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REVIEW

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Harnessing of plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi in agroecosystem sustainability

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Abstract

Background Soil microorganisms including rhizobacteria and fungi play a key role in soil health, biodiversity and productivity of natural and managed ecosystems. Plant growth-promoting rhizobacteria (PGPR) associated with plant roots enhance the uptake of nutrient and improve productivity. Similarly, mycorrhizal fungi particularly, arbuscular mycorrhizal fungi (AMF), form a mutualistic association with plants and enhance nutrients uptake and consequently promote plant growth and productivity.

Methods Here we show how harnessing beneficial soil microorganisms like PGPR and AMF with their positive effect on plant development can contribute to the green and clean economic growth strategy.

Results Through a review of the state-of -art knowledge in this area we demonstrate that this approach can improve uptake of nutrients, enhance plant growth, yield and tolerance to biotic and abiotic stress. We argue that this approach can reduce the need for agrochemicals that destabilizes the ecological system.

Conclusions This review provides a state-of-the-art synthesis of the knowledge generated so far and insight into the multifunctional strategies employed by AMF and PGPR toward ensuring sustainable agriculture.

Keywords Agricultural sustainability, Beneficial microbes, Nutrients uptake, Plant growth, Soil fertility

Background

The modern agricultural system is faced with two objectives, namely the need for more production of food to feed the growing world population and the need to reduce environmental damage (Jones et al. 2017). How these goals will be met is a great challenge to scientists. Food insecurity is an issue that needs serious attention due to climate change, soil infertility, increase in population growth, and scarcity of arable land for farming (Fasusi et al. 2021; Islam and Wong 2017). Over the past years, agrochemical (e.g., fertilizers, biocides, herbicides, etc.) have been widely promoted to increase food production and profitability of agriculture (Shuqin and Fang 2018). Chemical fertilizers help in improving nutrient deficiency in plants to improve plant productivity (Fasusi et al. 2021). The application of chemical fertilizers was reported by Itelima et al. (2018) to enhance several activities in the plants' roots because phosphorus, potassium, and nitrogen are important for plant growth and productivity. Nevertheless, its usage leads to loss of biological diversity, degradation of soil quality, and environmental pollution (Ramankutty et al. 2018). In addition, microbial diversity and the environment have been harmed due to an increase

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in the application of chemical fertilizers (Kumar et al. 2017; Nath et al. 2017). The application of chemical fertilizers did not only result in reduction in beneficial soil microbes' diversity, but it has also caused health hazards due to leaching and environmental pollutions (Alori and Babalola 2018). Therefore, there is a need to employ an environmentally friendly and biological-based approach that enhance plant growth and yield (Gouda et al. 2018). There are many factors that can enhance crop productivity and nutrients availability in plants; this could be influenced by beneficial microorganisms that live in the plant's rhizosphere (Teotia et al. 2016). Symbiotic interactions occur in the soil, which is beneficial in enhancing soil quality, fertility and increasing plant productivity. These interactions occur between the plant through the root system and the beneficial microbes that are present in the soil (Jacoby et al. 2017). For mutual interaction to occur between host plants and beneficial soil microbes that live near the plant root region through signaling pathways, the plant depends on the root system (Li et al. 2016). Some of the beneficial microorganisms that live in the rhizospheres and enhance plant growth include the genera *Alcaligenes, Serratia, Azospirillum, Bacillus, Frankia, Rhizobium, Mycobacterium, Azotobacter, Gigaspora, Glomus, Acaulospora, Streptomyces,* and *Arthrobacter* (Kehri et al. 2018; Meena et al. 2017).

Soil microbes perform an important function in improving soil fertility and cycling of nutrients to enhance plant development. AMF and PGPR are the main microorganisms present in the rhizosphere (Fasusi et al. 2021). In addition to improving plant development through nutrient uptake, these organisms also enhance plant tolerance to biotic and abiotic stress (Cabral et al. 2015; Ramakrishna et al. 2019). Through their symbiotic association with plants' roots, AMF mycelia colonize plant roots of different species and form a mycorrhizal network to improve soil quality, plant growth, and plant tolerance to adverse conditions (Borde et al. 2017).

The use of AMF and PGPR as bioinoculant in increasing plant growth and ensuring sustainable agriculture has recently gained interest among researchers and policymakers (Chatterjee et al. 2017). The application of AMF and PGPR in ensuring sustainable agriculture is becoming a new route to reduce the negative effect of chemical fertilizers. Although numerous studies exist on the use of PGPR and AMF in agriculture, the knowledge being generated has not been synthesized (Sagar et al. 2021). Substantial knowledge gaps also exist on the synthesis of PGPR and AMF in agriculture. Therefore, the objective of this review is to provide a state-of-the-art synthesis of the knowledge generated so far and insight into the multifunctional strategies employed by PGPR and AMF in ensuring sustainable agriculture.

Methods

Through a comprehensive review of the literature, this state-of-the-art synthesis and insight into the multifunctional strategies employed by PGPR and AMF toward ensuring sustainable agriculture. The literature review considered all types of relevant studies including those published in peer-reviewed journals, dissertations, and book chapters on the subject matter. We conducted the literature search using Google Scholar limiting the search to studies published in the English language covering the globe. We focussed the search on studies on the application of PGPR and AMF in ensuring agricultural sustainability. Accordingly, in the search engine we used various combinations of the following key words: Agricultural sustainability, beneficial microbes, mycorrhizal fungi, nutrients uptake, plant growth, plant growth promoting rhizobacteria and soil fertility. In total we found 163 published studies focussing on application PGPR and AMF in ensuring agricultural sustainability. We also found 16 studies providing practical effect of arbuscular mycorrhizal fungi (AMF) on plants under stress conditions. We confirmed and 9 studies providing information on mechanisms of action of plant growth promoting rhizobacteria that alleviate abiotic stress.

Synthesis

Plant growth-promoting rhizobacteria (PGPR)

The common rhizobacteria with plant growth-promoting potential are the PGPR that belongs to the phylum proteobacteria and firmicutes (Gontia-Mishra et al. 2017). Bacteria genera like *Pseudomonas*, *Acinetobacter*, *Enterobacter, Serratia,* and *Pantoea* in the class Gammaproteobacteria also possess plant growth-promoting activity. Two free-living bacteria that belong to Betaproteobacteria have also been identified; these are *Burkholderia* and *Achromobacter xylosoxidans* (Batista et al. 2018). Plants that are associated with PGPR are *Fabaceae*, *Poaceae*, *Asteraceae*, and *Brassicaceae*. *Fabaceae* is a group of leguminous families that contain important plants like soybean (*Glycine max*), and root nodule formation in this plant is caused by its symbiotic relationship with nitrogen-fixing bacteria (Igiehon and Babalola 2018). Proteobacteria gram-negative bacteria are the dominant group of microorganisms in maize, rice, and *Arabidopsis*. The root microbiome varied among plant species because there is specificity in the type of bacteria that is associated with different plant species (Fitzpatrick et al. 2018).

PGPR is a crucial component of the soil, and they enhance the nutrients uptake by plants to promote their growth (Verma et al. 2017). Soil microorganisms are the determining factor of the status of soil and plant health richness in nutrients (Francioli et al. 2018). These microorganisms play a crucial function in the mobilization and solubilization of nutrients by enhancing plant development and suppressing the action of disease-causing pathogens.

(Nath et al. 2017).

Role of plant growth-promoting rhizobacteria (PGPR)

Nitrogen fixation

Nitrogen is among the vital nutrients required to enhance plant development because it is classified as a building block for plants, microorganisms, and animals (Moreau et al. 2019). The nitrogen fixation (Fig. 1) process by rhizobacteria involves the conversion of atmospheric nitrogen to ammonia, and it is catalyzed by an enzyme-nitrogenase (Choudhary and Varma 2017; Kuypers et al. 2018). The nitrogen fixation process can also be referred to as biological nitrogen fixation (BNF), which consumes a broad range of energy in the form of Adenosine 5'- triphosphate (ATP). There is variation in nitrogen fixation among different genera of bacteria. The group of genes that is responsible for nitrogen fixation in a plant is known as the nitrogenase (*nif*) gene, which is known to be present in nitrogen-fixing microorganisms (Mus et al. 2018). The *nif* gene was reported to consist of a structural gene that activates iron protein and other regulatory genes that are involved in the synthesis of symbiotic and free-living systems. Biological nitrogen fixation microorganisms include symbiotic and free-living nitrogen-fixing bacteria which include *Herbaspirillum, Bradyrhizobium, Mesorhizobium, Rhizobium, Achromobacter, Frankia, Pseudomonas, Bacillus, Azoarus,* and *Azotobacter* (Xu et al. 2017).

Antibiotics production

Antibiotics production is the major mechanism that PGPR uses to overcome the negative effects caused by pathogens on plants (Alori and Babalola 2018). Antibiotics are compounds and some enzymes synthesized by plant growth-promoting microorganisms which inhibit the metabolism of plant pathogens, thus limiting their growth in causing plant diseases (Yadav et al. 2017). In the case where some plant pathogens develop resistance to a specific antibiotic, PGPR produces more antibiotics that will boost their ability against such pathogens. These antibiotics produced by PGPR can be biostatic or biocidal against plant pathogens (Katiyar et al. 2017). Recently, *Pseudomonas* and *Bacillus* were reported to produce different types of antibiotics such as subtilin, bacillaene, fengycin, sublancin, pseudononic acid, rhamnolipids, and cepaciamide (Alori and Babalola 2018).

Induction of systemic resistance (ISR)

PGPR promotes plant growth by inducing plant resistance to plant pathogens and the mechanism of inducing

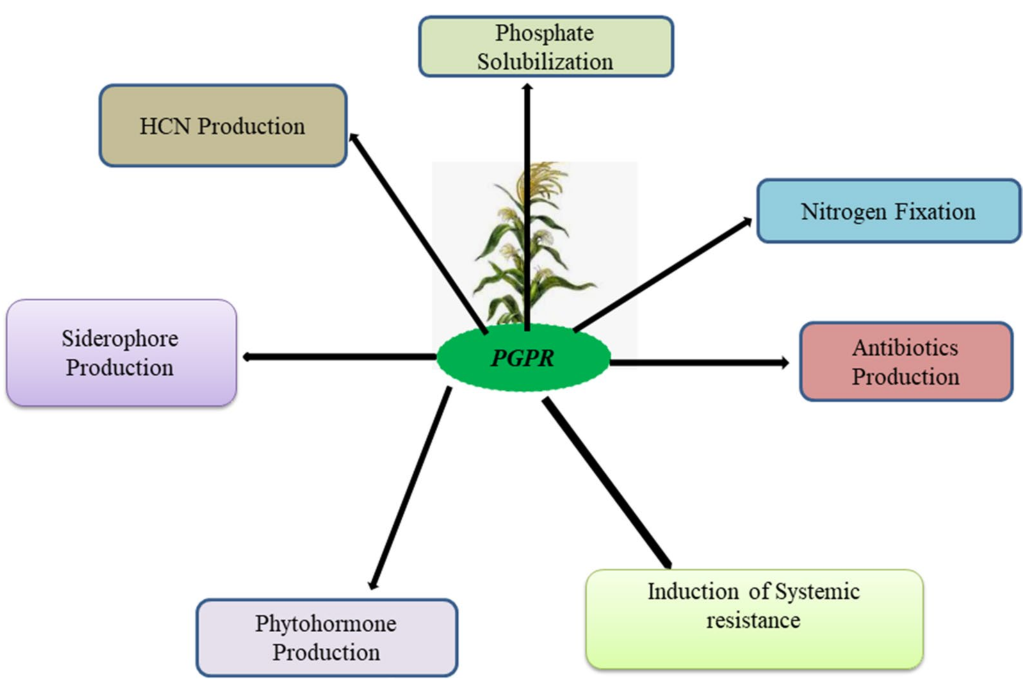

Fig. 1 Strategic mechanisms employed by plant growth-promoting rhizobacteria

systemic resistance is active when there is an attack on the plant by pathogenic microorganisms (Nguvo and Gao 2019). The induced systemic resistance in plants is initiated by Microbes Associated Molecular Patterns (MAMPs) like PGPR. The main receptor which first perceives the Microbes-Associated Molecular Pattern is known as the Pattern Recognition Receptors (PRRs). Upon reception by PPRs, the ISR is being triggered by the plant, which results in a defensive response of the plant against phytopathogens attack (Villena et al. 2018). Colonization of *Arabidopsis* root by *Bacillus amyloliquefaciens* has been reported to promote plant development through modulation of root defense, which is enhanced by jasmonic acid (Asari et al. 2017). It was reported that *Pseudomonas simiae* improves systemic resistance against *Mamestra brassicae* when it switches on JA/ET- regulated ORA59- branched in replacement of JA-regulated MYTC2- branch (Basu et al. 2017). Similarly, *Bacillus subtilis* was reported to confer resistance against *Fusarium oxysporum* by inducing accumulation of metabolites in onion (Abdel-Rahman and Sonomoto 2016). *Sclerotinia* stem rot disease of soybean (*Glycine max*) was recently reduced using *Trichoderma harzianum* as a biocontrol agent by triggering the expression of a defensive gene within the plant (Zhang et al. 2016). Similarly, plants protection against *Tobacco Mosaic Virus* by *Bacillus artrophaeus* HAB-5 through the action of salicyclic acid, jasmonic acid, and ethylene-dependent signalling increases the expression of genes that enhance plant growth (Rajaofera et al. 2020). Therefore, PGPR is helpful in plant protection by improving the internal systemic resistance of plants to a pathogenic agent (Enebe and Babalola 2018).

Phytohormone production

Phytohormones are chemical messenger substances that are responsible for gene expression, cell division, and thus promotes plant growth. Indole-3-acetic acid (IAA) as phytohormones that is produced by rhizobacteria are molecules that serve as an effector in the symbiotic association between plants and microorganisms, and it helps in the process of phytostimulation (Karthikeyan et al. 2019). The acquired IAA by the bacteria in the soil can alter the concentration of the IAA that is present in the plant (Manasa et al. 2017). IAA enhances plant growth by increasing the root surface to access the soil nutrients. The major functions that IAA performs in plants are cell division, elongation, cell differentiation, and increases the plant cell wall (Pholo et al. 2018). Auxin is among the phytohormones produced by PGPR. It is produced at the apex of the shoot and transported through the shoot to the apical meristem of the root; it also helps in root initiation and elongation (Olanrewaju et al. 2017). Another phytohormone that is produced by rhizobacteria is gibberellin. The major function of gibberellin is to activate growth processes in plants, including plant flowering, germination of seeds, elongation of the stem, and increase the rate of photosynthesis in plants (Vishal and Kumar 2018).

Siderophore production

Siderophore are small, high infinity iron chelating compound produced by microorganisms such as rhizobacteria especially under iron limiting conditions. Iron is among the nutrients that promote plant development. The problem caused by iron deficiency is a global issue that is affecting the production of crops on iron-deficient soil (Mahender et al. 2019). Iron occurs as Fe^{3+} ion where it forms hydroxide and oxyhydroxide in an aerobic environment, which makes it unavailable for the plant and microorganisms that may need it in the form of Fe^{2+} (Pahari and Mishra 2017). Fe^{2+} is acquired by bacteria through the secretion of siderophores. Fe^{3+} is reduced to Fe^{2+} when a complex membrane is formed by Fe^{3+} and siderophore; the Fe^{2+} is released into the cell by siderophore through a mechanism that links the membranes. The siderophore can be recycled during the process of reduction (Kashyap et al. 2017). Uptake of Fe^{2+} by a plant from siderophore producing bacteria is by uptaking Fe-siderophore complexes directly (Novo et al. 2018).

Hydrogen cyanide production (HCN)

HCN is a metabolite that reduces the growth of numerous microorganisms and also affects plant growth development (Gouda et al. 2018). HCN–producing rhizobacteria are effective biocontrol agents. PGPR that produces hydrogen cyanide secretes hydrogen cyanide synthases that break down the cell wall of pathogenic microorganisms (Bahadur et al. 2017). The rhizobacteria that produce HCN include *Rhizobium* spp., *Aeromonas* spp., *Bacillus* spp., *Pseudomonas* spp., *Enterobacter* spp., and *Alcaligenes* spp. (Tabassum et al. 2017). It was reported that most *Pseudomonas* spp. isolated from the rhizosphere of potato and wheat have the attribute of producing HCN when tested in the laboratory (Meena et al. 2017; Verma et al. 2017). The suppressive effect of diseases in rhizobacteria has also been attributed to the production of HCN. Rhizobacteria protect plants from pathogens by releasing HCN that can inhibit the growth of pathogenic microorganisms (Iftikhar et al. 2020). Recently, Zhai et al. (2018) reported that hydrogen cyanide-producing *Pseudomonas putida* 1A00316 was used as a biocontrol agent against *Meloidogyne incognita* egg collected from an infested tomato plant.

Phosphate solubilization

Phosphorus is among the important nutrients required for plant development (Mitran et al. 2018). The phosphorus that is available in the soil exists in two forms namely: the organic and inorganic, which are not available to plants, but through the process of phosphate solubilization by PGPR, phosphorus is made available for plant use (Etesami et al. 2017). Examples of microorganisms that act in this process are *Pseudomonas* spp., *Agrobacterium* spp., *Rhizobium* spp., *Bacillus* spp., and *Enterobacter* spp. (Alori et al. 2017). Production of mineral compounds like carbon dioxide, organic acid, inorganic acid, the liberation of enzymes, and OH^- are among the mechanisms that plant PGPR employ in solubilizing organic phosphorus (Khare and Yadav 2017).

Practical applications of plant growth-promoting rhizobacteria

PGPR through mechanisms such as antibiotics production and ISR has been able to protect plants against pathogen attack (Rahman et al. 2018). Devkota et al. (2020) has reported the effect of inoculating *pinus* spp. with PGPR *Bacillus velezensis* to prevent the plant against *Leptographium terebrantis* and *Grosmannia huntii* that cause root disease and wood blue stain in *Pinus* spp. Similarly, the biocontrol efficiency of PGPR *Bacillus subtilis* MML2476 was recently reported to inhibit *Rhizoctonia solani* MML4001 and *Fusarium solani* MML4002 growth, fungi that cause rhizome rot of turmeric (Chenniappan et al. 2019). Production of secondary metabolites in the plant has been enhanced by PGPR. Plant inoculated with PGPR was reported to enhance the synthesis of secondary metabolites which increase the survival and competitiveness of plants. Among the secondary metabolites produced by plants are resin, volatile oils, flavonoids, alkaloids, glycosides, and tannins, which are successfully exploited for industrial purposes (Thakur et al. 2019) (Table 1).

Arbuscular mycorrhizal fungi and their interaction with plants

The essential characteristics of most plants are the symbiotic associations that occur between the beneficial soil fungi and the plant roots referred to as mycorrhizae (Rich et al. 2017). The structures formed by mycorrhizal fungi in the plant roots determine the classification of mycorrhizal fungi as endomycorrhiza or ectomycorrhiza (Balestrini and Lumini 2018; Smith et al. 2018). The symbiotic relationship between mycorrhizal fungi with plant roots is based on nutrient exchange in the plant root (Bhantana et al. 2021). In mycorrhizal symbiotic association, the fungus absorbs carbohydrates and lipids from the plant as a source of organic matter (Luginbuehl et al. 2017), likewise, the regulation of nutrients in the soil such as soil aggregation, survival of seedlings, and decomposition of organic matter are among the functions performed by AMF in the ecological system (Powell and Rillig 2018). The symbiotic association between mycorrhizal fungi and plants enhance plant tolerance to favorable and unfavorable condition and influences growth performance in plants, thereby increasing plant productivity (Santander et al. 2017). To balance the concentration of micronutrients in the plant tissue, plants develop some mechanisms that include modification of root structure and root exudates through their interaction with soil microorganisms, like the arbuscular mycorrhizal fungi (Mahanty et al.

Table 1 Effect of plant growth-promoting rhizobacteria strain on plant growth

Plants	PGPR Strains	Effects	References
Apple	*Bacillus* spp., *Pseudomonas* spp., and *Mycobacterium* spp.	Increase fruit yield, weight, shoot length and the diameter	(Liu et al. 2020)
Pepper	*Pseudomonas fluorescence*, *Bacillus licheniformis*	Increase root and shoot length, root area, and stem diameter and act as a biocontrol agent against *Phytophthora capsici*	(Liu et al. 2020)
Lettuce	*Rhizobium leguminosarum*, *Serratia proteamaculans*	Enhance root promotion, increase chlorophyll content and fresh weight	(Stamford et al. 2019)
Cabbage	*Bacillus aryabhattai* H26-2 and *B. siamensis* H30-3	Increase plant growth and alleviate drought and heat stress	(Da Jeong Shin et al. 2019)
Cucumber	*Pantoea agglomerans*	Increase plant height and fruit yield	(Seymen et al. 2019)
Broccoli	*Brevibacillus reuszeri*, *Rhizobium rubi*	Increase chlorophyll content, plant yield and nutrient uptake	(Madende and Hayes 2020)
Grapevine	*Pseudomonas fluorescens*, *Azospirillum brasilense*	Increase nursery survival rate, fruit yield and shoot growth	(Kılıç and Cangi 2019)
Cherry	*Pseudomonas fluorescens*	Enhance plant growth, fruit weight and shoot length and as a biocontrol agent for phage	(Rabiey et al. 2020)
Maize	*Pseudomonas stutzeri* A1501	Enhance plant growth and promote yield	(Ke et al. 2019)

2017; Nanda and Wissuwa 2016). The dual functions performed by these fungi in the uptake of micronutrients by plants work either by increasing the absorption of micronutrients in a condition where there are limited nutrients or by preventing the accumulation of these nutrients by plant tissue when the soil is contaminated (Mnasri et al. 2017). AMF uses the mechanism of detoxification to reduce plant stress that is caused by excess micronutrients in the environment to enhance plant productivity. This makes AMF very useful in phytoremediation (Abu-Elsaoud et al. 2017; Bui and Franken 2018; Merlos et al. 2016). The absorption of micronutrients such as zinc, copper, iron, and manganese in a deficient condition and reduction in their accumulation under a toxic condition is achieved by AMF (Canton et al. 2016; Liu et al. 2018). The role played by AMF is dependent on the plant species that are involved. Recently, *Rhizophagus irregularis* has been reported to enhance the tolerance of a particular type of maize cultivar to copper, whereas, in another maize cultivar, it does not have any effect (Ruytinx et al. 2020). *Elsholzia spledens,* an indicator plant species of Chinese copper mining site, was reported to develop high adaptation to a copper that is available in high concentration in the soil as a result of its symbiotic association with AMF (Li et al. 2017). Plants that are colonized by AMF have the potential to develop an adaptation for a high concentration of zinc when compared to uninoculated plants without AMF. Examples of these plants are barley, maize, pepper, and soybeans (Ibiang et al. 2017; Watts-Williams and Cavagnaro 2018). The soil phosphorus concentration is the determining factor for the absorption of zinc by plants through their symbiotic association with AMF (Watts-Williams et al. 2019). Recently, inoculation of *Allium ampeloprasum* transplanted plants with *Glomus intraradices* increased zinc concentration, and inoculation of pepper and tomato plants with mycorrhizal fungi increased the phosphorus and zinc concentration in a soil that was deficient in zinc and phosphorus (Tran et al. 2019).

Effect of arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) in alleviating abiotic stress in plant

Inducing drought tolerance

Drought tolerance in plants is among the effective tools used by AMF in ensuring sustainable agriculture that can result in food security (Cardoso et al. 2017). The mutual association between plant and AMF causes modification of plant root architecture, which includes the root length, lateral root number, and root density. This association provides an opportunity for the extracellular hyphae of the fungi in the rhizosphere of the plant to extend beyond the zone of depletion, therefore making it possible for them to absorb water and nutrients more easily in the environment where water is deficient (Sharma et al. 2017). Kumar et al. (2017) reported that when *Pistacia vera* was inoculated with *Funneliformis mosseae* and *Rhizophagus intraradices* in the greenhouse under drought conditions, it improved the uptake of minerals like phosphorus and zinc, and also provided a conducive environment to enhance the relative water content of the leaf. The absorptive surface area of the plants can be increased by mycorrhizal fungi. In a moisture-deficient soil, the nutrient that is taken up by mycorrhizal hyphae can increase plant growth, productivity, and amelioration of stress as a result of an environmental factor (Jamiołkowska et al. 2018). The symbiotic association of mycorrhizal fungi with plants also enhances their tolerance to water stress through the expression of plant physiology and plant genes (Mathimaran et al. 2017). Recently, it was reported that inoculated lettuce plants with AMF regulate the level of abscisic acid faster than non-mycorrhizal inoculated plants, by creating an adequate balance between the transpiration in the leaf and water movement in the root during water stress conditions (Volpe et al. 2018). Similarly, inoculation of pepper plants with AMF increases their drought tolerance by increasing the leaf relative water content and the percentage of non-wilted plants in mycorrhizal inoculated plants (Pischl and Barber 2017). Also in dry soil, *Glomus mosseae* and *Glomus fasciculatum* inoculation on lettuce plants increase acquisition of nitrogen when compared to control plant (Adamec and Andrejiová, 2018). PGPR has also found its application in promoting the tolerance of plants to drought. The mechanisms of production of IAA promote the tolerance of a plant to drought. Recently, Jochum et al. (2019) reported inoculation of maize and wheat with two PGPR strains, *Bacillus* spp. 12D6 and *Enterobacter* spp. 16i under water stress conditions. It was reported that these PGPR (*Bacillus* spp. 12D6 and *Enterobacter* spp) inoculations on the maize plant increased the root surface area, root length, and the number of leaves when compared to the control, while the result obtained from the PGPR inoculation on wheat increased the root branching and length when compared with the control. Similarly, the plant growth promoting potentials of *Arthrobacter arilaitensis* and *Streptomyces pseudovanezuelae* have recently been reported by Chukwuneme et al. (2020) to enhance physiological parameters in maize under drought conditions.

Inducing tolerance to salinity

The role played by AMF in enhancing plant tolerance to salinity has been highlighted in several research findings (Elhindi et al. 2017). Recently, it was reported that inoculation of grapevine rootstocks (Table 2)

Table 2 The mechanisms of action of Plant Growth Promoting Rhizobacteria (PGPR) that alleviate abiotic stress

Stress	PGPR species	Plant growth-promoting mechanisms	Host plant	References
Drought	*Bacillus aquimaris*	IAA and ACC deaminase	*Helianthus tuberosus L*	(Namwongsa et al. 2019)
Drought	*Bacillus sp. Enterobacter sp*	IAA	*Zea mays and Triticum aestivum*	(Jochum et al. 2019)
Drought	*Bacillus megaterium*	Polyamine secretion	*Arabidopsis thaliana*	(Zhou et al. 2016)
Salt	*Burkholderia sp.*	IAA, ACC deaminase	*Oryza sativa L*	(Sarkar et al. 2018)
Salt	*Bacillus safensis*	IAA, ACC deaminase	*Brassica napus*	(Li et al. 2017)
Metal	*Streptomyces acidiscables*	Siderophore	*Vigna unguiculata*	(Dimkpa et al. 2009)
Heat	*Bacillus tequilensis*	GAs, IAA	*Glycine max*	(Kang et al. 2019)
Cold	*Bacillus spp*	ABA	*Triticum aestivum*	(Zubair et al. 2019)
Flooding	*Pseudomonas putida*	ACC deaminase	*Rumex palustris*	(Ravanbakhsh et al. 2017)

ABA abscisic acid, *GAs* Gibberellin, *IAA* indole-3-acetic acid, *ACC deaminase* 1-aminocyclopropane-1-carboxylate deaminase

with *Rhizophagus intaradices* and citrus seedling with *Funneliformis mosseae* and *Paraglomus accultum* increased the growth parameters of grapevine rootstocks when compared to uninoculated plants (Feldmane et al. 2020; Zhang et al. 2017). The increase in performance of grapevine and citrus inoculated with AMF was attributed to a decrease in the amount of sodium, calcium and an increase in potassium and magnesium concentration in the leaf tissue of the plant (Saxena et al. 2017). Also, it was reported that olive seedlings inoculated with AMF strains (*Funneliformis mosseae* and *Rhizophagus intraradices*) improved nutrient uptake, salt tolerance, and increased the shoot and root biomass in the seedlings (Pollastri et al. 2018). The role played by *Funneliformis mosseae* on olive growth occurred due to an increase in uptake of potassium under saline conditions. Basil (*Ocimum bacilicum* L 'Siam Queen) growth and tolerance to different salt concentrations were enhanced by *Rhizophagus irregularis* (Scagel et al. 2017). Similarly, plant tolerance to saline conditions when inoculated with AMF was demonstrated in tomatoes inoculated with *Rhizophagus intraradices.* There was an increase in uptake of potassium, phosphorus, and calcium in the plant which lowered sodium toxicity and increased the stomatal conductance as a result of improvement in the net photosynthesis, due to mycorrhization (Khalloufi et al. 2017). The increase in stomatal conductance shows an increase in the accumulation of phosphorus, copper, iron, and zinc in AMF inoculated plants when compared with uninoculated plants under controlled and saline conditions. AMF effect on the plant under salt stress conditions includes an increase in uptake of nutrients, potassium concentration and sodium ion ratio in the plant tissue, water use efficiency and photosynthetic in a plant (Saxena et al. 2017).

PGPR is beneficial to plant growth by enhancing plant tolerance to salinity. This was evident in the inoculation of maize (FH-1137) with a plant growth-promoting strain *Bacillus* spp. SR-2–1/1 increased the chlorophyll content, total phenolic content, and proline content in the plant (Rafiq et al. 2020). Also, inoculation of maize with *Bacillus* spp. SR-2–1/1 enhanced photosynthesis (RBCL) expression, antioxidants status (CAT1, APX1, APX2), and gene-related to homeostasis ion (NHX1, SOS1, H^+-PPase and HKT1) in plants. Similarly, Egamberdieva et al. (2019) reported that a salt tolerance strain *Bacillus licheniformis* SA03 promotes *Chrysanthemum* growth by increasing its tolerance to salt stress. A recent study by He et al. (2018) reported a novel salt tolerance PGPR strain *Pseudomonas* spp. M30-35 characterized from *Haloxylon ammodendron* rhizosphere to contain 34 genes associated with plant growth promotion and stress tolerance.

Reducing effects of adverse soil pH

Plants are generally sensitive to changes in soil pH which can have either a negative or positive effect on their growth and development. As regards tolerance of AMF inoculated plants to alkaline conditions, it has been reported that there was an increase in morphology and biochemical responses in zucchini squash and cucumber inoculated with *Rhizophagus intraradices* over the control when subjected to pH 6.0 and 8.1 (Gupta and Shukla 2017; Rouphael et al. 2017). The AMF reduced the negative effect of the alkalinity on the yield by maintaining high content of chlorophyll in the leaf and also enhancing the nutritional status of the plant. Recently, research was carried out on the application of *Funneliformis mosseae* in enhancing *Pyrus betulaefolia* tolerance to high alkalinity (Yang et al. 2020). The role of PGPR in enhancing plant tolerance to alkaline stress was recently reported by Dixit et al. (2020). Dixit et al. (2020) reported that *Bacillus* spp. NBRI YN4.4 inoculated on maize under greenhouse conditions was reported to enhance its tolerance to alkaline stress and promote maize growth with a significant increase in photosynthetic pigment and soluble sugar content when compared with uninoculated. Similarly, PGPR *Bacillus cereus* and *Pseudomonas fluorescens* inoculation on wheat when grown in infertile sandy soil increased chlorophyll content, sugar content, and protein content in the wheat plant (Khan et al. 2019).

Removal of heavy metals

AMF uses several mechanisms in removing heavy metal contamination from the soil, such as dilution of the heavy metal, enhancing the synthesis of organic acid by plant roots to prevent heavy metal from entering the plant root and enhancing the retention of metal ions by their hyphae (Basu et al. 2018). It was reported that the glycoprotein produced by AMF (glomalin) helps in removing contaminants in heavy metal contaminated soil (Mishra et al. 2017). Arbuscular mycorrhizal fungi perform a crucial role in ensuring agricultural sustainability by reducing the negative effects of heavy metal contamination on plants, increases plant productivity by acting as bioprotectants, biofertilizers, and biodegrades heavy metals (Choudhary et al. 2018). Several findings have reported the tolerance of AMF to heavy metal toxicity on plants. A research study was carried out on celery inoculated with *Glomus macrocarpum* in soil with a high concentration of Cd. The AMF was able to reduce the negative effects of Cd, increase chlorophyll content, and improve plant growth (Yasmeen et al. 2019). AMF potential in improving plant tolerance to Cd was also investigated on *Bromus kepotdaghensis* when inoculated with *Rhizophagus intraradices* (Azimi et al. 2016). Similarly, cucumber plant inoculated with *Funneliformis mosseae* BEG107 in an environment with a high concentration of Cd and Ni increased the plant biomass by reducing the rate of movement of metal to shoot system of cucumber when compared with uninoculated cucumber plants (Rakshit et al. 2017). The success recorded from this finding was attributed to the fact that when AMF acquires a high concentration of phosphorus, it stimulates the metal-rich substrate. A study was also conducted on basil grown on soil with a high concentration of Cr, Cd, Ni, and Pb when inoculated with *Rhizophagus intraradices*, high increase in shoot biomass was recorded in the inoculated plant. The tolerance potential of the AMF to heavy metal contamination was attributed to the binding of extraradical hyphae to the metal which limits their translocation to basil plant root (Wu et al. 2019). Studies conducted on *Solanum nigrum* and switchgrass also revealed this binding activity of AMF (Guo 2019; Sun et al. 2020). Using the mechanism of siderophore production, PGPR help in the bioremediation of heavy metal polluted soil. Singh et al. (2019) reported the effects of PGPR strain *Bacillus thuringiensis* PS-1 and *Azotobacter chroococcum* PS-2 inoculation on garden pea in enhancing garden pea physiological and biochemical parameters such as chlorophyll content, number of pods, root length, and plant relative water content when grown in soil polluted with heavy metal.

Practical applications of AMF

Inoculation of plants with AMF results in the formation of wider extra radical hyphae within the plant root (Thirkell et al. 2017). Also, inoculation of plants with AMF and PGPR improves plant growth by increasing nutrient uptake in plants and increase plant tolerance to *Sclerotium rolfsii* (Mohamed et al. 2019). Plants inoculated with AMF can adapt to changes in climatic conditions. AMF symbiotic association with plants was reported to enhance the resistance of plants to phytopathogens. However, the molecular mechanisms attributed to the function of mycorrhizal-induced resistance are still unknown. (Han et al. 2019). Through modulation of oxylipin pathway, which is identified by an increase in agglomeration of vitamins such as folic acid and riboflavin, tomato plant inoculated with *Rhizophagus irregularis* and *Funneliformis mosseae* showed higher resistance to *Botrytis cinerea* and early blight diseases caused by *Alternaria solani* (Sanchez-Bel et al. 2016). Moreover, tolerance in mycorrhizal fungi inoculated plants has also been reported by Formenti and Rasmann (2019) to be mediated by jasmonate signalling Induced resistance in plants by mycorrhizal fungi is also mediated by hormonal crosstalk. The effect of potato inoculated with *Rhizophagus irregularis* MUCL 41833 was reported by Singh and Giri (2017) to enhance its defense against *Rhizoctonia solani,* thereby suggesting its involvement in the ethylene pathway. Additionally, it was also reported that AMF inoculation protects plants against herbivory (Sharma et al. 2017). This was reported in tomato plants when inoculated with *Glomus mosseae*, the larval performance of chewing caterpillar *Helicoverpa arimigera* was inhibited by activation of jasmonates pathway and inducing the expression of the genes that are responsible for plant defense such as LOXD, AOC, PI-I, and PI-II (Basu et al. 2018). The potential AMF in inducing plant resistance to pathogenic attack was also established in corn plant inoculated with *Glomus mosseae*, where it developed resistance against sheath blight diseases by increasing the acquisition of genes responsible for plant defense such as PR2a, PAL, and AOS (Enebe and Babalola 2019) (Table 3). The induced acquisition of defense-related genes such as OsNPR1, OsAP2, and OsMPK6 in rice inoculated with mycorrhizal fungi, enhances rice resistance fungus pathogen (*Magnaporthe oryzae)* (Basu et al.

Table 3 Effect of arbuscular mycorrhizal fungi (AMF) on plants under stress conditions

Crop	Mycorrhizal species	Effect on crop and stress tolerance	References
Vitis vinifera	*Glomus mosseae*	Enhance plant growth and concentration of phosphorus and potassium in the leaf under drought stress condition	(Kamayestani et al. 2019)
Poncirus trifoliata	*Funneliformis mosseae, Paraglomus occultum*	Enhance plant growth under drought stress conditions by increasing photosynthesis and nutritional status of the plant	(Zhang et al. 2019)
Solanum lycopersium	*Rhizophagus intraradices* and *Claroidoglomus etunicatum*	Increase fruit yield and concentration of potassium and calcium in the plant under drought stress condition	(Khosravifar et al. 2020)
Zea mays	*Rhizophagus intraradices*	Increase plant biomass and rate of photosynthesis through tolerance to high temperature	(Mathur et al. 2018)
Triticum durum	*Rhizophagus intraradices, Funneliformis mosseae*	Increase plant grain yield and content of nutrient in the grain through tolerance to drought	(Bernardo et al. 2019; Goicoechea et al. 2016)
Olea europaea	*Arbuscular Mycorrhiza Fungi*	Increase in uptake of mineral and reduces drought stress	(Imane et al. 2019)
Triticum aestivum	*Glomus mosseae, Funneliformis mosseae*	Increase potassium and phosphorus uptake weight and chlorophyll content	(Rani 2016; Tarnabi et al. 2020)
Matthiola incana	*Rhizophagus intaradices*	Improved flower yield, shoot, root length and macronutrient content under salt stress condition	(Akať, 2020)
Pistachia vera	*Glomus mosseae*	Increase potassium, phosphorus, and zinc concentration in the leaf	(Rohani et al. 2019)
Solanum lycopersicum	*Rhizophagus intaradices*	Reduce the effect of Cd on the crop yield and development	(Kumar et al. 2015; Vilela and Barbosa 2019)
Pelargonium graveolens	*Rhizophagus intaradices Funneliformis mosseae*	Increase plant weight and potassium, calcium and phosphorus uptake under drought stress condition	(Amiri et al. 2015; Rydlová and Püschel 2020)
Prunus spp. Rootstock	*Rhizophagus intaradices*	Increase plant growth by increasing the concentration of phosphorus and potassium in the leaf	(Feldmane et al. 2020)

2018). Attack of plants by phytopathogens is among the limiting factors that affect agricultural productivity.

Secondary metabolites production in plants is enhanced by the symbiotic association of AMF with plants. Research has now focused on isoprenoid metabolism as a result of AMF inoculation on plants. Upon inoculation of leguminous plants with mycorrhizal fungi, two cyclohexenone derivatives of carotenoid origin (mycorradicin and blumenin) are accumulated in the plant. In mycorrhizal inoculated plants, analysis of the biosynthesis pathway for mycorradicin was identified to increase the accumulation of 1-deoxy-D-xylulose 5-phosphate synthase (DXS) and1-deoxy-D-xylulose 5-phosphate reductoisomerase (DXR) which was an indication that the biosynthesis takes place through on-mevalonate methylerythritol phosphate pathway (MEP pathway). Similarly, flavonoids have been helpful in mycorrhizal-inoculated plants by controlling hyphae growth, root colonization, and hyphae differentiation. The effect of flavonoids is dependent on AMF species specificity. Two flavonoids, such as phytoalexin and medicarpin, were build up in mycorrhizal colonized roots. The symbiotic association of mycorrhizal fungi with the plant has also initiated the production of phenolic compounds in the plant, which is helpful in AMF symbiosis. Furthermore, medicinal plants inoculated with AMF have been reported to improve the concentration of essential oil (terpenoid).

Future directions in research and development

In agricultural management, AMF and PGPR were found to exert positive effects on plant nutrition and increase soil quality and nutrients. Though, the application of chemical fertilizers and land-use disturbance may reduce and harm their role of symbiotic association with plants (Trejo et al. 2016). Therefore, the use of plant PGP strains of rhizobacteria and AMF in the management of the agricultural practice is important in the application of AMF and PGPR inocula for future use to ensure agricultural sustainability (Backer et al. 2018; Mensah et al. 2015).

For global food security to be realized despite the increase in world population, sustainable agricultural practices are needed that will not harm the environment. To make the application of AMF and PGPR technology a better choice in ensuring sustainable agricultural practices, there is a need to have a better understanding of the metabolic pathways of AMF and PGPR with their symbiotic interactions with the host plants in the rhizospheres (Desai et al. 2016). Additionally, in having the understanding of the factors that are responsible for AMF and PGPR potentials in promoting health and productivity, there is a need to investigate molecular techniques behind the host-microbe interaction of these beneficial soil microorganisms (Ma et al. 2016). The development of a biological network that involves the use of different omics data can be achieved by creating a genome-scale model mimicking the state of metabolism of microorganisms (Imam et al. 2017). More importantly, the use of omics data as a biological network permits the integration of a large database and spotting/picking out some core genes that can be manipulated to promote the symbiotic association of beneficial soil microbes with the host plant. In manipulating the expression of the genes of interest in the microbes after the regulatory key genes have been identified, the gene-editing method such as TALENs (Transcription Activator Like Effector Nucleases) or CRISPR-Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats, CRISPR/Cpf1 is performed (Fig. 2) (Gupta and Shukla 2017; Mosa et al. 2016). In addition to the integration of a systemic approach in promoting plant development, it is crucial to put into consideration the effect of environmental factors on beneficial microbes' colonization in the plant. It is also needful to acquire more information on the positive effect and synthesis of beneficial microbe technology in promoting plant growth. Also, it is essential to have a well-documented knowledge and complete understanding to improve the technology for future application.

Conclusion and recommedations

In this review we have demonstrated that PGPR and AMF can provide low-cost, eco-friendly pathways to reduce the use of synthetic inputs such as fertilizers and pesticides which causes deleterious effect on human and environment.

In conclusion, it is important for scientists and researchers to focus more attention on the application of these beneficial microorganisms as microbial inoculants for biofertilizer production and usage, to ensure more food production, food safety, food security and agricultural sustainability that will meet food demand, of the increasing world population. The need to intensify more research study on the isolation, characterization of beneficial soil microbe with plant growth promoting traits will be beneficial in enhancing plant growth, yield and improving plant tolerance to abiotic stress is important.

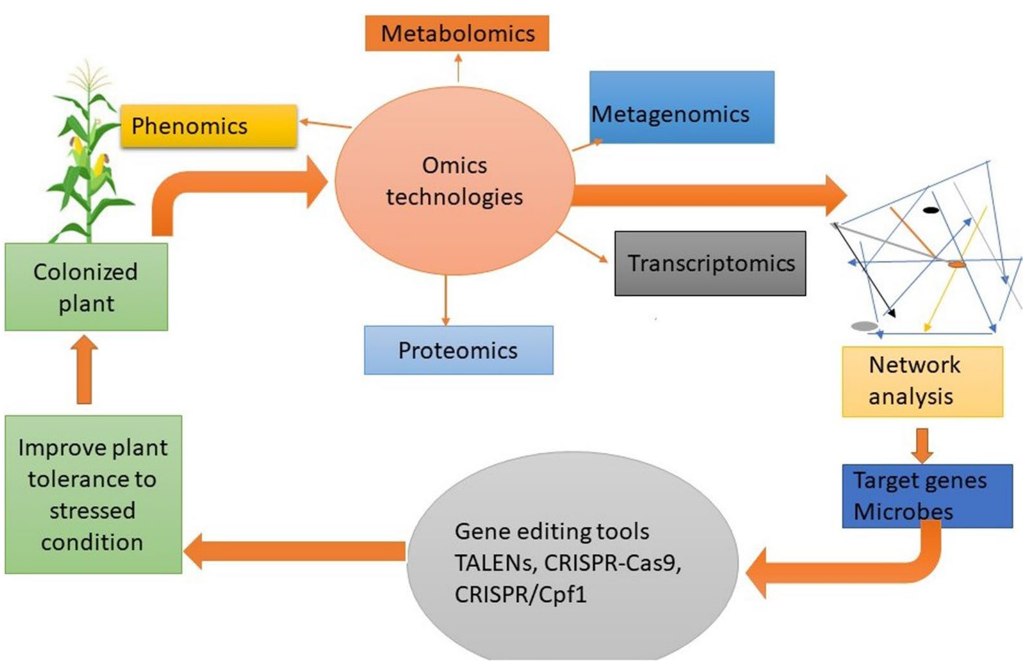

Fig. 2 A schematic representation of the biological technology involves understanding the interaction of beneficial soil microbes with plants for ensuring sustainable agriculture

Increase in availability of these beneficial microbes and more awareness on its acceptances by farmers is recommended for ensuring agricultural sustainability.

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