

Review

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Review

Arbuscular Mycorrhizal Fungi as Biostimulant and/or Biocontrol Agents? A Review

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Abstract: Arbuscular mycorrhizal fungi (AMF) are soil microorganisms living in symbiosis with most terrestrial plants. They are known to improve plant tolerance to numerous abiotic and biotic stresses through the systemic induction of resistance mechanisms. With the aim of developing a more sustainable agriculture, reducing the use of chemical inputs is becoming of a major concern. After providing an overview on the AMF history, phylogeny, development cycle and the symbiosis benefits, the current review aims at exploring the potential of AMF as biostimulants and/or biocontrol agents. Nowadays, AMF inoculums are already increasingly used as biostimulants, improving mineral nutrient plant acquisition. However, their role as promising tool into the biocontrol market, as alternative to chemical phytosanitary products, is underexplored and discussed. Thus, in the current review, we will address the mechanisms of mycorrhized plant resistance to biotic stresses induced by AMF, and highlight the various factors in favor of inoculum application, but also the challenges that remain to be overcome.

Keywords: arbuscular mycorrhizal fungi; biostimulant; biocontrol; AMF inoculum; sustainable agriculture

1. Introduction

Conventional agronomic techniques, such as agrochemicals inputs, have made it possible to guarantee access to food for humanity [1]. Nowadays, the human population keeps growing, approaching 9.7 billion people in 2050 according to the United Nations [2]. However, conventional agriculture is showing its limits, raises social concerns and is usually decried for their impact on all the ecosystems, both on wildlife and human societies (pollution, toxicity, reduced effectiveness of chemical plant protection products, destruction of ecological niches for the benefit of invasive species, etc.) [1,3–7]. Numerous policies and agronomic practices are being implemented around the world to foster a reduction in the use of chemical inputs and plant protection products. For instance, in 2022, the European Commission adopted the proposal 2022/0196 for the regulation (EU) 2021/2115, which aims at reducing at least 50% of chemical plant protection products by 2030 [8]. The Integrated Pest Management (IPM) implies the use of agronomic practices stopping or limiting diseases and pest growth in field, using as little as possible chemical phytosanitary products and employing preferably sustainable techniques and products [9]. The practice of organic farming prohibits the use of synthetic inputs and chemical phytosanitary products, as set out in the European directive 2018/848 [10]. Within this context, the agricultural world really needs alternatives to the synthetic products used in conventional farming.

Currently, biostimulant products, defined by du Jardin [11] as "any substance or microorganism applied to plants to improve nutritional efficiency, tolerance to abiotic stresses and/or important quality characteristics of the crop, irrespective of its nutrient content", are playing an important role in the agricultural products market for substituting or limiting chemical fertilizers. Among them, beneficial microorganisms are increasingly used as biostimulant products notably in fields,

horticulture and forestry [12]. These microorganisms are well-known as "Plant Growth Promoting Rhizobacteria" (PGPR) (e.g. *Azotobacter* sp., *Rhizobium* sp., *Azospirillum* sp.) [13] and "Plant Growth Promoting Fungi" (PGPF) (e.g. *Trichoderma* sp.) [14], which act as a support to crop growth, enhancers of nutrient supplies to plants (phosphate, nitrogen, etc.) and stimulants of plant organ development [13,14].

For many years, Glomeromycetes, a specific lineage of fungi and commonly called "arbuscular mycorrhizal fungi" (AMF) have drawn the attention of the scientific community. Like PGPR and PGPF, AMF are already used for their ability to improve plant nutrition and growth [15], and have been classified in European Union as biostimulant products according to the recent EU regulation 2019/1009 [16]. Also, they are often studied as interesting tools against diverse agricultural issues strengthened by climate change and mainly due to pedoclimatic stresses such as hydric, thermal, saline, osmotic, luminous, pollution and nutritional stresses [17].

Alongside their biostimulants' abilities, the AMF have also been studied in numerous biotic stress conditions. It has been shown that AMF are able to induce defense mechanisms leading to a "Mycorrhiza-Induced Resistance" [18], resulting in protection against attacks by various pests. For decades, controlling pest and crop diseases in conventional agriculture is mainly focused on the chemical pesticides' application and plant breeding. As alternative, biocontrol products, which limit pest and disease development in a more sustainable way by copying or using directly natural mechanisms [19], already employ a wide range of beneficial microorganisms such as PGPR and PGPF [20]. Thanks to their abilities to induce plant defenses, AMF could be used as biocontrol agents.

Firstly, this review aims to provide an overview of the history, phylogeny and development of AMF and plant symbiosis. Subsequently, the review will address their abilities to stimulate plant nutrition and growth, making them ideal for use as biostimulant products to replace chemical inputs, and recognized as plant tolerance inducers in front of numerous abiotic stresses. AMF could also take their place in the biocontrol industry, which is an eco-responsible alternative market to synthetic phytosanitary products used in conventional agriculture. The current state of research shows that this AMF-potential in biocontrol has its pros and cons. Thus, the present review aims at examining the potential of AMF as plant protection agents, by exploring all the plant defense mechanisms induced by mycorrhization upstream and during attacks by crop pests and diseases. Then, the review will state the persistent limits of AMF for crop protection, which require further research to confirm their biocontrol potential. Finally, a brief review of AMF inoculum production will be carried out to examine whether the current agribusiness can extend the use of AMF inoculum to biocontrol market.

2. Arbuscular Mycorrhizal Fungi (AMF)

2.1. History and Taxonomy

At the root level of most terrestrial plants, many edaphic fungi, described as "mycorrhizal" by Frank (1885), form a symbiotic relationship with plants. These include a monophyletic line of endophytic fungi known as "arbuscular mycorrhizal fungi". They were described firstly by von Nägeli in 1842 [22]. Unable to mineralize a very large proportion of soil organic matter due to their poor exo-enzymatic equipment [23], the AMF complete their development cycle through a highly compatible mutualistic symbiosis [24], forming a highly specific interface with the roots of the majority of vascular plants [25], with which they have co-evolved since their appearance in the Ordovician period 480 million years ago [26]. AMF are therefore obligate biotrophs [27].

In the past, AMF were identified by studying the morphological structures of the spores, which were considered to be difficult because of the structural diversity within and between species, often leading to inability or misclassification of AMF [28]. Nowadays, AMF taxonomy is based on the sequencing of certain parts of AMF genomes, using numerous molecular markers such as β -tubulin gene [29], nuclear large subunit 28S (LSU) rRNA gene [30], nuclear small subunit 18S (SSU) rRNA gene [31], the internal transcribed spacer (ITS) comprising the 5.8 rRNA gene [32]. Currently, AMF group belongs to the *Glomeromycota* phylum and the *Mucoromyceta* sub-range of fungi [33]. According to the AMF Phylogeny in 2024 (<http://www.amf-phylogeny.com/>), at least 352 species have been recorded currently. The taxonomic classification of AMF is evolving regularly. According to the last

proposed AMF-classification scheme by Wijayawardene et al. [33], Glomeromycetes are subdivided into three class (Archaeosporomycetes, Glomeromycetes, Paraglomeromycetes) and five orders that are Paraglomerales, Archaeosporales, Entrophosporales [34], Glomerales and Diversisporales [35,36] (Table 1).

Table 1. Current and evolving taxonomic classification of arbuscular mycorrhizal fungi.

Class	Order	Family	Genera	Reference
Archaeosporomycetes	Archaeosporales	<i>Ambisporaceae</i>	<i>Ambispora</i>	Confirmed taxa (2013) [36]
		<i>Archaeosporaceae</i>	<i>Archaeospora</i>	Formerly in <i>Intraspora</i> (2013) [36]
		<i>Geosiphonaceae</i>	<i>Geosiphon</i>	Confirmed taxa (2013) [36]
		<i>Polonosporaceae</i>	<i>Polonospora</i>	Recent taxa (2021) [37]
Glomeromycetes	Diversisporales	<i>Acaulosporaceae</i>	<i>Acaulospora</i>	Merged with <i>Kuklospora</i> (2013) [36]
			<i>Corymbiglomus</i>	Reclassified taxa (2012) [38]
			<i>Desertispora</i>	Recent taxa (2018) [39]
			<i>Diversispora</i>	Confirmed taxa (2013) [36]
		<i>Gigasporaceae</i>	<i>Otospora</i>	Uncertain taxa (2013) [36]
			<i>Redeckera</i>	Confirmed taxa (2013) [36]
			<i>Sieverdingia</i>	Reclassified taxa (2019) [40]
			<i>Tricispora</i>	Uncertain taxa (2013) [36]
			<i>Bulbospora</i>	Recent taxa (2014) [41]
			<i>Cetraspora</i>	Uncertain taxonomy (2013) [36], formerly in <i>Racocetraceae</i> (2011) [35]
			<i>Dentiscutata</i>	Formerly in <i>Quatunica</i> (2013) [36]
			<i>Fuscutata</i>	Formerly in <i>Dentiscutata</i> (2013) [36]
			<i>Gigaspora</i>	Confirmed taxa (2013) [36]
			<i>Intraornatospora</i>	Uncertain taxonomy (2013) [36], formerly in <i>Intraometosporaceae</i> (2011) [35]
			<i>Paradentiscutata</i>	Uncertain taxonomy (2013) [36], formerly in <i>Intraometosporaceae</i> (2011) [35]
			<i>Racocetra</i>	Confirmed taxa (2013) [36]
			<i>Scutellospora</i>	Formerly in <i>Orbispora</i> (2013) [36]
			<i>Pacispora</i>	Confirmed taxa (2013) [36]
			<i>Sacculospora</i>	Confirmed taxa (2013) [36]
			<i>Entrophospora</i> ³	Uncertain taxonomy (2013) [36]
	Entrophosporales ¹	<i>Pacisporaceae</i>		
		<i>Sacculosporaceae</i>		
	Glomerales	<i>Entrophosporaceae</i> ²		
	Glomerales	<i>Glomeraceae</i>	<i>Complexispora</i>	¹ Recent taxa [42], ² uncertain taxonomy (2013) [36], ³ formerly in <i>Claroideoglomus</i>
			<i>Dominikia</i>	Recent taxa (2023) [43]
			<i>Epigeocarpum</i>	Recent taxa (2015) [44]
			<i>Funneliformis</i>	Recent taxa (2021) [37]
			<i>Funneliglomus</i>	Confirmed taxa in 2013 [36]
			<i>Glomus</i>	Recent taxa (2019) [45]
			<i>Halonatospora</i>	Formerly in <i>Simiglomus</i> (2013) [36]
			<i>Kamienskia</i>	Recent taxa (2018) [46]
			<i>Microdominikia</i>	Recent taxa (2015) [44]
			<i>Microkamienskia</i>	Recent taxa (2018) [47]
			<i>Nanoglomus</i>	Recent taxa (2019) [48]
			<i>Oehlia</i>	Recent taxa (2019) [49]
			<i>Orientoglomus</i>	Recent taxa (2019) [48]
			<i>Rhizoglomus</i>	Recent taxa (2019) [48]
			<i>Rhizophagus</i>	Recent taxa (2019) [49]
			<i>Sclerocarpum</i>	Recent taxa (2014) [50]
			<i>Sclerocystis</i>	Reclassified taxa (2012) [38]
			<i>Septoglomus</i>	Recent taxa (2019) [51]
			<i>Silvaspora</i>	Reclassified taxa (2012) [38]
				Formerly in <i>Viscospora</i> (2013) [36]
				Recent taxa (2021) [37]
Paraglomomycetes	Paraglomerales	<i>Paraglomeraceae</i>	<i>Innospora</i>	Recent taxa (2017) [52]
			<i>Paraglomus</i>	Confirmed taxa (2013) [36]
		<i>Pervetustaceae</i>	<i>Pervetustus</i>	Recent taxa (2017) [52]

2.2. Developmental Cycle

Mycorrhizal symbiosis establishment begins with a pre-symbiotic phase. In an unfavorable environment, particularly in low inorganic phosphate soils, the roots secrete exudates into the soil (branching factors), like strigolactones, enabling the mycorrhizal symbiosis to be established [53,54]. Observed for the first time in the symbiosis between *Lotus japonicus* and *Gigaspora margarita* [55], strigolactones induce AMF spore germination [56]. AMF metabolism is changed, such as respiration,

mitochondrial reorganization and lipid catabolism [57], which act on the growth and branching of AMF extra-radical hyphae, leading to the formation of a new primary mycelium [58]. Without signals from plants, AMF stops growing, apical hyphae vacuolize, hyphae septate and a retraction of cell cytoplasm and nuclei happens [59,60]. Then, the AMF itself emits molecules towards the roots called "Myc factors" [61], such as lipochitooligosaccharides (LCOs) which activate genes involved in symbiosis establishment in the plant roots [62].

Then, the symbiotic phase of the fungus begins. On the arrival of AMF, the cells of the root epidermis modify their structures to form a "prepenetration apparatus" (PPA), which determines the entry of AMF into the root [63,64]. Then, the AMF forms an hyphopodium that burrows into the epidermal cell layer, with intra-radical mycelium colonizing the extracellular space between the cortical cells [63,64]. Intra-radical hyphae penetrate these cells and form arbuscules [65], branched structures where bidirectional exchange of signal molecules and nutrients occurs between the two partners in the symbiosis [63,64]. These arbuscules and cells are separated by the periarbuscular space [63,64]. The plant exchanges up to 20% of its carbon molecules from photosynthesis with AMF [66,67], in the form of carbohydrates [68] and fatty acids [69], against various macro- and micro-nutrients, taken from the soil via the extra-radical mycelium [70], such as phosphates [71], sulphates [72], nitrogen molecules [73], potassium [74], copper [74], iron [70,75], zinc [75], calcium, manganese, magnesium [76], and finally water [77,78]. Arbuscules have an average lifespan of 8.5 days, during which they are active for up to 5 days [79], and disappear by senescence, leaving the plant cell in its original state [80]. Intra-radical hyphae can also form other structures such as coiled hyphae and vesicles. These circular storage organs allow AMF to accumulate carbon into lipids for its own growth when photosynthesis does not produce sufficient carbon molecules [81]. Finally, new AMF spores are produced from extra-radical hyphae [82].

3. AMF as Biostimulant Agents

3.1. Plant Growth and Yield Improvements

AMF provide naturally various benefits to their host plants. Indirectly, AMF improve soil characteristics which is beneficial for plant growth. AMF increase soil resistance to water and wind erosions [83] by improving soil structure thanks to the excretion of glomalin, a glycoprotein acting as a biological glue binding soil particles together to form larger soil aggregates [84,85]. AMF can enhance soil water holding capacity [86] and reduce nutrients leaching, particularly those crucial for plant cultivation such as nitrogen and phosphate [87]. Also, AMF naturally contribute to better carbon sequestration in soils [86,88]: the improvement of soil aggregation by glomalin prevents the degradation and the leaching of soil organic matter [89].

AMF absorb carbon molecules from the plant's photosynthesis for their development and functioning [66,67]. This is not without consequences for the plant, because it creates a carbon sink for the plant: AMF will modify the primary carbon metabolism of the mycorrhizal plant, by deregulating photosynthesis and reducing the accumulation of photosynthates, to such an extent that a slowdown in growth has sometimes been observed in the establishment stage of AMF-plant symbiosis [90,91]. Under these conditions, the plant's photosynthesis rate increases to compensate for carbon loss [92,93]. After mitigating carbon loss, these increases in photosynthesis, added to enhance nutrient supply, can stimulate plant development and growth. In practical terms, this means that mycorrhizal inoculation can directly improve yield and crop qualities. Field trials using mycorrhizal inoculation have demonstrated a significant increase in yields for potatoes [94], maize [95] and yams [96]. Gao et al. [97] reported that cotton plants (*Gossypium hirsutum*) inoculated in the field with *Rhizophagus irregularis* CD1 produced higher yields of cotton, with more cotton bowl and higher quality cotton fibers, thanks to an increase in phosphate concentration into plants. Sorghum plants (*Sorghum bicolor*) growing in phosphate-poor soils and inoculated with *R. irregularis* produced higher yields and grains with superior nutritional richer in phosphate, iron and zinc [75]. Zhang et al. [98] showed that in mycorrhized rice plants, more nitrogen and carbon were observed in all the organs of the rice plants, and this had a positive influence on yield (up 28.2%) and protein concentration (up 7.4%) compared with non-inoculated plants. The composition in flavonoids, sugars, vitamin C,

organic acids and minerals in the fruit of lemon trees mycorrhized by *Glomus versiforme* can be enriched [99]. Anthocyanins, carotenoids and other phenolic compounds are increased in lettuce in response to *Rhizophagus fasciculatus*, *R. irregularis* and *Funneliformis mosseae* inoculations [100]. AMF can also boost essential oil yields in medicinal and aromatic plants and improve their composition in terpenoids and flavonoids [101–103]. For all these reasons, mycorrhizal inoculation became an agronomic tool for among biofertilizers and plant biostimulants [104–107].

3.2. Plant Tolerance against Abiotic Stress

Widely documented in the scientific literature, biostimulation with AMF improves plant tolerance to numerous abiotic stresses. Through a meta-analysis of 546 publications between 1950 and 2021, Wu et al. [108] explained that, in countries where agriculture is rainwater-dependent and crops are regularly subjected to abiotic stresses such as drought or heat stress, mycorrhizal inoculations helped to increase harvested crop biomass by an average of 23%, especially in nitrogen-fixing plants, and average root biomass by up to 29.6% compared to non-mycorrhized cultivations. Under water and salt stress, the biomass of AMF-inoculated plants was increased [109–111]. Thanks to AMF, the plant tolerance to climatic hazards can provide food and economic security to human population, and AMF inoculation become an interesting mean to alleviate the deleterious effects of climatic changes [112]. Symbiosis between AMF and the host plant improves plant physiology, enabling them to cope with abiotic stresses, such as water, thermal (cold, heat), salt, light, pollution, osmotic and oxidative stresses. This tolerance of AMF-inoculated plants is due to different mechanisms and changes occurring outside and inside the plants.

Mycorrhizal symbiosis improves plant mineral nutrition making the host plant more tolerant to abiotic stresses. Under salinity or metallic stresses, AMF can enhance plant mineral uptake, such as phosphate, nitrogen, iron, magnesium, copper or zinc [113–115]. Some mycorrhized plants have also been found to have higher concentrations of organic acids, which are used by plants to solubilize soil phosphate [116] and by AMF to mobilize essential mineral nutrients such as N, P that are difficult for plants to access [117]. Higher levels of organic acids enable mycorrhized plants to better tolerate alkaline [118] and saline [119] stresses.

AMF improve the plant's water use under water, salt, cold and light stresses [120–123]. The hyphae of extra-radical mycelium, 2 to 5 μm thin, act as an extension of the plant's roots, giving them access to micro-porosities into the soil that are difficult for the root's absorbing hairs to reach, and to more distant regions of the soil for the root system [124–126]. Then, AMF induce the overexpression of aquaporins genes in plant roots. Aquaporins (AQP) are membrane transport proteins involved in water movement, the water transport is done via an osmotic gradient [127]. These aquaporins are, for example, PIP (Plasma membrane Intrinsic Protein) 1 and 2, TIP (Tonoplast Intrinsic Proteins) 1, 2 et 4, NIP (Nodulin 26-like Intrinsic Protein) 1 et 2, SIP2 (Small and basic Intrinsic Proteins 2), AQP2, and they all have been found to be involved in abiotic stresses such as drought stress [128–133], salinity stress [134–137] and cold stress [138]. In the roots of inoculated plants, aquaporin genes overexpression is beneficial to obtain more water from the extra-radical mycelium, under low water availability [134]. At the above ground organs of inoculated plants, the closure of stomata is induced by water or salt stresses, reducing the entry of CO_2 into the plant and therefore photosynthesis activity [139]. In others cases, mycorrhizal symbiosis can moderate the consequences of these stresses, by inducing an increase in stomatal conductance, gas exchange, leaf water potential and photosynthesis, in particular chlorophyll levels [140–146]. In the face of low temperatures, mycorrhizal symbiosis can also reduce water loss [147] and an increase in leaf chlorophyll content [123,148]. Under water and salt stresses, the leaf area index is increased [109–111]. Finally, it should not be forgotten that glomalin, excreted by AMF, plays a positive role in soil structuring and facilitates water retention in the soil, this inevitably improves water availability for plants under abiotic stresses [83–86].

Linked to the enhancement of photosynthesis, a higher concentration of hexose is then observed in the tissues of the mycorrhized plants, which is partly metabolized by AMF into glucose [68] at the beginning of mycorrhizal symbiosis establishment [149] or in phosphorus-deficient conditions [67].

These higher sugar concentrations can be used by the mycorrhized plant for its own development [150]. Also, higher sugar concentrations give to mycorrhized plants greater tolerance to various abiotic stresses such as drought [151], cold [152], high soil salinity [119,153] or pollution [154], because sugars can prevent structural changes in soluble proteins, maintain cell membrane integrity and osmotic balance.

In response to the water, heat and salt stresses, the plant produces in excess "Reactive Oxygen Species" (ROS) such as hydrogen peroxide H_2O_2 , superoxide anion radicals O_2^- , singlet oxygen 1O_2 and hydroxyl radicals OH^\bullet , which can degrade by oxidation the plant's nucleic, lipid, pigments and protein molecules [155–158]. This oxidative stress is countered by producing non-enzymatic antioxidant molecules (ascorbic acid, reduced glutathione, tocopherols, carotenoids, flavonoids, phenols, proline) [159–162]. It is also countered by enhancing antioxidant enzymatic activities (ascorbate peroxidase [APX], catalase [CAT], glutathione peroxidase [GPX], glutathione reductase [GR], peroxidases [POD], superoxide dismutase [SOD]) [159–162]. These antioxidant enzymes detoxify the ROS excess and maintain cells' homeostasis [159–162]. The stimulation of antioxidant enzymes activities has also been observed into mycorrhized plant [163]. For example, Li et al. [164] attributed to mycorrhizal inoculation, the preservation of the photosynthetic process in C_3 and C_4 plants through the stimulation of antioxidant enzyme activities in drought stress. During a salt stress affecting bread wheat plants (*Triticum aestivum* L.), Talaat and Shawky [165] observed that the leaves of wheat plants inoculated with *Glomus spp.* spores contained less H_2O_2 than those of non-inoculated plants. Hormonal changes induced by mycorrhization, particularly the stimulation of abscisic acid (ABA) production, activate mechanisms for tolerance to water and salt stresses [166,167]. ABA prevents water loss [168] and osmotic and oxidative shocks by regulating the opening of stomatal guard cells (regulation of stomatal conductance) [169] and the induction of defense genes against abiotic stresses such as SOD genes [170]. Under metallic stresses, proline biosynthesis, root biomass or root nodulation and nutrient uptakes (iron, magnesium, phosphate, nitrogen) are stimulated by AMF in pigeonpea (*Cajanus cajan* L. Millsp.) [171].

Mycorrhizal symbiosis regulates osmotic adjustment in the tissues of inoculated plants stressed by lack of water, osmotic stress or excess salt. Because plants need to keep cellular processes and turgor pressure active, mycorrhized plants can accumulate organic osmolytes (glycine betaine, polyamines, prolines, soluble sugars) and ionic osmolytes (Ca^{2+} , K^+ , Mg^{2+}) [140,169,170,172–175].

Finally, AMF can detain the excess soil metallic ions into their hyphae, stopping them spreading into plant roots [176] and avoiding heavy metal pollution stress effects, such as denaturation or modification of proteins and cell membranes disruptions [177]. Otherwise, it was observed that mycorrhizae induced the metal fixation into their cell wall, accumulation into their vacuoles and chelation via siderophore into the cell cytoplasm [176]. As a result, mycorrhized plants cultivated under heavy metal stress developed better than non-mycorrhized plants [178].

4. AMF Inoculum as Biocontrol Agents?

According to the International Biocontrol Manufacturers Association (IBMA) [19], biocontrol products and agents offer sustainable pest and disease control strategies by using natural mechanisms. They include macro-organisms, chemical mediators (kairomones, pheromones), natural substances of animal, plant and mineral origin, and micro-organisms. The sale of micro-organisms is authorized on the biocontrol product market, such as bacteria (e.g. *Bacillus sp.*, *Pseudomonas sp.*, *Streptomyces sp.*, etc.), oomycota (e.g. *Pythium sp.*), virus (*Cydia pomonella granulosus* virus, Pepino mosaic virus, etc.) and fungi (*Ampylomyces sp.*, *Candida sp.*, *Trichoderma sp.*, etc.) [20]. AMF are not included in biocontrol products, although numerous studies highlighted the ability of AMF to induce resistance in plants to biotic stresses, through the stimulation of plant defense mechanisms.

4.1. AMF-Induced Plant Protection against Pathogens

As Comby et al. [179] summarized in their review, mycorrhizal symbiosis can protect plants against a wide panel of plant pathogens, such as virus, bacteria, phytoplasma, fungi and pests through inducing several biochemical and molecular mechanisms. Firstly, improved photosynthesis

and plant nutrition enhancement can help mycorrhized plants to overcome pathogen attacks [150,180]. Secondly, the extra-radical mycelium of AMF modulates the microbiota around the roots by competing spatially and nutritionally with belowground pathogenic microorganisms [181]. The mycorrhizal extra-radical mycelium also stimulates the activity of microorganisms, such as PGPR [182] (e.g. nitrogen-fixing bacteria) [183] and phosphate-solubilizing bacteria [184] that are beneficial to the plant in competition with belowground pathogenic microorganisms. Between plants of same or different species, the AMF can form a mycelial network (Common Mycorrhizal Network or CMN), which enables several sources of nutrients to be exchanged over long distances [185], and transfer of signal molecules between plants [186] or induction of membrane depolarization [187]. For example, a mycorrhized plant attacked by a caterpillar or a necrotrophic fungus [188,189] warns its neighbors through the CMN, which can then activate their own defense mechanisms [186,190] in anticipation of a future attack.

4.2. Mycorrhiza-Induced Resistance

During the first interactions between a plant and an AMF, various MAMPs (Microbe-Associated Molecular Patterns) secreted by AMF are recognized by the plant, leading to a local plant immune response in the plant roots known as MAMP-Triggered Immunity (MTI) [191,192]. This immune response is associated with salicylic acid (SA) production, leading to the generation of long-distance signals moving along the vascular tissues and responsible for a transient systemic priming of SA-dependent defenses in other parts of the plant [193].

However, high levels of SA in root tissues are not favorable to the establishment of the mycorrhizal symbiosis [194]. In response, AMF release effectors, which after recognition by plant, induce in roots ABA production [195]. ABA displays local immune suppressive effects, inhibiting SA-related defense mechanisms and resulting in root colonization. In addition, ABA could transit via the xylem from the roots to the aerial parts and activate cell wall defense mechanisms, useful for protecting plants against aerial diseases [196].

Once the symbiosis is well established, a protection against pathogens can be observed in distal parts of the plants [197]. This protection is the result of the Mycorrhiza-Induced Resistance (MIR) [18], due to the induction of a set of systemic defenses mechanisms throughout the plant by AMF located into the roots [198]. The split-root system experiment by Cordier et al. [199] confirmed the systemic nature of MIR by inoculating half the roots of tomato plants with the AMF *F. mosseae*, and infecting the other half with the oomycete *Phytophthora nicotianae* var. *parasitica*. Mycorrhization induced resistance in non-mycorrhized roots, which resulted in a reduction in root necrosis as well as a significant reduction in the development of the internal and external mycelium of the pathogenic fungus. This protection has been linked to the accumulation of non-esterified pectins and PR1a (pathogenesis-related protein 1) defense proteins in the cell walls, preventing penetration of the pathogen [200].

MIR relies on hormonal signaling. Depending the tripartite system plant / pathogen / AMF, MIR could be associated with systemic acquired resistance (SAR)-like priming of SA-dependent genes, but more often coincides with an induced resistance similar to the Induced Systemic Resistance (ISR) priming of jasmonic acid (JA)-dependent genes [196]. Moreover, mycorrhizal symbiosis makes increase the phosphate uptakes and the transport of photosynthesis products from the leaves to roots [201], which modify the composition of root exudates. Enriched root exudates permit the recruitment of rhizobacteria and stimulate the development of the mycorrhizosphere [197]. Signaling compounds released by the selected bacteria (including *Pseudomonas* and *Burkholderia* strains) are recognized by the plants, which generates long-distance signals that prime JA- and ethylene-dependent plant defenses and induce ISR [202–205].

These plant hormones, whose production is modulated in mycorrhizal plants, induce a variety of defense mechanisms protecting against different crop pests and diseases. The JA- and ethylene-dependent defense appeared to protect mycorrhized plants against necrotrophic organisms [204,206], chewing insects [206,207] and to a lesser extent, against hemibiotrophic pathogens [208]. The defense mechanisms are characterized by the up-regulation of defense genes, such as lipoxygenase D gene

(LOXD) and allene oxide cyclase gene (AOC) [209], the stimulation of polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) or β -1,3 glucanases activities [200,209–211], accumulation of phenolic compounds [211], PR1a protein, callose and pectin at the site of attempted penetration by the pathogen [200,209–211]. Against biotrophic pathogens, JA- and ethylene-dependent defenses efficacy is more fluctuating. The SA-dependent defenses are known to be effective against hemibiotrophic and biotrophic pathogens [193] and are characterized by the up-regulation of defense genes enabling the production and accumulation of PR (Pathogenesis-Related) proteins [189], ROS [212], cell wall reinforcing compounds (callose and phenolic compounds deposition) [200,213], and activation of the phenylpropanoid pathway in mycorrhized plants [214].

Thanks to the aforementioned abilities to strengthen the plant and lead to set up plant protection against biotic stresses via MIR mechanisms, it can be argued that AMF inoculums can constitute an alternative to chemical phytosanitary products in the control against a wide array of different pests and pathogens. However, numerous factors, specific to AMF or from the external environment, could temper these advantages mainly observed in laboratory-controlled conditions.

4.3. Limits to the AMF-Inoculum Application as Biocontrol Agents

The efficacy of mycorrhizal protection depends on various factors. Firstly, mycorrhizal protection rate depends on AMF species. Mustafa et al. [215] demonstrated that different AMF strains (*F. mosseae*, *R. irregularis* and Solrize® inoculum [mixtures of various *Glomus* sp.]) confer different rates of protection against powdery mildew in wheat. It has also been shown that the effectiveness of mycorrhizal inoculation depends on the plant species or varieties. Mora-Romero et al. [216] observed variable rates of protection through symbiosis with *R. irregularis* in tomato infected against *Xanthomonas campestris* and pea infected against *Sclerotinia sclerotiorum*. Similarly, Campo et al. [217] showed different rates of protection of twelve different rice cultivars against the rice blast fungus (*Magnaporthe oryzae*) in response to the roots inoculation with *F. mosseae* or *R. irregularis*. Then, few data are available on the effectiveness of AMF inoculums in inducing protection against aerial plants disease [179]. Indeed, the majority of studies concern the plant protection mediated by AMF against soilborne diseases [179,193,218–222]. There is a real need to explore more widely the relevance of AMF inoculum as biocontrol tool against foliar diseases.

Additionally, plant breeding played a major role in modulating the symbiosis between AMF and the species and cultivars used in agriculture. Several studies have shown that old varieties and even ancestral wheat species roots are more colonized by AMF [223,224]. Wilson and Cox [224] explained that modern wheat varieties bred from the 1990s onwards were less sensitive to mycorrhizal symbiosis. Sawers et al. [225] argued that the plant breeding of modern wheat cultivars has improved their ability to extract more phosphate from the soil, thereby reducing their need to form a symbiosis with AMF. In addition, Parvin et al. [226] observed that modern rice cultivars formed a symbiosis with a lower diversity of AMF strains. Plant breeding, which has been practiced intensively for several decades, may therefore be a limiting factor for the effectiveness of inoculums as a biocontrol product.

Afterwards, the choice of inoculum composition is important to obtain efficient protection against plant pests and diseases. Biocontrol effectiveness of commercial inoculums based on non-endemic AMF strains could be questionable. Commercial mycorrhizal inoculums on the market are composed of cosmopolitan AMF strains with low genetic diversity and are not necessarily adapted to the soil and climatic conditions of the regions in which they are used [227,228]. Elliott et al. [229] explained that, particularly in wheat, root colonization by commercial AMF propagules can be significant, but does not systematically increase nutrient uptake, thus not providing a biofertilizer effect for the crop targeted by the commercial mycorrhizal treatment. Consequently, several studies attested that the design and use of consortia of AMF strains isolated from autochthonous soils would be more relevant and effective in protecting local crops. Indeed, by being better adapted to local conditions [230,231], endemic AMF strains can allocate more nutrients to mycorrhized plants, induce greater above-ground biomass [230,232], and increased production of phenolic compounds useful for resistance to biotic stresses [233].

Furthermore, AMF from different clades can develop differently depending on favorable or unfavorable environmental conditions [234] by adopting completely divergent resource use strategies (R or K strategies), also known as "Life History Strategies" (LHS) [235–237]. For example, AMF from the *Glomeraceae* family allocate resources to grow mainly inside roots, forming structures such as arbuscules, vesicles, hyphae [238], reproducing quickly [239] and sporulating abundantly [240]. De facto, *Glomeraceae* can develop even under unstable environment (R strategies) [235]. Compared with *Glomeraceae*, *Gigasporaceae* grow slowly, produce more extraradical structures [241,242], no vesicles and propagate mainly with spores [237,238]. *Gigasporaceae* prefer stable environment (K strategists) [235]. Like the AMF *Gigasporaceae*, the *Acaulosporaceae* also grow slowly and have limited spore viability [243]. Consequently, it turns out that some AMF species used in commercial mycorrhizal inoculums could be invasive. Basiru and Hijri [244] reported that commercial inoculums are produced from strains of generic species (*F. mosseae*, *R. irregularis*, etc.), which can be considered invasive, as a result of their rapid development (R strategy) to the detriment of local AMF strains. As they have a faster reproductive capacity, they can also compete for nutritional resources with the native AMF populations [228]. The protective effect against pests and diseases induced by inoculated AMF could be considered relative if native soil biodiversity can be compromised by the addition of invasive AMF strains. Conversely, if the inoculated strains are not capable of developing there because of their LHS, there is no need to select this inoculum, particularly when seeking protection against plant pests and diseases. In summary, the choice of local AMF strains could probably be the most relevant for an environmentally-friendly usage and reliable plant protection [245]. However, Lutz et al [246] have shown an interest in using invasive AMF strains in their analyses of the modulation of the soil microbiome in the situation of a significant supply of AMF inoculum to maize crops. The SAF22 strain, that they inoculated to the maize plants, has largely competed with local AMF strains, but also with strains of edaphic fungal pathogens (*Olpidium* sp., *Cladosporium* sp., *Mycochaetophora* sp., etc.), providing indirectly to maize plants root protection.

Also, it should be noted that certain agronomic practices reduce the development and activity of AMF. For example, agricultural inputs such as the use of fungicides [247–250], nitrogen and phosphate fertilization has often been observed to reduce the abundance and diversity of AMF in soils and the development of mycorrhization [251–255]. Soil ploughing disrupts soil structure [256,257], where *Glomeraceae* seem to be more resilient compared to *Gigasporaceae* [258,259]. In addition to AMF inoculation application, agronomic practices therefore need to be adapted in order to benefit from the positive effects of mycorrhization, and consequently take advantage of the protective potential of mycorrhizal inoculums.

5. AMF Inoculum Production

Jakobsen et al. [90] estimated that 80% of the conventional use of chemical phosphate fertilizers in the field could be offset by mycorrhizal inoculation. In this context, AMF have been used in agriculture, since the 1990s [260], as biostimulants [104,105]. Today, the production and sale of AMF inoculums represent a booming market all over the world (Table 2). The worldwide size of this market is projected to exceed \$620 million by 2025 [261,262]. Producers are found mainly in Europa (United-Kingdom, France, Germany, Italy, Czech Republic, Spain, Austria, Estonia, Switzerland and Netherlands), North America (Canada and USA) and Asia (India and China mainly) (Table 2). At a lesser degree, AMF-inoculum producers can be found in central and south America (Mexico, Argentina, Brazil, Colombia) and Africa (e.g. Kenya) [12] (Table 2). According to Chen et al. [12] in 2018, AMF inoculums are mainly used in the sectors of horticulture, gardening and landscaping, agriculture and forestry. To a much lesser extent, AMF inoculums are found into soil remediation, golf course maintenance, renaturation of deteriorated soils, roof planting and research sectors [12]. According to Basiru et al. [262], commercial inoculums can contain one or more AMF species, including mostly *R. irregularis*, *F. mosseae*, and to a lesser extent *Claroideoglossum etunicatum*, *R. aggregatum*, *R. clarus*, *R. iranicus* and *Septoglossum deserticola*. They come in the form of fragments of mycorrhized roots, spores or mycorrhizal filaments, mixed with granules, powders, or in the form of a liquid solution, or in seed coatings [263], sometimes mixed with ectomycorrhizal fungi or PGPR.

According to the same study [262], 60% of inoculums were formulated as powders, produced under *in-vivo* conditions, and often composed of several species; 29% of inoculums were in the form of liquid inoculums, produced under *in-vitro* conditions and preferably composed of a single AMF species.

Estimating the economic impact of AMF inoculums as biostimulants is not widely discussed in the scientific literature. For example, Hijri et al. [94] demonstrated that the use of AMF inoculums was affordable in field trials in potatoes, because the profit from harvesting was greater than the cost of using AMF inoculum (US\$135 per hectare). Similarly, Tawaraya et al. [264] demonstrated that inoculation of Welsh onions (*Allium fistulosum* L.) with AMF was significantly more economically cost-effective (US\$2,285 per ha) than conventional superphosphate fertilization (US\$5,659 per ha). Furthermore, it has been observed that AMF can also help with phosphate fertilization reduction over several years, reducing the cost of using conventional phosphate fertilizers. In a rotation of maize and horse gram (year 1) and rice (year 2), Maiti et al. [265] demonstrated that the rice crop required 33% less phosphate input thanks to the AMF. Finally, the major economic advantage of using mycorrhizal inoculum lies in the fact that, unlike chemical inputs, it is not necessary to apply them every year in the field, provided that cultivation practices are compatible with the development of mycelium network.

Table 2. Examples of AMF-inoculum producers and companies grouped by country (2024).

Countries	Examples of AMF-inoculum producers
Austria	Biofa; Gefafabritz
Belgium	Glomeromycota IN vitro COllection (GINCO); Plantura
Canada	Premier Tech Ltd.; Canadian Collection of Arbuscular Mycorrhizal Fungi (CCAMF); Glomeromycota IN vitro COllection (GINCO); Lallemand Inc.; Mikro-Tek Inc.
Chile	Biosim; Idemitsu Kosan Co.; Ecological Resources; Inc./Oikos
China	Guangdong Microbial Culture Collection Center (GDMCC); Weifang Yuedong International Trade Co., Ltd.; Weifang Yuexiang Chemical Co., Ltd.; Zhejiang Shijia Technology Co., Ltd.
Spain	Agrotecnologias Naturales (Atens); Biohorti SLU; Mycosym Trition S; Mycovitro; Odd Distributions
United States of America	Accelerator Horticultural Products; AgBio, Inc.; AgroScience Solutions LLC; Albright Seed Co./S & S Seeds; Becker Underwood (BASF); Bio-Organics; BioScientific, Inc.; EcoLife Corporation; First Fruits, LLC; Fungi Perfecti; Gro-Power; Helana Agri-Entreprises LLC; Hoodridge International; Horticultural Alliance, Inc; International Collection of Vesicular Arbuscular Mycorrhizal Fungi (INVAM); JH Biotech; MYCSA Ag, Inc. EUA; Mycorrhizal Applications; Pathway BioLogic LLC; Poulenger USA, Inc.; Purely Organic Products LLC; Reforestation Technologies International; ROOTS, Inc.; Shemin Garden LLC; Sustane Natural Fertilizer; Tainio Biologicals Inc.; The Tree Doctor ; Tree Pro; Valent BioSciences; Ecological Resources; Inc./Oikos
Estonia	Mikskaar
France	Agronutrition; IF tech; InoculumPlus; International Bank for the Glomeromycota (IBG); MycAgro; Terra fertilis; Mycoterroir; Semences de France
Germany	Agromyc-Merck GmbH; Biofa GmbH; BioMyc™; Inoq GmbH; Mykolife; Symplanta GmbH & Co. KG
India	AgriLife; Ambika Biotech; Anand Agro Care; Biotrack Technology Pvt. Ltd.; Centre for Mycorrhizal Culture Collection (CMCC); Cosme Biotech; Dr. Rajan Laboratories; GreenMax AgroTech; Kiran Chemicals; Katayani; Majestic Agronomics Pvt. Ltd.; Neesa Agritech Private Limited; Neologie Bio Innovations Private Limited; PHMS Technicare Private

	Limited; Privi Life Sciences; Sikko Industries; Sundaram Overseas Operation; T. Stanes & Company Limited; TARI Biotech; TERI; ManiDharma Biotech Pvt. Ltd.
Israel	Groundwork AG
Italy	Altea; Agribios; Italtollina; Sacom; Micosat F
Japan	Central Glass Co., Chemicals Section; Idemitsu Kosan Co. Ltd.; Kyowa Hakko Bio Co. Ltd.
Kenya	Dudutech
Malaysia	Agri Hi-Tech Sdn; N-Viron Sdn Bhd
Mexico	Instituto Nacional de Investigación Forestales Agrícolas y Pecuaria (INIFAP); Biofabrica Siglo XXI; Biokrone; Biomic; OBA; Vergel de Occidente
Netherlands	BioTabs Organic Fertilizers; Global Horticare; Koppert
Poland	Mykofl or Włodzimierz Szaański
Portugal	Asfertglobal
Czech Republic	Symbiom SRO
United Kingdom	Biological Crop Protection Ltd.; Crop Intellect Ltd.; PlantWorks Ltd.; Zander Corporation
Switzerland	Swiss culture collection of Arbuscular Mycorrhizal Fungi; Vegalab S.A.

As mentioned previously, AMF are therefore obligate biotrophs [27]. This characteristic prohibits their multiplication alone on standard culture media used in microbiology, as Jones [266], Gallaud [267] and Peyronel [268] tried unsuccessfully. AMF inoculums can only be produced using whole plants or transformed alive plant roots [269]. Numerous methods are regularly used for the mass production of AMF inoculums. The first is the "classic" method based on the production of a monospecific or multispecific inoculum from plants growing into bag, pots or beds filled with sterilized substrate and done mostly in greenhouse conditions [143]. AMF are multiplied in contact with the roots of trap plants that are easily mycorrhized, such as sorghum, maize, leek, clover, onion [270–272]. After production, the roots containing AMF propagules can be dried and reused, and the substrate sieved and/or decanted to recover the spores [273]. The produced substrate, enriched with AMF propagules, can also be used as AMF inoculum [274]. This method requires ongoing management of plant nutrition, and is not immune to any contamination already present in the substrate [273].

Since the end of the 1970s, other techniques have been developed to enable mycorrhizal inoculums to be produced in conditions of less or non-contamination by other microorganisms. Some techniques, free of substrate, are using plants whose roots are bathing into a static nutrient solution (hydroponic cultivation) [275], located into a flowing nutrient solution (nutrient flow systems) [276,277] or sprayed with a nutrient solution (aeroponic cultivation) [278,279]. These methods are widely used nowadays at industrial scale [273]. However, contamination with algae and a lack of support for AMF can affect production [143]. Finally, techniques for growing AMF inoculum into *in-vitro* conditions do exist. They use either Ri T-DNA root transformed organs [280] placed into bioreactors comprising a solid support [281], airlift bioreactor [282] or small containers [283]. Whole plants can also be used with aerial organs outside a Petri dish while AMF and roots are into the Petri dish filled with a solid medium [284,285]. These *in-vitro* techniques are performed in complete sterile conditions. They should make it possible to produce large quantities, high quality and free-contaminant AMF inoculums [273,286]. Also, these techniques enable production to be carried out in much more confined spaces [286]. However, the high level of technical expertise required to operate and maintain these techniques on an industrial scale means that production costs remain relatively high [273,286]. Finally, these *in-vitro* techniques are limited to a few AMF species [286], from the genus *Rhizophagus* sp. and few *Gigasporaceae* species [287].

The production of AMF inoculums therefore concerns an increasingly developed market, with a whole range of production techniques used by a multitude of companies around the world. These economic players could be involved in AMF inoculum production for the biocontrol market.

5. Conclusions and Future Perspectives

AMF are symbiotic living micro-organisms, members of a lineage of fungi whose great diversity has yet to be explored. Overall, AMF provide nutritional benefits to the host plants which can improve plant growth and yields in unfavorable conditions. Nowadays, AMF are then used as biostimulant products in the form of inoculums of different compositions and natures, whose diversity is often limited to the same cosmopolitan mycorrhizal families (mainly from *R. irregularis*. and *F. mosseae*). These inoculums are produced using efficient but costly techniques, and are used by dozens of companies and research centers around the world, mainly located in Europe, Northern America, India and China. Furthermore, AMF are able to induce a wide range of systemic defence mechanisms, which are effective to protect plants against a variety of pathogens and pests with different lifestyles (biotrophic, hemibiotrophic, necrotrophic), responsible of root and foliar diseases. The inductions of defence mechanisms are dependent to plant hormones such as SA, JA and ethylene, whose production is modulated by mycorrhization. Thus, the use of AMF represents an interesting alternative solution for plant protection thanks to the induced plant resistance via MIR. The use of mycorrhizal inoculums could then constitute a new additional agronomic technique to reduce the use of phytosanitary products [179,288]. AMF can be considered as an ecosystemic service [196] and could complement innovative protective strategies in the development of more sustainable agriculture [289–291]. However, a number of factors, both specific to AMF and external to it (plants or environment), can modulate the protective efficacy mediated by AMF. Therefore, more research is required on plant diseases, to determine the protective effectiveness against biotic stress. Furthermore, the impact of AMF inoculum on the immediate environment, in particular on the soil microbiota must be investigated. In addition, as Lekberg and Helgason [292] pointed out, many biotic and abiotic factors in the field modulate the effects observed with mycorrhizal inoculums obtained under controlled conditions. This means that this research will have to be carried out more under uncontrolled conditions, i.e. through the implementation of many more experimental field trials.

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