

Soil Bacteria and Phytohormones for Sustainable Crop Production

Ummay Amara, Rabia Khalid and Rifat Hayat

Abstract Plant growth-promoting rhizobacteria (PGPRs) synthesizes and exports phytohormones which are called plant growth regulators (PGRs). These PGRs may play regulatory role in plant growth and development. PGRs are organic substances that influence physiological processes of plants at extremely low concentrations. Among five classes of well-known PGRs, namely auxins, gibberellins, cytokinins, ethylene and abscisic acid, the most common, best characterized and physiologically active auxin in plants is indole-3-acetic acid (IAA) that stimulate both rapid (e.g. increases in cell elongation) and long-term (e.g. cell division and differentiation) responses in plants. Some bacteria also release indole-3-butyric acid (IBA), Tryptophan and tryptophol, or indole-3-ethanol (TOL) that can indirectly contribute to plant growth promotion. On the other hand, cytokinins are usually present in small amounts, but enhance cell division leading to root hair formation and root development. Microorganisms have been found to contain over 30 growth-promoting compounds of the cytokinin group and about 90 % of microorganisms found in the rhizosphere are capable of releasing cytokinins when cultured in vitro. Soil bacteria also produce gibberellins (GAs) and over 100 GAs are known. The most widely recognized gibberellin is GA₃ (gibberellic acid), and the most active GA in plants is GA₁, which is primarily responsible for stem elongation. In addition, abscisic acid (ABA) has been detected by radioimmunoassay in supernatants of bacterial cultures held responsible for stomatal closure. Its presence in the rhizosphere could be extremely important for crop survival under a water-stressed soil environment, such as is found in arid and semiarid climates. Ethylene is a potent plant growth regulator that affects many aspects of plant growth, development and senescence. In addition to its recognition

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as a ripening hormone, ethylene promotes formation of adventurous root and root hair, stimulates germination and breaks dormancy of seeds. Soil bacteria promote plant growth especially seed germination by lowering the levels of ethylene in plants/seed rhizosphere. The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, hydrolyzes ACC, the immediate biosynthesis precursor of ethylene in plants. The products of this hydrolysis, ammonia and α -ketobutyrate, can be used by the bacterium as a source of nitrogen and carbon for growth. Soil bacterium acts as a sink for ACC and thus lowers ethylene level in plants, preventing some of the potentially deleterious consequences of high ethylene concentrations. Soil bacteria along PGPRs also play an important role in production of phosphatases, β -glucanase, dehydrogenase, antibiotic, solubilization of mineral nutrients, stabilization of soil aggregates, improving in soil organic matter and soil structure. PGRs producing soil bacteria help in reduction of/supplementing the need for chemical fertilizers N and P for sustainable crop productivity.

Keywords Soil bacteria · Phytohormones · IAA · Ethylene · ACC deaminase · Cytokinin · Gibberellins · ABA

1 Introduction

The soil supports large and energetic microbial population capable of exerting beneficial effects on plant growth. The importance of microbial population for maintenance of root health, nutrient uptake, tolerance of environmental stress and crop responses has been recognized and well-documented. The rhizosphere bacteria exert on beneficial effects ranging from direct mechanisms to an indirect effects and play an important role in growth of plants are termed plant growth-promoting rhizobacteria (PGPRs). Indirect effects are related to production of metabolites, such as antibiotics, siderophores, or hydrogen cyanide (HCN) that decreases the growth of phytopathogens and other deleterious microorganisms. Direct effects are dependent on production of plant growth regulators, or improvement in plant nutrient uptake (Kloepper 1993; Glick 1995) and synthesis of phytohormones (Glick 1995) like IAA (indole acetic acid), auxin, gibberellins, cytokinins and ethylene (Zhang et al. 1997; Cattelan et al. 1999). The effect of phytohormones is direct, as they stimulate root growth, providing more sites for infection and nodulation (García et al. 2004). Significant increases in growth and yield of agronomically important crops in response to inoculation with phytohormones yielding PGPRs have been reported (Chen et al. 1994; Amara and Dahdoh 1997; Biswas et al. 2000; Hilali et al. 2001; Asghar et al. 2002). Several species of bacteria like *Agrobacterium*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Klebsiella*, *Micrococcus* *Pseudomonas* and *Serratia* have been reported to serve as PGPRs and improve the plant growth (Hayat et al. 2010; Bhattacharyya and Jha 2012; Ahemad and Kibret 2014).

PGPR produces and distributes phytohormones which may play regulatory role in plant growth and development. These regulators are organic substances that stimulate physiological processes of plants at very low concentrations (Dobbelaere et al. 2003). There are five different classes of known phytohormones, namely auxins, abscisic acid, cytokinins, ethylene and gibberellins (Zahir et al. 2004). Auxin is the most dominant phytohormone among all and indole-3-acetic acid (IAA) is physiologically the most active auxin in plant. The hormone is identified to regulate both rapid and long-term responses in crop plants e.g. stimulate cell elongation, cell differentiation and division (Hagen 1990), apical domination, tropistic responses, flowering, fruit ripening and senescence. Regulating these processes by auxin is believed to involve auxin-induced changes in gene expression (Guilfoyle et al. 1998). In this regard, the use of PGPRs has found a potential role in developing sustainable systems in crop production (Shoebitz et al. 2009; Sturz and Nowak 2000). We previously reviewed the beneficial soil bacteria along with the detail mechanisms and their role in sustainable crop production (Hayat et al. 2010, 2012). The particular mechanisms of phytohormones-mediated enhancement of plant growth includes: (i) the ability to produce ACC deaminase to reduce the level of ethylene in the root of the developing plants thereby increasing the root length and growth; (ii) ability to produce hormones like auxin, abscisic acid (ABA), gibberellic acid and cytokinins; (iii) antagonism against phytopathogenic microorganisms by producing siderophores, β -1-3-glucanase, chitinases, antibiotics, fluorescent pigments and cyanide; (iv) enhanced resistance to drought and oxidative stress and production of water soluble B group vitamins niacin, pantothenic acid, thiamine, riboflavine and biotin. Phytohormones producing PGPRs can play an essential role in helping plants establish and grow in nutrient-deficient conditions. Their application can favor a reduction of agro-chemical use and support eco-friendly crop production. Trials with rhizosphere-associated PGP species indicated yield increases in wheat, rice, maize, sugar cane, sugar beet, legumes, canola, vegetables and conifer species (Hayat et al. 2010, 2012). In this way, PGPRs are becoming attractive alternates for bioinoculants and utilized as an additive to chemical fertilizers for improving crop yield in an integrated nutrient management system (Maheshwari 2013). Integrated nutrient management system help to minimize chemical input and to enhance nutrient use efficacy by combining chemical and biological sources of plant nutrients in an efficient and environmentally prudent manner (Adesmoye and Kloepper 2009) and also helps to minimize the use of chemical pesticides and fertilizers (Dilantha et al. 2006). In order to successfully utilize PGPRs in agriculture as bioinoculants, it is essential to identify their metabolic, phenotypic and genotypic diversities and their capability for the production of different ranges of antimicrobial metabolites. Conventionally, phenotypic identification methods play an important role but identifying at molecular level becomes much authenticated and reliable. Since the discovery of PCR and DNA sequencing, comparison of the gene sequences of bacterial species have showed that the 16S rRNA gene is highly conserved within a species and among species of the same genus, and hence can be used for identification of bacteria at species level (Olsen and Woese 1993). To understand genotypic and phenotypic

diversities of PGPRs and their potential role in plant growth promotion, it is essential to understand their role in the rhizosphere and their interaction with plants, also application as inoculant (Rameshkumar et al. 2012; Maheshwari et al. 2014).

2 Phytohormones Production by PGPRs

Plant growth regulators (PGRs) are organic substances present in extremely small concentrations that affect biochemical, morphological and physiological processes of plants. PGRs act as signal molecules working as chemical messengers and significantly participate in plants as growth regulators (De Salamone et al. 2005; Martínez et al. 2010). Five major PGRs, viz, auxins, abscisic acid (ABA), cytokinins, 1-Aminocyclopropane-1-carboxylate (ACC) deaminase and gibberellins are usually called phytohormones that have advantageous effects on plant growth and are endogenous in origin of plants (Arshad and Frankenberger 1993). Polyamines and Brassinosteroids are also PGRs produced naturally by tissues. Some synthetic compounds also trigger many physiological responses when they are artificially applied to plant tissues (Galston and Sawhney 1990; Salisbury and Ross 1992). Many bacterial and fungal species synthesize phytohormones and synthesizing ability is broadly distributed among plant- and soil-associated bacteria. Several studies confirmed that the PGPRs can improve plant growth through auxins production (indole acetic acid), ethylene, gibberellins and cytokinins (Bottini et al. 2004; Spaepen et al. 2008).

2.1 Indole-3-Acetic Acid (IAA) Production

Indole-3-acetic acid (IAA) is the most common, well-studied and naturally occurring auxin having the ability to control many aspects of plant growth. Some of them include the vascular tissues differentiation, growth elongation, apical dominance, initiation of lateral root, fruit setting and ripening. Plants produce active IAA produced by de novo synthesis from tryptophan which passes either through oxidative deamination (through indole-3-pyruvic acid formation) or decarboxylation (through tryptamine formulation by using indole-3-acetic acid aldehyde as an intermediate) (Ahemad and Khan 2011) and by releasing IAA from conjugates (Dilfuza 2012). There are different pathways involved in the synthesis of IAA by microbes (Fig. 1) (i) IAA formation via indole-3-pyruvic acid and indole-3-acetic acid aldehyde is present in most of rhizobacteria like *Agrobacterium*, *Azospirillum*, *Bradyrhizobium*, *Rhizobium*, *Enterobacter*, *Erwinia herbicola*, *Pseudomonas*, *Klebsiella*, etc.; (ii) Conversion of tryptophan into indole-3-acetic aldehyde and produce tryptamine, e.g. *Azospirilla* and *Pseudomonads*; (iii) Biosynthesis of IAA via indole-3-acetamide formation is reported by *Azospirillum*, *A. tumefaciens*, *E. herbicola*, *Rhizobium* spp., *Bradyrhizobium*

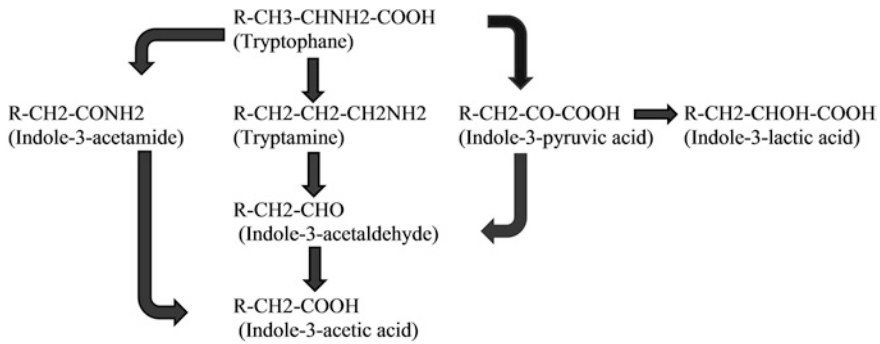


Fig. 1 Biosynthetic pathway of IAA synthesis in bacteria

sp. and Saprophytic *Pseudomonads*, etc.; (iv) In plant, biosynthesis of IAA via indole-3-acetonitrile is present, in the *Cyanobacteria* and *Alcaligenes faecalis* (v) Tryptophan independent pathway, mostly present in *Cyanobacteria* and *Azospirilla*. However, information of IAA using this pathway is non-significant and its mechanism is unknown. It is well-documented that more than 80 % bacteria isolated from rhizospheric soil of different crops have the capability to produce and release auxin (Loper and Schroth 1986). Among the auxin-producing PGPRs species, *Azospirillum* is the most studied IAA-producers (Dobbelaere et al. 1999). Other IAA-producing bacteria belong to genera *Aeromonas*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas* and *Rhizobium* (Swain et al. 2007; Ahmad et al. 2008; Hariprasad and Niranjana 2009; Shoebitz et al. 2009). The formation of different amount of IAA by bacterial strain could be varied because of participation of different biosynthetic pathway, regulatory sequences, genes location and availability of enzymes to convert active, free IAA to fixed form and could also be affected by environmental conditions (Patten and Glick 1996; Ahemad and Khan 2011). Regulation of these different physiological processes by auxin is believed to involve auxin-induced changes in gene expression (Guilfoyle et al. 1998). In addition to IAA, *P. polymyxa* and *Azospirilla* also release other compounds in the rhizosphere that could indirectly contribute to plant growth promotion.

2.2 Aminocyclopropane-1-Carboxylate (ACC) Deaminase Production

Ethylene is an important metabolite in regulating normal plant growth and developmental processes (Khalid et al. 2006; Ahemad and Kibret 2014). Ethylene has been recognized as a growth regulator and a good stress hormone (Saleem et al. 2007; Ahemad and Kibret 2014). Its production is due to various environmental

factors such as salinity, high temperature and drought, physical impendence, wounding, water logging, metal stress and during disease development (Arteca and Arteca 2007; Belimov et al. 2009; Bhattacharyya and Jha 2012; Ahemad and Kibret 2014). Low level of ethylene has a positive effect but higher levels inhibit normal plant growth. PGPRs with enzyme, ACC deaminase, support growth and development by declining level of ethylene, prompting salt tolerance and decreasing drought stress in plants (Ahemad and Kibret 2014). Presently, bacterial strains containing ACC deaminase enzymes belong to wide range of genera such as *Acinotobacter*, *Achromobacter*, *Enterobacter*, *Pseudomonas*, *Azospirillum*, *Agrobacterium*, *Burkholderia* spp., *Alcaligenes*, *Serratia*, *Ralstonia*, *Rhizobium*, etc. (Pandey et al. 2005; Shaharoon et al. 2007a, b; Zahir et al. 2009; Kang et al. 2010; Ahemad and Kibret 2014). Such rhizobacteria utilize ethylene precursor ACC and transform it into NH_3 and 2-oxobutanoate (Arshad et al. 2007). Numerous forms of stress, such as effects of phytopathogenic microorganisms (bacteria, fungi and viruses) and resistance to stress from flooding, extreme temperatures, polyaromatic hydrocarbons, heavy metals, high salt concentration, insect predation, radiation, high light intensity, draft and wounding (Lugtenberg and Kamilova 2009; Glick 2012) are overcome due to ACC containing rhizobacteria in plants. ACC deaminase containing PGPRs application show good effects on plant growth and development proving to be good candidates for biofertilizer preparation (Shaharoon et al. 2006).

Ethylene is an effective PGR synthesized by many species of bacteria (Primrose 1979), and serve as a ripening hormone, promotes adventitious roots and root hair formation, induces germination, breaks seed dormancy, enhance plant growth, development and delay senescence. However, higher ethylene concentration after germination proved to be toxic and inhibited root elongation as well as symbiotic N_2 fixation in leguminous plants. One of the mechanisms of growth promotion by PGPRs is by lowering the ethylene level in plants, which is accredited to the activity of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyzes ACC, the immediate biosynthesis precursor of ethylene in plants. The product of this hydrolysis, ammonia and α -ketobutyrate, can be utilized by the microbes as nitrogen and carbon source for growth. Therefore, the microorganisms act as a pool for ACC-deaminase and result in lowering of ethylene level in plants, thus preventing some of the precluding deleterious effects of high ethylene concentrations (Glick et al. 1998). PGPR with ACC deaminase activity is attributed to an improved plant growth and yield and thus, are potential candidate for biofertilizer formulation (Shaharoon et al. 2006).

2.3 Cytokinin Production

Cytokinins are good PGRs that control cytokinesis in tissues of crop plants (Skoog et al. 1965). Over 100 years ago, numerous scientists discovered the presence of substances that were capable to prompt cell division in cultured or damaged plant

tissue (El-Showk et al. 2013). Letham (1963) stated that zeatin was isolated from *Zea mays*. According to him, it was the first natural cytokinin with pure crystalline structure. Chemical synthesis proved the structure of zeatin to be (E)-4-(hydroxy-3-methyl-but-2-enyl) aminopurine. The most observable effect of cytokinin on plant is stimulation of shoot and root growth and enhancement in cell division (Hayat et al. 2010) and they have been involved in many other important developmental processes in plants, including seed germination, organ formation, shoot meristem formation and maintenance, and leaf senescence (Mok and Mok 2001). Above 30 different growth-promoting cytokinins compounds have been found in plants, plant-associated microorganisms and in in vitro conditions most of microorganisms are capable of releasing cytokinins with different proportions (Hayat et al. 2012). For biosynthesis of cytokinins two pathways have been proposed. Direct pathway, involving development of dimethylallyl pyrophosphate (DMAPP) and N6-isopentenyladenosine monophosphate (i6 AMP) from AMP, followed by formation zeatin-type compounds from hydroxylation of the side-chain and indirect pathway, in which cytokinins are released by turnover of tRNA containing *cis*-zeatin. Cytokinins play significant role during development processes, from germination of seed to plant senescence and regulate different physiological and morphological processes throughout the plant life, including respiration and photosynthesis (Arshad and Frankenberger 1993). The variable effects suggest that cytokinins might have different mechanisms of action depending on the type of tissues, or the impacts of primary and secondary effects caused by the variation in physiological states of the target cells (Salisbury and Ross 1992). Cytokinins phytohormones are usually present in small amounts in biological samples (Vessey 2003) and enhance cell division, root development and root hair formation (Frankenberger and Arshad 1995). Cytokinins are involved in processes such as photosynthesis or chloroplast differentiation. They are also known to induce the opening of stomata, to suppress auxin-induced apical dominance, and to inhibit senescence of plants organs, especially in leaves (Crozier et al. 2001). Plants and plant-associated microorganisms have been found to contain over 30 growth-promoting compounds of the cytokinin group. Nieto and Frankenberger (1991) studied the effect of the cytokinin precursor's adenine (ADE) and isopentyl alcohol (IA), and the cytokinin-producing bacteria *Azotobacter chroococcum* on the morphology and growth of maize under in vitro, greenhouse and field conditions, resultant, found improvement in plant growth.

2.4 Gibberellins Production

Gibberellins (GAs) are other important natural plant growth regulators in higher plants. They are usually derived from gibberellic acid and control seed dormancy, stem proliferation, expansion of leaves and flowering (Javid et al. 2011). GAs were discovered in 1938 and isolated from *Ibberella fujikuroi*, a pathogenic fungus of rice (Miransari and smith 2014). In root nodule symbiosis, GAs plays a

significant role. There are more than 80 different gibberellins, but among all GA₃ is the most commonly used form and GA₁ is the most active in plants, which is primarily responsible for stem elongation (Davies 1995). Several pathways are involved for the biosynthesis of gibberellins from geranyl diphosphate. DELLA proteins are involved in the regulation of gibberellins, C-terminal GRAS domain is the core part of structure of DELLA protein (eventually degraded by E3 ubiquitin ligase SCF (GID2/SLY1). Regulation of gibberellins is conducted by this protein (Miransari and Smith 2014). The accumulation of DELLAs in seeds becomes a cause to express the genes involved in the production of F-box proteins. The gibberellins receptor has recently been identified in rice. Gibberellin insensitive dawrf1 (GID1) protein interacts with DELLA proteins followed by their degradation in nucleus and binding with biologically active gibberellins (Willige et al. 2007). Role of gibberellins in plant growth and development is quite evident. The growth of stem is highly dependent on the production of gibberellins. Their low levels in plant metabolism results in shorter height as compared to natural height. In reality shorter and thicker stems are preferred as they can resist stress conditions and give better support; therefore, in grain production extensive use of gibberellin synthesis inhibitors is preferably chosen. On the other hand, they are considered beneficial for seed germination at breaking seed dormancy thereby positively considered for seeds that show resistance for germination. PGPR also produced gibberellic acid (GA) and gibberellins (GAs). Dobbelaere et al. (2003) reviewed that over 89 GAs are known to date and are numbered GA₁ through GA₈₉ in approximate order of their discovery. The most widely recognized gibberellin is GA₃ (gibberellic acid), the most active GA in plants is GA₁, which is primarily responsible for stem elongation. GAs also affects reproductive processes in a wide range of plants (Crozier et al. 2001). PGPRs like *Azospirillum* and *Pseudomonas* spp. produce cytokinins and gibberellins (gibberellic acid), in addition to IAA. Different genera of soil bacteria released variety of phytohormones and when inoculated, crops responded positively (Table 1).

3 Approaches to Develop PGPRs

Screening of PGPRs includes traditional as well as modern approaches. Modern approaches of screening these organisms from rhizospheric and non-rhizospheric soils are considered to be potent to improve the results of studying their effects on plant in lab. Soil and crop cultural practices, inoculant formulation and delivery are considered for rhizosphere management (Bowen and Rovira 1999; McSpadden and Fravel 2002). Root-associated traits to enhance the establishment and proliferation of beneficial organisms are being pursued by genetic manipulation of host crops (Smith and Goodman 1999; Mansouri et al. 2002). Multi-strain inocula formulations of PGPR with known functions may enhance the stability in the field (Jetiyanon and Kloepper 2002; Siddiqui and Shaikat 2002). Molecular techniques are playing lead roles in mounting our ability to understand and manage rhizosphere

Table 1 Plant growth regulator release by PGPRs and crop responses

PGPR	PGRs	Crops	Responses	References
<i>Azospirillum brasilense</i>	Indole-3-acetic acid, Gibberellins and cytokinin	Pearl millet	Increased lateral root and root hair	Tien et al. (1979)
<i>Bacillus firmus</i>	Indole-3-acetic acid	Rice	Increased grain yield and phosphate uptake	Datta et al. (1982)
<i>Pseudomonas polymyxa</i>	Indole-3-acetic acid	Wheat grass	Increased growth over uninoculated control	Holl et al. (1988)
<i>Azospirillum</i> spp. and <i>Bacillus</i> spp.	Gibberellin	Rice	Increased N ¹⁵ uptake	Kucey (1988)
<i>Azotobacter paspali</i>	IAA and other plant hormones	Canola, tomato and wheat	Increased plant growth	Abbass and Okon (1993)
<i>Bacillus firmus</i>	P-solubilizing and Indole-3-acetic acid	Rice	Increased grain yield and P-uptake of rice in a P-deficient soil	De Freitas et al. (1997)
<i>A. lipoferum</i>	Gibberellin	Maize	Alleviate temporary drought	
<i>Enterobacter cloacae</i> , <i>Pseudomonas putida</i> and <i>Achromobacter piechaudii</i>	ACC deaminase	Tomato	Inoculated tomato seed increased plant resistance in 55 days to nine consecutive days of flooding and increased resistance to salinity	Grinchko and Glick (2001)
<i>Bacillus circulans</i> , <i>Bacillus firmus</i> and <i>Bacillus globisporus</i>	ACC deaminase	Mustard	Increased root length	Ghosh et al. (2003)
<i>Achromobacter piechaudii</i>	ACC deaminase	Tomato	Increased fresh and dry weight of inoculated plants under saline and water stress conditions	Mayak et al. (2004)
<i>Pseudomonas asplenii</i>	ACC deaminase	Rape seeds	Significant increase in fresh and dry weight and biomass yield	Reed and Glick (2005)

(continued)

Table 1 (continued)

PGPR	PGRs	Crops	Responses	References
<i>Pseudomonas putida</i>	Indole-3-acetic acid	Canola	Two-threefold increases in the length of seedling roots	Ahmad et al. (2005)
<i>Pseudomonas fluorescens</i>	ACC deaminase	Maize	Increased root length and fresh weight under saline conditions	Kausar and Shahzad (2006)
<i>Splingomonas</i> spp. and <i>Mycobacterium</i> spp.	Indole-3-acetic acid	Orchid plant seeds	Increased seed germination rate	Tsavkelova et al. (2007)
<i>Bacillus subtilis</i>	Indole-3-acetic acid	Edible tubercle	Increased root and stem length and root and stem fresh weight	Swain et al. (2007)
<i>Splingobacterium</i> sp. and <i>Mycobacterium</i> spp.	Indole-3-acetic acid	Orchid plant seed	Significantly increase rate of germination and stimulate root growth	Tsavkelova et al. (2007)
<i>Pseudomonas fragi</i>	Hydrogen cyanide	Wheat seedlings	Significantly increases the germination percentage, germination rate, plant biomass and nutrient uptake	Selvakumar et al. (2008)
<i>Providencia</i> spp.	Hydrogen cyanide	Wheat	Twofold increase in germination percentage compared to untreated controls	Zarrin et al. (2009)
<i>Bacillus subtilis</i>	Indole-3-acetic acid	Sweet potatoes	Increase in root and stem length, fresh weight of the root and stem, root: stem ratio, and significantly enhanced numbers of sprouts	Martínez et al. (2010)
<i>Pseudomonas fluorescens</i>	ACC deaminase	Groundnut plants	Improved the saline resistance and yield	Siddikee et al. (2010)
<i>Pseudomonas putida</i> UW4	Indole-3-acetic acid and ACC deaminase	Canola	Under saline conditions, protected the seedling of canola from growth inhibition	Siddikee et al. (2010)

(continued)

Table 1 (continued)

PGPR	PGRs	Crops	Responses	References
<i>Providencia</i> spp. and <i>Pseudomonas aeruginosa</i>	Hydrogen cyanide	Wheat	Control fungus diseases and enhance defense against phytopathogen	Rana et al. (2011)
<i>Corynebacterium agropyri</i> , <i>Enterobacter gergoviae</i> , <i>Bacillus amyloliquefaciens</i>	Indole-3-acetic acid	Rice	Improved seed germination and seedling establishment	Ng et al. (2012)
<i>Pseudomonas chlororaphis</i>	Siderophore production	Maize	Increased root shoot biomass and seed germination rate	Hayat et al. (2012)

for obtaining improved and potent products (Nelson 2004). Large number of mechanisms has been studied yet for engineering the rhizosphere for improved productivity of crops. This includes manipulation of plant for the modification of rhizosphere. This plays vital role in promoting the nutrient availability to plants, immunity against pathogens and boosting PGPR bacterial growth (Ryan et al. 2008). A study conducted by Sundheim et al. (1998) reported during an in vitro technique that a modified strain of *Pseudomonas* with chitinase gene from *Serratia marcescens* had the potential to control *Fusarium oxysporum* f. sp. *redolens* and *Gaeumannomyces graminis* var. *tritici* effectively. Recent experiments performed on *Pseudomonas fluorescens* (DAPG-producing PGPR strain) have demonstrated that in rhizosphere different plant species have the ability to support and nourish unique microbial population and genotypes in rhizosphere (Fuente et al. 2006; Landa et al. 2006). DAPG accumulation by *Pseudomonas fluorescens* CHA0 with the expression of DAPG biosynthesis gene *phlA* has been significantly correlated by Notz et al. (2001). It was observed that the expression in rhizosphere of monocots was greater than that of dicots. Gregorio et al. (2006) noticed that in EDTA-amended soil, inocula with combined application (Triton X-100 and *Sinorhizobium* sp. Pb002) were beneficial for phytoextraction of lead by *Brassica juncea*.

4 Conclusion

PGPR synthesizes and exports phytohormones, also called as plant growth regulators (PGRs), may play regulatory role synthesized in defined organs of the plant that can be translocated to other sites, where it triggers specific biochemical, physiological and morphological responses in plant growth and development. PGRs are organic substances that influence physiological processes of plants at extremely low concentrations and are also active in the tissues where they are produced. Among different PGRs, auxins, gibberellins, cytokinins, ethylene and abscisic acid are well studied. In addition to IAA, abscisic acid (ABA) has also been detected by radioimmunoassay and TLC in supernatants of *Azospirillum* and *Rhizobium* spp. cultures. Role of PGPR in production of phosphatases, β -glucanase, dehydrogenase, antibiotic solubilization of mineral phosphates and other nutrients, stabilization of soil aggregates, improved soil structure and organic matter contents has been recognized. The mechanisms involved have a significant plant growth-promoting potential, retaining more soil organic N and other nutrients in the plant-soil system thereby reducing the need for fertilizer N and P and enhancing the release of nutrients. Another recently identified mechanism for plant growth promotion is due to production of volatiles by PGPR. PGPR release different volatile blends and the differences in these volatile blends stimulate the plant growth. Volatile compounds like 3-hydroxy-2-butanone (acetoin) and 2, 3-butanediol, produced by *Bacillus subtilis* and *B. amyloliquefaciens* stimulated the growth of *Arabidopsis thaliana* by in vitro experiments. The volatile-mediated growth promotion of plant accomplished by PGPR is due to activation of cytokinin-signaling pathways.

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