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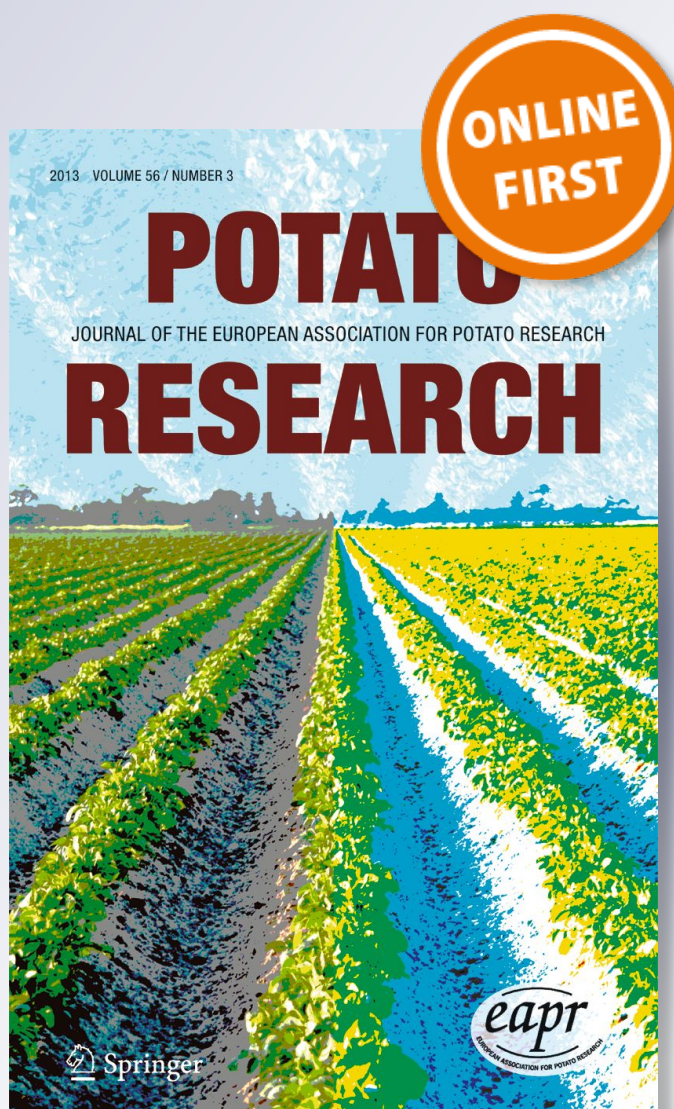
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Rhizobacteria-Based Technology for Sustainable Cropping of Potato (*Solanum tuberosum* L.)

B. N. Aloo¹ · E. R. Mbega¹ · B. A. Makumba²



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Abstract

Potato (*Solanum tuberosum* L.) is one of the most important food crops worldwide but its cultivation is affected by numerous challenges including pests, diseases and high fertiliser requirements which have associated environmental problems. The exploitation of plant rhizospheres and their associated rhizobacterial interactions has gathered momentum worldwide in search of environmentally-friendly approaches to crop cultivation. A lot of literature exists on rhizobacterial associations and their biofertilisation or bioprotection roles in many plants. However, very scanty information is available on rhizobacterial functions and communities of the potato, an indication that they are still understudied. In this regard, more research is needed to understand and exploit them for the successful application of rhizobacteria-based technology in potato cropping. This review updates our knowledge of the beneficial rhizobacteria of the potato and documents their roles in its bioprotection, phytostimulation and biofertilisation while highlighting their potential in enhancing its production and productivity. The future prospects regarding the research on these important potato microflora are further discussed as a guide and a baseline for future research on them. This review shows that rhizobacteria-based technology is a viable option for potato biofertilisation and bioprotection and could be the missing link in its sustainable cropping. The adoption and full exploitation of this technology can be fast-tracked if we increase our understanding of the subject matter.

Keywords Plant growth promotion · Rhizobacteria · *Solanum tuberosum* · Sustainable agriculture

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Introduction

Potato (*Solanum tuberosum* L.) is one of the most important non-cereal food crops and is consumed by more than a billion people worldwide (FAO 2014). It is ranked as the fourth most cultivated and consumed crop globally after maize, wheat and rice because of its high nutritive value and yield productivity to soil occupation ratio in comparison with other crops (FAO 2008, 2017). Reports also document it as a crop with the highest production rates for food energy and value per unit area of land and with the ability to grow in the widest range of altitudes, latitudes and climatic conditions (Wu et al. 2013). Furthermore, it is evidenced to give rise to more nutritious food, more quickly, on less land and in severer conditions than any other crop, and up to 85% of it is edible as compared with just about 50% in cereals in addition to containing the highest (2.1% of fresh weight) protein content among the tuber crops (FAO 2008). The latest statistics show that potato is produced in 82% of all countries in the world, with its production in 2014 estimated at 382 million tonnes (FAO 2017). As such, the potato is undoubtedly the world's most economically and nutritionally important crop, and as the world's population continues to rise and arable land continues to shrink, this crop will certainly become an integral part of the global food security systems (FAO 2008).

Despite its economic and nutritional importance, potato cultivation is affected by many factors worldwide (Wu et al. 2013). It is susceptible to numerous pests and diseases resulting in huge economic losses and increased production costs (Hill and Lazarovits 2005). The potato is also one of the heaviest fertiliser demanding crops (Wu et al. 2013), requiring as high as 250 kg ha⁻¹ of nitrogen (N) and 150 kg ha⁻¹ of phosphorus (P) (George and Ed 2011). Consequently, potato cultivation is heavily dependent on the application of synthetic fertilisers and pesticides for yield maximisation and pathogen control, respectively. As a direct result, production costs are often very high and this is coupled with environmental degradation from chemical-based production (Mohammadi and Sohrabi 2012).

Current efforts towards sustainable agriculture over the world are focused on environmentally friendly approaches (Hungria et al. 2013) such as the use of beneficial rhizosphere bacteria (Naqqash et al. 2016). These are indigenous bacteria localised in plant rhizospheres, with the capability of improving plant growth through several processes (Raza et al. 2016), either by direct mechanisms such as biofertilisation (Archana et al. 2013; Parmar and Sindhu 2013), stimulation of root growth, rhizoremediation and plant stress control (Govindasamy et al. 2010; Grover et al. 2011), or indirect mechanisms such as bioprotection through antibiosis, induced systemic resistance (ISR) and competition for nutrients and niches with plant pathogens (Nivya 2015; Singh and Jha 2015).

According to Hungria et al. (2013), rhizobacteria-based technology should be studied and exploited as an alternative to chemical-based agriculture. Reports indicate that beneficial rhizobacteria of potatoes are still largely unexplored and data relating to their colonisation and plant growth promotion (PGP) potential are also very limited (Andreote et al. 2009; Mohammed et al. 2013). Over the last two decades, some research has been done on effects of microbial inoculation on potato yield improvement (Duffy and Cassells 2000; Davies et al. 2005), bioprotection (Whipps 2004) and other aspects of PGP, but this is still far from enough considering the wealth of knowledge available on rhizobacterial communities and functions associated with other plants. In

this review, the beneficial rhizobacteria of the potato and the roles they play in its growth, as well as their potential in its production and productivity, are discussed. The review further tries to critically evaluate some future prospects and research regarding potato beneficial rhizobacteria while highlighting some of the knowledge gaps that still exist in this regard. Such information can guide future research work on potato beneficial rhizobacteria which will eventually contribute to its sustainable cropping.

Beneficial Rhizobacteria of the Potato

Over 60 bacterial genera including *Arthrobacter*, *Comamonas*, *Curtobacterium*, *Enterobacter*, *Paenibacillus*, *Pantoea*, *Serratia*, *Sphingobacterium*, *Stenotrophomonas*, *Variovorax*, *Xanthomonas*, *Agrobacterium*, *Bacillus* and *Pseudomonas* have frequently been identified by culture-dependent methods in potato rhizospheres (Diallo et al. 2011). Studies of potato rhizospheres and endospheres using culture-independent methods like the 16S rRNA gene-based techniques and sequencing analysis have also confirmed the presence of *Agrobacterium*, *Arthrobacter*, *Bacillus*, *Curtobacterium*, *Micrococcus*, *Pseudomonas*, *Sphingobacterium* and *Streptomyces* genera (Garbeva et al. 2001; Smalla et al. 2001; Reiter et al. 2003; Berg et al. 2005).

Previous culture-dependent and culture-independent studies have provided a complementary representation of rhizobacterial communities of potato and confirmed some level of specificity for different microenvironments (Berg et al. 2005). In a study done by Istifadah et al. (2018), isolation of bacterial endophytes from healthy potato roots and tubers resulted in a total of 88 isolates and 78% of these were from potato roots while only 18% were from potato tubers. Generally, bacterial densities in the potato rhizosphere have been shown to occur in the range of 10^7 – 10^8 colony forming units (CFU) g^{-1} of fresh weight (Berg et al. 2005), and endorhizal populations are approximately 100–1000 times less dense than the rhizospheric ones (Berg et al. 2005; Rasche et al. 2006). *Pseudomonas* spp. which are well-known for plant bioprotection are highly represented in potato endorhiza where their population can reach 36–48% of isolates (Garbeva et al. 2001). *Pseudomonas fluorescens* and *P. putida* are documented to extensively colonise potato rhizosphere soils in the range of 10^6 – 10^8 CFU g^{-1} root (Cirou et al. 2007). In previous studies, potato endophytic Proteobacteria, Actinobacteria, *Flexibacter*, *Cytophaga* and Bacteroidetes genera were identified by Reiter et al. (2003) and Sessitsch et al. (2004). Similarly, pyrosequencing analysis of potato root endophytes also revealed the presence of different Proteobacteria, Cyanobacteria, Firmicutes, Acidobacteria, Actinobacteria, Bacteroidetes, Chloflexi, Planctomycetes, Fusobacteria, Verrucomicrobia, Gemmatimonadetes and other unidentified bacteria families (Manter et al. 2010). Nevertheless, species of *Pseudomonas*, *Bacillus*, *Enterobacter* and *Agrobacterium* genera appear to be the most common culturable bacterial endophytes found in potato (Manter et al. 2010).

Despite the reports available on several potato rhizobacterial communities, very few reports exist on the beneficial functions of these rhizobacteria considering the wealth of information on beneficial rhizobacterial functions of other plants like cereals and legumes (Naqqash et al. 2016). Some studies have indicated that *Bacillus* sp. and *Pseudomonas* sp. are associated with the improvement of P-uptake in potato (Hanif et al. 2015), production of indole-3-acetic acid (IAA), biocontrol activities (Hunziker

et al. 2015) and ISR (Ardanov et al. 2011). In the study by Naqqash et al. (2016), *Pseudomonas* sp., *Azospirillum* sp., *Enterobacter* sp. and *Rhizobium* sp. isolated from potato rhizospheres were all shown to have PGP effects on growth of the plant in terms of height, fresh and dry weight of roots and shoots and total N levels. *Pseudomonas fluorescens* and *P. putida* have also been extensively shown to colonise potato rhizospheres (Cirou et al. 2007) and could thus be important regulators of potato growth.

Bacillus spp. are reported to contribute significantly to plant health in a number of ways including through atmospheric dinitrogen gas (N₂) fixation, P-solubilisation, antagonistic properties, ISR, production of siderophores and IAA (Ali et al. 2014). However, very little is known about the ecology, genomics and role of *Bacillus* spp. capable of P-solubilisation and phytate mineralisation in soils in the potato rhizosphere. Generally, a lot of investigations are still needed for the potato rhizosphere and endosphere since only a few reports exist on beneficial rhizobacteria associated with them. It is now recognised that potato rhizospheres host important bacterial diversity globally and since just over 60 genera have been found in these microenvironments, it is thought that numerous other rhizobacteria associated with this important plant are yet to be discovered (Diallo et al. 2011). It is also established that potato soil rhizobacterial communities, just like those of most other crops, shift according to site and cultivar, and in this regard, determination of rhizobiome common to all sites and cultivars could uncover potato competent microbes important for crop productivity and health in a variety of locations (Barnett et al. 2015).

Roles of Beneficial Rhizobacteria in Potato Growth

Just like in other crops, potato rhizobacteria exhibit several PGP mechanisms which are important in potato growth regulation. Figure 1 illustrates the different roles played by beneficial rhizobacteria in the potato rhizosphere. These roles are discussed in the 'Bioprotection of the Potato', 'Phyostimulation of the Potato' and 'Biofertilisation of the Potato' subsections.

Bioprotection of the Potato

The potato plant is prone to attack by several soil-borne pathogens which often result in poor yields and huge economic losses in the range of 15 to 25% globally (Oerke 2006). For some of these pathogens like *Fusarium* spp., causing dry rot, and *Phytophthora infestans*, causing late blight, effective chemical control can be difficult (Gachango et al. 2012). Beneficial rhizobacteria showing biological control activities which are commonly referred to as biocontrol agents, bioprotection agents or biopesticides (Diallo et al. 2011) offer suitable alternatives to chemical control of these pathogens which is often undesirable in a number of ways.

Biocontrol and bioprotection activities of beneficial rhizobacteria have been reported extensively in many plants but relatively few reports exist on potato bioprotection. According to Clermont et al. (2011), there is little information regarding the interactions between important potato pathogens and rhizobacteria which can be exploited for potential control of these pathogens. Species of *Pseudomonas* and *Bacillus* are the most studied biocontrol rhizobacteria in potato (Ardanov et al. 2011). *Bacillus* spp. are

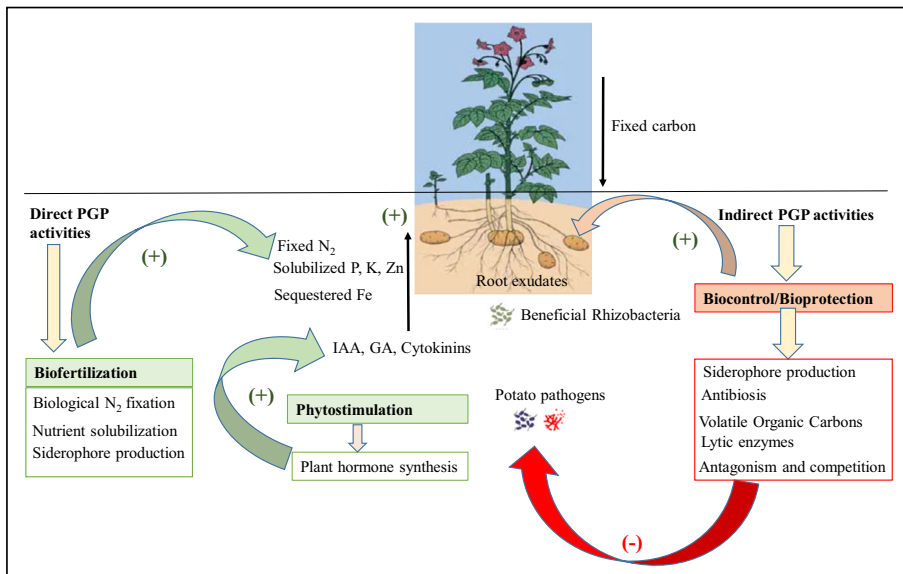


Fig. 1 Beneficial functions of rhizobacteria in the potato rhizosphere

especially important and have gathered a lot of attention not only because of their bioprotective abilities (Diallo et al. 2011), but also due to their ability to produce endospores which promotes their resistance to environmental stresses (Adesemoye et al. 2017). Reports show that different strains and species of *Bacillus* exhibit different biocontrol mechanisms; hence, understanding these mechanisms is a prerequisite to the facilitation of their selection, formulation and effective practical applications (Devi et al. 2016). Together, *Pseudomonas* and *Bacillus* spp. have widely been investigated as potato bioprotection agents under in vitro and screen-house conditions, but still not much data is available regarding their successful application under field conditions (Diallo et al. 2011). Some potato-associated endophytes are also reported to antagonise its fungal and bacterial pathogens by means of enzymes, antibiotics and siderophores (Sessitsch et al. 2004). For instance, *Lysobacter* sp. from the potato rhizosphere at the flowering stage can exhibit excellent antagonism to a number of the crop's pathogens (Van Overbeek and Van Elsas 2008). Other instances where beneficial rhizobacteria of potato have been shown to exhibit bioprotection to the crop are provided in Table 1.

Bioprotection by ISR occurs when the interaction between a rhizobacterium and a plant host induces the plant to resist a pathogen to which it was previously susceptible (Gouda et al. 2018). In potato, ISR has commonly been linked to *Rhizobium* sp. (Reitz et al. 2001). The literature suggests that *Bacillus subtilis* is also a promising biocontrol agent against potato pathogenic *Pectobacterium* spp. in planta via ISR (Aliye et al. 2008). For instance, the rhizobacterium *B. subtilis* GB03 is documented to reduce major soil-borne diseases of potato such as stem and stolon canker, blank scurf and common scab by 20–38%, 30–58% and 10–34%, respectively, through ISR (Larkin and Tavantvis 2013). It is hypothesised that ISR elicitors function to trigger changes in plant cell wall composition and production of pathogenesis-related proteins (Bakker et al. 2007), and can influence the activation of a number of plant defense mechanisms

Table 1 Beneficial rhizobacteria exhibiting biocontrol activities against potato pathogens

Pathogen	Disease	Rhizobacteria	Type of assay	Biocontrol mechanism	Reference
<i>Fusarium oxysporum</i>	Dry rot	<i>Bacillus</i> sp.	In vitro screening and tuber assays	Antibiosis, ISR and lytic enzymes	Kotan et al. 2009
		Fluorescent <i>Pseudomonads</i>	Tuber assays	Antagonism/antibiosis	Schlisler et al. 2000
		<i>Enterobacter cloacae</i>	Tuber assays	Antagonism/antibiosis	Schlisler et al. 2000
		<i>Burkholderia cepacian</i>	Pot assays	Antagonism	Kotan et al. 2011
<i>Phytophthora infestans</i>	Late blight	<i>Pseudomonas</i> sp, <i>Bacillus</i> spp.	Pot assays	VOCs ¹	Hunziker et al. 2015
		<i>P. korensis</i>	Greenhouse trials	Antagonism	Hullberg et al. 2010
		<i>P. putida</i>	Soil trials	Antibiosis/competition	Andreote et al. 2009
		<i>Arthrobacter</i> sp., <i>Pseudomonas</i> sp., Stenotrophomonads	In vitro screening	Antagonism	Bharadwaj et al. 2008
<i>Ralstonia solanacearum</i>	Bacterial wilt	<i>Lysobacter</i> sp.	In vitro screening	Antibiosis	Van Overbeek and Van Elsas 2008
		<i>Bacillus</i> sp., <i>Pseudomonas</i> sp., <i>Serratia</i> sp.	Field tests	Antagonism	Tahir et al. 2016
<i>Rhizoctonia solani</i>	Stem cankers	<i>B. subtilis</i>	In vitro screening	Antagonistic compounds	Brewer and Larkin 2005
		<i>Lysobacter</i> sp.		Antibiosis	Van Overbeek and Van Elsas 2008
		<i>Bacillus</i> spp.		Antibiosis/siderophores	Kumar et al. 2013
		<i>P. putida</i>		Hydrolytic enzymes	Berg et al. 2005
		<i>Arthrobacter</i> sp., <i>Pseudomonas</i> sp., Stenotrophomonads		Antagonism	Bharadwaj et al. 2008
<i>Verticillium dahliae</i>	<i>Verticillium</i> wilt	<i>P. putida</i> , <i>Cytophaga</i> , <i>Stenotrophomonas</i>	In vitro screening	Hydrolytic enzymes	Berg et al. 2005
		<i>Arthrobacter</i> sp., <i>Pseudomonas</i> sp., Stenotrophomonads	In vitro screening	Antagonism	Bharadwaj et al. 2008

Table 1 (continued)

Pathogen	Disease	Rhizobacteria	Type of assay	Biocontrol mechanism	Reference
<i>Streptomyces scabies</i>	Common scab	<i>Non-pathogenic Streptomyces</i> spp.	Field tests	Competition	Hiltunen et al. 2009; Wanner et al. 2014
		<i>P. fluorescens</i>	In planta	VOCs	Arseneault et al. 2013
		<i>Non-pathogenic Streptomyces</i>	In vitro screening	Antibiosis/competition	Hiltunen et al. 2009
		<i>B. amyloiliquefaciens</i>	Pot and field assays	Lipopolypeptides	Lin et al. 2018
<i>Pectobacterium carotovorum</i>	Soft rot	<i>P. mosselii</i>	Field tests	Not clear	Singhai et al. 2011
		<i>Arthrobacter</i> sp., <i>Pseudomonas</i> sp., Stenotrophomonads	In vitro screening	Antagonism	Bharadwaj et al. 2008

¹ Volatile organic compounds

(Borowicz 2001). Although ISR is not normally pathogen-specific (Kamal et al. 2014), this type of antagonism holds immense benefits due to its broad spectrum of action and its successful exploitation could transform crop production (Gouda et al. 2018). However, it should be noted that this has only been done at the laboratory trial level and its applicability in the field is still lacking.

Application of mixtures of different beneficial rhizobacterial strains to seeds and seedlings can result in increased ISR in some instances (Ramamoorthy et al. 2001). In potato, *Rhizobium* sp. and *Pseudomonas* sp. when inoculated together are capable of increased ISR (Reitz et al. 2001; Ardanov et al. 2011). Aliye et al. (2008) also demonstrated that *Ralstonia solanacearum*, causing bacterial wilt in potato, is controlled through ISR by Fluorescent Pseudomonads in field trials and by *B. subtilis* and *Paenibacillus macerans* in vitro. The development of ISR in potato plants against *Rhizoctonia solani* causing stem cankers after inoculation of tubers with different rhizobacteria is reported in several studies. Earlier reports show that ISR-eliciting rhizobacterial antagonists against *P. infestans* and *F. oxysporum* are more abundant in potato endorhiza than in the rhizosphere (Sturz et al. 1999). The preferential localisation of biocontrol rhizobacteria of different pathogens remains to be explored, but it is hypothesised that a higher level of intimacy between the endophytes and the potato plant could be responsible for better ISR elicitation (Diallo et al. 2011). Other studies have shown bioprotection capabilities of endophytic rhizobacteria in potato via ISR (Sessitsch et al. 2004; Hong-Xian et al. 2005; Palvo et al. 2011).

However, more investigations are required since the ISR-eliciting metabolic pathways are still poorly understood (Ramos Salano et al. 2008), and data on their successful field applications for potato bioprotection are scarce (Diallo et al. 2011).

Production of siderophores is widely reported as another mechanism that is commonly associated with rhizobacterial bioprotection of crops (Saha et al. 2016). Siderophores are low molecular weight (500–1000 Da) iron (Fe)-binding substances synthesised by microorganisms under low-iron conditions (Tank et al. 2012; Mhlongo et al. 2018). Very few potato rhizobacteria have been associated with the production of siderophores in iron-limiting conditions. Two *Erwinia* species were reported to produce siderophores during the screening of endophytic rhizobacteria with PGP abilities in potato cultivars in Spain (Garcia et al. 2005). A similar report has also indicated that certain potato endophytic rhizobacteria like *Pseudomonas* spp., *Arthrobacter* spp., *Methylobacterium* sp., *Paenibacillus* spp., *Clavibacter* spp. and *Microbacterium* spp. can reduce the in vitro growth of *S. scabies* and *Xanthomonas campestris* through the production of siderophores (Sessitsch et al. 2004). Several *Bacillus* spp., *Pseudomonas* spp. and one *Serratia* sp. are also documented as siderophore producers in a recent study (Tahir et al. 2016). Findings from older studies reveal that the ability to inhibit pathogen growth by siderophore-producing endophytic potato rhizobacteria tends to decrease in rhizobacteria colonizing deeper tissues, suggesting that siderophore production could be tissue-specific (Sturz et al. 1999), but this still needs more investigations.

The iron-chelation phenomenon is understood to create a state of iron deficiency in soil resulting in inhibition of plant pathogens and thus reducing their competitiveness (Tank et al. 2012; Solanki et al. 2014). Furthermore, the process is also very important in stimulating plant growth directly by increasing iron availability in the soil (Indiragandhi et al. 2008; Tank et al. 2012). Since Fe is one of the frequently limiting

m micronutrients in soils, (Rajkumar et al. 2010), by binding Fe, siderophore-producing rhizobacteria function to increase its availability to plants (Radzki et al. 2013; Mathew et al. 2014). According to Loaces et al. (2011), the ability of endophytic rhizobacteria to produce siderophores has barely been studied in many crops including the potato, yet it confers competitive advantages to plants through pathogen exclusion and improvement of Fe nutrition. Siderophore production is thus a classic example of how established beneficial rhizobacteria can increase their competence in the rhizosphere and due to its indisputable importance, further exploration of siderophore production and siderophore-producing rhizobacteria associated with potato should be investigated for better understanding.

Production of volatile organic compounds (VOCs) is another mechanism of PGP by beneficial rhizobacteria (Nivya 2015; Raza et al. 2016; Mhlongo et al. 2018). The PGP effects mediated through rhizobacterial VOCs production are recognised as a potential and environmentally sound way of controlling plant pathogens (Heydari et al. 2008). However, the spectrum of action of these VOCs is documented to depend not only on environmental conditions such as temperature and pH but also on the producing species (Saraf et al. 2014). In a previous study screening different potato-associated *Pseudomonas* strains for anti-oomycete potential, several strains showed various degrees of VOC-mediated efficacy against *P. infestans* mycelial growth (De Vrieze et al. 2015). Reports by Hunziker et al. (2015) document the ability of indigenous communities of *Pseudomonas* strains of potato plants to produce VOCs with high potentials for inhibiting *P. infestans* by significantly reducing mycelial growth, sporangium formation and spore formation and release. Fairly recent studies by Arseneault et al. (2013) illustrate the potential of the Fluorescent Pseudomonad, *P. fluorescens* LBUM233, to control common scab disease in potato, caused by *S. scabies*, under controlled soil conditions through the production of phenazine-1-carboxylic acid (PCA). However, these studies were not conclusive and their validation under field conditions is still required to further develop the isolate for biological control of potato scab (Arseneault et al. 2015). Previous studies on another PCA-producing *P. fluorescens* revealed that biocontrol efficiency was highly dependent on certain environmental factors such as nutrient availability, pH and soil silt composition (Ownley et al. 2003). Rhizobacterial PCA affects a large number of cellular activities in *S. scabies* but its effects on other potato pathogens, for example, the pathogenic *Streptomyces*, are still unknown and remain to be elucidated. More investigations into rhizobacterial VOCs and the sensitivity of important pathogens to them are therefore required to better understand their bioprotection systems in potato. The metabolite complexity of VOCs is also attributed to differences in rhizobacterial species and genotypes (Tyc et al. 2015; Kai et al. 2016), hence the need to investigate VOC-producing ability in different rhizobacterial strains and species of the potato.

Some rhizobacteria exhibit bioprotective qualities and subsequently PGP through the production of lytic enzymes (Meena et al. 2016). Examples of such enzymes include chitinases, dehydrogenases, glucanases, lipases, phosphatases, proteases and hydrolases, all of which are known for hyper-parasitic activity through cell wall hydrolysis (Goswami et al. 2016). In the study done by Sessitsch et al. (2004), several endophytic rhizobacteria of potatoes including *Sphingomonas* sp. and *Paenibacillus* sp. were shown to produce a wide spectrum of hydrolytic enzymes such as glucanases, chitinases, proteases and pectinases. The study by Berg et al. (2005) also identified

several potato rhizobacteria with the capability of expressing pectinolytic, cellulolytic, chitinolytic and proteolytic activities. Beneficial rhizobacteria that produce such enzymes can play significant roles in PGP by protecting plants from biotic stresses through pathogen inhibition (Upadyay et al. 2012; Nadeem et al. 2013). For example, glucanases synthesised by strains of *Paenibacillus* and *Streptomyces* spp. can easily degrade fungal cell walls of pathogenic *F. oxysporum* (Compant et al. 2005). Similarly, *B. cepacia* is also reported to synthesise glucanases that destroy the cell walls of a number of soil-borne pathogens including *R. solanacearum* (Sadfi et al. 2001). Both *F. oxysporum* and *R. solanacearum* are also pathogens of the potato (Sadfi et al. 2001); thus, such rhizobacteria and their lytic enzymes could be handy in its bioprotection. Rhizobacteria which produce lytic enzymes like *Pseudomonas* sp. and *Bacillus* sp. have commonly been isolated from potato rhizospheres (Hunziker et al. 2015). These and other potato rhizobacteria should be explored further for production of lytic enzymes and possession of other PGP traits to come up with novel species which can be applied and used as alternatives to synthetic pesticides and fertilisers (Gouda et al. 2018).

Reports show that potato-associated rhizobacterial antagonists are very specific for each microenvironment (Berg et al. 2005). Previous studies by Van Overbeek and Van Elsas (2008), investigating the effects of genotype, plant growth, soil and season on potato-associated rhizobacteria, revealed that plant growth stage overwhelmingly affects the diversity and composition of these bacterial communities. Such differences justify the need to ensure a compatible combination of host-rhizobacteria systems to ensure successful application in bioprotection and yield improvement (Davies et al. 2005), in potato (Klironomos and Hart 2002), even though local or indigenous isolates are usually recommended for biotechnological applications (Klironomos 2003).

Much attention has been drawn to the potential of plant rhizobacteria as biocontrol and bioprotection agents of soil-borne pathogens as an alternative or complementary strategy to synthetic pesticides (Murphy et al. 2000; Berg and Smalla 2009), and are promising for controlling potato pathogens (Wu et al. 2013). However, rhizobacterial biocontrol of many potato pathogens is still too poorly understood for their successful application and more knowledge is required on their dynamics, composition and complex disease suppression and regulatory mechanisms especially in response to biotic and abiotic factors (Normander and Prosser 2000). Rhizobacterial selection as potential biocontrol and bioprotection agents of potato pathogens must take into consideration different agroecosystem properties such as temperature, salinity and soil pH (Sturz and Christie 2003). Furthermore, knowledge of the mode of action and activity of different rhizobacterial siderophores, lytic enzymes, antibiotics and VOCs among the potato rhizobacteria could increase their applicability (Saraf et al. 2014). Further research on their ecology and biocontrol activities will improve our ability to use the potato rhizobacteria communities for effective disease control. Additionally, studies on their genomic sequences will provide useful insights into plant-microbe-pathogen interactions and possibly induce greater disease resistance (Saraf et al. 2014).

Phyostimulation of the Potato

The enhancement of crop productivity by beneficial rhizobacteria is largely attributed to the production of growth-stimulating phytohormones such as IAA, GA, zeatin,

ethylene and abscisic acid (ABA) that are responsible for increased foliage, root elongation and fruit yield (Fahad et al. 2015; Hassen et al. 2016; Mhlongo et al. 2018). A number of studies have illustrated IAA production by potato rhizobacteria and its role in stolon induction and tuber initiation in potato has been documented in a previous study (Dragivec et al. 2008). According to Naqqash et al. (2016), *Azospirillum*, *Pseudomonas*, *Enterobacter* and *Rhizobium* spp. can produce IAA with or without L-tryptophan supplementation. In a study by Hanif et al. (2015), *B. subtilis* isolated from potato rhizosphere was shown to produce up to $6.48 \mu\text{g ml}^{-1}$ IAA. Calvo et al. (2010) also report that *Pseudomonas* sp. and *Bacillus* sp. associated with potato are capable of IAA production. Earlier studies by Sessitsch et al. (2004) also revealed the ability of *Sphingomonas* sp., *Pseudomonas* spp., *Paenibacillus* sp., *Arthrobacter* sp., *Microbacterium* sp. and *Clavibacter* sp. isolated from potato to produce IAA. In a quite recent study, Henagamage et al. (2016) showed that certain rhizobacterial isolates from the potato rhizosphere can produce very high quantities of IAA in the range of $2.2\text{--}21.54 \mu\text{g ml}^{-1}$. Similarly, in a study by Tahir et al. (2016), several potato rhizospheric *Bacillus* spp. and *Serratia* sp. are documented to produce relatively high IAA ranging from $3.8 \pm 1.5 \mu\text{g ml}^{-1}$ to $40 \pm 1.29 \mu\text{g ml}^{-1}$.

Phytohormone production is a desirable trait alongside other PGP features among rhizobacteria (Marschner et al. 2011). For instance, IAA is known to promote plant growth by increasing root surface area and root tip elongation (Lu et al. 2015), and proliferation of lateral roots and root hairs and thus enhancement of plant uptake of minerals and nutrients from the soil (Sureshbabu et al. 2016). In some cases, IAA-producing rhizobacteria have been implicated in PGP by lateral root development alongside P-solubilisation potential (Venieraki et al. 2011). Interestingly, *Pseudomonas* spp. which are also commonly associated with the potato rhizosphere possess many other PGP traits in addition to IAA production and hence these organisms have a great potential to be exploited and developed as bioinoculants (Marathe et al. 2017), and such potential and application are worth investigating among other Pseudomonads and rhizobacteria associated with the potato.

Biofertilisation of the Potato

The global rise in potato demand has expanded production to seasons and agroecological conditions outside the crop's normal range. In a quest to avail nutrients for maximisation of yields, artificial fertilisers have constantly been used in its production. This has not only raised the costs of production, but it has also led to environmental degradation (Youssef and Eissa 2014). Rhizobacteria with the capability of solubilizing insoluble soil nutrients are promising biofertilisers (Daman et al. 2016) and are worth exploiting for potato production. Just like other crops, important nutrients that affect the growth of potato are N, P, K and Zinc, among others. Although the average P content in most soils is 0.05%, only about 0.1% of this is available for uptake by crops due to its immobilisation and low solubility capacity (Jorquera et al. 2011; Alori et al. 2017). Such low P concentration in soils makes this important nutrient very limiting for potato growth (Rosen et al. 2014). Adequate P nutrition is critical for tuber development in potato as well as high photosynthetic rate maintenance during tuber bulking (Wu et al. 2013), and improvement of protein contents (Mishra et al. 2007). Reports indicate that the potato has a much lower root density and limited ability to take up P fertilisers than

most crops; hence, P deficiency is usually a limiting factor in its cultivation (Rosen et al. 2014).

A number of studies have focused on P-solubilisation by potato rhizobacteria. For instance, during a study screening some endophytic potato rhizobacteria with PGP abilities in Spain, two *Erwinia* species showed inorganic P-solubilisation alongside the production of siderophores (Garcia et al. 2005). Similarly, in a study by Hanif et al. (2015), potato rhizospheric *Pseudomonas* sp. and *B. subtilis* inoculated on insoluble tricalcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$) exhibited remarkable P-solubilisation potential and the latter was able to solubilise $66.44 \mu\text{g ml}^{-1}$ of $\text{Ca}_3(\text{PO}_4)_2$ within 10 days of inoculation with a P-solubilisation index of 1.62. In the same study, a greenhouse experiment revealed that potato inoculation with *B. subtilis* showed increased root and shoot lengths as well as dry and wet weights of shoots and roots in pots supplemented with phytates, which are insoluble organic forms of P, as compared with uninoculated plants, showing that *B. subtilis* can mediate the conversion of organic P substrate (Richardson and Simpson 2011). In a different study, a number of potato rhizospheric bacteria were also reported to be involved in P-solubilisation, and their inoculation on potato tubers resulted in increased yields in comparison with uninoculated plants (Vosatka and Gryndler 2000).

Although P and phytate-solubilizing bacteria are commonly found in most soils, their establishment and activities are affected by different environmental factors (Ahemad and Khan 2012), and this should also be investigated for potatoes grown under different agroecosystems. The P solubilizing ability of rhizobacteria has been linked by some researchers to their genotypic constitution (Gyaneshwar et al. 2002). Understanding the genetic basis of P-solubilisation would be an important element in transforming more competent potato rhizobacteria into P-solubilizing rhizobacteria in the future (Wu et al. 2013). Such advances could eventually lead to their effective use as biofertilisers to reduce or eliminate the use of synthetic P fertiliser inputs (Asok and Jisha 2006; Shah et al. 2007) in potato production.

Bacteria having the ability of both P-solubilisation, and phytate mineralisation are widespread in the rhizosphere of different crops (Shahid et al. 2012) and offer a great promise for agricultural applications (Khan et al. 2006; Richardson and Simpson 2011). Evidence suggests that effective strains of P-solubilizing rhizobacteria can save up to $30\text{--}50 \text{ kg ha}^{-1}$ of inorganic P_2O_5 fertilisers (Richardson et al. 2009). However, several knowledge gaps still exist concerning the solubilisation of other important plant nutrients such as potassium (K) (Parmar and Sindhu 2013), in the potato (Kumar and Dubey 2012), yet K is one of the limiting nutrients in crop production (Gouda et al. 2018). In an Iranian study conducted by Hosni et al. (2016), it was shown that inoculation of potato tubers with *Pseudomonas* spp., *B. megaterium* and *B. subtilis* both as dual and separate cultures showed a significant positive effect on tuberisation and yield. Studies have indicated that the ability of rhizobacteria to solubilise K depends on soil type, microbial strain and the form of K available in soil (Sangeeth et al. 2012). Potassium-solubilizing rhizobacteria like *Rhizobium* spp., *Pseudomonas* spp. and *Bacillus* spp. have been implicated in increased plant growth and yield of different crops (Ahmed and El-Araby 2012; Guimarães et al. 2016; Yasin et al. 2016). These rhizobacteria have all also been isolated from potato rhizospheres and it would be important to study their K-solubilisation potential for the potato as well. Eventually,

such rhizobacteria can be harnessed and exploited to improve K availability in K-limiting soils (Bationo et al. 2012) for potato cultivation.

Nitrogen is one of the most important nutrients required for plant growth, but over 80% of this is unavailable to plants and therefore must be converted to forms which can be taken up by plants such as ammonia (NH_3) and nitrates (NO_3^-) (Thamer et al. 2011). Biological N_2 -fixing rhizobacteria produce the nitrogenase enzyme which they use to convert free atmospheric N_2 into NH_3 (Dighe et al. 2010) and hence have important potential in biofertilisation in the absence of nitrogenous fertilisers (Kuan et al. 2016). However, very few studies report on rhizobacterial N_2 fixation in potato. In the study done by Naqqash et al. (2016), rhizobacterial *Azospirillum* sp., *Pseudomonas* sp. and *Rhizobium* sp. were all implicated in N_2 fixation in the potato. The association between symbiotic N_2 -fixing rhizobacteria, commonly exhibited in legumes, has also been observed in some non-leguminous plants like sugarcane (*Saccharum officinarum* L.) (Thaweenut et al. 2011), implying that endophytic N_2 fixers can also form symbiotic interactions with non-legume crops. There is need, therefore, to investigate such potential among the endophytic rhizobacteria of potato as this can increase their applicability. It is especially important to understand endophytic N_2 fixation since endophytic rhizobacteria exhibit greater PGP abilities than the free-living external rhizobacteria (Diallo et al. 2011).

Future Prospects and Research on Rhizobacteria-Based Technology for Sustainable Cropping of Potato

Several beneficial rhizobacterial strains are now being formulated and made commercially available as biofertilisers and biocontrol agents (Jha and Saraf 2015; Mhlongo et al. 2018), and are substantially gaining popularity due to extensive research that has enhanced their effectiveness and understanding (Berg 2009). However, biofertilisers of the potato are still rare in the global market, hence the need for more research on their applicability. Research shows that potatoes harbor diverse communities of indigenous bacteria in their rhizospheres which can be important in growth promotion especially in nutrient deficient soils (Wu et al. 2013), as has also been demonstrated in different crops (Guimarães et al. 2016). Such rhizobacterial communities should be studied extensively if their successful application is to be realised for the sustainable cropping of the potato.

With regard to biocontrol agents, complications often arise because crops are grown under varying climatic conditions causing discrepancies in their potentiality (Gupta et al. 2015). Understanding the relationships between the potato and its rhizospheric communities under different climatic and agroecological conditions is therefore critical to the development and success of rhizobacteria-based technology for its production. It is also necessary to screen and optimise these microbes for more novel PGP abilities which could eventually lead to the full understanding of how they can successfully be harnessed for potato productivity. With time, researchers should be able to develop better biofertilisers and/or bioprotectants with improved shelf life and possessing better and efficient traits for the potato just as has been done for other plants.

Microbial formulations have immense advantages over their synthetic counterparts and rhizobacteria-based technology is a promising, sustainable and environmentally

friendly approach for fertilizing the potato. There is still a huge scope for enhancing potato productivity using this technology. Areas of research should focus on isolation and screening of potential beneficial rhizobacteria and their mass production, viability, safety and stability of biofertiliser formulations, as well as quality control and field efficacy tests (Vijay et al. 2017). The screening, selection and optimisation of novel beneficial rhizobacteria of potatoes will require comprehensive knowledge and controlled field trials for maximum exploitation and commercialisation (Bhattacharyya and Jha 2012). Furthermore, the effect of inoculations in field conditions is a complex phenomenon (Farmer et al. 2007), and more attention should be paid to the appropriate screening and selection of potato rhizobacterial communities (Wu et al. 2013). Such efforts will eventually increase our knowledge of the composition, diversity and community dynamics and offer possibilities for their advancement in potato production (Wu et al. 2013).

Molecular genetic studies have been used to reveal the interaction between rhizobacteria and potato plants as well as rhizobacterial genetic diversity (Wu et al. 2013). However, it is still unclear whether functional genes and their activities identified by such approaches can explain the effects of microbial communities on plant biofertilisation and biocontrol (Wu et al. 2013). Future research in potato rhizosphere biology should rely on developing molecular and/or biotechnological approaches to increase our knowledge of soil microbial populations (Vijay et al. 2017; Gouda et al. 2018). Researchers have indicated that current and future knowledge about rhizobacterial diversity, colonisation potential, mechanisms of action, formulation and application as well as assays for efficacy *in vitro* and *in vivo* in different plants, including the potato, could help facilitate their development and adoption as reliable components in crop production (Vijay et al. 2017). Hence, all these aspects must be investigated extensively for the potato. Over the past few decades, great strides have been made to enhance rhizobacterial antagonisms to improve their spectrum of activity against plant pathogens and enhance their tolerance to abiotic stresses (Saraf et al. 2014). For instance, several attempts have been made to improve biocontrol agents of different plant pathogens including *F. solani*, *R. solani* and *F. oxysporum* using physical mutagens (Wafa 2002). However, the literature on such attempts with rhizobacteria of the potato is still scarce and more needs to be done.

Some researchers have indicated that the production of PGP substances by rhizobacteria is related to the improvement of plant water stress tolerance (Khalil and El-Noemani 2015), but this is not clear for the potato. Such rhizobacteria can become immensely important especially in the wake of climate change. It is suggested that the application of multi-strain bacterial consortia over single inoculants is an effective approach to plant stress control (Wu et al. 2013; Vijay et al. 2017) and provides better PGP (Hungria et al. 2013), and this can also be investigated in potato to enhance its biofertilisation.

Current and future developments in understanding the functional diversity, rhizosphere colonizing ability, modes of action and optimisation of nutrient-solubilizing rhizobacteria are likely to facilitate their use as sustainable components in potato productivity. This will not only increase the field of the inoculants but also create confidence among the farmers for their use. Future research on beneficial rhizobacteria of potato should also focus on optimizing growth conditions, increasing shelf life, tolerance to diverse environmental conditions and cost-effectiveness to ensure their

adoption as viable alternatives to chemical inputs for increased production and productivity (Vijay et al. 2017). In the same perspective, current and future research also needs to focus on rhizoengineering of potatoes (Tewari and Arora 2013), by manipulating the rhizosphere to favor the growth of targeted rhizobacteria (Lugtenberg et al. 2001), and to optimise the rhizobacteria-based technology for their production. Matching appropriate rhizobacteria with the right potato cultivars and environmental conditions will also be helpful in achieving the best results from this promising technology (Arora et al. 2012).

Conclusion

Crop production, productivity and sustainable agriculture are some of the pressing issues in the world today. The potato holds a special place in present and the future global food security systems and the search for environmentally friendly and sustainable technologies for its production is both urgent and crucial. Previous studies have shown that this crop hosts numerous communities of native rhizobacteria which can be important in its growth promotion, as has been discovered in other plants. The literature also reveals that only a fraction of these root-inhabiting bacteria in the potato have been discovered and rigorous research is needed in this area. Future work should focus on fully understanding these communities and their associated roles in the potato rhizosphere and physiology. Such efforts could eventually show the magnitude of their potential as biofertilisers and bioprotectants of this crop and steer the way for the adoption and full exploitation of rhizobacteria-based technology for the sustainable cropping of the potato as food for the future.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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