

The multifaceted plant-beneficial rhizobacteria toward agricultural sustainability

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Citation: Fasusi O.A., Babalola O.O. (2021): The multifaceted plant-beneficial rhizobacteria toward agricultural sustainability. *Plant Protect. Sci.*, 57: 95–111.

Abstract: Agricultural practices depend mainly on the use of chemical fertilisers, pesticides, and herbicides which have caused serious health hazards and have also contributed to the pollution of the environment at large. The application of plant-beneficial rhizobacteria in agrarian practices has become paramount in increasing soil fertility, promoting plant growth, ensuring food safety, and increasing crop production to ensure sustainable agriculture. Beneficial rhizobacteria are soil microorganisms that are eco-friendly and serve as a modern method of improving the plant yield, protecting the plant and soil fertility that pose no harm to humans and the environment. This eco-friendly approach requires the application of beneficial rhizobacteria with plant growth-promoting traits that can improve the nutrient uptake, enhance the resistance of plants to abiotic and biotic stress, protect plants against pathogenic microorganisms and promote plant growth and yield. This review article has highlighted the multitasking roles that beneficial rhizobacteria employ in promoting plant growth, food production, bioremediation, providing defence to plants, and maintaining soil fertility. The knowledge acquired from this review will help in understanding the bases and importance of plant-beneficial rhizobacteria in ensuring agricultural sustainability and as an alternative to the use of agrochemicals.

Keywords: biofertiliser; biocontrol; crop yield; bioremediation; food security

Agriculture greatly contributes to the national income and earnings in developing countries, in a quest to ensure food security and employment. The act of practicing sustainable agriculture is crucial in the world today because it meets the need for more food production in the agricultural sector. The traditional method of practicing agriculture that involves the use of agrochemicals that are harmful to human health and the ecological system will not be able to meet the agricultural demand, because its harmful effects will keep increasing as the human population increases (Enagbonma & Babalola 2019b). The rhizosphere is a region of the soil where microbiological activity takes place as a result of the release of different kinds of plant metabolites called root exudates. These root exudates are made up

of various vitamins, proteins, sugars, and amino acids that are important to microorganisms that dwell in the rhizosphere. Various types of plant-beneficial microorganisms live in the soil and interact with plants and other types of microorganisms (Igiehon & Babalola 2018). Large numbers of rhizobacteria with plant growth-promoting traits and other beneficial microorganisms' growth are supported in the rhizosphere (Bhattacharyya & Jha 2012, Shoaib et al. 2016).

The major problems that have caused a reduction in the crop yields worldwide among farmers are soil infertility, heavy metal contamination, and the infestation of plants by pathogenic microorganisms (Gouda et al. 2018). This challenge could be tackled by improving the quality of the soil through a reduction in land degradation and encouraging the application

of plant-beneficial rhizobacteria as bioinoculants which require knowledge of good agricultural practices. It was reported by Mfilinge et al. (2014) that the major challenge facing the farming system is a reduction in the crop productivity. These low yields in most cereal and leguminous crops can be associated with a reduction in the soil fertility as well as attacks by pathogenic microorganisms. The microorganisms that live in the root region of a plant serve a beneficial purpose to the plant by improving its development and protection (Barea 2015). Rhizobacteria are among these beneficial organisms that can fix atmospheric nitrogen and phosphate solubilisers which are beneficial to plants (Bharti & Barnawal 2019). The application of agrochemicals has contributed to increasing the food production, but it has resulted in the pollution of water bodies, the air and has a deleterious effect on human health (Alori et al. 2017b; Ojuederie et al. 2019). Similarly, the application of agrochemicals has also increased the soil acidification (Gupta et al. 2015). The soil properties, soil fertility, structure, water holding capacity and diversity of the beneficial soil microorganisms have also been affected as a result of the prolonged use of agrochemicals (Enagbonma & Babalola 2019a). Considering the deleterious effect of agrochemicals on humans, plant health and the environment, which will keep increasing with an increase in the human population, there is a need for alternative methods of increasing the soil fertility, preventing pathogen attacks, and also improving food production, which should be inexpensive and should constitute no harm to humans, or the abiotic and biotic components (Iggehon & Babalola 2017; Pathak et al. 2018). The parameters used to assess a plant's health the function and structure of the microorganisms that live within the soil (Zhu et al. 2017). The potential role that beneficial rhizobacteria can play is the transformation of carbon-based organic materials that enhance plant health and promote sustainable agriculture (Olanrewaju et al. 2017).

Therefore, there is a need for the biological means of promoting plant growth and controlling attacks by pathogenic microorganisms which constitute one of the potential solutions and also play a crucial function in improving the crop yield and meeting the challenges caused by the application of agrochemicals.

Plant-beneficial rhizobacteria inoculants are preparations containing cells of efficient rhizobacteria strains that can be applied to the soil or plants to increase the metabolic processes in the plants by pro-

viding the plants with the nutrients that will enhance their growth and also serve as a defence for the plants against microbial pathogens and pests. This review summarises the beneficial role played by beneficial rhizobacteria as environmentally friendly and inexpensive microbial inoculants in improving plant growth, reducing heavy metal contamination, and controlling phytopathogens to ensure sustainable agriculture.

Agrochemical impact on the environment and human health

A large number of people are engaged in farming using agrochemicals to increase food production, which results in the consumption of contaminated farm products by the final consumer, which could constitute a health hazard and a reduction in the diversity of soil microorganisms that are beneficial to promote plant health and development (Alori et al. 2017a). The runoff of these agrochemicals also contributes to surface water and groundwater contamination (Burant et al. 2018). The major ways through which these agrochemicals that are applied to plants find their way into the human body and constitute health problems are through inhalation, penetration through the skin, and through the consumption of food products (Roychowdhury et al. 2014). Several health hazards that affect farmers and consumers of farm products have been recorded as a result of the use of agrochemicals. These include respiratory disorders, skeletal problems, and diseases that are related to the skin (Singh et al. 2018). The major contributing factor why the negative effects of using agrochemicals are more pronounced is inadequate knowledge of the precautions to be taken during application of the agrochemicals, especially those that are hazardous, and their effect in limiting the potential of the beneficial soil microbiota because only a few of these farmers have been trained on the harm attached to the application of agrochemicals and the preventive measures to take during application (Magauzi et al. 2011; Bhandari 2014). A report by the United States Environmental Protection Agency in 2016 has shown that, in some developing countries where the use of agrochemicals is high, there are health problem issues in the population. The major factors that cause the increase in health hazards due to the use of pesticides are the application of the cheapest, but the toxic type of agrochemicals and the presence, in residues, of agrochemicals on the consumable products (Dhananjayan et al. 2020).

<https://doi.org/10.17221/130/2020-PPS>

The novelty in the application of plant-beneficial rhizobacteria for agricultural sustainability

Rhizobacteria are microorganisms that are found in the rhizosphere of plants, those that form a beneficial association with the plant root are called plant growth-promoting rhizobacteria (Hashem et al. 2019a). These groups of bacteria form an interaction with the plant to promote their growth and development (Lobo et al. 2019). Bacteria are among the biotic components of the ecological system and their presence in the rhizosphere serves a beneficial purpose in promoting plants using a scale sequential bioreactor during the plant's growth (Alka et al. 2020).

More importantly, the plant root can stimulate the colonisation of beneficial rhizobacteria in the rhizosphere by releasing ions, enzymes, and some primary and secondary metabolites that are beneficial and can be absorbed by the bacteria (Olanrewaju et al. 2017). Additionally, through the beneficial association of the rhizobacteria with the plant root, their population becomes higher in the plant root region over the bulk soil and serves a beneficial purpose in plant growth promotion and protection (Pathan et al. 2020). The classification of beneficial rhizobacteria can be made into two categories which includes extracellular rhizobacteria that are found in the rhizosphere or the rhizoplane and intracellular rhizobacteria which are found inside the plant root (Gouda et al. 2018).

Beneficial rhizobacteria employ different mechanisms to ensure the nutrient availability and uptake by the plants to promote their growth, (Khan & Bano 2016), which act as biological control agents in protecting plants against pathogenic attacks (Jha & Saraf 2015), preventing plants from experiencing biotic and abiotic stress (Tiwari et al. 2017; Enebe & Babalola 2018) and helping in the bioremediation of heavy metal soil contamination which is beneficial to improve a plant's health (Vishan et al. 2019).

Furthermore, beneficial-plant rhizobacteria are considered crucial in ensuring sustainable agricultural practices with a greater worldwide demand and their eco-friendly approach when compared to the use of agrochemicals because of their beneficial interaction with the plant and other soil microorganisms. In developing countries, changes in the climatic conditions, an increase in the human population, and industrialisation have contributed to a negative impact on food security and the plants' accessibility to nutrient requirements for their growth (Myers et al. 2017). The application of rhizo-

sphere engineering using beneficial rhizobacteria is an ecological-friendly technique to meet the global demand for food and ensuring agricultural sustainability (Ahmadi et al. 2017). Recently, in increasing the interaction of rhizobacteria with plants, the application of a metaorganism approach is now being employed which involves bringing together different strains of microorganisms, conducting molecular investigations of the rhizobacteria strains, selecting specific host plants and investigating their sole and microbial consortium in situ (Thijs et al. 2016).

Additionally, the application of plant growth-promoting rhizobacteria is receiving more awareness because they are environmentally friendly, easy to handle, and cost-effective (Guo et al. 2020). The bigger delivery strength of applying plant growth-promoting rhizobacteria is their biological control activity against plant pathogens, their bioremediation ability in reducing heavy metal contaminated soil, promoting plant growth, and improving food safety and quality (Vejan et al. 2016).

Underlying plant-beneficial rhizobacteria mechanisms of action

Beneficial rhizobacteria promote plant growth through different mechanisms which include phosphatesolubilisation, nitrogen fixation, the production of siderophore, the production of phytohormones, the production of 1-aminocyclopropane-1-carboxylate deaminase (ACC), the induction of systemic resistance and could also act as biological control agents (Figure 1).

Phosphate solubilisation

Phosphorus can be regarded as a nutrient that is important to plants because it helps to improve their growth. Phosphate solubilising bacteria are beneficial rhizobacteria that solubilise phosphorus into a form that can be useful to plants and could equally enhance their growth (Alori et al. 2017b). The absence of phosphorus in the soil limits plant growth. The amount of phosphorus in the soil depends largely on the soil properties, such as the pH and type of soil. Organic phosphorus accounts for 29–65% of the total soil phosphorous content, but it contributes up to 90% of the total soil phosphorus in some soil types (Ghorbani-Nasrabadi et al. 2012). Usually, the phosphorus content in the soil must be present in large amounts for plant use. Nevertheless, a very little fraction of this huge amount is readily made available to the plants because phosphorus is highly reactive,

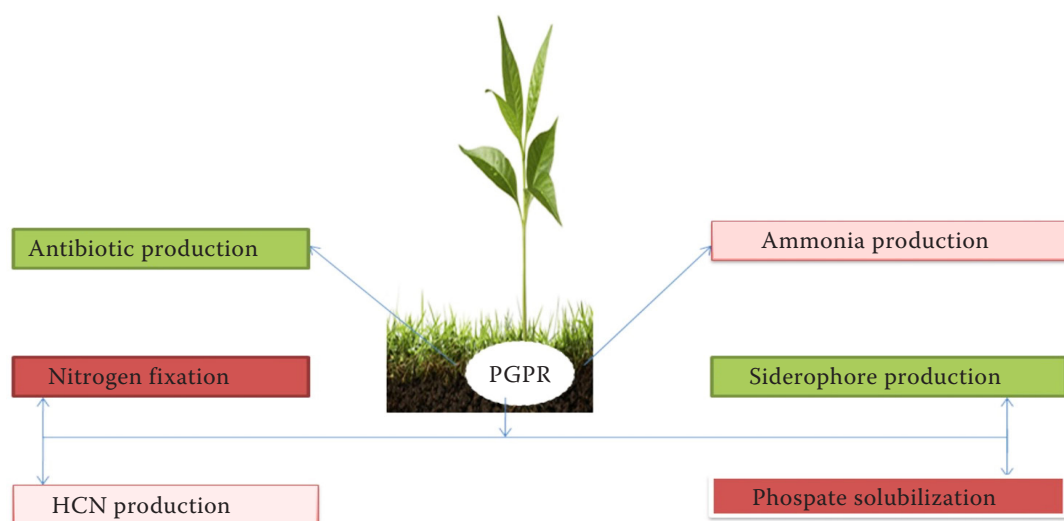


Figure 1. Mechanisms of beneficial rhizobacteria on plant
PGPR – plant growth-promoting rhizobacteria

which makes complexes with other elements that are not taken up by the plants. Plants can only uptake monobasic and dibasic forms of phosphorus. To fulfil the requirements of phosphorus, traditional agricultural practices make use of rock phosphate fertilisers, which result in the depletion of phosphate reservoirs. Several bacterial genera such as *Bacillus*, *Rhizobium*, *Pseudomonas*, *Azotobacter*, and *Azospirillum* species can be classified among phosphate solubilising rhizobacteria (Shah et al. 2018). Likewise, actinomycetes like *Streptomyces alboniger*, *S. venezuelae*, *S. aureofaciens*, and *S. lienomycini*, have been demonstrated to produce extracellular phytate-degrading enzymes, i.e., phytases which correspond to a group of phosphomonoesterases that initiate the stepwise breakdown of phytate (Barman et al. 2019). These phytases have been recorded as acid and alkaline phytases. The production of acidic compounds by soil microbial flora could also be a process by which phosphate can be solubilised, and it depends on the metabolic pathways to utilise different carbon sources. However, the mechanism of acidification in phosphate solubilisation by *Actinobacteria* has rarely been reported (Jog et al. 2014). Therefore, enzymatic degradation of phosphate complexes plays a crucial role in making the phosphorus and essential compounds available that are needed for plant growth.

Production of phytohormones

Plant growth is controlled by phytohormones like auxin and ethylene, which have a positive effect on plants. Phytohormones are messengers which are

chemicals that play an important function in improving the plant development, seed germination, and flowering time in plants (Jiang et al. 2017). More so, root exudates secreted by plants in the rhizosphere help to modulate the microflora around plant roots and construct a potential environment for the synthesis of indole-3-acetic acid (IAA) by the beneficial microorganisms in the rhizosphere. One of the major direct mechanisms of beneficial rhizobacteria is the production of phytohormones like gibberellic acid and IAA (García-Fraile et al. 2015). Interestingly, the biological synthesis of phytohormones by beneficial rhizobacteria can be associated with nutrient availability and the promotion of growth in plants (Stamenković et al. 2018). The major auxin that is found in the plant is called IAA. The roles performed by IAA in plants are cell division, root elongation, and cell differentiation. *Actinobacteria* have been studied to produce phytohormone belonging to a class of auxins, i.e., IAA which is a common hormone produced by plants (Ranveer et al. 2014). Likewise, ethylene, another important phytohormone, regulates plant growth by promoting root growth, flowers and fruits, as well as interacts with the microorganisms that are present in the plant root (Dubois et al. 2018). Besides plants, some beneficial bacteria genera produce IAA, such as *Streptomyces* (Vurukonda et al. 2018), *Rhizobium* (Tan et al. 2015), *Pantoea*, and *Agrobacterium* (Paiteir et al. 2019). However, Mishra et al. (2020) reported the production of IAA in *Pseudomonas* and *Ochrobactrum* species. Similarly, the production of cytokinins was reported

<https://doi.org/10.17221/130/2020-PPS>

in *Bacillus megaterium*, *Bacillus subtilis*, *Bacillus cereus*, and *Pseudomonas fluorescens* G20 (Hashem et al. 2019b). The production of IAA is an indication of the part of the communication between the plants and the beneficial bacteria that reside in the rhizosphere (Hassan et al. 2019). Their IAA producing trait makes them a potential candidate in agricultural practices as natural fertilisers in maintaining agricultural sustainability.

Utilisation of 1-aminocyclopropane-1-carboxylate (ACC)

Some rhizobacteria genera like *Actinobacteria* have the potential to utilise ACC that acts as a molecule for the biological synthesis of ethylene (Nascimento et al. 2018). However, ethylene performs a lot of biological activities in plants which helps in regulating the process of ripening fruits and in seed germination. Ethylene is often called the "ageing hormone" because of its role in enhancing plant developmental processes which include ripening, senescence, and abscission (Schaller 2012). An enzyme known as ACC-deaminase catalyses the hydrolysis of ACC into NH_3 and α -ketobutyrate. Some bacteria genera were reported to produce ACC-deaminase, this includes *Streptomyces*, *Pseudomonas*, *Bacillus*, *Azotobacter*, and they are considered as beneficial rhizobacterial strains in improving plant health (Glick 2014). A recent research study has revealed an increase in tomato growth (*Lycopersicum esculentum*) inoculated with *Streptomyces filipinensis* and *S. atroviens* due to the production of aminocyclopropane-1-carboxylate-deaminase (Buzón-Durán et al. 2020).

Production of siderophore

Siderophore can be referred to as a compound that is produced by some groups of microorganisms in the condition where the availability of iron is limited (Mhlongo et al. 2018). They are small peptide molecules that consist of side chains and a functional group where ferric iron can be attached (Goswami et al. 2016). Iron is an essential element in living things because it is responsible for the catalysis of numerous enzymatic reactions where it acts as a co-factor. Furthermore, microorganisms that produce siderophore reduce the amount of iron that is available to plant pathogens which could eventually reduce the percentage of pathogen proliferation by plants and promote plant growth (Etesami & Maheshwari 2018). Earlier, iron was usually present in the ferrous form (Fe^{2+}) in soils when the atmosphere

was oxygen-deficient and it was easily utilised by the microorganisms. However, with time, as the oxygen-deficiency in the atmosphere has been replaced by an oxygen-rich environment, iron gets oxidised into a ferric form (Fe^{3+}) which is not readily utilised by microorganisms. The competition for iron acquisition occurs between plants and phytopathogens as microbial siderophores have a higher affinity towards iron chelation making the iron unavailable to plants. High levels of siderophore production have been reported in *Bacillus* that were isolated from the maize rhizosphere (Bjelić et al. 2018).

More importantly, plant growth-promoting rhizobacteria that produce siderophores are becoming more relevant because they improve the iron nutrition in plants that are grown in iron-deficient soils (Figueiredo et al. 2016). Siderophores also help in alleviating heavy metal stress in a plant grown in a heavy metal polluted soil, which can be detrimental to plant health (Ahemad & Kibret 2014; Asad et al. 2019). Several bacteria genera have been reported to produce siderophores, this includes *Streptomyces* (Goudjal et al. 2016), *Azospirillum* (Banik et al. 2016), *Paenibacillus* (Liu et al. 2017), *Pseudomonas* (Deori et al. 2018), *Azotobacter* (Romero-Perdomo et al. 2017).

Production of hydrogen cyanide (HCN)

An important feature of some beneficial rhizobacteria is the production of HCN. The action mechanism of HCN is considered to inhibit the terminal cytochrome c oxidase in the respiratory chain as it binds to metalloenzymes which confers it as a property suppressing phytopathogens (Rosier et al. 2018). The *Rhizobium*, *Pseudomonas*, *Alcaligenes*, *Bacillus*, *Aeromonas*, and *Streptomyces* species are hydrogen cyanide producers. Hydrogen cyanide has also been reported to contribute to the mineral mobilisation and phosphate release which results in an indirect increase in the nutrient availability to both *Actinobacteria* and their host plants (Rijavec & Lapanje 2016). Based on the ability of HCN to prevent plant pathogens and to enhance nutrient availability, HCN producing rhizobacteria can be used as a biocontrol agent and biofertiliser for plant growth promotion and protection.

Nitrogen fixation

Approximately 80% of the nitrogen in the atmosphere cannot be made available to plants because it occurs as an inert gas (Patel & Minocheherhomji 2018). Besides, nitrogen is an important nutrient

that is responsible for plant growth. However, for atmospheric nitrogen to be used directly by plants, it must be converted to ammonia and this process is called nitrogen fixation (Byrne et al. 2019). The process of conversion of atmospheric nitrogen to ammonia is performed by beneficial microorganisms that can fix nitrogen and the action is aided by an enzyme called nitrogenase (Kumar et al. 2019).

The association built by nitrogen-fixing microorganisms with the host plant could be symbiotic or non-symbiotic. In a soil that is nitrogen deficient, a large amount of nitrogenous based fertiliser needs to be applied to the soil so that the amount of nitrogen required by plants to improve their growth is available to the plant. Some rhizobacterial species that have the ability to fix nitrogen are *Azospirillum*, *Acinetobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, *Azorhizobium* and *Serratia*. They colonise plant roots and fix the atmospheric nitrogen which improves the plant growth (Babalola 2010).

Production of lytic enzymes

The cell wall of microorganisms is responsible for maintaining the integrity of cells under all kinds of environments, i.e., isotonic, hypotonic, and hypertonic. The cell wall of different organisms is composed of various kinds of complex polymeric substances. For instance, the composition of the fungal cell wall is made up from chitin, while the bacterial cell wall is made up from peptidoglycan, i.e., a polysaccharide chain cross-linked with unusual peptides (Arroyo et al. 2016; Walter & Mayer 2019). The cell wall of pathogenic bacteria, fungi, and protozoa are hydrolysed by lytic enzymes, such as protease, acylases, and lactonases that are produced by beneficial rhizobacteria, thereby preventing pathogenic microorganisms from causing diseases in plants (Felestrino et al. 2018). Recently, *Streptomyces* spp. has been reported to produce chitinases, *Streptomyces* RC1071 isolated from cerrado soils was tested against a phytopathogenic fungus and was reported to have an antifungal activity (Shafi & Khattab 2020). Similarly, *Actinomycetes* have also been reported to produce proteases, lipases, chitinases, and cellulases (El-Sherbiny et al. 2017). The production of lytic enzymes by *Actinobacteria* grants them a biocontrol potential and helps improve plant growth characteristics (Wani & Gopalakrishnan 2019).

Several genera of bacteria have proved their importance as antagonistic agents against plant patho-

gens, these include *Bacillus*, *Azospirillum*, *Serratia*, *Pseudomonas*, *Pythium*, and *Coniothyrium* (Heidarzadeh & Baghaee-Ravari 2015). The application of these microorganisms over time has proved successful in colonising the plant rhizosphere and in promoting their growth (Becker et al. 2018).

Production of antibiotics

The production of secondary metabolites has been studied in beneficial rhizobacteria, i.e., by-products of metabolism that are not generally essential for their growth. These metabolites are known as antibiotics (Gislason et al. 2020). Antibiotic production by beneficial soil bacteria exhibits antitumor, antifungal, immunosuppressive, insecticidal, herbicidal and many clinically commercially important activities. Among the bacteria, *Streptomyces* spp. has been reported to produce a wide variety of antibiotics belonging to class β -lactam (Ogawara 2016). However, antibiotic production by beneficial soil bacteria differs in their chemical structure and effects on the different plant pathogens. In the rhizosphere, antibiotics produced by soil-dwelling bacteria inhibit plant pathogens fungistatically by targeting either the essential molecules or biosynthetic pathways and its production depends upon several factors like: the temperature, aeration, and presence of competing microorganisms (Shaikh & Sayyed 2015; Omran & Kadhem 2016). *Bacillus subtilis* has been reported to produce antibiotics known as zwittermicin and mycosubtilin that are effective against some fungal pathogens (Saraf et al. 2014). Recently, the deteriorative effect of *Rhizoctonia solani* on plants has been inhibited by pyrrolnitrin antibiotics produced by *P. fluorescens* BL915 (Tariq et al. 2017). Additionally, *Pseudomonas chlororaphis* that synthesised phenazine with an antagonistic activity have been reported by Chen et al. (2015) to inhibit the growth of pathogenic fungi *Fusarium oxysporum*, *Rhizoctonia solani*, and *Pythium ultimum*. Therefore, beneficial bacteria that live in the soil produce different types of antibiotics depending upon the environmental conditions to protect the plant against pathogen attacks which could be detrimental to the plant growth and productivity.

Multitasking role of beneficial rhizobacteria in agriculture

The role of rhizobacteria as biofertilisers in crop production. Microorganisms that are living in the soil are crucial because they decompose organic matter

<https://doi.org/10.17221/130/2020-PPS>

and also ensure that the nutrients needed for plant development are made available to the plants (Bahadur et al. 2016). The presence of beneficial bacterial in the soil certainly increases the nutrients that are present in the soil and improves the plant growth and yield which results in sustainable agriculture. A biofertiliser serves as an inexpensive source of nutrients to the plant so that the quality of the crop yield can be improved (Shabbir et al. 2019). Soil microorganisms help in the fixation of nitrogen to the plants by converting atmospheric nitrogen to a form that is assimilated by the plants and will result in improving their growth. *Rhizobium*, *Bradyrhizobium*, and *Azorhizobium* fix nitrogen to the legume through a symbiotic association which results in the formation of nodules in the plants (Iggehon & Babalola 2018). *Rhizobium* inoculation helps to enhance the root nodulation, improve the plant growth, and produce an increase in grain yield under cultivated conditions when compared to an uninoculated plant. The mi-

croorganisms used in the production of biofertilisers increase the plant yield through the fixation of atmospheric nitrogen, phosphate solubilisation, and phosphate mobilisation. The application of beneficial rhizobacteria fertilisers by farmers is increasing because they improve the soil quality, are cost-effective and pose no harm to humans and the environment, and result in limiting the application of chemical fertilisers (Singh et al. 2019).

More so, a lot of success has been recorded in the application of beneficial rhizobacteria as biofertilisers in promoting plant growth (Table 1). Recently, the research conducted by Bharti and Barnawal (2019) on the inoculation of wheat plants with *Dietzia natronolimnaea* was reported to increase the plant biomass and enhance its tolerance to salinity. In addition to this, Kuan et al. (2016) were able to screen some selected beneficial rhizobacteria like *Klebsiella pneumoniae*, *Bacillus pumilus* and the *Acinetobacter* species in improving maize

Table 1. Summary of the beneficial rhizobacteria strains used as a biofertiliser with their effect on the crop enhancement

| Plant growth-promoting rhizobacteria strain | Plants | Effect on crops enhancement | References |
|--|---|---|----------------------------------|
| <i>Pseudomonas granadensis</i> T6 | rice (<i>Oryza sativa</i>) | plant growth promotion | (Shen et al. 2019) |
| <i>Rhizobium leguminosarum</i> sv <i>viciae</i> NGB-FR 126 | fab beans (<i>Vicia faba</i>) | enhances the root length, weight and promote growth by 81% | (Youseif et al. 2017) |
| <i>Alcaligenes faecalis</i> | okra (<i>Abelmoschus esculentus</i>) | responsible for the production of IAA in okra (<i>Abelmoschus esculentus</i>) | (Perez-Harguindeguy et al. 2016) |
| <i>Azospirillum brasilense</i> | Wheat (<i>Triticum aestivum</i>) | responsible for an increase in height. | (Karimi et al. 2018b) |
| <i>Bradyrhizobium yuanmingense</i> VIBA-2 | cowpea (<i>Vigna unguiculata</i>) | promote growth by 38% when compared with uninoculated plant | (Gómez Padilla et al. 2016) |
| <i>Rhizobium leguminosarum</i> sv <i>phaseoli</i> HB-429 | common beans (<i>Phaseolus vulgaris</i>) | plant growth promotion | (Samago et al. 2018) |
| <i>Pseudomonas aeruginosa</i> | broad beans (<i>Vicia faba</i>) | promote the remediation ability of plant | (Babalola 2010) |
| <i>Rhizobium</i> spp. | mung beans (<i>Vigna mungo</i>) | promote the growth and improve weight in <i>Vigna mungo</i> | (Ravikumar 2012) |
| <i>Azospirillum brasilense</i> Ab-V5 and Ab-V6 | maize (<i>Zea mays</i>) | plant growth promotion | (Galindo et al. 2019) |
| <i>Bradyrhizobium</i> spp. | soybeans (<i>Glycine max</i>) | enhance nodulation in leguminous crop as their plant part grows | (Iggehon et al. 2019) |
| <i>Bacillus tequilensis</i> PBE1 | tomato (<i>Solanum lycopersicum</i>) | plant growth promotion | (Bhattacharya et al. 2019) |
| <i>Pseudomonas</i> , <i>Bacillus</i> | turmeric | plant growth promotion | (Kumar et al. 2015) |

IAA – indole-3- acetic acid

growth. In the research, it was reported that the plant growth-promoting rhizobacteria improved the maize ear yield when compared with the uninoculated plants. The positive effect of beneficial rhizobacteria *Pseudomonas* and *Agrobacterium* isolated from the root of *Arthrocnemum indicum* possessed plant growth-promoting activity which includes phosphate solubilisation, the production of indole-3-acetic acid, the ability to reduce acetylene and showed a positive reaction to ACC deaminase activity was recorded when the peanut plant was inoculated. They colonised the peanut roots and were capable of increasing the peanut growth over the uninoculated plants (Sharma et al. 2016). Similarly, Panwar et al. (2016) have also evaluated the effect of *Pantoea* and *Enterococcus* with plant growth-promoting traits on mung beans, the two rhizobacteria showed a better performance in increasing the plant growth over uninoculated mung bean plants under a salt stress condition. Likewise, the inoculation of the plant growth-promoting strain of *Bacillus* sp RZ2MS9 and *Burkholderia ambifaria* RZ2MS16 was reported by Batista et al. (2018) in promoting corn and soybean growth under greenhouse conditions when compared with an uninoculated control for both strains and crops. Chukwuneme et al. (2020) reported the plant growth-promoting potential of *Arthrobacter arilaitensis* and *Streptomyces pseudovenezuelae* in promoting maize growth under water-stressed conditions. In the research, the maize plants were protected against the deleterious effect of drought and a significant increase in the physiological parameters was recorded over the control plant.

Role of plant beneficial rhizobacteria as biological control agents against phytopathogens. The application of beneficial rhizobacteria as bioinoculants in controlling pests and pathogenic microorganisms that affect plants has been confirmed to be the best alternative to the use of agrochemicals because it is cheap, environmentally friendly and acts as a sustainable agricultural management approach in protecting plants. This makes plant growth-promoting rhizobacteria an acceptable biological tool for controlling plant diseases and ensuring good agricultural practices (Farha et al. 2018). There are a lot of biocontrol agents that are present in the market, but it is crucial to understand their interaction with plants, pathogens, and the environment before their use because the purpose of the application may not be achieved if the plant is already under attack from

diseases (Liang et al. 2015). A biocontrol can be defined as an interrelationship that occurs in plants through the action of some beneficial microorganisms, aimed at reducing the negative effects of pathogenic microorganisms that harm the plants, thereby enhancing the plant growth (Farha et al. 2018).

Some plant growth-promoting rhizobacteria have been reported for their potential to reduce diseases caused by pathogenic fungi and bacteria in plants which makes them the best option to be used as biocontrol agents (Table 2) (Rani et al. 2018). Adopting the use of beneficial rhizobacteria as a biocontrol agent in suppressing diseases in plants is also a low cost and safe method of crop management. Considering the toxicological aspect of chemical pesticides, it can be confirmed that most biopesticides are less toxic and more environmentally friendly than chemical pesticides. More importantly, the need to use beneficial rhizobacteria as an alternative that have not been chemically synthesised, especially biopesticides, are increasing globally because they pose no harm to the ecological system (Gross et al. 2014; Czaja et al. 2015). The action mechanisms that allow beneficial rhizobacteria to be used as biocontrol agents are the production of lytic enzymes, the competition for nutrient availability and the production of secondary metabolites/antibiotics that suppress the proliferation of plant pathogens (Alori & Babalola 2018). The application of beneficial rhizobacteria as biocontrol agents modulate hormones, like ethylene and auxin, in plants and reduce the rate of damage to the plants by pathogenic microorganisms.

Interestingly, the control of fungal infections and herbicidal activities is part of the important role played by plant growth-promoting rhizobacteria bioinoculants on plants, for example, *Aspergillus flavus*, in stored and field products, was reported to be controlled by *Bacillus subtilis*. *Rhizobium* had also served as a biocontrol agent against *Pythium* diseases (Alori & Babalola 2018). *Pseudomonas* was also used as a biocontrol agent for Fusarium wilt (Cepeda 2012). The biocontrol ability of plant growth-promoting rhizobacteria was conducted by Kumar et al. (2016), the report from the findings revealed that the inoculation of *Paenibacillus lentimorbus* with *Nicotiana tabacum* improved the plant growth and acted as a biocontrol agent against the mosaic virus in cucumbers. Beneficial rhizobacteria are seen as an alternative to the use of agrochemicals in suppressing soil-borne pathogens and are responsible for the mobilisation of nutrients in the soil (Meena et al. 2017).

<https://doi.org/10.17221/130/2020-PPS>

Table 2. Some beneficial rhizobacteria that have been tested as microbial inoculants in controlling plant diseases

| Microbial isolates | Host plant | Diseases causative agent | Diseases | Mechanisms involved | Effect on plants | References |
|---|---|--------------------------------|----------------------|---|---|----------------------------------|
| <i>Pseudomonas fluorescens</i> | olive trees (<i>Olea europaea</i>) | <i>Verticillium dahlia</i> | Verticillium wilt | improve plant growth and induce systemic resistance | reduce the severity of the disease caused by the pathogen | (Gómez-Lama Cabanás et al. 2014) |
| <i>Serratia plymuthica</i> | oilseed rape (<i>Verticillium longisporum</i>) | <i>Verticillium dahlia</i> | Verticillium wilt | interference of signal (Quorum sensing) | reduce the severity of the disease caused by pathogens | (Kaouthar et al. 2016) |
| <i>Bacillus subtilis</i> S499 | tomato (<i>Solanum lycopersicum</i>) | <i>Fusarium</i> spp. | | induction of systemic resistance | suppress the effect of pathogen attack on plant | (Tabassum et al. 2017) |
| <i>Pseudomonas fluorescens</i> | sugar cane (<i>Saccharum officinarum</i>) | <i>Colletotrichum falcatum</i> | red rot | activation of induced systemic resistance | production of defensive enzymes for treatment of the plant tissue | (Farha et al. 2018) |
| <i>Pseudomonas denitrificans</i> , <i>Pseudomonas putida</i> | oaks (<i>Quercus</i> spp) | <i>Ceratocystis fagacearum</i> | oak wilt | induced systemic resistance defence | reduce crown loss | (Zheng et al. 2012) |
| <i>Pseudomonas fluorescens</i> PNA1 | chickpea (<i>Cicer arietinum</i>) | <i>Fusarium</i> spp. | <i>Fusarium</i> wilt | induced systemic resistance defence | limit severity of diseases by causative organisms | (Babalola & Glick 2012) |

The application of *Bacillus cereus* TSH77 that are known to contain fengycin and surfactin through investigation of an acid cell-free culture filtrate has been reported by Chauhan et al. (2016) to suppress the proliferation of the *Fusarium solani* plant pathogen that caused rot disease in potatoes. Likewise, *Bacillus methylotrophicus* was reported for its antifungal activity against *Fusarium oxysporum* and *Rhizoctonia solani* (Devi et al. 2018). In the quest for more food production globally, the research conducted by Fu et al. (2017) revealed that the inoculation of a newly established banana plantation with *Bacillus amyloliquefaciens* NJN-6 suppressed Fusarium wilt. Likewise, the biocontrol activity of *Rhizobium* isolated from the rhizosphere of different plants was reported to suppress the growth of the plant pathogens *Rhizoctonia solani* and *Sclerotium rolfsii* under *in vitro* condition (Manasa et al. 2017). Similarly, the application of *Bacillus subtilis* and *Bacillus amyloliquefaciens* in suppressing the pathogenic effect of *Phytophthora sojae* was reported by Liu et al. (2019) to inhibit the *Phytophthora sojae* hyphae growth that causes soybean blight. The plant growth-promoting trait and biocontrol potential of the beneficial rhizobacteria strain *Acinetobacter* spp. PKA and *Ochrobactrum intermedium* TRD14 was conducted in a greenhouse against a root rot pathogen in the sugarcane *Colletotrichum falcatum*. The bacteria were reported to suppress pathogen growth and promote the plant growth parameters in the sugarcane (Patel et al. 2019). *Streptomyces cochorusii* have been reported by Yang et al. (2017) to be effective against *Rhizoctonia solani* that causes sheath blight diseases in rice. Rice sheath blight is among the worst rice diseases globally because it causes yield losses in rice of more than 50% approximately (Yang et al. 2017).

Significance of plant-beneficial rhizobacteria on heavy metal bioremediation

Bioremediation is a process that involves the use of beneficial rhizobacteria as inoculants to resolve the negative effects of industrialisation on the environment and plant health as a result of metal spillage (Ojuederie & Babalola 2017). Notably, agricultural practices are negatively affected by the presence of heavy metals because it results in soil contamination which makes it unfit for agricultural purposes and could be harmful for the plant development (Ayangbenro & Babalola 2017). Though metals are important to plants, their presence in excess

amounts becomes hazardous to the plant's health (Asati et al. 2016). Therefore, there is a need for metals to remain in a stable state for them to be useful to plants, but if they are available in an unstable state, they become detrimental to plant health by disrupting the biological processes that occur in the plant (Masood & Bano 2016). More so, metals can attach to some enzymes or molecules which cause stress to the plant and they can also attack protein formation, thereby becoming toxic to plants (Wang et al. 2016). The application of microorganisms like plant beneficial rhizobacteria in bioremediating metal polluted environments is an approach that is non-hazardous to the ecological system when compared with agrochemicals that pose harm to the biotic and abiotic components (Dixit et al. 2015). Similarly, rhizobacteria with a plant growth-promoting ability through the production of siderophores has helped in plant development by removing heavy metals from the polluted soil and providing the nutrients needed for plant survival in a soil polluted by heavy metals (Kumar et al. 2020). The application of plant growth-promoting rhizobacteria in the bioremedia-

tion of a soil polluted by heavy metals is attached to features such as the ubiquity, size, and ability to grow in both controlled and stressed conditions (Srivastava 2015). Several genera of plant growth-promoting rhizobacteria have been reported in the bioremediation of heavy metals such as the *Bacillus*, *Pseudomonas*, and *Micrococcus* species (Table 3). Some of the processes through which the microorganisms remediate their environment are rhizofiltration, biosorption, bioaccumulation, and biomineralisation (Wang et al. 2016).

The bioremediation ability of *Bacillus cereus* to remove mercury from a synthetic effluent was conducted in a laboratory experiment designed by Sinha et al. (2012) using a scale sequential bioreactor. In the research, it was reported that *Bacillus cereus* was able to remove approximately 104 mg/g of mercury on the third day. The report of *Micrococcus luteus* in removing a large amount of lead from a synthetic medium with the removal capacity of 1964 mg/g was reported by Puyen et al. (2012). Similarly, the application of *Desulfovibrio desulfuricans* in the removal of nickel, copper, and chromium from contaminated

Table 3. Summary of potential plant growth-promoting rhizobacteria strains employed in heavy metal bioremediation

| Plant growth-promoting bacteria strains | Tested plants | Plant growth-promoting trait | Heavy metal | References |
|---|----------------------------|---|-------------|-----------------------------|
| <i>Rhizobium leguminosarum</i> pr1 | <i>Vicia faba</i> | IAA | Pb, Cd, Cu | (Saadani et al. 2016) |
| <i>Pseudomonas aeruginosa</i> CPSB1 | <i>Triticum aestivum</i> | production of siderophore, HCN phosphate solubilization | Cr, Cu, Mn | (Hassan et al. 2017) |
| <i>Bacillus licheniformis</i> , <i>Micrococcus luteus</i> | <i>Vitis vinifera</i> | siderophore production, nitrogen fixation, phosphate solubilization | As | (Pinter et al. 2017) |
| <i>Pseudomonas</i> spp. | <i>Centaurea cyanus</i> | production of ACC deaminase siderophore | Pb | (Karimi et al. 2018a) |
| <i>Bacillus megaterium</i> H3 | <i>Bactris campestris</i> | production of siderophore and IAA | Cd, Pb | (Wang et al. 2018) |
| <i>Enterobacter</i> spp. HU38 | <i>Leptochloa fusca</i> | production of IAA and siderophore | Cr | (Ashraf et al. 2018) |
| <i>Acinetobacter iwoffii</i> RJB-2 | <i>Vigna radiata</i> | production of siderophore phosphate solubilization and IAA | As | (Das and Sarkar 2018) |
| <i>Pseudomonas agglomeran</i> RSO6 | <i>Spartina densiflora</i> | phosphate solubilization and nitrogen fixation | Zn, As, Pb | (Paredes-Páliz et al. 2018) |
| <i>Variovorax paradoxus</i> 5C-2 | <i>Pisum sativum</i> | production of ACC deaminase | Cd | (Kumar et al. 2020) |
| <i>Pseudomonas</i> spp. A3R3 | <i>Ricinus communis</i> | production of siderophore | Zn | (Ma et al. 2015) |

IAA – indole-3- acetic acid; ACC – aminocyclopropane-1-carboxylate; HCN – hydrogen cyanide

<https://doi.org/10.17221/130/2020-PPS>

seawater have been reported by Kim et al. (2015) with the capacity of removal ranging from 90–100 mg/g after seven days of the application.

Application of plant-beneficial rhizobacteria as biostimulant for plants

Biostimulants are materials of biological origin that contain microorganisms that can enhance the natural soil and, when applied in a small quantity, they promote plant growth (Yakhin et al. 2017). *Azospirillum*, which is the most popular genus of rhizobacteria, has been known to improve plant development in the plant's roots, where it can obtain a large carbon source and exudates that could serve as a nutrient for the beneficial rhizobacteria that live around the root region (Ramos et al. 2011). With this association of beneficial microbes with the plant root, the microorganisms will be able to produce some enzymes and plant hormones that will serve as protection for the plant against plant pathogens (Lawal and Babalola 2014). In the plant's roots and in the soil, millions of plant beneficial rhizobacteria are found that live symbiotically with them. Different strains of *Azospirillum* like *A. brasilense* and *A. lipoferum* have been used as a biostimulant in crops to improve their yield (Fei et al. 2019).

The benefits obtained by plants through the use of *Azospirillum* as a biostimulant are the nitrogen fixation and the production of indole-3-acetic acid, which enhances the root hair growth in the plants for the proper uptake of minerals (Lawal & Babalola 2014). Similarly, the stimulatory activity of plant growth-promoting rhizobacteria in promoting the plant have been reported in *Bacillus subtilis* KB105, *Peanibacillus graminis* FL400, *Bacillus amiloliquefaciens* SQR9 and *Bacillus pumilus* OS15, which makes the bacteria strains a good source of microbial inoculants in ensuring sustainable agriculture (Rouphael & Colla 2020).

CONCLUSION

The rate at which we use agrochemical products that caused ecological imbalance has encouraged industries responsible for the production. Therefore, there is a need to look for an alternative means of increasing food production, enhancing the plant health, reducing pathogen infections, and increasing the soil fertility, which will pose no harm to humans and the environment. The knowledge of the multifaceted role of plant-beneficial rhizobacteria

as bioinoculants can fill the gap in the food production, bioremediation, and pathogen control to meet the food demand by the increased global population. Also, it is important to appreciate the usefulness of beneficial rhizobacteria with their plant-growth-promoting and biocontrol potential as a modern way of improving crop productivity, food quality, and ensuring sustainable agriculture.

Conclusively, there is a need for more research to unveil the potential beneficial rhizobacteria as bioinoculants in increasing the plant development, plant defence and productivity toward ensuring sustainable agriculture.

Acknowledgement: OAF appreciates the National Research Foundation, South Africa, The World Academy of Science (NRF-TWAS) for PhD stipend.

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Received: September 4, 2020

Accepted: January 15, 2021

Published online: March 1, 2021