



Review

Development of agricultural bio-inoculants based on mycorrhizal fungi and endophytic filamentous fungi: Co-inoculants for improve plant-physiological responses in sustainable agriculture

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HIGHLIGHTS

- Agricultural inoculant formulations consist of several microorganisms on a carrier.
- Bioinoculants based on EFF* and MF** often act synergistically when co-inoculated.
- EF-MF consortia improve crop yield and quality under optimal conditions and stress.
- EF-MF consortia improve plant performance against biotic and abiotic stresses. *EFF: Endophytic filamentous fungi. **MF: Mycorrhizal fungi.

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ABSTRACT

A new more sustainable agricultural system needs to be developed to increase production without compromising human and animal health and preserving essential resources, such as soil, water and diversity. Bio-inoculants can be a tool to favor this transition, as they can replace or complement agrochemicals that do not meet the above premises. Bio-inoculants generated from endophytic filamentous fungi and mycorrhizal fungi, whether used individually, in combination with each other or with other microorganisms, stand out for their potential. This review provides information on how bio-inoculants based on these microorganisms have been shown to increase crop yield and quality through strategies, such as increasing nutrient uptake or levels of certain phytohormones. On how they can promote tolerance to abiotic stresses, including heavy metals, elevated temperatures, salinity or drought, through strategies, such as the accumulation of osmoregulatory substances or increasing the plant's root surface, among others. And finally, in the ability to protect the plant against pathogens and pests, either by inducing defense systems, competing for space or synthesizing metabolites with antibiotic activity. It should be noted that, although there are already commercial products using these microorganisms for agricultural purposes, such as biological control agents or biostimulants, it is expected that a deeper understanding of the mechanisms of action of the microorganisms, together with improved technical production processes, will lead to more effective, safer and cheaper products.

1. Introduction

Humankind faces a severe challenge, difficult to solve: ensuring food sovereignty. The world's population has reached 7.9 billion people in 2023 and it is estimated that by 2050 the world's population will reach

9.7 billion people (United Nations, 2019). This increase in population density must translate into an increase in available resources, such as food. In addition, climate change and global warming can be aggravating factors in this context, since an increase of extreme phenomena is predicted, such as torrential rains, droughts, heat and cold waves

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(Cramer et al., 2022). These phenomena can lead to water shortages, soil degradation or even the disruption of the biosphere. For example, the distribution patterns of certain pests, which act as vectors for the transmission of plant pathogens, can be altered, posing a threat to crops (Shiple et al., 2020). The agricultural system has to be able to cope with all these issues by increasing production, respecting the carrying capacity of the planet and avoiding overexploitation of soils and water sources (Gerten et al., 2020). During the green revolution, world production increased considerably, partly as a result of the indiscriminate use of agrochemicals (mainly fertilizers and pesticides). Although in those decades it was a great advance, today it has generated problems of immense depth. It is essential to modify the use we make of agrochemicals. It is evident that new fertilization strategies must be formulated, since the application rate is usually higher than the optimum, leading to an excess of fertilizer that contaminates the soil and water (Ullah et al., 2019). As an example, there are efforts to improve nitrogen use efficiency (NUE) since the excessive use of fertilizers rich in phosphorus and nitrogen can produce accumulation of these, generating human and animal toxicity (Mandal et al., 2020). In addition, the leaching of fertilizers from the soil is considered a global phenomenon that generates eutrophication and mortality of aquatic organisms (Khanna and Gupta, 2018). Moreover, nitrate in drinking water produces adverse health effects on population (Kotopoulou et al., 2021). The imbalance of mineral nutrients in the soil can generate a toxic impact on the edaphic microbiota. Alterations in the microbiome can affect the cycle of nutrients and, ultimately, the yield of crops (Mandal et al., 2020). On the other hand, pesticides contaminate the soil and water, generating wide-ranging concerns, since some heavy metals have been generated as residues, which have accumulated in the food chain, affecting the environment and human health (Parrón et al., 2014).

Therefore, the agricultural system must move towards more sustainable and context-sensitive solutions. New biocontrol strategies must be based on specific microorganisms that affect the target organisms, without harming other beneficial organisms such as insects or plant-symbiotic microorganisms. Similarly, biostimulants must specifically supplement the necessary nutrients, avoiding surpluses that may be toxic or harmful to the environment (Mandal et al., 2020). One proposal to try to reduce the use of agrochemicals is the use of microbial bio-inoculants, products formulated with the strains of interest of one or more microorganisms. These microorganisms can be bacteria or fungi that induce immune response against pathogens and pests, promote growth (producing phytohormones, improving the absorption of nutrients, mobilizing or solubilizing them) or generating tolerance to abiotic stresses (Chaudhary et al., 2020). In addition to improving plant performance, bioinoculants can also be used to improve the physicochemical properties of the soil and decontaminate or detoxify the soil (Maitra et al., 2022). For microorganisms to fulfil their function, they must be included in a uniform matrix (carrier) that allows their storage, transport and protection. The ideal carrier would be the one that allows the desired purpose to be fulfilled without polluting the environment. There are different types of carriers, among which we find: solid, liquid, metabolite and polymeric formulation. The ideal material should provide the necessary nutrients, be sterilizable, non-toxic and adaptable to different microorganisms (Chaudhary et al., 2020).

The benefit of mycorrhizal fungi (MF) in agriculture, either individually (Benami et al., 2020; Ejersa, 2021) or in co-inoculation with other microorganisms (Yadav et al., 2020; Santoyo et al., 2021), is well established. However, although numerous studies have demonstrated the efficacy of co-inoculation between MF and endophytic filamentous fungi (EFF), there was no review addressing the physiological responses of plant species to MF-EFF colonization. Therefore, the aim of this review is to gather the literature on the use of bio-inoculants based on filamentous endophytic fungi, mycorrhizal fungi, and their combination. In order to develop tools for sustainable agriculture that promote growth, increase crop yield and quality, promote tolerance to abiotic stresses and induce plant defense responses against pathogens and pests.

In addition, including information on their formulation and being critical of their efficacy, highlighting the weaknesses of this technology and proposing possible solutions.

2. Agricultural bio-inoculants based on mycorrhizal fungi (MF)

Mycorrhizae are defined as soil fungi associated with plant roots and establishing a symbiotic relationship with them. However, not all fungi associated with plants are mycorrhizas. Generally, mycorrhizas meet a number of distinctive structural (forming arbuscules, coils, pelotons, Hartig net, mantle...), functional (facilitating nutrient supply) and developmental synchronisation requirements with the host (Brundrett, 2006). In addition, the relationship is usually mutualistic, with the host plant benefiting from the supply of nutrients, such as phosphorus or nitrogen, and the fungus benefiting from a protected environment and carbon-derived compounds. Therefore, this definition must be understood within a broad spectrum of fungi that differ in function and structure from each other and may not strictly fit the definition. Within this amalgam of symbiont fungi we find various types of mycorrhizae, which have different origins, anatomy and ecology and, generating differences in their ability to protect against biotic or abiotic stresses, nutrient acquisition, carbon cycling and other nutrients (Tedersoo et al., 2020). They are usually classified by making a general division between ectomycorrhizae (ECM) and endomycorrhizae, among which we find orchid mycorrhizae (ORM), arbuscular mycorrhizae (AM) and ericoid mycorrhizae (ERM) (Genre et al., 2020).

2.1. MF as biostimulants

Mycorrhizal fungi (MF) can be used in agriculture for a wide variety of purposes. The most common way is to find them as biostimulants, because they increase nutrient uptake, mainly of phosphorus and other inorganic nutrients as nitrogen (Anand et al., 2022). In addition, crops associated with MF usually have in their tissues increased amount of some micronutrients, such as Cu, Zn, Fe or Mn (Baslam et al., 2011), essential for the human health but frequently scarce in the daily food intake, which induces the phenomenon termed 'hidden hunger'. In fact, there are numerous patents covering the use of MF as biostimulants. The most patented genus is *Glomus*, which accounts for 82.5% of all patented MF between 2000 and 2020, followed by the genera *Rhizophagus* (3.9%), *Sclerocystis* (3.9%) and *Gigaspora*.

2.2. Other benefits of AMF

MF can reduce the amount of fertiliser used, allowing a reduction in nutrient losses (Cavagnaro et al., 2015). These edaphic fungi favour soil aggregation through hyphal enmeshment and production of glomalin-related proteins, accelerate the decomposition of fresh N-rich residues and enhance the retention of organic C into soil aggregates in the longer term (Wei et al., 2019). The use of biostimulants is often linked to increasing yield in the form of dry and fresh weight, or/and grain weight, although this is not always correlated. In addition, some MF can increase grain quality (Tran et al., 2019), in wheat being this beneficial effect more evident when plants are exposed to water deficit (Goicoechea et al., 2016). Another of their main utilities is their use as bioprotectors against biotic stresses such as pests, plant diseases and weeds. They reduce crop diseases as they can activate plant defence systems and generate induced systemic resistance, as in the case of *Glomus* sp. which confers protection to tomato and pepper against *Phytophthora* (Nevalainen, 2021). This bioprotective effect, however, can be dependent on the species of MF as reported by Garmendia et al. (2004) working with pepper affected by *Verticillium dahliae*. Likewise, MF species can affect the competitive relationships between crops and weeds (Rashidi et al., 2021). In addition, MF have been shown to improve plant performance under abiotic stress conditions, such as high salinity, alkaline soils, low or elevated temperatures or high

concentrations of heavy metals. Therefore they can be used in bioremediation or recovery of natural areas (deserts, mines...) (Anand et al., 2022) and appear as a promising tool for increasing the resilience and quality of crops facing climate change scenarios (Torres et al., 2018a). MF also favour system performance and yield stability. Although not directly related to yield or short-term production, MF enhance plant stability by adding soil particles, promoting water acquisition, sequestering carbon and increasing soil organic matter, improving soil structure (Rillig et al., 2019). Finally, MF can induce the accumulation of mineral nutrients and antioxidant compounds in plant tissues and organs usually discarded as crop residuals, thus turning these vegetable wastes in an interesting material with potential use, not only as fertilizers, but also for human nutrition (Torres et al., 2018b) or even for biomedicine (Torres et al., 2019).

2.3. Co-inoculants: MF and other microorganisms

They were frequently co-inoculated with other microorganisms to enhance their effect. Bacteria were the most common microorganisms with which MF were associated. Co-inoculations with nitrogen fixing bacteria, phosphate solubilising bacteria and plant growth promoting rhizobacteria were predominant. The most predominant ones were *Bacillus licheniformis*, *B. subtilis*, *Bradyrhizobium japonicum*, *Pseudomonas fluorescens* and *Rhizobium meliloti* (Srivastava et al., 2021).

3. Agricultural bio-inoculants based on endophytic filamentous fungi (EFF)

Endophytic filamentous fungi (EFF) are microorganisms that colonize, partly or throughout their lifespan, the plant internal tissues or organs, such as roots, stems, seeds, leaves and fruits without causing any symptoms of disease (Petrini, 1991; Kumar et al., 2021). They are found in all plants on the planet and there is a great diversity of them. Some are specifically associated with certain species, while others are generalists. They can also occur in a specific tissue or colonise several different tissues (Zabalgoeazcoa, 2008). Depending on the tissue or organ, the abundance and diversity of EFF varies according to plant's genotype, nutrient availability, presence of other microorganisms and environmental conditions (soil characteristics, climate, agricultural management practices...) (Pozo et al., 2021). Different types of endophytes have been identified and are generally grouped into: clavicipitaceous endophytes associated with grasses, and non-clavicipitaceous endophytes associated with non-vascular plants, conifers and angiosperms (Rodríguez et al., 2009). The phylum with the greatest presence of endophytes is Ascomycota, followed by Basidiomycota, Zygomycota and Glomeromycota. Plant colonization can occur vertically, remaining through the seed, or horizontally, in which case it must recognize and colonize the host (Lugtenberg et al., 2016).

3.1. Benefits of EFF inoculation

Some EFF can maintain a mutualistic relationship with crops and provide them with certain advantages over uncolonized plants. Endophytes can increase yield or quality directly, by promoting growth, improving the uptake or use of the nutrient. They can also improve yield indirectly, by improving the plant's response to abiotic (drought, salinity, heavy metals...) or biotic stresses (plant pathogens such as viruses, bacteria, nematodes and fungi, herbivory...) (Poveda et al., 2022). The most popular and cost-effective strategy is the direct use of EFF by incorporating them into crops and allowing them to establish in plants. To a lesser extent, it has also been studied how exogenous application of compounds generated by EFF can improve plant performance. This is because EFF can produce antimicrobial compounds or activators of the plant's defence system, which could be applied to different crops like a traditional agrochemical (Khan et al., 2014; Numponsak et al., 2018).

3.1.1. EFF promote plant growth

To promote growth, they act as biostimulants, improving the uptake of nutrients that are difficult for the plant to access (Umesha et al., 2018; Poveda et al., 2021). Some examples are: *Trichoderma*, *Penicillium* or *Beauveria* sp. that increase nitrogen, phosphorus or iron uptake, respectively in various crops such as maize, wheat or habanero peppers (Wakelin et al., 2011; Rinu et al., 2014; Toscano-Verduzco et al., 2020). On the other hand, they can also promote growth by modifying the plant's hormone levels. Some endophytes produce hormone-like compounds that act as phytostimulators (auxins, cytokinins, gibberellins, etc.) (Chagas et al., 2018). As an example, *Aspergillus japonicus* and *A. niger* produces auxins and gibberellins that increases the growth of soybean, sunflower or rice (Asaf et al., 2018).

In order to improve plant performance in stressful conditions, endophytes present several strategies. According to Dastogeer and Wylie (2017), they can improve water uptake, the photosynthesis, the osmotic adjustment, reactive oxygen species (ROS) removal and hormone modulation. In addition, it has also been documented that endophytes can activate induced systemic tolerance (IST) (Chagas et al., 2018; Khan et al., 2013). Examples are *Exophiala pisciphila* which gives maize tolerance to cadmium at concentrations that would be phytotoxic or *Piriformospora indica* which protects against drought in Chinese cabbage (Sun et al., 2010) and against salinity in barley (Baltruschat et al., 2008).

3.1.2. EFF as biocontrol agents

Finally, endophytic fungi can increase resistance to pathogens, either locally or systemically. In this case, the formulated bioinoculant act as a biological control agent (BCA). Endophytes have been shown to protect plants against disease by reducing or suppressing the growth of the plant pathogen. To achieve this protection, endophytes activate induced systemic resistance (ISR), preventing pathogen colonization, compete for space and nutrients or synthesize defensive metabolites such as alkaloids, flavonoids, phenols, steroids, terpenoids or volatile organic compounds (VOCs) that inhibit the growth of certain plant pathogens. The latter strategy is also valid against herbivory, as has been demonstrated by some endophytic fungi of the genus *Epichloë* (Brem and Leuchtman, 2001). Another type of plant protection mediated by endophytic fungi may come from nematophagous or entomopathogens fungi which can inhabit plant roots as endophytes (Zabalgoeazcoa, 2008; Poveda et al., 2020; Pozo et al., 2021).

As an example, genus *Trichoderma*, act as BCA for nematode control (Poveda et al., 2020). Other examples of endophytes acting as BCAs are *Trichoderma asperellum* that protects against *Pseudomonas syringae* pv. *lachrymans* in cucumber, *Epichloë festucae* that generates an antifungal protein against *Sclerotinia homoeocarpa* (Tian et al., 2017) and *Heteroconium chaetospora* which reduces the symptoms of clubroot disease in oilseed roots (Adeleke et al., 2022). *Trichoderma*-based products are the most marketed ones. A large number of species within this genus have been shown to have fungicidal, fertilizer, insecticidal and inductors of ISR. As an example, products containing different *Trichoderma* species (*T. polysporum*, *T. harzianum*, *T. gamsii*, *T. atroviride* o *T. asperellum*, among others) have been registered in Europe. Some of these products are marketed as TUSAL WG, Trichomic, BioFlower, Sani-Root or Bioten and are formulated with one or more *Trichoderma* species. In addition, *Trichoderma* can appear associated with other microorganisms (Poveda and Eugui, 2022), as in the products Compete Plus and Suma Grow in which it appears combined with *Bacillus* spp. and *Streptomyces* in the former (Woo et al., 2014), or *Rhizobium* spp., *Pseudomonas* spp. and *Bacillus* spp. in the latter (Pirttilä et al., 2021).

3.2. Co-inoculants: EFF and other microorganisms

In general terms, these products consist of a microorganism, or a set of organisms (microbial consortium), associated with a carrier. Usually the microbial consortia offer better results than single-strain inoculants both as biostimulants (Kenneth Odoh et al., 2020) and in biological

control (Kumar et al., 2012; Whipps, 2001) especially in adverse environmental conditions. Although microbial consortia can potentially be made with a multitude of microorganisms (viruses, algae, archaea, oomycetes), the most commercialized products are the consortium between bacteria and fungi (Pirttilä et al., 2021; Poveda et al., 2022). This is probably due to the fact that most commercially available products are based on bacteria and are already accepted by the consumer and the regulation (EU, 2019; Kowalska et al., 2020). Moreover, bacteria have been shown to play a key role in biostimulation as they fix nitrogen (*Rhizobium*, *Azospirillum*, *Azotobacter*...), solubilise phosphorus (*Penicillium*, *Fusarium*, *Aspergillus*...), mobilise phosphate... And they are also used as biocontrol tools as they produce antibiotics, enzymes that degrade the cell wall of certain fungi and induce systemic resistance in plants (Tripathi et al., 2015; Vyas, 2018). Using them in combination can have a synergistic effect (Seenivasagan and Babalola, 2021), as an example *Pririformospora indica* and *Azotobacter chroococcum* promotes plant growth (Arora et al., 2020). In addition to the microorganisms that form the product, it is essential that the bioinoculants developed are cheap, easy to apply, easy to handle and remain effective throughout their useful life, which should be as long as possible. For this purpose, solid formulations (granules, microcapsules, emulsions or powder) and liquid formulations have been developed (Tripathi et al., 2015). In the case of biostimulants, they can also be different types of soils, either natural (peat and coal, soya bean oil, compost...) or inert (perlite, talcum, clay, vermiculite...). In general, the material must be non-toxic to micro-organisms, plants, animals and the environment. These tools are intended to be more environmentally friendly, safer for human health and the environment. In addition, bioinoculants are used in small quantities and their proliferation is controlled by the native microbiota and the plant (Baron and Rigobelo, 2022). The forms of application depend on the formulation. Usually, the most desirable form of application requires no additional material, either by the irrigation system itself or by spraying. Seed coating or dispersion by spreader centrifuges is also common. Crops that are transplanted, such as rice, onions or many ornamental plants can be dipped into this solution for several hours and then transplanted (Misra et al., 2020). It must be highlighted that EU Regulation allows only the drying or freeze-drying processes in the formulation of the product, limiting the range of micro-organisms that can be used to those that survive these processes (Kowalska et al., 2020).

4. Combined use mycorrhizal fungi-endophytic filamentous fungi

The plant-fungus relationship is never an isolated interaction, since both members interact in turn with the rest of organisms present (microorganisms, plants and animals). In the case of fungus-plant root interaction, the enormous complexity of interactions is encompassed under the concept of mycorrhizosphere. This includes the proportion of soil occupied by the roots and the fungal hyphae that interact with them, also colonizing the internal-plant tissues, together with all organisms present there (Kothe and Turnau, 2018).

In the plant-MF-EFF tripartite interaction we find a complex network of molecular dialogues that not only have effects on its members, but also on the rest of the organisms in the agro-system. Directly, it has been reported how different EFFs are capable of reducing or eliminating the ability of MF to colonize roots. In different grasses it has been possible to verify how the endophyte *Neotyphodium coenophialum* produces various allelochemical compounds that reduce the ability of MF to colonize the roots of these plants by 90% (Antunes et al., 2008). These antifungal allelochemical compounds against MF have been identified as alkaloids produced by the endophyte *Acremonium coenophialum* in *Festuca arundinacea* plants (Chu-Chou et al., 1992). On the other hand, MF can also act indirectly on endophytic fungi populations in different plant organs. It has been possible to describe how the root colonization of *Cirsium arvense* by different MF actively modifies the quantity and diversity of

EFF present in leaves and stems (Eschen et al., 2010). In turn, these EFF in the aerial part can also favor root colonization by MF, how has been reported in the grass *Poa bonariensis* with the endophyte *Neotyphodium* sp. (Victoria-Novas et al., 2009).

Simultaneous root colonization by MF and EFF has been described in a wide diversity of plant species, such as pteridophytes (Fernández et al., 2013), desert plants (Wagg et al., 2008; Wu et al., 2009), pines (Kernaghan et al., 2003), oaks (Toju et al., 2013; Yamamoto et al., 2014), orchids (Wang et al., 2017), medicinal and aromatic plants (Muthukumar et al., 2006; Dang et al., 2021), ginger (Pandey et al., 2020), switchgrass (Lee and Hawkes, 2021), rice (Vallino et al., 2009) or alfalfa (Saravesi et al., 2014). However, diversity and root/rhizosphere colonization of each fungal group can be very different depending on various factors, being the main: host phylogeny, geographic distance, soil and climate (Gooden et al., 2020; Wang et al., 2020). Within climatic factors, the most influential for MF and EFF are rainfall, sunlight hours and temperature (Olsson et al., 2004; Lingfei et al., 2005; Huo et al., 2021). Regarding the soil, the main conditioning factors are nutritional content (mainly, N and P), pH and the presence of heavy metals (Postma et al., 2007; Göransson et al., 2008; Bueno de Mesquita et al., 2018). Of course, the host conditions both directly and indirectly can modify the diversity and quantity of MF and EFF that colonize its roots. Differences have been reported at genotype level within the same species (Karliński et al., 2010; Bazghaleh et al., 2018), between different species within the same place (Fuchs and Haselwandter, 2004; John et al., 2014; Surendirakumar et al., 2021), and in different places with the same host (Chaudhry et al., 2009). On the other hand, it has also been described how this simultaneous root colonization by MF and EFF is modified according to the stage of plant development, with EFF being more present during the early part of the growing season, and MF during the peak growing season (Mandyam and Jumpponen, 2008).

In the next sections, all the studies carried out on the combined and directed use of MF and EFF in different crops, in order to promote their growth and yield, increase their tolerance to abiotic stresses and/or protect them from biotic stresses, are presented and discussed. In Fig. 1 we can find a summary infographic about the different effects and mechanisms of action reported with MF-EFF co-inoculation in plants.

4.1. Promotion of plant growth, yield and quality of crops

The ability of MF and EFF in isolation to promote plant growth and crop productivity is widely known. In this sense, the combination of both fungal tools can increase (even synergistically) the isolated effects of each microorganism. Table 1 compiles all MF-EFF co-inoculation studies related to plant growth promotion, yield and quality of crops.

There are numerous descriptive studies where only the effects of MF-EFF co-inoculation are reported, without identifying the mechanisms of action involved. In this sense, the promotion of plant growth has been reported additively with both types of fungi combined compared to each one in isolation. For example, in *Elymus hystrix* co-inoculated with different MF (*Glomus claroideum* and *G. mosseae*) and the EFF *Epichloë elymi* (Larimer et al., 2012); or in cucumber with *G. mosseae* and *Fusarium equiseti* (Saldajeno and Hyakumachi, 2011). Synergistic plant growth promotion effects have also been reported, such as in tomato co-inoculated with MF and *Trichoderma* spp. (Commatte et al., 2019). And even at a productive level, as is the case with the increase in tuber yield in *Helianthus tuberosus* plants co-inoculated with *Glomus etunicatum* and *Exserohilum rostratum* (Khaekhum et al., 2021).

In isolation, MF and EFF promote plant growth through various mechanisms of action, always dependent on the degree of root colonization (Jansa et al., 2008; Poveda et al., 2021). In this sense, it has been reported in several studies how MF-EFF co-inoculation increases root colonization by one or both fungi, significantly promoting the growth of the host plant. One of the mechanisms of action involved may be the production of exudates by EFF, favoring the growth and development of MF and the colonization of the host plant. In *Bromus auleticus* plants, the

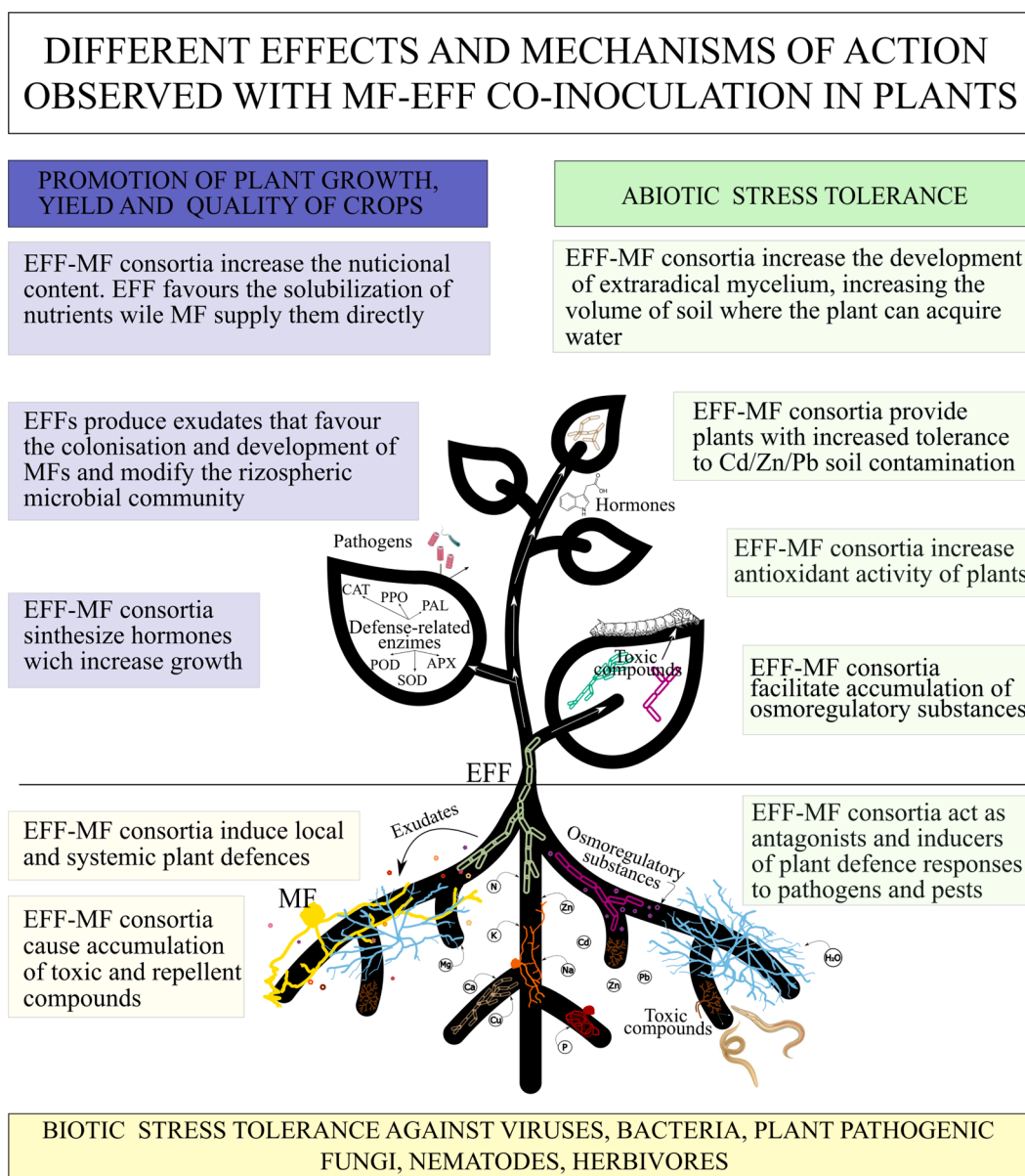


Fig. 1. Summary infographic about the different effects and mechanisms of action reported with mycorrhizal fungi (MF) and endophytic filamentous fungi (EFF) co-inoculation in plants. The acronyms PPO, PAL, POD, APX, SOD refer to the polyphenol oxidase, phenylalanine amino lyase, peroxidase, ascorbate peroxidase and superoxide dismutase enzymes, respectively.

exudates produced by *Epichloë tembladerae* promoted the growth and development of the MF *Rhizophagus intraradices* and *Gigaspora rosea*, significantly promoting plant growth (Vignale et al., 2018). These plant growth promotion effects, as a consequence of greater root colonization by MF, caused by its co-inoculation with EFF, have been reported with very different crops and fungal species. For example, in soybean with *G. mosseae* and *Fusarium* spp. (García-Romera et al., 1998), or in blueberry with the co-inoculations *Glomus viscosum*-*Phanerochaete chrysosporium* and *Glomus intraradices*-*Trametes versicolor* (Arriagada et al., 2012). However, these plant growth promotion effects because of a greater MF-root colonization are totally dependent on the MF-EFF combination performed. In this sense, co-inoculation with *G. mosseae* with *Trichoderma harzianum* in cucumber plants is effective, but when EFF is modified by *Penicillium simplicissimum*, the beneficial effect is not obtained (Chandanie et al., 2009). In a similar way, it occurs when the species MF is modified, having been observed how *T. harzianum* promotes root colonization of melon plants by *Glomus constrictum*, *G. claraideum* and *G. intraradices*, but not by *G. mosseae* (Martínez-

Medina et al., 2009). This same mechanism of action has been reported with ectomycorrhizae, promoting plant growth of *Picea abies* due to greater root colonization by *Laccaria bicolor* when co-inoculated with the EFF *Phialocephala fortinii* and *Acephala applanata* (Reininger and Sieber, 2012).

In addition to the promotion of plant growth, the increase in root colonization by MF can lead to an increase in the nutritional content of plant tissues. These results have been reported in very diverse crops and MF-EFF combinations, with the main nutrients quantified differentially being N, P, K, Ca, Na, Mg, Cu and Zn (Fracchia et al., 2000; Vaz et al., 2012; Zhou et al., 2018). Finally, both the promotion of plant growth and the increase in the acquisition of nutrients by the plant lead to an increase in crop yield and crop quality. In onions, MF-*Trichoderma viride* co-inoculation increases bulb yield by up to 20% (Metwally and Al-Amri, 2020), along with total free amino acids, and soluble protein content (Metwally et al., 2021). Similar increases reported in tuber yield of potato plants co-inoculated with *Rhizophagus irregularis* and *T. harzianum* (Buysens et al., 2016).

Table 1
Effect of promoting plant growth and increasing yield in crops by co-inoculations with mycorrhizal fungi (MF) and endophytic filamentous fungi (EFF).

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	BENEFICIAL EFFECTS	MECHANISMS OF ACTION	REFERENCE
<i>Acaulospora laevis</i>	<i>Trichoderma viride</i>	In greenhouse	Sunflower	Plant growth promotion Improved oil yield	Increased MF root colonization Increased P supply (MF)	Yadav et al., 2015
	<i>Phoma leveillei</i>	In greenhouse	Cucumber	Plant growth promotion Increased yield	Increased fungi root colonization	Gao et al., 2016
	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Increased bulb yield	Increased MF root colonization	Metwally and Al-Amri, 2020
<i>Dentiscutata nigra</i>	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Increased bulb yield	Increased MF root colonization	Metwally and Al-Amri, 2020
<i>Diversispora spurca</i>	<i>Piriformospora indica</i>	In field	Orange	Improved fruit quality	Increased P and water content in soil	Cheng et al., 2022
<i>D. versiformis</i>	<i>P. indica</i>	In field	Orange	Improved fruit quality	Increased P and water content in soil	Cheng et al., 2022
<i>Epulorhiza repens</i>	<i>Umbelopsis nana</i>	In greenhouse	<i>Cymbidium hybridum</i>	Plant growth promotion Increased nutrients content in plant tissues	Increased P, K, Ca, Mg and Zn supply (<i>E. repens</i>) Increased N, P and Ca supply (<i>U. nana</i>)	Liu et al., 2021
<i>Funneliformis constrictum</i> (= <i>Septoglonus constrictum</i>) (= <i>Glomus constrictum</i>)	<i>Trichoderma harzianum</i>	In greenhouse	Melon	Plant growth promotion	Increased MF root colonization	Martínez-Medina et al., 2009
	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Improved bulbs quality	Increased MF root colonization	Metwally et al., 2021
<i>Gigaspora margarita</i>	<i>T. harzianum</i>	In greenhouse	Bean	Plant growth promotion Increased nutrients content in plant tissues	Increased P and Zn supply P solubilization (<i>T. harzianum</i>)	Eke et al., 2019
	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Improved bulbs quality	Increased MF root colonization	Metwally et al., 2021
<i>G. rosea</i>	<i>Phialocephala turiciensis</i>	In growth chamber	<i>Trifolium repens</i>	Increased nutrients content in plant tissues	Increased P content in soil	Della Monica et al., 2015
	<i>P. glacialis</i> <i>Epichloë tembladera</i>	In greenhouse	<i>Bromus auleticus</i>	Plant growth promotion	Increased MF root colonization	Vignale et al., 2018
<i>Glomus aggregatum</i>	<i>Mortierella</i> sp.	In greenhouse	Leucaena	Plant growth promotion Increased nutrients content in plant tissues	P solubilization (<i>Mortierella</i> sp.) Increased P supply (<i>G. aggregatum</i>)	Osorio and Habte, 2001
	<i>T. harzianum</i>	In greenhouse	Rapeseed Arabidopsis	Increased siliques yield	Increased <i>T. harzianum</i> root colonization MF root colonization	Poveda et al., 2019
<i>G. claroideum</i> (= <i>Claroideoglonus claroideum</i>)	<i>T. harzianum</i>	In greenhouse	Melon	Plant growth promotion	Increased MF root colonization	Martínez-Medina et al., 2009
	<i>Epichloë elymi</i>	In greenhouse	<i>Elymus hystrix</i>	Plant growth promotion	Unidentified	Larimer et al., 2012
	<i>Mortierella</i> sp.	In greenhouse	Leucaena	Plant growth promotion Increased nutrients content in plant tissues	P solubilization (<i>Mortierella</i> sp.) Increased P supply (<i>C. claroideum</i>)	Osorio and Habte, 2015
<i>G. clarum</i>	<i>T. harzianum</i>	In greenhouse	Rapeseed Arabidopsis	Increased siliques yield	Increased <i>T. harzianum</i> root colonization MF root colonization	Poveda et al., 2019
	<i>Fusarium oxysporum</i>	In greenhouse In field	Pea Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Fracchia et al., 2000
<i>G. deserticola</i>	<i>F. oxysporum</i>	In greenhouse In field	Pea Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Fracchia et al., 2000

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Table 1 (continued)

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	BENEFICIAL EFFECTS	MECHANISMS OF ACTION	REFERENCE
<i>G. etunicatum</i> (= <i>Claroideoglossum etunicatum</i>)	<i>Epichloë</i> sp.	In field	<i>Achnatherum sibiricum</i>	Increased nutrients content in plant tissues	Increased P supply	Zhou et al., 2016
	<i>Epichloë gansuensis</i> <i>E. sibirica</i>	In field	<i>Achnatherum sibiricum</i>	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Zhou et al., 2018
	<i>Penicillium pinophilum</i>	In growth chamber	Tomato Lettuce	Plant growth promotion	P solubilization (<i>P. pinophilum</i>) Siderophore production (<i>P. pinophilum</i>) Increased root colonization (both)	Ibiang et al., 2020
<i>G. fistulosum</i>	<i>Exserohilum rostratum</i>	In field	<i>Helianthus tuberosus</i>	Increased tuber yield	Unidentified	Khaekhum et al., 2021
	<i>Mortierella</i> sp.	In greenhouse	Leucaena	Plant growth promotion Increased nutrients content in plant tissues	P solubilization (<i>Mortierella</i> sp.) Increased P supply (<i>G. fistulosum</i>)	Osorio and Habte, 2013
<i>G. hoi</i> (= <i>Simiglomus hoi</i>)	<i>Epichloë occultans</i>	In greenhouse	<i>Lolium multiflorum</i>	Plant growth promotion	Increased P supply (MF)	García-Parisi and Omacini, 2017
	<i>T. harzianum</i>	In greenhouse	Bean	Plant growth promotion Increased nutrients content in plant tissues	Increased P and Zn supply P solubilization (<i>T. harzianum</i>)	Eke et al., 2019
<i>G. monosporum</i> (= <i>Funnelformis monosporus</i>)	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Increased bulb yield	Increased MF root colonization	Metwally and Al-Amri, 2020
<i>G. mosseae</i> (= <i>Funnelformis mosseae</i>)	<i>F. oxysporum</i> <i>F. stilboide</i> <i>F. solani</i> <i>F. oxysporum</i>	In greenhouse	Soybean	Plant growth promotion	Increased MF root colonization	García-Romera et al., 1998
	<i>F. oxysporum</i>	In greenhouse	Pea	Plant growth promotion	Increased MF root colonization	Fracchia et al., 2000
	<i>F. oxysporum</i>	In field	Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Chandanie et al., 2009
	<i>T. harzianum</i>	In growth chamber	Cucumber	Plant growth promotion	Increased MF root colonization	Martínez-Medina et al., 2009
	<i>T. harzianum</i>	In greenhouse	Melon	Plant growth promotion	Increased MF root colonization	Saldajeno and Hyakumachi, 2011
	<i>Fusarium equiseti</i>	In growth chamber	Cucumber	Plant growth promotion	Unidentified	Larimer et al., 2012
	<i>E. elymi</i>	In greenhouse	<i>E. hystrix</i>	Plant growth promotion	Unidentified	Rane et al., 2015
	<i>P. indica</i>	In field	Maize	Plant growth promotion	Unidentified	Yadav et al., 2015
	<i>T. viride</i>	In greenhouse	Sunflower	Plant growth promotion Improved oil yield	Increased MF root colonization Increased P supply (MF)	Gao et al., 2016
	<i>P. leveillei</i>	In greenhouse	Cucumber	Plant growth promotion Increased yield	Increased fungi root colonization	Zhou et al., 2016
	<i>Epichloë</i> sp.	In field	<i>A. sibiricum</i>	Plant growth promotion Increased nutrients content in plant tissues	Increased P and N supply	García-Parisi and Omacini, 2017
	<i>E. occultans</i>	In greenhouse	<i>Lolium multiflorum</i>	Plant growth promotion	Increased P supply (MF)	Zhou et al., 2018
	<i>E. gansuensis</i> <i>E. sibirica</i>	In field	<i>A. sibiricum</i>	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Poveda et al., 2019
<i>T. harzianum</i>	In greenhouse	Rapeseed Arabidopsis	Increased siliques yield	Increased <i>T. harzianum</i> root colonization MF root colonization	Hallasgo et al., 2020	
<i>Serendipita williamsii</i>	In growth chamber	Tomato	Increased nutrients content in plant tissues	Increased N supply (both)		

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Table 1 (continued)

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	BENEFICIAL EFFECTS	MECHANISMS OF ACTION	REFERENCE
	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Improved bulbs quality	Increased MF root colonization	Metwally et al., 2021
<i>G. versiforme</i> (= <i>Diversispora epigaea</i>)	<i>P. leveillei</i>	In greenhouse	Cucumber	Plant growth promotion Increased yield	Increased fungi root colonization	Gao et al., 2016
	<i>Alternaria</i> sp.	In greenhouse	Maize	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization Increased P and K supply	Xie et al., 2021
<i>G. viscosum</i>	<i>Phanerochaete chrysosporium</i>	In greenhouse	Blueberry	Plant growth promotion	Increased MF root colonization	Arriagada et al., 2012
<i>Glomus</i> sp.	<i>Cylindrocarpon destructans</i> <i>C. pauciseptatum</i> <i>Eucasphaeria</i> sp. <i>Phoma schachtii</i> <i>P. columnaris</i>	In greenhouse	Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Vaz et al., 2012
<i>Laccaria bicolor</i>	<i>Phialocephala fortinii</i> <i>Acephala applanata</i>	In growth chamber	<i>Picea abies</i>	Plant growth promotion	Increased ectomycorrhizae root colonization	Reininger and Sieber, 2012
<i>Rhizophagus intraradices</i> (= <i>Glomus intraradices</i>)	<i>F. oxysporum</i>	In greenhouse In field	Pea Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Fracchia et al., 2000
	<i>T. harzianum</i>	In greenhouse	Melon	Plant growth promotion	Increased MF root colonization	Martínez-Medina et al., 2009
	<i>Trametes versicolor</i>	In greenhouse	Blueberry	Plant growth promotion	Increased MF root colonization	Arriagada et al., 2012
	<i>E. occultans</i>	In greenhouse	<i>Lolium multiflorum</i>	Plant growth promotion	Increased P supply (MF)	García-Parisi and Omacini, 2017
	<i>P. indica</i>	In greenhouse	<i>Miscanthus giganteus</i>	Plant growth promotion	Modification of hormonal content in plant tissues	Schmidt et al., 2017
	<i>E. tembladerae</i>	In greenhouse	<i>B. auleticus</i>	Plant growth promotion	Increased MF root colonization	Vignale et al., 2018
	<i>P. pinophilum</i>	In growth chamber	Tomato Lettuce	Plant growth promotion	P solubilization (<i>P. pinophilum</i>) Siderophore production (<i>P. pinophilum</i>) Increased root colonization (both)	Ibiang et al., 2020
<i>R. irregularis</i> (= <i>Glomus irregulare</i>)	<i>T. harzianum</i>	In field	Potato	Increased tuber yield	Increased MF root colonization	Buysens et al., 2016
	<i>T. harzianum</i>	In greenhouse	Rapeseed Arabidopsis	Increased siliques yield	Increased <i>T. harzianum</i> root colonization MF root colonization	Poveda et al., 2019
	<i>P. pinophilum</i>	In growth chamber	Tomato Lettuce	Plant growth promotion	P solubilization (<i>P. pinophilum</i>) Siderophore production (<i>P. pinophilum</i>) Increased root colonization (both)	Ibiang et al., 2020
	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Improved bulbs quality	Increased MF root colonization	Metwally et al., 2021
<i>Rhizoglomus clarum</i> (= <i>Rhizophagus clarus</i>)	<i>T. viride</i>	In greenhouse	Onion	Plant growth promotion Increased bulb yield	Increased MF root colonization	Metwally and Al-Amri, 2020
<i>R. fasciculatum</i> (= <i>Glomus fasciculatum</i>)	<i>F. oxysporum</i>	In greenhouse In field	Pea Sorghum	Plant growth promotion Increased nutrients content in plant tissues	Increased MF root colonization	Fracchia et al., 2000
	<i>Mortierella</i> sp.	In greenhouse	Avocado	Plant growth promotion Increased nutrients content in plant tissues	P solubilization (<i>Mortierella</i> sp.) Increased P supply (<i>R. fasciculatum</i>)	Tamayo-Velez and Osorio, 2016

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Table 1 (continued)

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	BENEFICIAL EFFECTS	MECHANISMS OF ACTION	REFERENCE
	<i>T. harzianum</i>	In greenhouse	Rapeseed <i>Arabidopsis</i>	Increased siliques yield	Increased <i>T. harzianum</i> root colonization MF root colonization	Poveda et al., 2019
<i>Scutellospora aurigloba</i>	<i>P. leveillei</i>	In greenhouse	Cucumber	Plant growth promotion Increased yield	Increased fungi root colonization	Gao et al., 2016
<i>S. gigantea</i>	<i>T. harzianum</i>	In greenhouse	Bean	Plant growth promotion Increased nutrients content in plant tissues	Increased P and Zn supply solubilization (<i>T. harzianum</i>)	Eke et al., 2019
<i>Suillus luteus</i>	<i>Mycena galopus</i>	In growth chamber	<i>Pinus contorta</i>	Plant growth promotion	Increased N supply	Dighton et al., 1987
Unidentified	<i>Trichoderma</i> spp.	In growth chamber	Tomato	Plant growth promotion	Unidentified	Commatteo et al., 2019
	Unidentified	In field	<i>Equisetum arvense</i> <i>E. sylvaticum</i>	Increased nutrients content in plant tissues	Increased N supply	Giesemann et al., 2020

However, MF-EFF co-inoculation is not able to promote plant growth only through increased colonization by MF, but also EFF can promote their growth, development and colonization of host roots. The co-inoculation of cucumber plants with different MF and *Phoma leveillei* significantly promotes the plant height, stem diameter, dry mass and yield per plant, due to greater root colonization by both types of fungi (Gao et al., 2016). Something even more innovative has been the work carried out by Poveda et al. (2019). Starting from the problem that the Brassicaceae family plants cannot form symbiosis with MF, since they have lost this ability evolutionarily, they formulated the hypothesis that using an EFF capable of colonizing the roots of these plants could facilitate colonization by MF. They co-inoculated *Arabidopsis* and rapeseed plants with different MF species and the endophyte *T. harzianum*, quantifying a significant increase in siliques yield. This was a consequence of an increase in root colonization by *T. harzianum*, by mycoparasitizing MF and using them as an energy resource, and the existence of colonization by MF. This colonization of the Brassicaceae roots by MF represents an enormous scientific advance in achieving the effective mycorrhization of important crops within this family of plants, being possible thanks to the modification of the root defenses by *T. harzianum*, “opening the door” for the entry of MF (Poveda et al., 2019).

Together with a greater root colonization, MF and EFF promote plant growth due to a direct supply of nutrients to the roots. With respect to N, both MF and EFF act as powerful decomposers of the organic matter present in the soil, making assimilable forms of the nutrient available to the plant (Dighton et al., 1987; Giesemann et al., 2020; Hallasgo et al., 2020). However, the main nutrient provided by both groups of fungi is P. It has been reported that greater root colonization by MF is related to a greater supply of P to the host plant, as occurs with *Acaulospora laevis*-*T. viride* co-inoculation in sunflower (Yadav et al., 2015), or *Glomus etunicatum*-*Epichloë* sp. in *Achnatherum sibiricum* (Zhou et al., 2016). In this sense, a complementary action between both fungi has been described, very important for the nutritional contribution to the plant: the solubilization of P by EFF and its greater supply to the plant by MF. Through these mechanisms of action, it has been possible to promote plant growth and increase the tissue content of P in various crops, such as leucaena and avocado with MF-*Mortierella* sp. co-inoculations (Osorio and Habte, 2001, 2013, 2015; Tamayo-Velez and Osorio, 2016), or bean with MF-*T. harzianum* (Eke et al., 2019). In addition, together with P supply, these fungi can favor the acquisition of other important nutrients by their host plant, such as K (Xie et al., 2021), Fe (Ibiang et al., 2020), Ca, Mg or Zn (Liu et al., 2021), and even improve the acquisition of water by the roots (Cheng et al., 2022).

On the other hand, it is widely known that rhizospheric fungi can promote plant growth through the production of plant hormones or the modification of the tissue contents of their host plant (Poveda et al.,

2021). In this sense, it has been reported how root colonization of *Miscanthus giganteus* by *Glomus intraradices* and *Piriformospora indica* leads to plant growth promotion as a consequence of an increase in leaf concentrations of abscisic acid (ABA) derivatives, auxin (indole-3-acetic acid) precursors and catabolites and numerous cytokinins (Schmidt et al., 2017).

Indirectly, root colonization by MF and/or EFF can also act on the fungal endophytic microbiota of the aerial part, and vice versa, modifying plant growth. For example, the foliar presence of EFF significantly reduces root colonization by MF, P uptake and shoot growth in several plant species (Park and Eom, 2007; Liu et al., 2020). But they can also have important positive effects on their host plant. In the wild grass *Bromus auleticus*, the presence of certain foliar EFFs, such as *Epichloë* sp., increases rhizosphere diversity and root colonization of P-solubilizing EFF and MF (Arrieta et al., 2015).

4.2. Abiotic stress tolerance

Environmental conditions, such as atmospheric CO₂, soil warming or drought, can significantly modify the diversity and quantity of MF and EFF that colonize plant roots (Staddon et al., 2004). It has even been possible to describe species of these filamentous fungi that are only present in situations of strong abiotic stress, such as salinity or pollution, and may play a key role in the ability of their host plants to survive in these extreme environments (Muthukumar and VEDIYAPPAN, 2010; Likar et al., 2011; Thiem et al., 2018). Table 2 compiles all the studies carried out to date where the MF-EFF co-inoculation has led to an improvement in the plant tolerance of crops to abiotic stresses.

4.2.1. MF-EFF inoculum against water stress

Drought is an increasing abiotic stress due to climate change and global warming. It is caused by a massive loss of soil moisture, causing serious losses in three quarters of the globally harvested land (Mishra et al., 2021). The co-inoculation of crops with MF and EFF has reported important results in improving plant tolerance under drought situations, although each type of fungus can by itself promote plant tolerance very effectively (Tyagi et al., 2017). As described above, co-inoculation can cause an increase in root colonization by one or both types of fungi. In a drought situation, the co-inoculation with *Gigaspora margarita* and *Phomopsis liquidambaris* in peanut plants caused a significant increase in root colonization by MF and a greater development of the extraradical mycelium, increasing the volume of soil where the plant can acquire water, and the plant tolerance to stress (Xu et al., 2020). Other mechanisms of action derived from co-inoculation under drought stress are the increase in the nutritional contribution to the plant, specifically P, facilitating the accumulation of osmoregulatory substances in plant

Table 2
Effect of abiotic stress tolerance in crops by co-inoculations with mycorrhizal fungi (MF) and endophytic filamentous fungi (EFF).

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	ABIOTIC STRESS AND BENEFICIAL EFFECTS	MECHANISMS OF ACTION	REFERENCE
<i>Claroideoglossum etunicatum</i> (= <i>Glomus etunicatum</i>)	<i>Epichloë</i> sp.	In greenhouse	Ryegrass	Drought / Increased plant tolerance	Increased P uptake Increased plant-tissues accumulation of osmoregulatory substances	Li et al., 2019
<i>Funneliformis geosporum</i> (= <i>Glomus geosporum</i>)	<i>Penicillium funiculosum</i> <i>Fusarium oxysporum</i>	In greenhouse	Wheat	Salinity / Increased plant tolerance and decreased Na and Cl accumulation in plant tissues	Increased MF root colonization (EFF) Increased nutrients uptake (both)	Elgharably and Nafady, 2021
<i>Funneliformis mosseae</i> (= <i>Glomus mosseae</i>)	<i>Serendipita indica</i> (<i>Piriformospora indica</i>) <i>P. indica</i>	In growth chamber	Wheat	Cd soil contamination / Increased plant tolerance	Unidentified	Shahabivand et al., 2012
	<i>P. indica</i>	In greenhouse	Wheat	Drought / Increased plant tolerance	Increased plant-antioxidant activity	Yaghoobian et al., 2014
	<i>Cadophora</i> sp.	In greenhouse	Ryegrass	Cd/Zn/Pb soil contamination / Increased Cd/Zn/Pb plant-tolerance and Cd accumulation in plant tissues	Reduce plant-oxidative stress (both)Increased P supply (MF)	Berthelot et al., 2018
	<i>Exophiala pisciphila</i>	In greenhouse	Maize	Cd soil contamination / Increased plant tolerance and reduction of Cd accumulation in plant tissues	Unidentified	He et al., 2020
	<i>P. funiculosum</i> <i>F. oxysporum</i>	In greenhouse	Wheat	Salinity / Increased plant tolerance and decreased Na and Cl accumulation in plant tissues	Increased MF root colonization (EFF) Increased nutrients uptake (both)	Elgharably and Nafady, 2021
<i>Gigaspora margarita</i>	<i>Phomopsis liquidambaris</i>	In greenhouse	Peanut	Drought / Increased plant tolerance	Increased MF root colonization	Xu et al., 2020
<i>Glomus deserticola</i>	<i>Trichoderma koningii</i>	In greenhouse	Eucalyptus	Cd soil contamination / Increased plant tolerance	Unidentified	Arriagada et al., 2004
<i>Rhizoglossum intraradices</i> (= <i>Glomus intraradices</i>) (= <i>Rhizoglossum intraradices</i>)	<i>Mucor</i> sp.	In greenhouse	<i>Lactuca serriola</i>	Cd/Zn/Pb soil contamination / Increased Cd/Zn/Pb plant-tolerance and Zn accumulation in plant tissues	Increased MF root colonization (EFF)	Wazny et al., 2018
<i>Rizophagus clarus</i> (= <i>Rhizoglossum clarum</i>) (= <i>Glomus clarus</i>)	<i>P. funiculosum</i> <i>F. oxysporum</i>	In greenhouse	Wheat	Salinity / Increased plant tolerance and decreased Na and Cl accumulation in plant tissues	Increased MF root colonization (EFF) Increased nutrients uptake (both)	Elgharably and Nafady, 2021
<i>Rhizophagus irregularis</i> (= <i>Rhizoglossum irregulare</i>) (= <i>Glomus irregulare</i>)	<i>Diaporthe</i> sp. <i>Cochliobolus sativus</i> <i>Phoma exigua</i> var. <i>exigua</i> <i>S. indica</i>	In greenhouse	<i>Verbascum lychnitis</i>	Cd/Zn soil contamination / Increased Cd/Zn plant-tolerance	Unidentified	Weżowicz et al., 2017
	<i>S. indica</i>	In greenhouse	Tomato	Salinity / Increased plant tolerance	Increased lipid content related to salinity tolerance in roots (both)	Heidarianpour et al., 2020
<i>Scutellospora persica</i> (= <i>Gigaspora persica</i>)	<i>P. funiculosum</i> <i>F. oxysporum</i>	In greenhouse	Wheat	Salinity / Increased plant tolerance and decreased Na and Cl accumulation in plant tissues	Increased MF root colonization (EFF) Increased nutrients uptake (both)	Elgharably and Nafady, 2021
Unidentified	<i>P. indica</i>	In greenhouse	Peppermint	Salinity / Increased plant tolerance	Increased antioxidant activity Increased P and K ⁺ uptake	Khalvandi et al., 2021

tissues (Li et al., 2019), and increasing its antioxidant activity (catalase, peroxidase, ascorbate peroxidase), reducing the adverse effects of stress (such as increased levels of hydrogen peroxide and lipid peroxidation) (Yaghoobian et al., 2014). However, negative effects of co-inoculation in drought situations have also been described, due to the great expense that the plant has to make to maintain the symbiotic relationship with both fungal groups (Liu et al., 2017).

4.2.2. MF-EFF inoculum against salinity

One of the main abiotic threats to world agriculture is the salinity of agricultural land. Currently, 20% of cultivated land and 33% of irrigated agricultural land have soil salinity, mainly as a result of human activity (overexploitation of aquifers and use of chemical fertilizers) (Mukhopadhyay et al., 2021). Increasing salinity tolerance in crops by using the

MF-EFF combination can be a sustainable and effective strategy. In wheat plants, co-inoculation with MF and the EFF *Penicillium funiculosum* or *F. oxysporum* caused an increase in plant tolerance to soil salinity, in addition to a lower accumulation of Na and Cl in the host plant tissues. This plant response was a consequence of an increase in MF-root colonization, due to the presence of EFFs, and an increase in the supply of nutrients to the plant (N, P and K) (Elgharably and Nafady, 2021). Moreover, with the combination MF-*P. indica* in peppermint, an increase in plant tolerance to salinity was reported due to an increase in P and K uptake, in addition to the antioxidant activity of the plant, reducing signs of stress (Khalvandi et al., 2021). This same fungal combination also increased drought tolerance in tomato plants, identifying the synthesis and plant accumulation of osmoregulatory lipids, such as ergosterol, as the mechanism of action implicated (Heidarianpour et al.,

2020).

4.2.3. MF-EFF mediated bioremediation

The contamination of agricultural soils and waters with heavy metals is a serious environmental and health problem of anthropogenic origin. The main heavy metals that can be found in the agricultural system are Pb, Cd and Zn (Zhu et al., 2018). To date, numerous MF-EFF combinations have been described with the ability to increase plant tolerance to the presence of these heavy metals in agricultural soils, for example, in crops such as wheat or maize; however, the mechanisms of action involved are still unknown in most cases (Arriagada et al., 2004; Wężowicz et al., 2017; He et al., 2020). The combination *Rhizoglyphus intraradices*-*Mucor* sp. entails an increase in MF-root colonization in *Lactuca serriola* plants, which may be the mechanism of action involved in a greater plant tolerance to Cd/Zn/Pb soil contamination, in addition to a greater Zn accumulation in plant tissues (Ważny et al., 2018). Other identified mechanisms of action include the increase in P supply to the plant by MF and a reduction in plant oxidative stress in the presence of heavy metals by both fungi (Berthelot et al., 2018).

4.3. Antagonists and inducers of plant defense responses against pathogens and pests

Both MF and EFF are widely used scientifically and commercially as BCAs in agriculture against pathogens and pests (Poveda et al., 2020; Poveda and Baptista, 2021). In addition, both fungal groups can be used in combination, reporting significant increases in their controlling capacity, which studies are compiled in Table 3.

4.3.1. MF-EFF inoculum against viruses

Viruses represent one of the main causes of plant diseases, assuming an estimated global economic impact up to \$30 billion annually (Jones and Naidu, 2019). In cucumber plants, it was reported that root inoculation with MF *G. mosseae* was not capable of reducing the incidence of the disease caused by Cucumber Mosaic Virus. However, co-inoculation with *Fusarium equiseti* resulted in a significant reduction of the disease, as a consequence of a systemic induction of SA-related defenses (Elsharkawy et al., 2012).

4.3.2. MF-EFF inoculum against bacteria

Bacteria represent a group of very important plant pathogens in agriculture, as they can cause significant losses, up to the entire crop (Álvarez and Biosca, 2017). MF-EFF co-inoculation has increased control of important soil bacteria compared to the isolated use of each fungus. In potato plants, MF-*Epicoccum nigrum* co-inoculation significantly reduced the incidence of blackleg disease caused by *Pectobacterium carotovora* subsp. *atrosepticum*, due to a root induction of plant defenses. These included a broad defensive battery, such as the accumulation of phenolic compounds and increased activity of defense-related enzymes superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione peroxidase (GPX) (Bagy et al., 2019). This same root defense induction response has been reported in tobacco plants inoculated with *G. mosseae* and *T. harzianum*, increasing the activity of polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) and peroxidase (POD). However, against the bacterium *Ralstonia solanacearum*, this fungal combination was also able to control the disease, 40% more than fungi alone, through an increase in root colonization by *G. mosseae* and a modifying the rhizospheric microbial community (Yuan et al., 2016).

4.3.3. MF-EFF inoculum against fungi

Plant pathogenic fungi represent the most dangerous group of microorganisms for global food stability, as they can seriously affect the most important crops globally (rice, wheat, maize, potatoes and soybean) and cause severe famine in almost 10% of the world population (Almeida et al., 2019). With regard to soil fungi, there are several studies

that describe a greater control of pathogens by MF-EFF co-inoculation than by isolated inoculations, without confirming the mechanism involved. For example, against *Fusarium oxysporum* in onion (f. sp. *cepae*) and melon (f. sp. *melonis*) with MF-*Trichoderma* co-inoculation (Martínez-Medina et al., 2011; Rajeswari et al., 2019). Although the mechanism possibly involved is an increase in root colonization by MF, since with *G. mosseae* neither increased colonization nor disease control was observed (Martínez-Medina et al., 2009), also in banana plants (Castillo et al., 2019). However, with *Penicillium simplicissimum* and *T. harzianum* in cucumber plants, co-inoculation with *G. mosseae* did report an increase in root colonization and control of the pathogen *Rhizoctonia solani* (Chandanie et al., 2009); existing, therefore, a specificity in all the variables involved in co-inoculation.

Other mechanisms of action described against soil fungi include the combination of direct antagonism by EFF and local activation of plant defenses by both beneficial fungi. In cumint plants, the co-inoculation MF-*T. viride* minimized *F. oxysporum* f. sp. *cumini* incidence and increased plant survival percentages, same as commercial chemical fungicides. This was a consequence of a direct antagonism by *T. viride* against the pathogen and the induction of root defenses, including the accumulation of phenolic compounds and the increase in POD and PPO enzymatic activity (Ghoneem et al., 2019). Similarly, the co-inoculation *G. intraradices*-*Penicillium pinophilum* in tomato plants reduced the incidence of the pathogen *Verticillium dahliae* through direct antagonism of EFF and increased root SOD activity (Ibiang et al., 2021). Although there may be no direct antagonism action, as in the co-inoculation MF-*T. harzianum* in bean plants, where a reduction of up to 90% in the incidence of *Fusarium solani* was achieved through the activation of root defenses (PPO activity) (Eke et al., 2019).

As far as aerial fungal pathogens, there are also studies where the mechanism of action of MF-EFF co-inoculation in disease control is not known. This is the case of anthracnose caused by *Colletotrichum orbiculare* in cucumber plants, being controlled by co-inoculation *G. mosseae*-*Fusarium equiseti* (Saldajeno and Hyakumachi, 2011). However, there are several studies where the main mechanism of action has been described as the induction of systemic resistance in the host plant. For example, in wheat plants co-inoculated with MF-*Trichoderma* against the pathogen *Puccinia graminis* f. sp. *tritici*, significantly reducing the severity of the disease by inducing systemic accumulation phenolic compounds and POD and PPO activity (El-Sharkawy et al., 2018). Or on ryegrass plants co-inoculated with *Claroideoglyphus etunicatum* and *Epichloë* sp. against *Bipolaris sorokiniana*, reporting higher POD, SOD, CAT and β -1,3-glucanase plant systemic activity, and lignin accumulation, JA-mediated (Li et al., 2018; Guo et al., 2019).

4.3.4. MF-EFF inoculum against nematodes

Plant-parasitic nematodes cause more than 20% of total global losses in horticultural crops (Kumar et al., 2020). With the MF-EFF co-inoculation, it has been possible to significantly reduce the attack of nematodes on crops, compared to isolated fungal inoculations. The mechanism of action involved is an increase in root colonization by MF, which leads to competition for root space and nematode penetration sites. For example, in sugarcane plants co-inoculated with *Rhizoglyphus fasciculatum* and *Arthrobotrys oligospora* against the root-damaging nematode *Pratylenchus zaei* (Sankaranarayanan and Hari, 2021). However, there are several studies where MF-EFF co-inoculation is not effective against plant-parasitic nematodes, mainly gall-forming nematodes (*Meloidogyne* sp.) (Diedhiou et al., 2003; Ban et al., 2004).

4.3.5. MF-EFF inoculum against herbivores

Regarding herbivores, they negatively affect the combined presence of MF-EFF in the plant, since the host selectively favors root colonization by MF and reduces that of EFF (Ruotsalainen and Eskelinen, 2011). Despite of this, MF-EFF co-inoculation reduces the attack and damage of different herbivorous insects on crops. The endophytic and entomopathogenic fungus *Beauveria bassiana* is capable of colonizing the roots of

Table 3

Biocontrol effects in crops by co-inoculations with mycorrhizal fungi (MF) and endophytic filamentous fungi (EFF).

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	PATHOGENS/PESTS	EFFECTS	MECHANISMS OF ACTION	REFERENCE
<i>Claroideoglossum etunicatum</i> (= <i>Glomus etunicatum</i>)	<i>Paecilomyces lilacinus</i>	In greenhouse	Tomato	Nematode: <i>Meloidogyne incognita</i>	Reduced gall index	Unidentified	Udo et al., 2013
	<i>Epichloë festucae</i> var. <i>lolii</i>	In greenhouse	Ryegrass	Fungus: <i>Bipolaris sorokiniana</i>	Reduced disease incidence	Induction of systemic plant defenses	Li et al., 2018
	<i>Epichloë</i> sp.	In greenhouse	Ryegrass	Fungus: <i>B. sorokiniana</i>	Reduced disease incidence	Induction of systemic plant defenses	Guo et al., 2019
<i>Funneliformis geosporum</i> (= <i>Glomus geosporum</i>)	<i>Epicoccum nigrum</i>	In greenhouse	Potato	Bacteria: <i>Pectobacterium carotovora</i> subsp. <i>atrosepticum</i>	Reduced disease incidence	Induction of local plant defenses	Bagy et al., 2019
<i>Gigaspora gigantea</i>	<i>Trichoderma harzianum</i>	In greenhouse	Wheat	Fungus: <i>Puccinia graminis</i> f. sp. <i>tritici</i>	Reduced disease severity	Induction of systemic plant defenses	El-Sharkawy et al., 2018
	<i>T. viride</i>	In greenhouse	Wheat	Fungus: <i>Puccinia graminis</i> f. sp. <i>tritici</i>	Reduced disease severity	Induction of systemic plant defenses	El-Sharkawy et al., 2018
<i>G. margarita</i>	<i>T. harzianum</i>	In greenhouse	Bean	Fungus: <i>Fusarium solani</i>	Reduced disease incidence	Induction of local plant defenses	Eke et al., 2019
	<i>T. viride</i>	In greenhouse	Bean	Fungus: <i>Fusarium solani</i>	Reduced disease incidence	Induction of local plant defenses	Eke et al., 2019
<i>Glomus aggregatum</i>	<i>T. viride</i>	In greenhouse In field	Cumin	Fungus: <i>F. oxysporum</i> f. sp. <i>cumini</i>	Reduced disease incidence	Direct antagonism (<i>T. viride</i>) Induction of local plant defenses	Ghoneem et al., 2019
<i>G. caesaris</i>	<i>E. nigrum</i>	In greenhouse	Potato	Bacteria: <i>Pectobacterium carotovora</i> subsp. <i>atrosepticum</i>	Reduced disease incidence	Induction of local plant defenses	Bagy et al., 2019
<i>G. claroideum</i>	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>Fusarium oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Increased MF colonization	Martínez-Medina et al., 2009
	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Unidentified	Martínez-Medina et al., 2011
<i>G. constrictum</i> (= <i>Funneliformis constrictus</i>)	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Increased MF colonization	Martínez-Medina et al., 2009
	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Unidentified	Martínez-Medina et al., 2011
<i>G. deserticola</i> (= <i>Septoglossum deserticola</i>)	<i>P. lilacinus</i>	In greenhouse	Tomato	Nematode: <i>M. incognita</i>	Reduced gall index	Unidentified	Udo et al., 2013
<i>G. fasciculatum</i> (= <i>Rhizoglossum fasciculatum</i>)	<i>T. viride</i>	In greenhouse In field	Onion	Fungus: <i>F. oxysporum</i> f. sp. <i>cepae</i>	Reduced disease incidence	Unidentified	Rajeswari et al., 2019
	<i>Arthrobotrys oligospora</i>	In greenhouse	Sugarcane	Nematode: <i>Pratylenchus zeae</i>	Reduced nematode populations	Increased MF colonization	Sankaranarayanan and Hari, 2021
<i>G. hoi</i>	<i>T. harzianum</i>	In greenhouse	Bean	Fungus: <i>F. solani</i>	Reduced disease incidence	Induction of local plant defenses	Eke et al., 2019
<i>G. mosseae</i> (= <i>Funneliformis mosseae</i>)	<i>Penicillium simplicissimum</i>	In growth chamber	Cucumber	Fungus: <i>Rhizoctonia solani</i>	Reduced disease incidence	Increased MF colonization	Chandanie et al., 2009
	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Unidentified	Martínez-Medina et al., 2011
	<i>Fusarium equiseti</i>	In growth chamber	Cucumber	Fungi: <i>Colletotrichum orbiculare</i>	Reduced disease incidence	Unidentified	Saldajeno and Hyakumachi, 2011
	<i>F. equiseti</i>	In growth chamber	Cucumber	Virus: Cucumber Mosaic Virus	Reduced disease severity	Induction of systemic plant defenses	Elsharkawy et al., 2012
	<i>P. lilacinus</i>	In greenhouse	Tomato	Nematode: <i>M. incognita</i>	Reduced gall index	Unidentified	Udo et al., 2013
	<i>T. harzianum</i>	In greenhouse	Tobacco	Bacteria: <i>Ralstonia solanacearum</i>	Reduced disease incidence	Increased MF colonization Modified rhizospheric microbial community Induction of local plant defenses	Yuan et al., 2016
	<i>T. harzianum</i>	In greenhouse	Wheat	Fungus: <i>Puccinia graminis</i> f. sp. <i>tritici</i>	Reduced disease severity	Induction of systemic plant defenses	El-Sharkawy et al., 2018
	<i>T. viride</i>	In greenhouse	Cumin	Fungus: <i>F. oxysporum</i> f. sp. <i>cumini</i>	Reduced disease incidence	Direct antagonism (<i>T. viride</i>) Induction of local plant defenses	Ghoneem et al., 2019
	<i>T. viride</i>	In greenhouse In field	Onion	Fungus: <i>F. oxysporum</i> f. sp. <i>cepae</i>	Reduced disease incidence	Unidentified	Rajeswari et al., 2019
<i>G. versiforme</i> (= <i>Diversispora versiformis</i>)	<i>T. harzianum</i>	In greenhouse	Cowpea	Fungus: <i>Erysiphe flexuosa</i>	Reduced disease incidence and severity	Induction of systemic plant defenses	Omomowo et al., 2018

(continued on next page)

Table 3 (continued)

MF SPECIES	EFF SPECIES	EXPERIMENT	CROP	PATHOGENS/PESTS	EFFECTS	MECHANISMS OF ACTION	REFERENCE
<i>Rhizoglyphus clarum</i> (= <i>Rhizophagus clarum</i> / <i>clarus</i>) (= <i>Glomus clarum/clarus</i>)	<i>T. harzianum</i>	In greenhouse	Wheat	Fungus: <i>Puccinia graminis</i> f. sp. <i>tritici</i>	Reduced disease severity	Induction of systemic plant defenses	El-Sharkawy et al., 2018
	<i>T. viride</i>	In greenhouse	Potato	Bacteria: <i>Pectobacterium carotovora</i> subsp. <i>atrosepticum</i>	Reduced disease incidence	Induction of local plant defenses	Bagy et al., 2019
	<i>T. viride</i>	In greenhouse In field	Cumin	Fungus: <i>F. oxysporum</i> f. sp. <i>cumini</i>	Reduced disease incidence	Direct antagonism (<i>T. viride</i>) Induction of local plant defenses	Ghoneem et al., 2019
<i>Rhizophagus intraradices</i> (= <i>Glomus intraradices</i>) (= <i>Rhizoglyphus intraradices</i>)	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Increased MF colonization	Martínez-Medina et al., 2009
	<i>T. harzianum</i>	In greenhouse	Melon	Fungus: <i>F. oxysporum</i> f.sp. <i>melonis</i>	Reduced disease incidence	Unidentified	Martínez-Medina et al., 2011
	<i>Beauveria bassiana</i>	In greenhouse	Tomato	Insect: <i>Spodoptera exigua</i>	Reduced larvae feed	Induction of systemic plant defenses	Shrivastava et al., 2015
Unidentified	<i>Penicillium pinophilum</i>	In greenhouse	Tomato	Fungus: <i>Verticillium dahliae</i>	Reduced disease incidence	Direct antagonism (<i>P. pinophilum</i>) Induction of local plant defenses	Ibiang et al., 2021
	<i>R. irregularis</i> (= <i>Glomus irregularis</i>) (= <i>Rhizoglyphus irregularis</i>)	<i>T. harzianum</i> <i>T. viride</i>	In greenhouse	Wheat	Fungus: <i>Puccinia graminis</i> f. sp. <i>tritici</i>	Reduced disease severity	Induction of systemic plant defenses
<i>Scutellospora gigantea</i>	<i>T. harzianum</i>	In greenhouse	Bean	Fungus: <i>F. solani</i>	Reduced disease incidence	Induction of local plant defenses	Eke et al., 2019
<i>S. persica</i> (= <i>Gigaspora persica</i>)	<i>E. nigrum</i>	In greenhouse	Potato	Bacteria: <i>Pectobacterium carotovora</i> subsp. <i>atrosepticum</i>	Reduced disease incidence	Induction of local plant defenses	Bagy et al., 2019
Unidentified	<i>Beauveria bassiana</i>	In greenhouse	Maize	Insect: <i>Phyllophaga vetula</i>	Reduction of the damaging effect of the pest	Increased nutritional content in systemic plant tissues	Zitlalpopoca-Hernandez et al., 2017

crops together with different MF, reducing the damage caused by insects, such as *Spodoptera exigua* in tomato or *Phyllophaga vetula* in corn. This is due to the induction of systemic plant defenses, causing the accumulation of toxic and repellent compounds for insects in plant tissues, such as monoterpenes and sesquiterpenes (Shrivastava et al., 2015; Zitlalpopoca-Hernandez et al., 2017). On the other hand, in the absence of root EFF, an increase in the populations and activity of foliar endophytic fungi has been reported as a mechanism of action of MF against herbivorous insects in their host plants (Vicari et al., 2002; Razak and Gange, 2021).

5. Description of molecular aspects of the mechanisms underlying the responses of plants inoculated with MF-EFF

It is well established that fungal co-inoculation can be beneficial to the host plant. However, the mechanisms underlying these benefits remain uncertain in many cases. This is due to the complexity of the interactions between the host plant and the microorganisms, taking into account that many other factors, such as climatic conditions or soil, also play a role (Ibiang et al., 2020). In this review, the mechanisms of action responsible for the benefit in MF-EFF co-inoculations have been listed (Tables 1, 2 and 3). In the effect of promoting plant growth and stress tolerance, the benefit was due to increased MF colonization in 40–35% of the cited articles. While biological control was mainly explained by the induction of defenses at local or systemic level (52%). It is worth noting that 30% of the cases cited in table 1 were due to the fact that the MF-EFF association increased the supply (18%), content (3%) or solubilization (10%) of P. If other nutrients are taken into account, this figure rises to 40%. A similar picture is repeated in table 2 under abiotic stress conditions. Other mechanisms, such as increased EFF colonization or siderophore formation, were also relevant in the case of growth enhancement. In the following, we will elaborate on these mechanisms.

5.1. Promotion of plant growth and increase of yield

EFF-MF association increases growth parameters in several ways. The extracellular hyphae increase absorptive surface area of the root, which allows a greater uptake of water and nutrients because the mycorrhizal hyphae penetrate into soil pores inaccessible to the plant. In parallel, certain EFFs, such as *Trichoderma* sp. secrete auxin-like compounds that elongate the root, enhancing this effect. On the other hand, the secretion of certain enzymes such as acid, neutral or alkaline phosphatase in this microenvironment can increase phosphatase activity, often resulting in an increase in soil available phosphorus (SAP) (Cheng et al., 2022). Increased access to P and other nutrients (N, Ca, K, Zn...) allows an increase in leaf area, resulting in a higher number of stomata. In addition, an increase in phosphorus uptake is related to an increase in chlorophyll concentration, resulting in a higher photosynthetic rate (Yadav et al., 2015).

Increased nutrient uptake may be related to higher crop quality. Co-inoculation with the AMF *Diversispora spurca* and the EFF *Piriformospora indica* increased fruit sugar content. This could be due to an interaction between *P. indica*, which has been shown to increase sugar content, and colonization by *D. spurca* and the latter's ability to increase chlorophyll level and photosynthetic rate (Cheng et al., 2022). It should be noted that mycorrhizae often need carbon supply from the host, in the form of sugars, so they must compensate for this disadvantage. Co-inoculation therefore makes this AMF-host relationship even more desirable.

Finally, it is worth mentioning that, although not a growth-promoting mechanism *per se*, mycorrhizal fungi can improve soil quality, which can improve plant performance in the short and long term. This is because mycorrhizae generate water stable aggregates (WSA), which is directly correlated with increased soil aggregate stability and soil quality. In addition, MF release organic acids and glomalin-related soil proteins (GRSP) that increase the amount of soil organic carbon (Cheng et al., 2022).

5.2. Induction of abiotic stress tolerance

Some of the molecular mechanisms of abiotic stress tolerance coincide with those mentioned above. Improved nutrition, vigor, increased access to water or secretion of certain hormones also increase yield under salinity or drought conditions (Waqas et al., 2012). In addition, the increase of soluble sugars (fructose, glucose, sugar alcohols) or osmoprotectants (proline, glutamic acid) produced by some endophytic fungi in co-inoculation with MF can increase plant turgor and photosynthetic efficiency. This mechanism was observed by Li et al., (2019), on perennial ryegrass co-inoculated with *Claroideoglossum etunicatum* and *Epichloë* and by Xu et al., (2020) in peanuts inoculated with *Gigaspora margarita* and *Phomopsis liquidambaris*.

One of the most effective mechanisms for increasing yield under stress conditions is to increase the chlorophyll content. Total chlorophyll content is reduced under these conditions. However, the co-inoculation of certain fungi, such as *G. mosseae* and *P. indica* can lead to increased levels of photosynthesis, compared to plants under the same conditions, but without inoculation. This may be because the fungi reduce photo-inhibition and photodestruction and increase chlorophyll synthesis (Yaghoobian et al., 2014).

In addition to reduced photosynthesis, another important damage of drought is lipid peroxidation, increased reactive oxygen species (ROS) and hydrogen peroxide (H₂O₂). Co-inoculation with certain fungi can lead to the induction or synthesis of enzymes with antioxidant function, which reduce ROS and H₂O₂ concentrations, such as POD, SOD and CAT, thus preventing lipid peroxidation (Farooq et al., 2009). Yaghoobian et al., (2014) showed that co-inoculation with *G. mosseae* and *P. indica* increased antioxidant enzymatic activity and reduced lipid peroxidation.

5.3. Biocontrol effect

The most important mechanism to induce biocontrol is the capacity of MF and EFF to activate pattern-triggered immunity (PTI). Phytohormones are key in this modulation and the levels of salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are key to adjust the precision of the response (Latz et al., 2018). This response has morphological and physiological consequences in plant cells such as callose deposition, stomatal closure, the induction of ethylene, the production and accumulation of ROS and antimicrobial secondary metabolites that helps the plant to survive to the attacks of pathogens. El-Sharkawy et al., (2018) shows how *Trichoderma* spp. have been reported as plant resistance inducers releasing elicitors that enhance signaling agents such as SA and triggering defense-related responses in co-inoculation with a group of MF (*Rhizophagus irregularis*, *Funneliformis mosseae*, *Rhizoglossum clarum*, *Gigaspora margarita* and *G. gigantea*).

Another mechanism is related to the antibiosis capacity of fungi. Fungi can synthesise defensive compounds (alkaloids, flavonoids, peptides, phenols, quinones, steroids, terpenoids, polyketides and volatile organic compounds) that inhibit the growth of certain plant pathogens. Ghoneem et al., (2019) shows how *Trichoderma* spp prevents the germination of spores of *Fusarium oxysporum* f. sp. *cumini* because it secretes certain volatile components. In turn, when co-inoculated with *G. mosseae*, *G. clarum* and *G. aggregatum* gives a response by induction of local plant defences.

Mycoparasitism is the main mechanism of action of *Trichoderma* spp. that penetrates pathogen cells by producing enzymes that degrade the cell wall and other compounds (Romero-Contreras et al., 2019). Finally, it is worth mentioning that, although this strategy is often weak, competition for space and nutrients can be a mechanism to prevent the establishment and proliferation of some pathogens. MF-EFF can prioritise establishment, deplete or sequester nutrients that prevent pathogens from colonising the plant.

6. Types and formulation of bioinoculants based on MF, EFF and MF-EFF.

6.1. What are bioinoculants?

An agricultural bioinoculant is a product whose use improves the yield of a given crop under optimal conditions or under biotic or abiotic stress. It is made up of a component of biological origin and a carrier, which allows its correct maintenance, distribution, application and addition. In general, the material must be non-toxic to microorganisms, plants, animals and the environment. In this case we will focus on those bioinoculants formed by one or several types of microorganisms (microbial consortium). It is essential that the bioinoculants developed be inexpensive, easy to apply, easy to handle and maintain their effectiveness throughout their useful life, which should be as long as possible.

6.2. What conditions its formulation?

The formulation should be chosen according to the needs of the microorganisms that form the bioinoculant, the needs of the crops in which they are to be applied and their commercial use. If the bioinoculants are biostimulants the formulation will depend mainly on the crop needs or soil properties while if they are BCA, the formulation will depend on the organism to be controlled, target specificity, effect on the non-target organism and human and environmental health (Thakur et al., 2020).

Regardless of its function, the mode of application will also have an influence. It can be applied to the seed, to the growing medium when the plant is still young, to the root or directly to the soil. One of the most effective methods is seed coating (Rocha et al., 2019). In this way, the inoculum concentration is uniform and easily controlled and treated seed can be acquired. Other formulations impede the control of application, e.g. those in powder or granules, directly in the soil or applied to the root (Nevalainen, 2021). Under these premises, solid, liquid or encapsulated products are generated. Solids are usually found in the form of granules, wettable powders, dusts, etc. while liquids in the form of suspensions and oily dispersions (Mishra and Arora, 2016). In the past it was common to find biostimulants in the form of peat, but their use is currently being reduced due to the high environmental impact it generates (Santos et al., 2019).

6.3. EFF, MF and MF-EFF formulations

MF inocula must be grown and formulated in a plant host. The main components or mycorrhizal products are fungal propagules constituted with fragments of colonised roots, fungal mycelium and spores. In contrast, EFF inocula can be generated independently and usually consist of hyphae and/or spores that may or may not be associated with the culture medium. MF-EFF combinations are therefore usually made after culture to form a compound inoculum (Vassilev et al., 2015).

In the case of co-inoculations with MF-EFF the co-immobilization of inocula in a matrix can increase the metabolic activity of both microorganisms and provide them with a microenvironment that reduces their susceptibility to biotic and abiotic stresses (Vassilev et al., 2015). Although they can be combined in solid or liquid products, the most common form of co-inoculation in a matrix is in the form of alginate beads. De Jaeger et al., (2011) demonstrated that co-immobilization of the AMF *Glomus* spp. and the EFF *T. harzianum* on alginate beads was possible. Subsequently, its scalability and validity in the field has been tested by studying how the administration of *T. harzianum* and *G. irregulare* co-immobilized on alginate beads increases potato yield (Buysens et al., 2016). However, it should be noted that compatibility testing is necessary, as a certain level of mycoparasitism may occur (De Jaeger et al., 2010).

Alginate is the most widely used biopolymer because it is safe and

versatile, capable of encapsulating different types of microorganisms, satisfying their needs for nutrients and oxygen. In addition, it favors the adhesion and colonization of microorganisms, promoting the formation of biofilms. However, this medium has limitations mainly due to its high sensitivity to chelating compounds. For this reason, additives are added to increase encapsulation efficiency. They are usually minerals, organic materials, polymers or osmoprotectants (kaolin, peat, gelatin, carbohydrates, amino acids...). In general, they improve the mechanical properties of the hydrogel, reduce the manufacturing cost, provide nutrients to the microorganisms or increase their survival during storage or subsequent treatments such as freeze-drying (Szopa et al., 2022).

7. Limitations in the use of EFF-MF bioinoculants in agriculture

7.1. Ineffective or harmful combinations

Bioinoculants can present detrimental performance. EFF, MF or combination of microorganisms can reduce the yield of the plant under optimal or stressful conditions. There are several studies where MF-EFF fungal combination did not have superior results to isolated inoculations (Kumar et al., 2018; Mack and Rudgers, 2008; Martínez-Medina et al., 2011), and even had negative effects on plant growth. The results obtained by Rillig et al., (2014) show that MF competes with EFF and can reduce root colonization by the latter. On the other hand, Martínez et al., (2004) demonstrated that the exudates and volatile compounds of some strains of *Trichoderma pseudokoningii* prevented the germination of spores from *G. mosseae* and *Gigaspora rosea*. In some crops, this resulted in a reduction in root length and dry matter. Nadeem et al., (2014) pointed out that fungal-bacterial interaction could also reduce crop yield. The presence of non-pathogenic bacteria could enhance fungal pathogenity. On the other hand PGPR associated with AM fungi that under optimal conditions promoted the growth of fungi (Kohler et al., 2010) or control pathogens (Tahmatsidou et al., 2006) were ineffective under stress conditions.

7.2. Inconsistency in the efficacy of commercial products and how to tackle it

Lack of efficacy or damage may be due to the characteristics of the host plant, the characteristics of the inoculated microorganisms themselves, soil conditions and soil management (Hoeksema et al., 2010). Under stress conditions, a change in root exudates may occur that modifies the plant-microorganism relationship (Nadeem et al., 2014). In addition, we must take into account the low efficiency in the application and establishment of the microorganisms on the host plant. During application, the right conditions of temperature, humidity, radiation or fertilization must be present so that the microorganisms can establish themselves on the plants (Lucy et al., 2004; Hoeksema et al., 2010; Babalola and Glick, 2012). It has been shown that all of these factors can negatively influence the establishment and usefulness of bioinocula. Therefore, it is currently unknown how effective many of the commercial products are under field conditions and inconsistency in field performance is reported (Pirttilä et al., 2021). The results of efficacy tests are varied and contradictory; the viability of a commercial inoculum may even depend on the batch tested (Owen et al., 2015). In commercial tests of MF inocula conducted by Faye et al., (2013) and Salomon et al., (2022) 80% of the products lacked viability and ability to colonize the plant and only 16–40% demonstrated the ability to promote growth.

To overcome these limitations, product formulation is essential. In addition to establishing adequate carriers and additives, a sufficient number of propagules must remain viable and active after processing, storage and distribution. The drying or freeze-drying process of the microorganisms can be properly performed as many microorganisms lose viability and not all of them can be subjected to this process. An alternative can be the use of liquid products as the shelf life is usually longer and they are easier to produce and scale up. However, they tend

to be less efficiently established (Silverstein et al., 2023). Therefore, to correct these limitations we should: (a) have clear and detailed labelling of the commercial bioinoculant with information on its production method, expiration dates and instructions for its application in different soils; (b) include enough amounts of viable microorganisms that can ensure a successful and quick association with the host plant; (c) be supported by greenhouse and field assays that certificate its beneficial effect. However, there is still a need for standardized quality control of bioinoculants and further tracing on their establishment and performance under field conditions (Salomon et al., 2022).

In addition to environmental conditions, it is important to note that the inoculum must be established in a previous microbial community. Under laboratory conditions, many experiments are done with autoclaved peat. However, in the field, the inoculum must compete with a pre-established community of microorganisms (Shrivastava et al., 2021). To increase the possibilities of establishment and maintenance of the inoculum we must take into account whether we inoculate with one or more microorganisms and how these combinations of microorganisms are designed. When the inoculum is composed of a community of metabolically interconnected microorganisms with a preference for the niche where they will establish, it is more likely that the inoculum will be maintained. Top-down designs in which an existing community is cultivated under selective conditions allow the generation of communities of microorganisms with a higher probability of success (Silverstein et al., 2023).

Finally, we should point out that bioinoculants can produce sensitizing effects or allergies when the concentration of these products, usually in the processing, is very high (Elnahal et al., 2022). In addition, the pathogenicity of the microorganisms must be studied, since several strains such as *Enterobacter* spp., *Burkholderia* spp. or *Pseudomonas* spp. have shown interesting characteristics as inoculants but may be related to human pathogens (Santos et al., 2019).

8. Conclusions and future perspectives

There is a solid bibliography demonstrating the efficacy of the use of EFF and MF in agriculture, whether they are applied individually, in combination (EFF-MF) or in formulations with other microorganisms (*Rhizobium*, *Azospirillum*, *Azotobacter*...). These inoculants can promote plant growth, increase yield and crop quality, increase tolerance to abiotic stresses or protect against pathogens, such as viruses, bacteria, fungi, nematodes and herbivores.

Integrated agriculture management is already being considered in Europe for all crops. However, Europe lags far behind in the market for BCA and biostimulants compared to other world regions, such as the North America (Köhl et al., 2019; Elnahal et al., 2022), and there is not yet a wide range of products developed and marketed based on this technology (Kowalska et al., 2020; Umesha et al., 2018). This may be because the European regulation requires process of registration and testing that can be long and costly. BCA takes 3–6 years and about USD 8 million to reach the market, while a biostimulant would take 1–2 years and about USD 1.8 million (Harman et al., 2010). Therefore, European regulations are expected to evolve or move towards more sustainable treatments (Kowalska et al., 2020). However, it is not only legislation that is holding back the development of these bioinoculants. Technical issues need to be resolved for EFF-MF biofertilizers to become widespread on the European market. Furthermore, our bibliographic compilation has reported that there are very few studies developed in trees and in the forestry sector, being a field of research with great potential.

Among the technical problems encountered, price is one of the main ones. The production and formulation of these microbial bioinoculants must become cheaper. There is a bottleneck in the development of fermenters, culture media and carriers. On the other hand, the stability of the product has to be ensured, as its efficacy is highly variable under field conditions (Mari et al., 2014). This may be because the effect of

BCA and biostimulants depends on the degree of colonization of the roots by the microorganism, its ability to displace the existing microbiota to establish itself or the environmental conditions at the time of product application. Very low temperatures, lack of moisture and high ultraviolet radiation can compromise the efficacy of the product (Babalola and Glick, 2012). Therefore, it is of utmost importance to study plant-microorganism, micro-organism-microorganism and microorganism-environment interactions in the agricultural context in order to develop appropriate formulations. Small changes in the formulation, the timing of application or the introduction of auxiliary microorganisms, which modulate the rhizosphere, can make the difference between a successful or unsuccessful bioinoculant.

Author contributions

JP proposed the review structure and content, and coordinated the work of all authors. MDU and JP wrote the first version. NG and PV contributed to the manuscript correction and critical reading, as well as to the knowledge on the mycorrhizal fungi and endophytic filamentous fungi field, respectively. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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