Exposing the Mycorrhizaes in Agriculture

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Abstract:
Mycorrhizal symbiosis is a highly evolved mutually beneficial relationship found between arbuscular mycorrhizal fungi (AMF) and vascular plants. The benefit of AMF to plants is mainly attributed to their ability to increase plant uptake of phosphorus and other non-mobile soil nutrients such as zinc and copper. Crop plants differ in their dependence on AMF mediated nutrient uptake, ranging from flax which is highly dependant on AMF for the uptake of phosphorus, to canola, a completely non-mycorrhizal crop. Agronomic practices such as crop rotation, fertilization and tillage affect the extent of mycorrhizal colonization and AMF mediated nutrient uptake of crops. Proper management of arbuscular mycorrhizal fungi has the potential to improve the profitability and sustainability of agricultural systems.

Introduction

Agricultural systems are composed of many organisms interacting in a multitude of complex relationships with their environment and each other. Biological relationships are found on a scale from antagonistic to beneficial. Mycorrhizal symbiosis is a highly evolved beneficial relationship found between arbuscular mycorrhizal fungi and plants. Arbuscular mycorrhizae improve plant fitness and productivity directly through increasing uptake of phosphorus and insoluble micronutrients, and indirectly by improving soil quality parameters.

Arbuscular mycorrhizal fungi (AMF) are thought to be ecologically important to most vascular plants. It has been said that it is easier to list the plants that do not form mycorrhizaes than those that do (Harley & Smith 1983). AMF are found in over 90% of vascular plants including most crop plants (Read et al., 1976; Harley & Smith, 1983). Mycorrhizae were present in the early ancestors of extant land plants and may have even facilitated the colonization of land by plants (Read et al. 1976; Simon et al. 1993). The persistence of the relationship over 460 million years indicates that mycorrhizaes confer an evolutionary advantage to plants.

It has been well established that arbuscular mycorrhizal symbiosis increases crop yields. A survey of 78 published field trials found that increased AMF colonization resulted in an average yield increase of 37% percent (McGonigle et al., 1988). Another study of 290 published field and greenhouse studies determined that increased colonization resulted in a 23% yield increase (Lekberg and Koide, 2005). Early season phosphorus supply is known to be critical for obtaining optimum crop yields. An inadequate phosphorus supply during early plant growth limits crop growth which cannot be recovered later in the season (Grant et al., 2001). Thompson (1994) found that mycorrhizal flax had higher seed yield than the un-inoculated control and dry weight of flax seed was linearly dependent on the degree of early AMF colonization. The degree to which AMF increases yields is also dependent on the soil type, nutrient status, crop and management (Karagiannidis and Hadjisavva-Zinoviadi, 1998). Karagiannidis and Hadjisavva-Zinoviadi (1998) found the effect of the AMF species *Glomus mosseae* on biomass of durum wheat (*Triticum turgitum* var. durum) in 10 different soils ranged from 11.6 to 3.6 times higher than the un-inoculated control.

In the past arbuscular mycorrhizal fungi were incorporated into the “black box” of soil microbial biomass and activities. The tremendous advancements in research on mycorrhizae physiology and ecology over the past 25 years have lead to a greater understanding of the multi-factorial role of mycorrhizae in the agroecosystem and how management practices influence the efficacy of mycorrhizal symbiosis.

Colonization and Symbiosis
The development of AM fungi prior to root colonization, known as presymbiosis, consists of three stages: spore germination, hyphal growth, and host recognition and appressorium formation (Douds & Nagahashi, 2000). Spores are thick walled multi-nucleate resting structures (Wright, 2005). AMF spores may germinate given suitable conditions of the soil matrix, temperature, carbon dioxide concentration, pH and phosphorus concentration (Douds & Nagahashi 2000). The germination of the spore is not thought to be under direct control of the plant as spores have been germinated under experimental conditions in the absence of plants both invitro and in soil. However, the rate of spore germination can be increased by plant host root exudates (Douds & Nagahashi, 2000).

The growth of arbuscular mycorrhizal hyphae through the soil is controlled by host root exudates and the soil phosphorus concentration. AMF colonization is higher in nutrient poor soils and decreased with the addition of phosphate fertilizer (Vivekanandan and Fixen, 1991; Hayman et al., 1975; Read et al. 1976). Low soil phosphorus concentrations increase hyphal growth and branching as well as induce plant exudation of compounds which control hyphal branching intensity (Nagahashi et al.1996, Douds & Nagahashi 2000). Arbuscular mycorrhizal fungi also have chemotaxic abilities which enable hyphal growth toward the roots of a potential host plant (Sbrana & Giovannetti 2005).

Once the arbuscular mycorrhizal fungal hyphae encounters the root of a host plant an apressorium is formed on the root epidermis from which the hyphae can penetrate into the host's parenchyma cortex (Gianinazzi-Pearson 1996). Once inside the parenchyma the fungi forms highly branching structures for nutrient exchange with the plant known as arbuscules (Figure 1). Arbuscules are the sites of exchange for phosphorus, carbon, water and other nutrients. The host plant exerts control over the intercellular hyphal proliferation and arbuscule formation (Gianinazzi-Pearson 1996).

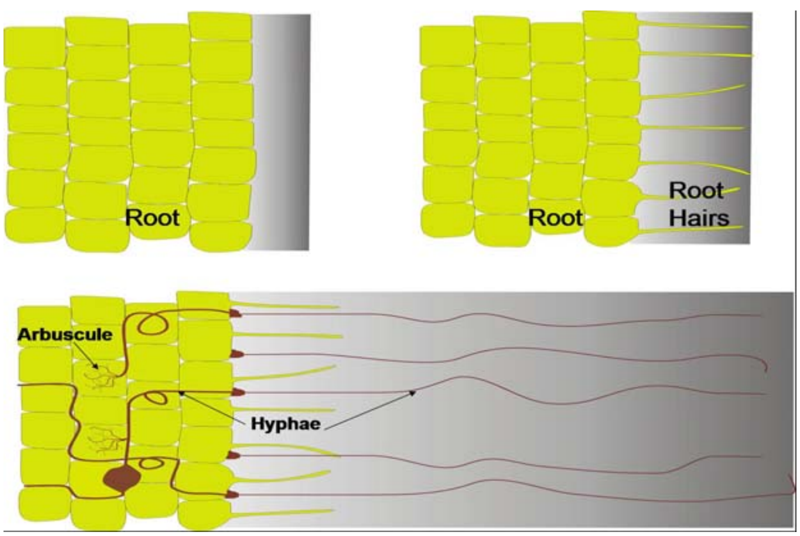

Figure 1: Mycorrhizal Colonization. Mycorrhizal hyphae greatly increase the surface area available for crop nutrient uptake. Arbuscules are the sites of nutrient exchange between the crop and mycorrhizal fungi.

There are two other types of morphologically distinct hyphae which originate from the colonized host plant root. Once colonization has occurred short lived runner hyphae grow from the plant root into the soil. These are the hyphae that take up phosphorus and micronutrients which are conferred to the plant (Figure 1). AM fungal hyphae have a high surface to volume ratio making their absorptive ability greater than that of plant roots (Tuomi et al. 2001). AMF hyphae are also finer than plant roots and can enter into pores of the soil that are inaccessible to roots (Bolan 1991). The third type of AMF hyphae grows from the roots and colonizes other host plant roots.

Nutrient Uptake and Exchange
The benefit of AMF to plants is mainly attributed to an increase in nutrient uptake, especially phosphorus. Phosphorus concentration had been shown to increase up to four times in mycorrhizal plants (Karagiannidis and Hadjisavva-Zinoviadi, 1998). This increase in uptake may be due to an increase in surface area of soil contact, increased movement of nutrients into mycorrhizae, a modification of the root

environment and increased storage (Bolan, 1991). Mycorrhizal hyphae prove to be much more efficient than plant roots at taking up phosphorus. Phosphorus travels to the roots via diffusion and AMF hyphae reduce the distance required for diffusion thus increasing uptake. The rate of inflow of phosphorus into mycorrhizae can be up to six times that of the root hairs (Bolan 1991). In some cases the role of phosphorus uptake can be completely taken over by the mycorrhizal network and all of the plant's phosphorus may be of hyphal origin (Smith et al. 2003).

Arbuscular mycorrhizal fungi may increase the plant uptake of other soil nutrients that, like phosphorus, low mobility in soil such as Zn and Cu. As with phosphorus, increased uptake by AMF is thought to be due to the increased surface area for uptake provided by the extraradical hyphal network. A decrease in mycorrhizal colonization due to high soil phosphorus levels has been reported to lead to plant deficiencies in other micronutrients that require mycorrhizal mediated uptake such as copper and zinc (Lambert et al., 1979; Timmer and Leyden, 1980; Pacovsky et al., 1986). Others (Liu et al, 2000; Lambert et al 1979) have also reported the effect of AMF on the uptake of micronutrients by plants is highly dependent on the level of nutrients in the soil.

Crop Dependency on Mycorrhizae

Crop plants differ in the extent and dependence on mycorrhizae for nutrient uptake. Some plants may be facultative mycotrophs while others may be obligate mycotrophs (Smith & Read, 2002). Crops with roots that are inefficient at seeking out phosphorus may receive the most benefit from mycorrhizal symbiosis. Crop plant root factors such as surface area, root hair abundance and length, growth rate, response to soil conditions and exudations determine the relative dependency on AMF for nutrient uptake (Smith & Read, 2002) Crops such as corn (*Zea mays*) and flax (*Linum usitatissimum*) are highly dependent on AMF to meet their early phosphorus requirements (Plenchette 1983; Thingstrup, 1999). Legumes (Leguminosae), beans (Fabaceae) and potatoes (*Solanum tuberosum*) also benefit significantly from mycorrhizae (Plenchett, 1983). Wheat (*Triticum* spp.), oat (*Avena sativa*) and barley (*Hordeum* spp.) benefit from mycorrhizal symbiosis but are not as dependent under conditions of high soil fertility (Plenchette 1983). Crops plants found in the families Polygonaceae, Brassicaceae do not form symbiotic relationships with AMF (Harley and Smith, 1983). This includes canola (*Brassica napus*), mustard (*Brassica juncea*)**,** beets (*Beta vulgaris*) and buckwheat (*Fagopyrum esculentum*).

Crop Rotation

Over the past 30 years much research has been done to elucidate how crop plant species influence AMF colonization, nutrient uptake and growth of subsequent crops in agricultural systems. A crop rotation is a system of growing crop plants in a repeated defined sequence (Harrier and Watson, 2003). Crop rotation is a tool for managing nutrient supply, weeds, pest and disease. It is well known that the preceding crop will affect the growth of the subsequent crop (Karlen et al., 1994). This phenomenon, known as the "rotation effect", cannot be explained entirely by nutritional effects (Bourgeois and Entz, 1996) and other factors such as AMF may play an important role in the success of crop rotations (Black and Tinker, 1979; Hendrix et al., 1995).

It has been well established that the AMF activity is decreased by non-AMF host plants and highly mycorrhizal host crops increase AMF inoculum potential of the soil and colonization of the subsequent crops (Black and Tinker, 1979; Gavito and Miller, 1998; Karasawa et al., 2002). For example, Karasawa et al. (2002) found an increase in AMF colonization and growth in maize following sunflower (*Helianthus annuus*, mycorrhizal) when compared to corn following mustard (non-mycorrhizal). Including non-mycorrhizal plants in the rotation reduces the rate of AMF colonization in following crops (Black and Tinker, 1979; Gavito and Miller, 1998). For example, Black and Tinker (1979) found that the rate of infection following the non-AMF host plant kale (*Brassica oleracea* L.) was lower than following the AMF host plant barley (*Hordeum distichon* L.). Gavito and Miller (1998) also observed delayed AMF colonization of corn (*Zea mays* L.) following canola (*Brassica napus* L.), a non-AMF host species, when compared to the colonization of corn following the AMF host species bromegrass (*Bromus inermis* Leys.) and alfalfa (*Medicago sativa* L.). The corn following canola had significantly lower AMF colonization for up to 62 days after planting after which the colonization was equal to the corn following an AMF host species. These observations suggest that AMF populations can be built up and the inhibitory effects of a non-mycorrhizal crop can be reversed after cropping with a mycorrhizal crop (Gavito and Miller, 1998).

The Effects of Fallow on AMF

Arbuscular mycorrhizal fungi are dependant on carbon input from their plant host for growth and reproduction. When the soil is cleared of AMF host plants the AMF population decrease and hyphal network deteriorate. Thus, mycorrhizal colonization and phosphorus uptake of host plants decreases with increasing length of the preceding fallow (Black and Tinker, 1979; Vivekanadan and Fixen, 1991; Kabir et al., 1999; Kabir and Koide, 2000). When the soil is left bare the viable hyphal network decreases over time which reduces the mineral uptake and growth of the subsequent mycorrhizal crop (Kabir et al., 1999). In a pot study by Kabir et al. (1999), a 90 day fallow was found to decrease active hyphae by 57%, AMF colonization of maize was decreased 33 % and the uptake of phosphorus by 19%, zinc by 54% and copper by 61% respectively. Clearly, fallowing is a practice that is detrimental to the AMF-plant symbiosis.

Management of weeds to increase mycorrhizal activity

Many common weed species of Manitoba are AMF hosts. This includes Green foxtail (*Setaria viridis*), Wild oats (*Avena fatua*), Canada Thistle (*Cirsium arvense*), Chickweed (*Stellaria media*), Cleavers (*Galium aparine*), Dandelion (*Taraxacum officinale*). Weeds in the families Chenopodiaceae, Amaranthaceae, Polygonaceae and Brassicaceae are non-mycorrhizal. This includes Wild buckwheat (*Polygonum convolvulus*), Lambs-quarters (*Chenopodium album*), Stinkweed (*Thlaspi arvense*), Redroot pigweed (*Amaranthus retroflexus*), Kochia (*Kochia scoparia*), Canola (*Brassica napus*).

There is evidence to suggest the presence of mycorrhizal weed hosts maintains a diverse AMF population and promotes highly effective symbiosis with the crop plant (Feldman and Boyle, 1998). Feldman and Boyle (1998) found that the AMF benefits to maize yield from maintaining a diverse weed cover crop outweighed any yield penalty due to competition. Indigenous AMF host weed species may provide an effective bridge for AMF in between cropping periods (Kabir and Koide 2000). Kabir and Koide (2000) compared a winter wheat cover crop to a dandelion cover and found that dandelion produced higher AMF colonization, P-uptake and yield in the following maize crop. Sorensen et al. (2005) found that a black medic cover crop was effective at increasing AMF colonization in leeks.

Tillage

Tillage reduces the inoculation potential of the soil and the efficacy of mycorrhizaes by disrupting the extraradical hyphal network (Miller et al. 1995; McGonigle & Miller 1999; Mozafar et al. 2000). Breaking apart the soil macro structure renders the hyphal network non-infective (Miller et al. 1995, McGonigle & Miller 1999). The disruption of the hyphal network decreases the absorptive abilities of the mycorrhizae because the surface area spanned by the hyphae is greatly reduced. This in turn lowers the phosphorus input to the plants which are connected to the hyphal network (McGonigle & Miller 1999). In reduced tillage system heavy phosphorus fertilizer input may not be required as compared to heavy tillage systems. This is due to the increase in the intact mycorrhizal network which provides access to greater surface area for crop phosphorus uptake (Miller et al. 1995).

Phosphorus Fertility

Phosphorus fertilizer can inhibit mycorrhizal colonization and growth. The benefits of AMF are greatest in systems where soil test P is low. As plant available soil phosphorus levels increases the plant tissue phosphorous increases and the plant carbon investment in mycorrhizae is not economically beneficial to the plant (Grant 2005). Encouragement of mycorrhizal symbiosis may increase early uptake of phosphorus, improving crop yield potential without starter P-fertilizer applications (Grant et al., 2005).

Conclusion

The role of arbuscular mycorrhizal fungi in agricultural ecosystems and the human impacts on mycorrhizae is increasingly being recognized. Management practices such as cropping rotation, tillage and phosphorus fertilization influence mycorrhizal activity. Promoting mycorrhizal activity ensures rapid colonization and effective symbiosis to plants during establishment. Early mycorrhizal symbiosis increases plant nutrition resulting in improved crop yields. Mycorrhizae are an essential element of successful low soil test phosphorus production systems. Encouragement of mycorrhizal symbiosis has great potential to benefit modern agricultural systems; therefore, it is important to consider mycorrhizae when making management decisions.

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