

Managing the Soil Mycorrhizal Infectivity to Improve the Agronomic Efficiency of Key Processes from Natural Ecosystems Integrated in Agricultural Management Systems

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Contents

1	Introduction.....	18
2	Ecological Importance of the Arbuscular Mycorrhizal Symbiosis in the Plant Phosphorus Acquisition.....	20
3	Application of AMF to Increase the Overall Yield of Important Staple Crops.....	21
4	Potentialities of Multispecies Plant-Cropping Systems to Sustainably Manage the Composition of AMF Communities.....	24
5	Conclusion and Future Prospects.....	25
	References.....	25

Abstract Phosphorus (P) is a major nutrient limiting plant growth in many soils. To reduce P deficiencies and ensure plant productivity, large quantities of soluble forms of P fertilizers are applied worldwide every year. However up to 80 % of P chemical fertilizer amendments are lost as it is easily precipitated into insoluble

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forms (CaHPO_4 , $\text{Ca}_3(\text{PO}_4)_2$, FePO_4 , and AlPO_4) and becomes unavailable for plant uptake. Some soil microorganisms are known to be involved in the solubilization of insoluble phosphate by excreting organic acids, phenolic compounds, protons, and siderophores. Among phosphate-solubilizing microorganisms, it has been reported that mycorrhizal fungi have the ability to actively mobilize and translocate nutrients from minerals and soil organic matter, directly to their host plant. Mycorrhizal fungi constitute a key functional group of soil biota that greatly contribute to productivity and sustainability of terrestrial ecosystems. These are ubiquitous components of most of the ecosystems throughout the world and considered key ecological factors in governing the cycles of major plant nutrients and in sustaining the vegetation cover. It has been suggested that the integration of key processes from natural ecosystems (plant-plant facilitation, positive plant soil feedback) in agricultural management systems could resolve increasing agricultural problems. Since these natural processes are frequently connected with arbuscular mycorrhizas, it is necessary to apply mycorrhizal inoculation technologies or to manage native arbuscular mycorrhizal fungus communities to replace or reinforce the mycorrhizal potential in these degraded areas. This chapter aims to describe the influence of some cultural practices (rotation, intercropping, mycorrhizal inoculation) that mimic these natural processes in agrosystems, on soil microbiota (i.e.: soil mycorrhizal infectivity) leading to a sustainable microbial complex with high efficiency against phosphorus mobilization and transferring phosphorus from the soil organic matter or from soil minerals to the host plant.

Keywords Facilitation • Plant soil feedback • Intercropping • Rotation • Mycorrhizal symbiosis • Mycorrhizosphere • P availability

1 Introduction

The Green Revolution has been designed from a series of researches, development, and technology transfer programs, performed between the 1940s and the late 1960s, in order to enhance agricultural production worldwide with a focus on the developing countries. These initiatives have begun more markedly in the late 1960s. This technological revolution was based on a package of modern inputs based on three main cultural practices such as irrigation, improved seeds, and use of fertilizers and pesticides. The Green Revolution had primary ambition to transform agricultural systems in developing countries to significantly enhance the productivity of cultivated areas and thus to ensure sustainable food security for the populations of these regions (Freebairn 1995).

Despite significant positive results in the fight against food insecurity, the intensive farming practices, ignoring the ecological characteristics of the environment, have led to a dramatic impact on the environment. Indeed, the recommended cultural practices have generated widespread soil pollution resulting from the

intensive use of pesticides and chemical fertilizers, and an overall loss of biodiversity and agro-biodiversity. They also altered soil quality due to a worsening of water and wind erosion. The social consequences were also recorded through an increased rural–urban migration and the emergence of slums on the outskirts of megacities.

In order to minimize the negative impacts of the expansion and intensification of modern agriculture, the development of sustainable farming practices that sustain yields and optimize the use of localized resources has been proposed. It has led to the emergence of new concepts such as sustainable agriculture in France, Ecoagriculture of IUCN (International Union for Conservation of Nature), and Agroecology. Hence the new concept of “doubly green revolution” has been suggested that combines the objectives of the Green Revolution and the maintenance of biological diversity and ecosystem resilience.

Agroecology is usually defined as the science that uses ecological theory to study, edify, manage, and evaluate agricultural systems in a context of a sustainable agricultural production (Wezel and Soldat 2009). This innovative approach considers all the interactions between the main components of farming systems (biophysical, technical, and socioeconomic components). In particular, it requires agricultural practice innovations to put agroecological technologies into practice.

The integration in agricultural cropping systems of some biological mechanisms governing the spatial and temporal evolution, productivity, and resilience of natural ecosystems has been suggested as models for the design of sustainable systems of land use. These long-term evolving natural processes result in ecosystems that are highly productive, resilient (rate of recovery after disturbance), and stable (the ability of an ecosystem to maintain a steady state) (Webster et al. 1975; Leps et al. 1982; Ewel 1999). These natural processes (i.e.: plant-plant facilitation, positive plant soil feedback) that improve plant stress resistance and plant mineral nutrition are usually connected to arbuscular mycorrhiza (AM) associations between plant roots and fungi belonging to the small fungal phylum Glomeromycota (Schüßler et al. 2001). AM symbiosis is an ubiquitous symbiotic process in all the terrestrial systems and on most plant species (80 % of plant families). Although enhanced plant phosphorus uptake is considered as the main benefit of AM fungi (AMF) to plants, this fungal symbiosis may also provide “non-nutritional” effects with improvements in soil structure and soil microbiology and in plant stress resistance. The potential of AMF to improve food security results from the ability of all globally important food crops to form mycorrhizal symbiosis in natural conditions. It is now well known that the magnitude of the benefits expected to the plant growth by appropriate application of AMF is mainly dependent to the AM propagule abundance, the AMF community structure, the composition of the cropping systems, the soil, and climate context (Burrows and Pfleger 2002). Hence managing AM soil infectivity in agro-systems could follow two different schemes that could be combined in practice: (1) the “reductionist” scheme and (2) the “holistic” scheme (Fig. 1). The reductionist pattern aims to improve plant performance in disturbed soils by adding specialized AMF inocula adapted to the environmental conditions and to the target crop. The objectives of the holistic pattern are rather at preserving and restoring the composition

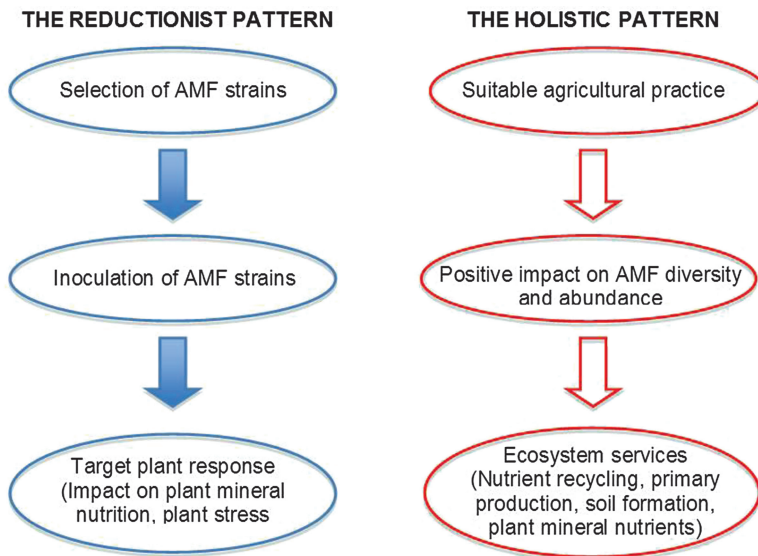


Fig. 1 Different patterns to manage the AM soil infectivity in agrosystems. The reductionist pattern aims to improve crop productivity by inoculating selected AM fungal strains whereas the holistic pattern allows to improve AM fungal diversity and abundance for ensuring AMF-dependent ecosystem services (adapted from Fester and Sawers 2011)

of native AMF communities. To present the benefits expected from the integration of AMF in agricultural practices through the combination of the “reductionist” and “holistic” approaches, we review (1) the importance of AMF in plant mineral nutrition, especially for the plant phosphorus nutrition, (2) the benefits to important staple crops resulting from the AMF inoculation (wheat, maize, vegetables, etc.), and (3) the potentialities of multispecies plant-cropping systems to sustainably manage the composition of AMF communities and their expected impact on plant growth.

2 Ecological Importance of the Arbuscular Mycorrhizal Symbiosis in the Plant Phosphorus Acquisition

Phosphorus (P) is an essential macronutrient for plant growth and its uptake from soil is effective almost exclusively in the form of soluble phosphate anions (Schachtman et al. 1998). Many studies have reported the significance of AMF for growth of crop species through different impacts on the nutrient supply and changes in plant physiology and morphology (Pellegrino and Bedini 2014). In general, the reported effect of mycorrhiza on plant P uptake is not always consistent because of the complexity and interactions between the involved components of the system (host plant genotype, AMF, environment conditions) (Baum et al. 2015). In

particular, it has been shown that the AM symbiosis promotes the inflow of slowly mobile nutrients to plant roots, predominantly P (Antunes et al. 2007). Koide and Kabir (2000) showed that extraradical hyphae of the AM fungus, *Glomus intraradices*, can hydrolize organic P (i.e., phytate) and that the resultant inorganic P can be taken up and transferred to host root. It has also been reported that mycorrhized plants respond positively to the soil amendment with insoluble forms of inorganic phosphorus such as rock phosphates (RPs) (Cabello et al. 2005; Duponnois et al. 2005). However the mechanisms involved in this plant response remain unclear although it has been hypothesized that AMF hyphae could excrete some chelating agents that could actively mobilize soluble P from the phosphate inorganic forms. Antunes et al. (2007) showed that the mechanisms underlying increased P uptake by the AM symbiosis establishment did not result from the fungal release of H⁺ ions alone or in combination with organic acid anions. It suggested that the positive AM effect on P uptake from RP was the result of interactions between AM symbionts and the soil microflora (Jayachandran et al. 1989). It is well known that extraradical hyphae of AMF provide an important area for interactions with soil microbes and a large pathway for the translocation of energy-rich plant assimilates to the soil (Johansson et al. 2004). The AM associations impact the composition of soil microflora leading to a zone influenced by both the mycorrhizal fungus and the host plant, commonly named the *mycorrhizosphere*, and a more specific zone resulting from the impacts of individual fungal hyphae, the *hyphosphere* (Linderman 1988; Johansson et al. 2004). Inside these two compartments occurred diverse multi-trophic interactions that influence the effects of the mycorrhizal symbiosis on the plant growth resulting from a direct positive effect (nutritional mechanisms) and an indirect positive effect via a selective pressure on microbial communities (Fig. 2) (Frey-Klett et al. 2005). Numerous studies have shown that some phosphate-solubilizing bacteria can interact synergistically with mycorrhizal fungi and facilitate phosphorus uptake by the plants (Muthukumar et al. 2001; Caravaca et al. 2004; Cabello et al. 2005). In field conditions, it has been reported that the abundance of phosphate-solubilizing bacteria belonging to the fluorescent pseudomonad group was correlated to the level of plant mycorrhizal colonization (Duponnois et al. 2011). The roles of the mycorrhizosphere microorganisms have to be considered in order to ensure the productivity and stability of agrosystems in the context of a sustainable agriculture.

3 Application of AMF to Increase the Overall Yield of Important Staple Crops

It is well known that mycorrhizal fungi are already present in all agricultural soils but AMF community structure is highly dependant to the environmental conditions (i.e., soil characteristics) and the cultural practices (Smith and Read 2008). Hence the implementation of AMF inoculation is particularly important when mycorrhizal

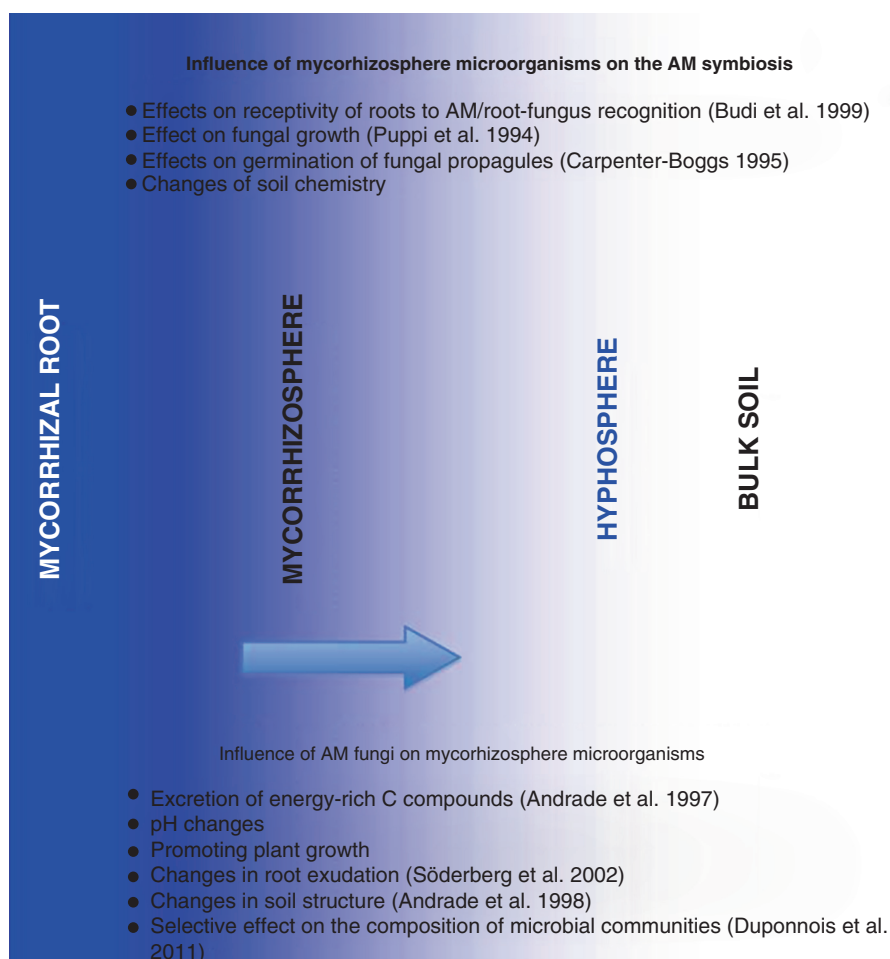


Fig. 2 Interactions between the AM symbiosis and the mycorrhizosphere/hyphosphere microbial communities (modified from Johansson et al. 2004)

potential of native soil is quantitatively and qualitatively inadequate (Requena et al. 1996; Koide and Mosse 2004). A meta-analysis of 38 published field trials has been conducted to determine the impacts of AMF inoculation on P, N, and Zn uptake, growth, and grain yield of wheat (Pellegrino et al. 2015). The results showed that AMF inoculation promoted aboveground biomass, grain yield, aboveground biomass, P content and concentration of aerial parts, straw P content, N content and concentration of aerial parts, grain N content, and grain Zn concentration. The positive impact of AMF inoculation on wheat growth was dependent on organic matter concentration, pH, total N and available P concentration, texture of soil, climate, and the AMF species inoculated. Lekberg and Koide (2005) reported the benefits on

yield, biomass, and phosphorus concentrations expected from AMF inoculation by conducting a meta-analyses of 290 published field and glasshouse trials. They concluded that the impacts of AMF inoculation were highly dependent on the levels of soil P and indigenous mycorrhizal soil infectivity. Most AMF inoculation field trials have been conducted in temperate agroecosystems where soil fertility (especially bioavailable phosphorus content) is higher than that frequently recorded in tropical and Mediterranean soils (Friesen et al. 1997). This lack of knowledge on the AMF potentialities to increase crop production is surprising since it is in these deficient soils that AMF application provides the strongest effect on the plant growth (Rodriguez and Sanders 2015). Some controlled mycorrhization field experiments performed in arid and/or tropical areas on field-grown wheat are listed in Table 1. However one important food plant in the tropics, Cassava (*Manihot esculenta* Crantz), has been widely studied for its response to AMF application. It has been demonstrated that Cassava was highly mycorrhizal dependent for its growth and mineral nutrition with a mycorrhizal dependency of 95 % (Sieverding and Howeler 1985; Howeler et al. 1987). In another experiment, the effect of inoculation with *Glomus clarum* on the growth of the cassava cultivar TMS 30572 has been investigated in field conditions in a low-nutrient tropical soil (Fagbola et al. 1998). The fungal inoculation provided an increase of the fresh tuber yield.

Table 1 Effect of AMF inoculation with arbuscular fungi on the growth and nutrient uptake of the productivity of field-grown wheat

Wheat cultivars	Country	AMF species	Biomass yield (%)	Grain yield (%)	References
Wheat cv. TAM-105	Iran	<i>Glomus etunicatum</i> <i>Glomus mosseae</i>	+21.6 +6.2	+41.4 0	Al-Karaki et al. (2004)
Wheat cv. Steady	Iran	<i>Glomus etunicatum</i> <i>Glomus mosseae</i>	+31.6 0	+41.8 0	Al-Karaki et al. (2004)
Wheat cv. Tetra	Mali	<i>Glomus intraradices</i>	+22.1	+22.4	Babana and Antoun (2006)
Unknown	India	<i>Glomus fasciculatum</i>	+77.9	+55.5	Khan and Zaidi (2007)
Wheat cv. UP-2338	India	Natural mycorrhiza consortium	nd	+81.0	Mader et al. (2011)
Wheat cv. HD 2643	India	<i>Glomus fasciculatum</i>	nd	+21.2	Mahanta et al. (2014)
Wheat cv. WH 147 × WH 533	India	<i>Glomus fasciculatum</i>	+8.7	+18.1	Singh et al. (2004)
Wheat cv. WH 533 × Raj 3077	India	<i>Glomus fasciculatum</i>	+5.5	+12.3	Singh et al. (2004)
Unknown	India	<i>Glomus mosseae</i>	+15.7	+12.6	Suri et al. (2011)
Unknown	India	<i>Glomus intraradices</i>	+15.4	+13.4	Suri et al. (2011)

nd not determined

4 Potentialities of Multispecies Plant-Cropping Systems to Sustainably Manage the Composition of AMF Communities

Alterations in plant diversity are known to impact aboveground ecosystem functioning (Cardinale et al. 2007; Hector and Bagchi 2007). Numerous studies studying the impact of plant diversity on the composition of soil microflora reported either positive (Milcu et al. 2008) or no influences (Habekost et al. 2008). Hence multispecies cropping systems may often be considered as a practical application of ecological principles based on biodiversity, plant interactions, and other natural regulation mechanisms (plant facilitation, positive soil feedback). Some studies have reported positive links between the composition of the cover plants and different ecological processes (i.e., primary productivity, soil nutrient content, and resilience capacity) (Erskine et al. 2006). In agroecosystems, multispecies plant-cropping systems can reduce pests and diseases resulting from an improvement of biological control or direct control of pests (Gurr et al. 2003). Different cropping systems can be designed according to their composition and their management (Table 2). In multispecies plant-cropping systems, the use of legume plants is fundamental to maintain soil fertility, mainly resulting from the tripartite symbiotic interaction between legumes, rhizobia, and AMF that positively influences P and N crop mineral nutrition (Scheublin et al. 2007) but also to maintain the mycorrhizal soil infectivity (Azcon-Aguilar et al. 1986).

Table 2 Forms of species mixture in annual crop agricultural systems (from Malézieux et al. 2009)

Type of system	Species number	Number of strata	Example/location
Combination (intraspecific mixture)	1	1	Cereals
Relay cropping (time overlap only during one part of the life cycle of each species)—crops or crop and service plant	2	1 or 2	Maize/beans, groundnut/cotton (Africa)
Row intercropping (growing two or more species in rows)—crops with crops or crops with service plant	2	1 or 2	Cereals/herbaceous legumes and grasses, e.g., rice/arachis pintoï (Europe, South America)
Mixed intercropping (no distinct row management)	2 – <i>n</i>	1	Two species (maize-sorghum, maize cassava, etc.) to <i>n</i> species (tropical garden, e.g., rice, maize, tomato, cassava) (humid tropics), annual grassland (Europe)

5 Conclusion and Future Prospects

Although numerous studies focussed on the potentialities of AMF application to sustainably improve crop productivity, this technical approach has not been widely integrated into modern agriculture practices. It has been frequently argued that the lack of high-quality mass produced AMF inoculum. However, it could also be noted that the AMF application remains too simplistic without taking into account the basic ecological concepts. Hence researches have to perform in order to explain (1) the biological determinants of the introduced AMF inoculant (soil receptivity to the AMF inoculation), and (2) the impacts of the AMF inoculation to the soil functioning and the composition of the soil microflora. Finally, the AMF potentialities have to integrate the design of multispecies agricultural systems in order to optimize the productivity of these innovative cultural practices.

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