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The Use of Mycorrhizae to Enhance Phosphorus Uptake: A Way Out The Phosphorus Crisis

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Abstract

In order to maintain crop yields, modern agricultural systems are highly dependent on continual inputs of Phosphate-based fertilizers. These fertilizers are processed from phosphate rock, which is a non-renewable natural resource. Therefore, the world could soon face a resource scarcity crisis that might affect global food security. Arbuscular mycorrhizal fungi, which form a symbiosis with the roots of nearly all vascular plants, could play a key role in solving the phosphate shortage problem. Mycorrhizal symbioses are recognized for their importance in plant nutrition, particularly in phosphorus uptake. Also, by improving the efficiency of nutrients uptake, and by increasing plant resistance to pathogens and abiotic stresses, mycorrhizal symbiosis can enhance plant growth and therefore reduce the need for Phosphate-based fertilizers. In this review, we provide an update of recent findings and reports on inorganic phosphorus and on mycorrhizae as the cornerstone of a "second green revolution".

Keywords: Phosphorus; Rock phosphate; Arbuscular mycorrhizal fungi; Symbiosis; Biofertilizer; Sustainable agriculture

Introduction

Fertilizer utilization to supplement soil nutrients, to promote plant growth and to increase crop productivity and food quality is prevalent in modern agriculture. As a result, crop production and global food security are highly dependent on fertilizers input to agricultural lands [1]. Fertilizer provide the three major nutrients (nitrogen, phosphorus and potassium) required by plants. Among these nutrients, phosphorus constitutes a particularly critical component because on one hand it is limiting for crop yield on a large proportion of global arable land and, on the other hand, it is a non-renewable resource [1-3].

Phosphorus is not a rare element on Earth, but it is often found in low concentrations [4]. Therefore, the deposits that are rich enough in phosphorous to allow economically viable extraction are limited [1,3-5]. Accurate and reliable data on phosphorus reserves are nearly inexistent or inaccessible [4,5] and the scientific community and the industry do not agree on the remaining quantity of phosphate. Nevertheless, all experts acknowledge that we will have to face a shortage sooner or later. Given the predicted global demand for food and the current rate of phosphorus extraction, the resource could be depleted in 50 to 125 years [1,3,5]. In the recent news feature "The disappearing nutrient", Gilbert [5] points to a potential crisis of agricultural phosphate availability brought by increasing use and decreasing worldwide supply. At present, modern agricultural systems are highly dependent on continual inputs of phosphate-based fertilizers: for example, the use of phosphate-based fertilizers has increased from 9 million tons per year in 1960 to 40 million tons in 2000 [3].

The issue of phosphorus scarcity can be addressed with different approaches. First, we can develop technologies to extract phosphorous from lower-quality, smaller or less accessible deposits, such as apatite deposits in northern Québec [6]. Second, we can find ways to recover and reuse phosphate. For example, the recuperation of phosphate from wastewater in the form of struvite and the use of urine to fertilize crops are very promising solutions [1,5]. Finally, we can promote practices and lifestyles that reduce the need for phosphate fertilizers, for example by avoiding over fertilization and encouraging people to shift their diet toward less phosphate-intensive food. Taking into consideration soil microorganisms, such as mycorrhizal fungi, that can greatly enhance phosphorus uptake, could also be a very effective approach for a more efficient resource use. In order to overcome the phosphate crisis, it is critical that we adopt a holistic and comprehensive vision to the management of the phosphorus cycle, and that we integrate all the potential solutions.

It is unfortunate that many authors interested in this issue overlook the potential of mycorrhizal symbiosis to reduce the need for phosphate addition in agricultural lands. Mycorrhizae, a fungal solution to the phosphate availability problem honed by over 450 million years of co-evolution with plants, could be a key factor in solving this crisis.

Mycorrhizae and phosphorus uptake

Mycorrhizae are mutualistic symbiotic associations based on bidirectional nutrient transfer between soil fungi and the roots of vascular plants. The plant supplies the fungi with sugars produced by photosynthesis, while the hyphae network improves the plant capacity to absorb water and nutrients [2,7,8]. Arbuscular mycorrhizae, also called endomycorrhizae, are the most ancient, common and widespread types of mycorrhizae (Figure 1) [7]. The arbuscular mycorrhizal (AM) fungi are a group of endophytes that constitute the phylum Glomeromycota. AM fungi form symbiosis with the roots of approximately 80% of all vascular plant species, including many important crop species, such as maize, wheat, rice and potato [7]. Demonstrations of the positive effect of mycorrhizal symbiosis on plant productivity are now abundant, stimulation of growth usually following colonization by the AM fungi [2,7] (Figure 2).

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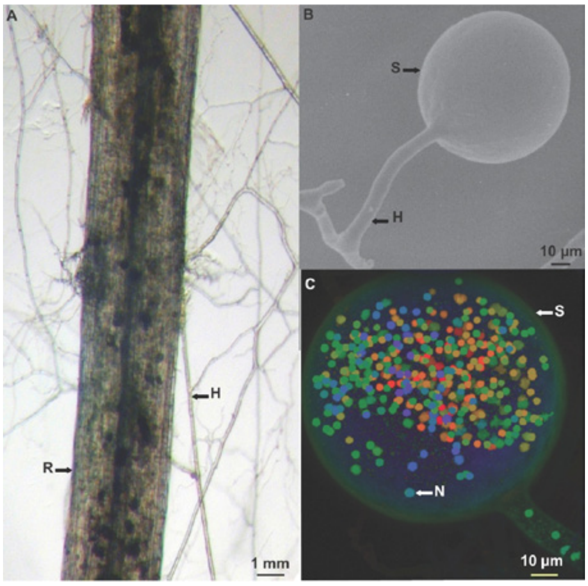

Figure 1: **A**, Colonized carrot-root showing fungal colonization that is restricted to the root cortex. **B** and **C**, show typical multinucleated asexual spores produced in the soil. **B**,spore of the AM fungus *G. irregulare* observed by scanning electron microscopy. **C**, spore of the AM fungus *G. diaphanum* observed by confocal laser scanning microscopy [28]. H: Hypha; N: Nucleus; R: Root; S:Spore.

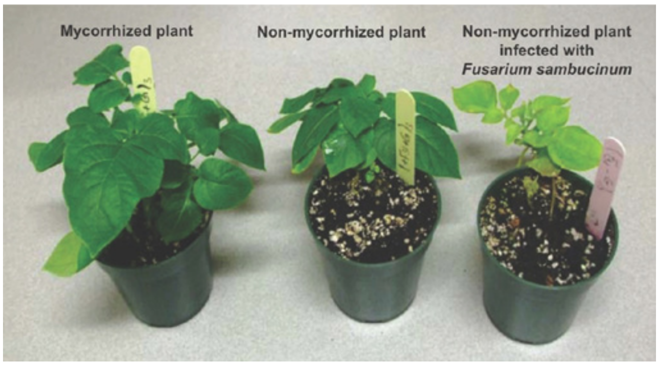

Figure 2: Potato plants (cultivar Riba) showing typical impact of AM fungi to promote plant growth and plant protection against soil-born pathogens.

Mycorrhizal symbioses contribute significantly to plant nutrition, particularly to phosphorus uptake [7]. First, because of its very large surface area, AM fungi hyphal network is very efficient in nutrient uptake [2,7]. The fungal partners form extraradical mycelium, which can be very extensive in the soil and increase prominently the absorbing area of roots [7]. Second, phosphorus is a highly immobile element because it is easily absorbed by soil particles and a phosphate-free zone rapidly occurs around plant roots [4]. Extra radical hyphae extend beyond this depletion zone, absorbing bio-available phosphate that is otherwise not accessible to the plant (Figure 3) [2,9]. Also, phosphate ions in soil become rapidly bound with cations, forming unsoluble complexes that are unavailable to plants [3,7,9]. It is known that the presence of mycorrhizal fungi in the soil improves phosphate solubility. Whether the fungus itself releases enzymes breaking the unsoluble P complexes is still debated. Nevertheless, it is certain that AM fungi interact with rhizosphere microorganisms and enhance the establishment of bacteria [10,11], many of which secrete phosphate-solubilizing enzymes [7]. These interactions have positive synergetic effects resulting in enhanced plant nutrition, growth and survival [7,10,12]. The nutrients mobilizing processes described above are particularly important in plant nutrition and explain why non-mycorrhizal plants require higher levels of soil fertility to maintain their health [7].

Other benefits of mycorrhizal associations

Improved phosphorus nutrition is probably the most widely known and most documented benefit of AM fungi for plants [9,13]. It is also recognized that mycorrhizal symbioses improve other nutrients (such as nitrogen, zinc and potassium) uptake [7,9] and enhance symbiotic N-fixation ability [7,9,10].

In addition, AM fungi have many non-nutritional benefits to plants. First, AM fungi hyphae enhance water uptake by increasing the absorbing surface of the root system and by accessing the smallest soil pores [7]. Mycorrhizae therefore contribute significantly to increase plant resistance to drought and can also relieve other abiotic stresses [9]. Second, AM fungi improve soils structure and contribute to soil aggregation, leading to increased soil stability and quality as well as decreased erosion [9,12]. The mechanisms implied (reviewed in Rilling and Mummey [14]) are biological, biochemical and physical processes. These mechanisms include, for example, the physical retention of aggregates by the mycelium and the secretion of glomalin, a glue-like fungal substance that bounds soil particles between them as well as to hyphae [9,12,14]. Finally, AM fungi also help plants to resist and overcome pathogen infections [13] (reviewed in St-Arnaud

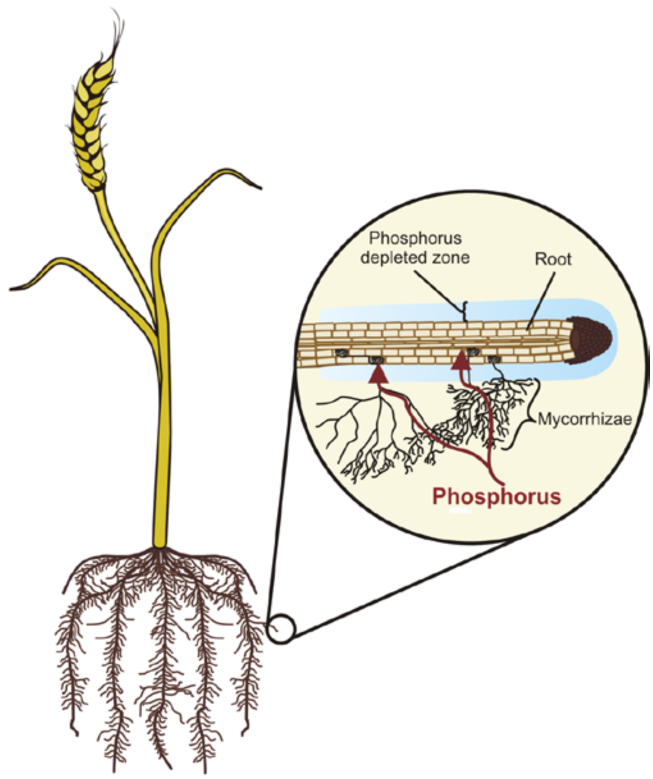

Figure 3: Typical mycorrhized plant showing extraradical hyphae of AMF. Mycorrhizal fungal filaments in the soil act as extensions of the root system and are more effective at nutrient and water absorption than the roots themselves; they also explore the soil and reach places inaccessible to roots.

and Vujanovic [15]. In recent years, the disease resistance induced in plants by AM fungi has become increasingly useful in biocontrol of plant diseases. For example, it is well documented that mycorrhizal associations significantly protect tomato and potato plants against the soil borne pathogens *Phytophthora parasitica* [16] *Furaium sambucinum* [17], respectively (Figure 2). Pozo et al. [16] found that bioprotection by AM fungi resulted from a combination of local and systemic effects, as showed by microscopical studies and biochemical analyses. Many literature reports indicate that AM fungi are antagonists of soil-borne disease pathogens [17], and either suppress the growth of the pathogen, or increase the resistance or tolerance of mycorrhizal plants to soil-borne diseases. Several hypotheses have been proposed to explain the mechanisms of the increased resistance in mycorrhizal plants: improvement of plant nutrition [7], competition for space [17,18], modified microbial flora in the rhizosphere [19], induced resistance or systemic resistance in the plant [15]. Recently Ismail Y, McCormick S, Hijri M [17] found that the AM fungus *Glomus irregulare* significantly inhibits *Fusarium sambucinum* growth, a mycotoxin-producing fungal pathogen. Using RT-PCR assays to assess the relative expression of trichothecene genes, [17] showed that AM fungi can indeed modulate mycotoxin gene expression by a plant fungal pathogen. In the presence of the AM fungus *G. irregulare, F. sambucinum* genes *TRI5* and *TRI6* were up-regulated, while *TRI4, TRI13* and *TRI101* were down-regulated. In brief, there are several ways by which AM fungi can be a key contributor to agro-ecosystems resilience, increased crop productivity and sustainable food production [14].

Applications of AM symbioses in agriculture

While the use of AM fungi in agriculture has not yet been widely integrated in the intensive agriculture typical of Europe and North America, impressive advances have been made by developing countries such as Cuba, India and Mexico, where chemical fertilizers are prohibitively expensive [20] (reviewed [9]) Following an intensive research program in the 1990s, Cuban scientists developed an inoculum called EcoMic specific to soils of that region. Used in many growing operations, it has been proven to be a very effective biofertilizer, and resulted in yield increases of 10 to 80% per hectare with a 6 to 10% application rate when used as a seedcoating [21]. In India, where a great deal of applied mycorrhizal research has also taken place, commercial inoculants are used on a large scale, with close to 2500 tons produced in 2006 by four different Indian companies. Used with rice crops, researchers found that mycorrhizal inoculation resulted in yield increases of around 10% with a 25–50% reduction in the amount of fertilizer required – real savings considering India's low phosphorous soils [22]. Premier Tech Biotechnologies (PTB), a Canadian company, is the leader in industrial bioreactor production of the AM inoculants. PTB produces and sells certified AM fungal inoculants for horticulture and agriculture in North America (Canada, USA and Mexico) and in Europe (Spain and France). In 2010, more than 20,000 ha of field crops in Canada were inoculated with AM fungi as biofertilizers (Serge Gagné, personal communication). In order to foster the use of AM fungi in modern agriculture systems, methods must be developed to analyze rapidly and at low-cost the mycorrhizal status of fields so that producers can respond accordingly. It is crucial to gain a more comprehensive picture of what AM fungal taxa are present, how they react to different host crops and to various soil treatments, and how they interact with other soil microbes [9].

Management and practices for a sustainable agriculture

Agriculture is the largest interface between humans and the environment, and is a major cause of climate change and ecosystem degradation. In particular, fertilizer use leads to fundamental changes in the pools and fluxes of carbon, nitrogen, and phosphorus [23]. Globally, a large proportion of the landscape has now been modified for food production. For example, in Canada, agriculture occupies a surface comparable to the total area of France: as much as 67.5 million hectares [24]. Consequently, improvements in agricultural land management will translate into large contributions to the reduction of greenhouse gas emissions, on a global scale, and to the protection of biodiversity, and of water and air quality. Given the numerous negative environmental impacts of phosphate, such as algal bloom and watercourse eutrophication, reducing the amount of phosphorus fertilizer applied on cropland would be a large step toward a more sustainable agriculture.

The phosphate requirements of a given cropland is difficult to forecast and P fertilizer recommendations are often imprecise. Most of these recommendations are based on soil tests ([25] estimating only the phosphorus potentially available in the soil solution, and ignoring the organic fraction of the soil P pool. These tests do not consider microbial interactions nor soil mycorrhizal potential, factors that importantly influence the P uptake ability of mycorrhizal plants. The failure to accurately predict and estimate phosphorus needs has been attributed to variations in the functionality of AM fungi indigenous to agricultural soils [26]. Not surprisingly, the correlation between soil test P values and crop response to P fertilizer is low [26].

As a result, P fertilizer is often applied in a wasteful and harmful way to non-responsive crops [1,5]. Over-fertilization leads to runoffs into the environment, pollution hazards, P build-up in soils and increased crop dependence on fertilizers [3,9]. Moreover, abundant phosphorus fertilization negatively impacts AM fungi. Although AM fungal strains tolerating high levels of phosphorus have been developed [27], over P fertilization reduces mycorrhizal-derived benefits to crops and society [2], which puts us in a dangerous vicious circle. In addition to reducing agriculture's footprint on the environment, accurate P fertilization recommendations are crucial in order to slow down the depletion of phosphorus deposits. This could be achieved by implementing more precise and accurate estimates of phosphate requirements prior to fertilization and by taking soil symbiotic associations such as mycorrhizae into account. Unfortunately, we are currently lacking the tools required for the management of AM fungi in cropping systems. Once again, the beneficial effects of AM fungi are extensive and permit among other things good yield under reduced fertilization. AM fungi were revealed as the cornerstone of the sustainability of soil-plant systems and it is important to integrate their management in food production systems.

There are two main approaches to manage AM fungi in cropping systems: applying inoculum of selected strains of AM fungi or adopting practices enhancing indigenous fungi proliferation and colonization [2]. As we discussed in the previous section of this review, inoculation with selected strains, such as EcoMic in Cuba or Myke® sold by PTB in Canada, produced impressive progresses in India, Mexico and India. However, the production of selected strains of AM fungi inoculum in large amount is still costly and, because they are obligate symbionts, their introduction can be complicated [2]. Indigenous fungi, even if they might have a lower efficiency than selected strains, have the advantage of being well adapted to local conditions. Whatever the chosen approach, we should adjust our agricultural practices and adopt a cropping system having positive effects on AM symbiosis. First, leaving off the use of chemicals killing soil microbes are important in order to maintain AM fungal communities in farmland [2]. Fumigants, such as methyl bromide, used in intensive agriculture to sterilize soils, destroy almost all soil organisms and are detrimental to AM fungi. Fungicides can also impair beneficial plants associations with soil microorganisms [2]. Second, the mycorrhizal dependency of plants varying from a species to another, the cultivation of more mycotrophic species impacts positively the diversity and the biomass of AM fungi in a cropping system [2,12].

Conclusions and Recommendations

To draw an analogy between dwindling petrol and phosphate supplies is inescapable, and to apply what has been learned from society's reaction to falling petrol supplies is essential. Tracking down new supplies and depending on higher prices to make harder-to-extract sources financially viable has been so far the preferred path to compensating for reduced worldwide petrol production. In the case of phosphate, however, there is already an available biological opportunity that has a significant impact on the efficiency of phosphate use. Mycorrhizae are undeniably a very promising approach to reduce the amount of phosphate fertilizers required for food production. It is therefore crucially important that we give more attention to biotic interactions in the rhizosphere of agricultural soils. What we need now is more research in order to gain a better understanding of the functions and ecology of AM fungi in agricultural soils, and to develop methods to easily quantify and identify mycorrhizal associations in farmlands. We also need continued development and refining of mycorrhizal inoculates, thereby providing producers with an ability to select the optimized products for different practices and conditions of cultivation. Most importantly, however, what seems a necessary prerequisite is an increased awareness within the agricultural industry itself of AM fungi and their potential in reducing fertilizer use.

Finally, a global issue like the phosphorus crisis requires that we seriously reflect on a long-term and large-scale plan, and that we rapidly adopt an integrated approach. Leaving mycorrhizal symbiosis out of this strategy would incontestably be a great mistake.

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