Review

Soil fertility and crop biofortification: is there potential improvement through arbuscular mycorrhizal symbiosis in Sub-Saharan Africa?

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Abstract
The transition from current production systems to sustainable soil and crop management practices is imperative for meeting increasing demands. This shift is essential for minimizing environmental impacts while enhancing productivity and resource efficiency. In this context, the use of beneficial soil microorganisms such as arbuscular mycorrhizal fungi (AMF) represents a promising avenue. The roles of AMF in improving crop growth, yield, and biofortification have been scientifically established, both under normal and extreme conditions. Additionally, the role of AMF in enhancing soil fertility by improving its physical, chemical, and biological properties has been recently elucidated in several experimental studies in Sub-Saharan Africa. However, the effective establishment of symbiosis and its impact are closely regulated by various factors, including the genetic characteristics of crop and AMF species, as well as environmental conditions. The lack of control over these parameters reduces crops responsiveness to AMF, thus limiting the full agronomic potential of this symbiosis. This review presents scientific evidence of the benefits of AMF in enhancing soil fertility, increasing yields, and crop biofortification, while examining the underlying mechanisms. Finally, we have identified the knowledge gaps that should be addressed by future research for optimal integration of AMF into cropping systems.

Keywords Mycorrhizal symbiosis · Crop biofortification · Nutrients cycling · Yield · Sub-Saharan Africa

1 Introduction

The modern intensive agricultural systems, which rely on the use of chemical inputs, have recently come under scrutiny due to their environmental impacts. These include soil degradation, decline in soil fertility, land acidification, eutrophication, increasing greenhouse gas emissions, and a reduction in ecosystem services [143]. In response to these challenges, agroecological technologies have been promoted as alternative practices to improve resource use efficiency while minimizing the negative impacts of conventional methods [175]. In this context, agriculture faces a major challenge: producing more food in both quantity and quality while reducing chemical inputs. This is necessary to ensure food and nutritional security for the growing population [156]. Furthermore, agriculture must address the issue of malnutrition, particularly in sub-Saharan Africa, through crop biofortification to prevent diseases related to

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micronutrient deficiency [51, 83]. Achieving this goal requires the adoption of sustainable production systems that promote the sustainable management of soil fertility [156, 175].

It has been recognized in the literature that microorganisms inhabiting the soil, such as mycorrhizal fungi (AMF), play a significant role in influencing both plant and soil health, as well as crop productivity [55, 101]. According to Lehmann et al. [91], soil health refers to the overall state of a soil in terms of its ability to function as a living ecosystem that supports plants, animals, and humans. A healthy soil is characterized by a balanced structure and composition, rich biodiversity, dynamic biological activity, and the capacity to absorb and retain nutrients and water.. Soil health also refers to the soil's ability to support an effective symbiotic association between plants and soil AMF [140]. AMF represent the most widespread group of fungal symbionts in plants and are associated with over 80% of terrestrial plants [23]. They are obligate biotrophs grouped within the phylum Glomeromycota, colonizing the root cortex by developing structures called mycorrhizae. The establishment of symbiosis is followed by the development of internal structures such as hyphae, vesicles, and arbuscules, along with a network of hyphae known as the extraradical mycelium (ERM), which extends beyond the root system of the host plant for a distance of 10–22 m [126]. This relationship is essential for enhancing the absorption of nutrients (such as phosphorus) and water by plants, increasing plant tolerance to abiotic stresses (such as drought and salinity), and protecting plants from pathogens [140]. During the interaction between the plant and AMF, the fungus also enhances the host plant's tolerance to drought and nutrient-poor soils, increases resistance to temperature stress and heavy metal toxicity, and stimulates the plant's defense mechanisms [34, 114]. In return, AMF acquire the carbon necessary for their growth and reproduction from the host plants [58].

In line with previous studies [53, 58, 112] that have reported the roles of the ERM of AMF in ameliorating nutrients absorption, primarily phosphate (inorganic phosphorus, Pi), it is also confirmed that this role is related to the fact that ERM exploring a larger volume of soil compared to non-mycorrhizal plants. In addition to Pi, other nutrients such as nitrogen, potassium, calcium, and micronutrients can also be absorbed by AMF and transferred to the host plant [94]. More recently, studies have shown that AMFs produce several compounds and molecules, the main ones being exopolysaccharides, primarily glomalin, hormones, volatile compounds, antimicrobial products, Myc factors, and Nod factors [18, 154]. These compounds are involved in molecular and biochemical processes that determine the initiation and efficiency of mycorrhizal symbiosis, as well as the influence of AMF on plant physiology and the stimulation of crop growth and productivity. These include, among others; Early Recognition and Communication between plant and fungi (secretion of chemical signals and fungal response), Activation of signaling pathways (Specific receptors and Gene expression), and formation of symbiotic structures (formation of prepenetration structures and development of arbuscules). For example, the production of strigolactones stimulates the germination of AMF spores, oxidative metabolism, hyphal branching, and consequently, root colonization [100]. Additionally, it has been revealed that during the later stages of mycorrhizal symbiosis, hormones such as auxins, abscisic acid, and brassinosteroids produced by AMF have a positive effect on symbiosis regulation [22, 74]. On the other hand, jasmonic and salicylic acids produced by AMFs induce resistance to insects and pathogens [44]. Finally, other research has reported that AMF to stimulate various transporters involved in the absorption and translocation of nutrients. These observations clearly indicate the potential role of AMFs in plant mineral nutrition and in promoting stability and quality of yields in different environments [55].

Over the last decade, research has focused on finding alternative methods to improve soil fertility and crop biofortification using soil microorganisms, with the aim of increasing both productivity and nutritional quality of crops [49, 113, 114]. It has been found that arbuscular mycorrhizal fungi (AMFs) impact not only crop growth and productivity but also enhance soil fertility and crop biofortification [49, 86, 97, 183, 190]. Regarding soil fertility, AMFs influence the physical, chemical, and biological properties of the soil through various processes such as soil aggregation, improvement of the biogeochemical nutrient cycle (absorption, immobilization, solubilization), soil pH neutralization, and interaction with other soil organisms [46, 50, 121, 140, 169]. For biofortification, AMFs facilitate the strong mobilization of micronutrients from the soil to the plant roots, enhancing their absorption and translocation to the edible parts of crops [55]. More recently, it has been reported that AMFs also play a role in the solubilization of micronutrients, thereby increasing their bioavailability [158]. The mechanisms involved include the chelating effect of certain AMF exudates (affecting Fe and Zn) and the production of organic acids and other phenolic compounds by AMF extraradical hyphae, which increase the bioavailability of micronutrients and facilitate their absorption by the plant [159]. Thus, the use of AMFs in agriculture is a sustainable and ecological approach to improve crop yield, biofortification, and soil fertility. In this review, we compile and synthesize recent scientific evidence on the role of AMFs in improving soil fertility, crop productivity, and biofortification. We also provide a general overview of the challenges related to soil fertility in sub-Saharan Africa, mycorrhizal

symbiosis, and crop biofortification, focusing on how to harness the potential of AMFs to improve soil fertility and crop biofortification.

2 Challenges related to soil fertility in Sub-Saharan Africa (SSA)

2.1 Concept and current status of the soil fertility in SSA

Soil is the most important factor for agricultural production since it supports crop growth and closely interacts with it. Africa has a great diversity of soils whose nature and main characteristics are determined by age, parent materials, and climatic conditions [150]. According to FAO [51] and Bado and Batioo [11], soil fertility implies its ability to support growth and optimize crop yields, while, soil degradation is the loss of the productive capacity of the soil in terms of loss of fertility, soil biodiversity, and natural resource degradation. In sub-Saharan Africa (SSA), land degradation is particularly intense and is a major problem negatively affecting crop yields, causing shortages of food staples, poverty, and food insecurity for vulnerable populations [51, 73, 200]. In this region, most soils are at a more advanced stage of degradation. It has been estimated that 70–80% of the cultivated land in the African continent is classified as one of the most degraded with a loss of about 40–60 kg of nutrients/ha/year [3, 51]. Soil degradation in SSA refers to several phenomena such as the deterioration of soil's physical, chemical, and biological properties [200]. Within agroecosystems, these phenomena have contributed significantly to the depletion of the fertility of cultivated soil [3, 150].

Research studies have reported the decline in agricultural soil fertility in many regions of sub-Saharan Africa in the last decade, by considering variation in the balance of key nutrients. It was be concluded that there is a high loss of essential soil nutrients due to poor implementation of soil fertility management practices by farmers, deforestation, overexploitation of land, and high demographic pressure on land, further accentuated by the unavailability or scarcity of land in Africa [70, 150, 179]. Added to this, there is variation in climatic conditions and the vulnerability of soils in several areas of SSA [10, 11]. The loss of essential nutrients significantly affects crop development and yield as it reduces nutrient availability. Crop activity related to nutrient exports without restitution or recycling is the main cause of soil nutrient losses because they create nutrient disequilibrium in soils [152]. Depending on their physiological needs, crops have different impacts on soil nutrient losses. Indeed, cereal crops and legumes can export up to 30–40 kg of NPK/ha annually. For legumes, these quantities can be lower than for cereals because they can enrich the soil in nitrogen through biological nitrogen fixation [79]. This exploitation of nutrients contributes to rapid soil depletion, which in turn limits the sustainability of agriculture. For example, it has been shown that the combined effects of soil erosion and crop activity are responsible for an estimated loss of soil fertility of about 660 kg N ha^{-1}, 75 kg P ha^{-1}, and 450 kg K ha^{-1} in SSA [3].

Moreover, the loss of soil organic matter affects both the soil's physical, chemical, and biological properties and also increases its degradation. It has been reported that in SSA, soils are characterized by nutrient poverty, low organic matter contents, and low cation exchange capacity [11]. Due to the climatic conditions of the region, there is a rapid decrease in soil organic matter leading to increased soil acidification and reduced nutrient availability. Next to nutrient and soil organic matter loss, soil acidification is one of the serious problems of tropical soils in general and Sub-Saharan Africa in particular. It leads to a decline in soil fertility and several other phenomena affecting numerous chemical and biological processes in the soil [15, 144]. Soil acidification involves a significant decrease in soil pH that is due to an unbalanced ratio between acidic (H+) and alkaline (OH−) ions in the soil–water solution surrounding the soil particles. Some other factors exacerbate this process, like the leaching of base cations following soil exposure to high rainfall, inadequate crop irrigation, use of ammonium-based fertilizers which lead to an increase in acidic ions (H+), and crop activity which lead to a reduction in base ions in the soil, most of which are accumulated in the fruit or seeds [124, 144]. Most soils in SSA (56%) are dominated by Oxisols and Ultisols according to the USDA Soil Taxonomy. These soil types are mostly the poorest and most acidic. While moderate fertility soils account for only 12% of soils in all cropland [51]. Soil acidity has a great influence on crop growth and productivity. This is because most crops grow best in the pH range between 5.8 and 6.5, below 5.5 the production potential of the soil tends to decrease. In addition, soil pH decreases nutrient availability, plant nutrition, and soil biological activity by increasing the fixing capacity of the soils and dependence on fertilizers [124].

2.2 Approaches to managing the soil fertility in SSA

As a response to the decline in soil fertility, the use of chemical and organic fertilizers has been long-term recommended to rapidly remediate soil nutrient imbalance through the application of sustainable soil fertility management techniques

[110, 179]. This is because the direct input of mineral fertilizers compensates the losses due to crop export, while organic matter supply provides nutrients to the soil that can compensate for crop export, but also improve soil retention capacity (water and nutrients), soil structure, and soil microbial activity [11, 64]. However, several study showed that the overuse of chemical fertilizers leads to soil acidification [144], on the other hand, the use of mineral fertilizers is still very low in Sub-Saharan Africa (the average amount being ≤ 8 kg N ha^{-1} yr^{-1}) compared to other continents such as America, Asia and Europe due to the high cost of fertilizers that are often not adapted to the socio-economic conditions of small farmers [118]. Several researchers have recommended adopting practices that effectively integrate organic matter in crop production [166, 173, 186]. Based on the above, it is clear that sustainable soil fertility management in SSA is a more complex problem, so other solutions should be investigated. More recently, several researchers have reported the importance of soil microorganisms in soil fertility management [112, 118, 174, 196]. In the context of SSA, several groups of beneficial microorganisms have been identified in the soil and in the roots of several crops, the main ones being bacteria and fungi identified as Plant growth promoting Microorganisms (PGPM). Experimental tests of these microorganisms have revealed several effects on soil fertility and crop growth promotion, the main ones being the improvement of soil properties, nutrient bioavailability, solubilization, mobilization, mineralization, dissolving, uptake and soil bioremediation, control of crop diseases, improvement of nodulation and biological nitrogen fixation (BNF), improvement of fruit yield and quality, and crop biofortification [49, 97, 192]. Within the main PGPM, a particular group of AMF has captured our interest whose effects on soil fertility, crop biofortification, and crop yields will be presented in this work. For example, it has been demonstrated that the use of arbuscular mycorrhizal fungi (AMF) in agricultural systems can hydrolyze the soil's organic phosphorus stock into inorganic phosphorus, making significant amounts available to plants [19, 115]. Similarly, improved nitrogen nutrition and other nutrients (N, P, K, Ca, Mg, Fe, Zn, etc.) have been observed in plants colonized by AMF compared to non-mycorrhizal plants [120]. It has also been reported that combining AMF with other organic fertilizers significantly enhances crop development and yield [49]. Additionally, Ji et al. [81] demonstrated that the inoculation of *Acaulospora colombiana* and *Acaulospora morrowiae* promotes glomalin production and the formation and stability of soil aggregates.

3 An overview of crop biofortification

Malnutrition poses a major challenge and a public health problem in developing countries, particularly in Africa, where the highest prevalence in the world has been reported (21% in 2020) with more consistent growth. It is the underlying cause of many diet-related diseases and one of the main sources of deaths among children [52]. Additionally, hidden hunger refers to another form of malnutrition caused by deficiencies in vitamins and essential micronutrients in the human diet. It is often overlooked, yet it affects more than 282 million people in Africa [52, 83]. Micronutrients are as important as macronutrients (proteins, fats, and carbohydrates) due to the role they play in nutritional balance and human health [83, 160]. It has been reported that in sub-Saharan Africa, the diet of the population is deficient in vitamins, Fe, Zn, Ca, Mg, Cu, Mn, Se, B, Mo, Ni, Cl, and I, which affect the health and longevity of individuals. These nutrients are categorized among the essential elements, and their deficiency weakens the immune system, delays physical and intellectual growth, and can even lead to death [52].

   To mitigate micronutrient deficiencies, several approaches have been employed. These include industrial fortification of foods, promotion of dietary diversification, and food supplementation. Due to various technical, political, and socio-economic constraints, these methods have not yielded satisfactory results. Therefore, crop biofortification has been proposed as an alternative to conventional methods to increase the concentration and bioavailability of micronutrients in the edible parts of plants through agronomic and/or genetic approaches [86, 160]. These micronutrients play a role in several plant metabolisms and are important not only for plant growth and development but also for human and animal nutrition [87]. According to Ku et al. [87], biofortification is also used to improve the concentration of other non-essential but beneficial secondary metabolites for human health.

3.1 Why crop biofortification is important?

The deficiency of essential minerals and vitamins affects human health by increasing the risk of diseases [52]. Indeed, micronutrients play a crucial role in human health. Among them, five elements—iron, zinc, iodine, calcium, and selenium—are present in very limited quantities in foods and are associated with most cases of observed chronic diseases due to deficiencies. For example, iron is an important cofactor for various enzymes involved in multiple metabolic

processes in both humans and plants [158]. Zinc plays a role in growth and development. Zinc deficiency leads to immune dysfunction, growth retardation, and cognitive disorders. On the other hand, selenium is also beneficial for human health. Selenium deficiency increases the risk of cardiovascular diseases, oxidative stress, thyroid and immune function impairments, and raises the risk of various cancers [133]. Calcium plays a structural role in the human body and is present in large proportions (1–2%). It also serves as a cofactor for enzymes. It plays a role in blood clotting, and its deficiency affects bone health, leading to rickets and osteoporosis [59]. Iodine is an essential component of thyroid hormones, thyroxine and triiodothyronine, which regulate growth and development and maintain basal metabolism [160]. As described earlier, biofortification increases the concentration of these nutrients in crops to combat malnutrition worldwide. The importance of this technique in improving the bioavailability of various micronutrients has been reported by several authors [34, 155, 190]. Firstly, it resides in the fact that biofortification targets crops whose products are part of daily consumption and constitute staple foods for all segments of the population. Secondly, biofortification is a highly sustainable approach once the adopted techniques are mastered. Thirdly, by providing naturally enriched foods to people, biofortification enables reaching poor populations with limited access to resources [116]. In addition, the investment costs in biofortification are low compared to traditional public health methods based on food supplementation and dietary diversification [27].

3.2 Approaches for crop biofortification: challenges and opportunity

Three main strategies have long made crop biofortification possible. These include agronomic methods, breeding (improvement) methods, and genetic engineering [27, 160]. Breeding methods are based on techniques or approaches of crop genetic improvement, such as selecting elite germplasms that already have preferred agronomic characteristics or introgressive hybridizations between elite varieties. Genetic engineering (metabolic) involves using advanced biotechnology techniques to introduce genes from various sources into improved elite varieties. Meanwhile, agronomic methods are based on agricultural practices aimed at increasing the nutrient content in the edible parts of plants, such as fertilization [83]. Among the three aforementioned strategies, only breeding improvement and genetic engineering can influence nutrient bioavailability. These two methods differ from agronomic methods in that they involve modifying the genotype of the target crop. They result in the creation of lines possessing genes that promote high accumulation efficiency and nutrient bioavailability. However, the two methods differ in that breeding and hybridizations occur between genetically compatible species, whereas genetic engineering presents no taxonomic obstacles, as it employs artificial and biotechnological techniques based on gene transfer [27, 155, 160].

Breeding and genetic engineering methods offer a dual advantage in improving the nutrient content of plants. Firstly, after the efforts invested in the variety development stage, the increase in nutrient content is guaranteed over time. Additionally, the increase in nutrient content also enhances the plant's vigor and thus its yield [83]. However, these methods have faced a major obstacle in terms of the time required for breeding selection and genetic engineering to develop a biofortified variety, as well as for the acceptance of genetically modified plants in the community. Additionally, there is the issue of high investment costs for developing biofortified varieties using either of these methods [86]. To overcome these obstacles, molecular biology techniques such as quantitative trait locus (QTL) analysis and marker-assisted selection (MAS) have been employed. In this case, it was necessary to consider the various soil properties that can significantly interfere with the absorption and accumulation of minerals. Additionally, for some nutrients, selecting cultivars rich in these nutrients is limited by plant genetics [83]. For example, for wheat, Connorton and Balk [35] demonstrated that developing wheat lines rich in iron was challenging using traditional breeding methods because the iron concentration was negatively correlated with yield. On the other hand, biofortification through genetic engineering required significant investments. Moreover, biofortification through agronomic methods based on fertilizer application is not sustainable and causes environnemental pollution [83]. Given the above, the search for new approaches is necessary to sustainably improve nutrient bioavailability in crops within a short timeframe and at an acceptable cost. Plant growth-promoting microorganisms are known for their ability to increase the levels of micro- and macronutrients in most staple food crops through various mechanisms depending on the groups considered [83, 86, 130, 160]. The study by Shi et al. [155] proposed the use of plant microbiomes to enhance iron content in wheat, while in rice, selenium content was significantly increased through the use of rice microbiomes [34]. Thus, the use of microorganisms associated with crops could be an alternative approach for crop biofortification. In particular, it has been reported that AMF play a particular role in biofortification in most crops [190]. Therefore, it would be important to exploit them to improve crop biofortification and reduce the prevalence of malnutrition in SSA.

Furthermore, with regard to agronomic biofortification methods, it has been reported that several constraints can hinder the development of crops in the field and their nutritional capacity, which could lead to decreased yields and, consequently, a situation of food insecurity in Africa. Among these constraints are climate change, the ever-increasing human population, depleted soil nutrients, drought, loss of biodiversity, as well as crop diseases and pests [136]. Climate change can cause extreme weather conditions, such as prolonged droughts or floods, which negatively affect plant growth and reduce agricultural yields. The increasing human population exerts growing pressure on food resources, necessitating increased agricultural production to meet demand [20]. Depleted soil nutrients, often caused by intensive and unsustainable farming practices, reduce soil fertility and the ability of plants to absorb the essential nutrients needed for their growth [39]. Drought, particularly in the arid and semi-arid regions of Africa, limits the water supply essential for crop growth. The loss of biodiversity can destabilize agricultural ecosystems, making crops more vulnerable to diseases and pests. Finally, crop diseases and pests can cause significant yield losses and affect the quality of harvested products. These constraints also limit the ability of plants to absorb essential nutrients such as macronutrients (carbohydrates, proteins, amino acids and lipids) and micronutrients (iron, zinc, iodine, selenium, molybdenum, Calcium, Magnesium, Copper, Manganese, Borum, and Nickel) in the harvested products. In light of this situation, it is interesting to note that soil microorganisms, particularly AMF, have long demonstrated their reliability and effectiveness for a wide range of crops [109].

AMF establish a symbiotic relationship with plant roots, thereby improving the absorption of nutrients and water. By colonizing the roots, AMF increase the root absorption surface and facilitate access to essential nutrients present in the soil. Moreover, they help strengthen plant resistance to environmental and biotic stresses, such as drought, diseases, and pests [112]. By integrating AMF into agricultural practices, farmers can overcome the various constraints that hinder agricultural production, thereby ensuring sufficient production in terms of both quality and quantity for most crops. This approach not only helps to improve food security but also promotes sustainable agricultural practices, which are essential to addressing the challenges posed by climate change and population growth in Africa [66].

4 An overview of arbuscular mycorrhizal symbiosis

Arbuscular mycorrhizal fungi (AMF) are the most widespread group of fungal symbionts in plants, associated with more than 80% of terrestrial plants [23]. This widespread distribution of arbuscular mycorrhizal symbiosis is believed to be related to its ancient origin, as confirmed by analyses of archaeological data obtained from ancient plant fossils [138]. Mycorrhizal symbiosis establishes an association between soil fungi and vascular plants, allowing for the bidirectional exchange of substances between the two partners. Several taxonomic studies of AMFs have been conducted over time, followed by diversity studies in various environments depending on the host plant species. In this section, we provide a brief overview of the taxonomy of AMFs and the functioning of arbuscular mycorrhizal symbiosis.

4.1 Diversity and classification of arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi form a very heterogeneous group with several species distributed in several fungal taxa. The first classifications of fungi (AMF), based on the morphological characteristics of the fungal spores, grouped arbuscular mycorrhizal fungi in the family Endogonaceae, before 1974, and then in four genera (Glomus, Sclerocystis, Gigaspora, and Acaulospora) between 1974 and 1990, which referred them to the polyphyletic group Zygomycetes [105]. Then, a new class of Glomeromycetes was described within the phylum Zygomycota with two distinct orders; the order Glomerales which includes the AMF, and the order Endogonales, without considering the relationships between the two orders [60] More recently, molecular and phylogenetic analysis of the generalized taxonomic structure of the AMFs, based on 18S ribosomal DNA (SSU) gene sequences, has grouped the AMFs into the monophyletic phylum Glomeromycota with four orders; the Glomerales, Paraglomerales, Archaeosporales, and Diversisporales. [138, 163]. Other studies have proposed a clearer classification based on morphological, phylogenetic, and molecular analysis (18S SSU, région ITS1, ITS2 et 28S LSU of ARNr). It has been suggested that arbuscular mycorrhizal fungi are not related to the zygomycetes group but are close to the ascomycetes and basidiomycetes and form a well-individualized phylum, the Glomeromycota [58, 117, 139]. This classification allowed to group the AMFs in 3 classes (Archaeosporomycetes, Glomeromycetes, and Paraglomero- mycetes), five orders (Archaeosporales, Diversisporales, Gigasporales, Glomerales, and Paraglomerales), sixteen families, forty-five genera and about two hundred and thirty species (Table 1).

Table 1 Current classification of the phylum Glomeromycota (arbuscular mycorrhizal fungi, AMF), as described by Castillo et al. (2016)

Class	Order	Family	Genous
Glomeromycetes	Glomerales	Glomeraceae	*Glomus, Dominikia, unneliformis, Funneliglomus, Kamienskia, Micro-dominikia, icrokamienskia, Nanoglomus, Oehlia, Orientoglomus, Rhizo-glomus, Septoglomus, Sclerocarpum, Sclerocystis, Simiglomus*
		Entrophosporaceae	*Entrophospora, Albahypha Claroideoglomus, Viscospora*
	Diversisporales	Diversisporaceae	*Diversispora, Desertispora, Otospora, Tricispora, Redeckera, Corymbiglomus*
		Sacculosporaceae	*Sacculospora*
		Pacisporaceae	*Pacispora*
		Acaulosporaceae	*Acaulospora, Kuklospora*
	Gigasporales	Gigasporaceae	*Gigaspora*
		Scutellosporaceae	*Scutellospora, Bulbospora, Orbispora*
		Racocetraceae	*Racocetra, Cetraspora*
		Dentiscutataceae	*Dentiscutata, Fuscutata, Quatunica*
		Intraornatosporaceae	*Intraornatospora, Paradentiscutata*
Archaeosporomycetes	Archaeosporales	Archaeosporaceae	*Archaeospora, Intraspora, Palaeospora,*
		Ambisporaceae (= Appendicispo-raceae)	*Ambispora (= Appendicispora)*
		Geosiphonaceae	*Geosiphon*
Paraglomeromycetes	Paraglomerales	Paraglomeraceae	*Paraglomus, Innospora*
		Pervetustaceae	*Pervetustus*

Recent advances in soil microorganism study techniques have profoundly transformed soil biology. Utilizing molecular biology-based approaches, it is now possible to uncover the vast diversity of microbial populations present in the soil [89]. In particular, arbuscular mycorrhizal fungi (AMF) have benefited from these advancements, enabling their direct identification in plant roots or soils. This approach has revealed that the actual diversity of AMF in ecosystems is potentially much higher than initially estimated. Moreover, the analysis of DNA polymorphism in AMF isolates from diverse geographical origins has been made possible by these molecular techniques [32]. The genetic diversity observed within AMF species or among their isolates arises from their complex genetic structure. Indeed, a single spore or hypha of AMF can contain hundreds or even thousands of nuclei, giving these organisms a "multi-genomic" genetic structure. Sperschneider et al. [165] revealed the coexistence of two nuclear genomes in AMF heterokaryons, while de Novais et al. [38] highlighted intraspecific polymorphisms in the 18s rDNA region within an isolate colonizingmaize. Similarly, Chen et al. [32] revealed high intraspecific genomic diversity among *Rhizophagus irregularis* isolates. Additionally, it has been scientifically proven that each nucleus within a spore is not genetically identical, indicating significant genetic variability within this group [85].

While the genetic diversity of arbuscular mycorrhizal fungi (AMF) has been revealed for most regions, their functional diversity under different environmental conditions and on different host plant types has not yet been well elucidated. Functional diversity refers to the variety of ecological roles that AMF can play, influenced by interactions with specific abiotic and biotic conditions. This includes their ability to enhance nutrient uptake, their resistance to environmental stresses, and their effectiveness in promoting host plant growth in various contexts [89]. Further studies should be conducted to clarify these functional aspects and bridge this knowledge gap. These studies could include various experimental approaches such as controlled and field trials, as well as the use of advanced sequencing and functional analysis techniques. Understanding the functional diversity of AMF is essential to optimize their use in agriculture and ecosystem management, in order to maximize their benefits in terms of agricultural productivity, soil fertility, and crop resilience to environmental changes.

4.2 Functioning of the arbuscular mycorrhizal symbiosis

Host plant root colonization by AMFs can be effective via the mycorrhizal propagules that are present in the soil. Three types of propagules are known to exist in the soil, including spores, fragments of mycorrhized roots, and hyphae [23,

163]. The establishment and functioning of the arbuscular mycorrhizal symbiosis require three principal steps. The first step is the hyphae development from the soil propagules, the second is the meeting of the hyphae with the host roots followed by the development of the mycorrhizal structures and the third step is the substances exchange between the two partners.

4.2.1 Hyphae development in the soil: initiation of root colonization

The establishment of the mycorrhizal symbiosis begins with the appearance of the first hyphae. These hyphae have two origins, either from spore germination or from mycorrhized roots [58]. In the absence of a host plant, hyphae derived from spore germination can be destroyed. They thus present a very limited life span in the absence of an appropriate energy source. This implies that arbuscular mycorrhizal fungi are the obliged biotrophs [23, 138, 157]. On the other hand, hyphae from mycorrhized roots are the result of a previously existing mycorrhization activity [58]. After germination, hyphae are fed by spores through their lipid storage catabolism for only a few days. During this phase, hyphae explore the soil trying to find the host plant (Fig. 1). They can retract into spores in case of the absence of a host plant or continue their development cycle in case of infection of a host plant. A presymbiotic mycelium is then established [23].

4.2.2 Meeting of the hyphae with the host roots

The perception of the host plant by the pre-symbiotic mycelium is possible through root exudates released into the rhizosphere by the host plant [128]. The most common are strigolactone molecules (5-deoxy-strigol) that stimulate the activity of the fungus mitochondria allowing it to reactivate its metabolic activity and ramification [58]. The hyphae attracted by the plant, penetrate the external part of the root through the development of a structure called "appressorium" and the pre-penetration apparatus, which would be stimulated by the wall of the epidermal cells [68, 161]. The formation of these two structures allows hyphae to propagate in the available intercellular spaces. After the penetration of the epidermis and the exodermal cells, the hyphae penetrate the cortex and branch by dichotomy forming the *arbuscules* (Fig. 2) surrounded by the periarbuscular membrane [163]. The arbuscules define a nutrient exchange zone between the two partners in the symbiosis [23].

4.2.3 Substance exchange between the two partners

One of the characteristics of mycorrhizal symbiosis is the bilateral transfer of nutrients [148]. This is possible through the establishment of the interface between the AMF and the host plant's roots. This allows the optimization of their own development [30]. Plant will benefit from good water and mineral nutrition (Phosphorus, Nitrogen, and trace elements) through the development of the extramatrical hyphae of the fungus (Fig. 1), while the fungus in turn will benefit from carbohydrate molecules derived from photosynthesis and provided by the host plant [58].

5 Role of AMF in the improvement of soil fertility

5.1 AMF and soil physical properties

Mycorrhizal fungi colonize both the rhizosphere and the adjacent soil area, thereby exerting an influence on soil structure through their involvement in soil aggregation processes at various levels and through diverse mechanisms. Studies have indicated that arbuscular mycorrhizal fungi (AMF) influence soil structure at three distinct levels: initially, they impact vegetation (plant species), constituting the primary level, followed by their effects on plant roots, and finally, their influence on the AMF mycelium [23, 141]. AMF alter the composition of vegetation growing in a given soil, which in turn affects soil aggregation dynamics [23]. Moreover, the colonization of plant roots by AMF influences root development processes, including soil penetration, water and nutrient uptake, and rhizodeposition (the release of organic compounds into the rhizosphere by living roots). Through their impact on root development within the soil, AMF significantly affect soil aggregation [141].

Regarding the influence of AMF mycelium on soil aggregation, three mechanisms should be considered. Firstly, biochemical mechanisms involve the production of aggregating agents such as glomalin, mucilage, and other proteins by the fungus [142]. Glomalin is a stable and persistent viscous glycoprotein produced in large quantities by CMA, acting
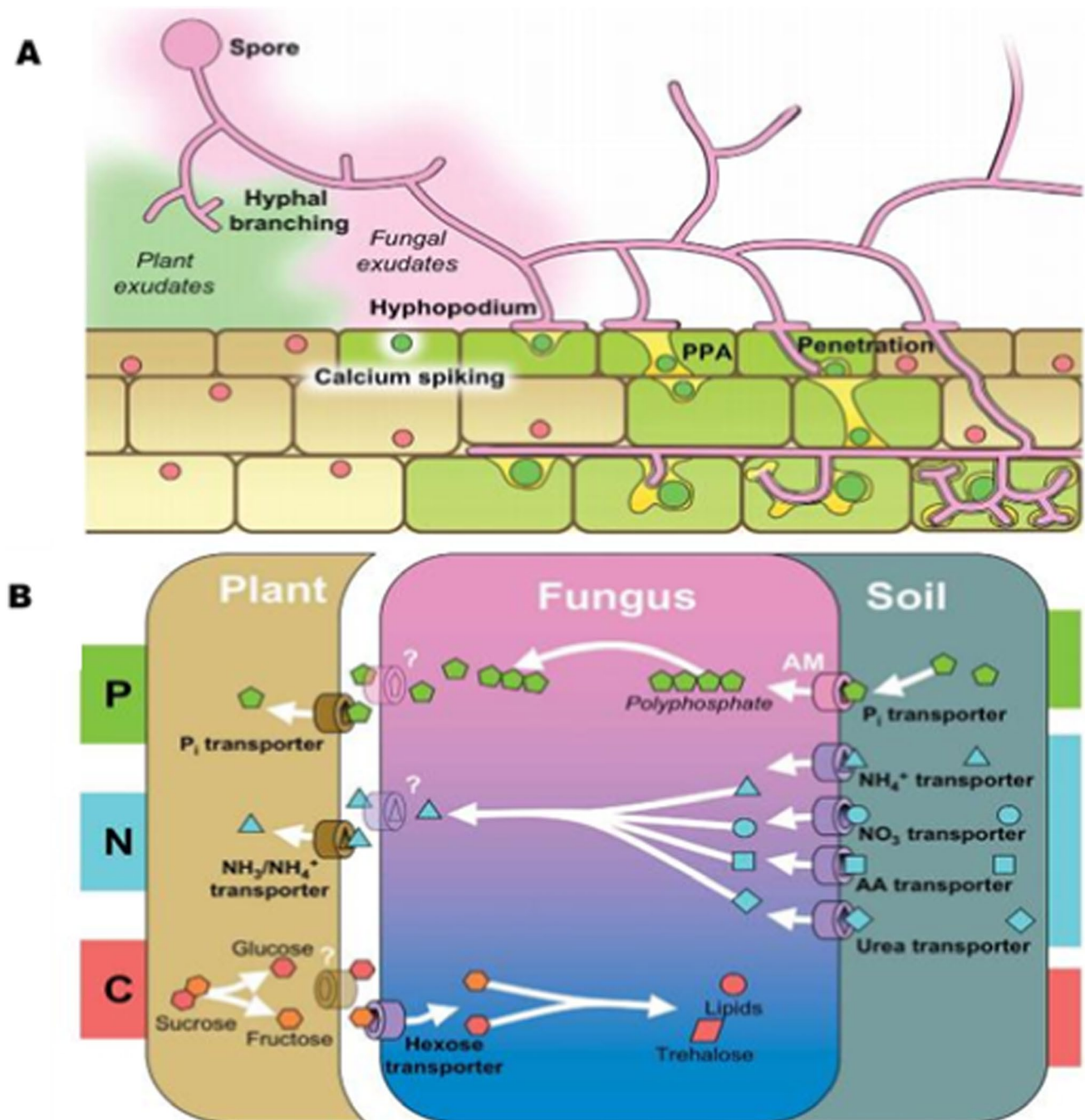
Fig. 1 Schematic representation of the initiation of mycorrhizal symbiosis (**A**): It involves the germination of spores, branching of fungal hyphae, perception of root exudates by the fungus, root infection, and formation of the pre-penetration apparatus (PPA), leading to the establishment of mycorrhizal structures such as arbuscules. Nutrient exchange process between the host plant and the arbuscular mycorrhizal fungus (AMF) (**B**): This process entails the enhancement of nitrogen (N) and phosphorus (P) absorption by the fungus through the stimulation of transporters for different nutrient forms. Additionally, there is a transfer of carbon from the host plant to the fungus in the form of sugars [23]

as a binder of soil particles and thus participating in soil aggregate formation. It also possesses the ability to bind ions present in the rhizosphere, contributing to soil quality rejuvenation and heavy metal sequestration [183]. The study by Syamsiyah et al. [169] demonstrated a significant and positive correlation between soil aggregation and both total glomalin content and available glomalin in the soil. Additionally, it has been shown that glomalin could be an important reservoir of organic nitrogen in the soil [57]. Next, biological mechanisms involve the influence of CMA on soil microbial
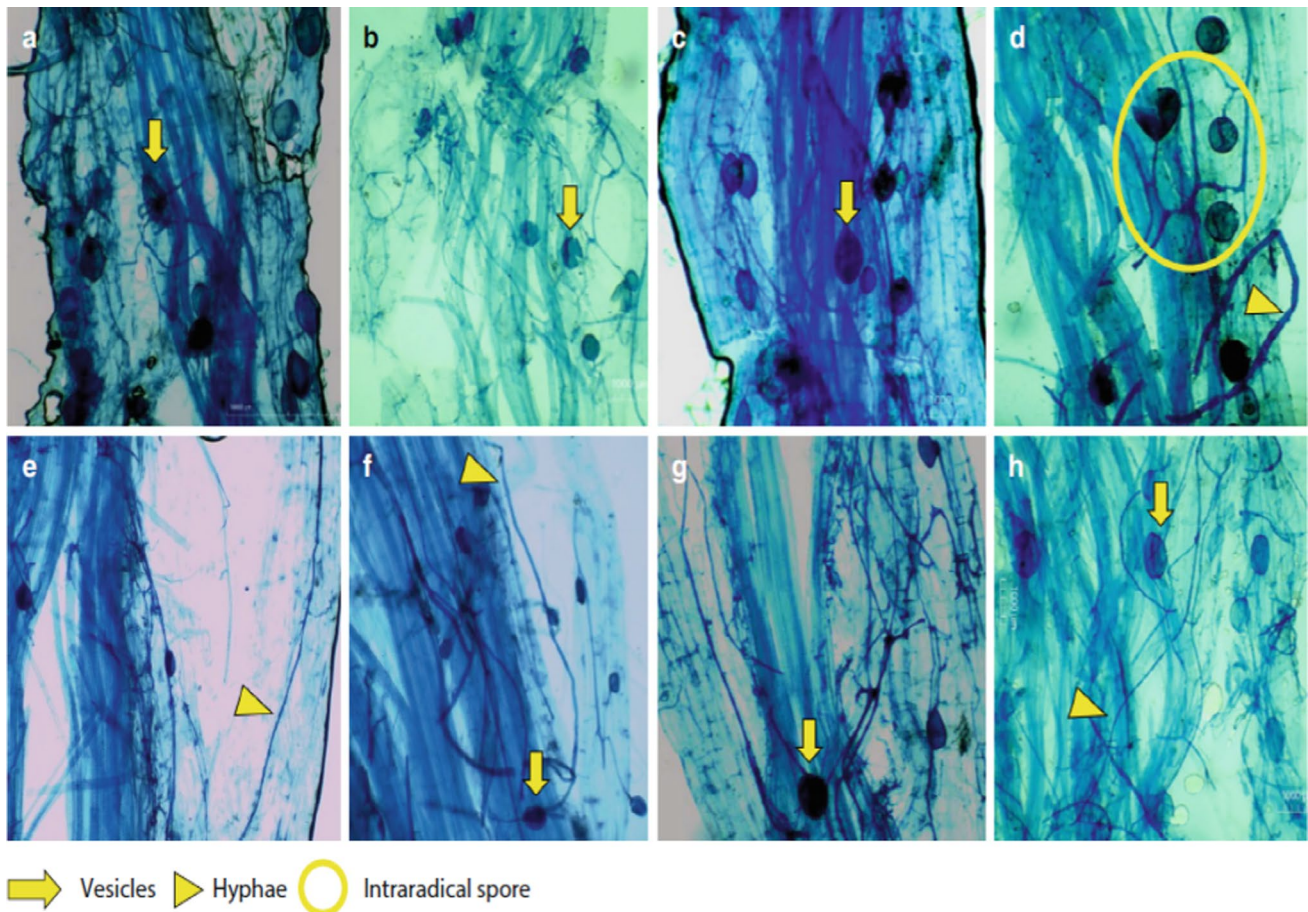
Fig. 2 Illustration of the various mycorrhizal structures (intraradical and extraradical hyphae, vesicles) and the endospores formed inside millet root fragments [114]

communities and interactions with other soil microorganisms. Indeed, CMA interact in various ways with other soil organisms, living in relationships of synergy, parasitism, or necrotrophism [169]. For example, CMA can coexist with certain bacteria such as exopolysaccharide-producing bacteria, which could influence soil aggregation processes [177]. Finally, biophysical mechanisms involve the modification of soil water status and the alignment and intertwining of hyphae, indirectly affecting soil aggregation [141]. Indeed, several studies have reported that CMA mycelium associated with plant roots, forming a dense mycelial network, contributes to soil aggregation, soil aeration, and erosion prevention [65]. Recent studies indicate that AMF hyphae affect the orientation of soil particles through mechanical action. Additionally, dead mycelium contributes to soil organic matter and acts as a physical binder through glomalin, which plays a crucial role in soil aggregation [14, 49].

5.2 AMF and soil chemical properties

One of the most scientifically evident assertions is that arbuscular mycorrhizal fungi (AMF) play a pivotal role in the biogeochemical cycling of nutrients in soil [180]. Numerous scientific studies have unequivocally demonstrated that these fungi, through their extramatrical hyphae, exhibit enhanced nutrient and water absorption capabilities beyond the rhizospheric zone, thereby significantly improving the growth and nutritional status of their host plants [43, 184]. Additionally, AMF are known to actively participate in various soil biochemical processes, thereby exerting a profound influence on the overall nutrient cycling dynamics within soil ecosystems [189] (Table 2).

Table 2 An overview of studies investigating the effect of AMF application on soil physical, chemical and biological properties

AMF species	Target plant species	Major effects on soil properties	References
Rhizophagus irregularis	Glyceria striata	AMF increase liming effect and an increase in nutrient availability	Moland et al. (2018)
Acaulospora colombiana and Acaulospora morrowiae	Urochloa brizantha	AMF enhances GRSP production and the formation and stability of soil aggregates	Barbosa et al. [14], Ji et al. [81]
Glomus etunicatum and Rhizophagus irregularis	Zea mays L	AMF improves the carbon mineralization rate	Xu et al. [189], Huang et al. [77]
Acaulospora sp and Glomus sp	Phaseolus vulgaris	AMF contributes to soil N concentration through the improvement of biological N2 fixation in low-fertility soils	Razakatiana et al. [137]
Glomus formosanum	Glycine max and Urochloa decumbens	AMF fungi facilitate bacterial translocation and the simultaneous associations of plants with beneficial fungi by their ERM, and after the establishment of symbiotic relationships	Barreto de Novais et al. [38]
Rhizophagus irregularis	Cucurbita pepo L	AM fungi facilitate mitigating the negative effects of acidity and aluminum toxicity, increasing the availability of N, P, K, and Fe in the soil	Rouphael et al. [145]
Gigaspora margarita	Ipomoea batatas	AM fungi reduce Al3 + and Mn2 + availability under acidic soil conditions	Yano and Takaki [191]
Rhizophagus irregularis	Trifolium subterraneum an Phalaris aquatica L	AM fungi reduce N and P loss via leaching with reductions in leaching of NH4 + and/or NO3-	Asghari et al. [9] , Asghari and Cavagnaro [8]
Glomus mossea	Pisum sativum	AMF increase rhizospheric soil aggregation in different soil types	Bethlenfalvay and Barea [21]
Glomus mosseae	ryegrass/clover sward	AM fungi enhance phytoremediation of polluted soils though degradation of polycyclic aromatic hydrocarbons	Joner et al. [82]
Funneliformis mosseae	Zea mays L	AMF enhanced the biomass and P uptake of maize, and decrease in phosphorus loss	He et al. [72]
Glomus deserticola and Gigaspora margarita	Olea europaea L	AM fungi induced changes in the soil chemical characteristics by increasing the electrical conductivity and an accumulation of Na + and Cl −, increased also the antioxidant enzyme activities, malondialdehyde and H2O2 contents, and electrolyte leakage rate	Hassena et al. [71]
Rhizophagus irregularis	Lycopersicon esculentum L.)	AMF decreased the C allocation to roots, in turn increased the net rhizodeposition, then enhance C sequestration by colonized plants	Zhou et al. [199]
Rhizophagus irregularis	Solanum lycopersicum L	Mycorrhizal plants reduced P lost via leaching in the sandy soil substrate	Tran et al. [176]

Table 2 (continued)

AMF species	Target plant species	Major effects on soil properties	References
Glomus caledonium	*Zea mays L*	AMF enhance C sequestration though improving hyphal aggregation, rhizo-C stabilization and soil priming and thus faster SOC turnover. AMF enhance soil aggregation and C sequestration.	Peduruhewa et al. [122]; Agnihotri et al. [4]

5.2.1 Effect on soil C cycling

The carbon cycle is one of the most critical biochemical processes, as it determines the flux of carbon in the soil, thereby influencing ecosystem functioning and resilience to climate change processes [77]. Currently, our understanding of the factors determining carbon fluxes in soil and associated processes remains incomplete [164]. Moreover, it has been demonstrated that soil organisms, particularly microorganisms, play a crucial role in the dynamics of soil decomposable carbon pools through processes such as respiration, decomposition, mineralization, and immobilization. However, their specific modes of action, which vary among organisms, are still poorly understood. Given their symbiotic relationship with the majority of plants, arbuscular mycorrhizal fungi (AMF) control the transfer of nutrients from the soil to the plant and vice versa [172]. Regarding carbon, AMF obtain their carbon demand from their host plants in the form of carbohydrates, which are transported via the phloem to the apoplast, reaching the cortical cells of the roots before being delivered to the AMF [178]. It has been estimated that approximately 20–50% of the plant host's photosynthates are allocated to AMF. In this context, various sucrose transporters (Sucrose Transporter, SUT) are involved in transporting carbon from the plant's upper parts to the roots. The carbon is then transported from the roots via intraradical hyphae to the extraradical hyphae to contribute to AMF development. Transfer to the soil is carried out by the extraradical hyphae in the form of chitin and glomalin. More recently, it has been discovered that, in addition to carbohydrates, lipid compounds are also directly transferred to AMF [121].

The dense mycelial network developed by AMF constitutes a significant portion of soil microbial biomass and one of the most important pools of soil microbial carbon. Therefore, AMF effectively contribute to soil organic matter and carbon sequestration due to the increased carbon demand from host plants and carbon redistribution within the mycelial network [121]. This carbon input to the soil significantly impacts soil microbial communities, particularly free-living microbial decomposers (bacteria and saprotrophic fungi), which in turn contribute to soil carbon flux. Conversely, antagonistic reactions may also be observed. In addition to carbon input to the soil, AMF control the decomposition of organic matter and determine whether carbon processes mineralization or sequestration. The impact of AMF on carbon sequestration could be explained by their preservation of carbon mineralization by reducing the activity of enzymes involved in organic matter decomposition produced by free-living microbial decomposers [162]. Indeed, according to Leifheit et al. [92], the rate of soil organic matter decomposition is negatively correlated with mycorrhizal fungal density. Thus, AMF influence soil fertility through their significant contribution to soil organic matter, which serves as a reservoir for soil nutrients and plays a role in soil carbon dynamics.

5.2.2 Effect on soil nitrogen and phosphorus cycling

Nitrogen and phosphorus are essential nutrients for crop growth and development. Their deficiency in the soil constitutes a major constraint to crop production as both are the most demanded macronutrients for optimal plant growth [28]. Apart from their role, AMF are primarily involved in phosphorus allocation to their host plants [183, 184]. More recently, it has been elucidated that in addition to phosphorus, AMF can absorb nitrogen in the form of nitrate, ammonium, and organic nitrogen, and transfer it to the plant [94]. According to Fellbaum et al. [54], the transfer of N by AMF to the host is directly related to the transfer of carbon from the host plant to the AMF (Sect. 5.2.1). The main implication of AMF in the nitrogen and phosphorus cycle is determined by nutrient allocation, nutrient immobilization, reduction of leaching losses, and improvement of nutrient use efficiency [178]. Indeed, studies aiming to evaluate the effects of AMF on nutrient uptake have shown that mycorrhizal plants absorb more than 80% of the phosphorus they need through AMF [117]. The work of Qi et al. [132] demonstrated the ability of AMF to facilitate phosphorus acquisition in phosphorus-poor soil conditions. Phosphorus is the least available macroelement for plants due to its low solubility, low mobility, and its sequestration by Fe^{3+}, Ca^{2+}, and Al^{3+} hydroxides in most acidic and calcareous soils [12].

In these conditions, AMF facilitate phosphorus nutrition in plants through the phenomenon of mobilization and solubilization, thereby increasing plant accessibility to Pi and orthophosphate ions in the soil solution [154]. Indeed, the extraradical hyphae of mycorrhizal roots extend beyond Pi-deficient zones, typically around the plants, and absorb the bioavailable Pi that would otherwise be inaccessible to plants [168, 184]. Additionally, mycorrhizal plants have the ability to release organic acids such as citrates and malates, which can chelate Al^{3+} and Ca^{2+} and dissolve Ca^{2+} and Al^{3+} phosphate [47, 129, 149]. Some AMF species are involved in the mineralization of organic P, converting it into inorganic phosphorus through the action of acid phosphatase enzymes they produce [154], recruiting P-solubilizing bacteria in the process [19].

As for nitrogen, in addition to absorption, AMF also play a role in nitrogen redistribution in the aboveground parts of the plant, such as leaves and fruits [55]. According to Veresoglou et al. [180], five pathways explain the influence of AMF on the nitrogen cycle. These include substrate availability, modification of the abiotic environment, modification of microbial communities, and effects on the host plant and plant community modification. Indeed, it has been reported that AMF can compete with free-living microbiomes that recycle nitrogen by immobilizing inorganic N in their mycelium or by transferring more ammonium to the host plant. This effect consequently limits denitrification and nitrogen leaching [172]. Additionally, AMF influence the activity of heterotrophic microorganisms involved in the nitrogen cycle by providing energy in the form of carbon in the soil, which is necessary for their development [54]. Given their influence on soil structure, AMF affect soil aeration, which could impact nitrification and denitrification, the two key stages of the nitrogen cycle influenced by soil oxygen concentration. The modification of soil pH due to AMF could influence the availability of nitrogen by favoring one process over the other [180]. AMF also increase the capacity of legumes to fix atmospheric nitrogen [63]. According to Etesami et al. [46], nitrogen is a constituent of chlorophyll, hence a key element in photosynthesis. The contribution of nitrogen through symbiotic fixation could therefore impact the transfer of photosynthates to the roots in the form of carbohydrates by increasing microbial activity in the soil, including that of AMF and other heterotrophic microorganisms involved in the nitrogen cycle.

5.3 AMF and soil acidity alleviation

Soil acidity is one of the major factors limiting the productivity of several crop species due to the aluminum toxicity it induces [119]. These conditions also affect the availability of essential nutrients, mainly phosphorus, altering their absorption and translocation in plants [36]. Soil acidity also determines the level and severity of phytotoxicity of elements such as aluminum (Al), manganese (Mn), and iron (Fe) [12, 129]. To address the issue of soil acidity, two approaches have been proposed: soil liming to raise the soil pH level and the use of crop genotypes tolerant to Al. However, liming is an unsustainable practice that requires significant time and financial resources, while improving tolerance/resistance to aluminum toxicity is a long-term and genetically complex process [145]. Furthermore, the use of soil organisms such as AMF could be an alternative method for managing soil acidity [6].

Numerous studies have reported the beneficial effects of AMF in alleviating the negative impacts of soil acidity and aluminium toxicity and on crop performance [145, 191]. One explanation for this is that AMF can alter the interaction between the plant and soil and also protect the plant against various stresses such as those caused by heavy metals, drought, etc. Under these conditions, AMF can enhance crop performance by limiting the absorption and translocation of Al^{3+} in the plant [90, 91]. Indeed, the extraradical mycelium of AMF produces exudates composed of organic acids capable of chelating Al^{3+}, Fe^{3+}, and other heavy metals, thereby preventing their absorption by the plant (Sect. 5.2.2). Rouphael et al. [145] conducted a greenhouse study examining the influence of inoculation with AMF strains on the agronomic and physiological performance of squash under conditions of soil acidity and aluminum toxicity. According to this study, inoculation with *Rhizophagus irregularis* and *Funneliformis mosseae* significantly improved plant performance in terms of biomass accumulation, yield, fruit quality, and concentration of macro and micronutrients, primarily phosphorus and iron. For sweet potato, inoculation with *Gigaspora margarita* in acidic soil limed (pH 4.2) and unlimed (pH 5.2) significantly improved biomass accumulation at pH 4.2 and not at pH 5.2. This suggests alleviation of aluminium and manganese toxicity under soil acidity conditions [191].

5.4 AMF and soil biological properties

Soil contains a complex network of organisms that interact directly with the physical and chemical properties of the soil. These organisms include bacteria, fungi, protozoa, nematodes, and insects [107, 108]. Among these organisms, microorganisms play a crucial role in the soil due to their importance and activities [88]. They interact with each other and perform various ecosystem functions such as decomposition of organic matter, nutrient mineralization, biological nitrogen fixation, soil aggregation, etc. Consequently, soil microorganisms contribute significantly to maintaining soil fertility (Sect. 5.2). Among these various microorganisms, arbuscular mycorrhizal fungi (AMF) are a particular group of beneficial soil microorganisms that form symbiotic relationships with the majority of plants, providing several ecological services (section). In addition to the relationships they develop with their hosts, AMF interact with other soil microorganisms, determining various types of relationships ranging from synergy to antagonism [13]. These interactions are involved in nutrient cycling, impacting soil fertility and crop growth [129, 131]. Moreover, due to their influence on the

quality and quantity of root exudates, AMF can also influence the structure of soil microbial communities and their activities [98, 141, 142].

Several microorganisms work synergistically with AMF to promote plant growth and soil health, especially under environmental stress. Indeed, numerous studies have reported the positive impacts of AMF on biological nitrogen fixation (BNF) due to the synergy they develop with nitrogen-fixing bacteria (Rhizobium). It has been observed that during the tripartite symbiosis (plant-AMF-Rhizobium), AMF fulfill the high demand for phosphorus required during the transformation of dinitrogen (N2), significantly enhancing BNF [195]. Additionally, AMF develop a synergistic relationship with plant growth-promoting bacteria (PGPB). For example, according to Nanjundappa et al. [107], the action of AMF in promoting crop growth is reinforced by different species of Bacillus bacteria. The study by Adriana et al. [2], evaluating the effect of double inoculation of three AMF isolates (two isolates of *Glomus constrictum* and one isolate of *Rhizophagus intraradis*) and a strain of PGPB (*Bacillus megaterium*), concluded that the combination of AMF isolates with *Bacillus megaterium* improved the growth of *Lactuca sativa* plants and enzymatic activities (glucose-6-phosphate dehydrogenase and glutamine synthetase) in the rhizospheric soil. In their study, Sarathambal et al. [153] observed that inoculation of *Rhizophagus sp.* in combination with zinc-solubilizing bacteria significantly improved the growth of Curcuma, enzymatic activity (dehydrogenase), microbial respiration, and the structure of soil bacterial communities. Similar effects were observed in maize inoculated with *Rhizoglomus irregularis* in combination with two PGPB species (*Pseudomonas reactans* and *Pantoea alli*) [104]. Other cases of synergy between AMF and endophytic bacteria (Frankia in actinorhizal plants), and diazotrophic bacteria (Azospirillum and Acetobacteria) in grasses have been reported in several studies [46, 80].

AMF also develop antagonistic relationships with other soil microorganisms through competition and parasitism. From a competitive standpoint, it has been reported that AMF can limit the growth of bacteria involved in the nitrogen cycle and regulate nitrogen flux in the soil by competing for substrates (Sect. 5.2.2). For example, the study by Veresoglou et al. [180] showed that mycorrhizal inoculation altered the structure of communities of ammonium-oxidizing bacteria due to competition for nitrogen. On the other hand, several researchers have reported the positive impact of AMF in controlling phytopathogenic microorganisms [45, 67]. According to Weng et al. [185], AMF utilize various mechanisms, the main ones being alteration of root structure, production of secondary metabolites acting as antimicrobial agents, and competition with pathogens either for infection sites in the root system or regulation of nutrient distribution in the soil. Apart from the influence of AMF on soil microorganisms, other studies have shown that certain endophytic microorganisms can disrupt mycorrhizal symbiosis within the host. Interactive effects, additive effects, or antagonism on host plant growth can be observed depending on the species present and environmental conditions. Under acidic soil conditions, Svenningsen et al. [168] observed suppression of mycorrhizal symbiosis due to the activity of Acidobacteria and other bacterial taxa acting as putative fungal antagonists.

However, based on the studies reported in the literature, understanding the determinants of mycorrhizal symbiosis remains challenging. Indeed, questions still remain regarding the adaptation of AMF and the functioning of mycorrhizal symbiosis in different environments. The various soil properties are often determined by environmental conditions, which could also influence the functioning of mycorrhizal symbiosis. How do bioclimatic parameters influence the overall diversity and functional diversity of AMF? What is the relationship between climatic parameters, soil properties, and the functioning of mycorrhizal symbiosis in the context of climate change? How do AMF interact with other soil organisms, and what is their impact on the biogeochemical cycle of soil nutrients?

6 Role of AMF in crop biofortification

In developing countries, crop biofortification is a key objective of the agricultural sector to ensure the bioavailability of essential micronutrients in sufficient quantities in food [86, 87]. So far, biofortification relies on two approaches: agronomic practices and crop genetic improvement. However, given the time required by these methods and sometimes unsatisfactory results, many researchers have turned to the use of beneficial rhizospheric or endophytic microorganisms to ensure crop biofortification [34, 87]. Among all targeted micronutrients, vitamins, Fe, Zn, selenium, and iodine are the most deficient in African diets. Microbial biofortification is an approach that utilizes beneficial soil microorganisms with effects on plant growth and mineral nutrition [158]. In particular, numerous researchers have reported the importance of AMF in crop biofortification [32, 190]. This section presents a synthesis of studies on the effect of AMF on crop biofortification and the mechanisms involved, focusing on the five most deficient micronutrients (Table 3).

Table 3 AMF-assisted biofortification of various micronutrients in different crop species

Crop species	AM fungal species	Impact on targeted micronutrients	References
Lactuca sativa L	*Funneliformis mosseae, Rhizophagus irregularis*	Improved ascorbate level and fresh weight	Baslam et al. [16]
Lactuca sativa L	*Rhizophagus irregularis, Glomus mosseae and Funneliformis mosseae*	Increased the levels of all major carotenoids, chlorophylls and tocopherols in green and red leaf lettuces and enhanced growth	Baslam et al. [17]
Allium cepa L	*Rhizophagus irregularis*	Improved biomass production, the abundance of vitamin B1 and its analogs, and organic acids concentration	Rozpadek et al. [146]
Allium cepa L	*Diversispora versiformis, Rhizophagus intraradices, Funneliformis mosseae*	Mycorrhizal inoculation increased total phenolic, pyruvic acid, and vitamin C of onion plants, phenylalanine ammonia-lyase (PAL) and antioxiodant enzyme activities such as catalase (CAT), and peroxidase	Mollavali et al. [103]
Chlorophytum borivilianum	*Glomus fasciculatum, Rhizophagus irregularis, and Glomus mosseae*	Improved saponin level and improved biomass of roots and shoots	Dave et al. [37]
Solanum Lycopersicum	*Rhizophagus irregularis, Funneliformis mosseae*	Increased higher antioxidant concentrations and carotenoid contents	Hart et al. [69]
Cicer arietinum	*Rhizophagus intraradices*	improved the intensity of I and Se accumulation, antioxidant levels, and higher protein and cellulose synthesis	Golubkina et al. [61]
Hordeum vulgare	*Rhizophagus irregularis*	Improved grain and straw Zn concentrations and HvZIP13 gene was significantly up-regulated by mycorrhizal colonisation at the lowest Zn treatment	Watts-Williams and Cavagnaro [184]
Cicer arietinum L	*Funneliformis mosseae, Rhizophagus irregularis*	AM Fungi improved yield and the nutritional value of grain by protein, Fe and Zn biofortification	Pellegrino and Bedini [123]
Triticum aestivum	*Glomus claroideum*	AM fungi increase total selenium content in plant tissues and substrate	Durán et al. [42]
Triticum aestivum	*Glomus versiform and Funneliformis mosseae*	AM fungi improved wheat selenate and selenite acquisition through up-regulating the expression of TaSultr1;1, TaSultr1;3, and TaSultr2;1 in the plant roots	Luo et al. [95]
Calendula officinalis L	*Claroideoglomus claroideum and Funneliformis mosseae*	AM fungi suppressed Pb and Cd accumulation and stimulated the accumulation of important secondary metabolites (total phenols, flavonoids, carotenoids)	Hristozkova et al. [76]
Oryza sativa L	*Funneliformis mosseae and Glomus versiforme*	AM fungi increase Se accumulation and modified the microbial community	Chen et al. [34]

6.1 Effect of AMF on *iron* and zinc biofortification

Inoculation with AMF strains positively affects the bioavailability of micronutrients in the soil as well as crop nutrition [90]. This function is carried out through extramatrical hyphae that absorb more nutrients from the soil towards the host plant [58]. The importance of AMF in improving plant nutrition in Fe and Zn has long been recognized and reported by several researchers. However, the mechanisms involved in the interaction between plants and their microbiome to ensure increased absorption of Fe and Zn are not yet well understood in most crops due to the strong relationship between P and Zn nutrition [55]. Additionally, the process of nutrient translocation and redistribution must also be considered to increase the micronutrient content in plants. Moreover, AMF are known for their potential to increase nutrient absorption and accumulation in roots, leaves, and seeds in several crops [31]. In addition to direct evidence demonstrating the impact of AMF on Fe and Zn nutrition, Pellegrino and Bedini [123] showed that inoculation with *Funneliformis mosseae* and *Rhizophagus irregularis* significantly improved Fe and Zn concentrations in chickpeas. These observations were corroborated by Watts-Williams and Cavagnaro [184], who demonstrated that under conditions of Zn-deficient soils, inoculation with *Rhizophagus irregularis* increased Zn content in leaves as well as the expression of 5 HvZIP genes encoding Zn and Fe transporters in barley. Lehmann et al. [90] conducted a meta-analysis assessing the influence of AMF on Zn nutrition and concluded that AMF positively affected the Zn concentration in tissues of different plant species under various conditions. Wang et al. [181] reported that mycorrhizal inoculation (*Glomus versiforme*) significantly increased iron absorption and translocation in *Citrus reticulata Blanco* and *Poncirus trifoliata* L. Additionally, an increase in Fe, Zn, and protein concentrations was also observed. Other studies have shown that the effect of AMF on Fe and Zn biofortification could be enhanced by dual inoculation with AMF strains and other rhizospheric or endophytic microorganisms [86]. For example, the study by Yadav et al. [190] demonstrated that inoculation of native soil bacteria in combination with AMF (commercial inoculum) significantly improved the Fe and Zn content in wheat.

Several mechanisms explain the role of AMF in the biofortification of iron (Fe) and zinc (Zn) in food crops (Fig. 3). These mechanisms include phytoextraction and translocation through phytostabilization. Phytoextraction refers to the enhancement of plants' ability to absorb nutrients from the soil into their roots. AMF facilitate this process by increasing the surface area of the root system and enhancing nutrient uptake efficiency. This is achieved through the fungal hyphae, which extend beyond the root zone, effectively accessing more soil volume and nutrient sources [66]. Translocation involves the movement of absorbed nutrients from the roots to the aerial parts of the plant. AMF play a crucial role in this process by aiding in the transport of Fe and Zn through the plant's vascular system, ensuring that these essential micronutrients reach the leaves and other edible parts of the crop [188]. Overall, the interaction between AMF and plants significantly enhances the bioavailability of iron and zinc, contributing to improved nutritional quality in food crops and addressing micronutrient deficiencies in human diets. Martino et al. [99] demonstrated that inoculation of AMF isolated from polluted and unpolluted soils induced strong mobilization of Zn. According to them, this effect is due to Zn solubilization resulting from increased production of organic acids, mainly malate and citrate, in the rhizosphere by AMF mycelium. Similarly, Pellegrino and Bedini [123] found that increased absorption and translocation of Fe and Zn in chickpeas were positively correlated with the level of mycorrhization and consequently with a large extraradical mycelial network of AMF. The production of organic acids by AMF mycelium has been reported as the main action mode of AMF to enhance Fe and Zn absorption and translocation in plants [99]. Indeed, through their mycelial network and high activity, AMF release more organic acids and other phenolic compounds that, by reducing soil pH, increase Fe and Zn availability [158]. Furthermore, some AMF exudates act as chelators of trivalent protons (Fe^{3+} and Zn^{3+}), thus favoring the reduced forms of Fe and Zn that are available to plants [159]. Particularly for Fe, plants use two strategies to absorb Fe from the soil, namely strategy I based on Fe^{3+} reduction and strategy II based on chelation by the production of root phytosiderophores [55], and demonstrated that Fe absorption via mycorrhizal structures is achieved through strategy II.

6.2 Effect of AMF on iode (I) and selenium (Se) biofortification

The essential nature of selenium (Se) and iodine (I) for human health and the relationship between these trace elements in human metabolism explain the importance of biofortification with these elements [61, 83]. Biofortification of crops with Se and I can be achieved through several pathways, including the use of beneficial microorganisms [55]. In addition to the known agronomic biofortification strategies, the importance of AMF in Se-I biofortification has long been reported by several researchers [61]. The results obtained so far have demonstrated the involvement of various AMF species in increasing Se-I concentration in most crops, both in poor soil conditions and when soil is fertilized with Se-I [61]. The work of Luo
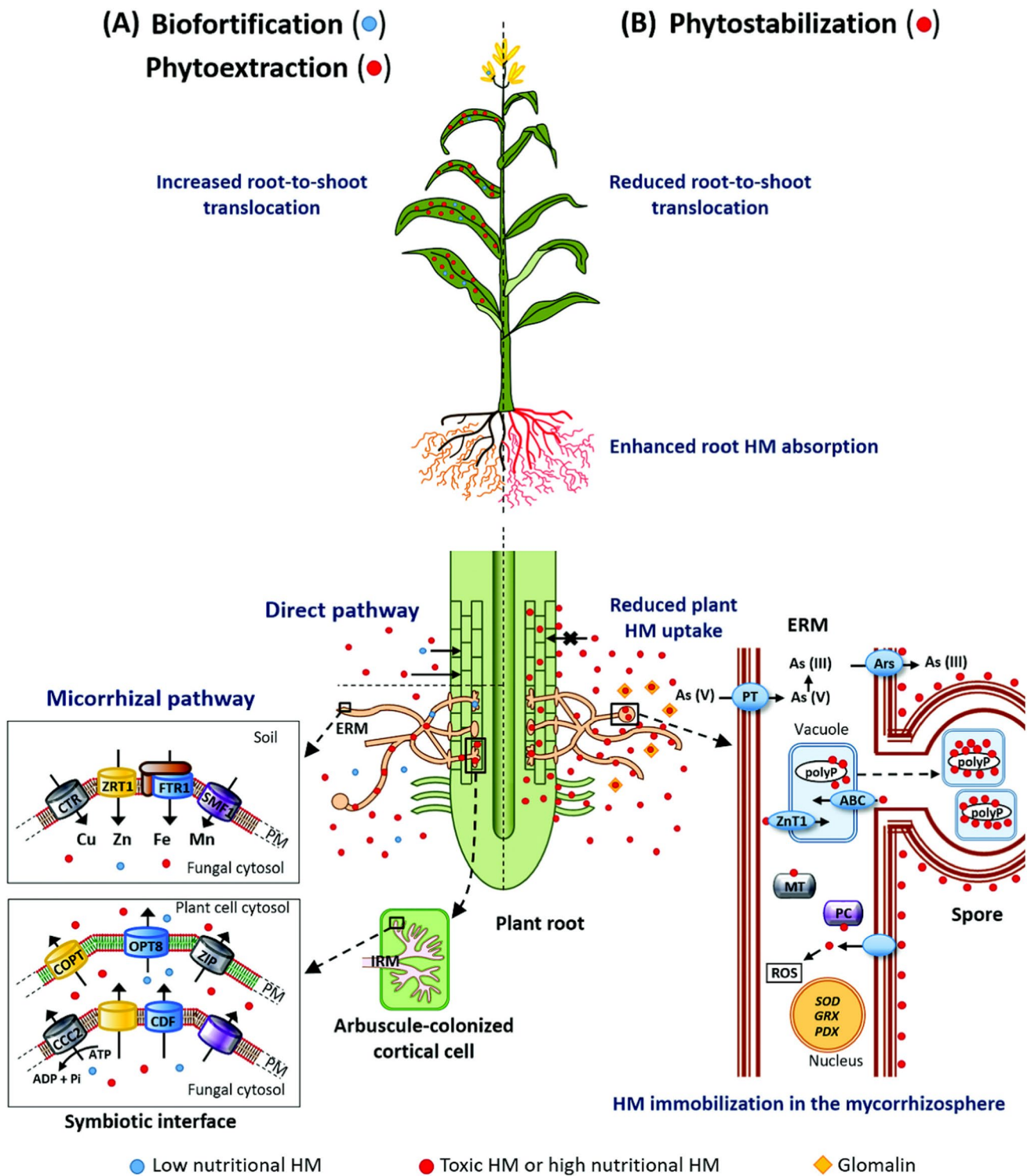
Fig. 3 Contribution of arbuscular mycorrhizal fungi to the acquisition and allocation of micronutrients in crops. **A** Illustrates biofortification and increasing micronutrient translocation from roots to leaves by phytoextraction and accumulation in the edible parts of the plant (biofortification). The diagram depicts direct mechanisms of micronutrient absorption and the mechanism involving AM fungi. **B** Explains micronutrient immobilization leading to micronutrient stabilization by reducing their translocation from roots to aerial parts of the plant, first by plant mechanisms themselves and by mechanisms involving AM fungi, primarily at the extraradical mycelium level. In both cases, AM fungi have a strong affinity with heavy metal transporters and can stimulate them [55]

et al. [95] showed that inoculation with *Funneliformis mosseae* increased Se concentration in wheat leaves and grains by enhancing root absorption surface area and improving the absorption of selenites and selenates by the host plant. These observations were corroborated by Chen et al. [34], who found that inoculation with *Funneliformis mosseae* and *Glomus versiforme*, in combination with Se fertilization, led to a significant accumulation of Se in rice leaves and grains compared to Se fertilization alone. In chickpea, Golubkina et al. [61] observed that inoculation with AMF increased the intensity of Se and I accumulation both when these elements were applied alone or together. To date, the literature reports the involvement of several AMF species in Se and I biofortification, including *Glomus claroideum, G. fasciculatum, G. intraradices, G. mosseae, G. versiforme, Rhizophagus intraradices, Funneliformis mosseae, Alternaria seleniiphila, Alternaria astragali, Aspergillus leporis, Fusarium acuminatum,* and *Trichoderma harzianum* [193]. Further research should be directed toward identifying other AMF species capable of enhancing Se-I biofortification.

The role of AMF in Selenium and –Iode absorption could be linked to their ability to regulate the expression of genes encoding heavy metal transporters at the plant roots' level [95]. Several genes encoding transporters involved in the absorption of Zn, S, Fe, Cu, and Mn have been found in AMF, specifically in the species *Rhizophagus irregularis* [55]. Additionally, other studies have shown that AMF may also decode Pi transporters [26]. The study by Li et al. [93] demonstrated that sulfate and phosphate transporters are involved in Selenium absorption due to their chemical affinity and similarity. According to this study, selenates would be transported by sulfate transporters while selenites would be transported by Pi transporters, and Se absorption would increase at low levels of Pi and sulfur in the soil.

Other mechanisms through which AMF mediate the biofortification of iodine and selenium involve several interconnected processes. AMF enhance the bioavailability of these micronutrients by extending their hyphae beyond the root zone, thereby increasing the root's access to a larger soil volume. They promote the solubilization of iodine and selenium by secreting organic acids and enzymes that convert these elements into more readily absorbable forms. Additionally, AMF can modify soil properties, such as pH and organic matter content, which can further affect the availability of iodine and selenium. The formation of arbuscules and vesicles within plant roots increases the surface area for nutrient exchange, facilitating the uptake of these micronutrients. Furthermore, AMF influence plant biochemical processes, potentially enhancing the accumulation of iodine and selenium [84]. They also improve plant stress tolerance, which can indirectly boost nutrient uptake. Lastly, AMF interact with other soil microorganisms, affecting the biogeochemical cycles of iodine and selenium. Collectively, these mechanisms contribute to the effective biofortification of crops with iodine and selenium when AMF are employed in agricultural systems [130].

6.2.1 Effect of AMF on vitamins allocation in staple food crops

Vitamins are the most important compounds for human health and are the primary targets in biofortification programs [160]. The literature describes a number of interventions undertaken to improve the vitamin content in crops, including varietal improvement approaches and transgenesis [86]. Vitamins of particular concern include vitamin A (β-carotene), vitamin B (B1 (thiamine), B6, B9 (folate), B12 (cobalamin)), and vitamin C. Some of these vitamins can be synthesized by plants, while others cannot. For example, vitamin B12 is synthesized by microorganisms but not by plants. This underscores the involvement of microorganisms in the accumulation of vitamins in crops and their allocation to consumable parts [17, 86].

Alternatively, the use of microorganisms, particularly AM fungi, has also been proposed by various authors to ensure the biofortification of vitamins in crops [16, 17]. The results of Hristozkova et al. [76] reported high concentrations of lutein, lycopene, and β-carotene in Calendula officinalis when plants were inoculated with Claroideoglomus claroideum and Funneliformis mosseae in a greenhouse. Similarly, Baslam et al. [16] observed a high concentration of various carotenoids, chlorophyll, and tocopherols in two lettuce genotypes when inoculated with *Glomus fasciculatum, Rhizophagus irregularis*, and *Funneliformis mosseae* in a greenhouse. These observations were corroborated by Rozpadek et al. [146], who observed a significant increase in vitamin B1 in onions inoculated with *Rhizophagus irregularis*. The synthesis conducted by Baslam et al. [17] indicates that AM fungi are actively involved in carotenoid metabolic pathways and stimulate their productio. Indeed, AM symbiosis activates the plastidial pathway of methylerythritol phosphate (MEP) by increasing the transcription levels of MEP genes and carotenoid biosynthesis and cleavage, which stimulates carotenoid production [167]. Regarding vitamin C, fruit crops have been targeted for vitamin C biofortification [55]. Thus, it has been reported that mycorrhizal inoculation effectively enhances biomass as well as ascorbate levels in lettuce leaves [16]. Similarly, inoculation with *Diversispora versiformis, Rhizophagus intraradices*, and *Funneliformis mosseae* led to a significant increase in the concentration of pyruvic acid, phenolics, and vitamin C in onion plants [103]. Based on the observations presented above, AM fungi are actively involved in crop biofortification and utilize various mechanisms, primarily enhancing nutrient bioavailability in the soil through mobilization and solubilization, nutrient absorption and translocation in the plant, and regulation of micronutrient transporters [159].

7 Role of AMF on crop growth, yield and nutrient use efficiency

Arbuscular mycorrhizal fungi offer numerous benefits to plants, as previously mentioned. Their primary role is to ensure adequate water and mineral nutrition for plants. Indeed, through their extramatrical mycelium, AM fungi absorb more water and mineral elements from the soil, primarily phosphorus, as well as other elements such as nitrogen, zinc, potassium, etc., and then transmit them to their host plants [117]. Additionally, AM fungi enhance soil fertility (Sect. 5) and nutrient use efficiency [101], thereby preventing fertilizer waste and allowing farmers to save money [183]. By ensuring adequate water and mineral nutrition for plants and improving soil fertility and nutrient use efficiency, AM fungi influence crop growth and yield (Table 4). This section will focus on two main points: the influence of AM fungi on crop growth and yield, and the effect of AM fungi on nutrient use efficiency Alshegaihi [7].

7.1 Effect of AMF on crop growth and yield

Currently, it is well known that the majority of crops benefit significantly from the relationships they establish with microorganisms living in their rhizospheres [106, 137]. These microorganisms are constantly influenced in turn by their host plants through the root exudates they release into the soil [141]. In the previous sections, we have shown that at the rhizosphere level, the plant–microbe and microbe–microbe relationships could influence several biochemical processes and the nutrient cycle in the soil, which could impact plant growth and development (Sect. 5.3). To date, the involvement of AM fungi in enhancing agro-ecosystem productivity is well established. The technique of inoculation with various efficient strains of AM fungi has received particular attention, resulting in improved plant growth, increased biomass production, enhanced nutrient uptake and translocation, and increased crop yields [97, 106, 111]. This technique indeed represents a sustainable solution to agro-environmental problems because AM fungi have the capacity to support plant and soil health [1]. However, too little information is available on the mechanisms involved in the plant response to inoculation with a consortium of AM fungi strains and co-inoculation of AM fungi with other beneficial soil organisms. Moreover, the effects of mycorrhizal inoculation under different environmental conditions are rarely studied.

The positive effects of AM fungi on promoting growth and improving crop yields are attributed to enhanced water and nutrient uptake and increased plant resistance to biotic stresses [41]. However, this is closely related to the proper functioning of symbiosis, which is determined by a strong mycorrhizal dependence of the plant (variety) host and the effectiveness of the inoculated AM fungi strains. Therefore, it is preferable to select optimal genotype plant/AM fungi species combinations for good efficiency [40]. In maize, field inoculation with AM fungi strains significantly increased P uptake and yield [1, 183]. These observations were corroborated by Yin et al. [194], but they specified that the response to mycorrhizal inoculation (*Funneliformis mosseae*) varies among maize cultivars. Similarly, Ndeko et al. [114] demonstrated that different millet lines responded differently to inoculation with *Rhizophagus aggregatus* and *Funneliformis mosseae*. The same trend was reported in sorghum by Nakmee et al. [106], who showed that inoculation with Acaulospora scrobiculata significantly increased nutrient concentration in leaves, plant biomass, and sorghum yield.

In leguminous crops, mycorrhizal inoculation not only improves growth and yield but also enhances biological nitrogen fixation (section). The study by Cely et al. [29] demonstrated that inoculation with Rhizophagus clarus increased mycorrhizal colonization of plants, P and N uptake, as well as soybean yield. Similarly, in common bean, it has been reported that inoculation with Rhizophagus irregularis significantly increased plant biomass and nutrient accumulation [24, 115]. The role of AM fungi in biological nitrogen fixation has also been noted by several researchers [38, 96, 195]. Indeed, as major symbionts, AM fungi and rhizobium bacteria share similarities in their signaling pathways [96]. They also exhibit synergistic effects in promoting plant growth and nitrogen fixation [38, 137]. Some authors suggest that AM fungi enhance nitrogen fixation by improving plant uptake of calcium and phosphorus. Calcium plays a role in the nodulation process, while phosphorus serves to meet the high demand for phosphorus required by bacteria during the nitrogen fixation process [195]. Moreover, it has been clearly demonstrated that AM fungi also increase yields in root and tuber crops such as cassava, as well as in vegetable crops such as tomato [181], lettuce [16], etc. (Fig. 4). Based on the beneficial effects of AM fungi on crop growth and yield as previously mentioned, scientific literature shows that the use of indigenous strains [106] and consortia of two or more strains are the most promising practices [56]. Some studies have also reported the low effectiveness of commercial inoculants compared to locally sourced inoculum based on indigenous strains [43]. It would therefore be prudent to locally develop techniques for the rapid production of inocula from indigenous AM fungal strains.

Table 4 An overview of AMF-assisted effects on plant growth, yield and nutrients use efficiency in different targeted crop species

Crop species	AMF species	Beneficial effects	References
Cucumis sativus	Rhizophagus irregularis	AM fungi caused growth and nutrients accumulation promotion in one of cucumber varieties	Ravnskov and Larsen [135]
Manihot esculenta Cranz	Rhizophagus irregularis (Genetically different isolates)	Influenced cassava physiological responses during water stress	Peña et al. [125]
Phragmites australis	Rhizophagus irregularis	AMF effectively improve the growth and photosynthetic activity under copper stress	Ishegaihi et al. [7]
Zea mays L	Funneliformis caledonium	AMF increased maize yield, foliar jasmonic acid, salicylic acid contents, Bt toxin contents, and Bt gene expression in Bt maize leaves and enhance the insect resistance capacity of Bt crops against Mythimna separate fed	Wang et al. [182]
Phaseolus vulgaris	Native AMF: C1-ART, C2-GEC, C3-PAR, C4-VIE, C5-CUC, C6-SAC, C7-SAB, and C8-MUZ	AMF increased plant height, root length, total fresh and dry biomass and N, P, K, Ca, Mg, Fe, Zn concentration in leaves	Paredes-Jácome et al. [120]
Glycine max L. Merr	Rhizophagus intraradices and Funneliformis mosseae	AMF improved plant production, photosynthetic efficiency and root activity under draught stress conditions	Takács et al. [171]
Lolium perenne L	Glomus mosseae	improve growth and the photosynthetic electron transport capacity of PSII in L under Cd stress, and reduce the toxicity of Cd	Zhang et al. [197]
Zea mays L	Glomus intraradis	AM fungi promoted plant growth, yields and nutrient accumulation than NH4NO3 and AMF + NH4NO3 treatements	Adesemoye et al. [1]
Ziziphus mauritiana Lam	Rhizophagus irregularis	AM fungi caused higher rates of plant survival and an increase of fruit production	Thioye et al. [174]
Zea mays L	Rhizophagus intraradices	AMF inoculation increased maize yield and NPK use efficiency in different agroecological zones	Aguégué et al. [5]
Cucumis sativus	Claroideoglomus sp., Funneliformis sp., Diversispora sp., Glomus sp., and Rhizophagus sp, Glomus intraradices, G. microaggeregatum, Funneliformis mosseae	AMF improved plant height, stem diameter, dry weight, root activity, chlorophyll content and net photosynthetic rate	Chen et al. [34]
Zea mays L	Rhizophagus irregularis	AM fungi increased both biomass (root biomass) and the nutrients content (	Ramírez-Flores et al.[134], Ndeko et al. [113]
Zea mays L	Funneliformis mosseae	AM fungi alleviated the toxicity of excessive Cd by increasing the leaf chlorophyll content, the net photosynthetic rate, and promoting plant growth	Yin et al. [194]
Torreya jackii	Rhizophagus irregularis	AM fungi inoculation with improved the plant height, shoot dry weight, total dry weight, maximal net photosynthetic rate, and the photosynthetic nitrogen use efficiency under nitrogen limitation	Lu et al. [94]

Table 4 (continued)

Crop species	AMF species	Beneficial effects	References
Hordeum vulgare	*Rhizophagus irregularis*	AM fungi increase macronutrients (phosphorus, magnesium, potassium and sulphur) concentration in gain	Ruytinx et al. [147]
Triticum aestivum	*Rhizophagus irregularis*	AM fungi increase micronutrients (zinc, iron, manganese, copper, cobalt and nickel) concentration in gain	Watts-Williams & Cavagnaro[184]
Sorghum bicolor	*Rhizophagusirregularis*	AM fungi inoculation improved yield, harvest indices, and grain P, Zn and Fe contents	Pereira et al. [127]
Vicia faba L	*Rhizophagusirregularis, Funneliformis geosporum and Claroideoglomus claroideum*	AM fungal inoculation significantly increased the yield parameters of faba bean plants	Sales et al. [151]
Saccharum officinarum	Native strains (*Acaulospora mellea, A. scrobiculata, Archaeospora trappei, Cetraspora pellucida, Funneliformis mosseae, Glomus sp., Septoglomus viscosum*	AM fungi increased enzyme activities (b-glucosidase, urease, phosphatase, and fluorescein diacetate hydrolysis), mycorrhizal colonization and sugarcane yield	Gomaa & Youssef [62]
Phaseolus vulgaris L	Mixture of *Glomus spp.*	AM fungi significantly increased growth, yield, and total carbohydrates and protein content in green pods and increases chlorophyll and nutrients content in the leaves	Ndeko et al. [115]
Phaseolus vulgaris L	*Rhizophagus irregularis*	Arbuscular mycorrhiza inoculation with increasing bean under low phosphate production and ensuring phosphate fertilizer savings	Xiao et al. [187]
Cinnamomum migao	*Glomus etunicatum and Funneliformis mosseae*	AM fungi inoculation improved growth and root vigor and upregulated antioxidant enzyme activities and osmotic adjustment substances under drought stress	Hussain et al. [78]
Zea mays L	*Funneliformis mosseae*	Improved root system, root colonization, and nutrient uptake	Cao et al. [25]
	Claroideoglomus etunicatum, Funneliformis mosseae, Rhizophagus intraradices, Diversispora versiformis	modulated AM fungi colonization, enhancing the nutrient (N, P, K) uptake, and reducing the root exudates	Hodge and Fitter [75]
Poncirus trifoliata L	*Diversispora versiformis, Funneliformis mosseae, Funneliformis mosseae and Rhizophagus intraradices*	Improved fruit quality parameters such as polar diameter, equatorial diameter, the weight of single fruits, fruit peel, and sarcocarp, coloration value, and soluble solids content	Chen et al. [33]
Plantago lanceolata	*Glomus hoi and Glomus mosseae*	AM fungi increased plant growth and N content and obtain substantial amounts of N from decomposing organic materials	
Wedelia trilobata	*Glomus versiforme and Glomus mosseae*	AM fungi improveed growth and reduced the infection of *Rhizoctonia solani* under both low-N under low-P nutrient conditions	

Table 4 (continued)

Crop species	AMF species	Beneficial effects	References
Ficus insipida Willd., Ochroma pyrami-dale, Luehea seemanii and Tabebuia rosea	*Native AM fungal species*	Inoculation improved acclimation of plant species though increasing whole plant, root, growth, ciomass allocation and shoot respira-tion rate	Fahey et al. [48]
Zea mays L	*Funneliformis mosseae*	AM fungi application increased phosphatase activity and mycorrhizal colonization, enhanced phosphorus uptake and overyielding	Wang et al. [183]
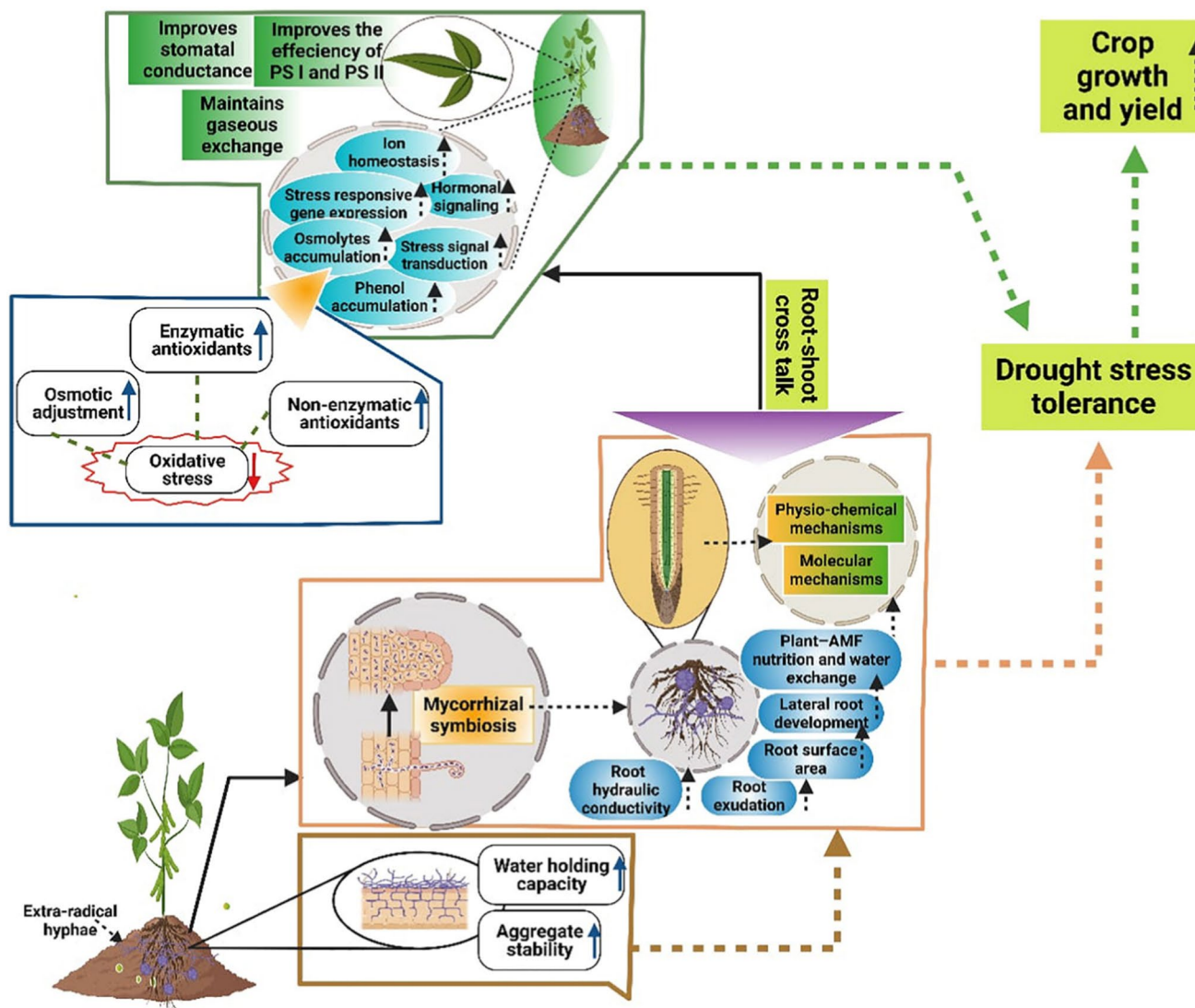
Fig. 4 Mechanisms employed by AMF to enhance crop growth and yield under environmental stress conditions: the case of drought. AMF improve soil aggregation, water retention capacity, plant water status, water absorption, root development, nutrient uptake, and hormone production (Tang et al. 2022)

7.2 Effect of AMF on nutrient use efficiency

Although fertilization is an essential practice for optimizing crop yields, it raises a number of questions regarding its sustainability and its impact on the soil and the organisms living within it. According to recent studies, overuse of chemical fertilizers is considered one of the causes of soil degradation due to soil acidification [144]. It is therefore important to develop alternative techniques and integrate them into integrated soil nutrient management practices to reduce the use of chemical fertilizers in agricultural soils [101]. Hence the concept of Nutrient Use Efficiency (NUE). Agronomically speaking, NUE is defined as the productivity gain per unit of nutrient applied or absorbed by the plant. It explains how nutrients absorbed by plants are used for biomass production [1].

As seen previously, due to their influence on soil fertility, AM fungi can greatly assist in sustainable nutrient management, particularly by improving nutrient use efficiency in various crops [183]. To date, it is known that the mode of action of AM fungi is to enhance nutrient availability in the soil through mobilization, solubilization, production of organic acids (malates and citrates), and chelation [86]. With a specific focus on nitrogen absorption in maize, Adesemoye et al. [1] observed a significant accumulation of nitrogen in the leaves and grains in the treatment inoculated

with commercial AM fungal inoculum compared to the control and the treatment fertilized with NH_4NO_3. Similarly, the treatment inoculated with AM fungi showed higher yields (7717 kg ha^{-1}) compared to the non-inoculated controls (5725 kg ha^{-1}) and the treatment fertilized with NH_4NO_3 (7470 kg ha^{-1}), suggesting an improvement in nitrogen use efficiency in maize. These observations were supported by Wang et al. [183], who demonstrated that AM fungi significantly improved phosphorus acquisition and utilization efficiency in different maize genotypes. Similar effects have been reported on micronutrients such as vitamins, iron, zinc, selenium, and iodine, thereby enhancing crop biofortification [86, 190]. Through these mechanisms, AM fungi influence the soil nutrient cycle and improve the availability of both macronutrients (N, P, K, etc.) and micronutrients (biofortification) in crops.

8 Conclusion and future prospects

In the context of climate change and rapid population growth, the adoption of sustainable agricultural practices is crucial for enhancing crop yields, ensuring food security, and mitigating environmental impacts. To achieve these objectives, several strategies have been proposed, including the use of biofertilization through arbuscular mycorrhizal fungi (AMF). This approach leverages the symbiotic relationship between AMF and plant roots to reduce the dependence on chemical fertilizers and improve soil fertility and nutrient availability. The role of arbuscular mycorrhizal fungi (AMF) in enhancing soil fertility and crop biofortification is both profound and multifaceted. AMF establish symbiotic relationships with plant roots, significantly improving nutrient uptake, particularly phosphorus, and aiding in the mobilization of other essential nutrients such as nitrogen, potassium, calcium, magnesium, iron, and zinc. These fungi contribute to soil fertility by enhancing soil structure through the production of glomalin, which aids in soil aggregation and stability. This improved soil structure not only facilitates better water and nutrient retention but also supports plant growth and resilience. In terms of biofortification, AMF play a crucial role in increasing the availability and uptake of micronutrients like iron and zinc. They enhance nutrient solubilization and increase the bioavailability of these essential elements through various mechanisms, including the production of organic acids and chelating compounds. This function is especially vital for addressing micronutrient deficiencies in crops, which can have significant implications for human health. A better exploitation of AMF requires a clear understanding of the factors that affect the functioning of symbiosis and the contribution of AMF to various functions, both globally and at the molecular level. This refers to factors influencing the plant-AMF interaction and environmental factors. This can be achieved by studying the effectiveness of AMF strains under different edapho-climatic conditions and on different host plant species, and on the other hand, by evaluating the genetic and functional diversity of AMF under these conditions in order to identify new species with specific functions. Looking ahead, future research should focus on further elucidating the specific mechanisms through which AMF contribute to biofortification, especially concerning iodine and selenium, and exploring their interactions with different soil types and environmental conditions. Additionally, more field-based studies and practical implementations are needed to translate findings obtained from experiments into effective agricultural practices. Addressing these areas will not only improve our understanding of AMF functions but also enhance their application in sustainable agriculture, leading to improved crop yields, soil health, and nutritional quality.

Author contributions ABN conceived the study and drafted the manuscript. GCB, AK, and GMN revised the final manuscript. All authors have read and approved the final version of the manuscript.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Consent for publication The data in the manuscript have been agreed upon by all of us, and we have submitted our final manuscript to the Journal of Discover Soil.

Competing interests The authors declare no competing interests.

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