Plant Growth-Promoting Bacteria: Importance in Vegetable Production

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Abstract

A large number of soil bacteria are able to colonize the surface/interior of root system and stimulate plant growth and health. This group of bacteria, generally referred to as plant growth-promoting rhizobacteria (PGPR), enhances the growth of plants including vegetables in both conventional and stressed soil. In addition, many PGPR facilitate crop production indirectly by inhibiting various phytopathogens. Conclusively, PGPR affects plant growth via nitrogen fixation, phosphate solubilization and mineral uptake, siderophore production, antibiosis, and hydrolytic enzymes synthesis. Some of the notable PGPR capable of facilitating the growth of a varied range of vegetables such as potato, carrot, onion, etc. belong to genera *Azotobacter*, *Azospirillum*, *Pseudomonas*, and *Bacillus*. Vegetables play a major role in providing essential minerals, vitamins, and fiber, which are not present in significant quantities in staple starchy foods. Hence, to optimize vegetable production without chemical inputs, the use of PGPR in vegetable cultivation is recommended. Here, an attempt is made to highlight the role of PGPR in vegetable production under both normal and derelict soils.

2.1 Introduction

Human population is growing very rapidly, and according to the United Nations estimate, it is expected to be 8.9 billion by the end of 2050 (UN 2004, 2015; Ashraf et al. 2012). In order to feed the growing populations, there is an increasing food demand whose production needs to be augmented alarmingly in the next few years.

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In this regard, the Center for Study of Carbon Dioxide and Global Change indicated that 70–100% increase in agricultural production is required to feed the ever-increasing human populations. It also published a presumptive model estimating that only 34.5–51.5% increase will be achieved between 2009 and 2050. Of the various food items, vegetables play an important role in human dietary systems. And hence, among vegetables, total potato production is estimated to raise from 329 to 416 million tons between 2009 and 2050 due to advancements in agricultural technology and scientific research (techno-intel effect) and to 466 million tons due to the combined consequences of techno-intel effect and CO_2 aerial fertilization effect. Also, total bean production is estimated to increase from about 21 to 26 and 32 million tons between 2009 and 2050 due to techno-intel effect alone or due to the combined techno-intel effect and CO_2 aerial fertilization (Idso 2011). However, the average vegetable supply available per person in the world was about 102 kg per person by the year 2000. In addition, between 1979 and 2000, it augmented from 45.4 to 52 kg in Africa and from 43.2 to 47.8 kg in South America, while the highest improvement was found in Asia (from 56.6 to 116.2 kg per person per year), noting that global vegetable production jumped from 326.616 to 691.894 million tons (Fresco and Baudoin 2002). However, due to environment degradation, biodiversity destruction, and soil fertility loses, considerable reduction in agricultural production including those of vegetable production leading to inadequate food supply to human populations has been recorded (Shahbaz and Ashraf 2013).

2.2 Place of PGPR in Food Safety and Agricultural Challenges

Because of different factors threatening agriculture, scientists are searching for alternatives involving natural and eco-friendly solutions. Among these options, microbe-based (bacteria, fungi) ecological engineering strategies have been developed for ecological conservation and to improve agronomic practices for enhancing food production (Ashraf et al. 2012). Among soil microflora, the use of plant growth-promoting rhizobacteria (PGPR) began about 100 years ago where some countries like China, European countries, the former Soviet Union, and the United States started practical programs to develop PGPR inoculants at a larger scale for the use in agriculture. However, the term “rhizobacteria” was introduced first by Kloepper and Schroth (1978) to qualify bacterial community that aggressively colonize roots and improve plant growth. The PGPR application is considered one of the most viable and inexpensive methods for increasing agricultural productivity through plant growth stimulation, plant pathogens control, and pollutant biodegradation, bioremediation (Bhattacharyya and Jha 2012; Landa et al. 2013). In this chapter, different mechanisms by which beneficial soil bacteria improve plant growth, plant defenses against phytopathogens, and soil health and how they participate in the interactive plant-soil-bacteria system are discussed. Furthermore, the importance of PGPR in vegetable production under different agroclimatic conditions is highlighted. It is important to mention that vegetables play a major role in providing essential minerals, vitamins, and fiber, which are not present in significant quantities in starchy foods, and represent an important supply of proteins and carbohydrates (Nichols and Hilmi 2009).

2.3 Mechanism of Growth Promotion by PGPR: A General Perspective

2.3.1 Nitrogen Fixation

Nitrogen fixation, one of the most important means of adding N to soil nutrient pool (Reddy 2014), is mediated both by symbiotic prokaryotic microorganisms like *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium*, and *Sinorhizobium* and asymbiotic/free-living organisms such as *Azoarcus*, *Azospirillum*, *Burkholderia*, *Gluconacetobacter*, *Pseudomonas*, *Azotobacter*, *Arthrobacter*, *Acinetobacter*, *Bacillus*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Klebsiella*, and *Acetobacter*. These bacterial genera and some others have been described as nitrogen-fixing PGPR with substantial ability to promote plant growth and yield (Gupta et al. 2015; Miao et al. 2014; Sivasakthi et al. 2014; Verma et al. 2013). Nitrogen fixation is carried out by a highly conserved and energetically expensive enzyme called nitrogenase. The conventional nitrogenase is composed of two metalloprotein subunits. The first one is composed of two heterodimers (250 kDa) and encoded by *nifD* and *nifK* genes; it contains the active site for nitrogen reduction. The second one (two identical subunits/70 kDa, encoded by *nifH* gene) ensures ATP hydrolysis and electron transfer between subunits that are coordinated by Fe-S containing Mo. Mo is replaced by V (*vnfH*) in “alternative nitrogenase” and by Fe (*anfH*) in “second alternative nitrogenase” (Zehr et al. 2003). Of the various nitrogen fixers, bacteria belonging to group “rhizobia” are known to establish symbiotic relations with host-specific legumes and to provide a major plant nutrient N to plants. The species *R. meliloti*, *R. trifolii*, *R. leguminosarum*, *R. phaseoli*, *R. japonicum*, etc. can supply N to plants such as lucerne, sweet clover, pea, lentil, bean, cowpea, etc. (Yamaguchi 1983). In addition, some other associative nitrogen fixers, for example, *Azospirillum* inoculation, have been reported to enhance growth and yield of several winter legumes such as pea and chickpea (Sarig et al. 1986). The role of two PGPR strains (*Serratia liquefaciens* 2-68 or *S. proteamaculans* 1-102) in increasing nodulation, nitrogen fixation, and total nitrogen yield of two soybean cultivars in a short season area was reported (Dashti et al. 1998). Strains increased soybean nodulation and accelerated nitrogen fixation onset. Fixed N, expressed as a percentage of total plant N, and protein and N yield were increased by PGPR inoculation. Pishchik et al. (1998) on the other hand reported the inoculation effect of nitrogen-fixing *Klebsiella* on yield of nonlegumes such as potato. A significant increase in potato yield and N content was obtained after inoculation with *K. mobilis* strains CIAM880 and CIAM853 when low doses of nitrogenous fertilizer were used. Recently, Naqqash et al. (2016) observed that inoculation of nitrogen-fixing bacteria, namely, *Azospirillum*, *Enterobacter*, and *Rhizobium*, under axenic conditions resulted in differential growth responses of potato. Of these, *Azospirillum* sp. TN10 showed the highest increase in fresh and dry weight of potato over control plants. In addition, a significant augmentation in N contents of shoot and roots of *Azospirillum* sp.-inoculated potato plants was observed.

2.3.2 Nitrification

Bacterial nitrification is a biological process in which energy is extracted by sequential oxidation of nitrogen that occurs as ammonia. Complete oxidation of nitrate is carried out by two metabolically distinct groups of bacteria: (i) ammonia-oxidizing bacteria, for example, *Nitrosomonas*, *Nitrosospira*, *Nitrosovibrio*, *Nitrosolobus*, and *Nitrosococcus*, transform ammonia to nitrite, and (ii) nitrite is transformed to nitrate by nitrifying bacteria like *Nitrobacter*, *Nitrococcus*, *Nitrospira*, and *Nitrospina*. Nitrification is important for soil and ecosystem health because it completes the mineralization of organic nitrogen started with ammonification process (nitrogen fixation) (Ardisson et al. 2014; Cohen and Mazzola 2006; Cohen et al. 2010). Among others, nitrification is considered as an important trait to select beneficial bacteria able to improve plant growth and crop yield (Prasad et al. 2015). It is believed that nitrification is the principal source of nitric oxide (NO) emitted from the soil. However, recent works have described NO as a signal molecule in plant-PGPR interaction. For example, *Azospirillum* strains produced tenfold of NO than the amount found in plant. Nevertheless, when bacterial nitric oxide was sequestered with specific scavenger (cPTIO), results clearly showed that the ability of *Azospirillum* inoculation to induce lateral root development in tomato was lost suggesting the involvement of NO in the *Azospirillum*-plant root association (Cohen et al. 2010; Skiba et al. 1993).

2.3.3 Denitrification

The first description of soil organic matter degradation that resulted in release of nitrogen gas into atmosphere was realized by Reyest in 1856. Later on, Gayon and Dupetit were the first to describe denitrification in 1886 (Elmerich 2007). Denitrification is defined as a microbial respiratory process during which soluble N oxides are used as alternative electron acceptor when O_2 is not available for aerobic respiration. It involves sequential reduction of NO^{3-} into dinitrogen in four steps coupled with energy conservation (NO to NO_2, NO_2 to NO, NO to N_2O, and N_2O to N_2). Denitrification completes the N cycle and usually balances the total biological N fixation in the global N cycle (Hofstra and Bouwman 2005; Philippot et al. 2007). Among denitrifying bacteria, *Agrobacterium*, *Aquaspirillum*, *Azoarcus*, *Azospirillum*, *Bradyrhizobium*, *Hyphomicrobium*, *Magnetospirillum*, *Paracoccus*, *Rhodobacter*, *Rhodopseudomonas*, *Cytophaga*, *Sinorhizobium*, *Flexibacter*, *Alcaligenes*, *Neisseria*, *Nitrosomonas*, and *Thiobacillus* are the most commonly found in nature, especially in soil (Knowles 2004).

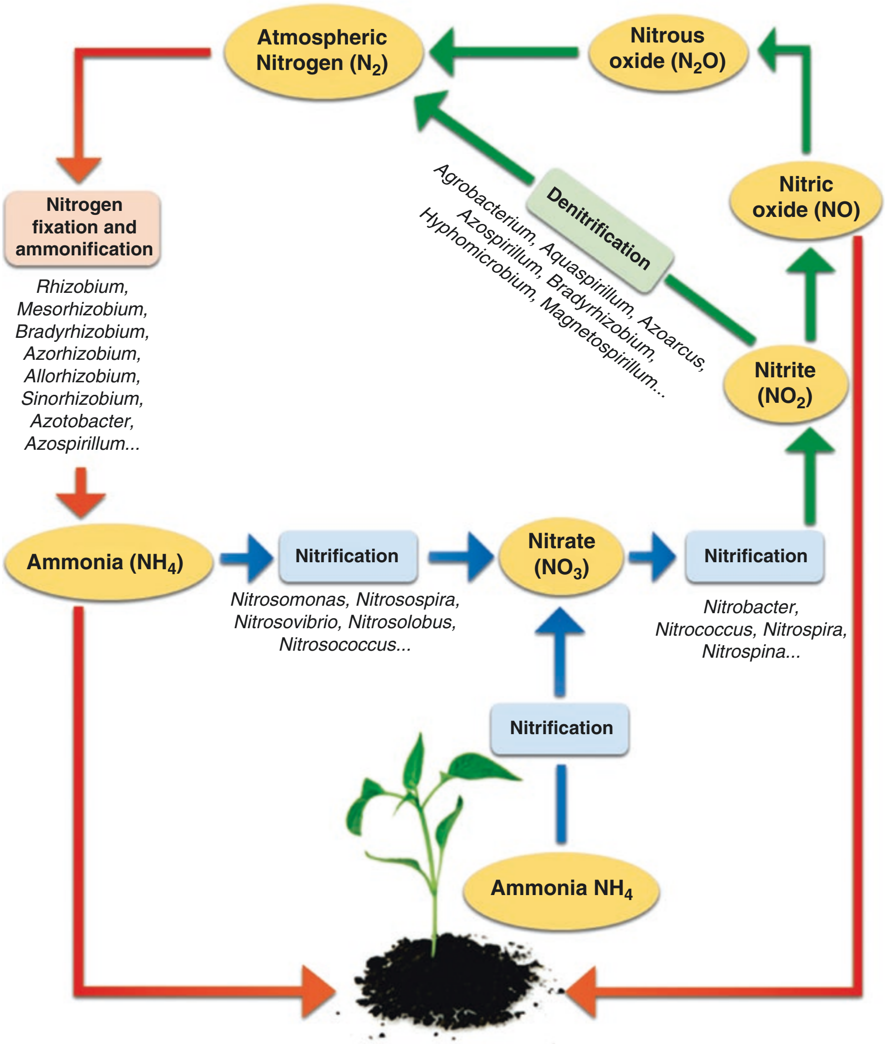

Fig. 2.1 Role of PGPR in nitrogen recycling and plant growth stimulation (modified from Cohen et al. 2010; Reddy 2014)

Ecologically, denitrification is a key mechanism for biological elimination of N. In fact, 15–70% of ammonium derived from organic matter mineralization is reported to be eliminated through nitrification and denitrification process (Bertrand et al. 2015). In rhizosphere, oxygen concentration could be lowered because of root and microorganism's respiration. In addition, organic compounds released by plants' roots can be used as electron donors in denitrification process, suggesting that denitrifiers could constitute highly competitive microorganisms in rhizosphere (Fig. 2.1). Denitrifying bacteria may prevent nitrogen accumulation to toxic levels, reduce nitrate contents in groundwater, and maintain a balance between soil and atmospheric nitrogen avoiding serious problems that could occur if no alternative mechanism is available to return nitrogen to atmosphere (Antoun and Prévost 2005; Gupta et al. 2000; Philippot et al. 2007). Due to these and in addition to the presence of positive correlation between bacterial denitrification ability and rhizosphere colonization, Kumar et al. (2014) considered nitrification as an important trait to isolate and select fluorescent PGP *Pseudomonas*. Furthermore, in a recent work conducted by Muriel et al. (2015), denitrification was regarded as an important plant growth trait in PGP *Pseudomonas fluorescens* F113. Otherwise, denitrification in legumes may be a species-dependent mechanism to maintain optimum rates of N_2 fixation within root nodule; hence, NO has been reported as inhibitor of nitrogenase activity (Williams et al. 2014). Denitrification in nodules could also ensure detoxification of cytotoxic compounds produced as intermediates during denitrification reactions or emerging from host plant such as nitrite and NO (O'Hara and Daniel 1985; Sánchez et al. 2011). In addition, Lombardo et al. (2006) reported that when lettuce plants were grown hydroponically, root epidermis did not form root hairs. The addition of 10 μM sodium nitroprusside (a nitric oxide (NO) donor) resulted in almost all rhizodermal cells differentiated into root hairs. They also found that treatment with synthetic auxin 1-naphthyl acetic acid exhibited a significant increase of root hair formation that was prevented by the specific NO scavenger carboxy-PTIO.

2.3.4 Phosphate Solubilization

After nitrogen, phosphorus (P) is the most important macronutrient for biological processes, for example, cell division and development, energy transport, signal transduction, macromolecular biosynthesis, photosynthesis, and plant respiration. Phosphorus is present at levels of 400–1200 mg/kg of soil. However, only a very small amount (1 mg or less) of P is in soluble forms, while the rest is insoluble and, hence, not available for plant uptake (Khan et al. 2009). It is important to mention that a big part of P applied to agricultural fields as fertilizer is rapidly immobilized and, hence, becomes inaccessible for plants (Oteino et al. 2015). In addition, the process of traditional phosphorus fertilizer production is environmentally undesirable because of contaminants release into the main product, gas stream and by-products, and accumulation of Cd or other heavy metals in soil and crops because of repetitive use of phosphatic fertilizers (Sharma et al. 2013; Song et al. 2008). To avoid these problems, a group of soil microorganisms, called phosphate-solubilizing microorganisms (PSM), is considered as one of the best eco-friendly options for providing inexpensive P to plants. Through their activities, insoluble forms of P are hydrolyzed to soluble forms through solubilization (inorganic P) and mineralization (organic p) processes. On the contrary, immobilization is the reverse reaction of mineralization, during which, microorganisms convert inorganic forms to organic phosphate (Sharma et al. 2013; Khan et al. 2014). Some of the notable PGPR possessing P-solubilizing activity are *Achromobacter xylosoxidans* (Ma et al. 2009), *Bacillus polymyxa* (Nautiyal 1999), *Pseudomonas putida* (Malboobi et al. 2009), *Acetobacter diazotrophicus* (Sashidhar and Podile 2010), *Agrobacterium radiobacter* (Leyval and Berthelin 1989), *Bradyrhizobium mediterranium* (Peix et al. 2001), *Enterobacter aerogenes*, *Pantoea agglomerans* (Chung et al. 2005), *Gluconacetobacter diazotrophicus* (Crespo et al. 2011), and *Rhizobium meliloti* (Krishnaraj and Dahale 2014). Among non-symbiotic bacteria, *Azotobacter* has also been found as phosphate solubilizer and plant growth-enhancing bacterium (Nosrati et al. 2014). Malboobi et al. (2009) evaluated the performance of three PSB *P. agglomerans* strain P5, *Microbacterium laevaniformans* strain P7, and *P. putida* strain P13 in potato's rhizosphere. All experiments proved that these isolates compete well with naturally occurring soil microorganisms in potato's rhizosphere. The combinations of strains P5 + P13 and P7 + P13 led to higher biomass and potato tuber in greenhouse and in field trials. The effect of other phosphate solubilizers such as *B. megaterium* var. phosphaticum, *P. agglomerans*, *M. laevaniformans*, *P. putida*, *P. cepacia*, *P. fluorescens*, *Xanthomonas maltophilia*, *Enterobacter cloacae*, *Acidovorans delafieldii*, *Rhizobium* sp., *A. chroococcum*, and *Burkholderia anthina* on some of the widely grown and consumed vegetables such as potato, tomato, pepper, cucumber, pea, brinjal, etc. has been reported by others (Bahena et al. 2015; Pastor et al. 2014; Rizvi et al. 2014 and Walpola and Yoon 2013).

2.3.5 Siderophores, a Powerful Tool for Antagonism and Competition

Iron is a central element for life on earth, especially for plant growth and development. It participates in formation of several types of vegetable proteins such as ferredoxin, cytochrome, and leghemoglobin (Fukuyama 2004; Liu et al. 2014). This element is relatively insoluble in soil solution. So why plants secrete soluble organic compounds (binders) which bind to ferric ion (Fe^{3+}) to form the chelator-Fe^{3+} complex (Tokala et al. 2002; Vessey 2003)? Several studies on iron utilization by plants allowed scientists to distinguish two strategies used by plants for iron acquisition from soil (Bar-Ness et al. 1992). In the first one, iron chelators (siderophores: from the Greek "iron carriers") secreted by plants are immediately absorbed with Fe^{3+} through the plasma lemma. In the second one, formed complex (chelator-Fe^{3+}) helps to keep ferric ions in solution, then exposes to root surface where they are reduced to ferrous ions (Fe^{2+}) and immediately absorbed (Neilands 1995; Vessey 2003). In addition to these two strategies, plants can also use microbial siderophores (fungi and bacteria) which are synthesized under iron-starved conditions. Broadly, siderophores are defined as low-molecular-weight compounds (500–1500 daltons) possessing high affinity for ferric iron. They are mainly produced by bacteria (Kümmerli et al. 2014), fungi (Renshaw et al. 2002), and graminaceous plants (Hider and Kong 2010) to scavenge iron from environment.

According to the chemical nature, siderophores are divided into five classes, (1) catecholates, (2) phenolates, (3) hydroxamates, (4) carboxylates, and (5) mixed siderophores, which contain at least two of the abovementioned classes. In agriculture, the secretion of bacterial siderophores is important for two reasons: (1) it provides iron to plants, and (2) it limits the availability of iron to plant pathogens (Miethke and Marahiel 2007; Tailor and Joshi 2012). Additionally, siderophores may stimulate biosynthesis of other antimicrobial compounds (Beneduzi et al. 2012; Laslo et al. 2011). Impressively, it has been reported that some nodule bacteria, for example, *Rhizobium*, can require an intact siderophore system to express some vital activities such as nitrogenase (Neilands 1995).

Until 2014, more than 500 siderophore-type molecules have been identified (Kannahi and Senbagam 2014). Genera like *Azotobacter* (Fekete et al. 1983), *Azospirillum* (Tortora et al. 2011), *Pseudomonas* (Tailor and Joshi 2012), *Agrobacterium* (Rondon et al. 2014), *Alcaligenes* (Sayyed and Chincholkar 2010), *Serratia* (Seyedsayamdost et al. 2012), *Enterobacter* and *Achromobacter* (Tian et al. 2009), *Rhizobium* (Datta and Chakrabartty 2014), *Bradyrhizobium* (Abd-Alla 1998), etc. are known to promote growth of many crops through siderophore production. Therefore, siderophores secreted by many PGPR are used as a specific trait for selection and application of effective bacteria in crop production. For example, the indigenous isolate *B. subtilis* CTS-G24 producing a hydroxamate type of siderophore was found to be efficient in inhibiting wilt and dry root rot disease caused by both *Fusarium oxysporum* f. sp. ciceri and *Macrophomina phaseolina* in chickpea (Patil et al. 2014). In other study, a yellow-green pigment (pseudobactin) exhibiting properties typical of a siderophore was isolated from broth cultures of fluorescent *Pseudomonas* strain B10, grown in iron-deficient medium (Kloepper et al. 1980). The application of B10 as inoculant and pure pseudobactin significantly improved potato growth in greenhouse assay compared to water-treated controls. In addition, strain B10 and pseudobactin significantly reduced fungal population in potato's rhizoplane (control, 5.5; B10, 2.3; pseudobactin, 1.4 CFU per 10 cm roots) suggesting that bacterial siderophores play a crucial role in enhancing plant growth by sequestering iron in root zone and by antagonism to potentially deleterious phytopathogens. The role of siderophore-producing bacteria in enhancing potato growth has also been reported by others (Bakker et al. 1986; Weisbeek et al. 1987). Moreover, in a hydroponic culture experiment, siderophores from bacterial strain *Chryseobacterium* C138 were found effective in supplying Fe to iron-starved tomato plants by roots inoculated with or without bacteria (Radzki et al. 2013). Similarly, the role of fluorescent siderophore (pyoverdin) in suppression of *Pythium*-induced damping-off in tomato by *Pseudomonas aeruginosa* RBL 101 has been reported by Jagadeesh et al. (2001). Thus, hyperactive mutants (Flu++ Sid++) (RBL 1015 and 1011) with higher siderophore production suppressed wilt disease more efficiently (75 and 37%, respectively) than the wild type (12.5%). In a follow-up study, Valencia-Cantero et al. (2007) observed a significant increase Fe content and growth of bean plants inoculated with *B. megaterium* UMCV1, *Arthrobacter* spp. UMCV2, *S. maltophilia* UMCV3, and *S. maltophilia* UMCV4, compared to uninoculated plants grown in sterilized soil. Similarly, the role of bacteria such as *Pseudomonas aeruginosa*, *P. fluorescens*, *P. putida*, and *S. marcescens* in inducing siderophore-dependent resistance in vegetables such as bean, tomato, radish, and cucumber against plant pathogens like *Colletotrichum lindemuthianum*, *C. orbiculare*, *Botrytis cinerea*, and *Fusarium* was also reported (Höfte and Bakker 2007).

2.3.6 Bacterial Phytohormones and Plant Growth Regulation

Phytohormones or "plant growth hormones" are naturally occurring organic substances that exert, at low concentrations, a major influence on plant growth and upregulation of physiological process. Among phytohormones, auxin, the term derived from Greek word αυξειν (auxein means "grow or increase"), was the first plant hormone discovered by Kende and Zeevaart (1997). Auxin remained the only synonym of phytohormone until 1973, when Went and Thimann published their book *Phytohormones*. Since then, other phytohormones such as gibberellin, ethylene, cytokinin, and abscisic acid have been discovered (Tran and Pal 2014). Phytohormones are produced by plants (Bari and Jones 2009), by microorganisms (Narayanasamy 2013), and even by algae (Kiseleva et al. 2012). Among microbes, PGPR can also modulate phytohormone levels in plant tissues affecting hormonal balance of host plant (Figueiredo et al. 2016). Some of the most common phytohormones affecting plant growth are discussed in the following section.

2.3.6.1 Auxins: Biosynthesis and Their Place in the Plant-PGPR Interaction

Among phytohormones, auxins have the ability to affect, practically, all plant physiological aspects from promotion of cell enlargement and division, apical dominance, root initiation, and differentiation of vascular tissue to modulation of reactive oxygen species (Tomić et al. 1998). Recently, it has been reviewed that auxins affect other plant hormone activities, such as cytokinin, abscisic acid, ethylene, jasmonate, and salicylic acid, and modulates various plant defense-signaling pathways (Vidhyasekaran 2015). Indole acetic acid (IAA) is the major naturally occurring phytohormone which is also produced by bacteria involved in plant growth and health enhancement (Gao and Zhao 2014; Etesami et al. 2015; Spaepen and Vanderleyden 2010). In most cases, tryptophan (Trp) serves as physiological precursor in IAA synthesis (Spaepen et al. 2007a). IAA biosynthesis in bacteria involves five Trp-dependent pathways: indole-3-acetamide pathway, indole-3-pyruvic acid pathway, tryptamine pathway, indole-3-acetonitrile pathway and Trp side chain oxidase pathway, and one Trp-independent pathway (Spaepen et al. 2007b; Di et al. 2016).

Beyeler et al. (1999) reported that a genetically modified strain of *P. fluorescens* CHA0, which overproduced IAA, was more effective for cucumber growth improvement than the wild strain. Accordingly, mutant strain CHA0/pME3468 increased fresh root weight of cucumber by 17–36%, compared to the effect of wild CHA0 strain; Gravel et al. (2007) found that IAA (10 μg/ml) application by drenching to the growing medium or by spraying on shoots reduced symptoms caused by *P. ultimum* on tomato plants. Furthermore, Khan et al. (2016) reported that among other tested strains, endophyte *B. subtilis* LK14 produced the highest (8.7 μM) amount of IAA on the fourteenth day of growth and significantly increased shoot and root biomass and chlorophyll (a and b) contents in tomato as compared to control plants.

2.3.6.2 Gibberellins: Miraculous Molecules for Plant Growth Regulation

Gibberellins were first isolated in 1962 from fungus *Fusarium moniliforme* (*Gibberella fujikuroi* in sexual form) by Kurosawa (Japan). In 1938, two other Japanese workers (Yakutat and Sumiki) isolated active principles as crystals from culture medium and named them gibberellins A and B (Takahashi et al. 1991). Macmillan and Suter (1958) identified the first plant gibberellin (GA1) from *Phaseolus coccineus* seeds. However, gibberellins are synthesized not only by plants and fungi but also by bacteria (Morrone et al. 2009). In this context, Maheshwari et al. (2015) mentioned that the bacterial gibberellins were reported first time in 1988 in *R. meliloti*. Later on, based on gibberellins pathways synthesis occurring in plant and fungi, it was suggested that its synthesis in bacteria started with geranyl-PP conversion into ent-kaurene via ent-copalyl diphosphate. After this, ent-kaurene is converted into GA12-aldehyde through ent-kaurene oxidase and ent-kaurenoic acid oxidase synthesis. GA12-aldehyde is then oxidized into GA_{12} and metabolized into other GA (Kang et al. 2014). Morrone et al. (2009) described an operon in *Bradyrhizobium japonicum* genome, whose enzymatic composition indicates that gibberellin biosynthesis in bacteria represents a third independently assembled pathway relative to plants and fungi.

Currently, gibberellins include a wide range of tetracyclic diterpene acids that regulate, in combination with other phytohormones, diverse processes in plant growth such as germination, stem elongation, flowering, fruiting, root growth promotion, root hair abundance, vegetative/reproductive bud dormancy, and delay of senescence in many plant organs (Cassán et al. 2014; Kang et al. 2012; Niranjana and Hariprasad 2014). Bacteria such as *Acetobacter diazotrophicus* (Bastian et al. 1998), *Azospirillum lipoferum* (Bottini et al. 1989), *A. brasilense* (Janzen et al. 1992), *Bacillus pumilus* (Joo et al. 2005), *B. cereus* (Joo et al. 2005), *B. macroides* (Joo et al. 2005), *Herbaspirillum seropedicae* (Kang et al. 2014), *Acinetobacter calcoaceticus* (Kang et al. 2009), *Burkholderia cepacia* (Joo et al. 2009), and *Promicromonospora* sp. (Kang et al. 2012) have been reported as gibberellin producers. In addition, Kang et al. (2012) described the role of gibberellin-producing *Promicromonospora* sp. SE188 in *Solanum lycopersicum* plant growth improvement. *Promicromonospora* sp. produced physiologically active (GA1 and GA4) and inactive (GA9, GA12, GA19, GA20, GA24, GA34, and GA53) gibberellins. In addition to plant growth improvement, tomato inoculated with this bacterium resulted in a downregulation of the stress hormone abscisic acid, while salicylic acid was significantly higher compared to control plants. Joo et al. (2004, 2005) reported the positive effect of gibberellin-producing bacteria (*B. cereus* MJ-1, *B. macroides* CJ-29, and *B. pumilus* CJ-69) on red pepper growth and its endogenous gibberellins content. Inoculation with *B. cereus* MJ-1 improved shoots and roots fresh weight of red pepper by 1.38- and 1.28-fold, respectively. Among 864 bacterial isolates tested on cucumber and crown daisy for growth promotion, the most efficient strain for plant growth enhancement, *Burkholderia* sp. KCTC 11096BP, was found to produce physiologically active gibberellins (GA_1, 0.23; GA_3, 5.11; and GA_4 2.65 ng/100 ml) and inactive gibberellins (GA_{12}, GA_{15}, GA_{20}, and GA_{24}) (Joo et al.

2009). Moreover, Khan et al. (2014) reported tomato growth-promoting activity of IAA and gibberellin-producing bacteria *Sphingomonas* sp. LK11 isolated from leaves of *Tephrosia apollinea*. In culture broth, the strain LK11 released active (GA4, 2.97 ng/ml) and inactive gibberellins (GA9, 0.98 and GA20, 2.41 ng/ml). Tomato plants inoculated with endophytic *Sphingomonas* sp. LK11 had significantly higher shoot length, chlorophyll contents, and dry matter accumulation in shoot and root compared to control suggesting the potential role of phytohormones in crop growth improvement.

2.3.6.3 Cytokinins and Plant Growth Regulation

Cytokinins are N6-substituted aminopurines or adenine compounds with an isoprene, modified isoprene, aromatic side chain attached to the N6-amino group, or zeatin and trans-zeatin. These molecules have the ability to influence physiological and developmental processes of plants. Cytokinins affect cell division, cell cycle, leaf senescence, nutrient mobilization, apical dominance, shoot apical meristems formation and activity, floral development, breaking of bud dormancy and seed germination, chloroplast differentiation, autotrophic metabolism, and leaf and cotyledon expansion (Maheshwari et al. 2015; Wong et al. 2015). Apart from plant roots, cytokinins can also be derived from microalgae, bacteria, mycorrhizal fungi, and nematodes in rhizosphere (Reddy 2014). For a long time, cytokinins have been considered as an important plant growth regulator. Hence, several works reported the role of cytokinin-producing bacteria like *Azotobacter* (Taller and Wong 1989), *Azospirillum* (Conard et al. 1992), *Agrobacterium* (Akiyoshi et al. 1987), *Pseudomonas* (Akiyoshi et al. 1987), *Paenibacillus* (Timmusk et al. 1999), *Bacillus* (Ortíz Castro et al. 2008), *Achromobacter* (Donderski and Głuchowska 2000), *Enterobacter* (Kämpfer et al. 2005), and *Klebsiella* (Conard et al. 1992) in plant growth regulation.

The impact of cytokinins produced by some bacterial strains isolated from rhizosphere on growth and cell division in cucumber cotyledons have been reported (Hussain and Hasnain 2009). Chlorophyll contents, cell division, and fresh weight were increased in cucumber cotyledons placed at 2 mm distance from cytokinin-producing *B. licheniformis* Am2, *B. subtilis* BC1, and *P. aeruginosa* E2 cultures under green light. Major cytokinin species detected were zeatin and zeatin riboside. Arkhipova et al. (2007) followed the consequences of inoculating growing medium with cytokinin-producing *Bacillus* (strain IB-22) under conditions of water sufficiency and deficit on 12-day-old lettuce seedlings. Inoculation increased shoot cytokinins, shoot abscisic acid, accumulation of shoot mass, and shortened roots, while it showed a smaller effect on root mass and root/shoot ratios by stimulating shoot growth, but did not raise stomatal conductance. Likewise, Arkhipova et al. (2005) evaluated the ability of cytokinin-producing *B. subtilis* in influencing growth and endogenous hormone content of lettuce plants. Recently, the osmotolerant cytokinin-producing *Citricoccus zhacaiensis* and *B. amyloliquefaciens* were found to enhance tomato growth under irrigation deficit conditions (Selvakumar et al. 2016). They observed that microbial inoculation significantly enhanced stomatal conductivity, transpiration rates, photosynthesis, and relative water contents of tomato plants across stress levels. Moreover, *C. zhacaiensis* enhanced the yield by 24 and 9%, while *B. amyloliquefaciens* increased the yield by 42 and 12.7%, at 50 and 25% water holding capacity, respectively. Ortiz Castro et al. (2008) described the important role played by cytokinin receptors in plant growth promotion by *B. megaterium*, initially isolated from bean plants rhizosphere. Inoculation with *B. megaterium* promoted biomass production of bean plants. This effect is related to altered root system architecture in inoculated plants (inhibition in primary root growth followed by an increase in lateral root formation and root hair length). These promoting effects on plant development were found to be independent of auxin and ethylene signaling.

2.3.6.4 Ethylene

Ethylene is a gaseous hormone produced by plants and plays an important role in various developmental processes, such as leaf senescence, leaf abscission, epinasty, and fruit ripening (Gray and Smith 2004; Vogel et al. 1998). Ethylene is synthesized from methionine in three steps that starts with methionine activation to S-adenosyl-L-methionine by the enzyme SAM synthetase. The second step consists to convert S-adenosyl-L-methionine to 1-aminocyclopropane-1-carboxylic acid (ACC), which is catalyzed by ACC synthase. After that, the enzyme ACC oxidase ensures ACC conversion to ethylene via an oxygenation reaction (Ma et al. 2014). At the beginning, ethylene was considered as a stress hormone because under stress conditions (salinity, drought, water logging, heavy metals, and pathogenicity), plants synthesize high amount of ethylene, leading to the alteration of their physiological performance and, consequently, to the reductions in root and shoot growth. Later, other vital functions such as seed germination, root hair development, adventitious root formation, nodulation, leaf and fruit abscission, and flower and leaf senescence have been found to be influenced by ethylene (Bakshi et al. 2015; Shrivastava and Kumar 2015).

2.3.6.5 Abscisic Acid

Abscisic acid (ABA) is a sesquiterpene phytohormone, synthesized by plants, bacteria, fungi, algae, and animals (Gomez-Cadenas et al. 2015; Karadeniz et al. 2006; Tuomi and Rosenquist 1995). ABA affects many physiological processes of plants including vegetables (Porcel et al. 2014). For example, ABA regulates several events during late seed development and plays an important role in circumventing environmental stresses such as desiccation, salt, and cold. Abscisic acid also controls plant growth and inhibits root elongation (Pilet and Chanson 1981) suggesting that a negative correlation exists between growth and the endogenous ABA plants content (Pilet and Saugy 1987). The prokaryotic pathway for abscisic acid biosynthesis originates from isoprene known as isopentenyl pyrophosphate that is synthesized from mevalonate pathway (Endo et al. 2014). Abscisic acid is the main hormone that balances many plant physiological responses to abiotic stress. However, its signaling pathways act in a complex interconnection with other hormone signal (Gomez-Cadenas et al. 2015).

2.3.6.6 Bacterial ACC Deaminase: A Hormone Balancing Signal Molecule

The enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase synthesized by a wide range of rhizospheric bacteria (Glick et al. 2007) decreases the deleterious ethylene amounts and balances ABA levels in stressed plants. Enzyme ACC deaminase degrades ACC into α-ketobutyrate and ammonia to supply N and energy and, hence, lowers the ethylene levels in plant (Glick et al. 2007; Penrose and Glick 2003). It has been reviewed that many biotic (viruses, bacteria, fungi, and insects) and abiotic (salt, heavy metals, drought, radiation, etc.) stresses could be relieved by ACC deaminase-producing bacteria (Lugtenberg and Kamilova 2009; Shaharoona et al. 2012). Among microorganisms, soil bacteria belonging to genera *Agrobacterium*, *Azospirillum*, *Alcaligenes*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Methylobacterium*, *Pseudomonas*, *Ralstonia*, *Rhizobium*, *Rhodococcus*, *Sinorhizobium*, *Kluyvera*, *Variovorax*, and *Paradoxus* have been reported to produce ACC deaminase (Barnawal et al. 2012; Glick 2014; Hao et al. 2010; Saleem et al. 2007; Toklikishvili et al. 2010).

The bacterial strain *M. ciceri* LMS-1 was transformed by triparental mating with plasmid pRKACC containing ACC deaminase gene (*acdS*) of *P. putida* UW4 cloned in pRK415. By expressing ACC deaminase under free-living conditions, ACC deaminase-producing mutant *Mesorhizobium* LMS-1 (pRKACC) increased chickpea nodulation performance and plant total biomass compared to LMS-1 wild-type strain (127 and 125%, respectively). These results suggest that the use of bacteria with improved ACC deaminase activity might be very important to develop microbial inocula for agricultural purposes (Nascimento et al. 2012). Like other crops, the role of ACC deaminase positive bacteria in vegetable growth is reported. As an example, Mayak et al. (2004) described the role of ACC deaminase-producing *Achromobacter piechaudii* in conferring resistance in tomato plants to salt stress. This bacterium significantly reduced ethylene levels in seedlings and increased fresh and dry weights of tomato grown in presence of up to 172 mM NaCl. Under salt stress, the bacterium also increased water use efficiency by plants compared to the control, suggesting the usefulness of such ACC deaminase-producing bacteria in alleviating salt stress. Similarly, ACC deaminase-producing and halotolerant *Brevibacterium iodinum*, *B. licheniformis*, and *Zhihengliuela alba* were found to regulate ethylene levels and consequently enhanced growth and salt tolerance of red pepper, grown in salt-stressed conditions (Siddikee et al. 2011). The inoculation with *B. licheniformis* RS656, *Z. alba* RS111, and *B. iodinum* RS16 reduced ethylene production by 44, 53 and 57%, respectively. In addition, when red pepper was grown in salt-stressed condition, salt stress caused 1.3-fold reduction in root/shoot dry weight ratio, while bacterial inoculation on the contrary relieved the stress, and the red pepper plants grew normally similar to those of control plants. Numerous other studies have also been conducted to validate the role of PGPR in vegetable improvement across many production systems (Ali et al. 2014; Belimov et al. 2015; Husen et al. 2011).

2.4 PGPR Hydrolytic Enzymes

Bacterial lytic enzymes such as urease, esterase, lipase, protease, chitinase, amylase, and cellulase are key protagonists in the biological transformation processes of N, H, and C (Rana et al. 2012; Reddy 2013; Xun et al. 2015). Enzymes like chitinase and cellulase play a major role as biocontrol agents by degrading fungal cell walls (Sindhu and Dadarwal 2001). Kathiresan et al. (2011) reported that an *Azotobacter* sp. produced high amounts of amylase, cellulase, lipase, chitinase, and protease and participated in biodegradation process of soil organic matter. Bacteria belonging to *Bacillus* and *Pseudomonas* sp. reduced growth of filamentous fungi by secreting lytic enzymes such as chitinases and glucanase. The application of such bacteria for biological protection of crops from pathogens, especially those that contain chitin and glucans within their cell wall structure, is widely assumed (Prasad et al. 2015). Kohler et al. (2007) observed that inoculation of lettuce plants with *B. subtilis* increased significantly urease, protease, and phosphatase activity in rhizosphere, hence participated in plant growth enhancement and potassium/calcium uptake. A bacterial isolate (MIC 3) produced lytic enzymes (protease, amylase, cellulase, chitinase, and pectinase) and exhibited high in vitro antagonistic activity against *F. oxysporum* and *Phoma* sp. (Avinash and Rai 2014). Recently, the role of chitinolytic *Streptomyces vinaceusdrappus* S5MW2 in enhancing tomato plant growth and biocontrol efficacy through chitin supplementation against *Rhizoctonia solani* is reported (Yandigeri et al. 2015). Under greenhouse experiment, chitin supplementation with S5MW2 showed a significant growth of tomato plants and superior disease reduction as compared to untreated control and without CC-treated plants. The role of chitinase-producing *S. maltophilia* and *Chromobacterium* sp. in inhibiting egg hatch of potato cyst nematode *Globodera rostochiensis* was reported by Cronin et al. (1997). Xu and Kim (2016) evaluated the role of cellulase-/protease-producing *Paenibacillus polymyxa* strain SC09-21 as biocontrol agent of *Phytophthora* blight and growth stimulation in pepper plants. Strain SC09-21 significantly reduced *Phytophthora* blight severity and increased phenylalanine ammonia-lyase, peroxidase, polyphenol oxidase, and superoxide dismutase activities. In addition, SC09-21 boosted pathogenesis-related protein gene expression in pepper plants. Singh et al. (1999) observed that two chitinolytic bacterial strains, *Paenibacillus* sp. 300 and *Streptomyces* sp. 385, suppressed *Fusarium* wilt of cucumber caused by *F. oxysporum* f. sp. *cucumerinum* in non-sterile, soilless potting medium.

2.5 Systemic Tolerance and Systemic Resistance Induction by PGPR

Apart from extreme temperatures, salinity, drought, unfavorable pH, heavy metals, and organic pollutants that hit the vegetable production hardest around the world, losses due to phytopathogens are equally substantial in many countries. As an example, about 28–40% of potatoes, cotton, wheat, rice, and maize yields loss are reported due to biotic factors, where the highest loss (40%) was observed in potato due to pathogen diseases (Ashraf et al. 2012; Schwarz et al. 2010). Recently, several works have been published highlighting the PGPR role as enhancers of plant tolerance to abiotic stress. PGPR-induced physiological and biochemical changes in plants that result in enhanced tolerance to environmental stress (drought, salinity, heavy metals, etc.) is known as induced systemic tolerance (IST) (Choudhary and Varma 2016; Nadeem et al. 2015). Species belonging to the genera *Bacillus*, *Halomonas*, *Planococcus*, *Azospirillum*, *Azotobacter*, *Rhizobium*, *Achromobacter*, and *Pseudomonas* can promote potato, chickpea, tomato, bean, lettuce, and cucumber growth under high salinities (Egamberdieva and Lugtenberg 2014; Gururani et al. 2013; Qurashi and Sabri 2012). In growth chamber experiment, Barassi et al. (2006) reported that lettuce seeds inoculated with *Azospirillum* had better germination and vegetative growth than non-inoculated plants exposed to varying levels of NaCl. Several other workers have also reported that *Bacillus*, *Pseudomonas*, *Achromobacter*, *Variovorax*, *Citrobacter*, *Bacillus*, and *Mesorhizobium* could be used to improve potato and tomato growth under drought stress (Belimov et al. 2015; Bensalim et al. 1998; Gururani et al. 2013; Ullah et al. 2016). Also, a novel osmotolerant plant growth-promoting *Actinobacterium citricoccus zhacaiensis* B-4 (MTCC 12119) was found to enhance onion seed germination under osmotic stress conditions (Selvakumar et al. 2015). On the other hand, Wang et al. (2015) evaluated the effect of a bacterial consortium (*Bacillus cereus* AR156, *B. subtilis* SM21, and *Serratia* sp. XY21) on alleviating cold stress in tomato seeds after 7 days of chilling treatment (4 °C) and 1 week recovery at normal 28 °C. Treated tomato plants had a survival rate of 93% on average six times more than control plants (16%). The same consortium (*B. cereus* AR156, *B. subtilis* SM21, and *Serratia* sp. XY21) was previously reported to be an efficient eco-friendly tool to induce drought tolerance in cucumber plants (Wang et al. 2012).

There are numerous reports where PGPR have been found to stimulate plant defense by inhibiting phytopathogens. They induce physical or chemical changes in plants and, hence, improve plant resistance, which is designated by induced systemic resistance (ISR) (Nadeem et al. 2015; Niranjana and Hariprasad 2014). For instance, *Bacillus subtilis* B4 and *B. subtilis* B5 when tested in pot trials against *Sclerotium cepivorum*, causing onion white rot, decreased disease incidence by 33.33% and 41.67%, respectively, compared with the control. In contrast, under field conditions, disease incidence was declined by 25% (*B. subtilis* B5) and 16.67% (*B. subtilis* B4) compared with the control. Due to their disease-reducing ability, strains of *Bacillus* were considered suitable for enhancing growth and productivity of onion plants (Shalaby et al. 2013). Furthermore, the ability of endophytic *Pseudomonas* sp. strain to promote growth and resistance of potato plants toward infection by necrotroph *Pectobacterium atrosepticum* is also reported (Pavlo et al. 2011). Apart from its ability to promote potato shoots growth, *Pseudomonas* sp. increased plant resistance toward soft rot disease. Disease inhibition was inversely proportional to the size of inoculated bacterial population. Raupach et al. (1996) studied the effect of two bacterial strains *P. fluorescens* 89B-27 and *S. marcescens* 90–166 to protect cucumber and tomato against cucumber mosaic *Cucumovirus* (CMV). The two strains showed high ability to stimulate tomato and cucumber defenses against phytopathogen virus CMV, and the results suggest that the two strains should be evaluated for their potential to contribute toward management of viral plant diseases. Equally, PGPR such as *Pseudomonas*, *Alcaligenes*, *Paenibacillus*, and *Chryseobacterium* have been reported as systemic resistance inducers in potato, tomato, pea, bean, and Chinese cabbage against pathogens like *Bemisia tabaci*, *Fusarium*, *Macrophomina phaseolina*, *Rhizoctonia*, *Ralstonia solanacearum*, *C. orbiculare*, *Botrytis cinerea*, and *Pectobacterium carotovorum* (Ben Abdallah et al. 2016; Lee et al. 2014; Moradi et al. 2012; Murthy et al. 2014; Valenzuela-Soto et al. 2010). Recently, Konappa et al. (2016) reported the role of lactic acid bacterium *Lactobacillus paracasei* in mediating induction of defense enzymes to enhance resistance against *Ralstonia solanacearum* causing bacterial wilt in tomato. Inoculation of tomato seedlings with bacterial isolate induced a significant amount of peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase, total phenolics, and β-1,3-glucanase activities. In field experiment, treatment with lactic acid bacteria increased the yield by 15% (8.2 kg/m^2), and pathogen-infected plants as well as pretreated with bacteria gave an average of 55% yield (28.3 kg/m^2 compared to infected plots). The results indicated that bacterial inoculation reduced the bacterial wilt by 61% in tomato.

Conclusion

Vegetables constitute an important part of human healthy foods. They provide many important nutrient elements such as calcium, magnesium, potassium, iron, beta-carotene, vitamin B complex, vitamin C, vitamin A, vitamin K, and antioxidants. Vegetables also provide soluble as well as insoluble dietary fiber collectively known as non-starch polysaccharides (NSP) such as cellulose, mucilage, hemicellulose, gums, pectin, etc. Like many other crops, vegetables are threatened by biotic and abiotic stresses. Thus, scientists and vegetable growers are working hard to develop different strategies to overcome these problems. Among various strategies, the use of PGPR in agricultural practices has received greater attention. It is clear that until now, there is no clear antithesis about beneficial and eco-friendly effect of PGPR in a sustainable agriculture establishment worldwide. However, there are many challenges that need to be addressed in order to make full use of this technology. Among various reasons, the lack of uniformity and variation in responses are of prime concern. Moreover, the detection of vegetable-specific PGPR and understanding the interactive relationship between PGPR and vegetable require special attention so that vegetable-specific inoculant is developed. In addition to these, the difficulties encountered in inoculum production, storage, delivery, viability, and its competitiveness in the new environment after application are some of the other major challenges that require immediate and considerable attention of both scientists and farmers to make full use of this technology for enhancing the vegetable production in different agroecological niches.

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