Chapter 7
Status and Prospects of Bacterial Inoculants for Sustainable Management of Agroecosystems

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Abstract Bacterial inoculants are bacterial species that are applied directly or indirectly to enhance the growth and yield of plants. The application of bacterial inoculants is largely due to their compatibility and complementarity with natural processes of nutrient cycling, plant protection and other related biological processes in agroecosystems. As a nature-based solution, bacterial inoculants are able to drive many beneficial biological processes in agroecosystems with little or no negative impacts. However, their applications have been limited by factors such as awareness, production quality and quantity, storage and compatibility. Although there are studies that are already investigating many of these challenges, the future prospects of the application of bacterial inoculants will be determined by the adoption of new technologies that include multi-omics approach for improving the quality as well as applicability of these beneficial microorganisms.

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7.1 Introduction

The core objective for sustainable agriculture is promoting a healthy environment while producing sufficient yield of crops to meet the requirements of an increasing world population. Generally, the vision of sustainable agriculture guarantees biosafety, nutrient-rich yield and efficient soil nutrient utilisation as well as increased crop productivity without compromising environmental integrity or public health (Lesueur et al. 2016; Lichtfouse et al. 2009). The application of chemical inputs such as inorganic fertilisers, pesticides and herbicides in agriculture has, without doubt, led to increased crop productivity over the years (Chianu et al. 2012; Hermary 2007). Nevertheless, their excessive application and inefficient management have contributed to soil degradation and environmental pollution, along with associated human, animal and crop health risks (Wallace and Knausenberger 1997).

Globally, there is an evolving consensus that encourages the adoption of suitable practices for management of both the agroecosystems and the environment in general. Of great importance is the use of beneficial plant and soil microorganisms, also known as biofertilisers or inoculants. They are regarded as active biological agents, free of agrochemicals, but contain microorganisms that are known to drive the biogeochemical cycles (Szilagyi-Zecchin et al. 2016; Trabelsi and Mhamdi 2013; Sayyed et al. 2012). These microorganisms hold huge potential in improving crop health through their ability to produce plant growth-promoting (PGP) substances such as siderophores, antifungal metabolites and 1-aminocyclopropane-1-carboxylate acid (ACC) (Khan et al. 2016a; Vejan et al. 2016; Glick 2014).

Microbial inoculants are classified based on different factors, which include type and functional capabilities of microbial components, method of application and market segmentation of the inoculant product (Huang et al. 2014; Malusá et al. 2012; Lucy et al. 2004). Although inoculants could be made of bacteria, fungi or blue-green algae (BGA) in combination or separately, this chapter only focusses on bacterial inoculants. Effects of bacterial inoculants are expressed through enhancement of growth and development by nitrogen fixation, macro- and micronutrient solubilisation and the production of PGP substances (Hassen et al. 2016; Singh et al. 2016; Gupta et al. 2007). In addition, these inoculants have secondary roles such as inducing systemic resistance on plants as well as biocontrol capabilities of pathogenic microorganisms. In this chapter, we write about different types of bacterial inoculants and their applications. In addition, future prospects of bacterial inoculant applications in the agroecosystem are also discussed.

7.2 Bacterial Inoculants as a Nature-Based Solution

A combination of factors that include climate change and the increasing world population and anthropogenic pollution of soils and water bodies pose a significant challenge to crop productivity (García-Fraile et al. 2015). Although cross-interactions between physicochemical and biological properties of the soil are important for plant productivity, microbes are key drivers of many processes in the soil-plant interphase (Huang et al. 2014). The interactions of plant and its beneficial microbes, especially in the soil, is important for maintenance of plant health and perhaps the continued existence of plants (Jain and Khichi 2014; Patel et al. 2014). Due to their biological origin and potential beneficial influence on the environment, fertilisers consisting of beneficial microbes have become an indispensable part of sustainable environmental practices (Vessey 2003). They are utilised not only for soil productivity but to also deal with many environmental and socioeconomic challenges such as climate change, water security, soil and water pollution, mineral purification, food security, plant and human health and disaster risk management (Raimi et al. 2017; Adeleke 2014; Patel et al. 2014).

Of the diverse types of soil beneficial microorganisms used for inoculant formulation, the bacterial group also known as plant growth-promoting rhizobacteria (PGPR) are, perhaps, the most promising with various agricultural applications (Glick 2014; Suyal et al. 2016; Vessey 2003). Activities of these microbes in the soil contribute to plant nutrient uptake, regulation and control of microclimate and hydrological processes, plant disease control and detoxification of noxious chemicals in the soil (Fig. 7.1) (Ambrosini et al. 2015). Examples of these beneficial rhizosphere bacteria include *Rhizobium*, *Azospirillum*, *Azotobacter*, *Azomonas, Bradyrhizobium*, *Pseudomonas* and *Bacillus.* In appreciation of their huge beneficial roles in promoting plant growth, these bacterial species have been widely utilised for the production of commercial inoculants (Malusà et al. 2016; Singh et al. 2016; Ahemad and Kibret 2014). Harnessing these essential beneficial microbes for increased crop productivity is a strategy towards achieving the objectives of sustainable agricultural production. Sustainable agriculture supports the development of a safe ecosystem for all plants and animals by promoting efficient use of diverse resources through the integration of biochemical, economic and physical sciences to develop new and eco-friendly techniques (Patel et al. 2014; Lichtfouse et al. 2009; Gupta et al. 2007). Hence, the adoption of an environmentally friendly nutrient management approach fits well into this scope.

7.3 Sources of Microbes Used for Inoculant Formulation

A large number of bacteria used for inoculant formulation are present in the rhizosphere and phyllosphere (Fig. 7.1). Some also exist as endophytic or free-living bacteria, for example, bacterial endophytes inhabit inter- and/or intracellular healthy tissues of host plants, for the entire or a part of their life cycle, without causing damage or disease (Singh et al. 2017; Shridhar 2012; Andrews and Harris 2000). The plant-endophyte

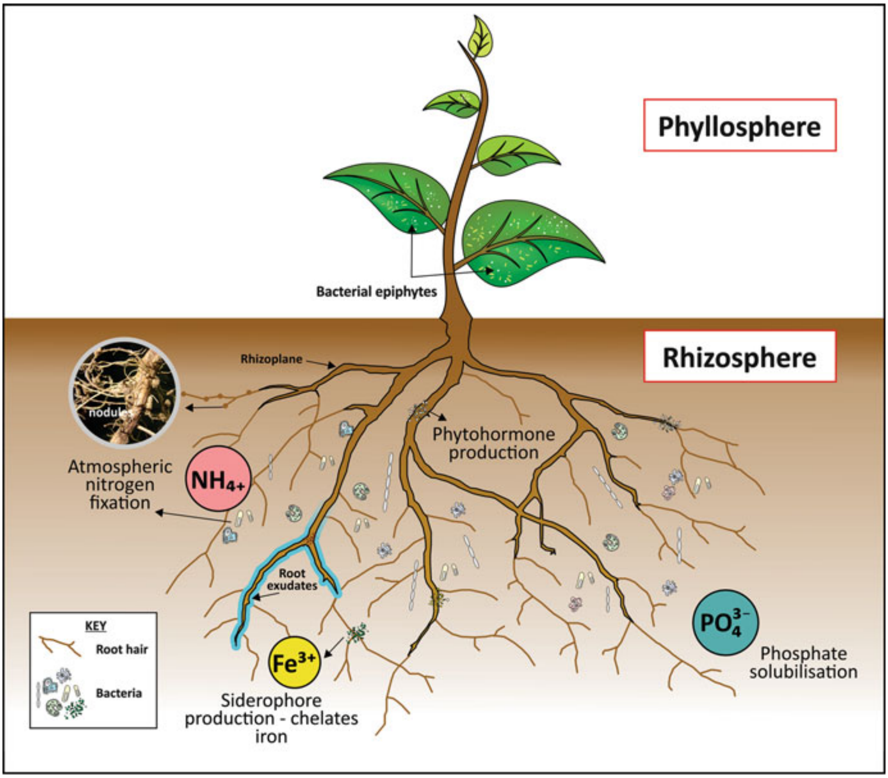

Fig. 7.1 Schematic overview of mechanisms of action and habitat of bacteria used for inoculant formulation. Different soil bacteria found in the phyllosphere and rhizosphere are involved in plant and soil nutrient management through atmospheric nitrogen fixation, nutrient solubilisation and the production of plant growth-promoting substances

association, mostly found in vascular plants, has been shown to enhance plant growth and development by protecting the host plant from pathogenic attack and improving their adaptability in adverse conditions. The endophytes accomplish this by secreting bioactive compounds such as alkaloids, steroids, flavonoids, phenols and azadirachtin (Singh et al. 2017). They exist in the host roots, leaves, stems, meristems, reproductive structures as well as seeds. Endophytes have been considered essential components of biodiversity that can be harnessed for sustainable production of bacterial inoculants for increased agricultural production (Gupta et al. 2012; James 2000).

Furthermore, epiphytic bacteria used for the production of inoculants are found on plant surfaces such as leaves, stems, buds, roots and flowers (Andrews and Harris 2000; Lindow and Brandl 2003). Various studies have reported bacteria as a major colonist of plant leaves with their population averaging up to 10^8 cells/g of leaf (Andrews and Harris 2000). This large population of bacteria on leave surfaces is an indication of the potential contributions of bacterial epiphytes to many essential global processes as well as plant behaviour and physiological condition (Lindow and Brandl 2003).

Other beneficial microbes freely inhabit the rhizosphere, the narrow region of the soil that is in close proximity to the plant roots. The rhizosphere is directly influenced by the microbial colonists, respiration and metabolism of the plant root (Zhang et al. 2010; Chung et al. 2005). The rhizosphere has a higher concentration and diversity of bacteria than any other part of the soil. Soil bacteria use root exudates as a source of nutrition while in return promote plant growth through soil nutrient management processes including nitrogen fixation, phosphorus solubilisation, sulphur oxidation as well as siderophore production and stimulation of the production of various phytohormones (Fig. 7.1) (Huang et al. 2014). The nutrient management in the rhizosphere is tailored towards high-efficiency crop production by enhancing the supply of nutrients in the plant root zone, regulating root architecture and physiological traits as well as influencing biological processes (Zhang et al. 2010). These processes are crucial and are reflected in the properties of bacteria that are considered in the formulation of specific and efficient inoculant products (Huang et al. 2014). Some of these processes occur at the rhizoplane, the surface of plant roots, comprising the epidermis and outer cortex, where microbes and plant exchange different types of nutrients and metabolic products (Huang et al. 2014; Johri et al. 2003). Microorganisms attach to the rhizoplane using structures such as flagella, fimbriae and polysaccharides. Generally, the rhizoplane and rhizosphere appear as a whole; this is because the thin boundary that separates the two habitats is difficult to differentiate (Johri et al. 2003).

7.4 Types of Bacterial Inoculants and Their Mechanisms of Action

7.4.1 Nitrogen-Fixing Bacterial Inoculants

Although the atmosphere consists of approximately 80% nitrogen, atmospheric nitrogen (N_2) is inaccessible to plants due to its stability. However, it may become accessible when converted to compounds such as ammonia and nitrate during biological nitrogen fixation (BNF) (Fig. 7.2) (Chianu et al. 2010; Guinness and Walpole 2012; Bloem et al. 2009). Biological nitrogen fixation is usually carried out by prokaryotic microorganisms that are collectively known as diazotrophs. Diazotrophs interact with host plant root in the soil under symbiotic or non-symbiotic associations to fix N (Bloem et al. 2009). Some of the well-known diazotrophs including symbiotic (rhizobia and *Frankia*) and non-symbiotic (free-living and associative) N-fixers of great importance in BNF are discussed in the section below.

Biological nitrogen fixation involves different biological and chemical transformations and/or processes that are performed by various rhizosphere beneficial microbes. Such processes are key components of the N cycle during which organic nitrogen and atmospheric nitrogen are transformed to ammonia through

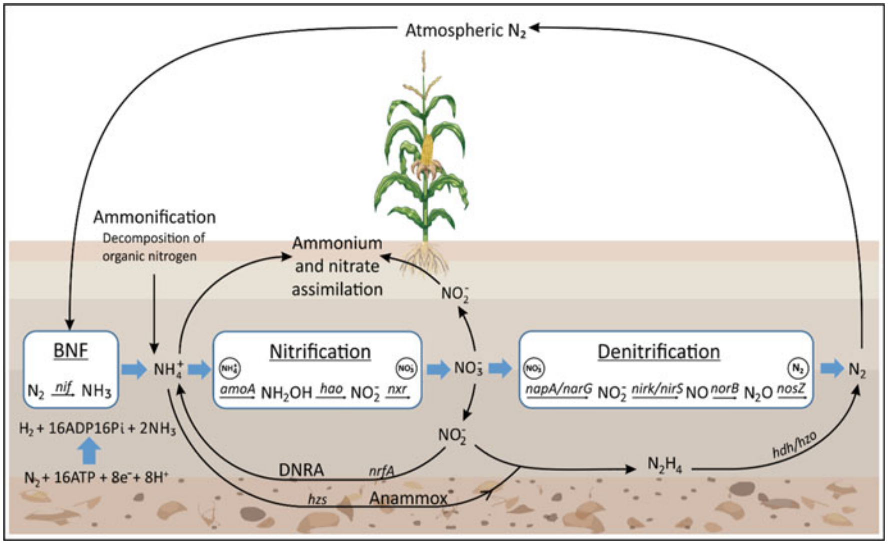

Fig. 7.2 Overview of the nitrogen cycle showing biological nitrogen fixation (BNF), nitrification and denitrification processes. The genes involved in the processes are in italics on the arrows that indicate the path of the reaction, where nitrogenase (*nif*), ammonium monooxygenase (*amoA*), hydroxylamine oxidoreductase (*hao*), nitrite oxidoreductase (*nxr*), periplasm nitrate reductase (*nap*), respiratory nitrate reductase (*nar*), nitrite reductase (*nir*), nitric oxide reductase (*nor*), nitrous oxide reductase (*nos*), multiheme nitrite reductase (*nrf*), and hydrazine synthase (*hzs*) are all enzymes involved in the reactions. The enzyme *nrf*A is involved in the dissimilatory nitrate reduction to ammonia (DNRA), while *hzs* is involved in the anaerobic ammonium oxidation (anammox). Adapted from Kox and Jetten (2015), Klotz and Stein (2008)

ammonification and BNF, respectively (Zehr and Kudela 2011; Klotz and Stein 2008). The cycle also involves the regulation of organic nitrogen in the soil through mineralisation and immobilisation. Mineralisation is the release of ammonia and nitrate during microbial decomposition of organic matter, whereas immobilisation occurs when soil microorganisms take up ammonia and nitrate for cell metabolism and growth. Mineralisation involves two major processes: ammonification and hydrolysis. The former transforms organic nitrogen into ammonia, while the latter converts ammonia to ammonium (Zehr and Kudela 2011).

Diazotrophs fix dinitrogen gas from abiotic to biotic environments employing a mechanism that involves the enzyme called nitrogenase (*nif*) (Zhang et al. 2017). Nitrogenase is an oxygen-sensitive enzyme complex that comprises dinitrogenase reductase and dinitrogenase, which both function in reducing the atmospheric nitrogen into a reactive form of ammonia and nitrate (Fig. 7.2) (Swain and Abhijita 2013; Shridhar 2012). The ammonium produced may be converted to nitrites (NO_2^-) and then nitrates (NO_3^-) through nitrification process (Fig. 7.2) (Zehr and Kudela 2011). In this process, ammonium is usually converted to nitrites by bacteria called *Nitrosomonas* spp., which possess key enzymes such as ammonium monooxygenase (*amoA*) and hydroxylamine oxidoreductase (*hao*) (Kox and Jetten

2015). The toxic nitrite produced is then converted to nitrate by *Nitrobacter* spp., using the nitrite oxidoreductase (*nxr*) (Fig. 7.2) (Klotz and Stein 2008). Nitrate is further transformed into nitrogen through denitrification process. In this process, nitric oxide (NO) and nitrous oxide (N_2O) released from the reduction of nitrate (NO_3^-) and nitrite (NO_2^-) are subsequently reduced to atmospheric nitrogen by nitrite reductase (*nir*), nitric oxide reductase (*nor*) and nitrous oxide reductase (*nos*) (Kox and Jetten 2015; Klotz and Stein 2008). Denitrification process completes the N cycle, and microbes such as *Pseudomonas* are involved in this process.

7.4.1.1 Symbiotic Nitrogen Fixers

Historically, rhizobia have been a major bacterial inoculant used for enhancement of plant and soil health. They are a group of well-known soil bacteria that are efficient in BNF (Somasegaran and Hoben 2012; Oldroyd et al. 2011). Most rhizobia belong to the family *Rhizobiaceae* and inhabit the intracellular spaces of the host in a symbiotic association. This synergy may be mutualistic, resulting in the formation of specialised structures called nodules (Fig. 7.1). Such mutualistic symbioses are most prominent in *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Mesorhizobium* and *Sinorhizobium* in association with several hundreds of legume plants (Oldroyd et al. 2011; Peoples et al. 2009). The nodule-forming, rhizobia-legume association has enormous agronomic and ecological significance due to its substantial role in global BNF (Fig. 7.2). For instance, legumes cultivated with *Rhizobium* inoculants fix up to 300 kg N/ha and can also supply over 90% of the total nitrogen requirement of the host plants through BNF (Swain and Abhijita 2013; Hayat et al. 2010). By and large, rhizobial inoculants are most efficient in agricultural soils when the rhizobia in the local soil are lacking, less efficient or have low population (Lupwayi et al. 2000).

Another important nitrogen-fixing bacterium is *Frankia.* The first isolated species of *Frankia, F. alni* strain CpI1, which was isolated from the root nodules of *Comptonia peregrina*, is commonly referred to as CpI1 (*Comptonia peregrina* Isolate No.1) (Callaham et al. 1978). The soil actinomycete genus *Frankia* fixes nitrogen both in free-living and symbiotic association with the host, actinorhizal plants (Sellstedt and Richau 2013). It belongs to the family *Frankiaceae* and has been found to nodulate actinorhizal plants, which represent a diverse group of almost 220 species belonging to 8 plant families including Betulaceae, Casuarinaceae, Myricaceae, Rosaceae, Elaeagnaceae, Rhamnaceae, Datiscaceae and Coriariaceae (Santi et al. 2013). Its wide distribution, broad range of plant hosts and the ability to differentiate into sporangium and vesicles, which are specialised cells for nitrogen fixation, have increased its ecological importance (Santi et al. 2013; Boonkerd 1998). Similarly, the diazo-vesicles produced during the growth stage of *Frankia* can supply adequate amounts of nitrogen to the host plant under the symbiotic association. Thus, *Frankia* can support the growth of plants where nitrogen is a major limiting factor in the growth of the host (Sellstedt and Richau 2013). It has been reported that *Frankia* is responsible for about 15% of BNF in the world, mostly in symbiotic relationship with plants and shrubs, especially dicot plants (Rascio and Rocca 2013). Under a symbiotic system, this important genus also secretes extracellular enzymes such as cellulases, pectinases and proteinases that are involved in bacteriolysis, hydrolysis and virulence (Santi et al. 2013).

7.4.1.2 Non-symbiotic Nitrogen Fixers

Free-Living Nitrogen Fixers

This group of N-fixers exist freely in the rhizosphere without necessarily having any association with the plant. Several non-symbiotic, free-living, N-fixing bacteria have been employed for the production of inoculants used on a large expanse of agricultural land. These include *Azotobacter*, *Beijerinckia*, *Bacillus*, *Pseudomonas* and *Clostridium* (Mirza and Rodrigues 2012; Ahmad et al. 2008). *Azotobacter* spp. are gram-negative bacteria belonging to the phylum *Proteobacteria* with extremely high rates of respiration, which makes it an efficient nitrogen fixer under nitrogen-deficient soil conditions (Hayat et al. 2010). *Azotobacter* species including *A. vinelandii*, *A. beijerinckii*, *A. nigricans*, *A. salinestri* and *A. chroococcum* are widely used in inoculant formulation. Apart from the nitrogen-fixing ability, *Azotobacter* also contributes to the production of PGP substances such as gibberellins, indole acetic acids and vitamins (Verma et al. 2001). Other free-living N-fixers that participate in BNF and also produce the aforementioned PGP substances are *Azoarcus* sp., *Klebsiella pneumoniae* and *Pantoea agglomerans* (Yanni et al. 2001; Reinhold-Hurek et al. 1993).

Associative Living Nitrogen Fixers

Other non-symbiotic nitrogen-fixing bacteria, including the genera of *Azospirillum* and *Enterobacter*, occur in an associative relationship with the host plant. The genus *Azospirillum* is a facultative endophyte, mostly inhabiting the intercellular space, vascular tissues or root surfaces of several kinds of cereal crops and grasses (Shridhar 2012; Wagner 2012). The species *Azospirillum brasilense* has been widely used on various crops to increase yield, while *Azospirillum diazotrophicus* has been reported to fix approximately 60–80% of nitrogen in sugarcane plantations (Ohyama et al. 2014; Lucy et al. 2004). Similarly, some of the species in the *Acetobacteraceae* family have the ability to fix N when in association with the host. These include *Swaminathania*, *Gluconacetobacter* and *Acetobacter*. For example, *Gluconacetobacter diazotrophicus* fixes nitrogen non-symbiotically or symbiotically, especially in association with sugarcane plants (James 2000). These bacteria have been isolated in countries such as Brazil, Argentina, the United States, Mexico and Egypt (Reis and Teixeira 2015). *Gluconacetobacter diazotrophicus* has been reported with the ability to colonise intracellular space of both leguminous and nonleguminous plants without the formation of nodules. They produce enzymes such as cellulase, hemicellulase and pectinases that enhance host cell wall penetration (Dent and Cocking 2017). Under different field trials, the inoculant NFix® of *G. diazotrophicus* significantly increased crop yield such as maize, oilseed rape and wheat with or without the application of N fertilisers. It was suggested that the intracellular symbiotic N-fixation improved the level of photosynthesis and production of plant growth substances, which are essential for improvement of crop yield (Dent and Cocking 2017).

7.4.2 *Solubilising Bacterial Inoculants*

For increased crop productivity, agricultural soil must have adequate plant nutrients such as phosphorus, potassium, magnesium and zinc. These nutrients are frequently lacking and, when present, form stable complexes with iron, aluminium and calcium, which cannot be easily metabolised by plants (Shanware et al. 2014; Parmar and Sindhu 2013; Han and Lee 2005). This situation has resulted in limitations of plant growth due to nutrient deficiencies especially for phosphorus, which is the second most essential macronutrient after nitrogen for crop metabolism, growth and development (Cordell et al. 2009; Roy et al. 2006). Hence, solubilisation and mobilisation of insoluble nutrients in the soil using bacterial inoculant technology are essential strategies in nutrient management.

7.4.2.1 Phosphate-Solubilising and Phosphate-Mobilising Bacterial Inoculants

Phosphorus is essential for the formation and effective functioning of key plant enzymes. In spite of the large reservoir of phosphorus, it remains inaccessible by plants (Jenkins and Jenkins 2005). To improve crop productivity, phosphorus fertilisers are commonly used to augment phosphorus-deficient agricultural soils. However, most of the phosphorus fertilisers applied are immobilised, leaving a minimal amount available for plant use. Thus, phosphate-solubilising and phosphate-mobilising bacteria are essential for alleviating this situation (Mukhuba et al. 2018; Ma et al. 2011; Jenkins and Jenkins 2005). Phosphate-solubilising bacteria (PSB) have been in use since 1950 after it was first reported by Pikovskaya in 1948 (Krasilinikov 1957). Its application in crop cultivation, being a sustainable alternative to inorganic phosphorus fertiliser application, supports the world's campaign for the green revolution. Most PSB belong to the genera *Pseudomonas*, *Klebsiella*, *Serratia*, *Rhodococcus*, *Flavobacterium*, *Bacillus*, *Arthrobacter*, *Xanthomonas* and *Micrococcus* (Bello-Akinosho et al. 2016; Suyal et al. 2016; Mohammadi 2012). Some of the most efficient phosphorus solubilisers that have been reported in different studies include *Enterobacter*, *Erwinia*, *Bacillus (B. polymyxa*, *B. megaterium*, *B. subtilis)* and *Pseudomonas (P. striata*, *P. rathonis)* (Adeleke et al. 2017; Pindi and Satyanarayana 2012; Bhattacharyya and Jha 2012; Mohammadi 2012).

There are different mechanisms through which beneficial rhizosphere bacteria solubilise insoluble phosphate. Such mechanisms are based on the form of available phosphorus, either inorganic or organic phosphorus (Mukhuba et al. 2018; Adeleke et al. 2017). Other factors such as soil pH, temperature and nutritional content as well as bacterial growth and physiological status greatly affect solubilisation efficiency (Goldstein and Krishnaraj 2007; Chung et al. 2005). For organic phosphorus, a major mechanism of solubilisation is by mineralisation through the secretion of phosphatase, an enzyme which hydrolyses organic phosphate to release phosphorus (Goldstein and Krishnaraj 2007). Conversely, the PSB solubilise inorganic phosphate by secreting low-molecular-weight organic acids (oxalic, citric, malic, fumaric, acetic and lactic acids), siderophores as well as hydroxyl and carboxyl groups (Fig. 7.3) (Adeleke et al. 2017; Sarkar et al. 2017). These chemical substances use a chelating mechanism to bind the cation to the insoluble phosphate compounds thereby releasing the soluble form of phosphate (Mohammadi 2012; Richardson and Simpson 2011). Many phosphorus-solubilising bacteria can effectively solubilise $Ca_3(PO_4)_2$ and phosphorite to monobasic ($H_2PO_4^{-}$) and dibasic (HPO_4^{2-}) ions, which are easily taken up by plants (Oliveira et al. 2009).

The field efficiency of phosphate inoculants is dependent on several factors such as bacterial inoculant type, soil carbon and nitrogen, available phosphorus and level of hydrogen ions in the soil. Most *Enterobacter* and *Klebsiella* sp. are able to solubilise $Ca_3(PO_4)_2$ more efficiently than other phosphate compounds such as $FePO_4$ and $AlPO_4$ (Chung et al. 2005). Similarly, the metabolic activities of bacterial inoculants also directly contribute to the solubilisation of phosphorus through the efflux of protons and organic ions (Richardson and Simpson 2011).

Apart from the aforementioned, bacteria inoculants can also improve the ability of plants to acquire available phosphorus in the soil through hormonal stimulation of root growth, development and elongation (Adeleke et al. 2017; Goldstein and Krishnaraj 2007). In addition, variations in the soil sorption balance may increase the amount of orthophosphate ions in soil solutions. This may also enhance the mobility of organic phosphorus through microbial turnover (Richardson and Simpson 2011; Richardson et al. 2009).

7.4.2.2 Potassium-Solubilising Bacterial Inoculants

Major compounds of potassium including mica, muscovite, illite, orthoclase and biotite are unavailable for plant use (Raimi et al. 2017; Meena et al. 2014). This situation has adversely affected crop productivity in many agricultural fields. However, rhizosphere bacteria are capable of solubilising insoluble potassium compounds through the secretion of biochemical substances such as metabolites,

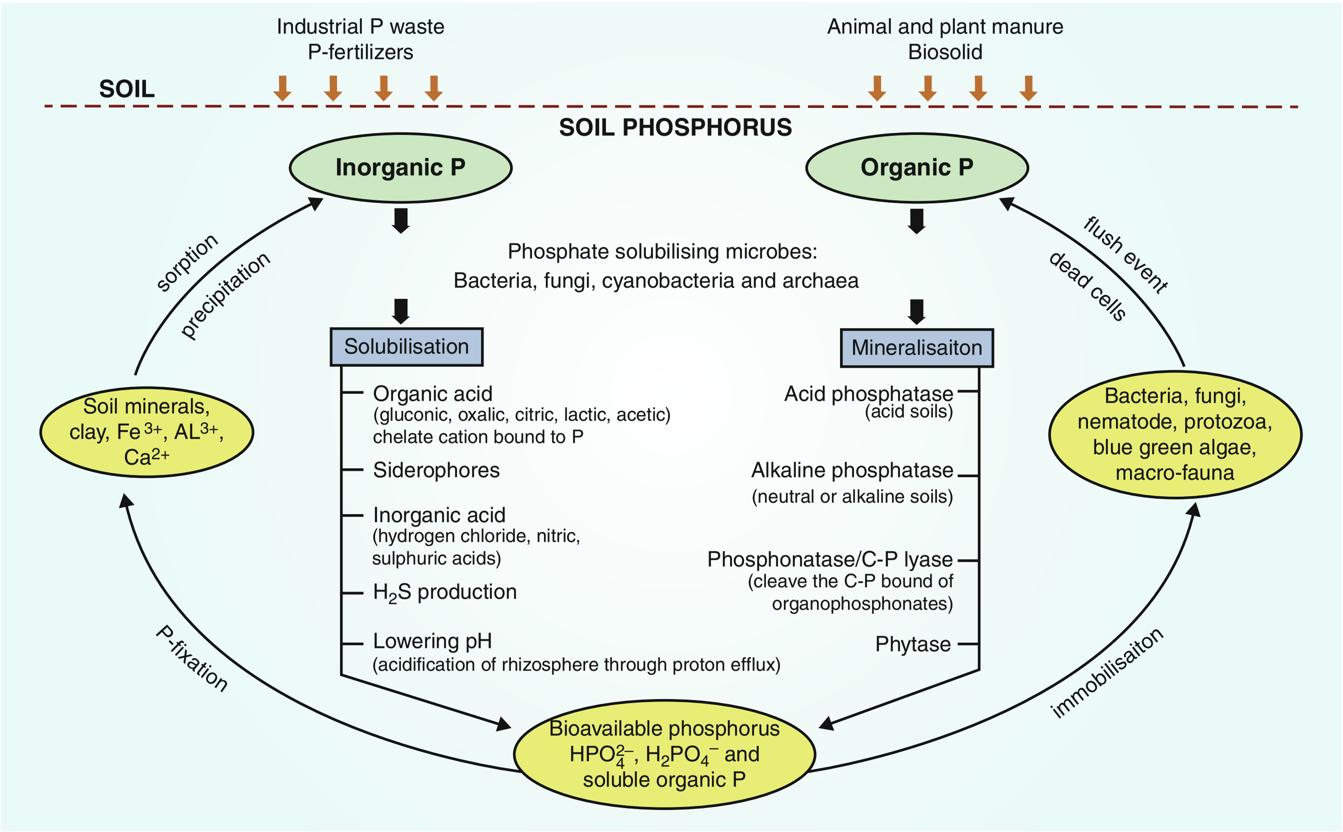

Fig. 7.3 Phosphorus cycle showing different mechanisms by which organic and inorganic soil phosphorus is solubilised. Source: Raimi et al. (2017)

organic ligands, hydroxyl anions and enzymes (Shanware et al. 2014; Han and Lee 2005). Bacteria with this ability are referred to as potassium-solubilising bacteria, and their solubilisation efficiency greatly depends on soil, microbial type and the form of potassium compounds (Meena et al. 2014; Shanware et al. 2014). Several bacterial genera such as *Acidothiobacillus*, *Bacillus*, *Pseudomonas*, *Burkholderia*, *Frateuria* and *Paenibacillus* are widely used for the production of K-solubilising inoculants. Important species of *Bacillus* with high K-solubilising and K-mobilising capabilities include *B. mucilaginous*, *B. edaphicus* and *B. circulans* (Parmar and Sindhu 2013; Sangeeth et al. 2012; Adeleke et al. 2010). These bacteria directly solubilise potassium by secreting viscous-like substances such as exopolysaccharides that invade silicate mineral and chelate silicon to release soluble potassium (Parmar and Sindhu 2013; Hutchens et al. 2003). It has been reported that organic ligands such as exudates, enzymes, secondary metabolites, siderophores and organic compounds (oxalic, gluconic, citric and lactic acids) aid in the solubilisation of potassium from its parent compounds such as feldspar and aluminosilicate (Sarkar et al. 2017; Hutchens et al. 2003). The application of potassium bacterial inoculants on agricultural soil is a sustainable measure to increase plant-available potassium in the soil, thereby reducing the cost of potassium fertiliser application for increasing crop production.

7.4.2.3 Micronutrient-Solubilising Bacterial Inoculants

Various micronutrients including zinc, iron and manganese are essential for the survival and multiplication of plants and microorganisms (Roy et al. 2006). Under different soil conditions, such as pH and oxygen levels, these compounds are transformed into various mineral complexes and become isolated, thereby preventing plants from accessing them (Adeleke et al. 2017). Under the oxic condition, iron occurs primarily as iron (III), an insoluble compound that forms hydroxides and oxyhydroxides (Hayat et al. 2010). These important elements drive the enzymatic and metabolic processes of plants and are needed in low quantity for metabolism. However, their absence or presence at high concentrations hinders plant growth and development (Berraho et al. 1997). To deal with this challenge, soils deficient in micronutrients are usually treated with fertilisers, but the majority of applied fertilisers are immobilised in the soil. For example, in zinc-fertilised soil, approximately 25% of applied zinc is available, with less than 4% of this being used by plants (Mahdi et al. 2010). However, bacterial inoculants such as *Bradyrhizobium*, *Rhizobium*, *Bacillus*, *Pseudomonas* and *Thiobacillus* are well known for the production of metabolic by-products and siderophores, which have a high affinity for soil micronutrients such as zinc and iron. These inoculants have been widely employed to overcome soil nutrient immobilisation in several agricultural soils (Ndakidemi et al. 2011; Esitken et al. 2010; Altomare et al. 1999).

7.4.3 Plant Growth Regulators Synthesised by Bacterial Inoculants

Bacteria and plant interactions in the rhizosphere have been used as indicators of soil and plant health (Huang et al. 2014). Several soil beneficial bacteria promote soil fertility and plant health through the production of different growth-promoting substances, also known as growth regulators. The production of these regulators may be facilitated through direct or indirect mechanisms (Chaiharn and Lumyong 2011; Hayat et al. 2010). Apart from participating in soil nutrient management, beneficial bacteria directly participate in plant growth promotion through biosynthesis of different plant hormones including auxins, gibberellins, cytokinins and 1-aminocyclopropane-1-carboxylate (ACC) acid, which is an ethylene precursor (Khan et al. 2016a; Karadeniz et al. 2006). These phytohormones have been found to increase leaf and root length as well as yield in plants, while also improving the interactions between plant and the rhizosphere microbes (Vacheron et al. 2013). Different types of auxins exist, and some of these include 1-naphthalene acetic acid (NAA), indole-3-butyric acid (IBA), phenylacetic acid (PAA), indole-3-pyruvic acid (IPyA) and indole acetic acid (IAA) (Patten and Glick 1996). The most common and physiologically active auxin in plants is indole acetic acid (IAA), which promotes accelerated and long-term responses in plants. Indole acetic acid affects plant root architecture and cell division, elongation and differentiation, thereby stimulating increased root development (Patten and Glick 2002). Bacteria such as *Bacillus subtilis,* which are efficient in producing IAA, have been reported to promote tuber elongation and increased number of sprouts when used on *Dioscorea rotundata* (Swain et al. 2007). Similarly, inoculant of *Azospirillum* producing IAA-mediated ethylene stimulated an increase in the number of root hairs, root surface area and total biomass in tomato plants (Ribaudo et al. 2006). Rhizosphere beneficial bacteria including *Azospirillum* and *Paenibacillus* also produce indole-3-butyric acid, tryptophol and indole-3-ethanol, which indirectly contribute to plant growth promotion (Solaiman and Anawar 2015; Hayat et al. 2010). Approximately 80% of isolated rhizosphere bacteria have been reported to produce IAA (Patten and Glick 1996), while about 90% of isolated bacteria from the rhizosphere of different crops were found to be involved in cytokinin production, under in vitro cultivation (Barea et al. 1976). According to Vacheron et al. (2013), the biosynthesis of cytokinins has also been documented in bacteria such as *Bradyrhizobium japonicum, Pseudomonas fluorescens* and *Bacillus licheniformis*. Similarly, gibberellic acid produced by *Bacillus megaterium*, *B. aureus* and *Klebsiella pneumoniae* stimulates increased flowering, stem and internode elongation as well as fruit setting and growth in different plants (Kumar et al. 2014; Zalewska and Antkowiak 2013; Karadeniz et al. 2006). Maize, tomato and rice planted with gibberellic acid had a substantial increase in growth and yield when compared to the control (Kumar et al. 2014; Zalewska and Antkowiak 2013; Fulchieri et al. 1993). 1-Aminocyclopropane-1-carboxylate acid (ACC) plays an essential role in the biosynthesis of ethylene hormone found in higher plants (Khan et al. 2016a, Onofre-Lemus et al. 2009).

Ethylene hormone acts as a modulator of growth and development in plants. Although ethylene is a key factor in plant defence response to a wide range of stress, high levels of ethylene could be detrimental to plant growth. Fortunately, ACC can be degraded by bacterial ACC deaminase, an enzyme that indirectly facilitates plant growth (Glick 2014). Rhizosphere bacteria with ACC deaminase function as a sink for ACC by producing alpha-ketobutyrate and ammonia from ACC hydrolysis, instead of ethylene (Onofre-Lemus et al. 2009). This process lowers the amount of ACC and ethylene levels in plants, thereby promoting steady plant growth and development, through the reduction of damages such as plant death and growth inhibition usually caused by high concentration of plant ethylene (Glick 2014; Hayat et al. 2010; Onofre-Lemus et al. 2009; Saleem et al. 2007).

Furthermore, rhizosphere bacteria also produce siderophores, particularly under iron-deficient soil. Siderophores are low-molecular-weight (~200–2000 Da) substances with an extraordinary chelating ability for iron (Ahmed and Holmström 2014). A wide range of siderophores have been reported in different bacteria, and most of these are catecholates (enterobactin), carboxylates (rhizobactin) and hydroxamates (ferrioxamine B). Most of the soil iron is not readily available for rhizosphere beneficial microbes and plant use (Shanmugaiah et al. 2015; Ahmed and Holmström 2014). The bacteria producing siderophores are able to overcome this condition through iron-chelation mechanism (Sarkar et al. 2017; Radzki et al. 2013). The mechanism of siderophore-bound iron transport systems varies between gram-positive and gram-negative bacteria (Ahmed and Holmström 2014). In gram-negative bacteria, the Fe(III)-siderophore complexes bind to TonB-dependent outer membrane receptor and cross the membrane through an energy-dependent system involving outer membrane receptor proteins, periplasmic binding proteins and inner membrane transport proteins (Fukushima et al. 2013; Braun and Hantke 2011). Subsequently, the complex is transported into the cytoplasm through the cytoplasmic membrane by an ATP-binding cassette (ABC) transport system after the Fe(III)-siderophore complex, bounded by periplasmic binding protein have been released into the periplasmic space (Ahmed and Holmström 2014; Noinaj et al. 2010). Finally, the Fe(III)-siderophore complex is reduced to Fe(II). For gram-positive bacteria, the membrane receptors are absent due to lack of the outer membrane. Hence, the Fe(III)-siderophore complexes are bound by periplasmic binding proteins that are attached to the cell membrane due to lack of periplasmic space. Similar to gram-negative bacteria, the Fe(III)-siderophore complexes are then transported into the cytoplasm using ATP-binding (ABC) transport system (Fukushima et al. 2013; Braun and Hantke 2011). Some of the bacterial species used for inoculum formulation and their plant growth-promoting functions are presented in Table 7.1.

Table 7.1 Bacterial species used for inoculum formulation and their plant growth-promoting functions

Bacterial genera	Species	Function	Reference
Sinorhizobium	*Sinorhizobium meliloti*	Fix-N	Villegas et al. (2006)
Bradyrhizobium	*B. japonicum*, *B. elkanii*, *B. betae*, *B. canariense*, *B. liaoningense*	Fix-N, P-solubilisation, siderophore and IAA production	Antoun et al. (1998), Wu et al. (2011)
Azospirillum	*A. brasilense*, *A. lipoferum*, *A. amazonense*	Fix-N, P-solubilisation, IAA and siderophore production	Rodrigues et al. (2008), Thakuria et al. (2004)
Azotobacter	*Azotobacter chroococcum*	Fix-N, P-solubilisation, gibberellin, IAA, kinetin and siderophore production	Ahmad et al. (2005), Verma et al. (2001)
Azoarcus	*A. communis*, *A. indigens*	N-fixer	Reinhold-Hurek et al. (1993)
Bacillus	*B. mucilaginous*, *B. megaterium*, *B. licheniformis*, *B. edaphicus*, *B. subtilis*, *B. cereus*, *B. pumilus*, *B. circulans*	K- and P-solubilisation, gibberellin, auxin, and cytokinin production	Parmar and Sindhu (2013), Mohammadi and Sohrabi (2012), Karadeniz et al. (2006)
Burkholderia	*B. unamae*, *B. tropica*	1-Aminocyclopropane-1-carboxylate (ACC), N-fixer, IAA, P-solubilisation and siderophore	Onofre-Lemus et al. (2009)
Enterobacter	*E. asburiae*	IAA, P-solubilisation, siderophore ammonia	Ahemad and Khan (2010)
Klebsiella	*Klebsiella* sp.	IAA, P-solubilisation, siderophore ammonia	Ahemad and Khan (2011)
Pseudomonas	*Pseudomonas putida*, *P. jessenii*, *P. aeruginosa*, *P. chlororaphis*	P-solubilisation, siderophore and IAA	Parani and Saha (2012), Shaharoona et al. (2008)
Alcaligenes	*Alcaligenes faecalis*	P-solubilisation, IAA and siderophore production	Sayyed et al. (2010)
Acinetobacter	*Acinetobacter* spp.	IAA, P-solubilisation and siderophore	Rokhbakhsh-Zamin et al. (2011)
Rhizobium	*Rhizobium cicero*, *R. phaseoli*, *R. undicola*	Siderophore, Fix-N, IAA	Berraho et al. (1997), Ghosh et al. (2015)
Serratia	*Serratia nematodiphila*	IAA, siderophore, HCN and P-solubilisation	Dastager et al. (2011)
Flavobacterium	*Flavobacterium* sp.	IAA, P-solubilisation	Soltani et al. (2010)

Adapted from Raimi et al. (2017), Ahemad and Kibret (2014)

7.5 Applications of Bacterial Inoculants in Agroecosystems

7.5.1 Bacterial Inoculants for Increased Crop Productivity and Soil Restoration/Maintenance

The application of bacterial inoculants in agriculture has robust benefits in enhancing soil fertility and crop productivity (Raimi et al. 2017; Hassen et al. 2016; Singh et al. 2016). The efficiency of agronomic input is enhanced where inoculants are used in combination with other integrated nutrient management methods (Duarah et al. 2011; Kumar et al. 2010; Shaharoona et al. 2008). In general, these benefits lead to the reduction of inorganic fertiliser application, while also improving the economic status and profitability of farmers (Singh et al. 2016; Suyal et al. 2016; Geetha and Joshi 2013; Catroux et al. 2001; Bashan 1998). Cost-effectiveness of bacterial inoculants is usually estimated based on the fraction of the value of possible benefits correlated to the total real costs of applied inoculants over a specific period of time (Mulongoy et al. 1992). For legume inoculants, the benefits are based on the N-fixing capability of the product. For example, white clover plant had cost/benefit ratio of 416 with a N-fixing capability of 200 kg/ha, while soybean had a cost/benefit ratio of 17 and fixes about 100 kg of N/ha from inoculation which cost as low as half a dollar (US$ currency) per kg of bacterial inoculant (Mulongoy et al. 1992). In addition, the cost of bacterial inoculants that will provide the same quantity of nutrient supplied by mineral fertiliser is low. For example, NoduMax® inoculant costs only $5 per ha in application as opposed to $100 per ha cost of urea fertiliser needed to supply the same quantity of nutrients (N2Africa 2015).

The soil is the farmer's most precious asset and must be made productive through a systematic application of nutrients. It has been estimated that about 28.8 million tons of plant nutrients are needed for the production of 321 million tons of grain crops by the year 2020. Due to high market price and unavailability, only 21.6 million tons will be supplied through chemical fertiliser application, leaving a shortfall of 7.2 million tons (Pathak et al. 2017). This deficit is a major challenge for increasing food supply, especially in developing nations. However, the application of bacterial inoculants, which is more economically viable, is an efficient nutrient management technique for augmenting the gap (Chianu et al. 2010; Graham and Vance 2003).

7.5.2 Availability of Soil Nutrients and Increased Crop Yield

Crop yield, especially for legumes, is improved when cultivated with nitrogen-fixing bacterial inoculants such as *Sinorhizobium*, *Bradyrhizobium*, *Rhizobium* and *Azorhizobium*, which can fix appreciable amounts of soil nitrogen through BNF (Wagner 2012; Oldroyd et al. 2011). The symbiotic relationship of the *Rhizobium*-leguminous plant has been reported to fix between 24 and 584 kg N/ha annually under different crop and soil types (Martínez-Romero 2009; O'hara et al. 2002). For example, soybean yield and soil organic matter were improved under *Rhizobium*-inoculated soil which was attributed to the biological fixation of approximately 80% of nitrogen (Smaling et al. 2008). In addition, *Frankia* and *Casuarina equisetifolia* symbiotic relationship resulted in the fixation of up to 362 kg N/ha, whereas *Azotobacter*, a free-living bacteria, contributes about 15 kg N/ha/year (Elkan 1992). Depending on crop types, co-inoculation of *Azotobacter* and *Azospirillum* increases the yield of crops in the range of 5%–10% (Pathak et al. 2017). Likewise, the increased growth of *Phaseolus vulgaris* (common bean) was attributed to *Rhizobial* inoculant application (Ndakidemi et al. 2011). In addition, pomegranate (*Punica granatum* L.) treated with inoculants containing N-fixing bacteria (*Azotobacter chroococcum*) and arbuscular mycorrhiza fungi (*Glomus mosseae)* had increased growth and yield (Aseri et al. 2008). The combined treatment of the inoculants enhanced microbial activities, nutrient uptake as well as the activities of dehydrogenase, alkaline phosphatase and nitrogenase in the plant rhizosphere compared to the control (Aseri et al. 2008).

Similarly, solubilising bacteria also have positive influence on crop growth and development. For instance, *Bacillus magisterium* var. *phosphaticum* applied on sugarcane plants stimulated plant growth and yield with high sugar content (Sundara et al. 2002). In the same vein, the cultivation of rice (*Oryza sativa*) and yardlong bean (*Vigna unguiculata*) with P inoculants such as *Pseudomonas*, *Bacillus* and *Erwinia* was also found to promote seed germination (germination index > 2.5) as well as increased shoot, root length and biomass (Duarah et al. 2011). Peanut (*Arachis hypogaea*) and sunflower (*Helianthus annuus*) had high yield when inoculated with *Bacillus* inoculants (Wang et al. 2014; Ahmed and El-Araby 2012). In addition, *Pseudomonas aeruginosa* strain $\mathrm{PSBI_3}$-1 and *Aerococcus* sp. strain $\mathrm{PSBCRG_1}$-1 solubilise tricalcium phosphate at different sodium chloride concentrations for plants grown under saline soil, while *Burkholderia cepacia* increased maize plant yield under sodium chloride concentration of up to 5% (Alori et al. 2017; Srinivasan et al. 2012).

Furthermore, under low P and K soil, eggplant (*Solanum melongena*), pepper (*Capsicum annuum* L.) and cucumber (*Cucumis sativus* L.) plants were reported to have improved mineral uptake with an increase in nutrient (NPK) content and yield of crops when cultivated with a combination of potassium and phosphate inoculants (Han and Lee 2005, 2006). The potassium and phosphate inoculants contained *Bacillus megaterium* var. *phosphaticum* and *Bacillus mucilaginosus,* respectively (Han and Lee 2005). Similarly, under soil inoculation with K-solubilising *Bacillus edaphicus*, an increased yield of rape (*Brassica napus* L.) and cotton (*Gossypium hirsutum* L.) was achieved (Sheng 2005). Inoculants of *Pseudomonas*, *Mycobacterium* and *Bacillus* have also been reported with high ability to increase the growth and yield of maize (*Zea mays*) plants (Egamberdiyeva 2007).

In iron-deficient soil, inoculants producing siderophores caused an increase in the yield of groundnut (*Arachis hypogaea*) and tomato (*Solanum lycopersicum*) plants compared to the control (Radzki et al. 2013; Sayyed et al. 2010). Likewise, mung bean (*Vigna radiata* L.) had increased chlorophyll content and yield under iron-deficient soil when inoculated with *Pseudomonas* strain (GRP3) (Sharma et al. 2003). In addition, available soil iron is of great importance for effective functioning of N-fixing bacterial inoculants. This is because iron is necessary for the formation of iron-molybdenum and iron proteins that play crucial roles in the effective functioning of the nitrogenase, an important enzyme in BNF (Sickerman et al. 2017). Thus, for increased N-fixation, especially under iron-deficient soil, siderophore-producing bacterial inoculants are essential (Hassen et al. 2016; Duval and Hungate 2008). These observations highlight the positive influence of inoculant application in increasing crop nutrient uptake and productivity.

7.5.3 Biocontrol Ability of Bacterial Inoculants

The iron-chelation mechanism of siderophores creates an indirect competition for soil iron amongst rhizosphere microbes. This process reduces the available soil iron, thereby indirectly suppressing pathogens and their ability to cause diseases (Shanmugaiah et al. 2015; Sayyed et al. 2010). For example, the fusarium wilt of potato and maize has been controlled by siderophore-producing *Pseudomona*s and *Bacillus* inoculants, through their ability to make iron unavailable to the pathogen (Beneduzi et al. 2012). In the same vein, inoculants of *Pseudomonas aeruginosa* have been widely used for controlling bacterial blight disease caused by *Xanthomonas oryzae* pv. *oryza* and *Rhizoctonia solani* (Yasmin et al. 2017). *Fusarium* spp. and *Pythium* spp., mainly attacking both maize and wheat crops, have also been controlled with inoculants of *Bacillus* spp. and *Burkholderia cepacia* (Whipps 2001). The application of inoculants for biocontrol of crop pest and diseases is a sustainable alternative to pesticide application.

On the other hand, the direct inhibition of pathogens by bacterial inoculants is usually through their metabolic activities and production of antibiotics (Solanki et al. 2012; Akgül and Mirik 2008). For example, *Fusarium udum* Butler and *Erwinia carotovora* cause *Fusarium* wilt of pigeon pea (*Cajanus cajan* L.) and soft rot of potato (*Solanum tuberosum*), respectively, thereby reducing the productivity of these crops (Sharma et al. 2016; Pérombelon 2002). However, these pathogens can be controlled by inoculants of *Pseudomonas fluorescens* and *Sinorhizobium* that synthesise chitinase and β-1,3-glucanase (Gupta et al. 2013; Kumar et al. 2010). These enzymes are able to break down the cell wall components of fungal pathogen. Chitinases hydrolyse chitin, the major components of fungal cell walls, while glucanases catalyse hydrolytic cleavage of the glucosidic linkages in the (1, 3) β-glucan and break down the glucans present in the fungal cell wall (Gupta et al. 2013). Furthermore, plant-microbe interactions in the rhizosphere can strengthen the defence mechanisms of plants against pest attack through cyanogenesis, a process through which hydrogen cyanide is produced (Rudrappa et al. 2008). The cyanogenic defence substances produced in the legume-*Rhizobium* symbiotic relationship promote resistance in plants against herbivore attack (Thamer et al. 2011; Kempel et al. 2009). Similarly, about 26% reduction in the population of predatory insects was achieved when maize (*Zea mays*) plants were cultivated with bacterial inoculants (Megali et al. 2015).

7.5.4 Volatile Organic Compounds

One of the major groups of secondary metabolites produced by rhizosphere bacteria is known as volatile organic compounds (VOCs). Volatile organic compounds are essential components of plant growth regulators that have been found to stimulate increased crop productivity through induced resistance of plants to pathogens and as a direct source of plant nutrients (Santoro et al. 2011). These metabolites play an essential role in plant-microbe signal communication (Insam and Seewald 2010). Some of the well-known VOCs include acetone, 3-butanediol, terpenes, jasmonates and isoprene. These compounds have a high vapour pressure, low boiling point and low molecular mass (<300 Da). Several factors have been reported to affect the production of microbial VOCs in the soil. These factors include the pH, moisture content, temperature, oxygen level and nutrient content of the soil (Insam and Seewald 2010). The microbial growth stage also influences VOCs production. Several studies have shown that microbial VOCs can indirectly affect root development, secretion of hormones and plant growth (Piechulla et al. 2017; Schulz-Bohm et al. 2017; Ryu et al. 2004). For example, in a study by Santoro et al. (2011), the biosynthesis of essential oils and increased growth parameters observed in *Mentha piperita* (peppermint) were attributed to the VOCs produced by *Pseudomonas fluorescens*, *Bacillus subtilis* and *Azospirillum brasilense*. Similarly, biocontrol potential of different species of *Pseudomonas* and *Bacillus* has been attributed to the antibacterial activities of their various VOCs (Schulz-Bohm et al. 2017). Volatile organic compounds such as benzothiazole and 1-methylnaphthalene produced by *Pseudomonas fluorescens* WR-1 have bacteriostatic effects against *Ralstonia solanacearum,* a tomato pathogen (Raza et al. 2016). Likewise, benzaldehyde and 1,3-butadiene produced by *Bacillus* spp. suppress the growth of *R. solanacearum* and induces systemic resistance in tobacco plant against bacterial wilt diseases (Tahir et al. 2017).

7.6 Bacterial Inoculants for Environmental Sustainability

7.6.1 Bioremediation of Polluted Agricultural Soil

Of recent, rhizosphere beneficial bacteria have found application in soil bioremediation, especially in toxic metal-polluted soils (Adeleke et al. 2012; Adeleke 2014; El-Kabbany 1999). Bioremediation process is an eco-friendly and cost-effective technique that employs microorganisms to effectively remove or reduce pollutants of water, soil and sediments. This process is based on the ability of microbes such as bacteria to degrade organic and inorganic substances in polluted environment (Adeleke 2014; Chorom et al. 2010). In addition, the diverse rhizosphere beneficial processes such as nutrient cycling, biochemical synthesis, detoxification as well as soil structure conservation have been harnessed in bioremediation (Jiao et al. 2015; Panda and Mishra 2007).

The main advantage of using bacterial inoculants for bioremediation of polluted soil in agroecosystems is the potential additional capabilities of microorganisms to drive the processes involved in nutrient cycling. For instance, *Rhizobacteria* in association with arbuscular mycorrhizal fungi (AMF) have been used to clean up toxic heavy metal-contaminated agricultural soil (Khan 2014). Such approach will allow the ecosystem, especially the agroecosystem, to benefit comprehensively from the bioremediation process. Similarly, Bello-Akinosho et al. (2016) in an in vitro study also reported the potential of *Pseudomonas* sp. strain 10–1B in the degradation of polycyclic aromatic hydrocarbons (PAH) as well as in soil fertility management. Several beneficial bacteria including *Burkholderia, Pseudomonas, Bacillus, Rhizobium* and *Enterobacter* have also found application in bioremediation (Bello-Akinosho et al. 2015, 2016, 2017; Jain and Khichi 2014; Mathew et al. 2014). *Burkholderia* spp. have been used to remediate Cd- and Pb-polluted agricultural soil (Jiang et al. 2008), while species of *Bacillus*, *Streptococcus*, *Pseudomonas* and *Micrococcus* have also been reported with bioremediation potential for Cd-, Pb- and Cu-contaminated soil (Mani and Kumar 2014; Fulekar et al. 2012). Importantly, the twofold functions, viz. soil nutrient management and bioremediation, have made rhizosphere beneficial bacteria a significant soil fertility management technology for increasing agricultural land productivity in polluted soils (Raimi et al. 2017).

7.6.2 Drought or Water Stress Resistance

Plant-microbe interactions have vital influences on the diversity, abundance and survival of both plants and their associated microbes (Huang et al. 2014; Whipps 2001). Due to this close interconnection, stress and sudden changes in the abiotic environment of plants also affect their associated microbial communities (Naylor and Coleman-Derr 2018). One of such environmental stress conditions is drought, which adversely affects crop productivity. Under repeated water stress conditions, interactions between plants and microbes have evolved adaptive strategies (Cruz-Martínez et al. 2009). This involves improved association of plants with microbes. These microbes can directly or indirectly improve the metabolism and development of the host plant, thereby making such plants drought-resistant (Naylor and Coleman-Derr 2018). Many of the root-associated bacterial communities of plants cultivated under drought conditions have the capability to enhance water stress tolerance through their growth-promoting mechanisms (Kaushal and Wani 2016). The production of antioxidant defence substances, VOCs, dehydrins, PGP substances and exopolysaccharides (EPS) and modification of phytohormone levels are some of the common mechanisms used by bacteria to enhance water stress resistance of plants (Cruz-Martínez et al. 2009; Glick 2014; Kaushal and Wani 2016). Unfortunately, no single bacterial isolate possesses all these attributes. Hence, utilisation of a microbial consortium rather than single isolates could be important in the formulation of bacterial inoculants with drought-resistant capabilities (Naylor and Coleman-Derr 2018). For example, in a study conducted by Khan et al. (2016b), a consortium of ten endophytic strains improved water stress resistance of hybrid poplar (*Populus* sp.) through multiple distinct drought response pathways.

Another example is the ability of such consortium to produce a combination of PGP substances such as auxins, cytokinins, gibberellins, siderophores and ACC, which promote high water stress tolerance in plants (Kaushal and Wani 2016; Molina-Romero et al. 2017). Hence, inoculants known for the production of these PGP substances have immense application in drought-prone environments (Figueiredo et al. 2010; Wang et al. 2012). For instance, cucumber (*Cucumis sativus*) plants inoculated with a consortium of PGPR strains (*Bacillus cereus* AR156, *Bacillus subtilis* SM21 and *Serratia* sp. XY21) under drought stress conditions had increased leaf proline and chlorophyll content, darker green leaves and improved root recovery intension when compared to the control (Wang et al. 2012). Similarly, a bacterial consortium formulated with *Pseudomonas putida* KT2440, *Sphingomonas* sp. OF178, *Azospirillum brasilense* Sp7 and *Acinetobacter* sp. EMM2 improved the yield of maize (*Zea mays*) compared to the control. This was attributed to the abilities of the strains to solubilise phosphorus and produce high levels of siderophore and IAA (Molina-Romero et al. 2017). According to Gururani et al. (2013), *Bacillus* inoculant, which produces ACC and siderophores, enhanced water stress tolerance of potato (*Solanum tuberosum*). Also, pepper (*Capsicum annum*) and tomato (*Solanum lycopersicum*) plants inoculated with *Achromobacter piechaudii* ARV8 had increased water stress resistance when cultivated under water-stressed soil conditions (Mayak et al. 2004).

7.7 Current Status and Hurdles in the Formulation of Efficient Inoculants

Efficient bacterial inoculants must not only have the ability to enhance plant growth, but they should also be highly potent with sufficient capabilities to dominate in the rhizosphere environment (Lupwayi et al. 2000). It is also important to ensure that inoculants have high association compatibility with the plant host and other beneficial rhizosphere microbes, as well as a broad range of beneficial functions with diverse crops (Herridge et al. 2002). In addition, bacteria used for inoculant production must be easily multiplied (both in the laboratory and field), environmentally friendly and have the capability to perform under various ecological conditions (Reddy and Giller 2008). Quite a number of rhizosphere bacteria have been reported to possess a combination of the aforementioned abilities. As earlier highlighted, no single inoculant can effectively perform all these functions under the different ecological conditions. This has encouraged the formulation of inoculants with microbial consortium, which perform diverse field functions (Herrmann and Lesueur 2013). In addition, it is also necessary to screen and select beneficial plant growth promoters under different ecological conditions for the formulation and production of efficient bacterial inoculants for increased crop productivity (Arora et al. 2010). For instance, several species of *Pseudomonas*, *Bacillus*, *Azospirillum* and *Azotobacter* have found extensive applications in soil nutrient enhancement, not only for their high nutrient solubilisation capability but also for their abilities to produce different PGP substances and fix appreciable amounts of nitrogen, especially under extreme environmental conditions (Bello-Akinosho et al. 2016; Ghosh et al. 2015; Parani and Saha 2012; Sharma et al. 2003).

In spite of the need for increased production and application of inoculant in sustainable agriculture, there exist some challenges that limit full commercialisation of inoculants. One of the limiting factors is the field efficacy, which affects the overall acceptability and success of the products (Parnell et al. 2016). Generally, the field efficacy of inoculants cannot always be guaranteed. Several successful laboratory and greenhouse experiments are rarely translated to field success. In addition, several quality assessments have shown that poor-quality inoculant products unable to improve crop productivity are sold in the agro market (Herrmann et al. 2015; Olsen et al. 1996; Raimi and Adeleke 2018). More so, efforts to formulate inoculants that can perform under all ecological conditions have been unsuccessful (Stephens and Rask 2000). Specific plants recruit a range of beneficial bacteria based on the plant's metabolites or exudates in the form of carbon, VOCs and organic acids (Parnell et al. 2016). Moreover, efficiency of inoculants on different crops may differ due to differences in their associated microbial community, developmental stages, environment and nutrient availability or preferences (Herrmann and Lesueur 2013).

Furthermore, the success of inoculants greatly depends on the target crop, product availability and cost as well as ease of application and environmental challenges. Developing an efficient product suitable under different field conditions, which combines all the aforementioned characteristics, has become a major challenge in the inoculant industry (Stephens and Rask 2000). Another important factor is the carrier formulation for inoculant production. This is a challenge that affects product application, quality and field efficiency. It is essential that carrier materials support the growth of specific inoculant strains and maintain the desired population of these strains over an acceptable shelf life. Unfortunately, carriers for consortium products are usually less selective; a desired quality that is required to support the diverse microbial strains used for consortium product formulation. However, the disadvantage of the less selective carrier is the potential to support growth of other microbial contaminants. This is a major challenge affecting the formulation of good-quality inoculants, especially the consortium products (Herrmann et al. 2015; Olsen et al. 1996).

An additional challenge in the production of efficient inoculants is the lack of stringent quality control measures. Better quality control system should be put in place to assess the quality of the numerous emerging products in the market as well as the activities of the growing industry (Lupwayi et al. 2000). It is essential that the products meet all quality criteria through regular quality assurance performed by the manufacturers during production processes. In addition, quality control assessment by independent bodies or government should be performed regularly to confirm quality standards of inoculants (Herrmann and Lesueur 2013).

7.8 Commercial Bacterial Inoculant Products

Bacterial inoculants have been established for over a century, with the first reported inoculant, Nitragin®, produced by a Dutch scientist, Hiltner L. in 1896 (Bhattacharjee and Dey 2014). The growing need for sustainable agricultural production has increased awareness and use of bacterial inoculants. This has caused an increase in the commercialisation and market share of inoculants with different types of products being supplied to the agromarket (Raimi et al. 2017). Recently, the majority of inoculants produced and used are mostly rhizobia products, which constitutes approximately 79% of the global inoculant demand. This may be attributed to the major role nitrogen plays in crop productivity. Apart from rhizobia, the phosphate-solubilising inoculants account for approximately 15%, while other inoculants including mycorrhizal products make up the remaining percentage (Transparency Market Research 2014; Suyal et al. 2016). According to Transparency Market Research (2014), the bioinoculant global market demand is growing and has been estimated to increase at a robust cumulative average growth rate (CAGR) of approximately 13% from 2017 to 2025. It is projected to be valued at US$4.09 billion in 2025 from the value of US$1.25 billion as at 2016. *Azospirillum* sp. and *Bacillus subtilis* are commonly used for the formulation of commercial free-living PGPR products, *Bacillus subtilis* has been used under different trade names such as Serenade® and Kodiak® for crops including beans, pea, rice, maize and soybean (Transparency Market Research 2014). Another important bacterial species in inoculant production is *Agrobacterium radiobacter*, which have been produced by different manufacturers under the trade names Diegall® and Nogall®. These products are used for the cultivation of fruit, trees and ornamentals. Similarly, *Pseudomonas fluorescens* has been produced under trade names such as Conquer® and Victus®, used on various types of crops (Suyal et al. 2016). Some of these inoculant products are listed in Table 7.2.

7.9 Conclusions

Bacterial inoculants play several essential roles in agroecosystems. Their direct and indirect impacts on plant growth and development are expressed through various mechanisms including nutrient solubilisation and mobilisation as well as the production of PGP substances. Therefore, traditional nutrient management strategies, which are greatly dependent on the application of agrochemical inputs such as inorganic fertilisers and pesticides must realign with contemporary integrated nutrient management systems such as bacterial inoculant technology. In spite of the many success stories attributed to the use of bacterial inoculants for improving agricultural production, many questions regarding their sole utilisation to improve soil quality and enhance plant health remain unanswered.

Table 7.2 Global representation of inoculants, bacterial components and manufacturers

Continent	Product	Active component	Manufacturer
Africa	Firstbase, Biostat, Landbac, Waterbac, lifeForce	*Bacillus* sp.	Microbial solution (Pty) Ltd, South Africa
	Likuiq Semia	*Bradyrhizobium elkanii*	Microbial solution (Pty) Ltd, South Africa
	Nitrasec Alfalfa (Lucerne)	*Sinorhizobium meliloti*	Microbial solution (Pty) Ltd, South Africa
	Organico	*Bacillus* spp. *Enterobacter* spp., *Pseudomonas*, *Stenotrophomonas*, *Rhizobium*	Amka Products (Pty) Ltd, South Africa
	Soil Vital Q	*Bacillus subtilis*, *Bacillus thuringiensis*, *Azotobacter chroococcum*, *Pseudomonas fluorescens*, *Lactobacillus* sp.	BioControl Products SA (Pty) Ltd
	Bac up	*Bacillus subtilis*	BioControl Products SA (Pty) Ltd
	Azo-N	*Azospirillum brasilense*, *Azospirillum lipoferum*	BioControl Products SA (Pty) Ltd
	Azo-N Plus	*Azospirillum brasilense*, *Azospirillum lipoferum*, *Azotobacter chroococcum*	BioControl Products SA (Pty) Ltd
	B-RUS, Extrasol	*Bacillus subtilis*	Ag-Chem Africa (Ltd) Ltd, South Africa
	NAT-P	*Pseudomonas fluorescence*	BioControl Products SA (Ltd) Ltd
	N-Soy	*Bradyrhizobium japonicum*	BioControl Products SA (Ltd) Ltd
	SoilFix	*Brevibacillus laterosporus*, *Paenibacillus chitinolyticus*, *Lysinibacillus sphaericus*, *Sporolactobacillus laevolacticus*	BioControl Products SA (Ltd) Ltd
	Composter	*Bacillus* spp.	BioControl Products SA (Ltd) Ltd
	N-Bean	*Rhizobium phaseolus*	BioControl Products SA (Ltd) Ltd
	Histick	*Bradyrhizobium japonicum*	BASF SA (Pty) Ltd, South Africa
	Nodumax	*Bradyrhizobia*	IITA Business incubation platform, Nigeria
	BIOFIX	Rhizobia	MEA Fertilizer Ltd, Kenya
	Soyflo	*Bradyrhizobium japonicum*	Soygro (Ltd) Ltd, South Africa

(continued)

Table 7.2 (continued)

Continent	Product	Active component	Manufacturer
	Rhizostim	*Azospirillum* sp.	Soygro (Ltd) Ltd, South Africa
	Mazospirflo	*Azospirillum brasilense*	Soygro (Ltd) Ltd, South Africa
Europe	Legume fix (common bean)	*Rhizobium* spp.	Legume Technology (UK)
	Legume fix (soybean)	*Bradyrhizobium japonicum*	
	Twin N	*Azorhizobium* sp., *Azoarcus* sp., *Azospirillum* sp.	Mapleton Ltd, UK
	Nitrasec	*Rhizobium tropici*	Lage y Cía. S.A, Uruguay
Australia	Bio-N	*Azotobacter* spp.	Nutri-Tech Solution, Australia
	B.Sub	*Bacillus subtilis*	Nutri-Tech Solution, Australia
	Accelerate	*Bacillus polymyxa*, *Streptomyces* spp.	Nutri-Tech Solution, Australia
	Bioplex	*Azotobacter* spp.	Nutri-Tech Solution, Australia
	Myco tea	*Azotobacter chrococcum*, *Bacillus polymyxa*	Nutri-Tech Solution, Australia
	Twin-N	*Azorhizobium*, *Azoarcus*, *Azospirillum*	Mapleton Int. Australia
	NIB PGPR peat inoculant	*Pseudomonas* sp.	Murdoch University, Australia
North and South America	Vault NP	*Bradyrhizobium japonicum*	Becker Underwood, USA
	Chick Pea Nodulator	*Mesorhizobium ciceri*	Becker Underwood, USA
	Cowpea peat inoculant	Rhizobia	Becker Underwood, USA
	Excalibur Gold	*Natural bacteria for field seed*	America's Best Inoculant, USA
	Graph-Ex	*Bradyrhizobium japonicum*	America's Best Inoculant, USA
	Green gram peat and Groundnut peat	Rhizobia	Becker Underwood, USA
	Myco Apply Soluble Maxx	*Bacillus licheniformis*, *B. megaterium*, *B. pumilus*, *B. amyloliquefaciens*	Mycorrhizal Application, Inc. USA
	Vault HP	*Bradyrhizobium* spp.	BASF, Canada

(continued)

Table 7.2 (continued)

Continent	Product	Active component	Manufacturer
	PHC Biopak	*Bacillus azotofixans*, *B. licheniformis*, *B. megaterium*, *B. polymyxa*, *B. subtilis*, *B. thuringiensis*	Plant Health Care Inc. USA
	PHC Biopak colonise AG	*Paenibacillus azotofixans*, *Bacillus licheniformis*, *B. megaterium*, *B. polymyxa*, *B. subtilis*, *B. thuringiensis*	Plant Health Care Inc. USA
	Rizo-Liq (green gram, common bean, soybean, groundnut, chickpea)	*Bradyrhizobium* sp. (green gram, ground nut and soybean), *Mesorhizobium ciceri* (chickpea), *Rhizobium* spp. (common bean)	Rizobacter, Argentina
	Rizo-Liq Top	*Bradyrhizobium japonicum*	Rizobacter, Argentina
Asia	Bioplant	*Clostridium*, *Achromobacter*, *Streptomyces*, *Aerobacter*, *Nitrobacter*, *Nitrosomonas*, *Bacillus*	Artemis & Angelio Co. Ltd, Thailand

Adapted from Raimi et al. (2017), Herrmann et al. (2015)

Furthermore, several research works have focussed on rhizobia, possibly because of its huge biological N-fixation capability, especially in symbiosis with legumes (Reis and Teixeira 2015; Zahran 1999). However, beyond rhizobia-legume interactions, there is more to be discovered and developed for improving N-fixation, particularly in nonleguminous crops. Similarly, bacterial inoculants that have multiple field applications (e.g. nitrogen fixation, nutrient solubilisation and syntheses of PGP substances) should be further investigated for efficient inoculation and sustainable crop production.

Globally, to improve quality, acceptance and adoption of bacterial inoculants, ideas should be borrowed from new technologies that include multi-omics approach. This approach could lead to the development of ‘super-inoculants’ that can be used not only to improve plant health but also to eliminate unwanted microbes that directly or indirectly inhibit plant development. This could involve development of a biomarker strategy for manipulating plant microbiome ecosystems, thus improving the production of efficient bacterial inoculants for sustainable management of agroecosystems.

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