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Abstract

One of the most anticipated challenges in the field of agriculture is to ensure high production levels while limiting the use of environmentally harmful synthetic chemicals. One of the most interesting strategies to overcome this challenge is the exploitation of the interactions between soil microorganisms and plants which result in stimulating plants' natural activity. The interactions among mycorrhiza, growth-promoting microorganisms and plants play a crucial role in soil fertility, biocontrol and protection. The use of mixed microbial products can simulate interactions between fungi and bacteria, realising all the benefits that can be obtained from these associations in terms of quantity and quality of agri-cultural production and ensuring a significant reduction in the chemicals usually used in agriculture.

Keywords

Mycorrhizal fungi; Symbiotic microorganisms; Abiotic stress; Growth promoting microorganisms

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REVIEW ARTICLE

Role of Microorganisms in Horticulture to Improve Plant Quality

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Abstract

One of the most ongoing challenges in the field of agriculture is in terms of maintaining high production levels ensuring, at the same time, the reduction of environmentally harmful synthetic chemicals use. One of the most interesting strategies to overcome this challenge is the exploitation of the interactions between soil microorganisms and plants, which result in stimulating plants' natural activity. The interactions among mycorrhiza, growth-promoting microorganisms and plants play a crucial role in soil fertility, biocontrol and protection. The use of mixed microbial products can stimulate interactions between fungi and bacteria, obtaining all the benefits of these associations in terms of quantity and quality of agricultural production, promoting a significant reduction in the chemicals usually used in agriculture.

Keywords: Mycorrhizal fungi, Symbiotic microorganisms, Abiotic stress, Growth promoting microorganisms

1. Introduction

In recent years, research has acknowledged a significant environmental sensitivity that presupposes the reduction of agricultural practices that are harmful to the soil and plants (excess herbicides, monocultures, intensive cultivation). In the long run, such practices lead to a loss of soil fertility and biodiversity, reducing the sustainability of production [1]. The soil microbial community plays a fundamental role in maintaining the sustainability of fruit and vegetable production. Complex interactions happen between biotic and abiotic components in the rhizosphere. These are relevant in order to have chemical and physical changes in the soil structure that influence plant growth [2–4]. Microorganisms, in particular, regulate the biogeochemical cycles of soil mineral elements that are responsible for plants' physiological health status [5]. Interactions between plants and microorganisms take place in the rhizosphere, where bacteria and fungi can often create a real symbiosis, that is, a mutually beneficial relationship and interaction

between different organisms. Evolutionarily, symbiosis benefits both organisms and ensures better growth and survival of the species, promoting their spread and adaptation in the environment. In the biosphere, symbiosis is a widespread phenomenon that assumes great ecological significance when they involve plants and microorganisms [6,7]. Plants provide an alternative habitat to organic substrates and plant residues when microbial competition is high. Through symbioses, microorganisms fulfil their trophic needs by obtaining adequate nourishment and protection against competing microorganisms and environmental adversities [8]. The colonization of endophytes, localized or systemic, is inter- and intracellular, that often shows organ and tissue specificity based on adaptation to different physiological conditions in plants [9]. They may colonize various parts of the plant, such as only the leaves, the roots or the bark. Among the best-known endophytic microorganisms are mycorrhizal fungi and plant growth-promoting bacteria. In this paper, we describe the potential of using these microorganisms in agriculture, as well as their functions and

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their use in controlling biotic and abiotic stresses [10,11].

2. Mycorrhizal symbiosis and benefits in agriculture

Mycorrhizal fungi are an example of a mutualistic symbiosis between a fungus (symbiont) and a plant (host). In fact, in mutualistic symbioses, the endophyte receives trophic support from the plant and, in turn, benefits the plant in the form of improved uptake of mineral elements, ensuring better growth and excellent resistance to insects and telluric pathogens [12,13]. Likewise, the symbiont organisms receive physiological, nutritional and ecological benefits. Recent years have witnessed a growing interest in the symbiotic structures between fungal hyphae and plant roots, especially considering the benefits of nutrient uptake, improved soil quality and increased resistance to biotic and abiotic stresses [14,15]. About 95% of plants in nature have roots characterized by symbiosis or associated with mycorrhizal fungi. Depending on their structure and function, mycorrhizae can be classified into ectomycorrhizae and endomycorrhizae [16]. Ectomycorrhizae are a specific class of mycorrhizae belonging to the Ascomycetes and Basidiomycetes, characterized by their inability to penetrate host cells. The ectomycorrhizal fungus forms a mantle in the apical portion of the root, called a mycelial sheath or mantle. Hyphae develop from the mycelium, which penetrate the cells of the cortical parenchyma to form the Hartig reticulum, through which the exchange of sugars produced by the plant and water and mineral salts absorbed by the fungus takes place [17]. In conifers, the Hartig reticulum reaches the central cylinder, whereas, in broad-leaved trees, it only colonizes the cortical layer.

Under appropriate conditions, the hyphae of this network extend into the soil, leading to the production of reproductive structures called carpophores. This class of mycorrhizae is widespread mainly in the woody plants of temperate forests, while they are scarcely present in herbaceous species [18,19]. Due to their role in promoting agriculture, the most widespread mycorrhizae are the arbuscular mycorrhizae. Endomycorrhizae differ from ectomycorrhizae in their ability to interact with the plant's root cells, although they do not produce the outer fungal coat. Endomycorrhizae have been found in various fruit and vegetable species, as well as deciduous and coniferous trees [20]. In addition, these fungi have been found in desert areas or marine dunes. The plant releases chemotactic molecules such as strigolactones and cellular proteins

into the rhizosphere, which after being recognized by the fungi's membrane receptors, activates signal transduction processes, leading to spore germination with the production of the germinal tubule [21]. Through the signals released by the germinative tubule, the plant can detect the location of the fungus. The hyphae produce structures called vesicles, which accumulate lipids as a reserve source [22]. After colonizing a large part of the cell, the hypha begins to explore a volume of soil not accessible to plant roots. Although there are a large number of plant species involved in the colonization of arbuscular mycorrhizae, only a few fungal species establish this type of symbiotic interaction. The essential arbuscular mycorrhizae include *Glomus intraradices*, whose spores, abundant in the soil, are round in shape, yellow/brown and have a thick wall [23].

Mycorrhizal fungi are considered in reforestation projects, as they provide the trees they associate with (e.g. of the genus *Cistus*) with numerous benefits, such as an improved ability to absorb water and mineral elements (such as phosphorous and nitrogen). For example, *Pisolithus albus* has been demonstrated to enhance the growth of *Acacia spirorbis* and *Eucalyptus globulus*, leading to a significant increase in biomass and mineral nutrition (P, K and Ca), as well as a limited uptake of metals, acting as a protective barrier in nickel-rich soils [24]. Sousa et al. demonstrated that select mycorrhizal fungi could be used in horticulture, particularly *Pinus pinaster*, in order to reduce the use of chemical fertilisers [25]. A finalised study of eight pepper cultivars, sown in pots on substrate inoculated or non-inoculated with two arbuscular fungi (*Rhizophagus irregularis* and *Gigaspora margarita*) and grown in a growth chamber for nine weeks, showed that dry biomass was increased in the mycorrhized plants compared to the non-inoculated control [26]. On processing tomatoes grown in calcareous soil, the application of *Rhizoglyphus irregularis* at transplanting near the root system delayed plant senescence and increased root mycorrhization, growth, flowering, marketable yield and phosphorus content in the fruit [27]. An increase in growth and production was found in courgette and lettuce inoculated with *Rhizoglyphus irregularis* with positive effects on nutrient uptake (P, Fe, Mn, Zn and B) [28]; the same effects were observed in artichoke grown using seed coated with a mycorrhizal fungi inoculum [29]. A positive effect was also found on tomato and lettuce plants grown in 104-hole honeycomb containers in which *Rhizoglyphus irregularis* was inoculated with beneficial effects on seedling height, stem diameter and epigeal and hypogean biomass [30].

3. Plant growth-promoting microorganisms

Associative bacteria capable of enhancing plant growth, plant growth-promoting rhizobacteria (PGPR), have been described as a crucial microbial group in agronomy [31]. Characteristics of these bacteria related to plant growth are as follows: i) the synthesis of phytohormones such as auxins and cytokinins; ii) the production of chelating siderophores that promote the uptake of iron by plants; iii) the solubilization of mineral elements; iv) nitrogen-fixing activity; v) the production of antibiotics [32]. PGPRs include the genera *Azospirillum* spp., *Pseudomonas* spp. and *Burkholderia* spp., which have been studied for several years. These bacterial genera play a fundamental role in the adaptive physiology of plants, as they can interact with their host plants [26]. Some studies suggest that microbial biodiversity depends on the ability of soil bacteria to colonize the rhizosphere and plant tissues [33,34] effectively. The bacterial genera *Azospirillum* spp., *Burkholderia* spp., *Bacillus* spp. and *Pseudomonas* spp. can colonize not only at the root level but also in other plant tissues. Endophytic colonization is characterized by the ability to grow sexually through biofilm formation, developing various chemotactic and metabolic capacities [35]. Numerous studies show that plants can communicate simultaneously with the rhizospheric and mycorrhizospheric microbial community through a complex system of species- and strain-specific communication involving a highly specialized dialogue at the germplasm strain level [36–38].

In recent decades, bacteria have been demonstrated to be capable of communicating, and this is critical for their survival and competitiveness [39]. This results in outcomes as diverse as inhibiting competitors through cooperative behaviour that provides both individual and group benefits [40–42]. Communication between bacterial microbes is undoubtedly an important factor in root microbiome dynamics [40–42]. In order for bacteria to communicate, signal molecules must be synthesized and diffused and then perceived by the other members of the community. Signal molecules alter the physiology and activity of recipients by altering gene transcription after perception [40]. In order for bacterial functions to continue effectively,

communication is crucial to community coordination. The formation of biofilm, adhesion and motility [43] have also been demonstrated to be associated with signal molecule mediated communication [41], control of virulence associated factors [43], and propagation [40]. Population density is often correlated with the regulation of these aspects of bacterial behaviour. As a result of density-dependent stimuli and responses, this phenomenon is referred to as quorum sensing (QS) [40–44]. It has also been found that the beneficial plant growth-promoting effect exerted by these endophytic cell populations can be significantly more effective than their non-endophytic and rhizospheric counterparts, boosting plant physiology and adaptation to both biotic and abiotic environmental stressors (Table 1) [45].

4. Beneficial interactions between plants and microorganisms

The main benefit obtained by plants through microbial symbiosis is certainly related to the increase in surface area and root volume (Fig. 1), which improves interactions with the soil and enables greater plant stability in the soil [46,47]. From a physiological point of view, the main advantage is the increased transfer of mineral elements present in the soil to the plant, which is absorbed by microorganisms, mainly fungi, and passed on to the plants. The main mineral element generally absorbed in mycorrhizal symbioses is phosphorous, followed by nitrogen, zinc and copper. On the other hand, the plant provides the microorganisms with sugars and vitamins that enable them to produce spores in the soil [48]. Mycorrhizal fungi in the soil form aggregates of mineral particles that, through cementing by polysaccharides and organic compounds, including a protein called glomalin, form micro-aggregates that not only provide nutrient reserves but also facilitate soil stability by reducing erosion. Usually, rhizospheric microbial environments are colonized by many PGPRs, which perform an intense metabolic activity in the presence of organic matter, promoting plant growth and root development through different mechanisms such as phytohormone production and solubilization of soil nutrients [49]. Plants that facilitate a symbiotic relationship, particularly mycorrhizae,

Table 1. List of PGPRs capable of eliciting a response in plants as biotic elicitors.

PGPR	Plant	Metabolite induced
<i>Pseudomonas fluorescens</i>	<i>Catharanthus roseus</i> L.	Ajmalicine
<i>Pseudomonas putida</i>	<i>Hyoscyamus niger</i> L.	Hyoscyamine and Scopalamine
<i>Bacillus subtilis</i>	<i>Crocus sativus</i> L.	Picrocrocin, Crocetin and Safranal
<i>Bacillus cereus</i>	<i>Salvia miltiorrhiza</i>	Tanshinone

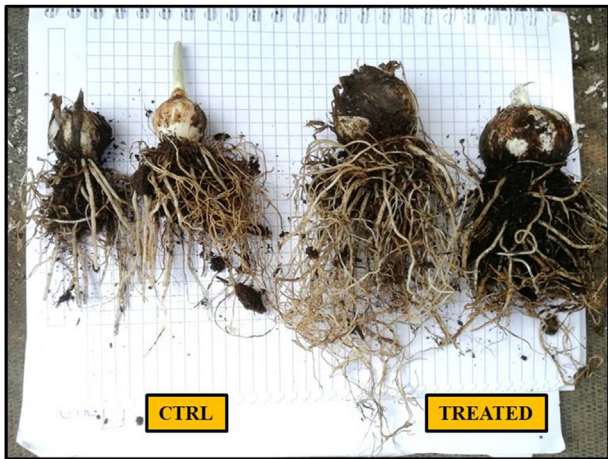


Fig. 1. Increased root growth of *Allium sativum* following microbial colonisation. The plant can thus explore a larger soil surface.

can transform organic phosphorous into inorganic phosphorous by releasing enzymes such as acid phosphatases into the soil, allowing immediate uptake [50]. While for nitrogen, many studies have shown that the release of various enzymes by microorganisms leads to an increase in the pool of readily available inorganic nitrogen from organic forms. PGPRs such as the rhizobia of leguminous plants and azospirilli favour the uptake of iron, nitrogen and phosphorous. Several studies demonstrate the ability of PGPRs to act as biofertilizers providing phosphate nutrition; plant root systems alone can influence phosphorus availability, but they are almost always also supported by the activity of growth-promoting bacteria such as *Bacillus* spp. and *Pseudomonas* spp. or *Rhizobium*, which have proven helpful in this respect [51,52]. Many PGPRs can enrich the soil with phosphorous, promoting the mineralization of inorganic phosphate through the production of phytase and phosphatase enzyme activities, enhancing solubilization through the production of organic acids such as those found in *Burkholderia* spp. The efficacy of PGPRs in increasing phosphate nutrition has been demonstrated in several trials on ornamental and vegetable plants [53]. The secretion of siderophores by certain microorganisms can be considered a fundamental phenotypic trait in favouring the plant's uptake of mineral nutrients and iron. Several bacteria and fungi have developed iron acquisition strategies through the secretion of molecules capable of forming complexes characterized by a strong affinity for Fe^{3+} ions. The diversity of siderophores, consisting of different classes of organic compounds, depends on the microorganism that can exclusively utilize and assimilate the iron–siderophore complex via a specialized receptor [54]. Metabolic activity

influenced by soil organic matter and carried out by plant growth-promoting microorganisms can contribute to intensifying nutrient mineralization and mobilization processes. The development of root systems is influenced by the presence of microorganisms; auxin hormones, which are responsible for root development, are a derivative of bacterial metabolism in soils with good organic matter content and root exudates [55]. The impact of this hormone on root development is essential. It is especially noticeable in poor-quality soils, where it can significantly increase root growth and mineral uptake, as found in various experiments on vegetable plants [56].

5. Role of microorganisms in increasing resistance to abiotic stresses

Another interesting use of symbiotic microorganisms is their ability to protect plants against specific abiotic stresses. Microbial symbioses positively affect plant growth under conditions of nutritional deficiency [57]. In addition, there is often an induction of tolerance to water and salt stresses that, in various environments, limits crop growth and survival when subjected to extreme drought situations. PGPRs constitute an important microbial group for plant stimulation, as they can enhance plant defences against stresses. Soil microorganisms are generally more resistant than plants to nutrient deficiencies, osmotic changes or salinity [58]. Thus, they can perform a protective role in helping plants under critical stress conditions. Microorganisms can provide different types of protection, which can be traced back to physiological-adaptive bacterial responses that include the following.

- metabolic production of osmoprotective compounds;
- production of hormones that act on the plant under stress by promoting root growth;
- production of antioxidants and bioactive molecules

For example, some bacteria ensure the development of lateral roots in cereals. Several PGPRs remain active even under high-stress conditions, providing nutritional support even when plants suffer from significant nutritional stress [59]. Adverse effects attributable to water stress are a reduction in photosynthetic activity due to stomatal closure and, consequently, reduced availability of carbon dioxide at the chloroplast level, resulting in reduced vegetative development, leaf senescence and unhealthy reproductive organs. The presence of

microorganisms, particularly mycorrhizae, increases tolerance to water stress due to an increase in the hydraulic conductivity of the roots, which allows water to be extracted from the soil under low-gradient conditions. Indeed, mycorrhizae can limit water stress by increasing the external water potential of the roots due to their ability to reach areas far away from the roots [60]. The water potential draws water inside the roots, which positively influences stomatal conductance, preventing the closure of guard cells and promoting gas exchange. Other factors influenced by mycorrhizal symbiosis in water stress tolerance are lack of tissue dehydration and good photosynthetic activity. From a metabolic point of view, mycorrhizae in plants induce carbohydrate accumulation and compartmentalization, suggesting a greater capacity for photosynthesis [61]. Root colonization by plant growth-promoting microorganisms can limit water stress in cereal, vegetable and ornamental plants by controlling ethylene levels and their growth-inhibiting activities [62]. In fact, several rhizobacteria are, producers of the enzyme ACC deaminase, which helps stressed plants by hindering ethylene synthesis. Microbial activity can reduce the rhizospheric concentration of ethylene in plant tissue. Another stress that can adversely affect plant growth is saline stress, as the absorption of toxic ions disturbs nutrient uptake [61]. Plants under these conditions suffer toxic, nutritional and osmotic damage, leading to a lack of vegetative growth, reduced gas exchange and photosynthetic activity. Microorganisms can increase resistance to salt stress, as depicted by the example of *Crassula Ovata* in Fig. 2, by limiting sodium ion uptake at the cellular level in favour of nutrients. The main



Fig. 2. Ability of microorganisms to increase plants' resistance to abiotic stresses. In this case, *Crassula Ovata* plants inoculated with *Glomus* spp. are more resistant to salt stress than non-inoculated plants.

advantage, therefore, is not the immediate increase in plant biomass but the uptake of mineral elements. Inoculations of *Glomus intraradices* on different crops under salt stress conditions showed less direct damage on treated plants than on non-inoculated plants [63].

The protective effect of microorganisms against salt toxicity is achieved through.

- production of exopolysaccharide matrices;
- production of osmolytes;
- biostimulation of root development;
- production of ACC deaminase

The production of exopolysaccharide matrices is accompanied by the development of biofilms that can bind toxic elements capable of entering the plant [64]. In bacteria, cellular adaptation to salt stress also occurs through the production of amino acids, sugars and osmolytes. Various studies also highlight the possibility that microorganisms can produce bioactive and biostimulant molecules like plant growth regulators, such as cadaverine in *Azospirillum* spp., which plays an essential role in regulating plant adaptation to salinity [65].

6. Soil bioremediation with microorganisms

Microorganisms, particularly mycorrhizae, can reduce plants' heavy metal uptake. In several experiments with mycorrhizae, both a reduction in copper uptake and an increase in antioxidant activity were observed in vegetable crops. Plants grown in soils polluted with heavy metals such as mercury adapted better when colonized in the root system by symbiotic microorganisms [66]. Endophytic strains can increase the mobility of heavy metals in the soil and promote phytoextraction by improving plant growth and biomass in polluted sites. Many microorganisms can bioaccumulate metals in the cell biomass by reducing their mobility in the plant–soil system. In contrast, others can enhance plant development without stimulating the uptake of heavy metals by plants. Several strains of growth-promoting microorganisms promote physiological adaptation in heavy metal-polluted soils without leading to the concomitant accumulation of toxic products in roots and leaves [56].

7. Use of microbial products in agriculture

Many experimental trials have reported the efficacy of the application of products based on several different microorganisms. As depicted in Fig. 3, microorganisms can be used to alleviate various situations resulting from biotic and abiotic stresses.

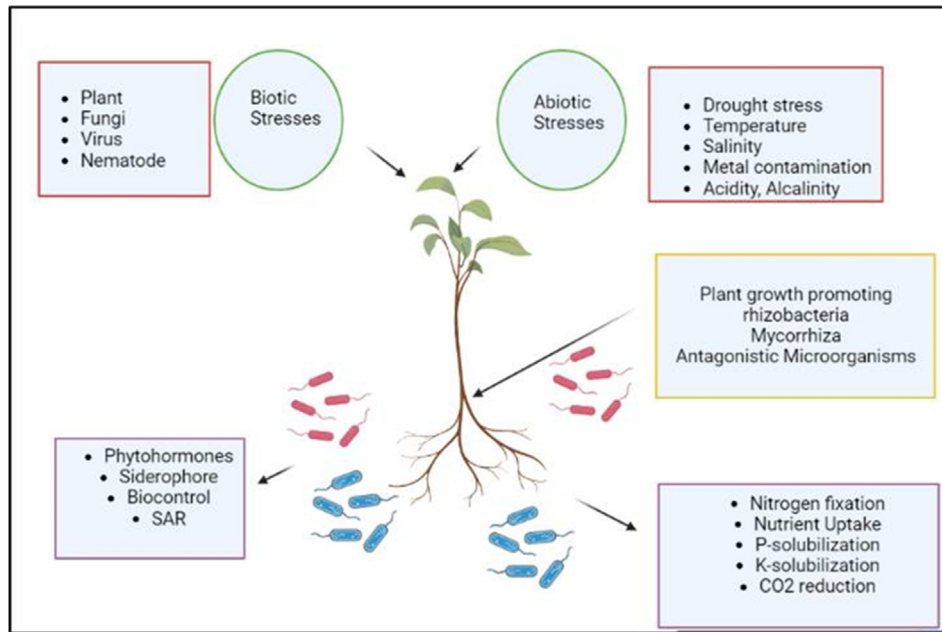


Fig. 3. Positive effects of the use of microorganisms on crops.

However, their compatibility and anti-microbial synergism must be verified at the level of the species and the plant to be treated [67,68]. Numerous works highlight the positive symbioses between *Glomus* spp. and *Rhizobium* or *Glomus* spp. and *Azotobacter* spp. and *Bacillus* spp. that have led to an increase in biomass and mineral content in the tissue. These symbioses appear suitable for open-field treatments [69]. Diverse applications of mycorrhizae and PGPR, particularly *Pseudomonas* spp. and *Bacillus* spp., have provided exciting results in the case of vegetable plants by increasing their antioxidant content. Mixed inoculants enhanced and ensured plant growth in cereals and vegetables despite water-stress conditions; further, mycorrhizae and growth-promoting bacteria resulted in increased yields and root growth. In many cases, bioprotective activity against severe salt stress was also evident when a combination of mycorrhizae and PGPR was used [70,71]. Mixed formulations can be applied in polluted soils to ensure control of plant uptake processes by reducing phytoextraction and accumulation in the edible part of leaves and fruits [72].

8. Conclusions

The application of microorganisms in soil or growing media fulfil the need for improved product quality and sustainable agro-system management. Mycorrhizae or plant growth-promoting microorganisms can enhance the ability of roots to absorb nutrients and increase plant defence, providing

innovations in crop defence and fertilization management. This is also critical for improving plants' tolerance phenomena related to different types of stress – water and salt – that cause significant losses annually. All these features make the optimization of microbiological potential can revolutionize conventional farming practices in favour of less impactful agriculture. Sustainability in agriculture will be promoted through careful management of microbial biodiversity, particularly with PGPRs, which can improve nutrient availability in plants and stimulate the growth of many vegetables, cereal and fruit plants. These are especially necessary in some conditions like water and salt stress or in polluted soils. Commercial products involving a mix of mycorrhizae and PGPR can act as biofertilizers, fortifying agents and phytostimulants, particularly helpful during the germination and rooting phases of plants. Combinations of mycorrhizae and PGPR can be a viable alternative to synthetic fertilizers and are widely used as biofertilizers.

Conflict of interest

The author declares no conflict of interest.

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