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Mycorrhizal biofertilizer: advantages and hindrances in its application

Biofertilizante micorrízico: ventajas y desventajas en su aplicación

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Abstract

Global climate change, rising population growth, and the overuse of agrochemicals have led to various problems, including soil degradation, a decline in food production, and environmental issues affecting the agricultural sector. To overcome these challenges, biofertilizers (particularly, those of mycorrhizal origin) have emerged as a sustainable and eco-friendly alternative. Arbuscular mycorrhiza (AM) is an association between plant roots and fungi from the subphylum Glomeromycotina, found in approximately 72% of land plants, and is one of the most common and ancient types of symbiosis on Earth. AM fungi provide with numerous benefits in exchange for plant photoassimilates. Although AM fungi may represent a viable biofertilizer option, their use is significantly limited due to various issues, ranging from their production to field application. This review sheds light on the potential of AM fungi as biofertilizers, analyzing their diverse benefits while also addressing the limitations associated with their production and application for enhancing agricultural productivity.

Keywords: Agricultural productivity; agrochemicals; biofertilizers; global climate change; mycorrhiza.

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Resumen

El cambio climático global, el aumento de la población y el uso excesivo de productos agroquímicos han dado lugar a diversos problemas, como la degradación del suelo, la caída de la producción de alimentos y cuestiones medioambientales que han arrinconado al sector agrícola. Para superarlos, los biofertilizantes, en particular los micorrícicos, han surgido como una alternativa sostenible y respetuosa con el medio ambiente. La micorriza arbuscular (MA), una alianza entre las raíces de las plantas y los hongos del subfilo Glomeromycotina, que se encuentra en aproximadamente el 72% de las plantas terrestres, es uno de los tipos de simbiosis más comunes y antiguos de la Tierra. Los hongos MA proporcionan a las plantas multitud de beneficios a cambio de fotoasimilados vegetales. Aunque los hongos MA pueden ser una buena opción biofertilizante, su uso es muy limitado, ya que existen diversos problemas que van desde su producción hasta su aplicación. Esta revisión arroja luz sobre el potencial de los hongos MA como biofertilizantes, analizando sus diversos beneficios y abordando al mismo tiempo las limitaciones asociadas a su producción y aplicación para aumentar la productividad agrícola.

Palabras clave: Productividad agrícola; agroquímicos; biofertilizantes; cambio climático global; micorrizas.

INTRODUCTION

Global climate change, the exponential rise in the human population, the energy crisis, and the limited availability of natural resources have placed immense pressure on the agricultural sector (Kinge *et al.*, 2022). In addition, the long-term injudicious use of synthetic chemical fertilizers and pesticides to raise agricultural productivity has given rise to many problems, such as deterioration of soil quality, which has resulted in a decrease in food production (Naik *et al.*, 2020; Fasusi *et al.*, 2023) and has given rise to many environmental problems, such as eutrophication of water bodies (Bakhshandeh *et al.*, 2017; Ammar *et al.*, 2023). This, in turn, has led to the degradation of ecosystems and has jeopardized trophic interactions (Barros-Rodríguez *et al.*, 2024). This unprecedented situation has put various stakeholders, such as governments, policymakers, scientists, and farmers, in an alarming state (Stephenson *et al.*, 2013). The growing awareness of the environmental and ecological consequences of heavy reliance on synthetic fertilizers has prompted a shift towards more sustainable agricultural practices to ensure food security for this expanding population while simultaneously conserving Earth's natural resources, with biofertilizers emerging as a viable, eco-friendly, sustainable, and cost-saving solution (Hunter *et al.*, 2017; Nosheen *et al.*, 2021).

Biofertilizers are formulations containing microorganisms or microbial-derived molecules that enhance plant growth and productivity by approximately 10–40% (Shahwar *et al.*, 2023; Ferreyra-Suarez *et al.*, 2024). Among biofertilizers, mycorrhizal biofertilizers have garnered significant attention because of their ability to enhance plant nutrient acquisition and overall growth performance (Kour *et al.*, 2020; Ammar *et al.*, 2023). Mycorrhizae, first reported by Frank (1885), is the mutualistic association between fungal hyphae and plant roots in which there is a reciprocal exchange of nutrients in the form of photo-assimilates like hexose sugars and lipids from plants to fungi and mineral nutrients from fungi to plants (Kaiser *et al.*, 2014; Luginbuehl *et al.*, 2017). Mycorrhizal association can be categorized into four types: arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), orchidioid mycorrhiza (OrM), and ericoid mycorrhiza (ErM) (Brundrett & Tedersoo, 2018). Among these, arbuscular mycorrhiza, a symbiotic association between plant roots and obligate biotrophic fungi of the subphylum Glomeromycotina (Spatafora *et al.*, 2016), is one of the most ancient and widespread symbioses on Earth (Kenrick & Strullu-Derrien, 2014). It is found in approximately 72% of terrestrial land plants (Genre *et al.*, 2020), ranging from bryophytes to angiosperms from a wide range of ecosystems (Redecker *et al.*, 2013), which played a pivotal role in allowing plants to transition from an aquatic environment before the evolution of true roots (Kenrick & Strullu-Derrien, 2014; Kuyper & Jansa, 2023). In contrast, ectomycorrhizal associations are found in only 2% of land plants, primarily those associated with temperate trees (Brundrett & Tedersoo, 2018). The other two types of mycorrhizal associations, Orchidioid and Ericoid, were restricted to specific plant families, Orchidaceae and Ericaceae, respectively (Brundrett & Tedersoo, 2018).

In addition to their widespread occurrence and distribution across ecosystems, arbuscular mycorrhizae provide plants with an array of benefits, such as providing them access to immobile soil nutrients (Smith & Smith, 2011; Yu *et al.*, 2022), promoting plant growth (Nadeem *et al.*, 2014), and helping plants adapt and survive under various abiotic (Begum *et al.*, 2019) and biotic stresses (Dey & Ghosh, 2022). They also improve soil structure through soil aggregation (Gosling *et al.*, 2010) and mediate communication between plants through a Common Mycorrhizal Network (CMN) (Walder *et al.*, 2012; Heklau *et al.*, 2021) (Fig. 1). In addition, they provide various ecosystem services, such as the breakdown of organic matter (Powell & Rillig, 2018), maintenance of belowground microbial diversity, and regulation of plant community diversity (Van Der Heijden *et al.*, 2015; Fall *et al.*, 2022). Thus, they have huge potential to be harnessed as a sustainable biofertilizer option for boosting agricultural productivity, with the potential to reduce reliance on synthetic fertilizers and pesticides while improving plant growth and resilience. However, they remain underutilized owing to inherent challenges associated with mass production, the risk of contamination, the need for skilled labour (Gianinazzi & Vosátka, 2004; Madawala,

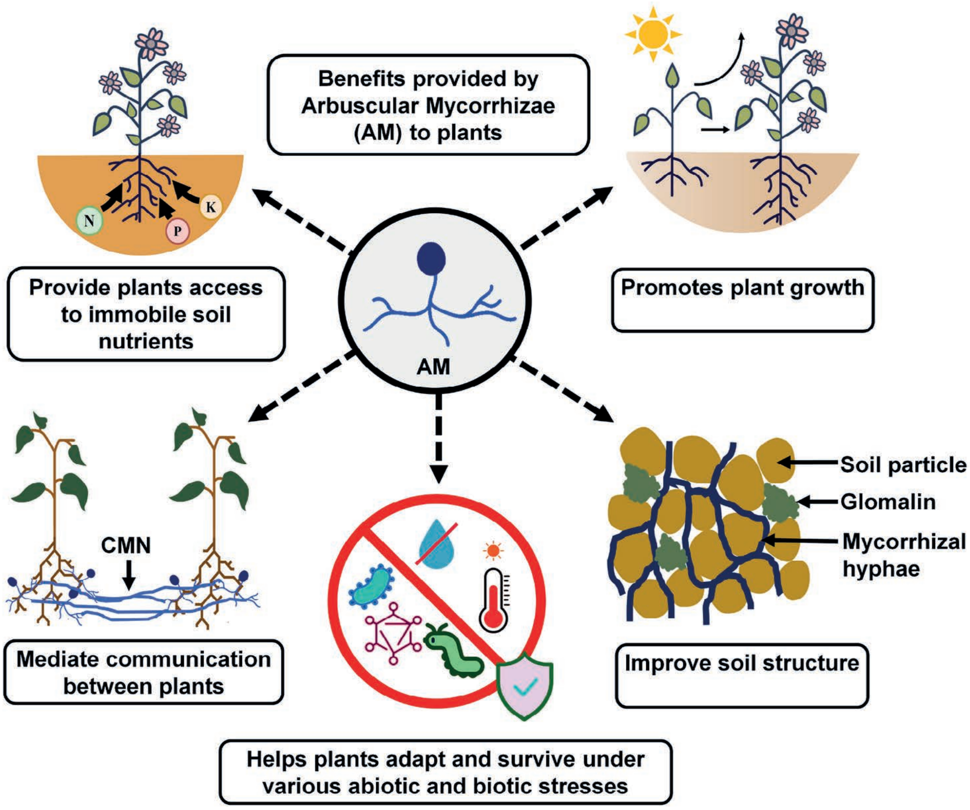

Fig. 1. Benefits provided by AM (Arbuscular Mycorrhizal) fungi to plants. Common Mycorrhizal Network (CMN).

Fig. 1. Beneficios que aportan los hongos MA (micorrizas arbusculares) a las plantas. Red común de micorrizas (CMN).

2021), and conventional agricultural practices, such as the application of agrochemicals, tillage, and crop rotation, which disrupt mycorrhiza development (Brito *et al.*, 2012; Bakhshandeh *et al.*, 2017). Among mycorrhizas, arbuscular mycorrhiza (AM) will be considered in this review, as they are found inclusively in all habitats and form symbiosis with nearly 72% of terrestrial land plants, whereas ectomycorrhizae associate with only 2% of land plants, mostly with trees found in forests of temperate regions (Brundrett & Tedersoo, 2018).

This review elucidates the potential of arbuscular mycorrhizal (AM) fungi as biofertilizers by discussing the numerous benefits they offer. Furthermore, this paper highlights the various challenges that may arise in the application of AM fungi as biofertilizers intended to enhance agricultural productivity.

ADVANTAGES

The symbiotic association between plants and mycorrhizae provides the plants with an array of benefits and services that promote their growth and, at the same time, help them to cope with various stresses, which are discussed below.

Facilitation of nutrient uptake

Mycorrhizal colonization induces changes in the morphological characteristics of plant roots that are crucial for hosting mycorrhizal structures within the cells and enhancing nutrient uptake and accumulation by mycorrhizal plants (Neumann & George, 2010). The morphological modifications in the plant root system triggered by mycorrhizal colonization include an increase in total root length, a change in root-shoot ratio, an increase in root branching, and an increase in the number of root tertiary branches (Vierheilig *et al.*, 2008). Along with these root modifications, the hyphae of mycorrhizal fungi have the capacity to expand beyond the root surface by a distance greater than 10 cm (Jakobsen *et al.*, 1992). These hyphae are very thin, with an average diameter of 3 to 4 μm, which is much smaller than the finest root hairs, which have an average diameter of 10 μm (Johansen *et al.*, 1993); thus, they are able to extend their growth into the tiniest micropores of soil, which enhances their nutrient absorption efficiency (Bennett & Groten, 2022). Altogether, the root modifications induced by AM fungi and the AM hyphae form an extensive nutrient-absorbing network that expands the root zone absorption area by 10% to 100% (Etesami *et al.*, 2021) that stretches beyond the nutrient depletion zones that form around roots in the rhizosphere (The narrow zone of soil surrounding plant roots), which enables the AM-colonized roots to access a larger volume of the soil than roots that are not colonized by AM fungi (Cavagnaro *et al.*, 2015). AM also promotes the expression of phosphate transporters (PTs) in various host plants, including *StPT3* in potato (Rausch *et al.*, 2001), *MtPT4* in *Medicago truncatula* (Harrison *et al.*, 2002), and *OsPT11* in rice (Paszkowski *et al.*, 2002). These transporters play a critical role in facilitating the uptake of phosphate released by AM fungi at the symbiotic interface into plant cells (Wang *et al.*, 2017). In addition to phosphate transporters, plant ammonium transporters such as *GmAMT4.1* and *ATM2;3* in soybean and *Medicago* are induced by the presence of the fungus within arbuscule-containing cortical cells in the roots (Wang *et al.,* 2017).

Mycorrhizal fungi secrete enzymes, like acid phosphatases and proteases, which facilitate the solubilization of both organic and inorganic phosphorus compounds in the soil (Miransari *et al.*, 2009). This enzymatic activity enhances the bioavailability of phosphorus, thereby improving the availability of phosphorus to the plant host (Samantaray *et al.*, 2024).

Some mycorrhizal fungi produce siderophores (Low molecular weight organic compounds that have a high affinity for ferric ions) that complex iron and oxalate to increase potassium absorption from the soil, resulting in improved plant nutrition (Lindahl *et al.*, 2007).

Improvement of water absorption capacity

Mycorrhizal hyphae are very thin, usually having a diameter of 2–5 μm, which is approximately two times smaller than plant roots, which have an average diameter of 10–20 μm, which allows them to transport water through small soil cavities inaccessible to plant roots (Diagne *et al.*, 2020). In addition, the hyphal tips are also hydrophilic, which enhances the transport of water from the soil to the plant cells (Miransari, 2011).

AM fungi also produces glomalin, which is a glycoprotein containing 30–40% carbon compounds that is deposited on the soil particles and holds the soil particles together, forming stable soil aggregations that improve the water holding capacity of soil and protect the soil from desiccation (Verbruggen *et al.*, 2012; Sharma *et al.*, 2017).

Mycorrhizal fungi also induce the expression of plant aquaporin genes in mycorrhizal roots, which encode integral membrane transporters that transport water, signalling molecules, and ions through cell membranes (Santander *et al.*, 2021). Aquaporins enhance the water absorption capacity of plants and improve their tolerance to drought stress. Thus, AM fungi improves plants resilience to drought stress through multilayered, controlled protection mechanisms.

Enhancement of growth and yield of crops

Mycorrhizal symbiosis plays a significant role in enhancing the productivity and quality of tropical agricultural crops, particularly in regions where phosphorus deficiency is prevalent in the soil (Hildermann *et al.*, 2010). Nziguheba and Smolders (2008) stated that 75% of the phosphorus applied to crops is not utilized by plants. *Zea mays* and flax are very dependent on AM fungi to meet their primary phosphorus requirements (Bai *et al.*, 2003; Thompson *et al.*, 2013). AM fungi inoculation can provide up to 90% of plant phosphorus and 20% of plant nitrogen due to the hyphal network in the soil formed after symbiotic associations with the host plant (Johnson *et al.*, 2012). Most of the major agricultural crops are mycorrhizal hosts and increase the inoculum potential of the soil and colonization of future crops (Schliemann *et al.*, 2008). AM fungi have a widespread distribution, and their use in agroecosystems as mycorrhizae-based inoculants is increasing (Igiehon & Babalola, 2017). In the case of potatoes, AM inoculation was observed to increase the total crop yield by 9.5%.

When AM fungi inoculant (*Rhizophagus irregularis*) was applied to potatoes over a period of four years in North America and Europe under real field conditions and showed a highly significant increase (42.2 tons/ha) in potato yield compared to non-inoculated controls (38.3 tons/ha) (Hijri, 2016). AM fungi also contributes to enhancing crop yield in rainfed agricultural systems by promoting drought resistance in host plants, which is particularly important in mitigating yield losses attributed to phytopathogens and herbivores (Dowarah *et al.*, 2022).

Furthermore, AM fungi have been engaged in large-scale field production of maize (Sabia *et al.*, 2015). The inoculation of the AM fungus *Rhizophagus irregularis* with the cotton cultivar Lumian No. 1 reduced the requirement of fertilizer application in the field (Gao *et al.*, 2020). Thus, AM fungi possess a considerable potential for enhancing the yield of crops.

A positive relationship between mycorrhizal spore population and fruit yield (number and weight of fruits) has been observed in various fruit trees (Bona *et al.*, 2017). Zeng *et al.* (2014) observed increased levels of sugars, organic acids, vitamin C, flavonoids, and minerals in citrus fruits due to *Glomus versiforme*, resulting in improved quality. The inoculation of *Glomus macrocarpum*, *G. coledonicum, and Acaulospora sp*. resulted in enhanced plant height, stem diameter, and biomass in trifoliate and troyer oranges (De Souza, 2000). Inoculation with *Gigaspora rosea* and *Glomus mosseae* enhanced the growth of different grape rootstocks and cultivars compared to uninoculated plants (Linderman & Davis, 2001). Arbuscular mycorrhizal fungi also increased the yield and productivity of apple trees when plants were co-inoculated with phosphate-solubilizing bacteria (Aslantaş *et al.*, 2007).

Contributes to soil sustainability

Arbuscular mycorrhizae are an essential component of the pedosphere that regulate important soil processes and are considered to have immense potential for improving soil sustainability (Powell & Rillig, 2018; Zhang *et al.*, 2024). AM fungi contribute to soil sustainability by regulating three major factors: the structure of the soil, physiological processes in plants, and ecological dynamics (Fall *et al.*, 2022).

Mycorrhizal fungi form a large amount of mycelia in the soil, which continuously regenerates and forms a matrix that wraps and interconnects soil particles, improving the stability of soil aggregates, minimizing soil compaction, and improving the water-holding capacity of soil (Chen *et al.*, 2018). Mycorrhizal fungi also secrete a negatively charged, hydrophobic, and thermotolerant glycoprotein, glomalin (Fall *et al.*, 2022). Glomalin acts as a glue that binds soil particles and stabilizes soil aggregation (Lehmann *et al.*, 2020). Furthermore, the hydrophobic nature of glomalin provides soil aggregates with water resistance. Additionally, glomalin is slowly biodegradable by soil microorganisms (Hu *et al.*, 2019).

Together, the formation of soil aggregates by the enmeshment action of hyphae and the increase in their stability by glomalin minimize the risk of soil compaction and increase the water-holding capacity of the soil, which results in reduced soil erosion, nutrient leaching, and denitrification, thereby improving soil fertility (Pellegrino *et al.*, 2020). The mycelial network, in addition to forming stable soil aggregates, also contributes to the formation of soil organic matter after death (Hawkins *et al.*, 2023).

Thus, AM fungi participate in various types of essential soil functions, such as nutrient cycling (Powell & Rillig, 2018; Frey, 2019), reducing soil nutrient loss by minimizing nutrient leaching from the soil (Cavagnaro *et al.*, 2015), and improving the soil structure by producing a hydrophobic glycoprotein glomalin (Leifheit *et al.*, 2014). AM also regulates various physiological processes in plants, such as enhancing their nutrient acquisition capacity from the soil (Rouphael *et al.*, 2015), modulating phytohormone levels in plants, and reprogramming the secondary metabolism of plants (Rivero *et al.*, 2015). AM also influences the ecological dynamics of soil by recruiting beneficial soil microorganisms, such as phosphate-solubilizing bacteria (PSB), nitrogen-fixing bacteria, and plant growth-promoting rhizobacteria (PGPR), to the mycorrhizosphere (The zone of soil surrounding the plant roots colonized by mycorrhizal fungi) (Yu *et al.*, 2022).

Strengthens plant immunity to biotic stress

AM induces disease control by both indirect and direct means. Indirectly through nutrition improvement; synthesis of plant hormones (Song *et al.*, 2015) and competing with other harmful microbes on the root surface and within the root. AM fungi also produce some antifungal (Bencherif *et al.*, 2019) and antibacterial compounds (Kaur & Sussella, 2020) and toxins that act against pathogenic organisms (Wang *et al.*, 2018).

AM fungal symbiosis directly inhibits pathogens by mycorrhiza-induced resistance (MIR) (Nguvo & Gao, 2019) by creating systemic protection against a wide range of pathogens. MIR includes characteristics of both systemic acquired resistance (SAR), which occurs after pathogen infection in plants, and induced systemic resistance (ISR), which occurs following root colonization by non-pathogenic rhizobacteria (Cameron *et al.*, 2013). MIR activates both pathogen-specific and broad-range defence genes (Fiorilli *et al.*, 2018) to produce enzymes and pathogenesis-related (PR) proteins (Sanmartín *et al.*, 2020).

AM fungi are active against different types of nematodes (Da Silva Campos, 2020), bacteria (Sanmartín *et al.*, 2020), viruses (Aseel *et al.*, 2019), and fungi (Song *et al.*, 2015) in different hosts, though the protective effects vary with AM and host species or other conditions.

Enhancement of abiotic stress tolerance

Water stress, caused by drought and salinity, is one of the main abiotic stresses that impact plant growth and productivity. The symbiosis between plant roots and AM fungi is a common strategy for adapting to water stress (Brachmann & Parniske, 2006). Mycorrhizal fungi employ various strategies to sustain host vitality during water stress. Water stress decreases the turgor pressure and water potential of plant cells, which results in the formation of reactive oxygen species like superoxide and hydroxyl radicals (Laxa *et al.*, 2019). As mycorrhizal hyphae can explore a large volume of the soil, they enhance plants water absorption, which improves turgor potential, stomatal conductance, and hence elevates transpiration rate (Augé *et al.*, 2015). AM colonization also improves osmotic balance by inducing accumulation of osmo-protectants such as proline, polyamines, glycine betaine, non-structural carbohydrates, and inorganic solutes like K^+, Ca^{2+}, and Mg^{2+} (Baslam & Goicoechea, 2012; Yooyongwech *et al.*, 2013) inside plant cells, which maintains the turgor pressure and protects plant cells from the adverse effects of water stress (Grümberg *et al.*, 2015).

Under salinity stress conditions, AM fungi enhance the uptake of nutrients like phosphorus (P), nitrogen (N), potassium (K), zinc (Zn), and copper (Cu) and maintain ionic homeostasis (Hanin *et al.*, 2016). AM fungi also enhance the levels of the abiotic stress hormone abscisic acid (ABA) in plants to cope with the detrimental effects of water and salinity stress (Martín-Rodríguez *et al.*, 2016). ABA regulates transpiration rates, stomatal movements, root hydraulic conductivity, and the expression of aquaporin-encoding genes (Ouledali *et al.*, 2019). ABA triggers stomatal closure, which in turn reduces transpiration and minimizes water loss during drought stress (Chitarra *et al.*, 2016). AM fungi also augment antioxidant activities to defend against damage by reactive oxygen species (ROS) and promote photosynthesis to minimize the detrimental effects of salts on the growth and development of plants (Evelin *et al.*, 2009). Crop plants inoculated with AM fungi have been reported to enhance growth and yield, while mitigating osmotic and ionic imbalances to normal levels, allowing crops to thrive under salinity stress (Hanin *et al.*, 2016).

All these adjustments by AM fungi improve plant resilience to various abiotic and biotic stresses, which improves plant growth and ultimately their productivity. Thus, AM can be utilized as a bioinoculant in the soil, which can maximize the output without compromising soil health while simultaneously ensuring soil sustainability.

HINDRANCES IN APPLICATION

Despite the multitude of benefits offered by mycorrhiza, their widespread adoption and successful implementation as biofertilizers in modern agriculture face several challenges (Fig. 2).

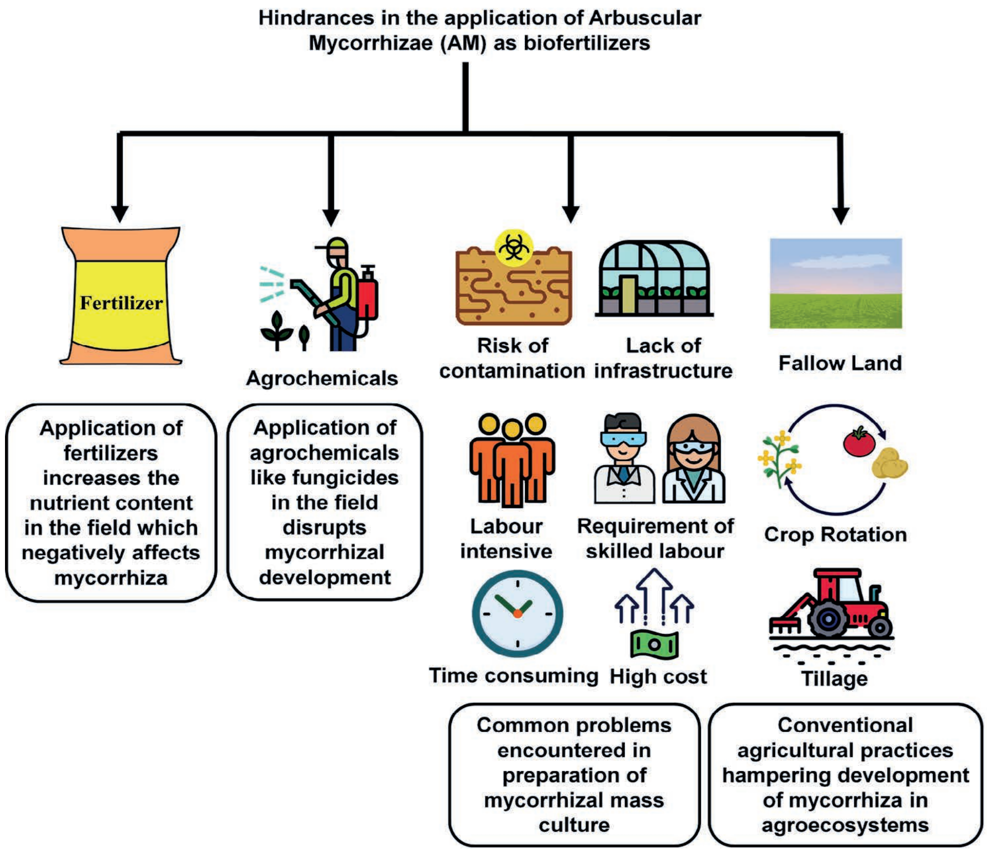

Fig. 2. Challenges associated with the use of arbuscular mycorrhiza as a biofertilizer in agroecosystems.

Fig. 2. Desafíos asociados al uso de micorrizas arbusculares como biofertilizante en agroecosistemas.

High nutrient content in soil

Under nutrient-poor conditions in the soil, plant roots release strigolactones (A family of carotenoid-derived phytohormones that promote seed germination in parasitic plants and facilitate the establishment of symbiosis between plants and AM fungi) into the soil, which induces the germination of AM spores and stimulate hyphal branching (Waters *et al.*, 2017). The AM fungi in response release *myc* factors that are perceived by plant receptors, resulting in the induction of the common symbiotic pathway leading to the establishment of symbiosis (Zhang *et al.*, 2015). However, in agroecosystems with high fertilizer input, the level of nutrients, especially phosphorus (P), becomes high, and plants can take up phosphorus (P) from the soil without seeking any help from the AM fungi, and the symbiotic association transforms to a parasitic one in contrast to mutualism under low soil N and P levels (López-Ráez *et al.*, 2017). Therefore, it is no longer feasible for plants to remain in this association, as there is a carbon cost; thus, the allocation of carbohydrates and lipids to AM fungi is reduced (Qin *et al.*, 2024).

Additionally, the release of strigolactones from plant roots decreases (López-Ráez *et al.*, 2011). Finally, plants also downregulates the expression of *phosphate transporter (PT) genes* (Sawers *et al.*, 2017). As a result, the AM fungal colonization and sporulation are reduced (Tiamtanong *et al.*, 2015). In addition to phosphorus (P), the mycorrhizal community is greatly affected by chronic nitrogen deposition. Many nitrogen fertilizers have been reported to decrease colonization in both field and pot experiments (Getman-Pickering *et al.*, 2021). Nitrogen fertilization alone or in combination with phosphorus disrupts AM symbiotic efficiency. Potassium (K) more than the natural soil K content decreased mycorrhizal colonization in maize (Ardestani *et al.*, 2011).

Application of agrochemicals

Agrochemicals (fungicides, pesticides etc.) are now integral part of technology dependent modern conventional agriculture as most high yielding crops are more susceptible to diseases than their wild genotypes. Systemic fungicides have selectivity and specificity for certain pathogens while non-systemic fungicides are broad spectrum and kill all organism exposed to these. Common non–systemic fungicides like *pentachloronitrobenzene* (PCNB), *thiram, fotran, arsan, langstan, Chlorothalinol, Captapol, chloroneb, metaxyl* and *ethazole* are highly toxic; while Captan, *Mylone*, *Vapram* and *Volax* are moderately toxic to mycorrhizal fungi. Daconil, Sodium azide, terrazole, captain, and copper sulphate may favour AM activity and development at low doses under specific environmental conditions (Vyas & Vyas, 2000).

Systemic fungicides are more detrimental to AM fungi as they get accumulated inside the roots (Jin *et al.*, 2013). As systemic fungicides are mostly fungi static, they have less effect on spore germination and hyphal growth, but they affect infection, colonization and sporulation. *Benomyl, Tridemorph, Triforine, Ethirimol, Etridiazole, Thiophanate methyl, Thiabendazole, Thiademifom* and *Carboxin* show detrimental effects on the development of AM in the root (Wang *et al.*, 2018). Almost all non-systematic fungicides adversely affect AM and are retained in soil (Ghosh *et al.*, 2024).

Selection and preparation of mass culture

The primary challenge in producing an AM fungi inoculum is the obligate symbiotic nature of AM fungi, which requires a host plant to grow and complete its life cycle. Thus, they cannot be cultivated in pure culture without their host plants (Säle *et al.*, 2015). Consequently, their propagation must include a cultivation phase with host plants maintained in fields, greenhouses, or growth chambers. This is labour intensive, costly, and at the same time requires considerable time and space (Gianinazzi &

Vosátka, 2004). Additionally, AM fungal inoculum is a combination of soil and AM propagules; therefore, these inocula cannot be entirely free from contamination with pathogens and weedy seeds (Kumar *et al.*, 2017). Furthermore, the soil makes AM inocula bulkier, and their transport becomes more challenging and expensive (Ceballos *et al.*, 2013). Apart from these evident limitations associated with the production of AM inocula on a large scale, there are additional obstacles like lack of infrastructure for inoculum production, storage, and skilled labour, as well as lack of a suitable carrier material, short shelf life, and inconsistency in the inoculum (Mukhongo *et al.*, 2016). Additionally, there is a lack of quality control protocols for AM fungal inoculum production; thus, the species listed in commercial products may not be entirely accurate (Hart *et al.*, 2018). Again, not all AM fungi species may be suitable for all hosts, soil types, or climates (Jansa *et al.*, 2014). Thus, screening is necessary.

Conventional agricultural practices like fallowing land, rotation with non-host plant and tillage

Conventional agricultural practices, aside from the application of agrochemicals, such as tillage and crop rotation, which inhibit the development of mycorrhizae, particularly in topsoil layers, are two commonly encountered challenges that prohibit the effective utilization of mycorrhizae as a biofertilizer in agroecosystems.

As an obligate symbiont, prolonged fallowing of land devoid of vegetation or with non-host vegetation leads to the depletion of arbuscular mycorrhizal (AM) propagules in the soil as AM spores are unable to germinate and proliferate in the absence of a host. Similarly, the cultivation of non-host crops, such as those belonging to the Brassicaceae family, which release glucosinolates into the soil, adversely affects AM propagules. Upon their release, glucosinolates decompose into isothiocyanates, which are antimicrobial compounds that further reduce the prevalence of AM propagules in the soil, even following the rotation with host plants (Kirkegaard & Sarwar, 1998; Ghosh *et al.*, 2004).

Intensive tillage disrupts the hyphal networks of mycorrhizae within the soil (Feilinezhad *et al.*, 2022) which can selectively affect various arbuscular mycorrhizal fungi (AMF) groups based on their life and colonization strategies, either promoting or impairing specific groups, leading to a 40% reduction in AM fungal diversity (Brito *et al.*, 2012). Furthermore, mycorrhizal root colonization consistently demonstrates lower levels under tillage conditions compared to no-tillage environments (Castillo, 2006). During the initial stages of colonization, the direct impacts of conventional tillage systems are attributed to the physical disruption of the extraradical mycelium network, resulting in a slowdown of symbiotic efficiency. This disruption hampers AM activity related to nutrient and water uptake, glomalin-associated soil aggregate formation (Brito *et al.*, 2012), and bioprotection against soil pathogens (Patanita *et al.*, 2020).

Thus, conventional agricultural practices, aside from the application of agrochemicals, such as tillage and crop rotation, can inhibit the development of mycorrhizae in different agroecosystems. However, adopting practical alternatives such as utilizing organic fertilizers (manures and compost) and slow-release mineral fertilizers (like rock phosphate) (Cavagnaro, 2014), implementing reduced tillage (Ghorui *et al.*, 2024), and shortening the fallow period through crop rotation with mycorrhizal-dependent cover crops such as *Vicia villosa* Roth. and *Trifolium* spp. instead of non-mycorrhizal hosts like Brassicaceae can stimulate arbuscular mycorrhizal (AM) fungi in the field (Njeru *et al.*, 2015). Furthermore, the application of fungicides that do not negatively affect mycorrhizal fungi can lead to an increase in AM propagules and their species diversity (Rouphael *et al.*, 2015).

Methods of plant inoculation with mycorrhizal fungi

Inoculating plants with AM fungi employs advanced techniques that can significantly enhance plant health and productivity. These methods can be broadly categorized as follows.

Seed inoculation.— This method consists of coating seeds with a slurry of AM spores, ensuring that upon germination, the seeds are immediately exposed to the AM fungi (Kafle *et al.*, 2019).

Direct root inoculation.— This approach involves dipping the roots of seedlings into a suspension of AM spores during transplanting, thereby establishing direct contact between the AM fungi and the root system (Eulenstein *et al.*, 2017).

Soil inoculation.— This strategy involves broadcasting granular or powdered inoculum over the soil surface at the time of tillage or planting, making it suitable for large-scale agricultural operations where direct root inoculation may not be feasible (Aliyu *et al.*, 2019).

While these methods demonstrate potential for enhancing soil health and agricultural productivity, challenges persist in standardizing these practices.

Dual applicationof AM fungi and plant growth promoting bacteria (PGPB)

The simultaneous application of Arbuscular Mycorrhizal (AM) fungi and Plant Growth Promoting Bacteria (PGPB), represents an effective ecological strategy to enhance plant performance and soil health compared to single inoculation (Feng *et al.*, 2023). AM fungi colonize the roots of terrestrial plants; on the other hand, PGPB colonizes the rhizosphere. The combination of these two groups can lead to improved plant performance by providing numerous benefits, such as nitrogen fixation, phosphate solubilization and mineralization, phytohormone production, and enhanced tolerance to various biotic and abiotic stresses (Wahid *et al.*, 2022).

The mechanism behind this synergistic effect is attributed to several factors, including PGPB enhancing AM spore germination and hyphal growth, which leads to more efficient mycorrhizal colonization (Sagar *et al.*, 2021). In return, the PGPB receive nourishment in the form of carbon-rich exudates from the AM fungi. This mutual enhancement results in a more robust root system that better absorbs nutrients and water, promoting plant growth and improving performance under various stresses (Wahid *et al.*, 2022).

The synergistic effect of dual inoculation with AM fungi and PGPB has been validated by several scientific studies. For example, in two wheat (*Triticum aestivum*) cultivars, HD-3086 and HD-2967, the co-application of *Bacillus subtilis* CP4 and the AM fungi *Glomus fasciculatum* significantly increased plant biomass and yield compared to single inoculation and uninoculated controls (Yadav *et al.*, 2021). Additionally, inoculating a strawberry variety (*Fragaria ananassa* var. Selva) with a consortium of AM fungi (*Rhizophagus intraradices, Glomus aggregatum, G. viscosum, Claroideoglomus etunicatum, and C. claroideum*) and *Pseudomonas fluorescens* Pf4 resulted in earlier flowering and fruiting, as well as increased yield and nutritional content (Bona *et al.*, 2015). In *Melissa officinalis* L., dual inoculation with the AM fungi *Glomus mosseae* and the PGPB *Azospirillum brasilense* Sp245 promoted plant growth and yield under water deficit conditions (Gorgi *et al.*, 2022). El-Sharkawy *et al.* (2022) found that inoculating *Rhizophagus irregularis* with the bacterium *Streptomyces viridosporus* HH1 improved growth parameters and induced defence responses in pea (*Pisum sativum* L.) against infection of *Fusarium oxysporum* f.sp. *pisi*.

CONCLUSION

The use of mycorrhizae as biofertilizers is a cost-effective strategy for supplying essential nutrients and water and enhancing resilience to various environmental stresses, thereby contributing to sustainable, eco-friendly production that minimizes the use of agrochemicals and reduces environmental and human health risks. To fully harness the potential of AM fungi in enhancing the productivity of agroecosystems, it is essential to troubleshoot the negative effects of conventional agricultural practices on AM fungi, soil quality, ecosystem functioning, and human health. Therefore, to maximize the benefits of AM fungi, it is essential to develop an integrated management system, which is a comprehensive strategy that combines multiple agricultural practices to increase the number, variety, and functioning of AM fungi. This enhancement aims to improve their symbiotic interaction of AM fungi with their host plants, thereby optimizing mycorrhizal advantages, leading to improved crop performance and agroecosystem sustainability while remaining within economic boundaries.

To achieve such a sustainable system, soil management practices like no-tillage farming or reduced tillage should be adopted, and cover crops should be implemented to promote soil aggregation and increase organic matter content in fields, creating a more favourable environment for mycorrhizal fungi, which will facilitate their growth and colonization of plant roots within agroecosystems. Besides soil management practices, nutrient management strategies should include the judicious application of fertilizers tailored to the specific needs of the crops and the existing soil nutrient levels to mitigate the suppression of mycorrhizal activity caused by excessive fertilization. Also, selecting crop varieties known to be highly responsive to mycorrhizal colonization is crucial to ensure that plants can successfully capitalize on the benefits provided by AM fungi.

An integrated management system should also incorporate strategies to introduce beneficial mycorrhizal fungi populations in the soil, taking into account the broader ecological context of the agroecosystem. This can be achieved by exploring native AM fungi and plant growth-promoting bacteria instead of relying on commercially available bioinoculants, as native populations are pre-adapted to the environment and can establish themselves better in the soil without promoting weed growth, which is often a concern with commercial bioinoculants (Duell *et al.*, 2022). Furthermore, fostering collaborative partnerships between government, researchers, and farmers is vital to facilitate the exchange of knowledge and best practices related to mycorrhizal management.

Additionally, investment in research and development for enhancing the infrastructure for propagule production and building a skilled workforce in this domain are critical to ensure their widespread adoption and success.

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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