



The potential of Bacilli rhizobacteria for sustainable crop production and environmental sustainability

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ABSTRACT

Conventional agricultural practices often rely on synthetic fertilizers and pesticides which have immense and adverse effects on humans, animals and environments. To minimize these effects, scientists world over are now deeply engaged in finding alternative approaches for crop production which are less dependent on chemical inputs. One such approach is the use of rhizospheric bacteria as vital components of soil fertility and plant growth promotion (PGP) through their direct and indirect processes in plant rhizospheres. Among the most studied rhizobacteria are the Bacilli, particularly for production of antibiotics, enzymes and siderophores all of which are important aspects of PGP. Despite this, little information is available especially on their potentiality in crop production and their direct application only involves a few species, leaving a majority of these important rhizobacteria unexploited. This paper gives an overview of the unique properties of Bacilli rhizobacteria as well as their different PGP mechanisms that if mined can lead to their successful application and agricultural sustainability. It further points out the missing aspects with regards to these important rhizobacteria that should be considered for future research. This information will be useful in analyzing the PGP abilities of Bacilli rhizobacteria with an aim of fully mining their potential for crop production and environmental sustainability.

1. Introduction

The demand for food will continue to rise annually and proportionally to the rising population worldwide (Patel and Minocheherhomji, 2018). This will consequently lead to intensification of agriculture for food security and the continued use of synthetic fertilizers and pesticides for maximization of yields (Kumar et al., 2010). As a result, deleterious effects of synthetic pesticides on non-target organisms and destabilization of ecosystems through pollution will also increase (Yu et al., 2009). Research world over is now directed to alternative environmentally-friendly means of improving crop growth and controlling plant pathogens (Bhattacharyya and Jha, 2012), and one most researched areas is the exploitation of plant-microbe associations to develop sustainable crop production systems (Naqqash et al., 2016).

Plant rhizospheres are special environments with complex plant root-soil microbes interactions (Jha et al., 2013). These complex interactions are propounded to follow roots exudations which serve to attract beneficial soil bacteria to the plant roots (Bhattacharyya et al., 2016; Mhlongo et al., 2018; Zhang et al., 2017) and as a result, plant

rhizospheres support a large number of bacteria which are commonly referred to as plant growth promoting rhizobacteria (PGPR) or beneficial rhizobacteria (Bhattacharyya and Jha, 2012; Raza et al., 2016). Evidence suggests that rhizobacteria are capable of enhancing plant growth either directly or indirectly through multifarious ways (Patel and Minocheherhomji, 2018; Raza et al., 2016), including nitrogen (N₂) fixation, nutrient solubilization and biosynthesis of phytohormones, antibiotics, hydrolytic enzymes, siderophores and induced systematic resistance (ISR) in plants to their pathogens (Beneduzi et al., 2012; García-Fraile et al., 2015; Gupta et al., 2015). Rhizobacteria which contribute to PGP through enhanced nutrient availability and N₂ fixation, phosphorous solubilization or iron acquisition are commonly referred to as biofertilizers (Kuan et al., 2016; Sharma et al., 2013). It is evidenced that such rhizobacteria are very useful in mobilization and solubilization of soil nutrients compared to their non-rhizospheric counterparts (Hayat et al., 2010), and are therefore very critical in redressing soil fertility (Glick, 2012). Rhizobacteria that contribute to suppression of plant pathogens by antagonism and competition are referred to as biocontrol agents or biopesticides (Beneduzi et al., 2012; Chowdhury et al., 2013), while those which contribute to degradation

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of organic pollutants and reduction of metal toxicity in contaminated soils are called bio remediators, rhizo-remediators or phytoremediators (Goswami et al., 2016). Similarly, rhizobacteria that produce phytohormones such as IAA, ethylene, GA and others are collectively referred to as phytostimulators (Somers et al., 2004). Endophytic rhizobacterial strains colonize plant root tissues internally (Verma et al., 2010), while the external types occur on the exterior portions of plant roots (Ilangumaran and Smith, 2017; Martinez-Viveros et al., 2010). As opposed to their external counterparts, endophytic rhizobacteria have been shown to be better candidates for plant growth promotion because of the intimate relationships they form with plant root tissues (Castanheira et al., 2017; Souza et al., 2015).

Rhizobacterial-based technologies have been investigated for their use as alternatives to synthetic fertilizers for sustainable crop production (Patel and Minocheherhomji, 2018). Some commonly studied rhizobacteria include *Pseudomonas*, *Azospirillum*, *Azotobacter*, *Enterobacter*, *Arthrobacter*, *Alcaligenes*, *Bacillus*, *Serratia*, *Burkholderia*, *Acinetobacter* and *Klebsiella*, all of which are reviewed by Bhattacharyya and Jha (2012) and Adesemoye et al. (2017). Their potential has been illustrated in several crops including wheat (Govindasamy et al., 2014), bean (Stefan et al., 2013), potato (Dawwam et al., 2013), maize (Krey et al., 2013), cucumber (Islam et al., 2016), and many others (Hayat et al., 2010). All these studies have demonstrated that PGPR-based formulations can improve different attributes of plant growth such as shoot and root length and biomass, seed germination and size of leaves (Wang et al., 2016). However, there still remains the need for further understanding of not only the mechanisms through which the PGPR perform their ecological roles, but also how such roles can be utilized and exploited for sustainable crop production and subsequently, improved food security (Rosier et al., 2018).

In this review, a critical discussion has been made on the Bacilli rhizobacteria. The Bacilli are among the most investigated rhizobacterial species (Souza et al., 2015), after *Pseudomonas* mostly for their bio-control activities (Idris et al., 2007). Reports indicate that bacilli are also the most abundant in plant rhizospheres (Sivasakthi et al., 2014), making up to 95% of the Gram positive rhizobacterial populations in plant rhizospheres ((Prashar et al., 2013). According to Kumar et al. (2012a), these bacteria are efficient PGPR and capable of enhancing plant growth through production of a number of substances such as antibiotics and antifungal metabolites (Chowdhury et al., 2013), such as siderophores (Compant et al., 2005), and lytic enzymes (Nelson, 2004). Members of the *Bacillus* genus are particularly popular candidates for PGP because they sporulate and are easier to subject to commercial formulation (Mendis et al., 2018). Evidence seems to suggest that many of the Bacilli rhizobacteria can promote plant growth in more ways than one or a combination of several processes. For instance, *B. polymyxa* BFKC01 can not only improve nutrient availability to plants, but also produces phytohormones and enhances plant host ability to tolerate biotic and abiotic stresses (Zhou et al., 2016). Despite this information, complete exploitation of these rhizobacteria for crop production has not yet been realized in many parts of the world, especially considering the many desirable qualities they possess which make them suitable for use as plant biofertilizers and biopesticides. In fact, it is propounded that these unique rhizobacteria have received far much less attention even as potential bio-control agents than the *Pseudomonas* yet they offer several PGP activities and several advantages over the latter and other rhizobacteria (Idris et al., 2007). In this review, we highlight the many ways in which the Bacilli rhizobacteria are important in PGP, the desirable qualities they possess and the different ways in which they can be exploited for crop production and environmental sustainability. The present paradigms of applications of these rhizobacteria in different countries are presented explicitly to shed light on their applicability or lack thereof. Most importantly, this paper shows their multifarious PGP potential, which if adequately mined, can greatly contribute to increased crop production while at the same time, redressing environmental conservation.

Table 1

Endophytic Bacilli rhizobacteria of several host plants.

<i>Bacillus</i> sp.	Host plant	Reference
<i>B. amyloliquefaciens</i>	Tomato	Tan et al., 2013
<i>B. aryabhatai</i>	Mung bean	Bhutani et al., 2018
<i>B. cereus</i>	Mung bean	Bhutani et al., 2018
	Sophora	Zhao et al., 2011
<i>B. licheniformis</i>	Saffron	Sharma et al., 2015
<i>B. pumilus</i>	Saffron	Sharma et al., 2015
<i>B. megaterium</i>	Soybean	Subramanian et al., 2015
	Maize, Corn, Carrot, Citrus	Surette et al., 2003
	Mung bean	Bhutani et al., 2018
	Wild legumes	Muresu et al., 2008
	Common bean	Korir et al., 2017
<i>B. polymyxa</i>	Soybean	Hung et al., 2007
	Common bean	Korir et al., 2017
<i>B. simplex</i>	Various plants, Pea	Schwartz et al., 2013
	Wild legumes	Muresu et al., 2008
<i>B. subtilis</i>	Wheat	Li et al., 2013
	Soybeans	Bai et al., 2003
<i>B. thuringiensis</i>	Soybeans	Bai et al., 2003
<i>Bacillus</i> sp.	Chickpea	Saini et al., 2013
	Mung bean	Pandya et al., 2013
	Pigeon pea	Rajendran et al., 2008
	Peanuts	Figueredo et al., 2014
	Tomato	Wei et al., 2015
	Wheat	Selvakumar et al., 2008
	Maize	Ikedo et al., 2013

2. Types of Bacilli rhizobacteria

Just like other PGPR, Bacilli rhizobacteria can be external or internal rhizobacteria with respect to plant roots (Gadhav et al., 2018). Literature indicates that *Bacillus* spp. are among the most common endophytes in plants (Rajendran et al., 2008), and that endophytic *Bacillus* spp. form more intimate relationships with their host plants because they are protected within the host tissues (Zhao et al., 2015), and possess better bio-control properties against plant pathogens (Dey et al., 2014; Timmusk et al., 2005). Hence, there is need to further investigate their potential in PGP as well as bioprotection. Examples of endophytic Bacilli rhizobacteria alongside their specific host plants are provided in Table 1.

Literature shows that some endophytic *Bacillus* spp. exist in nodules of non-specific hosts and are important in promoting growth and nodulation in such plants (Deng et al., 2011; Li et al., 2008a, 2008b; Muresu et al., 2008; Saini et al., 2013; Selvakumar et al., 2008; Stajković et al., 2009). Interestingly, such bacilli can be exploited for agricultural value. For instance, a very recent study by Zhao et al. (2018), demonstrates that nodule symbiotic *Bacillus* strains can be valuable candidates for exploring as biofertilizers. Some Bacilli rhizobacteria have also been implicated in enhanced nodulation and plant yield, especially when co-inoculated with *Rhizobium* (Bai et al., 2003; Rajendran et al., 2008).

This potential thus opens an interesting possibility for harnessing the Bacilli rhizobacteria for biofertilizer formulations. However, there is need for further investigations on the occurrence, conditions and interactions of endophytic Bacilli rhizobacteria with different plant systems and how this can be made a beneficial option for improved crop yields and ultimately environmental sustainability.

3. The plant growth promotion functions of Bacilli rhizobacteria

The Bacilli rhizobacteria are known for many unique functions and properties in plant rhizospheres including phytostimulation, biofertilization and bioprotection. Detailed descriptions of the functions are elaborated in the following sub-sections.

Table 2

Phytohormones produced by different Bacilli rhizobacteria from different host plants.

Phytohormone	Bacilli rhizobacteria	Host Plant	Reference
IAA	<i>B. amyloliquefaciens</i>	Duckweed	Idris et al., 2007
	<i>B. amyloliquefaciens</i>	Soybean	Sharma et al., 2013
	<i>B. amyloliquefaciens</i> , <i>B. subtilis</i>	Pepper	Wu et al., 2015
	<i>B. aryabhattai</i>	Soybean	Park et al., 2017a
	<i>B. cereus</i>	Wheat	Hassan et al., 2018
	<i>B. cereus</i>	Rice, Chickpea	Chakraborty et al., 2011
	<i>B. cereus</i> , <i>B. megaterium</i> , <i>B. aryabhattai</i>	Mung bean	Bhutani et al., 2018
	<i>B. licheniformis</i>	Wheat	Singh and Jha, 2015
	<i>B. megaterium</i>	<i>Trifolium repens</i>	Marulanda et al., 2009
	<i>B. megaterium</i>	<i>Vinca rosea</i>	Khan et al., 2017
	<i>B. megaterium</i> , <i>B. subtilis</i> , <i>B. cereus</i>	Banana, Maize, Cotton, Wheat	Mohite, 2013
	<i>B. polymyxa</i>	Pepper	Phi et al., 2010
	<i>B. pumilus</i>	Wheat	Tiwari et al., 2011
	<i>B. pumilus</i> , <i>B. furmus</i>	Potato	Gururani et al., 2012
	<i>B. subtilis</i>	<i>Acacia gerrardii</i>	Hashem et al., 2016
	<i>B. subtilis</i>	Wheat	Upadhyay et al., 2012
	<i>Bacillus</i> sp.	Grapevines	Liu et al., 2016
	<i>Bacillus</i> spp.	Maize	Bjelčić et al., 2018
	<i>Bacillus</i> spp.	Bitter gourd	Ahmad et al., 2016
	<i>Bacillus</i> spp.	Maize	Rayavarapu and Padmavathi, 2016
GA	<i>B. amyloliquefaciens</i>	Rice	Shahzad et al., 2017
	<i>B. aryabhattai</i>	Soybean	Park et al., 2017b
	<i>B. cereus</i>	Wheat	Hassan et al., 2018
	<i>B. pumilus</i> , <i>B. cereus</i>	Red Pepper	Joo et al., 2005
	<i>B. pumilus</i> , <i>B. licheniformis</i>	<i>Alnus</i>	Gutierrez-Manero et al., 2001
		<i>Glutinosa</i>	
	<i>B. subtilis</i>	Cucumber	Park et al., 2013
	<i>B. amyloliquefaciens</i>	Rice	Shahzad et al., 2016
	<i>Bacillus</i> spp.	Maize	Rayavarapu and Padmavathi, 2016
ABA	<i>B. amyloliquefaciens</i>	Rice	Shahzad et al., 2017
	<i>B. aryabhattai</i>	Soybean	Park et al., 2017b
	<i>B. cereus</i>	Wheat	Hassan et al., 2018
	<i>B. licheniformis</i>	Grape vines	Salomon et al., 2014
	<i>B. licheniformis</i>	<i>Chrysanthemum morifolium</i>	Zhou et al., 2017
Cytokinin	<i>B. licheniformis</i> , <i>B. pumilus</i> , <i>B. subtilis</i>	<i>Alnus glutinosa</i>	Gutierrez-Manero et al., 2001
	<i>B. megaterium</i> UMCV1	Beans	Ortiz-Castro et al., 2008
	<i>Bacillus</i> sp.	Cucumber	Sokolova et al., 2011
Ethylene	<i>B. subtilis</i>	<i>Arabidopsis</i>	Ryu et al., 2004
	<i>B. subtilis</i>	Rice	Chandler et al., 2015

3.1. Bacilli rhizobacteria as phytostimulators

Production of phytohormones such as gibberellic acid (GA) and indole-3-acetic acid (IAA) is one of the direct PGPR mechanisms exhibited by Bacilli rhizobacteria (García-Fraile et al., 2015). Several Bacilli rhizobacteria are known to produce IAA but little has been reported on their ability to produce abscisic acid (ABA) (Table 2). Phytohormone biosynthesis by these rhizobacteria has been directly linked to nutrient availability and subsequent growth promotion in different plants (Stamenkovic et al., 2018). For instance, inoculating potted tomato seedlings with cell suspensions of *B. subtilis*, was reported to enhance shoot and root growth, seedling vigor and leaf area of the plants and higher levels of GA and IAA were detected in treated plants compared with non-treated plants (Chowdappa et al., 2013). Some *Bacillus* strains such as SH1RP8 has also been shown to enhance 10.9% shoot growth and 51.7% dry weight of *Peucedanum japonicum* (Hong and Lee, 2014). Indole-3-acetic acid has an important role in enhancement of shoot and root development by influencing cell division and elongation (Pin-Ng et al., 2015).

The isolation of IAA-producing rhizobacteria and their application on crops has been put forward as a promising way of increasing soil fertility and plant production (Vejan et al., 2016).

The GAs are also known to influence many developmental processes such as seed germination, stem elongation, flowering, and fruiting in plants (Hedden and Phillips, 2000), and as well as enhanced shoot elongation and leaf bud formation (Srivastava, 2002). On the other

hand, ABA regulates many physiological processes in plants including seed germination and tolerance to environmental stresses (Vijayabharathi et al., 2016). Just like IAA and GA, the presence of cytokinin in plant rhizospheres is reported to result in enhanced plant growth (Ortiz-Castro et al., 2008; Patel and Minocheherhomji, 2018). Studies show that cytokinin promotes plant growth by facilitating seed germination, leaf enlargement, and root and shoot development among others (Jha and Saraf, 2015).

Similarly, ethylene is important for growth and development of plants at lower concentrations but at higher concentrations, it can induce defoliation and premature senescence (Patel and Minocheherhomji, 2018). The production of such phytohormones and the subsequent enhancement of root branching, root numbers and/or development of root hair cells roots development is recognized to enhance nutrient uptake in plants (Kumar, 2015).

3.2. Bacilli rhizobacteria as plant bio-protectors

Bacilli rhizobacteria are among the most studied plant bio-protection agents (Przemieniecki et al., 2018), and use and number of antagonistically important Bacilli rhizobacteria is increasing rapidly especially because of their broad spectrum of activity against plant pathogens (Shafi et al., 2017). Some examples of Bacilli plant bioprotectors include to *B. simplex* (Schwartz et al., 2013), *B. amyloliquefaciens* (Idris et al., 2007), *B. thuringiensis* (Bai et al., 2003), *B. megaterium* (López-Bucio et al., 2007), and *B. subtilis* (Ashwiri and Srividya, 2013).

For instance, *B. amyloliquefaciens* has been shown to have antifungal activity against *Puccinia striiformis* (Reiss and Jørgensen, 2017). Investigations by Wei et al. (2011), revealed the ability of *B. amyloliquefaciens* in reducing infections caused by *Ralstonia solanacearum* in potato plants. In another report by Etesami and Alikhani (2017), *B. cereus* was highlighted as having the potential of controlling many rice phytopathogenic fungi. *Bacillus cereus* has also been shown to be effective in bio-protection of Pigeon Pea against several fungal pathogens (Rani et al., 2011). In a very recent study, *Bacillus* sp. were shown to have significantly high antifungal properties when compared with other rhizobacteria including *Pseudomonas* spp. (Bjelić et al., 2018). In laboratory analyses performed by Przemienjecki et al. (2018), *B. subtilis* was reported to be antagonistic against a wide range of phytopathogens including *Alternaria alternata*, *Aspergillus flavus*, *Botrytis cinerea*, *Colletotrichum acutatum*, *Fusarium oxysporum*, *F. graminearum*, *Verticillium dahlia*, and *Xanthomonas compestris*. In general, *B. subtilis*, *B. amyloliquefaciens* and *B. cereus* are documented as the most effective of all rhizobacterial species in controlling plant diseases (Francis et al., 2010). Many of these special Bacilli rhizobacterial species with the potential to manage important plant diseases are reviewed by Shafi et al. (2017).

Bacilli rhizobacteria contribute to plant bioprotection in a number of ways, including by production of siderophores, enzymes, antibiotics and volatile organic compounds (Patel and Minocheherhomji, 2018), as discussed in the sections below.

3.2.1. Production of siderophores

Siderophores are iron-chelating low molecular weight (200–2000 Da) compounds produced by some microorganisms and plants under iron-limiting conditions (Mhlongo et al., 2018; Shaikh and Sayyed, 2015). The mode of pathogen suppression by siderophores has been put forward as restriction of pathogen survival through inhibition of iron nutrition by chelation of available iron (Chaiharin et al., 2009). As such, a lot of siderophore-producing rhizobacteria, including Bacilli have been implicated in biocontrol of several plant diseases (Sayyed et al., 2005). *Bacillus* sp. from the maize rhizosphere were shown to have a high capacity to produce siderophores (Bjelić et al., 2018) and antagonism elicited by other siderophore-producing *Bacillus* sp. against *Rhizoctonia solani* causing black scurf and stem canker was reported by Kumar et al. (2013). In another study, siderophores produced by *B. antiquum* were reported to control charcoal rot disease caused by *Macrophomonia phaseolina* in sorghum (Gopalakrishnan et al., 2011). Other examples of siderophore producing Bacilli rhizobacteria include *B. niabensis*, *B. subtilis* and *B. mojavensis* (Kesaulya, 2018), *B. megaterium* (Chakraborty et al., 2006), *Bacillus* sp. from maize and peeper (Beneduzi et al., 2012), *B. cereus* from rice, mung bean and chickpea (Chakraborty et al., 2011), *B. pumilus* and *B. furvus* from potato (Gururani et al., 2012), *B. polymyxa* from pepper (Phi et al., 2010), *B. subtilis* from Chickpea (Karimi et al., 2011), and *B. pumilus* from wheat plants (Hafeez et al., 2006; Shaikh and Sayyed, 2015).

Siderophore-producing rhizobacteria are quickly gaining commercial significance not only because target organisms cannot develop resistance (Sayyed et al., 2005), but also because they also enhance iron nutrition to plants grown in iron limiting soils (Sayyed et al., 2007; Tank et al., 2012). Apart from iron, there is evidence indicating that siderophores also form stable compounds with other heavy metals like Al, Cd, Cu, Pb and Zn (Gururani et al., 2012). This phenomenon is advantageous to plants not only because of increasing availability of mineral nutrient to plants (Hassen et al., 2016), but also because they can help alleviate heavy metal stress especially in polluted soils (Ahemad and Kibret, 2014). The usefulness of siderophores and siderophore producing Bacilli rhizobacteria in plant health and nutrition can therefore not be overlooked and is worth more investigations.

3.2.2. Production of antibiotics

Bacilli rhizobacteria are reported to be among the most important

genera for antibiotic production (Jayaprakashvel and Mathivanan, 2011). Evidence shows that *B. subtilis* 168 and *B. amyloliquefaciens* FZB42 (Chang et al., 2007), produce a wide variety of antibacterial and antifungal antibiotics, including subtilin, bacilysin, mycobacillin, rhizocitins and diffidin (Leclerc et al., 2005). In fact, these two *Bacillus* species are evidenced to have an average of 4–5% (Stein, 2005), and 8% (Ruckert et al., 2011), respectively of their genomes respectively coding for structurally diverse antimicrobial compounds. *Bacillus subtilis* also produces lantibiotics (Stein, 2005), which exhibit strong antibacterial properties against Gram-positive bacteria but their involvement in the biocontrol activity against plant-associated pathogens has not been clearly demonstrated (Cawoy et al., 2011). *Bacillus brevis* and *B. polymyxa* produce gramicidin S and polymyxin B peptide antibiotics that strongly inhibit *Botrytis cinerea* causing grey mold disease in strawberry under both *in vitro* and field conditions (Haggag, 2008) and reports also indicate that other *Bacillus* species can produce several antibiotics such as oomycin, pyoluteorin, and zwittermicin A (Fernando et al., 2005). Zwittermicin and mycosubtilin from *B. subtilis* are reported to be very effective against a number of fungal pathogens (Saraf et al., 2014), including *Pythium aphanidermatum* (Leclerc et al., 2005). Also implicated in production of antibiotics are *B. cereus*, *B. licheniformis*, *B. megaterium*, *B. mycoides* and *B. pumilus* (Cawoy et al., 2011).

Antibiotics have been reported to suppress different plant pathogens through fungistasis (Shaikh and Sayyed, 2015). For instance, old reports indicate that a number of antibiotics such as iturin (Yu et al., 2002), surfactin (Ongena and Jacques, 2008), and aminopolylol produced by *B. subtilis* have strong antimicrobial activities against major plant pathogens like *Rhizoctonia solani*, *Fusarium oxysporum* and *Pythium ultimum* (Constantinescu, 2001) and *Podosphaera fusca* causing powdery mildew of cucurbits (Romero et al., 2007). These reports have been confirmed by a more recent study by Grover et al. (2010). Romero et al. (2007) also showed the connection between iturin and fengycin antibiotics from four *B. subtilis* strains (UMAF6614, UMAF6616, UMAF6639, and UMAF8561) in the suppression of powdery mildew of cucurbits caused by *Podosphaera fusca*. Bacillomycin D produced by *Bacillus* sp. A3F and *B. amyloliquefaciens* FZB42 (Koumoutsis et al., 2007), has also shown remarked effectiveness against *Sclerotinia sclerotiorum* (Kumar et al., 2012b), and other fungal plant pathogens (Chen et al., 2009). Similarly, other antibiotics from *B. cereus* (KBS5-H) and *B. subtilis* (KBS6-3), were also reported to show significant efficiency against *F. oxysporum* and *Pythium ultimum* respectively (Idris et al., 2007). It is reported that the basis of antibiosis in bacteria is secretion of compounds which are deleterious to the metabolism of other microorganisms (Sayyed et al., 2008), and has been put forward as one of the processes that rhizobacteria use to suppress plant pathogens (Glick et al., 2007). Additionally, studies have established that each family of *Bacillus* antibiotics display specific antimicrobial activities and may thus be differentially involved in the antagonism of the various plant pathogens (Cawoy et al., 2011). A detailed review on the different classes of antibiotics produced by Bacilli rhizobacteria is available (Engelbrecht et al., 2018). Maksimov and Khairulin (2015), also reviewed some important antibiotics produced by Bacilli rhizobacteria. Likewise, a detailed analysis of all known antibiotics produced by *B. subtilis*, one of the most studied Bacilli rhizobacteria is provided for in an earlier review by Stein (2005).

3.2.3. Induced systematic resistance in plants

The isolation of important biocontrol rhizobacteria but with no apparent antagonistic activities led to the discovery of an interesting class of plant associated bacteria that activate plant defense systems (Cawoy et al., 2011). As such, ISR occurs when a plant acquires the ability to resist a pathogen it was initially susceptible to through the interaction with a rhizobacterium (Patel and Minocheherhomji, 2018). As a result, rhizobacteria which result into ISR in plants may not necessarily produce metabolites like antibiotics and siderophores but are still capable of protecting plants through alteration of host defense

systems (Shaikh and Sayyed, 2015). Defense elicitation during ISR is reported to occur as a result of cell wall thickenings or rapid death of diseased cells to prevent spread of pathogens (Lugtenberg et al., 2002). Several rhizobacterial species, have been implicated in triggering ISR in various plants against a broad range of diseases (Van Wees et al., 2008). Experimental results show that *Bacillus* species can induce a broad spectrum of resistance against various bacterial and fungal plant pathogens under both greenhouse and field conditions (Kloepper et al., 2004; Shafi et al., 2017).

The main components of ISR have been identified as phenolic compounds, genetic and structural modifications, plant resistance activators, and activation of enzymatic weapons (Shafi et al., 2017). However, many studies maintain that the biochemical and structural modifications in plants are key sources of disease reduction by defending pathogen attack (Shafi et al., 2017), and can lessen the spread of pathogens in host plants (Guo et al., 2004). For instance, cytological studies of root colonization of pea by *B. pumilus* limited *Fusarium oxysporum* from the epidermis and outer cortex by strengthening the cell wall and epidermal cells. In an older study with the same species, reduced fungal colonization by changing the host physiology by enhancing host cell wall density was reported (Benhamou et al., 1998). Instances of *Bacillus*-triggered ISR in different plants are illustrated in Table 3. Further, an old review is available on ISR elicitation in different plants against a wide spectrum of pathogens under greenhouse and field conditions (Kloepper et al., 2004).

Although rhizobacterial mediated ISR is not normally pathogen-specific and cannot confer total protection to plants, the phenomenon is highly desirable since it is long-lasting and confers a broad spectrum of protection to plants (Cawoy et al., 2011), and should definitely be explored and understood further. Out of the numerous *Bacillus* species involved in ISR in plants, *B. subtilis* is the most common and most efficient. It should however be noted that although *B. subtilis* is not always entirely rhizospheric and can be found in non-rhizospheric soils (Idris et al., 2007), it has often been associated with antifungal activities against plant pathogens (Bais et al., 2004).

The level of ISR has been shown to vary for different strains of rhizobacteria and in different plant species (Shafi et al., 2017). It is therefore important to investigate ISR elicitation by Bacilli rhizobacteria in different plants. ISR has also been demonstrated to be higher under plant-stress conditions than in non-stress conditions, thus ISR is highly favorable and recommended for biological control of plant pathogenic diseases even under environmentally-stressing conditions (Shafi et al., 2017). Their ability to produce heat-resistant spores can also be harnessed for successful plant protection in dry and hot conditions as will be the case in the wake of climate change and global warming. The application of Bacilli rhizobacterial species that can develop ISR in plants is a novel plant protection strategy (Idris et al., 2007; Wiesel et al., 2014), that should obviously call for more investigations to fully understand the mechanisms behind it and how they can fully be exploited for plant protection. In addition, most of the ISR elicited by these rhizobacteria has only been demonstrated under laboratory or greenhouse conditions and it is important that this promising attribute of the Bacilli should be investigated thoroughly under field conditions to increase applicability.

3.2.4. Production of volatile organic compounds

Rhizobacterial Volatile Organic Compounds (VOCs) are low molecular weight compounds (< 300 g/mol) with high vapor pressure and include alcohol, aldehydes, ketones, hydrocarbons, acids and terpenes (Bhattacharyya et al., 2016; Mhlango et al., 2018). Such VOCs have been directly and tightly linked to plant defense mechanisms by ISR (Shafi et al., 2017). For instance, the 2,3-butanediol (Ryu et al., 2004), and lipopeptides produced by *B. subtilis* plays an important role in PGP by activation of ISR (Compant et al., 2005) including the bio-control of *Fusarium* wilt of cucumber (Cao et al., 2011), *Phytophthora* blight of pepper (Chung et al., 2008), and damping off in tomato (Mizumoto et al., 2007). Experiments conducted on bean and tomato plants, the production of both surfactin and fengycin biosynthetic genes in *B. subtilis* S168 was also associated with a significant increase in ISR. Additionally, *B. polymyxa* that elicits ISR in *Arabidopsis* is documented

Table 3
Selected examples of *Bacillus*-induced systematic resistance in different host plants.

Bacilli rhizobacteria	Host plant	Pathogens	Evaluation conditions	Reference
<i>B. subtilis</i>	<i>Arabidopsis</i>	<i>Pseudomonas syringiae</i>	Greenhouse	Rudrappa et al., 2010
	Rice	<i>Xanthomonas oryzae</i>	Greenhouse	Jayaraj et al., 2004
	Tomato	<i>Alternaria solani</i> , <i>Phytophthora infestans</i>	Greenhouse	Chowdappa et al., 2013
	<i>Arabidopsis</i>	<i>Erwinia carotovora</i>	Greenhouse	Compant et al., 2005
	Rice	<i>Xanthomonas oryzae</i>	Laboratory, Greenhouse	Udayashankar et al., 2011
	Rice	<i>Rhizoctonia solani</i>	Greenhouse	Chandler et al., 2015
	Tomato	<i>Alternaria solani</i> , <i>Phytophthora infestans</i>	Laboratory, Greenhouse	Chowdappa et al., 2013
	Tomato	<i>Fusarium oxysporum</i>	Greenhouse	Akram et al., 2016
	Wheat	<i>Puccinia striiformis</i>	Greenhouse, field	Li et al., 2013
	Cucurbits	<i>Podosphaera fusca</i>	Laboratory	Romero et al., 2007
	Tomato, Tobacco and cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
	Tomato	<i>Ralstonia solanacearum</i>	Greenhouse	Tan et al., 2013
	Tobacco	<i>Nicotiana tabacum</i>	Laboratory, Greenhouse	Wang et al., 2016
<i>B. amyloliquefaciens</i>	Pepper	<i>Xanthomonaas axonipodis</i>	Field	Choi et al., 2014
	<i>Panax ginseng</i>	<i>Phytophthora cactorum</i>	Field	Lee et al., 2015
	Tomato, Tobacco, Cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
<i>B. cereus</i>	Tobacco, Corn	<i>Fungal pathogens</i>	Greenhouse & field	Huang et al., 2012
	Tomato, Tobacco and cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
<i>B. pasteurii</i>	Soybean	<i>Rhizoctonia bataticola</i> , <i>Sclerotium rolfsii</i>	In vitro	Hung et al., 2007
<i>B. polymyxa</i>	French bean	<i>Xanthomonas campestris</i>	Laboratory, Greenhouse	Mageshwaran et al., 2012
	Wheat	<i>Septoria tritici</i>	Field	Kildea et al., 2008
<i>B. megaterium</i>	Tomato, Tobacco, Cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
	Sugar beet	<i>Cercospora beticola</i>	Laboratory, Glasshouse	Bargabus et al., 2004
<i>B. mycoides</i>	<i>Arabidopsis</i>	<i>Erwinia carotovora</i>	In vitro	Ryu et al., 2004
	Tomato, Tobacco, Cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
<i>B. spheericus</i>	Tomato	<i>Ralstonia solanacearum</i>	Greenhouse	Park et al., 2007
<i>B. vallismortis</i>	Chilli pepper	<i>Colletotrichum acutatum</i>	Greenhouse	Park et al., 2013
	Tomato	<i>Fusarium oxysporum</i>	Greenhouse	Akram et al., 2016
<i>B. fortis</i> LAGS162	Tomato, Tobacco and cucumber	Various pathogens	Greenhouse & field	Kloepper et al., 2004
<i>B. pumilus</i>	Sugar beet	<i>Cercospora beticola</i>	Laboratory, Glasshouse	Bargabus et al., 2004

to produce a number of VOCs including isoprene and acetoin (Lee et al., 2015). In studies done by Jiang et al. (2015), it was reported that *B. amyloliquefaciens* strain 54 enhanced the level of resistance in plants against bacterial fruit blotch of cucurbitaceae crops by eliciting accumulation of H₂O₂ and other VOCs in their tissues. These studies also confirmed the activity of VOCs such as 2,3-butanediol, 2-pentanol and acetoin by *B. subtilis* and *B. amyloliquefaciens* as earlier reported by Choong-Min et al., (2004).

Some rhizobacteria are capable of producing hydrogen cyanide (HCN) (Rezzonico et al., 2007), a VOC that is important in controlling plant pathogens by inhibiting the electron transport chain leading to death of cells (Patel and Minocheherhomji, 2018). Of the many VOCs produced by rhizobacteria, HCN is probably the most common and highly toxic compound that is reported to interfere with pathogen electron transport systems and therefore their energy supply systems (Patel and Minocheherhomji, 2018; Shaikh and Sayyed, 2015). Bacilli rhizobacterial species are documented to produce HCN and ammonia (Liu et al., 2016; Wani and Khan, 2010). Other VOCs which are highly effective against plant pathogens include decadienal and phenolic compounds (Shafi et al., 2017). In a recent *in vitro* study, several VOCs including 2,4 decadienal from *Bacillus* and *Paenibacillus* spp. were reported to show intensive antagonistic activities against a number of soil borne pathogens (Wei-wei et al., 2008). Evidence suggests that *B. pumilus* facilitates ISR development in pea roots in response to attack by *F. oxysporum* f. sp. *pisi* through accumulation of phenolic compounds (Jetiyanun and Kloepper, 2002), which contribute to pathogen suppression either by facilitating plant ISR by enhancing the mechanical strength of host cells or by directly inhibiting the growth of pathogen cells (Ramamoorthy et al., 2002). Production of VOCs is a very promising attribute of the Bacilli rhizobacteria that can be exploited for effective control of plant pathogens particularly those which are soil-borne. Reports indicate that production of VOCs is a strain specific phenomenon (Bhattacharyya et al., 2016), that can be attributed to rhizobacterial genotypes (Kai et al., 2016). More investigations on functionality and applicability of different *Bacillus* strains are definitely required. More knowledge is also needed on the nature and accumulation of these compounds in rhizobacteria to clearly understand the mechanisms by which they signal plant defense systems against specific pathogens (Bhattacharyya et al., 2016).

3.2.5. Production of lytic enzymes

Besides production of siderophores, antibiotics and VOCs, several Bacilli rhizobacteria also produce lytic enzymes such as chitinases, glucanases and chitosanases (Shafi et al., 2017), whose defense-related activities have been proven against various plant pathogens (Shafi et al., 2017; Thilagavathi et al., 2007).

Enzymes are normally produced by several bacteria mainly to hydrolyze and utilize nutrients stored in substrates but the production of these unique metabolites transcends nutrient acquisition and often include outcompetition of other microbes in the rhizosphere (Shafi et al., 2017). Table 4 illustrates some of the rhizobacterial *Bacillus* species from a number of host plants which have been shown to produce lytic enzymes. Bacilli rhizobacteria that produce these important defense-eliciting enzymes hold an immense potential for the management of important fungal diseases of plants (Shafi et al., 2017). The cell walls of many plant pathogenic fungi are often made up of chitin and therefore rhizobacterial Bacilli which produce chitinases are particularly very important in biological control of such pathogens and ultimately lead to reduced dependence on chemical fungicides (Shaikh and Sayyed, 2015). The potential and major biocontrol agents with chitinolytic activities include *B. licheniformis*, *B. cereus*, *B. circulans*, *B. subtilis* and *B. thuringiensis* (Sadfi et al., 2001).

3.3. Bacilli rhizobacteria as biofertilizers

3.3.1. Nutrient solubilization

Most soils have sufficient amounts of plant nutrients but these are often present in insoluble forms which are unavailable for uptake by plants (Shafi et al., 2017). Rhizobacterial *Bacillus* species secrete a number of metabolites which can strongly increase nutrient availability to plants (Sivasakthi et al., 2014; Verma et al., 2010). For instance, Jiang et al. (2015), after studying 100 bacterial strains for their PGP activities reported that *B. amyloliquefaciens* S54 significantly increased plant growth by enhancing the Nitrogen, Phosphorus and Potassium as well as the chlorophyll content of plants. Inoculation of peanut seedlings with *B. thuringiensis* was reported to improve the solubilization of sparingly soluble phosphate compounds in soils resulting in a higher crop yield and increase the concentration of soluble P (Wang et al., 2014). In yet another study, inoculating wheat plants with *B. thuringiensis* was also reported to improve P uptake by the plants when compared with untreated plants (Delfim et al., 2018). In studies done by Han and Lee (2006), *B. megaterium* var. *phosphaticum* inoculated in nutrient deficient soils resulted into increased P availability and uptake in pepper and cucumber. In a different study, Hafeez et al. (2006), also reported nutrient solubilization ability of *B. pumilus* of wheat in Mongolia. In terms of nutrient solubilization, *Bacillus* spp. are perhaps the most efficient rhizobacteria comparable only to *Pseudomonas* (Podile and Kishore, 2006). Furthermore, evidence now seems to suggest that Bacilli rhizobacteria could actually be better PGP candidates than *Pseudomonas* sp. (Malleswari and Bhagyanarayana, 2013), and probably unmatched by all other rhizobacteria. In a recent study by Bjelić et al. (2018) for instance, *Bacillus* spp. were found to be better P-solubilizers than all other isolates that were studied, including *Pseudomonas* spp.

The mechanisms of P-solubilization have been associated with the release of organic acids through which their hydroxyl and carboxyl groups chelate the cations bound to the phosphate, ultimately converting it into soluble forms (Bhattacharyya et al., 2016; Patel and Minocheherhomji, 2018). Evidence suggests that these P solubilizing bacteria (PSB) utilize the sugars in root exudates and in turn produce the organic acids which are responsible for P solubilization (Goswami et al., 2014). Several studies have identified and quantified organic acids from Bacilli rhizobacteria and defined their role in the solubilization process (Marra et al., 2012). However, the efficiency of solubilization depends on the kind of organic acids released into the medium and their concentration (Delfim et al., 2018). The identification of specific Bacilli rhizobacteria that can produce several organic acids simultaneously could also mean greater solubilization potential of insoluble inorganic phosphates and other nutrients (Marra et al., 2012), and probably suffice with regards to provision of nutrients to plants.

Among the soil bacterial communities, ectorrhizospheric *Bacillus* species for example *B. megaterium*, *B. circulans*, *B. coagulans*, *B. subtilis*, *B. sircalmous* (Govindasamy et al., 2011), and *B. cereus* (Rani et al., 2011), are recognized as some of the most effective P solubilizers (Goswami et al., 2014). Other Bacilli rhizobacteria which have been implicated in P solubilization include *B. pumilus* and *B. furmus* (Gururani et al., 2012), *B. cereus* (Chakraborty et al., 2011), *B. thuringiensis* and *B. sphaericus* (Sivasakthi et al., 2014), *B. flexus* (Ibarra-Galeana et al., 2017), *B. polymyxa* (Ei-Yazeid and Abou-Aly, 2011), and other *Bacillus* spp. (Liu et al., 2016). Phosphate solubilization by *B. megaterium* has also been reported by other workers (Chakraborty et al., 2006; Ibarra-Galeana et al., 2017; Surette et al., 2003). It goes without saying that the application of PSB can contribute immensely to increased P availability for plants and reduce the need for the application of synthetic P fertilizers and the environmental effect associated with excess of P applications.

Potassium (K), is also one of the essential nutrients required for plant growth (Patel and Minocheherhomji, 2018), but is also often limiting in most soils. Hence, the need to find indigenous sources of soil enrichment with K-solubilizing rhizobacteria present in soil can provide

Table 4
Lytic enzymes produced by some rhizobacterial *Bacillus* species in different host plants.

<i>Bacillus</i> sp.	Enzyme(s)	Host plant	Reference
<i>B. subtilis</i>	Phenolics lyases, Catalases	Tomato	Ramyabharathi and Raguchander, 2014
	Chitinases	Tobacco	Das et al., 2010
	Chitinases	Grapevine	Trotel-Aziz et al., 2008
	Catalases	Wheat	Przemieniecki et al., 2018
	Proteases	Chickpea	Karimi et al., 2011
	Chitinases, Glucanases, Proteases, Cellulases	Chickpea	Patil et al., 2014
	Chitinases	Peanut	Kishore et al., 2005
<i>B. circulans</i>	Glucanases, Chitinases, Peroxidases,	Sugar beet	Bargabus et al., 2004
<i>B. mycoides</i>	Glucanases, Chitinases	Sugar beet	Bargabus et al., 2004
<i>B. pumilus</i>	Peroxidases, Glucanases, Chitinases	Sugar beet	Bargabus et al., 2004
<i>B. thuringiensis</i>	Chitinases	Soybean	Liu et al., 2010
	Chitinases	Cotton	Shaikh and Sayyed, 2015
	Chitinases	Sorghum	Idris et al., 2007
<i>B. cereus</i>	Catalases, Proteases, Chitinases	Rice, Mung bean, Chickpea	Chakraborty et al., 2011
	Chitinases, Chitosanase, Proteases	Cabbage	Chang et al., 2007
	Chitinases, Glucanases	Loquat	Wang et al., 2014
	Proteases	Pepper	Sivasakthi et al., 2014
<i>B. licheniformis</i>	Chitinases	Cabbage	Chang et al., 2007
<i>Bacillus</i> sp.	Cellulases	Grapevines	Liu et al., 2016
<i>B. polymyxa</i>	Lytic enzymes	Maize	Bjelić et al., 2018
	Chitinases, Glucanases, Proteases, Peroxidases	Tomato	Solanki et al., 2014
	Peroxidases, Oxidases, superoxide dismutases	Tomato	Chowdappa et al., 2013
	Cellulases, Pectinases	Soybean	Hung et al., 2007

K to plants in K deficient soils (Setiawati and Mutmainnah, 2016). A number of *Bacillus* species from Pepper and cucumber rhizospheres are documented to be involved in K solubilization (Han and Lee, 2006). Also commonly implicated in K mobilization are *B. circulans* (Liu et al., 2012), *B. mucilaginosus* and *B. edaphicus* (Bhattacharya et al., 2016). Bacilli rhizobacteria have also been implicated in solubilization of other nutrients. For instance, Zinc solubilization and mobilization ability of *B. subtilis* have been demonstrated in wheat and soybean plants (Ramesh et al., 2014), and in soybean and mung bean (Sharma et al., 2013). Zinc solubilization has also been reported in studies involving *B. aryabhattai* (Mumtaz et al., 2017). However, most of these demonstrations have been conducted under laboratory conditions and little information is present on the transferability of these qualities under field conditions. According to Parmar and Sindhu (2013), generally little is known of K solubilization and mechanisms of solubilization by most rhizobacteria in different crops and there are possibilities for further enhancing the production of crops by application of K solubilizing rhizobacteria as biofertilizers.

3.3.2. Nitrogen fixation

More than 80% of N₂ occurs in the atmosphere as inert gas which is not available to plants (Patel and Minocheherhomji, 2018). To supply this important nutrient to plants, nitrogenous fertilizers are often applied during crop production. Recent reports indicate that less than half of applied nitrogen is effectively absorbed by plants with the rest being lost through volatilization or leaching resulting into environmental pollution (Le Mire et al., 2016). For instance, nitrous oxide (N₂O) which is one of the gases evolved during application of nitrogenous fertilizers is one of the most important greenhouse gases (Adesemoye et al., 2009). A lot of these problems can adequately be solved by exploiting the biological N₂ fixing microorganisms (Calvo et al., 2014).

Biological nitrogen fixation (BNF) is the process through which atmospheric N₂ is reduced to ammonia which can be taken up by plants (Gothwal et al., 2007). The BNF process can occur symbiotically or asymbiotically (Gupta, 2004). *Bacillus* sp. among other rhizobacteria such as *Azospirillum*, *Azotobacter* and *Paenibacillus* are some of the asymbiotic N₂ fixers in plant rhizospheres (Ahmad and Kibret, 2014; Goswami et al., 2015). In a study done by Ding et al., (2005), investigating N₂-fixing strains from plant rhizospheres in Beijing region, the presence of *nif* genes in *Bacillus* was reported. The N₂-fixing *B. megaterium* has previously also been isolated from maize and rhizospher

es (Liu et al., 2006). Older studies also report the N₂-fixing ability of *Bacillus* spp. and *B. polymyxa* isolated from grass (Idris et al., 2007) and wheat roots (Omar et al., 1996) respectively. The species *B. polymyxa* has also been reported to increase the foliar N content in pine seedlings by up to 38% higher than control seedlings (Tang et al., 2017), and by up to 118% and 22% for canola and tomato seedlings respectively (Padma et al., 2016). *Bacillus pumilus* S1r1, and *B. subtilis* UPMB10 are also reported to have the capacity to fix N₂ (Gouda et al., 2018)). These studies agree with older reports on the ability of a number of Bacilli rhizobacteria including *B. megaterium*, *B. cereus*, *B. pumilus*, *B. circulans*, *B. licheniformis*, *B. subtilis*, *B. brevis* and *B. firmus* to contain nitrogenase activities (Xie et al., 1998).

Interestingly, quite recent reports indicate that some Bacilli rhizobacteria can be involved in symbiotic N₂ fixation (Bhattacharyya and Jha, 2012; Ikeda et al., 2013). Szilagy-Zecchin et al. (2014), also report of three endophytic *Bacillus* spp. isolated from corn roots with N₂ fixing capacity evaluated through acetylene reduction assay and identification of N₂ fixation (*nif*) genes. However, these reports only refer to the possibility of symbiotic N₂ fixation under *in vitro* conditions by use of Nitrogen free media. Due to the important nature of symbiotic N₂ fixation, such phenomena in Bacilli rhizobacteria are worth investigating and exploiting even *in planta*. Most symbiotic N₂ fixation even in Bacilli rhizobacteria have been reported in leguminous plants and it will also be immensely important to investigate the ability of Bacilli rhizobacteria to fix N₂ symbiotically in non-leguminous plants which form the bulk of human food worldwide (Gouda et al., 2018). Nitrogen fixation is an important trait of PGPRs as it directly provides N₂ to the plant and N₂-fixing rhizobacteria have been marketed as biofertilizers for over 20 years (Goswami et al., 2015). Although not many studies report the ability of Bacilli rhizobacteria to fix N₂, there are a number of studies which report on increased nitrogen nutrition in plants especially when Bacilli rhizobacteria are co-inoculated with other rhizobacterial species. For instance, co-inoculation of *Azospirillum lipoferum* and *B. megaterium* was reported to improve both N₂ and phosphorus nutrition in wheat plants (El-Komy, 2005). Similarly, co-inoculation of some *Bacillus* strains along with effective *Rhizobium* spp. has been shown to stimulate growth, nodulation and N₂ fixation, for instance in chickpea (Qureshi et al., 2009), and common bean (Korir et al., 2017). *Bacillus* spp. isolated from soybean root nodules can promote plant growth and nodulation either individually or with co-inoculation with *Bradyrhizobium japonicum* (Bai et al., 2003). These

interesting findings seem to signify some form of cooperation between Bacilli rhizobacteria and N₂-fixing bacteria which calls for more investigations

4. Factors that contribute to suitability of Bacilli rhizobacteria for plant growth promotion

The efficiency of *Bacillus* species over other rhizobacteria has constantly been attributed to their ability to produce spores which are resistant to environmental stresses (Rayavarapu and Padmavathi, 2016). The Bacilli rhizobacteria have found wide applications in several sectors because of the unique properties they possess (Ongena and Jacques, 2008). For example, they are known to be resistant to adverse environmental conditions due to their ability to produce hard, resistant endospores which have made them very attractive biological control agents. According to a number of workers, the spores make them survive extreme temperatures, pH and osmotic conditions and provide them with competitive advantages over other microorganisms (Kumar et al., 2014). The ability of the spores to survive for extended periods of time is especially attractive because it helps in increasing the shelf life of products, hence making them readily adaptable and attractive commercial formulations for field applications (Adesemoye et al., 2017). It is documented that *B. subtilis* endospores contribute to their hyperactivity against many fungal pathogens as a result of the ability of the spores to endure the extreme environmental conditions (Shafi et al., 2017). Moreover, sporulation is advantageous because bacterial suspensions can be converted into powdered formulations which are not only easy to handle but also increase their stability, something which cannot be realized with non-sporulating bacteria (Loloo et al., 2010).

Apart from sporulation, Bacilli rhizobacteria possess many other important properties that increase their chances of survival in the environment (Rosas-Garcia, 2009). For instance, reports indicate that although they are aerobic, they also possess qualities to enable them survive under extreme anoxic conditions (Silini-Cherif et al., 2012). This enables them to survive under different oxygen conditions and equip them with a competitive advantage over other rhizobacteria (Cawoy et al., 2011). Additionally, Bacilli rhizobacteria are well studied and understood organisms which helps to facilitate their use (Cawoy et al., 2011). For example, one of the major Bacilli rhizobacteria, *B. subtilis* is recognized by the US Food and Drug Administration (US FDA) as a GRAS (generally recognized as safe) organism (Denner and Gillanders, 1996). However, some species like *B. cereus*, although also good at PGP, are not suitable for formulation and commercialization because they are also opportunistic pathogenic to human beings (Nakreen et al., 2005).

The ability of Bacilli rhizobacteria to replicate rapidly has also made them suitable candidates for PGP as this is one of the critical factors required for successful bio-control activities (Cavaglieri et al., 2005). The rapid colonization potential of Bacilli rhizobacteria has been demonstrated in cucumber (Cao et al., 2011), cotton (Li et al., 2013), maize (Cavaglieri et al., 2005), banana (Zhang et al., 2011), water melon, (Jiang et al., 2015), and rice (Nautiyal et al., 2013). Rapid root colonization is documented as a prerequisite for PGP activities (Kamilova et al., 2015) and is subsequently one of the factors that are considered important during selection of rhizobacteria for commercial formulation (Shafi et al., 2017). Competitive colonization by some Bacilli rhizobacteria has been attributed to some of the metabolites they produce. For instance, surfactins synthesized by *B. amyloliquefaciens* FZB42 are documented to not only confer them with competitive advantage but also competitive colonization of the rhizosphere (Chen et al., 2009). Similarly, the successful application of *B. subtilis* as a commercial product for PGP has been attributed not only to its ability to produce numerous antifungal metabolites but also to its competitive colonization potential (Cao et al., 2011; Compant et al., 2010; Li et al., 2013). Furthermore, Bacilli rhizobacteria being motile species, are capable of moving towards and locating host plants through

chemotaxis, facilitating the colonization potential (Cawoy et al., 2011). In an earlier study done by Zheng and Sinclair (2000), motile and chemotactic strains of *B. megaterium* were shown to have better rhizosphere colonization ability and suppression of *Rhizoctonia solani*.

Bacilli rhizobacteria produce a wide array of antagonistic compounds such as wide spectrum antibiotics, siderophores and enzymes (Goswami et al., 2016; Shafi et al., 2017), all of which are known to suppress phytopathogens (Ashwiri and Srividya, 2013), and increase their competitive ability over the other microflora in the rhizosphere (Koumoutsis et al., 2004). The antibiotics they produce are reported to belong to different classes and capable of suppressing diverse microbial competitors, including phytopathogens (Choudhary and Johri, 2009). Additionally, some of the antifungal metabolites like siderophores and other VOCs double up as phytostimulators (McSpadden and Fravel, 2002). Moreover, Bacilli rhizobacteria are generally easy to subject to industrial production and commercialization because they do not have complex nutritional requirements (Cawoy et al., 2011).

5. Current and future prospects of use and application of Bacilli rhizobacteria

Bacillus species produce numerous compounds that can be applied in the management of a broad range of plant pests (Shafi et al., 2017) and plant growth promotion. Formulation, commercialization and application of efficient PGPR strains like the Bacilli has been put forward as one of the ways in which the agricultural losses cause by biotic and abiotic stresses can be controlled (Glick, 2014). However, there is still a huge potential of enhancing their usage for agricultural productivity (Kamilova et al., 2015). Table 5 portrays some of the commercial products that have been developed and commercialized using different Bacilli rhizobacteria as used in different countries on different crops.

Despite the fact that the Bacilli rhizobacteria possess many different and unique qualities which make them promising for commercial formulations, their use and application has not been adopted in majority of countries in the world. According to Shafi et al. (2017), their formulation and commercialization is concentrated mainly in America, Europe and Asia. In Africa for example, utilization has only been reported in South Africa. Still, although most of the commercialized rhizobacteria consist of *Bacillus* spp., only a few species of *Bacillus* have been put to practical use in crop production. Reports indicate that of all the Bacilli rhizobacteria, commercial formulations are commonly just made out of two prominent species: *B. subtilis* and *B. amyloliquefaciens* (Dey et al., 2014), and the rest are almost untouched in terms of formulation, commercialization and application despite the huge potential they hold. According to Pérez-García et al. (2011), *Bacillus* species such as *B. amyloliquefaciens*, *B. licheniformis* and *B. pumilus* are also available in the market as bio-fungicide formulations. As such, there is still a huge potential and possibility of exploiting many other *Bacillus* species and strains of rhizobacteria for formulation and commercialization.

A number of factors are reported to contribute to the slow rate of exploitation of these beneficial rhizobacteria, for instance, complexity of field conditions, call for extensive studies to fully understand and characterize their modes of action (Shafi et al., 2017). Studies show that many rhizobacteria perform well under controlled conditions but applications under field conditions do not perform as well (Shafi et al., 2017; Shaikh and Sayyed, 2015). The greatest challenge faced during development of bio-formulations is the fact that crops are grown under a multiplicity of climatic and environmental conditions causing disparities in the potentiality of PGPR biofertilizers (Kamilova et al., 2015). The development of stable formulations of biological agents under field conditions is also still problematic due to diverse environmental conditions (Shafi et al., 2017). As a result, more investigations on field viability of other Bacilli rhizobacteria which have currently not been commercialized for such applications are still required. Part of the solution to this problem will be to continue investigating plant, soil and region-specific Bacilli rhizobacteria to enhance their adoption in

Table 5
Examples of Bacilli rhizobacterial Commercial Formulations in different countries.

<i>Bacillus</i> sp.	Commercial product	Plants under application	Country	Reference
<i>B. subtilis</i>	Serenade [®]	Fruits, Vegetables, Onions, Potato	USA, Chile, Israel, Italy, Turkey	Mendis et al., 2018
	Rhizocell [®] GC	Cereals	Canada	Le Mire et al., 2016
	Sonata [®]	Tomato, Potato, Fruits, Pepper	USA, Mexico	Cao et al., 2011
	Yield Shield [®] , Companion [®]	Soybean, Cotton, Bean	USA	Cawoy et al., 2011
	Avogreen [®]	Avocado	South Africa	Cawoy et al., 2011
	Epic [®]	Cotton, legumes	USA	Sayyed et al., 2012
	Bio safe [®]	Soybean, Bean	Brazil	Cawoy et al., 2011
	Biosubtilin [®]	Cotton, Cereals	India	Cawoy et al., 2011
	Pro-Mix [®]	Soybean	USA, Canada	Cawoy et al., 2011
	Rhizo Plus [®]	Several crops	Germany, USA	Cawoy et al., 2011; Tabassum et al., 2017
	Ecoshot [®]	Fruits, Legumes	Japan	Cawoy et al., 2011
	Cease [®]	Several crops	USA, Mexico	Cawoy et al., 2011
	Inomix [®]	Cereals	Spain	Le Mire et al., 2016
	Bacillus SPP [®]	Several crops	Chile	Cawoy et al., 2011
	Sutilex [®]	Cotton, Soybean	USA	Tabassum et al., 2017
	EM Biocontrol	Vegetable, Fruits	Pakistan	Tabassum et al., 2017
	FZB24 [®]	Potatoes	Germany	Sharaf-Eldin et al., 2008
	VoTiVo [®]	Different crops	USA	Castillo et al., 2013
	BioPromotor [®] BioPhospho [®]	Wheat, Maize, Rice	India	Tabassum et al., 2017
	Quantum [®] 4000	Cabbage, Lettuce, Pepper, Tomato	USA	Chet and Chernin, 2002
	Kodiak [®]	Cotton, legumes	USA	Sayyed et al., 2012
	Kiwa [®]	Rice	China	Tabassum et al., 2017
<i>B. amyloliquefaciens</i>	Rhizo Vital [®]	Potato, Corn, Tomato, cucumber	Germany	Chowdhury et al., 2013
	BioYield [®]	Tomato, cucumber, Pepper, Tobacco	USA	Tabassum et al., 2017
<i>B. cepacian</i>	Green Relief [®]	Various crops	USA	Choudhary and Johri, 2009
<i>B. licheniformis</i>	Botrycid [®]	Several crops	Colombia	Cawoy et al., 2011
<i>B. megaterium</i> var. <i>phosphaticum</i>	EcoGuard [®]	Different crops	USA	Goswami et al., 2016
<i>B. polymyxa</i>	Symbion [®] -K	Vegetables	India	Le Mire et al., 2016
<i>B. pumilus</i>	Inomix [®]	Cereals	Spain	Le Mire et al., 2016
	Ballad [®]	Cereals, Sugar beet	USA	Cawoy et al., 2011
	Nortica [®]	Turf grasses	USA	Mendis et al., 2018
	Yield Shield [®]	Soybeans	North America	Govindasamy et al., 2010
<i>B. velezensis</i>	Botrybel [®]	Tomato, Lettuce	Spain	Cawoy et al., 2011
<i>Bacillus</i> sp.	PGA [®]	Fruits, vegetables	USA	Govindasamy et al., 2010

different regions (Kloepper et al., 2004). Successful application and use of Bacilli rhizobacteria for plant bio-protection and growth promotion by other mechanisms will therefore require stable formulations using suitable carriers that can optimize their activities under field conditions (Shafi et al., 2017). Development of formulations with enhanced and stable shelf lives will be extremely important in paving way for commercialization and application of these rhizobacteria for crop production and environmental sustainability (Shaikh and Sayyed, 2015). It should however be noted that although some *Bacillus* species may not show good PGP activities *in vitro* tests, the same can show significant bio-control efficacy *in vivo* (Idris et al., 2007). Research has shown that greater PGP is realized when mixed inoculants are used (García-de-Salamone et al., 2012), and investigations into combined PGP ability of different Bacilli rhizobacteria could yield even better results at plant growth promotion. However, care should be taken not to include species with antagonistic effect against the other biological control agents.

Introducing spore-forming *Bacillus* species into plants through genetic engineering has been provided as an effective solution to plant pathogens. Spore forming ability of Bacilli rhizobacteria is one of the desirable and promising qualities for their application as plant growth promoters. Thus, attention should be paid to development of cost-effective and stable spores-based products.

Bacillus species have the ability to produce compounds that belong to multiple classes of antibiotics which can be used for control of a broad range of plant pathogenic diseases. However, quantification of these biologically active compounds is difficult because of low quantities. Current biotechnology can be employed to select not only for better producers of these important compounds, but also for stability and competent root colonization for enhanced performance (Shaikh and Sayyed, 2015). To realize this, proper knowledge and

understanding of the rhizobacterial active compounds is necessary for a stable and efficient formulation. For successful application of Bacilli rhizobacteria, understanding of their modes of action, diversity, ecological distribution will be valuable. More knowledge on diversity, distribution and activities mediated by these rhizobacteria will be useful not only in identifying better inoculants but also the specific crops onto which their application will be successful (Choudhary and Johri, 2009). Similarly, since root colonization has been identified as a prerequisite for PGP (Kamilova et al., 2015), investigations on Bacilli rhizobacteria colonization potential in different plant roots are still very necessary and quantification methods should be able to differentiate the inoculated strain from indigenous rhizosphere bacterial communities (Mendis et al., 2018). According to Compant et al. (2010) understanding the colonization potential of rhizobacteria is very important in predicting their suitability as successful plant growth promoters under field conditions. It will also be important to investigate the genetic diversity within antagonistic Bacilli rhizobacteria with common biocontrol traits to build knowledge on the mechanisms and exploit the genetic differences for purposes of selecting and developing strains with better rhizosphere colonization and competition potential (Choudhary and Johri, 2009).

6. Conclusions

Application of rhizobacterial inoculants as biofertilizers and bio-control agents is an integral component of sustainable agricultural practices (Babalola, 2010), and has been the subject of investigation for a long time now (Stamenkovic et al., 2018). With the rising emphasis on sustainable agriculture, environmental protection, and food security, the exploitation of beneficial soil microbiota is inevitable (Ilanguaran

and Smith, 2017). Bacilli rhizobacteria present not only environmentally-friendly but also an efficient technology (Shafi et al., 2017), for PGP through different mechanisms including plant bio-protection, hormone production and nutrient solubilization. The formulation, commercialization and real time application of Bacilli rhizobacteria in crop production does not reflect the volume of research that has been done on them plus their multifarious PGP abilities and unique properties. More investigations are needed concerning their modes of action, practical formulation and application, stability under field conditions and to screen for efficient strains. The way to go will be rhizoengineering (Dessaux and Grandclément, 2016), using species specific rhizobacteria and eventually, this could allow for significant progress in implementing the application of the Bacilli rhizobacteria for crop production and environmental sustainability. Continued research focusing on endophytic types of Bacilli rhizobacteria and their colonization potential in different plants will pave way for development of better performing biofertilizers, bioprotection agents and phytostimulators (Govindasamy et al., 2011). Finally, biotechnology can help in screening and development of better stains with multiple and over-expressed PGP qualities.

Declaration of interest

None.

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