed in native ecosystems. Successful creation of soil structure is only possible after the mycorrhizal network is in place (St John, 2005).

As the medium of soil structure, mycorrhizae determines the flow of water, nutrients, air, directs the pathways of root growth, and opens channels for the movement of soil animals. As the moderator of the microbial community, it determines the metabolic processes of the soil. In other words, the mycorrhizal network is practically synonymous with ecosystem function (St John, 2005).

Influence of temperature

It seems that more effective colonisation of new plants occurs where the hyphal network is largely undisturbed. The role of extraradical hyphae as principal propagules for AM colonisation might be of considerable importance, particularly in cool climates where populations of viable spores in agricultural spores may be extremely low following winter. (Kabir 2004).

Farm and landscape practices

1. Tillage and ground disturbance

Any serious disturbance takes a heavy toll on the soil microbes, and such activities as grading (e.g. laser levelling), erosion or overgrazing can destroy the fungi completely. The fungi can only move by moving from root to root or by the physical transportation of inoculated soil (St John, 2005).

Tillage can modify the physical, chemical and biological properties of a soil and consequently may also affect AM fungi. In tilled soil, certain AM species may survive while others may disappear. Because AM fungi are more abundant in the top soil, deep ploughing may dilute their propagules. Tillage is particularly detrimental to AM hyphae if the soil is tilled in the autumn and the hyphae are detached from the host plant. Under no-till AM fungi survive better particularly when they are close to the host crop on which they developed. There is speculation that in NT systems, plants may follow old root channels and potentially encounter more AM fungal propagules than plants growing in soil that has been tilled (Nasim, 2005)

Kabir (2004) reports that in one trial, AM species diversity in a soil under 12 years of conventional tillage was significantly lower than that of a no-till soil. Other research cited by Kabir (2004) suggests that tillage practices may select AM fungi with certain characteristics and eliminate others.

A 40% reduction in AM inoculum in field soil after leaving the land fallow for one season has been reported in India. Long-fallow periods (more than one year) in northern Australia were associated with a decline in mycorrhizal colonisation and AM sporulation in various crops (Thompson, 1987). This reduction in AM fungal inoculum may be exacerbated by adverse winter conditions. In a no-till system in eastern Canada, winter alone caused a reduction of approximately 31 and 40% of total and metabolic active hyphae, respectively (Kabir, 2004). It is important therefore to maintain the level of AM inoculum in soil over winter to maximise the benefits of AM fungi on the following crop.

Conventional tillage practices tend to destroy perennial grass populations and encourage annual grasses and forbs to grow between crop phases. Since many annual species are not

highly responsive to mycorrhizal associations they probably tend to diminish mycorrhizal species and diversity in farm lands.

2. Crop rotation

While mycorrhizal propagules can build up during cropping not all crops produce equal quantities of inoculum. For example crops and weeds from the brassica and mustard families are non-hosts and so behave like a weed free fallow (Qld DPI).

3. Fire and heating

Burning of windrows of stubble or timber can heat soil to temperatures that kill mycorrhizae (Qld DPI)

4. Waterlogging

Excessive soil waterlogging results in poor root colonisation with AM due to lack of oxygen (Qld DPI)

5. Pesticides

The Qld DPI says that broad spectrum fumigants and some fungicides are very toxic to AM under ideal soil moisture and temperature conditions. Recommended rates of insecticides and nematicides generally do not inhibit AM fungi (Qld DPI).

6. Fertilisation

Fertilisation often suppresses mycorrhizal formation. Fertilisation cannot increase plant diversity; it tends to favour large individuals of the few most vigorous species. Fertilisation cannot improve plant survival, but rather tends to favour a few large plants rather than many smaller ones. Fertilisation does not make the site unfit for weeds, but instead gives them a nearly insurmountable competitive edge against native plants. Fertilisation does nothing to decrease root disease, favour beneficial bacteria, or improve soil structure, perhaps the most important effects of mycorrhiza in natural systems. In a revegetation project, fertilisation is often a serious mistake (St John, 2005).

7. Grazing management

Livestock trampling also reduces the number of soil mycorrhizae. Many exotic weeds do not require or benefit from these fungi. As trampling reduces concentrations of mycorrhizae in the soil, the ability of native grasses to acquire nutrients and water is reduced, giving the exotic weeds a competitive advantage over the native plants (Belsky and Gelbard).

Hetrick et al (1989) showed that repeated clipping of *Andropogon gerardii* rhizomes resulted in reduced mycorrhizal root colonisation. Maximum shoot and root biomass of mycorrhizal plants was produced at 12 and 18 weeks, respectively. Fungicide treated plants did not grow appreciably after the first clipping. They showed that mycorrhizae improved clipping tolerance, but with repeated intensive clipping, significant changes in root/shoot ratio occurred and eventually mycorrhizal root colonisation and growth benefit were lost.

When grazing practices favour bare ground, annual grass species often proliferate. Since many annual grass species are not highly responsive to mycorrhizal associations they probably tend to diminish mycorrhizal species and diversity in rangelands. Also, since the mycorrhizal infection area is usually on relatively young roots, repeated grazing/defoliation resulting in roots being shed, causes depletion of mycorrhizal fungal populations.

As already discussed above, low mycorrhizal fungal populations caused by overgrazing and proliferation of annual grasses may be further exacerbated by cold winters.

Inoculation of agricultural crops

The value of inoculating an agricultural crop will vary from zero to great, depending on, for example, the crop and history of the site. There have been good results in the establishment of nursery transplants, orchards and vineyards on newly fumigated ground (St John, 2005).

Even with fumigation, the heavy fertilisation typical of modern agriculture will very likely mask the growth benefits of inoculation (St John, 2005). Since many current fertilisers are soluble and causing environmental damage in places such as the Great Barrier Reef it may be that in time that only less soluble forms of phosphorus such as rock phosphate, for example, will be allowed. In this situation until mycorrhizal fungal species recover it may be necessary to inoculate crops.

While viable mycorrhizal propagules have been documented in soil stockpiles as much as 12 years of age, in general two to three years is the longest that stored soil should be considered reliable mycorrhizal inoculum (St John, 2005).

While spores are considered to be the resistant structure and may be viewed as 'long term' propagules when viable host plants are not present, hyphae are considered to be the main source of inocula when host plants are present and the soil is not disturbed. (Kabir, 2004)

Temperatures over about 50° C may be lethal for many temperate zone isolates. The life span for mycorrhizal spores as given in the scientific literature is in the neighbourhood of 6 months to a year. Certain kinds of carriers appear to provide protection, and in good storage conditions, with the original production vessel kept intact, inoculum in calcined clay has retained its viability for two years or more (St John, 2005).

Possible inhibitory conditions include excessive fertilisation, frequent discing, soil compaction, or the presence of root disease.

Salinity management

Mycorrhizal fungi also play a vital role in alleviating the effects of salinity (Nasim, 2005). By improved nutrient acquisition, AM fungi compensate for the nutritional imbalances imposed by salinisation. AM fungi also plays a positive role in protecting plants from pH extremes.

Glomalin, soil structure and carbon sequestration

USDA researcher Dr Sara Wright (2005) reports that glomalin extracted from active cultures of AM fungi contains 40% glomalin, and glomalin from soils averages 28% carbon. The turnover time for glomalin has been estimated to be in the range 7 to 42 years. Wright also says that glomalin contributes about seven times more carbon to total soil organic carbon than do humic acids.

Glomalin permeates organic matter, binding it to silt, sand, and clay particles. Not only does glomalin contain 30 to 40 percent carbon, but it also forms clumps of soil granules called aggregates. These add structure to soil and keep other stored soil carbon from escaping.

Arbuscular mycorrhizal fungi, found living on plant roots around the world, appear to be the only producers of glomalin.

As a plant grows, the fungi move down the root and form new hyphae to colonize the growing roots. When hyphae higher up on the roots stop transporting nutrients, their protective glomalin sloughs off into the soil. There it attaches to particles of minerals (sand, silt, and clay) and organic matter, forming clumps. This type of soil structure is stable enough to resist wind and water erosion, but porous enough to let air, water, and roots move through it. It also harbours more beneficial microbes, holds more water, and helps the soil surface resist crusting (St John, 2005).

Wright and colleagues found that glomalin contributes much more nitrogen and carbon to the soil than do hyphae or other soil microbes (St John, 2005).

Climate change

Rillig *et al* (1999) studied three different ecosystems: two grasslands in northern California and chaparral in southern California. In all three, they found as carbon dioxide was pumped into open-top chambers placed over grassland plants growing outdoors, or in a greenhouse built around shrubs, glomalin levels rose, along with soil stability. The high carbon dioxide levels in the air increased the amount of carbon taken in by plant roots. That gives the fungi more food and enables them to produce more glomalin

An interesting piece of research was conducted by Sara Wright and others on the effect of rising carbon dioxide levels on the production of glomalin. When carbon dioxide levels were increased to 670 ppm (the level predicted by mid to late 21st century) VAM hyphae grew three times as long and produced five times as much glomalin as fungi on plants growing with today's ambient levels of 370 ppm.

CONCLUSION

AM fungi can represent 70% of the microbial biomass in undisturbed soils and the glomalin that they produce can account for around 28% of soil carbon. Given that soil carbon and glomalin in particular are the major contributors to soil structure and hence water holding capacity, farm and landscape managers should have as one of their major goals the building and maintenance of AM fungal populations. Tools available to these managers include low to nil soil disturbance such as no-till practices, low to nil use of pesticides, use of plants with well developed root systems and grazing practices that prevent soil compaction.

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