

Sustainable approaches in modern agriculture: The role of arbuscular mycorrhizal fungi



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Abstract An effective, practical, and sustainable nutritional crop supplementation strategy for crops is achievable through the application of biostimulants, which can also mitigate environmental issues associated with excessive fertilization. Plants benefit from biostimulants when their metabolism is increased, which leads to higher yields and improved quality crops; it protects plants from stress caused by water shortage, soil salinization, and suboptimal growth temperatures; and it promotes plant growth by increasing nutrient absorption. In addition, it enhances soil fertility by nurturing the development of complementary soil microbes, enhancing soil enzymatic and microbial activity, changing root architecture, enhancing micronutrient solubility and mobility, and changing root architecture. It is possible to categorize biostimulants as microbial, such as arbuscular mycorrhizae fungi (AMF), plant-growth-promoting rhizobacteria (PGPR), nonpathogenic fungi, protozoa, and nematodes, or nonmicrobial, such as seaweed extract, phosphite, humic acid, other inorganic salts, chitin and chitosan derivatives, protein hydrolysates, free amino acids, and complex organic materials. It is important for sustainable agriculture to cultivate better, healthier, and more functional foods with the help of arbuscular mycorrhizal fungi, which are among the best known microbial biostimulants. As a sustainable and environmentally friendly source of crop supplements, AMF helps plants acquire nutrients and water, improves plant stress tolerance for salinity, drought, and heavy metals, and reduces soil erosion. To better understand how biostimulants can be used in sustainable agriculture, further studies are needed. Several examples of how biostimulants can be used to produce various crops are presented in the current manuscript. This review presents examples of biostimulant applications in various crops and discusses the role of AMF in bridging yield gaps between organic and conventional farming by improving nutrient availability, uptake, and assimilation, thus addressing the nutrient limitations often found in organic systems.

Keywords: arbuscular mycorrhizal fungi, biostimulant, microbial biostimulants, mycorrhizal fungi, sustainable agriculture

1. Introduction

In addition to being environmentally friendly and novel, biostimulant farming can also be applied to two otherwise contrasting concepts: crop sustainability and intensification (Sun & Shahrajabian, 2023). Over the years and in the future, biostimulant products have become an important part of global agriculture (Sun et al., 2023). There are many reports regarding their positive impacts on crops, especially under biotic and abiotic stress conditions, and substantial research is constantly being conducted to find and/or produce new biostimulatory products, as well as to elucidate the mechanisms of action behind the observed impacts. The variance in the composition of biostimulant products, as well as the lack of ordinary application protocols, may cause inconsistencies between the observed results and complicated attempts to uncover the actual mechanisms behind the biostimulatory effects, which include physiological processes, hormonal control, and changes in morphology. A number of biostimulants have been shown to improve nutrient uptake, stimulate root growth, and produce phytohormones; they also appear to have the ability to adjust the osmotic environment through the synthesis of organic osmolytes. As an environmentally friendly tool with no significant negative impact on fruit quality or total yield, biostimulants can also be used to decrease the application of mineral inorganic fertilizer. Plant biostimulants include humic acids, fulvic acids, protein seaweed extracts, hydrolyses, N-containing compounds, botanicals, seaweed extracts, chitosan and other related biopolymers, beneficial bacteria and fungi, and inorganic compounds. Various biotic and abiotic stressors affect crop production, such as the salinity of soil and irrigation water, extreme weather phenomena, water limitations, infections from pathogens, and pests, which adversely affect crop performance and product quality (Shahrajabian et al., 2022; Shahrajabian, et al., 2023; Shahrajabian & Sun, 2023). Plant responses are stimulated by biostimulants, operating costs are reduced, fertilizers are applied less frequently, roots are better protected from soil pathogens, and drought tolerance is improved. In addition, they repel pests, accelerate root establishment, increase fertilization, increase stress tolerance, improve fertilization, alleviate leaching, detoxify heavy metals and chemicals, open stomata and increase plant transpiration (Shahrajabian et al., 2022; Shahrajabian, et al., 2023; Shahrajabian & Sun, 2023; Calvo et al., 2014). In addition to stimulating



soil biology, biostimulatory compounds are also well known for being effective in restoring degraded ecosystems and semiarid areas (Calvo et al., 2014; Karapouloutidou & Gasparatos, 2019; Tejada et al., 2011). However, revealing the mechanisms of action of biostimulant products is more difficult because of the variable composition of the raw materials used in production (Calvo et al., 2014).

Among the different sources of chitin and chitosan in nature are crustaceans (lobsters, shrimp, king crabs), fungi (*Mucor rouxii*, *Penicillium chrysogenum*, *Aspergillus niger*, *Lactobacillus vellereus*), insects (ladybugs, waxworms, silkworms, butterflies), and mollusks (shell oysters, squid pens). There are three steps involved in chitin recovery: demineralization, deproteinization, and removal of pigments and lipids (Philibert et al., 2017; Meramo-Hurtado & Gonzalez-Delgado, 2020; Koleska et al., 2017). *Lactobacillus* sp., *Bacillus* sp., *Pseudomonas* sp., *Serratia marcescens*, etc., are the most significant strains used to make chitin and chitosan (Philibert et al., 2017). The growth, yield, and shelf-life of onion bulbs are increased by biostimulants containing organic substances, humic acids, amino acids, algae extracts, carbon, and boron (Shehata et al., 2017), whereas diluted honey extract (DHE) improves photosynthetic parameters, antioxidant activity, and biomass production. In a previous study (Anbarasi & HariPriya, 2020), seaweed extracts, vermicompost, and animal waste were used to increase bulb yields and characteristics. In soil from goldmines, foliar application of vermicompost leachate, smoke water, *Ecklonia maxima* extracts, and indole3-butyric acid increased phytoremediation activity by increasing the accumulation of heavy metals. When carrots are applied with Kelpak SL or Asahi SL, their nutritional value increases, and their storage life improves (Wszelaczynska et al., 2019). When protein hydrolysates are applied to lettuce plants grown under saline conditions, oxidative stress is mitigated, and glucosinolate and osmolyte levels increase (Halpern et al., 2015; Lucini et al., 2015). Biostimulants can also increase nutrient use efficiency and partially replace chemical fertilizer inputs in intensive cropping sectors such as horticulture and floriculture (Petropoulos et al., 2020; Shahrabian et al., 2021). The heterogeneous family of biostimulants includes microstimulants derived from microorganisms, which are related to a microorganism (or mixture of microorganisms) that can stimulate biochemical and physiological processes affecting plant growth, nutrient efficiency, nutrient uptake, tolerance to abiotic stress, crop quality, and/or yield (Joly et al., 2021), thereby moderately mitigating the damaging effects of intensive agriculture. Biostimulatory products are typically composed of bacteria such as *Azotobacter*, *Rhizobium*, and *Azospirillum*, which are not pathogenic or toxic to plants, and mycorrhizal fungi, which are not toxic to plants. Several forms of mycorrhizae exist according to the fungal taxonomy and the host plant, and they are symbiotic associations between fungi and plant roots. Among the key parameters influencing the distribution of these forms (Hart & Reader, 2002; Yang et al., 2012) are climatic and soil conditions as well as the distribution of the host plants. Among mycorrhizae, there are two major types, namely, endotrophic and ectotrophic, which can significantly increase mineral absorption efficiency (Cruz et al., 2021). Arbuscular mycorrhizal fungi are mostly classified into the subphylum *Glomeromycotina* of *Mucoromycota* (Spatafora et al., 2016), where four orders of AMF have been recognized within this subphylum, which contains 25 genera (Redecker et al., 2013; Zhu et al., 2022), including *Glomerales*, *Paraglomerles*, *Archaeosporales*, and *Diversisporales*. In addition to reducing oxidative stress, arbuscular mycorrhizal fungi increase rapid water uptake and nutrient absorption and alter gene transcript levels associated with signaling pathways and stress responses (Cui et al., 2022; Sales et al., 2022; Liang et al., 2023), and the effectiveness of AMF depends on the soil conditions and environmental variables (Paymaneh et al., 2023). This review aims to synthesize recent findings on the practical applications of microbial biostimulants in enhancing crop productivity, quality, and resilience to environmental stressors. Additionally, emerging methodologies and tools for investigating the underlying mechanisms by which microbial biostimulants exert beneficial effects on crops have been explored. Finally, the challenges related to biostimulant formulation, application protocols, and consistency of the observed results are identified and analyzed to promote effective biostimulant utilization in sustainable agriculture.

2. Types of Biostimulants

Biological stimulants can be divided into two categories on the basis of their origin: the first group includes pathogens or plant-derived products, whereas the second group includes products with no biological origin (Rafiee et al., 2016; Bosi et al., 2023; Vasconsuelo & Boland, 2007). In addition, microbial biostimulants are made from arbuscular mycorrhizal fungi and plant growth-promoting bacteria, whereas nonmicrobial biostimulants are made from plant microalgae extracts, humic substances, and biopolymers such as chitosan (Ahemad & Kibret, 2014; Perez-Montano et al., 2014; Lugtenberg & Kamilova, 2009). The growth and development of plants can be accelerated by the use of a variety of biostimulants (Askari-Khorasgani et al., 2019) that have bioactive properties. In addition to being economical, quick-acting, environmentally friendly, and linked with other elicitors to increase secondary metabolite biosynthesis (Ali, 2021), salicylic acid is also an efficient elicitor. In addition to increasing plant growth, humic acid can also increase water retention, enrich nutrients, and suppress disease (Guo et al., 2019). In addition to changing plant primary and secondary metabolism, fulvic acids can improve root growth, nutrient uptake, and crop tolerance to environmental stresses (Canellas et al., 2015). A mixture of soluble amino acids and peptides is used to produce protein hydrolysate biostimulants, which are produced mainly by chemical and enzymatic hydrolysis of plant- and animal-derived proteins. In addition to improving plant nutrient uptake and tolerance to abiotic stress, protein hydrolysate biostimulants can increase yields and product quality. The most common brown seaweeds used for this purpose



are *Ecklonia maxima*, *Ascophyllum nodosum*, and *Macrocystis pyrifera*, which contain promoting hormones and trace elements such as Zn, Fe, Mn, and Cu. The biostimulatory activity of humic-like substances such as fulvic and humic acids may also be observed, since several reports suggest that crop performance improves mainly due to auxin- and cytokinin-like effects. In addition to improving soil physical-chemical properties and improving the availability of nutrients in the rhizosphere, they also play roles in plant growth. They are derived from the decomposition of organic matter and metabolic products of soil microbes. The actual mechanisms of action seem to result from synergy between the many bioactive components of raw materials, although the impacts vary depending on crop type, soil type, and rhizosphere microbes. Chitin and its derivatives have the major benefits of stimulating and protecting against seed germination; stimulating stress resistance; mitigating the negative impacts of abiotic stress; stimulating plant growth; improving soil properties; preventing nutrient leaching; improving the shelf-life of crops; chelating heavy metals; increasing crop yields and quality; and protecting against pests and pathogens, such as bacteria, viruses, fungi, insects, and nematodes (Goni et al., 2016). Stress tolerance can be increased by amino acids through osmoprotection, ROS scavenging, metal chelation, and nutrient availability (Oosten et al., 2017), which can significantly affect the synthesis of enzymes and gene expression. They can also be applied as signal molecules, such as for inducing stomatal closure, as sensors of the nutrient content of cells, or as regulators of their own catabolism. In addition to strengthening plant growth, photosynthesis, and yield formation, amino acids can help regulate protein synthesis; improve nutrient assimilation, use, and translocation; and improve constituent quality (Shahrajabian & Sun, 2023).

Abiotic stresses can be mitigated by amino acids (Popko et al., 2018), which are well-known biostimulants that improve yield and plant growth. Ammonium fixation and C4 metabolism and the biosynthesis of various components, including isoflavonoids, flavonoids, cutins, auronones, sporopollenin, stilbenes, proanthocyanidins, suberin, lignins, catechins, phenylpropanes, lignans, and other alkaloid derivatives, are also dependent on amino acids. A major group of secondary metabolites in plants are phenols, which are antioxidants that play important roles in photosynthesis, physiological activities, and oxidation–reduction procedures (Ozyigit et al., 2007). Coumarins, stilbenes, quinones, lignans, flavonoids, curcuminoids, and tannins, which are derivatives of phenolic acids, play significant roles in plant development, especially in pigment and lignin biosynthesis, as well as protecting plants against stress (Sharma et al., 2019). In addition to increasing the quality and yield of products and plant uptake and abiotic stress tolerance, protein hydrolysate biostimulants are derived through the enzymatic and chemical hydrolysis of plant-derived and animal proteins. By producing proteins with chaperone-like functions (Albertsen et al., 2006), members of the phylum *Glomeromycota* can withstand drought and form symbiotic relationships with plant roots. These proteins enable plants to withstand drought. *Trichoderma* fungi promote plant growth as they act as antagonists of phytopathogenic fungi (Schubert et al., 2005), interact with microorganisms, soil, arthropods, and plants at a variety of trophic levels, and act as biopesticides and biocontrol agents. In addition to biofuels, antibiotics, and enzymes, *Trichoderma* members are used in a variety of industrial branches. The main effects of *Trichoderma*-plant interactions include morphology, plant physiology, nutrient absorption, yield improvement, disease resistance, and tolerance to abiotic stresses. *Trichoderma reesei* is a filamentous fungus that produces proteins, such as enzymes, cellulases, hemicellulases, and hydrophobins (Katenkamp et al., 1989), as well as superior industrial cellulose sources. Additionally, the endophytic fungus *Heteroconium chaetospira* can penetrate the outer epidermal cells of its host, enter the inner cortex, and colonize cortical cells, including those at its root tip, without being apparently pathogenic (Hashiba & Narisawa, 2005). This provides plants with even more nitrogen than the organic nitrogen they mineralize. *Arthrobacter* species, gram-positive chemoorganotrophs and obligate aerobics, are commonly identified in soil bacteria (Orlandini et al., 2014), and they make up the majority of aerobic bacteria in the *Micrococcaceae* and *Actinobacteria* families (Mukhia et al., 2021), with their main characteristic being nutritional flexibility (Cacciari & Lippi, 1987). This species of gram-negative coccobacilli is aerobic, nonmotile, oxidatively negative, and does not ferment glucose; it can be found in a variety of environments (Wu et al., 2018). In addition to fixing nitrogen, solubilizing minerals, producing siderophores, and acting as plant endophytes, they can help hosts deal with environmental stresses and detach pollutants (Khaksar et al., 2017). In addition to phosphate solubilization, IAA, and siderophores, *Actinobacteria* also promote plant growth (Lin et al., 2018). In addition to promoting phosphorus content and plant growth, they can also increase radical scavenging, plant phenolics, and antioxidant activity (Joe et al., 2016). Figure 1 illustrates the different classifications of plant biostimulants.

3. The Use of Microbial Biostimulants

Microbial inoculants are categorized as biopesticides or biofertilizers (Bashan & Holguin, 1998). Biofertilizers are classified as biostimulants. When applied to plants, seeds, or soil, they are known as bioinoculants, which contain living organisms that stimulate plant growth via a variety of procedures, including increasing biomass and root growth, supplying nutrients, and increasing nutrient uptake. A number of beneficial functions are associated with microbial biostimulants, including solubilization, uptake, metabolism, and translocation of macronutrients and micronutrients, resulting in phytochemical accumulation, establishing robust root systems that can forage on the soil, increasing photosynthetic activity to increase growth, reducing the oxidative stress burden, and increasing nutrient use efficiency (Younes et al., 2023). There has been a growing interest in biostimulants derived from living microorganisms because they can increase plant growth and

development more easily in the field (Jacobs-Hoffman & Hills, 2021). Microbes produce enzymes efficiently and can be used as alternatives to form beneficial microbial consortia that can be combined with gelatin to increase biostimulant activity (Costa et al., 2023). The majority of microorganisms that act as biostimulants are beneficial fungi that include arbuscular mycorrhizal fungi and free-living bacteria (Berg, 2009). Many factors are involved in the development of microbial inoculants as biofertilizers, including the variety of plants and their compatibility with soil, chemical fertilizers, and environmental conditions (Dalmastri et al., 1999). In addition to affecting the activity of microbial inoculants, root exudates (extracellular secretions by plants) also act as substrates for the formation of bioactive substances (Khalid et al., 2004). Several mechanisms are involved in the stimulation of plant growth by AMF: (i) increasing water absorption, since AMF increase the root surface area, making it easier for the plant to take up water; (ii) changing the root structure; (iii) making nutrients available under nutrient-deficient conditions; (iv) changing enzymatic and physiological activities, particularly in plants that produce antioxidants; and (v) activating ABA plant hormones (Begum et al., 2019). Microbial primary degraders prefer polyhydroxyalkanoates (PHAs) as carbon sources (Botti et al., 2023).

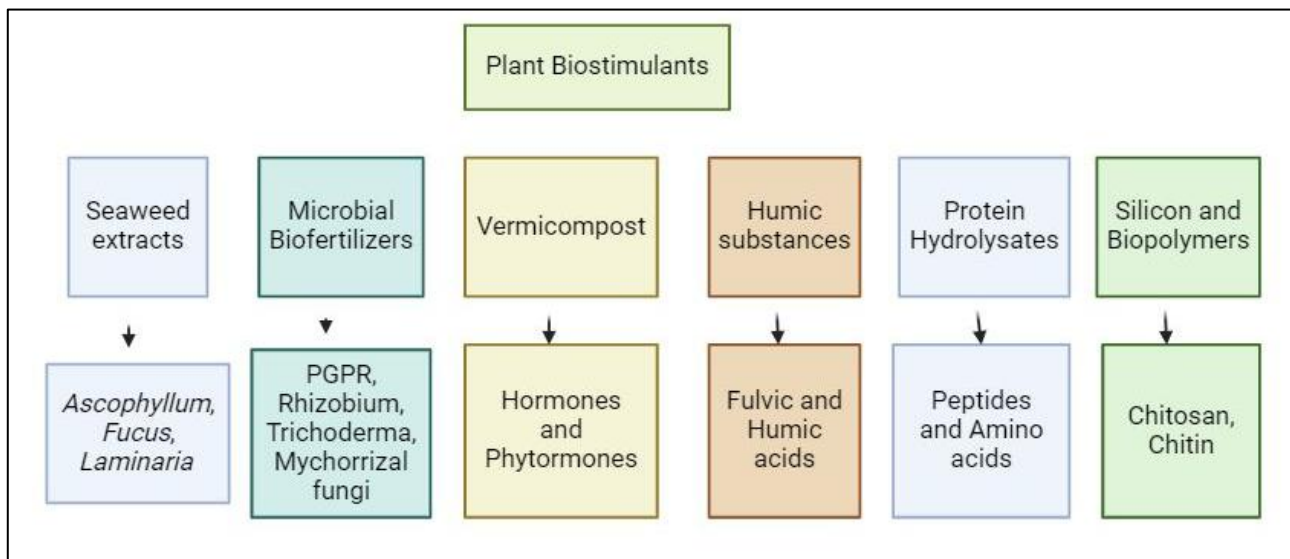


Figure 1 Plant biostimulant classification.

4. Microbial Biostimulants and Their Mechanisms of Action

There are several notable protective mechanisms utilized by microbial biostimulants under different stresses, including osmolyte production, the modulation of phytohormone levels, an increase in antioxidant activity, and the secretion of extracellular polymeric substances (EPSs) when water is stressed (Lindow & Brandl, 2003). Under thermal stress conditions such as freezing and extreme heat, phytohormone levels are modulated, volatile organic compounds are emitted, ice nucleation activity is antagonistic, senescence is delayed, and osmo- and thermal protection are achieved (Mishra et al., 2008). During nutrient stress, soil exploration and mineral nutrient solubilization increase, whereas during biotic stress, system resistance is induced, pathogen direct antagonism occurs, and phytohormone levels are modulated. According to Bozhinova (Bozhinova, 2023), Europlus® and PH Trainer® were effective at increasing tobacco yields by 5.5% and 6.7%, respectively, compared with those of untreated plants. Additionally, Bozhinova (Bozhinova, 2023) reported that applying the microbial inoculant Europlus to leaves increased the N, P, and K concentrations, and the Ca, Mn, Zn, and Cu concentrations were slightly greater when the microbial inoculant Europlus was applied. According to this study, microbial biostimulants could be used to increase the yield and quality of oriental tobacco on sustainable tobacco farms. Under drought stress, AMF can increase the *Glycine max* dry weight, photosynthesis, and fresh yield of seeds. In *Triticum aestivum* grains under drought stress, *Gigaspora decipiens* and *Glomus mosseae* can increase chlorophyll levels, whereas *Rhizophagus intraradices* can increase magnesium, zinc, copper, and iron contents (Goicoechea & Antolin, 2017).

Zea mays can increase N, P, and K uptake under drought stress when *Rhizophagus intraradices* are present (Zhao et al., 2015), and *Fragaria ananassa* can use more water effectively if *Funneliformis geosporus* BEG11 is present (Boyer et al., 2015). The proline level of *L. majus* can be improved by *Glomus deserticola* (Asrar & Elhindi, 2011), and the mineral level of *Vigna subterranea* can be increased and the proline content can be reduced by *Gigaspora gregaria* (Tsoata et al., 2015). *Poncirus trifoliata* can benefit from the increased water absorption and hyphal length of *Paraglomus occultum* under water shortage (Tsoata et al., 2015). *Digitaria eriantha* can benefit from *Rhizophagus irregularis*'s increased conductivity and dry matter of shoots, and *Glomus* species are capable of increasing water uptake, phenolic, metabolite, and glutathione levels in *Saccharum arundinaceum* (Mirshad & Puthur, 2016) and improving osmotic potential adjustment in *Ipomoea batatas* (Yooyongwech et al., 2016) and *Saccharum arundinaceum* (Mirshad & Puthur, 2016). The fresh weight and number of leaves of *Solanum*

lycopersicum can be increased by *Rhizophagus irregularis* under salinity stress (Khaloufi et al., 2017). *Claroideoglossum etunicatum* can increase the conductivity of stomata and the level of soluble sugars in *Aleurites moluccanus* (Hajiboland et al., 2015), and *Aeluropus littoralis* can benefit from *Claroideoglossum etunicatum* and increase the conductivity of stomata. The antioxidant defense system of *Solanum melongena* can be activated by *Rhizophagus irregularis* and *Funneliformis mosseae* when cold stress is applied (Pasbani et al., 2020). The photosynthetic efficiency of *Solanum lycopersicum* plants can be improved by *Rhizophagus irregularis* under heat stress (Calvo-Polanco et al., 2016). In tomato cultivars, AMF containing *Rhizoglossum irregulare* and *Funneliformis mosseae* can significantly influence growth, productivity, and nutraceutical and nutritional quality, as AMF increase the biosynthesis and nutrient uptake of notable molecules involved in cellular pH and oxidative stress (Carillo et al., 2020).

A mixture of AMF strains (*Glomus manihotis*, *Glomus gigantea*, *Entrophospora colombiana*, *Acaulospora laevis*, *Acaulospora scrobiculata*, *Gigaspora gigantea*, *Entrophospora colombiana*, and *Scutellospora heterogama*) and six single strains (*Acaulospora laevis*, *Acaulospora scrobiculata*, *Gigaspora gigantea*, *Acaulospora scrobiculata laevis*, *Acaulospora scrobiculata*, and *Gigaspora gigantea*) inoculated with *Chloris gayana* increased survival, increased tolerance of stress stress stress, and increased nutritional status, relative water content, photosynthesis, and P, N, Mg, and Fe contents (Krishna et al., 2005). With the application of *Rhizophagus irregularis*, *Pseudomonas fluorescens*, and *Funneliformis mosseae*, APX and GPX enzyme activities increase, plant growth parameters increase, water deficit damage is alleviated, H₂O₂ and lipid peroxidation are reduced, and drought tolerance is improved (Aalipour et al., 2020). Under salt stress, *Glomus mosseae*, *Rhizobium leguminosarum*, and *Arthrobacter protophormiae* decreased proline content and lipid peroxidation, improved plant weight, increased nutrient uptake, increased pigment content, and relieved salt stress in *Pisum sativum* (Barnawal et al., 2014). To reduce salt stress, *Acaulospora* sp., *Claroideoglossum etunicatum*, *Rhizobium* sp., and *Burkholderia* sp. In *Schizolobium parahyba* var. *amazonicum* under salt stress, chemical fertilizers are better absorbed, and the wood yield increases. As a result of *Bacillus megaterium*, *Rhizophagus irregularis*, and *Frateuria aurantia*, nutrient uptake responses are enhanced, low-mobility nutrient uptake is improved, microbial biomass is increased, microbial metabolism is improved, plant growth is increased, and gluten quality is improved in *Triticum aestivum* L. under salt stress (Dal Cortivo et al., 2017). The application of microbial biostimulants altered seedling growth and responses to various stresses and was found to promote growth among unstressed seedlings, increasing dry and fresh biomass, leaf area, and leaf number, making it an appropriate option for improving seedling salinity tolerance, particularly when stressed.

5. Practical Applications of Microbial Biostimulants

A microbial biostimulant has two types of mechanisms of action. For direct mechanisms, microbes are active in the synthesis of components that can increase the adsorption of nutrients, whereas indirect mechanisms include siderophore production, zinc solubilization, phosphorus solubilization, indole acetic acid biosynthesis, the production of antioxidant enzymes, the production of ammonia and hydrogen cyanide, nitrogen fixation biologically, and phytohormone production (Kumar et al., 2022). Plant growth and final yield can be positively impacted by microbial biostimulants that produce hormone-like stimulants to alleviate the adverse effects of environmental stress. Plants can be protected against various stressors by microbial biostimulants that act on molecular processes that play a role in interactions between plants and microorganisms, resulting in secondary metabolites (Ganugi et al., 2021). It is possible to produce protective molecules via the shikimate pathway, which involves the enzyme phenylalanine ammonia lyase (PAL) to produce phenylpropanoids after microbial elicitation (Mansoor et al., 2020), which may have significant effects on adjusting external pressures, termed induced systemic resistance (ISR). Various biostimulants can target shoot targets, such as stomatal regulation and xylem hydraulic conductance, as well as root targets, such as root ethylene and auxin levels, via ROS scavenging, membrane stability, and osmoprotection. The plant phenotype, cell level, and molecular level can all be affected by biostimulants. Shoot and root growth, flowering, yield parameters, leaf number and vigor, improved abiotic stress tolerance, improved fruit nutritional quality, increased relative water content, increased stomatal conductance, and increased nutrient uptake and transport are among the effects affecting plant phenotype. At the molecular level, the effects include increased gene expression of SOD, CAT, APX, nutrient transporters, and stress-related genes, whereas the effects at the cellular level include increased antioxidant activity, improved primary and secondary metabolism, increased chlorophyll content, and increased photosynthetic rates. In addition to alleviating abiotic stress, balancing plant hormone levels, altering root biomass and morphology, and increasing nutrient availability, microbial biostimulants can also improve crop cold tolerance and increase crop heat tolerance (Behera et al., 2021). Biostimulants derived from microorganisms have been reported to increase lettuce production, copper and calcium contents, and isochlorogenic acid contents. The influence of biostimulants on lettuce nutritional and functional quality is largely independent of water availability (Saia, et al., 2021). A microbiome analysis of chickpea seeds and plants revealed a positive correlation between soil health and yield, and microbial biostimulants can improve carbohydrate, protein, sugar, K, Ca, Mn, Zn, and Fe contents (Mukherjee et al., 2022). A number of mechanisms can be used by microbial-based biostimulants to improve crop growth and yield, and microbial-based biostimulants can increase nutrient uptake, reduce phytopathogen infection, promote root system development, reduce heavy metal toxicity, and increase nutrient uptake and use efficiency (Mrid et al., 2021). Agriculture and horticulture crops can be more resilient to



abiotic stresses and more productive under environmental stress with natural biostimulants (Kaushal et al., 2023). The effects of microbial biostimulants on native plant growth and emergence were demonstrated by Alfonzetti (Alfonzetti et al., 2023), but the exact effects are dependent on the plant species, the type of amendment, and the soil characteristics of the planting site. An appropriate microbe can also produce secondary metabolites such as volatile organic components to improve plant growth with the help of microbial biostimulants. The effects of microbial biostimulants are not limited to direct effects on molecular procedures. They also affect morphological changes, such as changes in root morphology and increases in the root surface area, both of which can increase the uptake of nutrients and water, assisting plants in coping with stressors. Additionally, inoculating water-stressed plants with *Penicillium* sp., *Phoma glomerata*, *Glomus intraradices*, *Exophiala* sp., and *Paecilomyces formosus* may lead to increased soil exploration by roots or fungal hyphae with improved root conductivity (Aroca et al., 2007).

6. Mycorrhizal Fungi (AMF)

Many terrestrial herbs can establish symbiotic relationships with advantageous microorganisms such as AMF. AMFs belong to 11 families, 25 genera, and more than 250 species (Shubler et al., 2001). As a result of the mutualistic relationship between fungi and plants, arbuscular mycorrhizal symbiosis plays an important role in nutrient exchange, ecosystem sustainability, plant stress resistance, and host plant development. The natural environment contains AMFs that are useful in several ways. They enhance plant nutrition acquisition, improve plant tolerance and resistance to stress, increase soil fertility and structure, and have several beneficial applications in agriculture (Chen et al., 2018). Plants can absorb nutrients through both mycorrhizae and their own pathways through symbiosis, increasing host plant nutrition. In addition, AMF alter soil physicochemical characteristics, microbial communities, and nutrient cycling to influence nutrient availability (Kan et al., 2023). According to plant and fungal functional group identities and soil nutrient availability, AMF affect herbaceous plant element stoichiometry, such as the plant C:N:P ratio. Through the regulation of gene expression levels associated with these pathways, AMF promoted the utilization and accumulation of calcium in apple rootstock (*Malus robusta*). AMF increase the uptake of ZnO nanoparticles by barley roots, possibly through the mutualistic relationship between roots and fungi, which promotes water absorption through the more efficient rhizosphere (Kimura et al., 2023). Plant biomass is significantly increased by the combination of humic substances and AMF (Zhao & Naeth, 2022). Compared with those of single-inoculated and uninoculated forages, the effects of *Rhizobium* and AMF on the growth and yield of *Lablab purpureus*, *Vigna unguiculata*, and *Mucuna pruriens* were analyzed. AMF and *Rhizobia* dual inoculation improved legume growth and biomass yield, and dual inoculation might be an ideal alternative for reducing the overreliance on chemical fertilizers to produce forage (Mpongwana et al., 2023).

As a result of AMF, the lettuce plants grew taller, heavier, longer, and heavier, and the functional composition profiles revealed that several functions, such as cell motility and environmental adaptation, increased, and AMF significantly influenced the lettuce endophytic bacterial networks and structural functionality. Under greenhouse conditions, AMF containing high levels of Cu components improved stomatal conductivity and transpiration, contributing to the growth and survival of grapevine rootstocks (Betancur-Agudelo et al., 2023). A key component of the eco-engineered mining pedogenesis of iron ore tailings is the role of AM fungi (*Glomus* species) in the upregulation of plant growth and nutritional status in technosols of plants such as sorghum (Li et al., 2023). After inoculation with AMF (*Gigaspora albida* and *Acaulospora longula*), *Anadenanthera colubrina* (Vell.) Brenan contains more saponins and flavanols and has significant antioxidant activity (Falcao et al., 2023). In addition to improving *Iris tectorum* biomass and nutrient levels, AMF also reduce the number of soil Cr constituents; furthermore, AMF can increase the abundance of functional genes related to nutrient cycling (N, P) in rhizosphere microbial communities and increase rhizosphere microbial community complexity and stability by increasing the abundance of functional genes associated with heavy metal resistance and transporters (Zhao et al., 2023). The reduction in As and Cd accumulation caused by AMF depends on the plant family, and AMF reduces plant uptake and bioavailability of Cd and As. Additionally, AMF–*Glomus versiforme* (Gv) symbiosis leads to increased P uptake, plant growth, and photosynthesis in upland rice, and Gv inoculation decreases Nramp5 expression, reducing Cd absorption, transfer, and accumulation in upland rice and increasing catalase (CAT) and peroxide (POD) activities (Zhu et al., 2022). It is mainly *Glomeraceae* and *Paraglomeraceae* that affect the available P content the most.

AMF communities are sensitive indicators of the quality of soil-available P in *Eucalyptus plantations*, and applying *Glomeraceae* and *Paraglomeraceae* to *Eucalyptus plantations* may increase soil P availability (Liu et al., 2023). By accumulating Pb in fungal structures, AMF reduce the toxicity risk of Pb but not its abundance. Flooding and Pb stress reduced AMF diversity but not abundance. In terms of the species of fungi, fungal inoculation partly improved fruit quality and mineral elements, whereas inoculation with *Piriformospora indica*, a cultured mycorrhiza-like fungus, has replaced AMF in citrus plants (Cheng et al., 2022). With respect to AMF, lemon balm (*Melissa officinalis* L.) has good dry weight and yields a high amount of essential oil (Alves de Assis et al., 2020). The combination of AMF inoculants promoted plant productivity and flower quality in chamomile cultivation, particularly in terms of phenolic compounds (Baczek et al., 2019). As a result of AMF inoculation (Chen et al., 2022), raspberry (*Rubus idaeus* L.) yields are positively affected, while the combination of biochar and AMF improves AMF colonization potential, and the photosynthetic potential of *Tamarindus indica* significantly increases



with increasing chlorophyll and carotenoid contents (Ndiata et al., 2022). Through the production and release of secondary metabolites, filamentous endophytic fungi, such as *Trichoderma*, can control pathogens such as *Xylella fastidiosa* and *Pseudomonas savastanoi*; they can also control *Oomycetes* and *Colletotrichum* (Poveda & Baptista, 2021). Under saline conditions, GA3 (gibberellic acid) and AMF (*Rhizophagus irregularis*) significantly reduce growth impairment by altering the hormonal balance of plants. In the presence of salinity stress, sweet basil plants (*Ocimum basilicum*) are able to increase productivity, and AMF and mycorrhizal inoculation significantly increase water efficiency and chlorophyll content (Elhindi et al., 2017). Owing to the protection of the PSII system from damage under high temperatures (Yan et al., 2021), AMF formation significantly increased lettuce tolerance to high temperatures. A study has also suggested that mycorrhizal symbiosis lowers sodium and chlorine concentrations in olive plants, increases the ratio of water to dry matter, and improves their photosynthesis (Hassena et al., 2021). Both in the nursery and in the field, mango rootstocks improved nutrient uptake, plant growth, and yield after AMF inoculation (Mohandas, 2012). Table 1 shows the major impacts of AMF on different plants. The effects of mycorrhizal activity on plants and roots are presented in Figure 2.

Table 1 Major effects of AMF on plants.

Type	Plant	Effects	Reference
Mycorrhizal fungi (AMF)			
<i>Glomus mosseae</i> , <i>Gigaspora gigantea</i>	Carrot (<i>Daucus carota</i> L.)	Under salinity stress, AMF inoculation can lead to successful carrot production. Plant growth and the total N content of the plants were positively affected by coinfection with AMF and rhizobia, along with synergistic effects on the total P content, the number of nodules, and mycorrhizal rate of the plants. Myrtle drought resistance was boosted as a result of the increased water and nutrient supply caused by the AMF, as well as the stimulation of antioxidant defenses.	(Yadav et al., 2021)
<i>Acaulospora</i> sp., <i>Glomus</i> sp.	Common bean (<i>Phaseolus vulgaris</i> L.)	Biological control factors in greenhouse agroecosystems showed promising results through the AMF consortium in inhibiting <i>Fusarium</i> wilt of cucumber.	(Razakatiana et al., 2020)
<i>Funneliformis mosseae</i> , <i>Rhizophagus irregularis</i>	Common myrtle (<i>Myrtus communis</i>)	A couple of mycorrhizal fungi directly affect plant growth, and they can also reduce chemical pesticide inputs in eggplant.	(Azizi et al., 2021)
<i>Glomus</i> spp., <i>Acaulospora</i> spp.	Cucumber (<i>Cucumis sativus</i> L.)	The leaf and stem ratios increased after inoculation, while ear ratios decreased.	(Hu et al., 2010)
<i>Gigaspora gigantea</i> , <i>Glomus mosseae</i>	Eggplant (<i>Solanum melongena</i> L.)	To alleviate marigolds' Cd stress, it can increase the ability of plants to scavenge reactive oxygen species (ROS).	(Sharma et al., 2021)
<i>Glomus intraradices</i>	Maize (<i>Zea mays</i> L.)	In seedlings colonized by AMF species, P and N contents increased.	(Celebi et al., 2010)
<i>Glomus intraradices</i> , <i>Glomus constrictum</i> , <i>Glomus mosseae</i>	Marigold (<i>Tagetes erecta</i> L.)		(Liu et al., 2011)
<i>Glomus mosseae</i> , <i>Glomus intraradices</i>	Mulberry (<i>Morus alba</i> L.)		(Lu et al., 2015)

7. Using Microbiostimulants in Crop Production

Different bacterial taxa have been isolated from the mycorrhizospheres of *Glomus margarita*, *Glomus versiforme*, *Rhizobium irregular*, *Rhizobium clarus*, and *Funneliformis mosseae* via culture-dependent approaches (Mayo et al., 1986). In horticulture and agriculture, microbes and fungi have different effects (Figure 3); *Pseudomonas putida* increases iron uptake

in rice, whereas *Pseudomonas fluorescens* improves yields, plant height, and biomass in rice, sweet potato, and rapeseed (Hasani & Aminpanah, 2015). Several studies have indicated that *Streptomyces* strains are beneficial to tomato and rice plant growth (Rungin et al., 2012). The application of *Azospirillum brasilense* Sp245, along with *Aeromonas* spp., improved dry shoot weight and leaf length. As a consequence, the rice root area increases (Mehnaz et al., 2001). Plant growth and cytokinin constituents in shoots and roots are significantly improved by *Comamonas acidovorans* and *Bacillus subtilis* (Arkhipova et al., 2005). In cucumber (Hussain & Hasnain, 2009), *Bacillus licheniformis* application increased fresh weight, cell division, and chlorophyll concentration, whereas *Azospirillum lipoferum* application improved maize seedling root hair density. Wheat is more salinity tolerant when *Azospirillum lipoferum* is used (Bacilio et al., 2004), and white clover is more water soluble and shoot rich when *Pseudomonas putida* is applied (Bae et al., 2009). *Alternaria* sp. stimulated drought tolerance in wheat (Singh et al., 2011). Additionally, *Azoarcus* sp. increased plant nitrogen nutrition and root growth and reduced nutrient deficiency in wheat (Dal Cortivo et al., 2020), and *Azorhizobium* sp. increased plant nitrogen nutrition and root growth and alleviated nutrient deficiency (Dal Cortivo et al., 2020). In peanut plants, *Rhizobium meliloti* improved plant growth, nitrogen use efficiency, and pod quality, whereas in soybean seedlings, *Rhizobium leguminosarum* increased yield and growth under drought stress. Root and shoot length, chlorophyll content, and root and leaf numbers are increased by *Azotobacter chroococcum* and *Azotobacter vinelandii* (Jain et al., 2021).

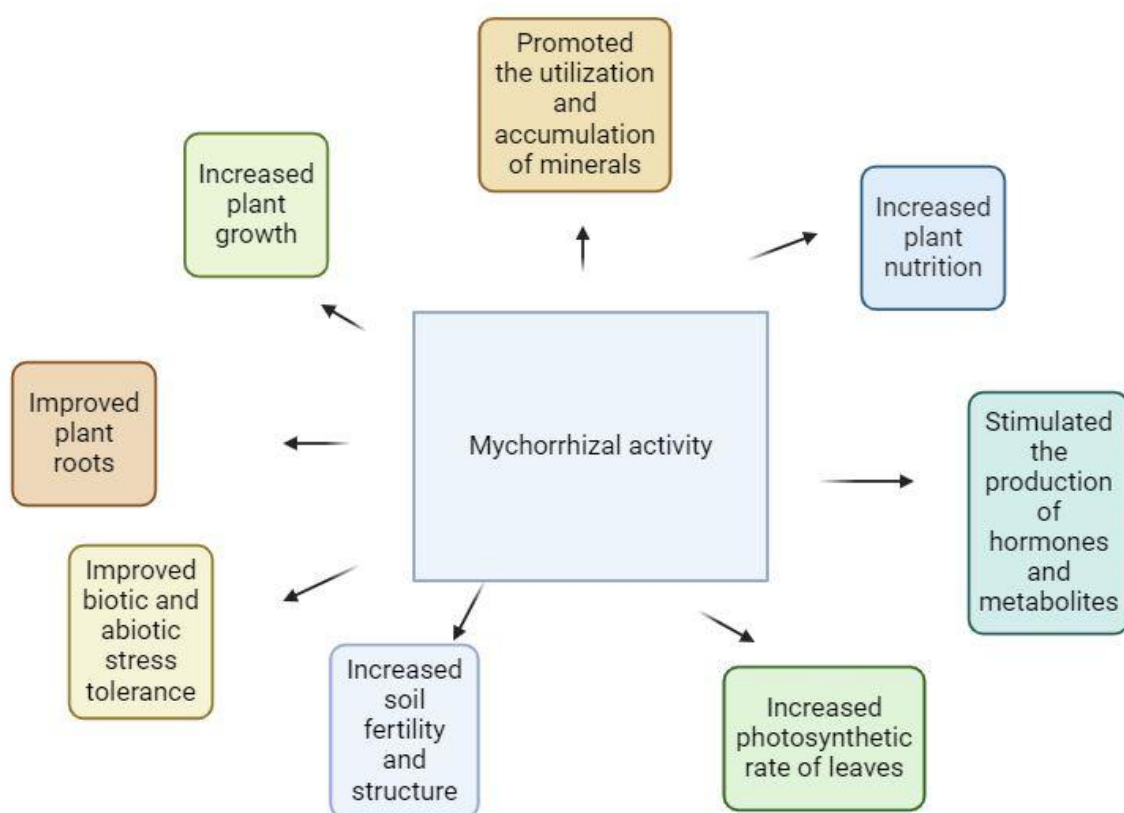


Figure 2 Mycorrhizal activity in plants and roots.

Germination, growth, and yield are increased by the application of *Bacillus halotolerans*, *Pseudomonas frederiksbergensis* RG2, and *Enterobacter hormaechei* (Fahsi et al., 2021). Under drought conditions, *Rhizogloium irregulare* *Aoufous* improved growth characteristics and physiological characteristics related to nitrogen and phosphorus absorption, protein and sugar content, and MDA and H₂O₂ reduction; improved soil pH; and increased electrical conductivity, organic matter, and total organic carbon in date palms (Anli et al., 2020). The basal diameter, dry biomass, seedling length, and germination index of date palm roots improved under heavy metal stress conditions in *Glomus* species (Ghadbane et al., 2021). PGPR can also interact with AMF (Karthikeyan et al., 2016). Among other factors, *Bacillus subtilis* and AMF have positive and significant synergistic interactions with respect to nitrate, nitrate reductase, and nitrogenase activities, as well as with the phenols, lipids, fibers, and osmoprotectants proline, betaine, and glycine (Hashem et al., 2016). Zamljen (Zamljen et al., 2023) reported that adding microbial biostimulants to nutrient solutions improved the basil volatile content, primary metabolism, and yield. Anton-Herrero (Anton-Herrero et al., 2023) reported that the origin and composition of microbial biostimulants determine their physiological impact on pepper plants. Cherry tomato cultivars with microbial biostimulants presented relatively high levels of lipophilic antioxidants and reduced sugars.

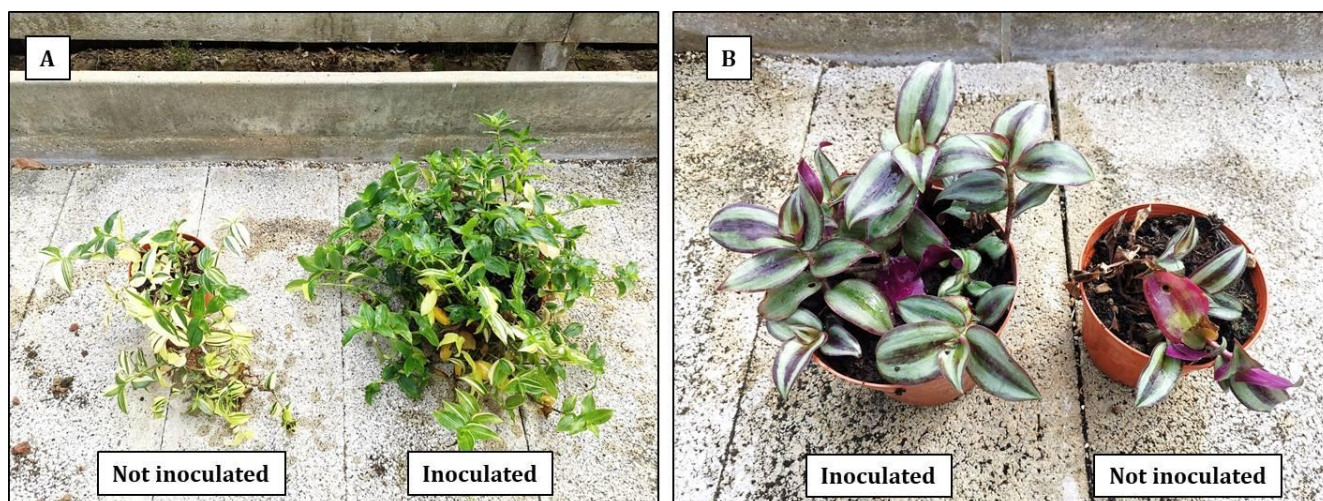


Figure 3 Effects of mycorrhizal inoculation on the development of *Tradescantia fluminensis* (A) and *Tradescantia zebrina* (B).

8. Conclusions and Future Observations

The application of biostimulants offers a promising approach to increase plant yield, productivity, and crop quality while increasing resistance to abiotic stresses by promoting metabolic and enzymatic processes. Biostimulants, which may include special formulations of natural components or microorganisms, can significantly stimulate plant growth. Major categories of biostimulants include humic and fulvic acids, fungi, bacteria, amino acid-containing products, and hormone-based formulations. As a vital alternative to mineral fertilizers, biostimulants are crucial in organic farming and sustainable crop production management. Its use in sustainable agriculture can stimulate shoot and root growth, increase stress resistance, and reduce the need for nitrogen fertilizers. Arbuscular mycorrhizal fungi (AMF), which colonize plant roots, have shown potential in enhancing specific secondary metabolite production through root organ culture (ROC), an efficient alternative for multiplying mycorrhizal species. Studies have revealed that AMF can significantly modify the quality and quantity of secondary metabolites in medicinal and aromatic plants. Owing to their wide use in agriculture and horticulture, AMF species such as *Rhizophagus intraradices* and *Funneliformis mosseae* improve crop yield, stress tolerance, pathogen resistance, and sustainability in agricultural ecosystems. In mycorrhizal plants, studies have shown that AMF increase the production of secondary metabolites and activate antioxidant defense enzymes. Given their ability to improve mineral uptake, AMF are pivotal to plant nutrition and performance, contributing to enhanced food quality and quantity for a growing global population. In addition to other microbial biostimulants, AMF increase the sustainability of agricultural and horticultural production systems. Further studies into the molecular mechanisms driving these effects will clarify the physiological pathways involved, allowing the development of tailored biostimulant products for various agricultural needs. However, these positive effects require greater reproducibility, and production processes must be standardized from laboratory to industrial scales. According to this review, AMF inoculation has the potential to increase secondary metabolite production. To improve the consistency of outcomes, future research should focus on understanding the interaction mechanisms between AMF and other biostimulants, as well as on validating the reproducibility of their positive impacts.

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Ethical Considerations

Not applicable.

Conflict of Interest

The authors declare that they have no conflicts of interest.

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