

Chapter 17: Arbuscular Mycorrhizal Associations and Their Significance for Wheat Production



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Arbuscular mycorrhizal (AM) fungi have the capacity to form symbiotic relationships with important crop species, such as wheat, corn, soybean and rice. The colonization with AM fungi provides numerous benefits for the host plant including an increased uptake of nutrients and an enhanced resistance against plant pathogens and other stresses such as drought, salinity, and heavy metals. In return, the plant transfers up to 20% of its photosynthetically produced carbohydrates to the fungus. The AM fungus is an obligate symbiont that relies on the host-derived carbon to reproduce and to complete its life cycle.

In South Dakota, research on using soil microorganisms to improve nutrient and water- use efficiency is just starting. The key role of these ubiquitous soil fungi for plant productivity and health, however, has prompted agronomic interest in these interactions with regard to a potential use as ‘biofertilizers and bioprotectors’ in sustainable agriculture. This chapter summarizes our current knowledge on the significance of AM fungi for wheat productivity and discusses agricultural practices that stimulate the AM colonization of the plant.

Nutrient uptake of arbuscular mycorrhizal plants

The most important benefit of the AM symbiosis for the plant is the improvement in the supply with nutrients, such as P, N, K and S, but also with trace elements, such as Cu and Zn. In general, an AM colonization is beneficial for the host plant as long as the net costs of the symbiosis for the host plant (carbon costs) are lower than the net benefits (increase in nutrient uptake) (Johnson et al. 1997).

Plants can take up nutrients via the ‘plant pathway’ or via the ‘mycorrhizal pathway’ (Fig. 17.1). The ‘plant pathway’ involves the uptake via the nutrient-absorbing surface area of the root, particularly the root hairs. The low mobility of many nutrients in the soil (e.g., P), however, leads to the development of depletion zones around the roots that often limit further nutrient uptake.

The ‘mycorrhizal pathway,’ on the other hand, involves the uptake of nutrients from the soil via the extraradical mycelium (ERM) and the transfer to highly branched, tree-like structures within the plant root

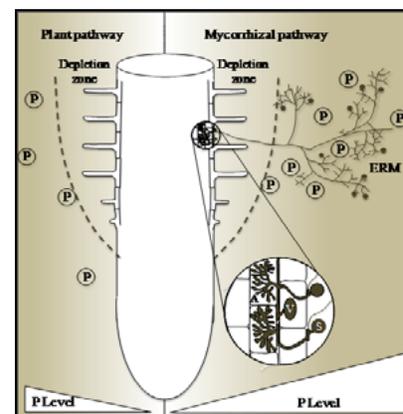


Figure 17.1. Model demonstrating the uptake of nutrients via the ‘plant pathway’ or the ‘mycorrhizal pathway’.
ERM – extraradical mycelium
S – spore, V – vesicle, A – arbuscule

cells, the arbuscules, which release the nutrients to the host plant. The ERM of the fungus extends the nutrient-absorbing surface of the root substantially beyond the depletion zone, thus providing access to nutrients in a larger soil volume. In addition, AM fungi are also able to take up organic nutrient resources that are not available for the host. According to estimates, the ‘mycorrhizal pathway’ is responsible for 50 to 80% of the plant’s P (Li et al. 2006) and for 75% of the plant’s N uptake (Tanaka and Yano 2005).

Despite relatively high total P soil contents, crop productivity in many soils is limited by P, and many crops show a relatively low responsiveness to P fertilizer (Holloway et al. 2001). The P fertilizer use efficiency (PUE) of wheat can be as low as 8 to 16%, and decreases with increasing P soil concentrations. The grain purchasing power of P fertilizer is low (Karamanos 2007; Mosali et al. 2006). This is due to the fact that plants are not able to store nutrients very efficiently and the nutrient uptake capacity is regulated by the demand. AM fungi, on the other hand, are able to store P as polyphosphate, which allows the fungus to provide the host plant continuously with P even if soil P levels decrease. This characteristic of AM fungi could be helpful in increasing the PUE of agricultural systems (Singh and Singh 2008).

Mycorrhizal fungi contribution to nutrient uptake and productivity in wheat

Published data about the mycorrhizal colonization rate in wheat roots range from 10 to 80% colonized root length (Li et al. 2005; Sharif and Nasrullah 2009). Despite relatively high colonization rates, the mycorrhizal dependency of wheat has been considered as relatively low with potential yield losses of 10 to 30% without an AM colonization (Queensland Government 2011). It has been suggested that wheat may not benefit from the AM symbiosis due to its relatively large and highly branched root system and dense root hairs (Graham and Abbott 2000; Zhu et al. 2001).

However, our own studies and the results of other authors suggest that wheat cultivars differ in their response to AM fungi and that mycorrhizal benefit depends on the nutrient supply conditions. We examined the mycorrhizal dependency of different wheat cultivars under various nutrient supply conditions and found that under low nutrient level, some wheat cultivars showed yield increases of 60% after colonization with AM fungi. The yield gains of mycorrhizal plants was higher in some varieties than in others.

Azcón and Ocampo (1981), who tested the mycorrhizal responsiveness of thirteen different wheat cultivars, found biomass gains of more than 40% in some cultivars, and low or slightly negative growth responses in other cultivars (Fig. 17.2, blue bars). However, it should be noted that, in general, the plants with negative or low positive growth responses showed relatively low mycorrhizal colonization rates (Fig. 17.2, red line).

Hetrick et al. (1992) concluded that genotypic differences depend on the root architecture and that higher mycorrhizal benefits can typically be found in genotypes with a lower root fibrousness.

Zhu et al. (2001) reported that wheat varieties developed before 1900 had a higher responsiveness than modern varieties. However, modern varieties from the U.S. or Great Britain also showed biomass increases of 29 to 100% following an inoculation with AM fungi (Hetrick et al. 1992). Even wheat varieties that were considered not susceptible to AM fungi showed high colonization rates under field conditions (Li et al. 2005).

In our experiments, the mycorrhizal dependency was, in general, lower when more nutrients were supplied. Under high nutrient supply conditions, no effects or growth reductions were observed as a result

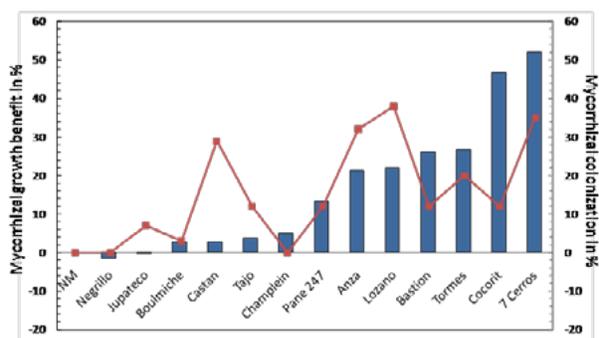


Figure 17.2. Biomass growth benefit or mycorrhizal responsiveness (blue bars) and mycorrhizal colonization (red line) of thirteen different wheat cultivars and non-mycorrhizal control plants (NM). (Data of Azcón and Ocampo 1981)

of the AM colonization. However, a low mycorrhizal responsiveness does not mean that the AM fungus does not contribute to wheat nutrient uptake (see above, Li et al. 2006; Schweiger and Jakobsen 1999). It has been suggested that the uptake via the plant pathway is not affected by the AM symbiosis and that the 'plant pathway' and 'mycorrhizal pathway' act additively. This has led to the assumption that the uptake via the mycorrhizal pathway can be neglected, when P fertilizers are added and AM plants don't show a positive growth response. This view, however, is now being questioned (Smith et al. 2009a; Smith et al. 2009b).

Mycorrhizal wheat has been shown to take up more P from the soil than non-mycorrhizal plants, regardless of growth responses (Ravnskov and Jakobsen 1995). Li et al. (2006) estimated that in non-responsive wheat plants, 50 to 80% of the P was taken up via the mycorrhizal pathway. Schweiger and Jakobsen (1999), who studied the P uptake and transport via the mycorrhizal ERM to winter wheat, reported that, even at typical field soil fertility levels of 28 $\mu\text{g NaHCO}_3$ -extractable P g^{-1} soil, the AM fungus contributes significantly to the P uptake of the plant. This indicates that:

1. In mycorrhizal plants, the P uptake via the plant pathway is reduced.
2. Mycorrhizal wheat changes its nutrient uptake strategy and shifts the responsibility for nutrient uptake from the plant to the mycorrhizal pathway.
3. Even under conditions in which P fertilization limits the mycorrhizal responsiveness, the AM fungus contributes to P uptake.

These findings should have important implications and demonstrate that the mycorrhizal responsiveness should be considered as an important trait in crop breeding programs that seek to increase the nutrient efficiency of wheat.

AM colonization impacts on stress resistance in wheat

In addition to the positive effects on nutrient uptake, AM fungi can also increase the resistance of plants to a variety of other stresses. For example, drought stress is often considered to be the most significant factor restricting crop productivity world-wide, and therefore the development of wheat genotypes and management techniques that improve drought stress tolerance represents an urgent research priority (Hagyó et al. 2007).

Many authors have shown that the AM symbiosis can improve the drought resistance of plants, and mycorrhizal wheat plants had an almost 40% higher biomass and grain yield under drought stress compared to non-mycorrhizal control plants (Al-Karaki et al. 2004).

The cadmium levels in grains of Durum wheat harvested in some areas of the Northern Great Plains already exceed the maximum permissible concentration recommended by the World Health Organization (Wolnick et al. 1983). It can be expected that these levels will further increase, since the declining purity of phosphate rock reserves and P fertilizers will increase the heavy metal input in agricultural soils. AM fungi alleviate the stress response of plants to heavy metals (Aloui et al. 2011), and have also been shown to increase the tolerance of wheat to high salt concentrations (Daei et al. 2009).

Spring and winter wheat productivity in South Dakota and the Northern Great Plains is challenged by many fungal pathogens, such as *Fusarium* head blight, rusts, the leaf spot complex and the root rot complex. *Fusarium* head blight, for example, was responsible for \$34 million in crop losses in 2005. AM fungi have been shown to increase plant resistance particularly against root pathogens.

Particularly important is the bioprotection conferred to plants against *Aphanomyces*, *Cylindrocladium*, *Fusarium*, *Macrophomina*, *Phytophthora*, *Pythium*, *Rhizoctonia*, *Sclerotinium*, *Verticillium*, *Gaeumannomyces graminis* (Take-all), *Thielaviopsis*, and various nematodes (Behn 2008). The AM colonization can lead to quantitative and qualitative changes in the microbial community composition, and there are indications that the ERM of AM fungi supports plant growth promoting rhizobacteria (PGPR), but suppresses plant pathogens (Andrade et al. 1998). While poorly understood, several

mechanisms have been proposed to explain the improved disease resistance, including:

1. Changes in the microbial community composition and an increase in the number of antagonistic microbes.
2. Reduction in the availability of nutrients for pathogens.
3. Stimulation of plant defense mechanisms.
4. Increase in plant fitness resulting from an improved nutrient supply.

Effects of agricultural management practices on AM colonization

AM fungi have the potential to reduce the required fertilizer inputs and the susceptibility to abiotic and biotic stresses, and to increase productivity and environmental sustainability of wheat production. However, agricultural management practices such as P and N fertilization, tillage or no-tillage, crop rotations, conventional or organic farming practices can affect the AM spore density in the soil and mycorrhizal colonization of food crops. It is long known that the reliance on fertilizers to meet plant nutrient requirements can decrease the AM spore density and mycorrhizal colonization (McGonigle et al. 1990; Singh and Singh 2008).

The greater disturbance by tilling can also lead to a reduction in AM spore density and mycorrhizal colonization of crops (van Groenigen et al. 2009) and can negatively affect the AM community composition by favoring less beneficial AM species. A combination of no-tillage and crop rotations has been shown to lead to a greater richness and biodiversity of microbial communities, including AM fungi. Non-mycorrhizal preceding crops such as Brassica species have been shown to reduce the mycorrhizal colonization of wheat, whereas mycorrhizal susceptible plants such as wax flax increase the spore density and mycorrhizal colonization of wheat (Gao et al. 2009).

As a rule of thumb, AM communities and the mycorrhizal colonization of wheat can be increased by a reduced tillage intensity and application of fertilizers, by an increase in crop diversity and crop rotations particularly with mycorrhizal plants, and by using appropriate techniques to inoculate the soil with AM fungi.

Conclusions

Mycorrhizal fungi can represent an important tool to increase the environmental sustainability of wheat production in the future with their unique effect on nutrient uptake and stress resistance. More research is needed to identify AM fungal species that provide the highest benefit for the host plant along with management practices that are able to facilitate the AM colonization and the benefit for the plant. The high colonization rates of wheat under field conditions and the impact of AM fungi on nutrient uptake strategies, indicate that the mycorrhizal responsiveness should be included as an important trait into breeding programs for nutrient-efficient and stress-resistant wheat cultivars.

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